Master's Thesis, D-UWIS, Ecology & Evolution Zürich, 01.06.2010

Impacts of Different-Sized Herbivores on Above- and Belowground Productivity in Alpine Grasslands

Bigna Stoffel

Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland.

Composed during the period between 01.12.2009 – 01.06.2010

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Abstract

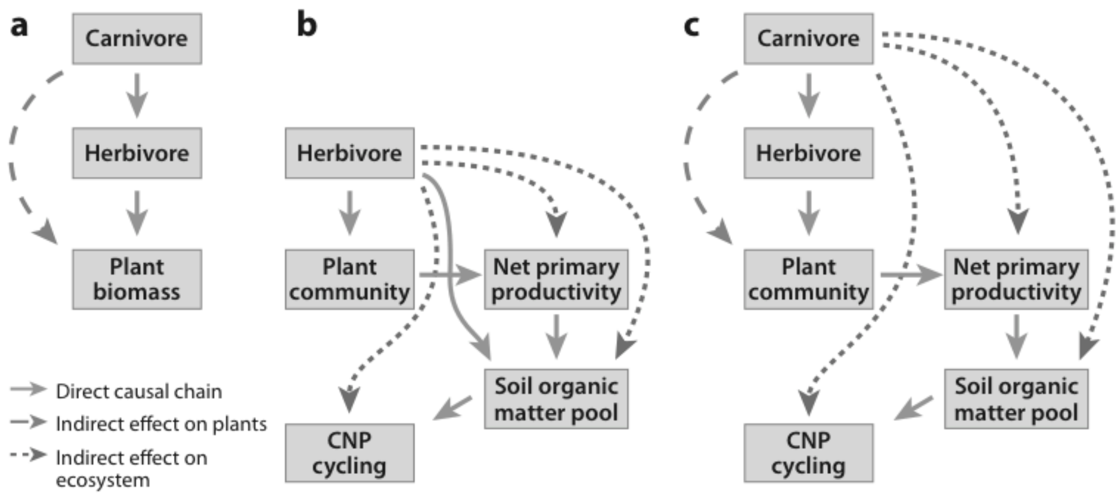
Herbivores can be key determinants and important regulators for grassland processes. Consumption rates and therefore grazing intensity of herbivores are shown to be related to their body size. While small herbivores require high quality forage and can exist with low quantities, larger herbivores need high quantity and can better exploit low quality. A large-scale exclusion experiment, in the Swiss National Park (SNP), was established in 2009 that assesses the impacts of different-sized herbivores on subalpine grasslands of different productivity. This thesis focuses on changes in above- and belowground biomass after the first season of herbivore exclusion. In nutrient rich short-grass communities, large herbivores were shown to have large negative effects on aboveground biomass, whereas they had only little effect on changes in tall-grass. There was a slight trend in terms of herbivore exclusion on belowground biomass, which was decreasing with decreasing size of herbivores. Finally, the data suggests that succession is depleted in the presence of large herbivores. Large herbivores promote diverse landscape patterns and thus diversity of plants and animals. For conservation management it is suggested that there is no need for human induced regulations of large herbivore densities in SNP. However, short-term observations make it difficult to predict future states and may lead to misinterpretation. To better understand the complexity of the grassland system and thus to be able to predict impacts of different-sized herbivores on its functions, there is a need to focus on the whole ecosystem over a longer time-scale, which will be done in subsequent studies from Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) and SNP.

Keywords: Aboveground biomass, alpine grasslands, belowground biomass, herbivores, trophic cascades

INTRODUCTION

Top-down and bottom-up control of different trophic levels across an ecosystem are a key issue of ecology (McNaughton et al. 1997, Pastor and Cohen 1997, Polis 1999, Pastor et al. 2006, Gruner et al. 2008, Schmitz 2008). In grasslands, large vertebrate herbivores can determine and regulate above- and belowground productivity through selective grazing (Krüsi et al. 1995, Hobbs 1996, Krüsi et al. 1996, Polis 1999, Bakker et al. 2006, van Wieren and Bakker 2008; Fig. 1 a). By reducing biomass and by profiting from protein-rich re-growth, grazing of large herbivores leads to short vegetation but in high forage quality and therefore improved feeding conditions for large herbivores (McNaughton 1984, Frank and McNaughton 1992, Pastor and Cohen 1997, Kuijper et al. 2006, Van der Graaf et al. 2005). Further, foliar herbivory has the potential to stimulate rhizosphere processes that feedback positively on plant productivity and induce compensatory growth (Bardgett and Wardle 2003; Fig. 1 b).

Consumption rates and therefore grazing intensity of herbivores are assumed to be related to their body size (e.g. Hobbs 1996, Bakker et al. 2004). While large herbivores consume greater quantities of lower quality food, small herbivores consume less food of higher quality because they are constrained by their high metabolism and limited digestive capacity (Olff et al. 2002, Cromsigt and Olff 2008). Del-Val and Crawley (2005) reported changes in plant species abundances in dependence of the composition of herbivore communities. By changing plant species composition, vegetation structure and nutrient content, large and medium sized herbivores affect the living conditions for smaller species (e.g. Achermann 2000, Bakker et al. 2006, Van Wieren and Bakker 20089) e.g. as shown in the case of cattle facilitating rabbits, but disadvantaging voles in the Netherlands (Bakker et al. 2009). Herbivores can also have large effects on vegetation biomass, microbial biomass and nutrient content through input of urine and feces (Bardgett et al. 2001, Wardle et al. 2002, Wardle et al. 2004; Fig. 1 d) and trampling (Pastor and Cohen 1997, Wardle et al. 2002, Wardle et al. 2004, Bakker et al. 2009).



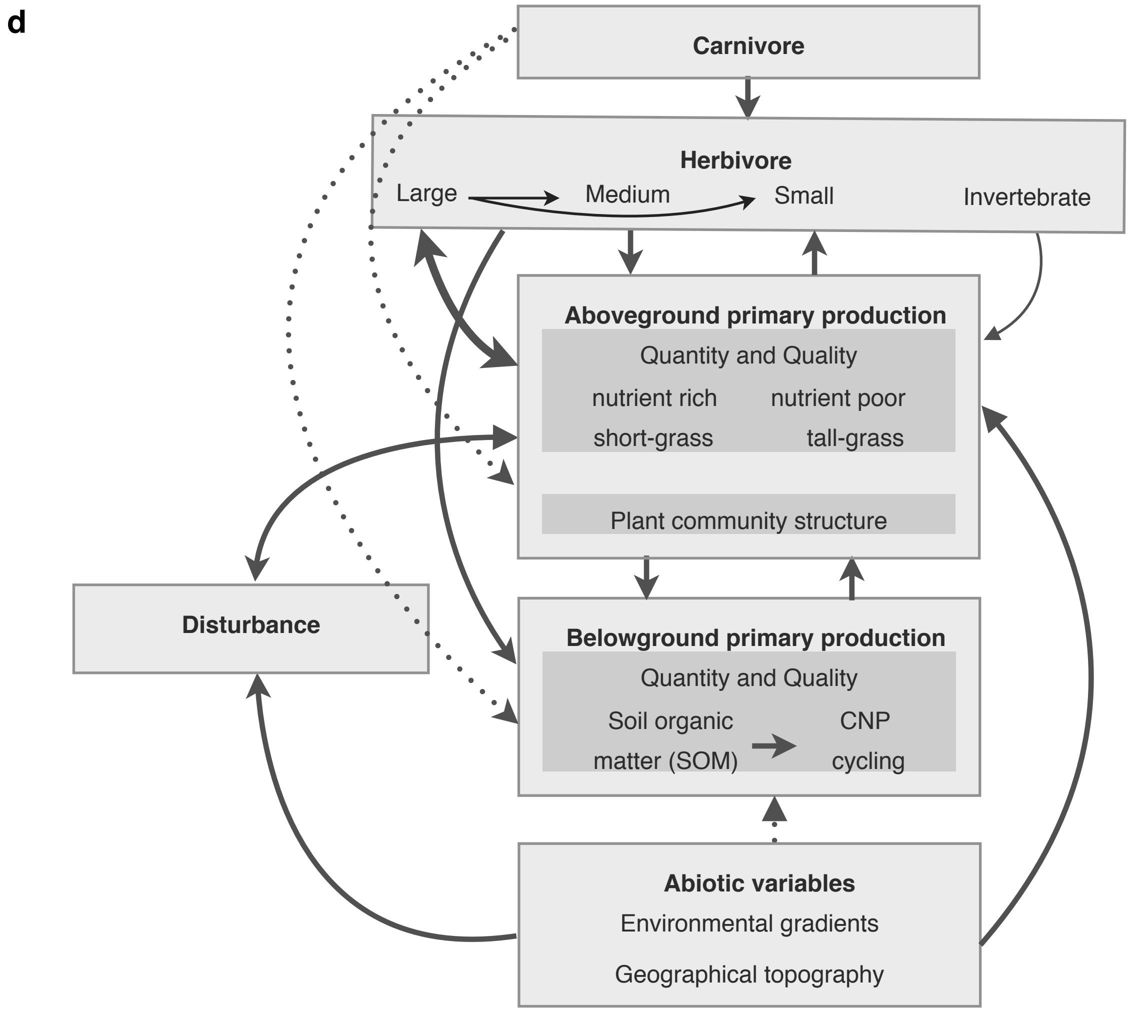


Figure 1: Factors influencing herbivores and plant productivity. a) - d) Conceptualization of the way to extend classic green world hypothesis to ecosystem function. (a) According to classical theory for a three-trophic-level food chain (HSS), predators have indirect effects on the plant trophic level by directly limiting herbivore abundance. (b) Classic HSS theory can be extended to understand multitrophic effects on ecosystem function by first recognizing that herbivores directly impact the species composition of the plant community through selective foraging. Ensuing changes in mean leaf tissue chemistry owing to preponderance of uneaten plants will propagate indirect effects on ecosystem properties and functions. (c) HSS is then completely linked to ecosystem function by recognizing that carnivore indirect effect on ecosystems is mediated through direct effects with herbivores in ways that change the nature of herbivore indirect effects on ecosystems (from Schmitz et al. 2009). (d) The abundance of herbivores is regulated by top-down processes, such as predation, and by bottom-up processes through the quality versus the quantity of primary production (arrows indicate the direction of influence). Herbivores showing strong functional divergences based on body size. Through consuming high quantities large herbivores have large impacts on aboveground productivity while smaller herbivores are dependent on quality. Environmental gradients have direct and indirect effects on the plant community structure and on the quality and quantity of primary production. Biotic disturbances, such as grazing lawns, modify the vegetation by altering the competitive balance between grazing-tolerant and grazing-intolerant grass species (Cromsigt and Olff 2008, adapted from Hopcraft et al. 2009).

Even though influences on grassland productivity is an important issue in ecology, there is a lack of studies considering the complexity of multilevel trophic cascades and different-sized herbivores in terrestrial systems (Gruner et al. 2008). Most studies which treat this issue only consider one or two groups of herbivores (e.g. McNaughton 1979, Frank and McNaughton 1992, Kuijper et al. 200, Smit et al. 2001). More complex studies either are restricted to one grassland only (Bakker et al. 2004) or investigate in human changed grasslands and assess the alterations of productivity and diversity due to human introduced cattle (e.g. Bakker et al. 2006, Van Wieren and Bakker 2008).

Very little is known about how several groups of different-sized herbivores affect vegetation types of different productivity on multiple trophic levels in alpine grasslands. In a large-scale exclusion experiment in Swiss alpine grasslands, it is assessed how different vegetation types, i.e. short- (nutrient-rich) and tall-grass (nutrient-poor), respond to grazing by different groups of herbivores (top-down effects). As a part of a broad project on trophic cascades, this thesis focuses on changes of biomass. It is expected that depending on the body size and the vegetation type the exclusion of one or more herbivore groups induces appropriate changes during the first growing season (Fig. 2).

It is assessed, that impacts of herbivores are positively related to their body size. It is expected that the exclusion of larger herbivores will induce larger and faster effects on above- and belowground biomass under study than the exclusion of smaller herbivores. As short-grass is the preferred grazing site of large herbivores (Wildi and Schütz 2000, Schmitz et al. 2008), exclusion results in a small amount of aboveground biomass of high quality and in high changes of belowground biomass. In tall-grass, exclusion will result in high amounts of aboveground biomass but in low quality and only in small changes of belowground biomass.

By assessing how the single and combined effects of herbivory incluences above- and belowground processes, it may be possible to predict future changes in vegetation composition and its feedback on foraging patterns of herbivore communities if one or several groups of herbivores disappear. Different reasons for changes in herbivore densities could be both, biotic factors, e.g. re-immigration of predators, and abiotic factors, e.g. changes in the climate regimes (Fig. 1 c and d).

Expected effects after 1. season

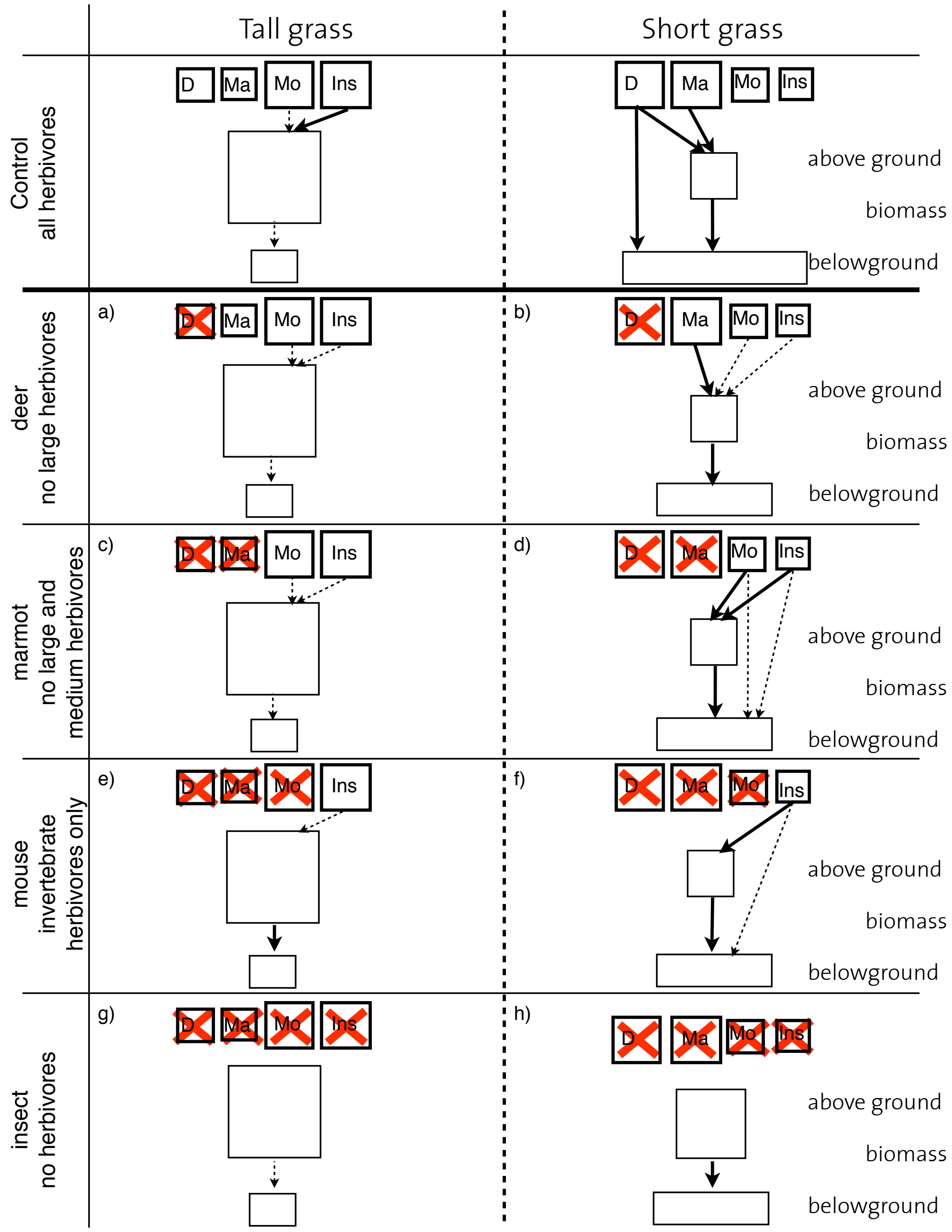


Figure 2: Hypothesized top-down effects on above- and belowground biomass of grazing treatments (Control, deer (exclosure of deer), marmot (exclosure of marmot), mouse (exclosure of mouse) and insect (exclosure of insect, respectively all herbivores) within two different grass types (short/tall) after one season.

METHODS AND MATERIAL

Study area

The Swiss National Park (SNP) is located in the southeastern part of Switzerland in the Central Alps. It extends over an area of 170.3km² with 85km². Vegetation in the SNP consists of 3% subalpine, 18% alpine grasslands and 28% by forests and 51% of boulders and rocks (SNP homepage). It's elevation ranges from 1400 to 3174m a.s.l. Mean annual temperature and precipitation are 0.2±0.7°C and 925±162mm (mean ± SD; Risch et al. 2008, recorded at the park's weather station: Buffalora 1977 m). Since the early 1600 many pastures were used as grazing sites for domestic animals (Risch et al. 2008, Parolini 1995). Agricultural activities ceased in 1914 when the SNP was founded (Wildi and Schütz 2000), and human disturbance has been kept to a minimum ever since (Achermann 2000).

Study design

Eighteen sites on six grasslands (Stabelchod, Stablechod dadaint, Margunet, Val dal Botsch, Alp Grimmels, Alp Minger) were selected where large patches (>1ha) of both short-grass and tall-grass vegetation occurred. Meadows were chosen to be as similar as possible in animal diversity (Table 1). The underlying parent material of all sites consists of dolomite sediments (SNP, Schütz et al. 2006). The two vegetation types found on those grasslands can easily be distinguished. Short-grass pastures are dominated by red fescue (*Festuca rubra* L.), perennial quaking grass (*Brisa media* L.), and milfoil (*Achillea millefolium* L.; Mächler 2009, Risch et al. 2008, Werhahn 2009, Wildi and Schütz 2000). As a result of intensive grazing, the vegetation height of the short-grass type is approximately 2cm. The tall-grass pastures in contrast, is dominated by evergreen sedge tussocks (*Carex sempervirens* Vill.), exceeding 20cm in height (Risch et al. 2008, Schütz et al. 2006).

Exclusion Design

Within each site effects of different-sized herbivores were experimentally separated. Four fences were built with different mesh size on each of the eighteen sites. The control treatment (control) remained unfenced allowing all herbivores to graze (Fig. 3). The complete electric fence powered by a solar panel with integrated battery (AGRARO Sunpower S250, Landi, Bern, Switzerland), which contained 4 time 2m x 3m exclusion plots, is designed 900 (length) x 700 (width) x 200cm (height) and was electronically . The four sides remained open the lowest 80cm to allow medium and small herbivores to enter.

Grazing type 1 (deer) within the matrix excludes large herbivores, i.e. red deer and chamois, and is unfenced. Grazing type 2 (marmot; mesh size 5 x 5cm) excludes medium herbivores (marmots and snow hares), but still allows small herbivores and insects to enter. Grazing type 3 (mouse; mesh size 1.5 x 1.5cm) allows invertebrate herbivores to enter. Finally grazing type 4 (insect; mesh size 1 x 1mm) excludes all herbivores. The insect treatment was checked regularly and sprayed with a biodegradable insecticide (biokill, Doetsch Grether AG, Switzerland) if it was necessary (Fig. 3).

Within each grazing treatment 6 Plots (P1 - P6) of 1m² were placed where species composition, biomass, microbial activity, UV, PAR, ground temperature, soil moisture and nutrient content was assessed (Mächler 2009, Werhahn 2009, Kukielka 2010; AppendixC). Herbivore densities are reported in complementary studies and summarized in table 1 (Wittker 2008, Schäfer 2009).

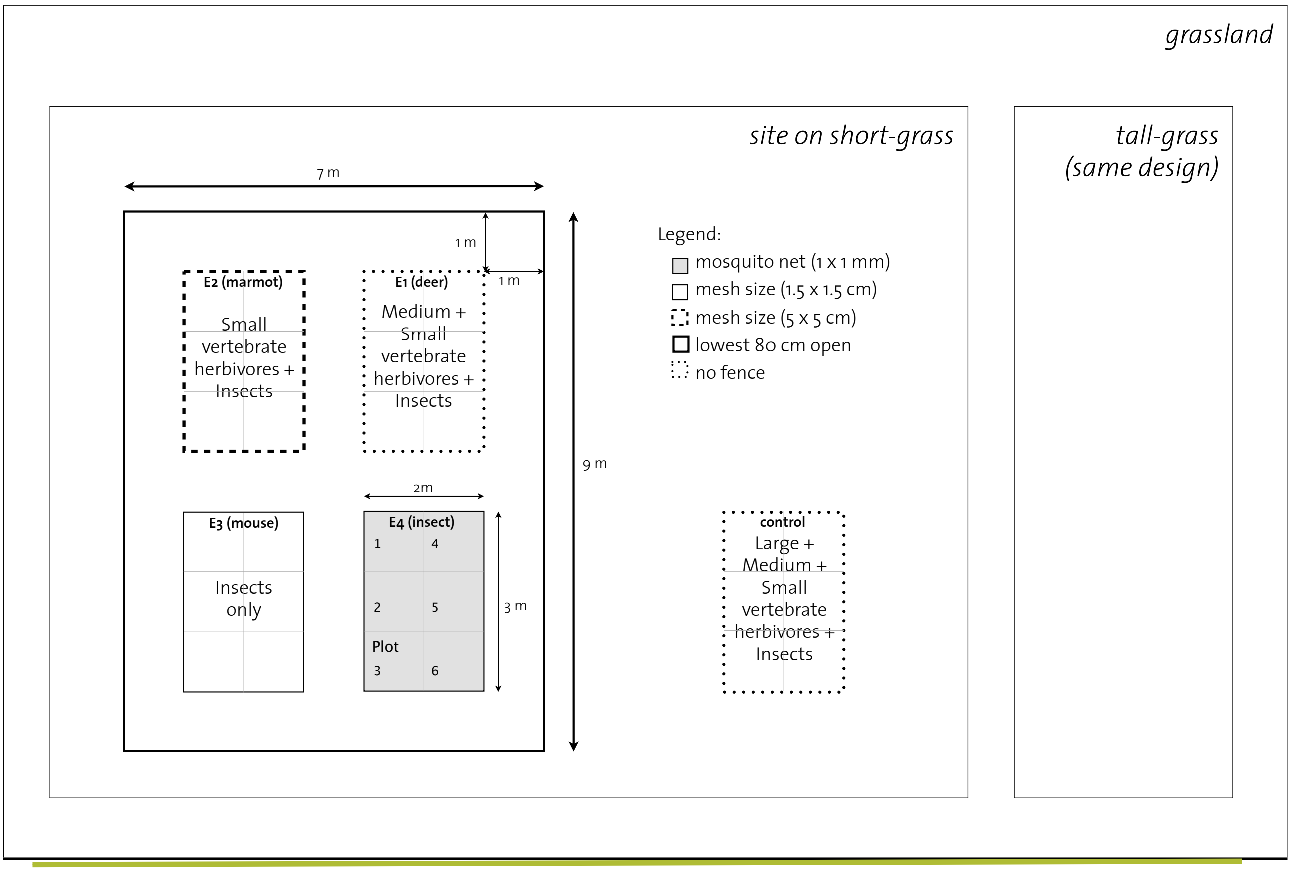


Figure 3: Block design indicating the study design. Within each grassland 1 to 2 sites were selected on short and tall-grass. Within each site the four grazing treatments were experimentally excluded (control, E1: deer, E2: marmot, E3: mouse, E4: insect). Within each grazing treatment 6 plots were distinguished. P1 was used to monitor vegetation, i.e. aboveground biomass, P3 to determine belowground biomass and soil nutrient content and finally P6 to measure CO_2 for microbial activity and abiotic factors.

Table 1: Characteristics of different grasslands and overview on herbivore densities (data from Wittker 2008, Schäfer 2009, SNP and unpublished data).

Grassland	Deer pellets	Observed marmots	Insects	Elevation [m a.s.l.]	Geographical position (Latitude / Longitude)
Stabelchod	18.34	5	2.67	1960-1975	46°39'49.64"N 10°14'30.07"E
Stabelchod dadaint	25.71	3	9.66	2125-2135	46°40'19.58"N 10°14'45.39"E
Grimmels	35.84	17	4.17	2015-2065	46°39'55.91"N 10°11'18.72"E
Margunet	17	9	1.83	2328-2348	46°40'29.30"N 10°14'39.55"E
Minger	34.27	11	1.34	2090-2100	46°42'27.49"N 10°15'42.76"E
Val dal Botsch	7.67	2	0.67	2065-2075	46°40'25.92"N 10°13'55.40"E

Field sampling and estimation of biomass

Aboveground net primary production was measured at peak growth in August 2009. It was assessed on every site in plot 1 (18 sites x 5 grazing treatments = 90 samples) and was estimated using the canopy intercept method (McNaughton 1984). The canopy intercept method relates standing crop to the number of hits a pin makes when passed at an angle through vegetation. However, results are strongly affected by plant growth form, therefore, calculations of slopes of regression require data modification.

In a first step, we conducted pin counts on reference plots next to each plot on all the sites. Vegetation was clipped afterwards. For shrubs only current year grown was collected (Bakker et al. 2006). Freshly clipped biomass was dried 48 h at 65°C, and weighted to assess the dry weight (gm^{-2}). The relationship between leaf counts (litter and flower counts were excluded) and standing crop was calculated as follows; Narrow-leafed graminoids *Elyna myosuroides* Vill., *Festuca ovina* L., *F. rubra* L. and *Nardus stricta* L. were modified by dividing the pin counts by two to acknowledge the relatively small biomass of these species. To exclude variations due to different people who did the recordings, records were adjusted (Appendix A). The relationship between adjusted leaf counts and standing crop was calculated and applied to the dataset (Fig. 4).

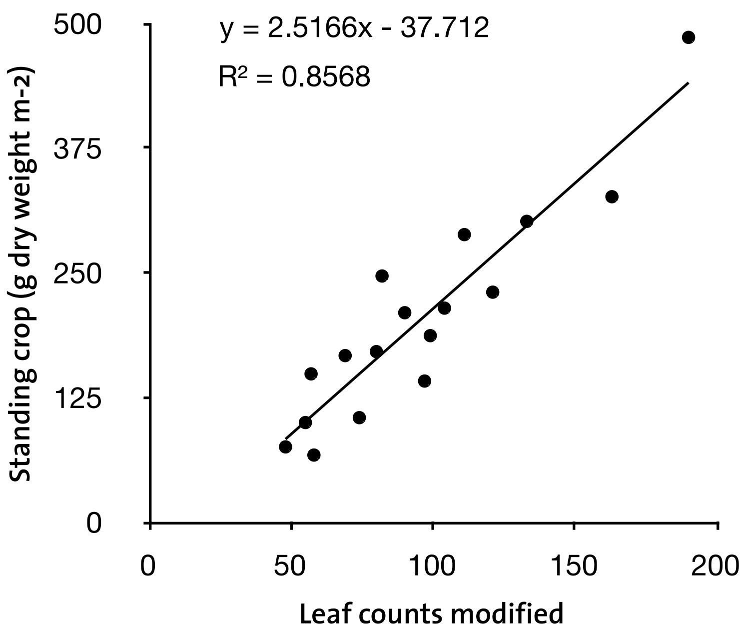


Figure 4: Relationship between adjusted pin counts and standing biomass.

estimated standing crop = 2.517 x adjusted pin counts - 37.712

To determine belowground biomass, soil core samples were taken (core diameter: 1.1 cm). Within each grazing treatment 5 samples from 0 to 10 cm depth were collected in reference plot 3 (18 sites x 5 grazing treatments x 5 replications = 450 samples). The samples were dried at 30°C and fine roots were manually separated from soil material. Roots were dried for 48 hours at 65°C and weighted to determine belowground biomass (g/per core; i.e. $10cm \times 1.1^2cm \times \pi = 38.013cm^3$).

Abiotic variables and nutrient contents

Additionally, abiotic data (photosynthetic active radiation (PAR) at 0cm and 30cm above ground, ultraviolett radiation (UV) at 0cm and 30cm above ground, soil temperature, soil moisture; Appendix C) and nutrient content (nitrogen (N), carbon (C) and phosphorous (P); Kukielka 2010) was collected by other members of the project group but is used in this thesis to further investigate and interpret biomass results.

Statistical data analysis

To analyze the impact of different-sized herbivores on biomass, a two way type I ANOVA was run for each target variable i.e. aboveground and belowground biomass, separately based on linear mixed effect models (Pinheiro and Bates 2000). Explanatory factors of different levels were grazing treatment (control, deer, marmot, mouse, insect) and grass type (short/tall). These factors were treated as fixed effects. Site nested in grassland as a random effect. Above- and belowground biomass were taken as dependent variables. In a second step, one way ANOVAs were performed on subsets of short- and tall-grass separately. All significant interactions were further analyzed by Tukey honestly significance (HSD) test (p=0.05) for pairwise comparisons. The ANOVA of this model does not provide a correct sum of squares, why it is not indicated in the results.

Where effects of exclosure were significant, possible effects of other variables (geographical topography, soil moisture and temperature, light conditions, nutrients and diversity) are tested through manual backward selection based on P values of summary tables and stepwise model selection based on Akaike's information criterion (Sakamoto et al. 1986).

Model assumptions are tested with Shapiro-Wilk normality test and Bartlett test of homogeneity of variances (Bartlett 1937, Royston 1982). Analyses were performed on log transformed data to better meet assumptions of normal distribution of residuals. To meet assumptions of homogeneity of variance, data were corrected as follows: First, all data were log transformed. Second, aboveground biomass measurement number 1 is treated as an outlier in the analysis of total biomass. In total belowground biomass measurement 17, 27, 37 and 42 are treated as an outlier. By skipping these measurements, model assumptions are better met. Outliers were skipped in statistical analysis but included in the calculations of means and standard derivations in tables and figures. Outliers are highlighted in scatter plots (Appendix B2). All statistical tests were performed in R version 2.10.0 using the packages „nlme“ (Pinheiro and Bates 2000).

RESULTS

In summary, results of productivity indicate an increasing trend in aboveground biomass and a decreasing trend in belowground biomass of exclusion, after the first season. Significant effects, occur mainly in aboveground biomass in nutrient-rich short-grass (for a summary of detailed results see Appendix B2).

After one season, exclusion showed a significant impact on total aboveground biomass ($F_4 = 9.613$, $p < 0.001$). Biomass in control was significantly lower than in other grazing treatments (Fig. 5 a). The effect of exclusion also differed significantly within grass type ($F_4 = 4.286$, $p = 0.004$). The effect of grass type was not significant ($F_1 = 0.703$, $p = 0.420$). Whereas biomass in control was significantly lower than in all other grazing treatment, biomass in insect was significantly higher than in deer ($p=0.028$) and mouse ($p=0.009$). In short-grass, exclusion resulted in a significant effect ($F_4 = 11.424$, $p<0.001$). The absence of large herbivores indicates a significant increase of biomass on short-grass as shown in Tukey HSD test. In nutrient-poor tall-grass, exclusion showed no significant effect ($F = 2.008$, $p = 0.117$; Fig. 5 b).

Results of total belowground biomass showed no significance (Appendix B1). There is a non significant trend where total belowground biomass is decreasing with the exclusion of herbivores ($F=1.973$, $p=0.110$; Fig. 5 c). In nutrient-rich short-grass, biomass was lowest in the deer treatment but differed only significantly from mouse ($p=0.045$). In nutrient-poor tall-grass, exclusion showed a significant effect ($F=2.888$, $p=0.003$; Fig. 5 d). Biomass of deer was in contrast highest and differed significantly from mouse ($p<0.001$) and insect ($p<0.001$) (Appendix B2).

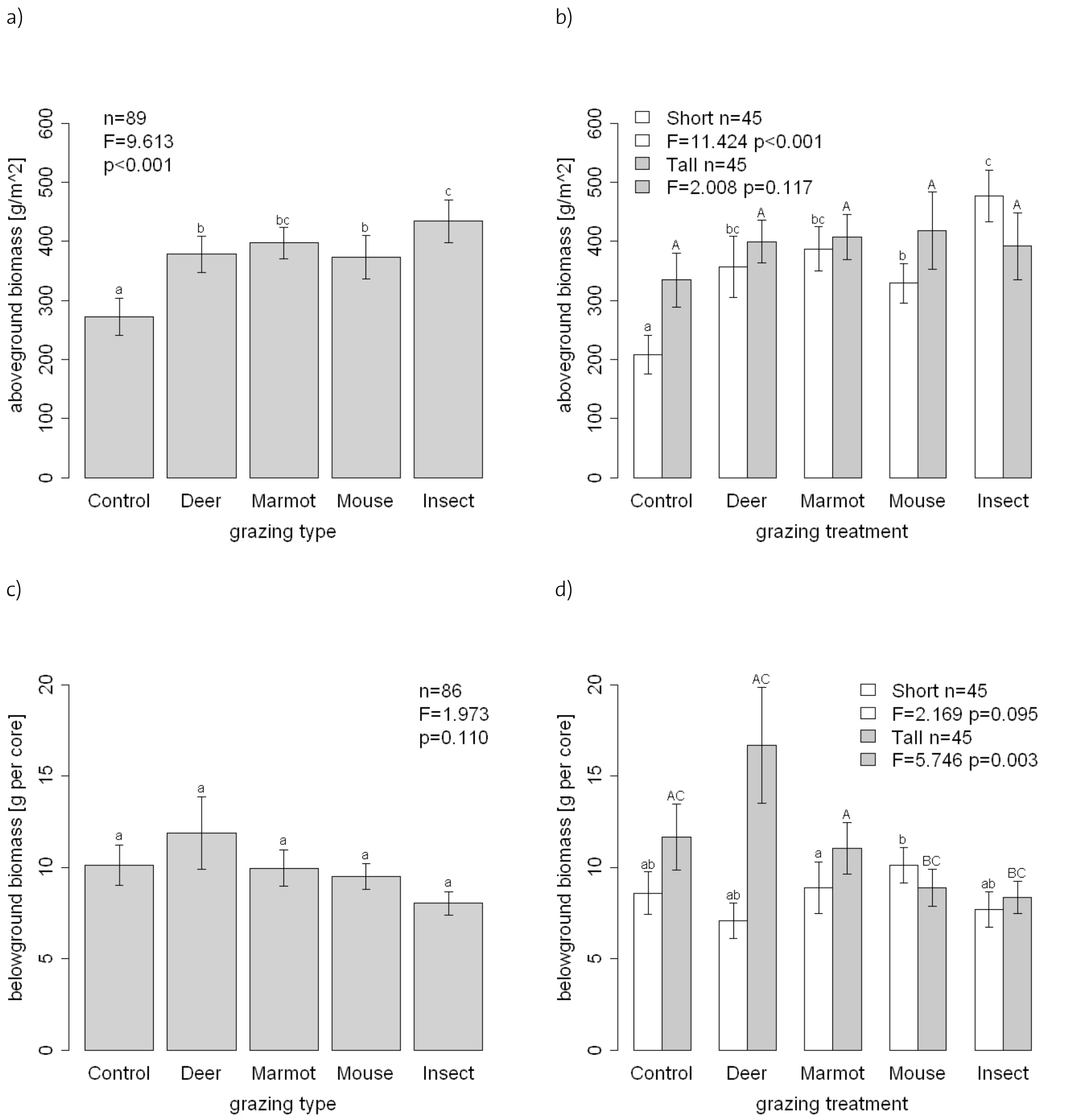


Figure 5 shows how various grazing treatments affect biomass. Figures show the effect of different-sized herbivores on a) total aboveground biomass b) short- and tall-grass biomass, c) total belowground biomass, d) short and tall-grass biomass. Same letters represent no significant difference between grazing treatment (significant: $p<0.05$). Whereas outliers are considered in figures, they are skipped for the statistical analysis

DISCUSSION

To sum up, results of this exclusion experiment corroborate that grazing intensity and therefore impacts on biomass are directly related to herbivores body size. As expected, the exclusion of large herbivores induced larger and faster changes in aboveground biomass than the exclusion of smaller herbivores. The removal of large herbivores induced a significant increase in aboveground biomass. Since nutrient-rich short-grass are preferred grazing sites of red deer and chamois (Wildi and Schütz 2000), the high grazing pressure exhibited major effects and grazing resulted in a significantly lower amount of aboveground biomass. These findings generally agree with those reported by others, e.g. Frank and McNaughton (1993), which showed an increase of 47% in aboveground production after exclosure of bison and elk in the Yellowstone National Park. Jacobs and Naiman (2008) reported a threefold increase of plant biomass after three years of herbivore exclusion in African Savannas. In nutrient-poor tall-grass, the low grazing pressure of smaller herbivores resulted in high amounts of aboveground biomass. Finding no significant treatment effect can be explained by the relatively short time span of the exclusion experiment so far.

Results on belowground biomass indicate a trend of decreasing biomass, when all herbivores are excluded. The most eye-catching results are biomass in deer. While belowground biomass was lowest on short-grass, it was highest on tall-grass. In nutrient-rich short-grass it was shown that C and N values contribute to the pattern of belowground biomass distribution (Appendix B3). In a complementary study Kukielka (2010) reported increasing N and P, but decreasing C levels. These results are comparable with Bakker et al. (2004). They showed that N mineralization rates directly depend on the composition of herbivore communities and on the species-specific patterns of N return to the soil through feces and urine. Based on results of exclusion of bisons and elks in the Yellowstone Park, Frank and McNaughton (JAHRGANG), stated the grazing optimization hypothesis. According to this, plants compensate for defoliation. Additionally, foliar herbivory can stimulate rhizosphere processes (Bardgett and Wardle 2003) which induce compensatory growth. After exclusion of deer and chamois, mechanisms of plant available nutrient input and growth simulation ceased, which could be a reason for low belowground biomass in deer on short-grass.

Milchunas et al. (1993) showed that nutrient-poor sites are grazing-limited and therefore these sites may react more sensible to grazing. This could be a possible explanation for high belowground biomass in deer on nutrient-poor tall-grass. Even though large herbivores prefer nutrient-rich short grass, they may feed on tall-grass due to high competition. Another explanatory factor of patterns of biomass distribution in tall-grass, is UV radiation, which was lowest in insect and showed as only abiotic factor effects (Appendix 3B).

Competition and facilitation between different groups of herbivores are not assessed separately. Based on results of this study, it can be conducted that, due to ceasing competition through exclosure and higher protective cover through increasing aboveground biomass, extended foraging areas for medium sized and smaller herbivores develop. This is comparable to Wildi and Schütz (2000) who showed extended foraging areas for smaller herbivores where large herbivores are excluded.

The small timespan makes it difficult to make exact predictions about how different groups of herbivores compete with or facilitate each other. In general, effects on belowground processes are mostly indirect and more complex than aboveground processes (Bardgett and Wardle 2003), thus it is probable that belowground biomass has a delayed response to herbivory. Although that aboveground biota can have important effects on the belowground subsystem, for a feedback to occur it is necessary that belowground organisms can influence aboveground community structure and functioning (Wardle et al. 2004). In this study, only short-term effects of foliar herbivory were assessed. The recording of belowground herbivores was not feasible. In the long-term perspective, these effects may become more acute (Bakker et al. 2009).

Some abiotic factors (soil temperature, soil moisture, PAR, UV etc.) contribute as well to the found pattern of biomass distribution. Geographical effects of elevation are negligible. North and east exposition may influence microclimatic variables like soil temperature which may again influence nutrient cycling, which was of importance in grazing dominated short-grass. In tall-grass mainly UV radiation was of importance. In general these factors were shown not to dominate the exclusion effects and are considered in the model selection as random site effects (Appendix B3).

The great differences of control treatment compared to other treatments in aboveground biomass and the confusing pattern in belowground biomass, may be traced back to not homogeneously chosen treatment plots, since control is placed further distanced to other treatments. This assumption was already stated by Wehrhahn (2009) who found high differences between the mean species richness on the control treatment compared to the exclusion treatments.

CONCLUSION

Even though the exclusion have only be applied over one season yet, some of the results are quite interesting. The results hold implications for the impacts of different sized herbivores on productivity-diversity and on their role on succession. Since SNP management focuses on conservation, questions related to resistance and resilience of grasslands or changes in biodiversity are fundamental and may have implications for sustainable management strategies. Habitat productivity and thus biomass, is an important factor in predicting the impact of mammalian herbivory on grassland diversity (Bakker et al. 2006).

According to Grime's (1973) intermediate disturbance hypothesis, intermediate levels of disturbance can maximize species diversity. As shown in Milchunas et al. (1988) intermediate disturbance such as intense grazing modify the quantity and quality of vegetation by altering the competitive balance between grazing tolerant and grazing-intolerant grass species. At low disturbance, competitively dominant species exclude subordinate species, but excessive disturbance leads to local extinctions. By reducing biomass of specific plants and increasing spatial vegetation heterogeneity, grazing allows more species to coexist (Jacobs and Naiman 2008). In this study, in nutrient-rich short-grass diversity was dependent of aboveground biomass but was not related to grazing treatments so far (Werhahn 2009). Beside effects on plant diversity, grazing of large herbivores leads to diverse vegetation patterns, and thus facilitate the abundance of other smaller herbivores. E.g. Klein and Bay (1994) reported that species-specific foraging patterns of muskoxen, hares and lemmings minimized food resource competition between these herbivores. And Kujiper et al. (2008) showed cattle induced facilitated grazing conditions for hares.

Bardgett and Wardle (2003) and Wardle et al. (2004) pointed out that effects of herbivory on ecosystems are not only dependent on their size but also on the productivity of the ecosystem itself. In the course of grazing, large herbivores stimulate growth of nutrient-rich grass and return most of the organic material to soil as fecal material. Thus positive effects of herbivory on soil biota and soil processes are generally found when productivity and grazing intensity are high. Thus, grazing in nutrient-rich short-grass may lead to a retardation in succession from short- to tall-grass (Fig. 6 a). Whereas negative effects are to be expected in unproductive systems with low consumption rates (Skarpe and Hester 2008; Fig. 6 b). Changes of plant community composition will occur. After a while nutrient poor tall-grass pastures would develop followed by forests (Wildi and Schütz 2000).

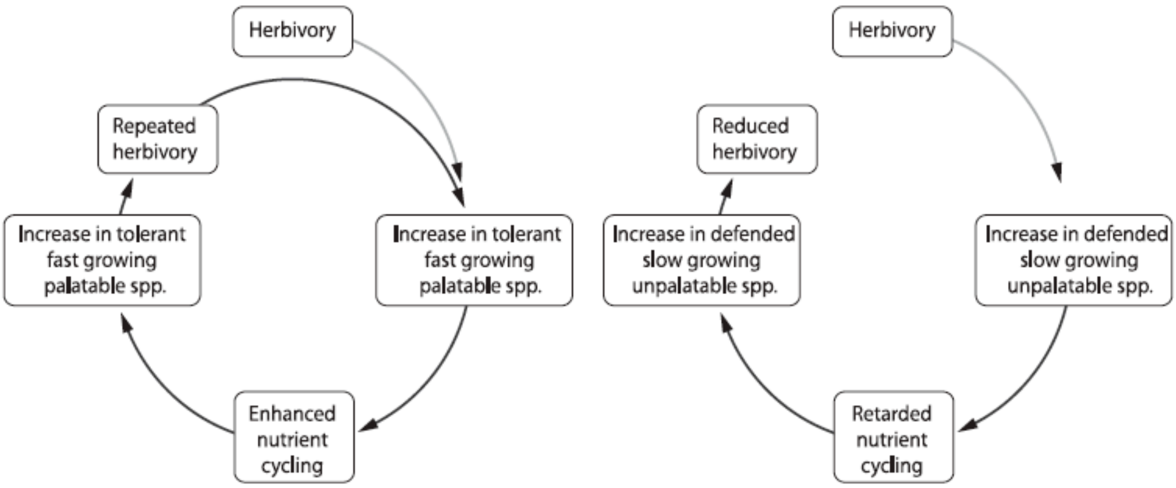


Figure 6: a) Feedback loop enhancing repeated herbivory in resource-rich environment. b) Herbivory leading to reduced forage quality and a decrease in herbivory in resource-poor environment, (from Skarpe et al. 2008).

In a long-term perspective the abundance of large herbivores in the SNP could perform positive effects on both, plant and animal diversity. Considering biodiversity as a management focus, it is suggested that there is no need for human interference to regulate density of large herbivores. However, short-term observations make it difficult to predict future states and may lead to misinterpretation. To better understand the complexity of the grassland system and thus to be able to predict impacts of herbivores on its functions, there is a need to focus on the whole ecosystem and on a longer time-scale. In particular, belowground processes and animal-animal interactions require further investigation. Since after one season results do not lead to profound understanding, the WSL and the SNP will continue to assess and combine results of different biotic and abiotic factors on ecosystem functions in further studies, as parts of the ongoing project, for another 3-4 years.

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APPENDIX A

Above ground biomass: Regression parameters for bio-mass calculation

The relationship between leaf counts (litter and flower counts were excluded) and standing crop was calculated as follows; Narrow-leafed graminoids *Elyna myosuroides* Vill., *Festuca ovina* L., *F. rubra* L. and *Nardus stricta* L. were modified by dividing the pin counts sampled in the field by two to acknowledge the relatively small biomass of these species. To exclude variations due to different people who did the recordings, records were adjusted. Correlation between modified leaf counts of Werhahn (GW) and Mächler (MJM) to those of Schütz (MS) with equation 1.

$$y = 0.724x - 7.187 \quad (1)$$

y: adjusted pin counts of GW and MJM

The relationship between adjusted leaf counts and standing crop was calculated and applied to the dataset equation 2.

$$SC = 2.5166y - 37.712 \quad (2)$$

SC: Estimated Standing Crop

y: adjusted pin counts (MS)

APPENDIX B1: DETAILED RESULTS OF STATISTICAL ANALYSIS

Results of ANOVA

Table S1: Results of the ANOVA of the factors affecting target variables. * p<0.05, ** p<0.01, *** p<0.001, outliers: total above:1, total below: 17,27,37,42

		aboveground biomass		*belowground biomass*	
	df	*F*	*p-value*	*F*	*p value*
grass type	1	0.703	0.420	1.672	0.223
exclusion	4	9.613	<0.001***	1.973	0.110
exclusion x grass type	4	4.286	0.004**	2.985	0.026*

Results of Tukey HSD post hoc tests

Table S2: Results of Tukey HSD on aboveground biomass

	control	*deer*	*marmot*	*mouse*
total above				
deer	<0.001***			
marmot	<0.001***	0.838		
mouse	<0.001***	0.997	0.642	
insect	<0.001***	0.028*	0.320	0.009**
above short	effect of exclosure F= 11.424, p>0.001			
deer	<0.001***			
marmot	<0.001***	0.902		
mouse	0.002**	0.998	0.764	
insect	<0.001***	0.089	0.485	0.041*
above tall	effects of exclosure F=2.008, p = 0.117			
deer	0.140			
marmot	0.107	1.000		
mouse	0.194	1.000	0.999	
insect	0.451	0.968	0.942	0.988

Table s3: Results of Tukey HSD on belowground biomass

	control	*deer*	*marmot*	*mouse*
total below				
deer	0.738			
marmot	1.000	0.706		
mouse	0.541	0.054	0.578	
insect	0.882	0.998	0.858	0.097
below short	***F=2.169, p=0.095***			
deer	0.595			
marmot	1.000	0.563		
mouse	0.680	0.045*	0.710	
insect	0.929	0.968	0.913	0.209
below tall	***F=5.746 0.001***			
deer	0.172			
marmot	0.999	0.100		
mouse	0.446	<0.001***	0.600	
insect	0.230	<0.001***	0.350	0.995

APPENDIX B2: SCATTERPLOTS OF GRAZING TREATMENTS

Scatterplots of above biomass

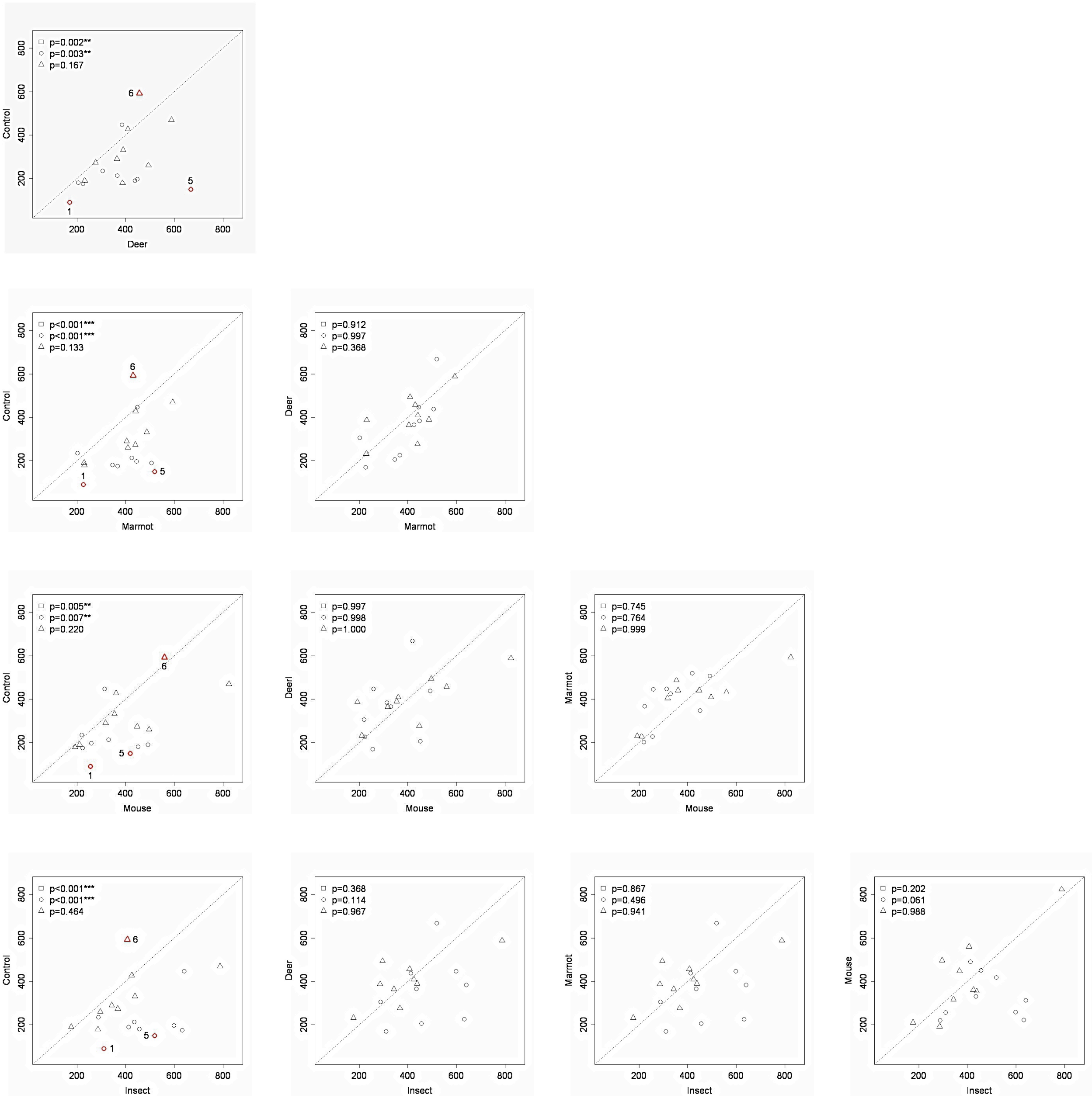

Figure S1: Overview on significant effects on aboveground biomass [gm^{-2}]. Circles symbolize short-grass and triangles represent tall-grass. P values are from total(rectangle), short-grass (circle) and tall-grass belowground biomass (triangle). * p<0.05, ** p<0.01, *** p<0.001.

scatterplots of belowground biomass

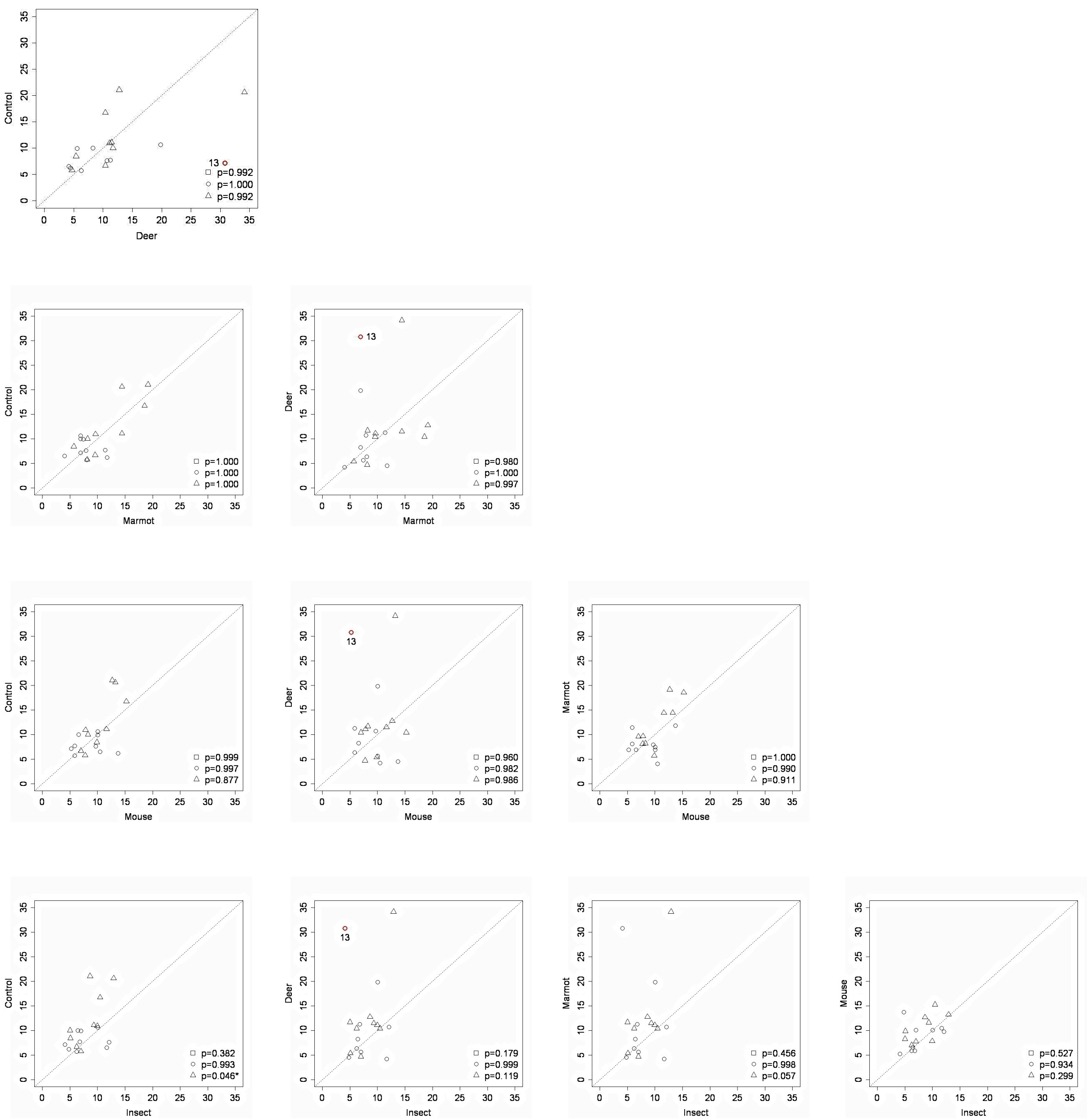

Figure: S2 Overview on significant effects on belowground biomass [g/core]. Circles symbolize short-grass and triangles represent tall-grass. P values are from total(rectangle), short-grass (circle) and tall-grass belowground biomass (triangle). * p<0.05, ** p<0.01, *** p<0.001.

APPENDIX B3: EFFECTS OF ABIOTIC FACTORS

Abiotic factors which do significantly contribute to the patterns of biomass

Table S4: Results of abiotic variables on biomass

	aboveground biomass		*belowground biomass*	
	short-grass	*tall-grass*	*short-grass*	*tall-grass*
factor	*p-value*			
north	-	0.023	-	-
east	-	-	0.006	-
soil temperature	0.183	-	0.009	-
PAR at 30cm aboveground	0.089	-	-	-
C contents	0.065	-	0.079	-
N contents	0.095	-	<0.001	-
UV at 0cm aboveground	-	<0.001	-	0.077
UV at 30cm aboveground	-	0.067	-	0.055
diversity (no. of species)	0.004	0.034	-	-

APPENDIX B4: COMPARISON OF DIFFERENT GRASSLANDS

Above and belowground biomass in different grasslands

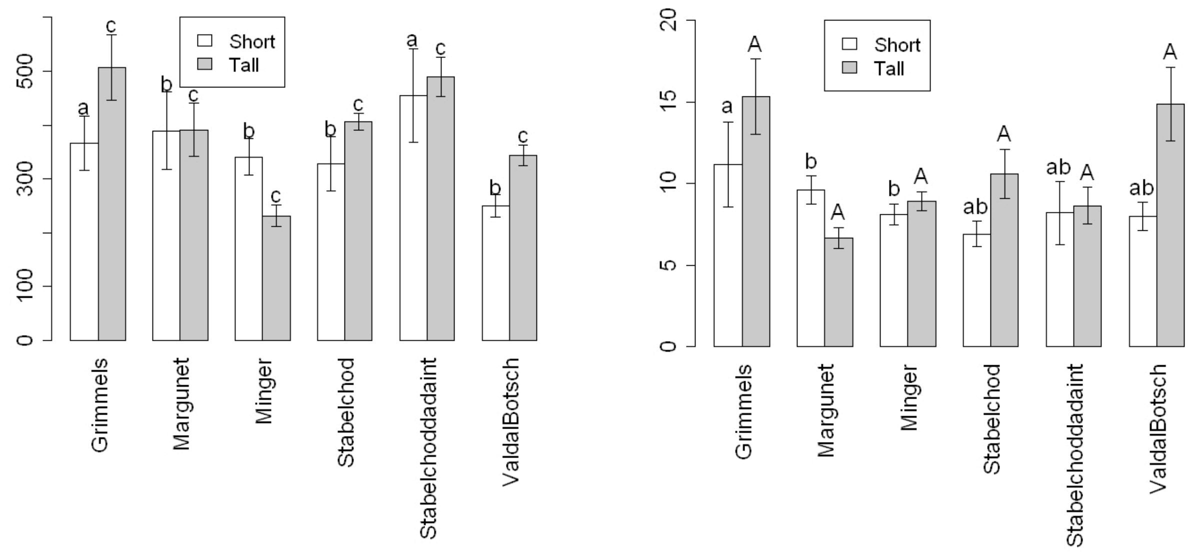

Figure S3: Overview on the distribution of biomass in different grasslands.

APPENDIX C: RAW DATA