Vegetation Composition of a High-Elevation Grassland
From small to large herbivore-how do they interact with a subalpine grassland ecosystem?

Semester project by Geri Werhahn D-BIOL ETH, June-August 2009
Supervised by Dr. Anita Risch and Dr. Martin Schütz, WSL Birmensdorf

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Abstract

Vegetation composition from 18 sites on six subalpine grasslands in the Swiss National Park was sampled. Half of the sites were established in nutrient-rich short-grass and the other half in nutrient-poor tall-grass vegetation. The vegetation of these grasslands is interacting with foraging herbivores. Formerly used by cattle, they constitute important food resources today for native herbivores of various sizes. Multivariate analysis of vegetation composition and a quantitative analysis of species flowering were conducted. The vegetation composition largely reflected the experimental setup. The two vegetation types, as well as the location of the six grasslands can be distinguished in terms of vegetation composition.
Species richness did not differ between the vegetation types, but more flowering species were found in the tall grass vegetation. A higher graminoid/herb ratio in the tall grass vegetation together with the fact that herbivores prefer the flowers of herbs over those of graminoids can help explain this finding.

Introduction

Grazing patterns of herbivores are closely linked to vegetation composition and productivity as well as nutrient contents of plant tissues. The responses of plants to grazing can range from changes in biomass production, nutrient content of plant tissue to altered flow of carbon from root to soil (Frank et al. 2002, Wardle et al. 2002, Bardgett and Wardle 2003).
Different sized herbivores have different requirements on their environment. While small herbivores require high quality forage but can exist with low a forage quantities, larger herbivores need high forage quantities but can exploit lower quality plant material (Olff et al. 2002).
The impact of different sized herbivores on the ecosystem is highly variable in respect of e.g. size and distribution patterns of faeces, physical impacts such as trampling or burrowing activity (Bakker et al. 2004). Herbivory acts as a disturbance vector by reducing biomass of specific plants and increasing spatial vegetation heterogeneity, which allows more species to coexist(Jacobs and Naiman 2008).
Schütz et al. (2003) found a significant positive correlation between plant species richness and deer density in the Central Alps, which is a pattern frequently observed in herbivore-grassland ecosems (Bardgett and Wardle 2003, Schutz et al. 2003). In African savannas, for example plant species richness declined by 64% and biomass increased threefold after three years of herbivore exclusion(Jacobs and Naiman 2008). Over long periods of time, herbivory often significantly changes the functional composition of the plant community (Olff et al. 2002). Whether the influence of herbivory on the system is neutral, positive or negative highly depends on soil fertility and mechanisms like changes in resource quality, quantity and functional composition

induced by the foraging animals (Bardgett and Wardle 2003). On a global scale herbivore diversity is positively correlated with available soil nutrients, which together with soil moisture determine vegetation productiviy, composition and nutrient content (Olff et al. 2002, Bardgett and Wardle 2003). Vegetation which is regularly grazed on high nutrient soils, maintains a high nutrient concentration in the plant tissue (Olff et al. 2002, Schutz et al. 2003). This distinct grazing pattern has consequences for plant community composition, where heavily grazed plots undergo larger changes than rarely grazed plots (Schutz et al. 2003). Grazing by ungulates gives advantage to short growing species, such as plants with morphological protection and short life spans (Schutz et al. 2006). It is shown that ungulates prefer feeding on flowers and fruits, and prefer those of herbs over graminoids, which causes a relative reduction in seed numbers of herbs compared to graminoid species present (Hulber et al. 2005). Blumer and colleagues found that grasshoppers removed between 19 and 30% of the aboveground biomass at an elevation of 2470m a.s.l. in the Swiss Central Alps, of which 36% was actually ingested by the animals (Blumer and Diemer 1996).

Increasing herbivore diversity, both on the functional group and species level, will lead to greater resource partitioning and by this increase the net resource utilization (Bardgett and Wardle 2003). In grassland herbivore communities, species can either compete for food resources or facilitate each other, as was shown in the case of cattle facilitating rabbits, but disadvantaging voles in the Netherlands (Bakker et al. 2009). Greenwald et al. (2008) found an increased number of salamanders, gastropods, snakes and invertebrate species in plots grazed by white-tailed deer compared to plots, where deer were excluded by fences. They hypothesized bottom-up effects to be the driving mechanisms, where grazing indirectly increased invertebrate species diversity (Greenwald et al. 2008).

To investigate the herbivore-vegetation-soil interactions in high-elevation grasslands in a more detailed manner, the Animal ecology and Plant ecology group of the Swiss Federal Institute for Forest, Snow and Landscape (WSL) setup an experimental design in the subalpine vegetation belt in the Swiss National Park (SNP). It examines how four different groups of herbivores of different body size affect plant biomass, nutrient content and composition, root biomass and nutrient content, microbial biomass as well as nutrient content of the soil in two different grassland vegetation types over the course of multiple years.

In the year 1914, when the SNP was founded, agriculture was abandoned in the area of the park (Parc). The old cow pastures were left to natural dynamic, which was strongly influenced by the herbivores foraging on them. The vegetation today still reflects this formerly agricultural use. The nutrient-rich short-grass vegetation is found around huts and stables were cows and sheeps rested and defecated (Thiel-Egenter et al. 2007). It is dominated by *Festuca rubra* and is the preferred grazing site for wild ungulates today (Thiel-Egenter et al. 2007). The nutrient-poor tall-grass vegetation, dominated by *Carex sempervirens*, is found where the agriculture animals were formerly grazing (Schutz et al. 2003, Schutz et al. 2006, Thiel-Egenter et al. 2007).

In this thesis the vegetation relevés of the first year of the experiment were conducted on all experimental plots. These will be repeated over the course of the study to detect changes in plant composition due to manipulated herbivore foraging pressure.

The aim of the following analysis made with the vegetation data was to search for differences in plant composition between the short- and tall-grass plant community, as

well as analyzing the presence of flowering species in relation to vegetation type and herbivore exclusion. The first question considered was, if there are differences in the vegetation composition between the nutrient-rich short-grass and the nutrient-poor tall-grass vegetation type? The second question investigated was which environmental parameters might explain these differences? And the third question addressed was if the quantity of flowering species present depends on vegetation type or herbivores foraging on it?

The hypotheses are:

(H1) There are differences in the vegetation composition between the nutrient-rich short grass and the nutrient-poor tall-grass type and between grassland locations.

(H2) Environmental parameters act as explaining variables for detected differences between vegetation types and grassland locations.

(H3) The quantity of species flowering is dependent of vegetation type and/or herbivore exclusion treatment.

I expect to find differences in the vegetation composition between vegetation type and grassland location and that these differences can be explained by environmental variables. I expect to find differences in the quantity of species flowering between vegetation type and herbivores foraging on it.

Methods

Study area

The Swiss National Park (SNP) is located in the Central Alps in Graubünden, Switzerland. It ranges from 1400 – 3174 meters above sea level and covers an area of 172km^2, of which 86km^2 is covered by vegetation. Subalpine grasslands occupy 3km^2 of the area (Schutz et al. 2003). Six subalpine grasslands located on Engadine Dolomites were selected for the experiment.

Table 1:Location of the experimental sites.

Grassland	Experimental site	Elevation [m a.s.l.]	Latitude	Longitude
Val dal Botsch	9, 10	2065 - 2075	46°40'25.92"N	10°13'55.40"E
Grimmels	11,12,13,14	2015 - 2065	46°39'55.91"N	10°11'18.72"E
Minger	15, 16, 17, 18	2090-2100		
Margunet	7, 8	2328-2348	46°40'29.30"N	10°14'39.55"E
Alp Stabelchod	1,2,3,4	1960 - 1975	46°39'49.64"N	10°14'30.07"E
Alp Stabelchod dadaint	5,6	2125 - 2135	46°40'19.58"N	10°14'45.39"E

Eighteen experimental sites were established in these six grassland; nine in each of the two dominant vegetation types short-grass and the tall-grass.

On each experimental site five different treatments were established(Fig.1): four fences with different mesh size to exclude four different-sized groups of herbivores. The excluded herbivores are divided into the following categories: deer/chamois, marmot/hare, mice and insects. An unfenced control plot completes the experiment. Each treatment consists of six plots.
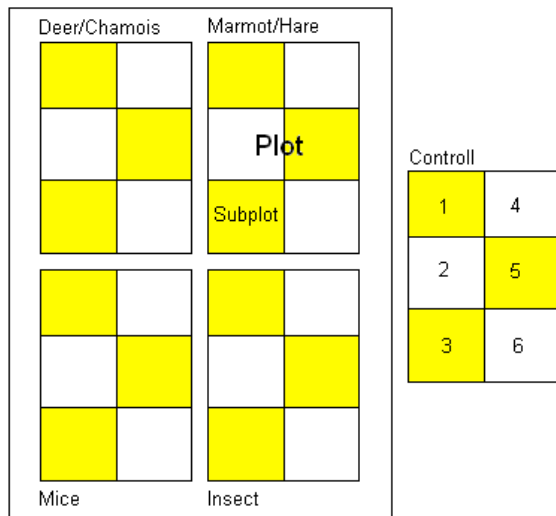
Experimental Site

Figure 1: Arrangement on the experimental site. On each colored plot a vegetation relevé was conducted.

Vegetation relevés

On each experimental site 15 vegetation relevés were conducted, namely on three plots per treatment. One plot has the size of one square meter. All vascular plant species found on each plot were noted, as well as presence or absence of reproductive structures. Buds, flowers, faded flowers and fruits counted as reproductive parts. In a final step the cover was estimated continuously in percent for each species found. The nomenclature used for plant species follows Lauber and Wagner (2001). Field work was conducted during the month of June, July and August of 2009.

Environmental data

Data for different environmental data was collected during the whole field season in regular intervals on each treatment. Data for the following parameters was collected: photosynthetic active radiation (PAR) at 0cm and 30cm above ground, ultraviolett radiation (UV) at 0cm and 30cm above ground, soil temperature, soil moisture and CO_2. This data was collected by other members of the project group and is used in this thesis to further investigate and interpret vegetation composition results.

Statistical analysis

Multivariate statistical analysis of the vegetation relevés was conducted with Canoco Version 4.5. Absolute cover data of plant species was arcus sin-square root transformed. A detrended correspondence analysis (DCA), with detrending by second order polynomials, was performed. With the coordinates of the first and second axis provided by the DCA, an analysis of variance(ANOVA) was conducted to check for explaining variables.

The data describing presence/absence of reproductive parts was quantitatively analyzed with an ANOVA to check for differences between vegetation type and treatment. It is handled in the rest of this report as the flower data. The number of total species and flowering species was averaged for each treatment. All analysis of variance was conducted with the program SYSTAT 11.

Results

Vegetation relevés

The total inertia of the DCA is 0.9096, which indicates a high variability in the dataset. The eigenvalue of the DCA-axis one is 0.3477, and DCA-axis two has a eigenvalue of 0.2700. These eigenvalues indicate a medium good dispersion of the data along the two axis.

The ordination axis one reflects in part the location of the grasslands in the field (Fig.2). Stabelchod, DD Stabelchod and Val DalBotsch are located close to each other, while Grimmels is located a bit farther away but on a similar altitude as is Val Dal Botsch. These four locations are clustered in the ordination. In the ordination Grimmels and Stabelchod appear to have a higher variability and in fact they cover a larger area than DDStabelschod and Val Dal Botsch. Margunet is situated farther away and on the highest altitude. Mingier is the grassland separated from the others by the longest distance and a mountain chain. Species like *Salix reticulata* and *Gentiana nivalis* are characteristic for Mingier, while species like *Nigritella nigra* and *Trifolium dubium* are typical for Margunet (Fig.3). Species like *Nardus stricta*, *Briza media* and *Festuca rubra* were found on all six grasslands.
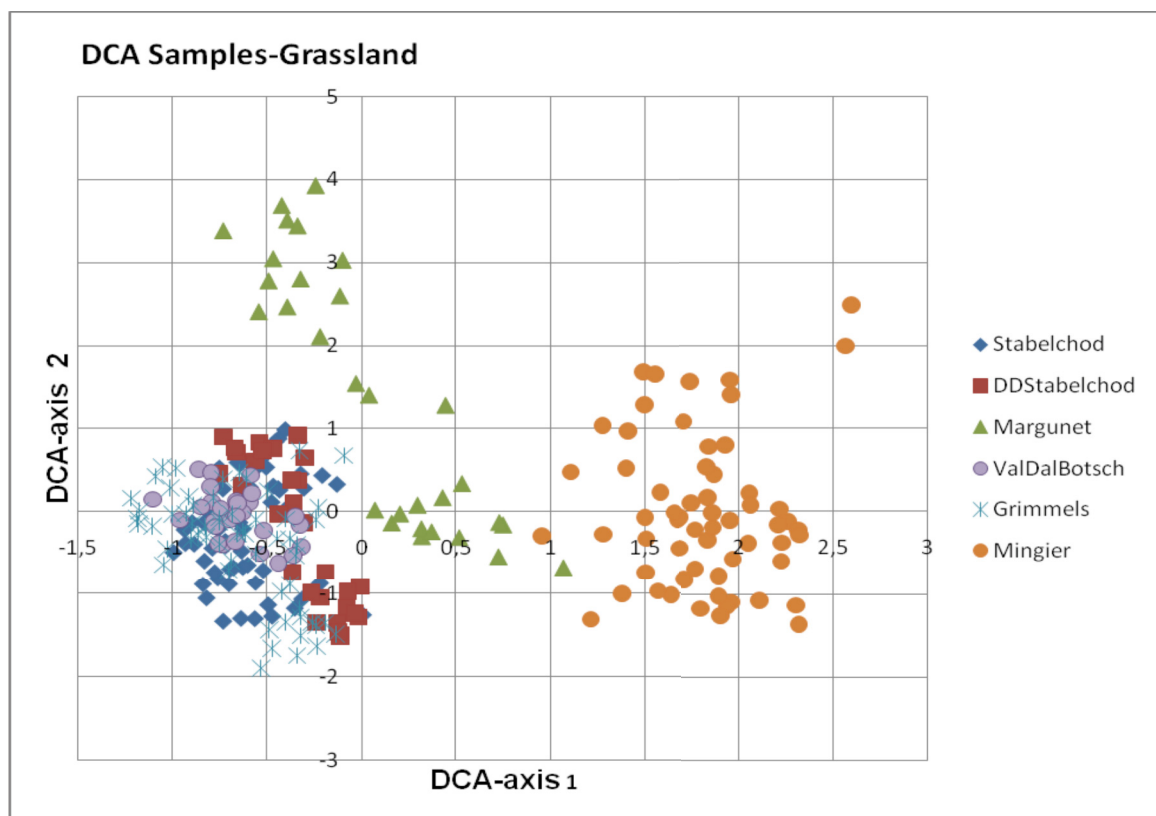

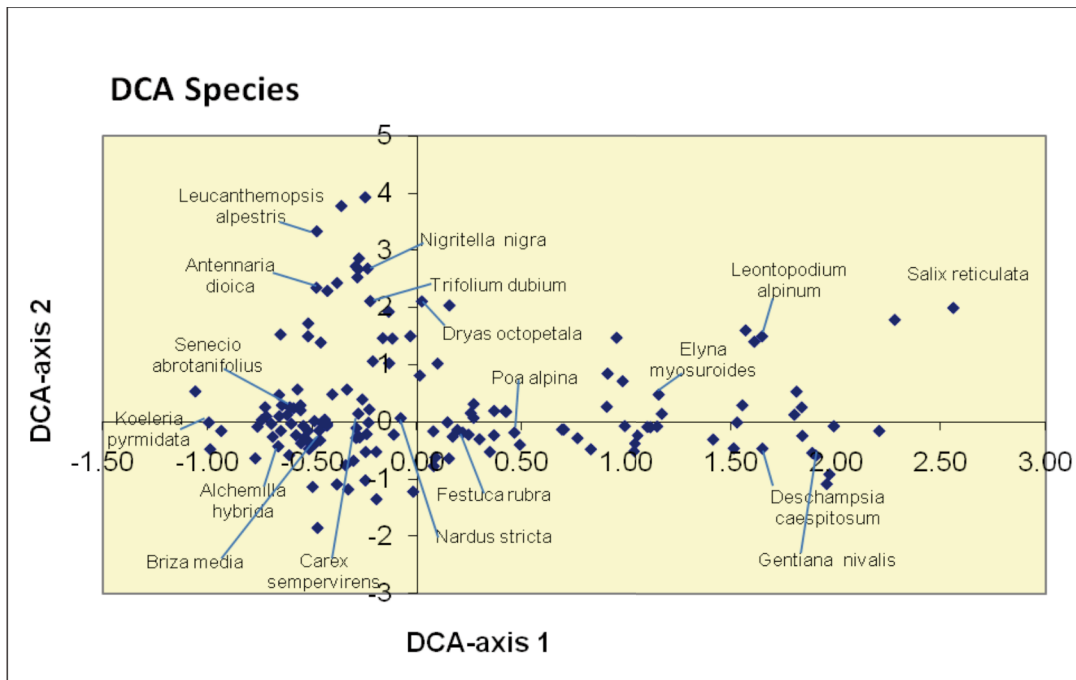Figure 2: DCA ordination of samples with the different grassland locations.

Figure 3: DCA ordination of species.

The ordination axis two reflects the vegetation type, but the short grass vegetation on Margunet constitutes an exception (Fig.4 and 5). On Margunet, Mingier, Stabelchod and DDStabelchod the two vegetation types can be clearly distinguished, while this distinction is less clear for Grimmels and Val DalBotsch (Fig.5)
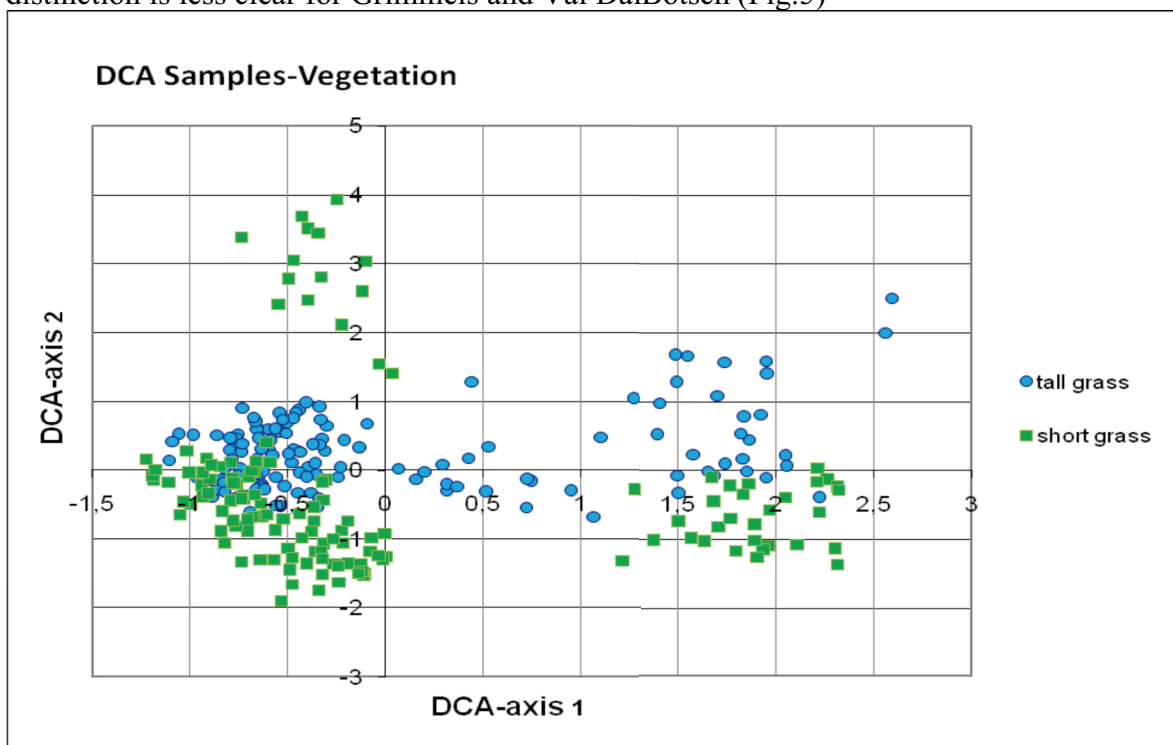

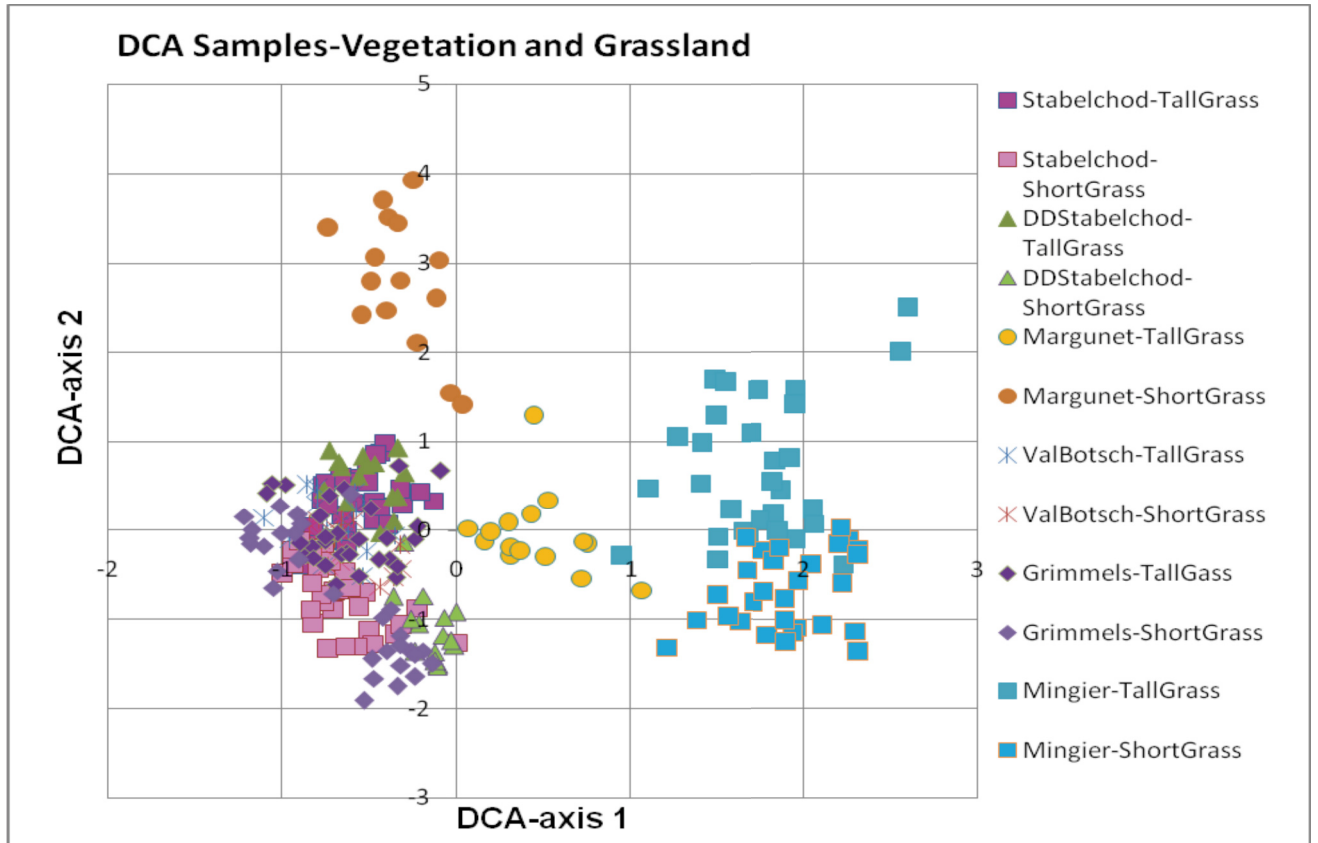Figure 4: DCA ordination of samples with the two vegetation types.

Figure 5: DCA ordination of samples with the different grassland locations and the two vegetation types.

The ordination axis one differs significantly between the locations of the grasslands (Figure 6). One environmental variable possibly explaining this is the soil temperature. It correlates significantly with DCA-axis one (Fig.7). Soil temperature differs significantly between the grassland locations, but is not linearly correlated to height above sea level of the location (Figure 8).
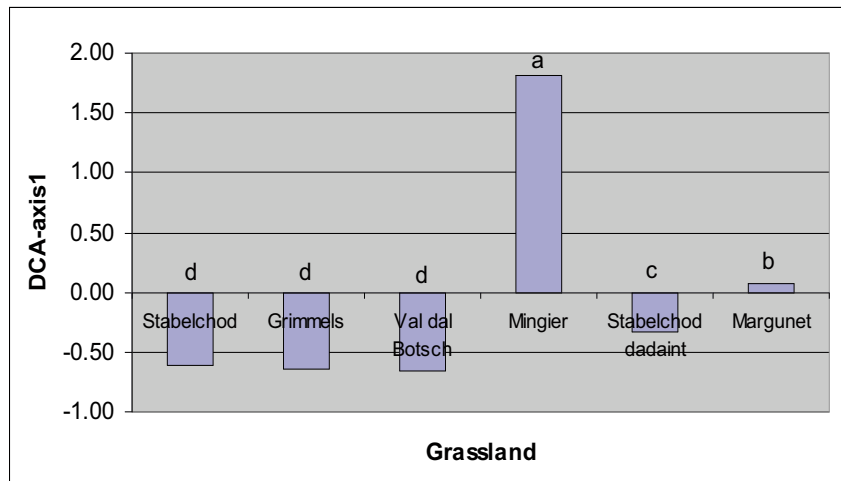

Figure 6: Mean coordinate values of DCA-axis one for the six grassland locations. ANOVA, p-value>0.001, n=270.
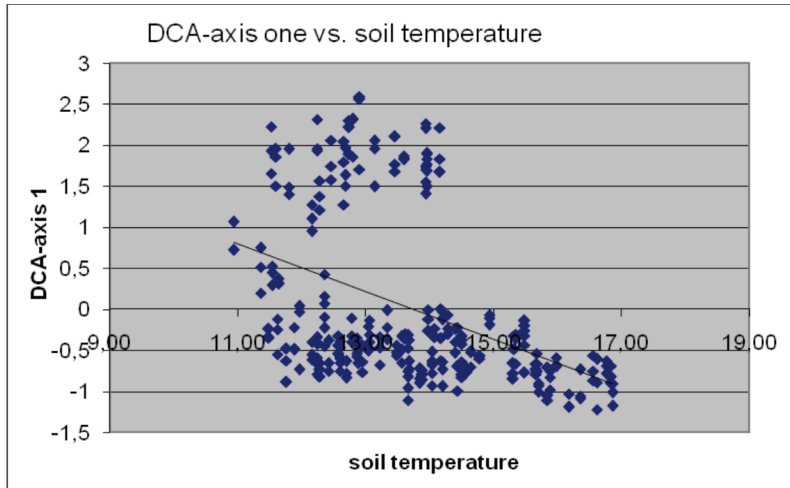
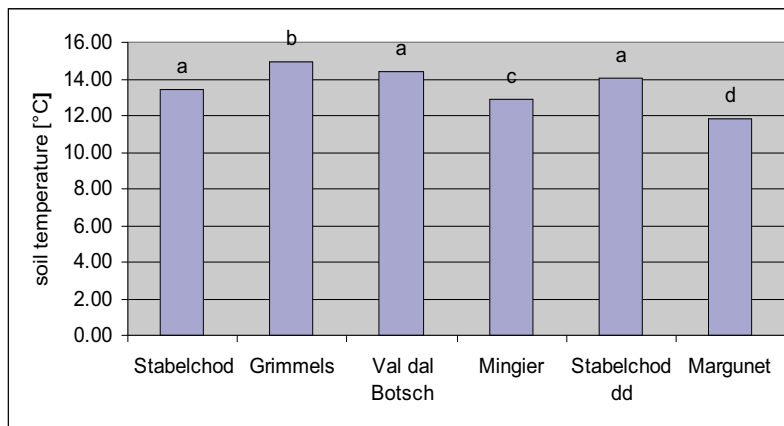Figure 7: Regression of soil temperature and DCA-axis one. ANOVA, p>0.001, n=270.

Figure 8: Mean soil temperature for grassland locations. ANOVA, p-value>0.001, n=270. Grasslands are arranged from left to right with increasing altitude.

The ordination axis two is significant for vegetation type (ANOVA, n=270, p>0.001). The tall grass vegetation has a mean value of 0.28 and the short grass vegetation has a mean of -0.32 for the DCA-axis two. This axis as well differs significantly between the grasslands, where especially Margunet but also Mingier are distinguishable from the others (Fig. 9).
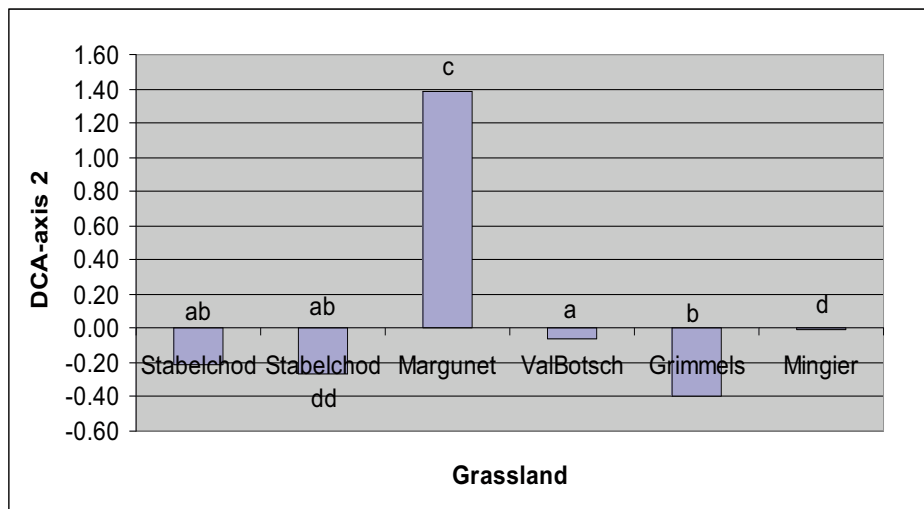

Figure 9: Mean coordinate values of DCA-axis two for the grassland locations. ANOVA, p-value= 0.000, n=270.

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Environmental variables explaining at least part of the difference between the vegetation types are CO_2 and PAR (at 0cm). Both variables correlate significantly with DCA-axis two and are significantly different between vegetation types(Fig.10 and 11).
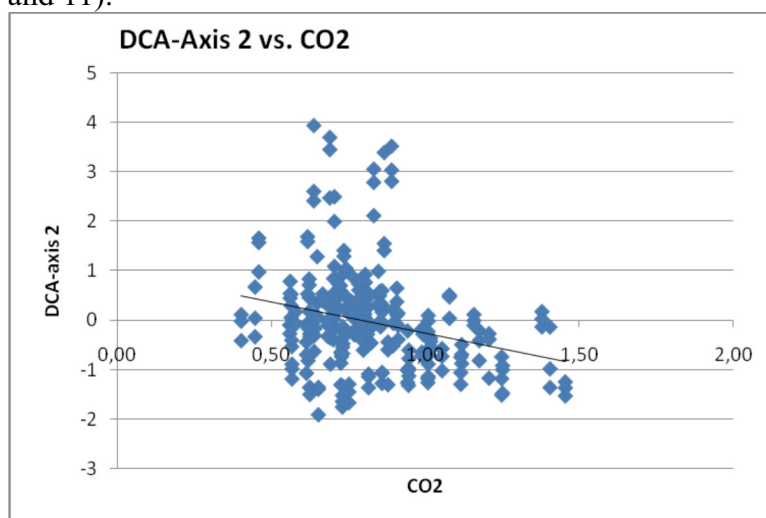

Figure 10: Regression of DCA-axis two and CO_2. ANOVA n=270, p>0.001.

The CO_2 has a mean of $0.75 gCO_2\ m^{-2}\ s^{-1}$ in the tall-grass and a mean of $0.87 gCO_2\ m^{-2}\ s^{-1}$ in the short-grass.
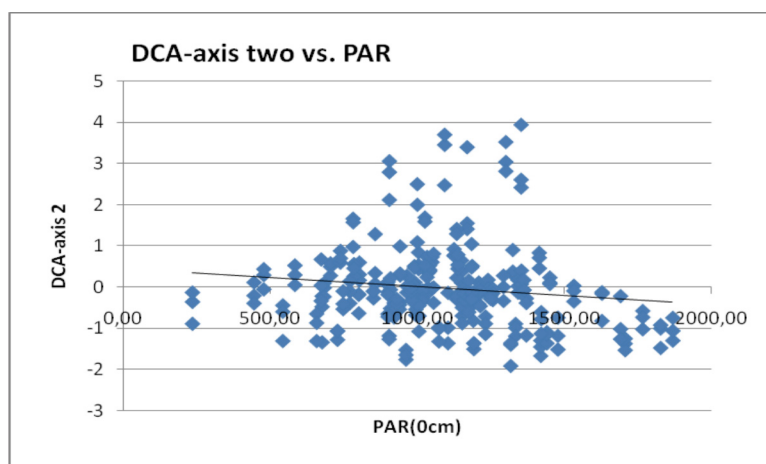

Figure 11: Regression of DCA axis two and PAR(0cm). ANOVA, n=270, p-value>0.027.

The PAR has a mean of 985.53nm in the tall grass and a mean of 1183.26nm in the short grass.

Flower Data

The mean species richness present per square meter differs significantly with treatment but not with vegetation type. But more species were flowering in the tall grass vegetation compared to the short grass vegetation type (Tab.2).

Table 2: ANOVA of flower data. p-values for vegetation type and herbivore exclusion treatment (n=90). Significant values are marked with a *.

Variable/Factor	vegetation type	treatment
mean species	0.078	0.037*
mean flower species	0.015*	0.072

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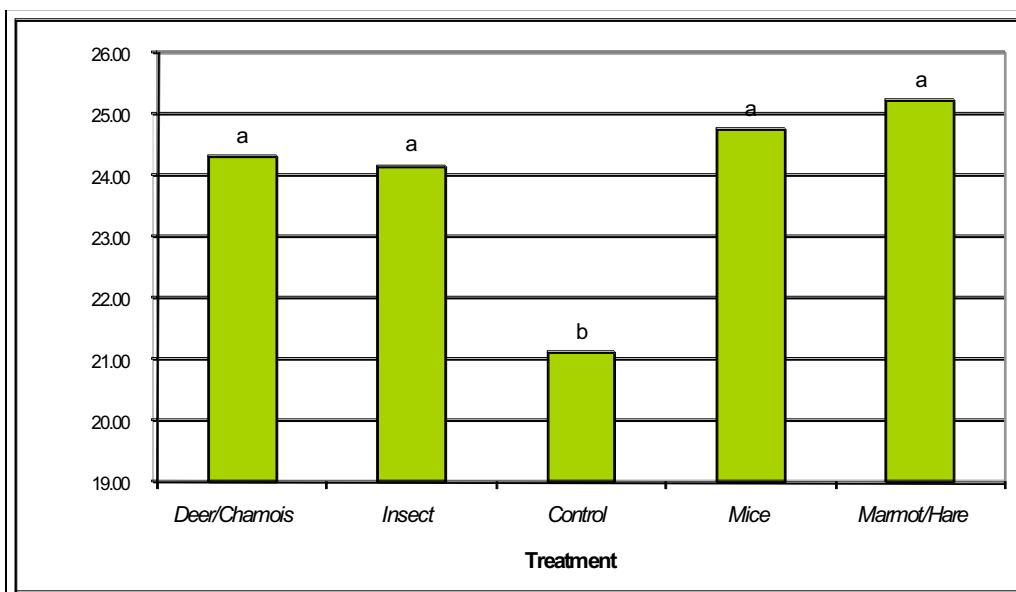The control treatments have a lower plant species richness considering all experimental sites (Fig.12).

Figure 12: Treatment effect on the mean plant species richness.
ANOVA, n=90, p-value=0.037.

The mean number of species with flowers is significantly higher in the tall grass vegetation type compared to the short grass (19.44 vs. 17.10, p-value=0.015, n=90).

While species richness does not differ between the vegetation types, the ratio of graminoid to herb species present is significantly higher in the tall-grass vegetation (ANOVA, p-value >0.001, n=270). The tall-grass vegetation has a mean ratio of 0.34 and the short-grass vegetation a mean ratio of 0.27.

Discussion

Vegetation relevés
The DCA-axis one reflects the location of the grassland. These differences between the locations are partly caused by the difference in the soil temperature, as shown by the correlation between the DCA-axis one and soil temperature. Since the soil temperature is not linearly increasing with altitude above sea level of the grassland locations, it seems to be determined by microclimatic factors.
The DCA-axis two correlates with the vegetation type as well as with the grassland location. The short grass vegetation on Margunet constitutes a exception concerning DCA-axis two. This indicates a distinct short grass vegetation there, compared to the short grass vegetation found on the other grasslands. This difference might be due to the fact, that Margunet is located on the highest altitude. Environmental variables like CO_2 and PAR might explain the different conditions in the two vegetation types, which enhances different plant species to grow there.
No significant differences in vegetation composition were found between exclusion treatments. This fact is very reasonable considering the short time span of the experiment so far. Vegetation composition changes due to different herbivore foraging pressure will take longer time spans than one vegetation period. It can be

expected that changes take place in the coming years of the experiment and that these changes proceed faster in the short-grass vegetation type compared to the tall-grass vegetation type (Schutz et al. 2003).

Flower data
The difference between the mean species richness on the control treatment compared to the exclusion treatments indicates that the treatment plots on the experimental sites were not homogenously chosen. It appears that control plots were established on species poorer spots. This is enhanced by the arrangement of the fence, where the four exclusion treatments are in a square with equal distance separating them, whereas the control is outside the square with more distance separating it from the others.
A possible explanation for more flowering species found in the tall-grass vegetation is found in the fact that short-grass vegetation experiences a higher herbivore foraging pressure and the fact that herbivores prefer the flowers of herbs over those of graminoids (Hulber et al. 2005). The tall-grass vegetation has a higher graminoid/herb ratio than the short-grass, while species richness does not differ between the two vegetation types. Tall-grass graminoid species like *Nardus stricta* and *Carex sempervirens* produce a large amount of flowers and are avoided by the herbivores. So the possibility of all flowers of a species present in a subplot being eaten increases with higher foraging pressure and is lower in graminoid species than in herbs.
Finding no treatment effect on the number of flowering species can be explained by the relatively short time span of the exclusion experiment so far. It can be assumed that density of flowers in species is affected first and then number of species flowering change.

Conclusion
The DCA of the vegetation relevés reflects in part the setup of the experiment, with the vegetation types significantly different on DCA-axis two and the grassland locations significantly different on both DCA-axis. These differences in vegetation types and grassland locations can be explained by environmental variables.
Hypothesis one and two are supported by the data. Differences in vegetation composition between vegetation types and grassland locations are found and environmental variables partly explaining these differences could be identified.
Hypothesis three is supported as well, since the amount of flowering species is correlated with vegetation type but it is not correlated with the treatment.

Acknowledgement

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