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The impact of grazing on mountain vegetation and the arbuscular mycorrhizal symbiont

Hvussu seyðabit ávirkar fjallavøkstur og arbuskul sopprót

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Abstract

In 2000 an enclosure experiment was established at one lowland (70 m a.s.l.) and one alpine (600 m a.s.l.) site in the Faroe Islands. After five years of enclosure, significant increases were seen in vegetation biomass at both altitudes as both the cover and vegetation height increased. Five species changed their abundance significantly. Only minor changes of species loss and gain were seen. Palatable grasses increased their abundance in enclosed plots, both at the lowland and the alpine site.

Roots from *Agrostis capillaris* were examined for arbuscular mycorrhizal (AM) colonisation, and the colonisation found to be greater at grazed plots. The plant species that had a significantly negative response to grazing were typically classified as normally mycorrhizal, while species that proliferated in grazed plots were either classified as rarely mycorrhizal or as less palatable.

Úrtak

Í 2000 varð farið undir at kanna gróður við at seta girðingar upp til at halda seyði burtur. Ein girðing var gjørd í láglandi (70 m oman sjóvar) og ein í hálendi (600 m oman sjóvar). Tá ið fimm ár vóru liðin, var greitt, at plantunøgdin var størri innan fyri girðingar-

nar; tað sást bæði á hæddini á plantunum og gróðrarlagnum. Títtleikin hjá fimm plantusløgum broyttist munandi, men eingin týðiligur munur kom á plantusamansetingina orsakað av girðingini. Meira av grøsum, sum seyði dámar at bita, vóru inni í girðingunum. Hetta hendi bæði í láglandi og hálendi.

Røtur á vanligum finagrasi (*Agrostis capillaris*) vóru kannaðar fyri arbuskul-sopprót, og nøgdin av sopprót var størri uttan fyri girðingarnar, har sum bit er. Tey plantusløgini, sum minkaðu munandi í títtleika, tá ið tey vórðu bitin, vórðu slík, sum vanligu hava sopprót, og tey sløg, sum tóku seg fram uttan fyri girðingarnar, hava annaðhvørt ikki vanligu nakað serligt av sopprót, ella eru ikki serliga átulig hjá seyði.

Introduction

Many studies have shown that herbivory has a profound effect on plant communities through processes of grazing, trampling, and urination. Grazing affects species richness by changing the competition relationship between species and thus the spatial heterogeneity of the vegetation due

to changes in habitat conditions (Adler *et al.*, 2001).

Herbivores do not only have direct effect on plants by removing biomass but they may also result in changed competition for light when biomass is increased as a result of excluding herbivores. Moderate grazing in productive areas such as tall herb and grass meadows normally increases local plant diversity (Austrheim and Eriksson, 2001; Dupré and Dickmann, 2001) compared to areas where grazing is excluded. Huisman *et al.* (1999) considered the interaction between herbivores and competition for light. He predicted that competition for light is more evident in communities with high productivity. Here small palatable herbs are out-shaded by taller less palatable species.

In less productive habitats, grazing will, however, reduce species richness (Austrheim and Eriksson, 2001) although the impact of grazing is seen to be strongest in areas with low biomass where competition for light is less (van der Wal *et al.*, 2000).

There is an increasing recognition that many of the herbivore driven ecosystem changes are predictable stepwise transitions from one vegetation state to another. In northern and arctic areas, herbivory changes lichen-dominated vegetation to moss-dominated vegetation (Thing, 1984; van der Wal *et al.*, 2001) and from moss-dwarf shrub heath to grass-dominated tundra (Olofsson *et al.*, 2001; 2004; Olofsson, 2006). These transitions are also seen in alpine Skandinavian areas (Wielgolaski, 1975; Austrheim and Erikson, 2001) as well as Scottish uplands (Alonso *et al.*,

2001, van der Wal *et al.*, 2003). These transitions toward a grass dominated vegetation increase the capacity of the area to sustain a greater population of herbivores (van der Wal, 2005).

Similar results are seen from Scottish *Calluna vulgaris* heath, where the mosses replace lichens in the understorey vegetation under moderate grazing pressure (Welch and Scott, 1995), and when the heather is replaced by grass dominated communities after increased grazing pressure.

Relatively few studies have attempted to quantify the interacting effects of herbivory and resource availability of the competitive balance between plant species in terms of below-ground growth parameters as well as above-ground parameters, but knowledge of the differential effects of herbivory and nutrient availability on plant performance is important in understanding the mechanisms by which one species replaces another (Hartley and Amos, 1999).

One such mechanism is mycorrhizas, which are beneficial symbioses between fungi and plants. The arbuscular mycorrhizal (AM) symbiosis is the most frequent. In the Faroes, where the current study is conducted, around 70% of the native plant species are AM mycorrhizal, while other forms of mycorrhiza account for 15% (Olsen and Fosaa, 2002). It is known that the symbiosis can provide a range of benefits to plants, including protection from pathogens, uptake of micro-nutrients, and possibly improved drought resistance (Newsham *et al.*, 1995).

Studies examining the effect of defolia-

tion on AM fungi have shown both positive, negative, and neutral responses. Daft and Al-Giahmi (1978), Bethlenfalvai and Dakessian (1984), Bethlenfalvai *et al.* (1985), Gehring and Whitham (1994) all found a decrease in the colonisation due to herbivory. However, more recent studies have suggested an increase in the colonisation due to herbivory (Eom *et al.*, 2001, Gehring *et al.*, 2002, Kula *et al.*, 2005). Bentivenga and Hetrick (1992) and Lugo *et al.* (2003) found no change in the colonisation. Hokka *et al.* (2004) found that the effects of grazing depended on the plant species, as they found a decrease in some grasses, and increase in others. Hokka *et al.* (2004) concluded that there is an interaction between mycorrhizal infection and defoliation, which is likely to be extremely complex.

In the present study, we investigated one grassland site in the lowland and one alpine vegetation type, where sheep has been excluded from both sides. The aim was to follow the changes in the vegetation composition and arbuscular mycorrhiza symbiont and to see if there was an interaction between these changes. No previous experimental study of the grazing impact on the vegetation in the Faroe Islands has been carried out before. Neither has the interaction between the vegetation and the mycorrhizal symbiont been studied. Thus, there was limited knowledge, which plant species would be the best indicators for grazing impact. We chose the most common grass in the Faroes, *Agrostis capillaris*, as a representative for palatable grasses. With this material we have tried to

answer the following questions: How does sheep grazing change the vegetation composition? Does grazing by sheep change the arbuscular mycorrhizal colonisation pattern? And, lastly: Does grazing by sheep change the interactions in arbuscular mycorrhizal symbiosis in terms of combined plant and fungal responses?

Description of sites

The study sites used in this experiment are two enclosures, established in 2000. One of the sites is located at 600 m a.s.l., the other enclosure at 70 m a.s.l. The study sites are on the mountain Sornfelli (62°04'10''N, 6°57'25''W) on Streymoy in the central part of the Faroe Islands.

The vegetation at 600 m a.s.l. reaches from sparsely vegetated open grassland to richly vegetated *Racomitrium* heath. The plant communities found on the site are the species-poor *Koenigia islandica*-community, and the species-rich communities *Festuca vivipara-Agrostis capillaris*-community, *Racomitrium*-community and *Racomitrium-Salix herbacea*-community (Fosaa 2004).

The vegetation at 70 m a.s.l. is moist grassland vegetation. The most common plant community at this site is *Nardus stricta-Potentilla erecta* community but *Festuca vivipara-Agrostis capillaris*-community, *Racomitrium*-community are also present (Fosaa 2004).

The whole area is grazed by sheep, about 45 ewes per km² (Thorsteinsson, 2001).

Methods

Sampling method

In 2000, two 25 x 50 m enclosures were established in the area in order to exclude the sheep. The vegetation was sampled in eight meso-plots of 0.25 m². These plots were subdivided into 25 (0.01 m²) micro-plots and the presence of all plant species was measured. The abundance of each species, ranging from 1-25, was determined for each meso-plot. The same method was used to classify the vegetation into plant communities (Fosaa, 2004).

At 600 m a.s.l., the vegetation was sampled in 2000, used grazed plots, and again in 2005 used as enclosed plots. At 70 m a.s.l., the vegetation was sampled both inside and outside the enclosure in 2006. Thus the method for selecting vegetation plots in the grazed vegetation was different for the two altitudes. The vegetation cover and the length of the tallest graminoid were measured for each mesoplot.

For the mycorrhizal samples, three small soil cores with *Agrostis capillaris* were sampled randomly from grazed plots (outside the fence), and from the enclosure (inside the fence). In 2002, samples were taken from both low and high altitude, a total of 36 samples, but in 2003 only at high altitude, a total of 18 samples.

Percent root length colonisation

The root clearing was a modified procedure after Grace and Stribley (1991), Koske and Gemma (1989) and Walker and Vestberg (1994). The staining procedure followed Vierheilig *et al.* (1998). Colonisation was measured following McGonigle

et al. (1990). In addition to mycorrhizal structures, an estimate of whether the plant root at the intersection point was coarse or fine was recorded (percent fine roots, %FR). A typical fine root was between 0.1 and 0.15 mm diameter, but a diameter up to 0.20 mm could be considered as a fine root if the stele was poorly developed.

Statistics

The composition of plant species in grazed and ungrazed vegetation plots was compared at 70 m a.s.l. and at 600 m a.s.l. by comparing richness of plant species and abundances of plant species. All plant species recorded were assigned to six life-forms, which are herbs, graminoids, sedges, woody, mosses, and lichens and compared with a one way ANOVA. The vegetation cover and the length of the longest graminoid leaf in grazed and ungrazed plots at 70 m a.s.l. and at 600 m a.s.l. was also compared with a one way ANOVA. Species richness was calculated by summing up the number of species in each plot.

Statistics for fine roots and mycorrhiza were computed using univariate GLM in SPSS 11.01 for Mac.

Results

After four years, changes were seen in the vegetation. The mean increase in vegetation cover at the alpine site (600 m a.s.l.) was 14% and the mean length of the highest grass leaf increased 25%, from 4.4 to 5.5 cm (Fig. 1).

At the lowland site (70 m a.s.l.), the dif-

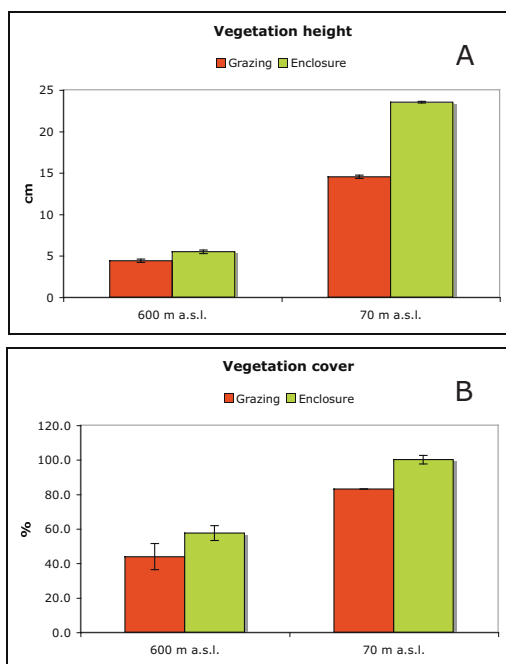


Fig. 1. Mean vegetation height in cm (a) and cover in % (b) in grazed and ungrazed plots at 600 m a.s.l. and 70 m a.s.l. Bars indicate \pm SE.

ference was even more profound as the vegetation cover inside the enclosure increased 17% and the mean length of the highest grass leaf had increased 62%, from 14.5 to 23.5 cm (Fig. 1).

The plant species were grouped in the following functional groups: graminoids, herbs, mosses, and lichens (Fig. 2). At 70 m a.s.l., the abundance of graminoids was lower in ungrazed plots than in grazed plots. The same was the case for mosses, but the opposite was the case for the herbs. The abundance of lichens was in general very low. The changes in abundance of the functional types were not significant. Of the functional types at 600 m a.s.l., graminoids and mosses had higher abundance in ungrazed plots than in grazed plots. For the other functional types, only small differences were found between grazed and ungrazed plots.

Five plant species changed their abundance significantly, three at low altitude

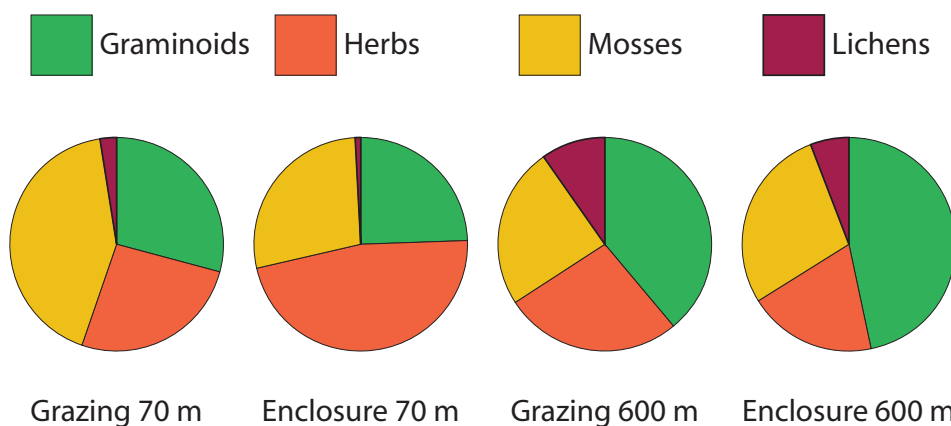


Fig. 2. The abundance of the four functional groups graminoids, herbs, mosses and lichens in grazed and ungrazed plots at 600 m a.s.l. and 70 m a.s.l.

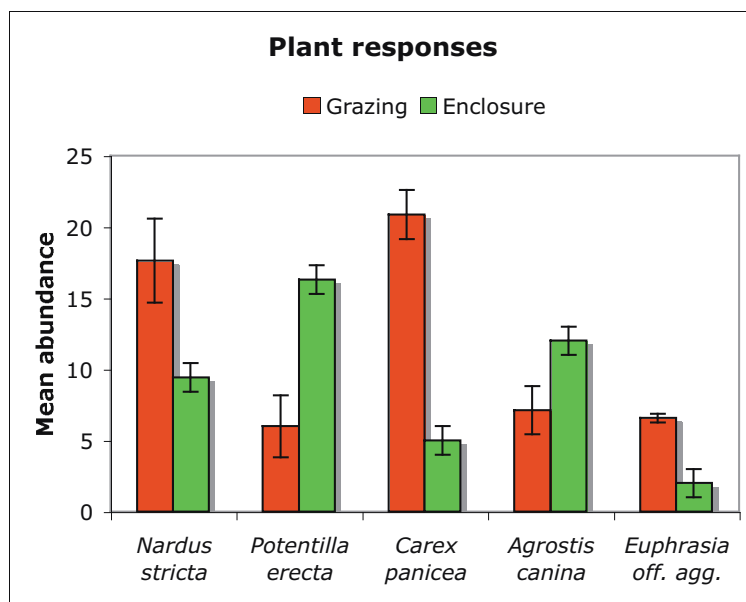


Fig. 3. Mean abundance of plant species with significant response to grazing, in grazed and ungrazed plots.

and two at high altitude (Fig. 3). The three species that changed their abundance significantly ($p < 0.01$) at low altitude were *Nardus stricta*, which had the highest abundance in grazed plots, while more palatable grasses like *Agrostis capillaris* and *A. canina* had the opposite trend. Herb species like *Potentilla erecta* increased their abundance in ungrazed plots significantly ($p < 0.01$) and the same trend was seen for *Narthecium ossifragum* although these changes were not significant. *Carex panicea* had a significantly higher ($p < 0.01$) abundance in grazed plots.

The two species that changed their abundance at high altitude were *Agrostis canina*, which was found to have significantly ($p < 0.05$) higher abundance in ungrazed than in grazed plots, and *Euphrasia* sp., which had a significantly ($p < 0.05$) higher abundance in grazed plots. In un-

grazed plots, we found that the abundance of *Deschampsia cespitosa*, *Bistorta vivipara*, and *Salix herbacea* increased while the abundance of *Festuca rubra* increased in grazed plots.

Most of the plants that had a significant response to grazing were normally mycorrhizal, and form symbiosis with arbuscular mycorrhizal fungi (Table 1). The species examined for mycorrhiza in this study was *Agrostis capillaris* whose mean abundance was found to be slightly greater in ungrazed plots. The difference was not significant (Fig. 4). The roots were finer in grazed plots at high altitude than in ungrazed plots at high altitude, while there was no significant difference in the roots from low altitude ($p < 0.01$). The percent root length colonisation (%RLC) was significantly greater in roots from grazed *Agrostis capillaris* at high altitude than at

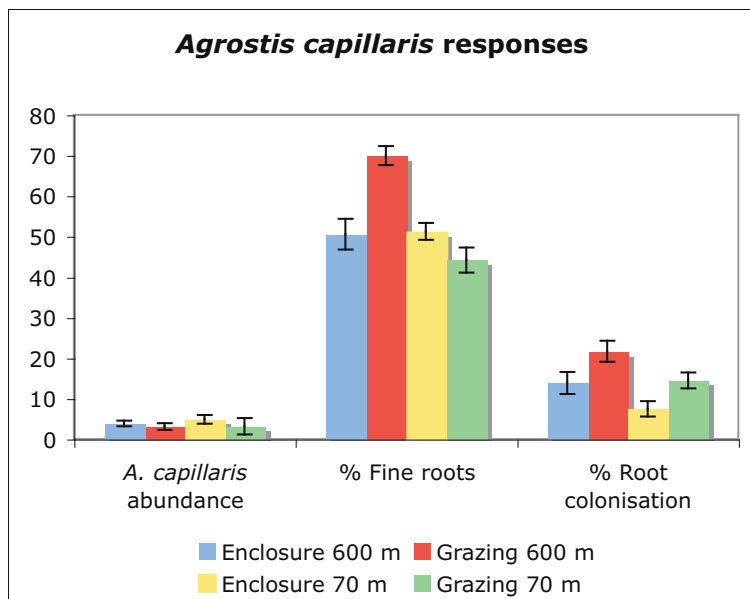


Fig. 4. Mean responses of the plant species *Agrostis capillaris*: the abundance, the percent fine roots and the percent root length colonisation in grazed and ungrazed plots at 600 m a.s.l. and 70 m a.s.l. Bars indicate \pm SE.

low altitude, and the colonisation in roots from the enclosure was similar to that found at low altitude ($p < 0.01$). The fraction of fine roots (%FR) and %RLC were positively correlated ($r = 0.49$), and using %FR as a covariate removed the signifi-

cant response of %RLC to grazing at high altitude, indicating that the increase in %RLC in grazed plots at high altitude might be a plant rather than a fungal response to grazing.

Plant species	Altitude 70 m a.s.l.	Altitude 600 m a.s.l.	Mycorrhizal status	Minimum soil requirements
<i>Nardus stricta</i>	Increase***		Normal	Infertile
<i>Agrostis capillaris</i>	Decrease*	Decrease*	Normal	Fertile
<i>Agrostis canina</i>	Decrease*	Decrease***	Normal	Infertile
<i>Potentilla erecta</i>	Decrease***		Normal	Very infertile
<i>Carex panicea</i>	Increase***		Rare	Infertile
<i>Scirpus cespitosus</i>	Decrease*		Rare	Infertile
<i>Festuca rubra</i>		Increase*	Normal	Very infertile
<i>Salix herbacea</i>		Decrease*	Normal§	Very infertile
<i>Euphrasia officinalis</i> agg.		Increase***	Absent	Infertile
<i>Bistorta vivipara</i>		Decrease*	§	Very infertile
<i>Deschampsia cespitosa</i>		Decrease*	Normal	Infertile

Table 1. Plant response to grazing in grazed plots compared with enclosure, their mycorrhizal dependency, and minimum soil requirements. *** Significant ($p < 0.05$) response. * Non-significant trend. § Indicates that the plant species can be colonised by both arbuscular and ectomycorrhizal fungi.

Discussion

Several short term studies of exclusions of herbivores have shown that the vegetation biomass increases (e.g. Austrheim and Eriksson, 2001). We found some changes in the vegetation, some of them significant, as a result of sheep grazing. During the study period, the biomass increased considerably in the enclosures, which can be seen by the increase in length of grass-leaves and vegetation cover.

Our short term results gave a significant increase in both cover and vegetation height in the lowland site as well as the alpine site for the ungrazed plots. As the vegetation cover and the vegetation height is much higher in lowland plots than in the alpine plots it would be expected that the gain in biomass was higher in the lowland site compared to the alpine site. This was also the case, but the difference was much smaller than would be expected. We must also take into consideration here that the alpine site was sampled after five years of enclosure and the lowland site after six years of enclosure. These findings indicate that the alpine site also is a productive site (Körner, 1999) and that the herbivores have a profound effect on the alpine ecosystem.

We have seen that five plant species changed their abundance significantly. Only small changes in loss and gain of new species had occurred at this stage, and maybe the time to detect such changes must be longer. The abundances of graminoids increased in grazed plots in the lowland while the opposite was the case in the alpine area. In the lowland plots, this

increase was due to increased abundance of the non-palatable *Nardus stricta* while other grass species were decreasing. This finding could be explained by competition between species instead of the grazing effect. This is also seen by others (e.g. Welch and Scott, 1995). At the alpine site, *Nardus stricta* was not found, but here all grass species increased their abundance in the enclosures. This result can be explained by the stronger effect of grazing in areas of low biomass and lesser effect due to competition (van der Wal *et al.*, 2000).

In the Scottish heathland, a 20-years study showed that *Calluna* declined at four sites where there were increases in herbivores. At these sites, graminoids and herbs showed a general rise in cover, and ericoids and lichens decreased. Species increasing significantly included *Agrostis capillaris*, *Anthoxantum odoratum*, *Festuca ovina*, *Galium saxatile*, *Luzula multiflora*, *Nardus stricta* and the moss *Rhytidadelphus squarrosus*. In contrast, *Deschampsia flexuosa* was reduced in cover at the same sites (Welch and Scott, 1995).

The response of *Agrostis capillaris* to grazing is variable. Some studies have found the abundance of *Agrostis capillaris* to decrease when grazed (Magnússon and Magnússon, 1990; Crawley, 1990). According to Magnússon and Magnússon (1990), the abundance and cover of *Agrostis capillaris* decreases with increasing grazing intensity. This study from Iceland might be the best predictor for what to expect in the Faroe Islands, as the climatic conditions are quite similar.

Other studies have found the abundance

of *Agrostis capillaris* to decrease when the grazers were removed (Hartley and Mitchell, 2005; Hulme *et al.*, 1999). This decrease has been explained by a change in the plant composition to more grazing-intolerant plant species such as *Deschampsia flexuosa* and *Molinia caerulea* (Hulme *et al.*, 1999).

The palatable grass *Agrostis capillaris* did not have a significant response to grazing, but the response was very similar to the response of *Agrostis canina*, which had significant increase in abundance inside the enclosure, indicating that these palatable grasses were affected by grazing. The response of grazing was more root growth and greater %RLC. Both these factors are known to increase nutrient uptake by the plant. While keeping sheep out of the plots, the enclosure also had one more unintended impact: it also eliminated one nutrient resource otherwise available for the plants, namely sheep urine and sheep dung. This could make species like *Agrostis capillaris* more vulnerable than other species, as *A. capillaris* has the highest nutrient requirements in Table 1. A study using *Agrostis capillaris* to examine the impact of defoliation on the distribution of nitrogen between shoot, roots, and soil nitrogen pool found that root biomass was decreased by regular defoliation and this coincided with greater amounts of nitrogen stemming from sheep urine (in this case ¹⁵N-labelled synthetic sheep urine) (Williams *et al.*, 2003).

The good correlation between %FR and %RLC might suggest that greater colonisation would be expected if increased fine

root production occurred. The observed differences in mycorrhizal colonisation in response to grazing may have been due to changes in the fraction of fine roots in response to grazing, rather than a direct response of the mycorrhizal fungi themselves.

Conclusions and future perspectives

Three questions were posed. Firstly, how sheep grazing changes the vegetation composition. In this study we have found that sheep grazing decreased the biomass of the vegetation in both lowland and alpine areas in terms of lower vegetation cover and lower vegetation height. We also found that the abundance of palatable graminoids decreased in grazed plots.

Secondly, whether grazing by sheep changes the arbuscular colonisation pattern. This can also be answered positively as we found a higher fraction of fine roots as well as greater colonisation in grazed plots, in particular at the alpine site.

This study did not give a clear answer to the third question, whether grazing by sheep changes the interactions in arbuscular mycorrhizal symbiosis in terms of combined plant and fungal responses. The grass species used may not be appropriate, as *A. capillaris* might be more dependent on nutrient availability than other grasses. Future studies should include nutrient availability as a factor, as well as include several plant species, which should be studied both in terms of specific biomass, grazing preferences as well as mycorrhizal colonisation.

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