Eidgenössische Technische Hochschule Zürich
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"Who likes flowers most?" - Influence of different herbivore groups on flower number.

Semester project

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Abstract

Vertebrate and invertebrate herbivores feed on reproductive organs of plants. The absence of herbivores can induce a higher number of inflorescence due to a reduced loss of floral tissue. Contradictionary they also might cause a reduction of floral stems due to the lack of stimulation for compensating investment of plants in reproductive parts. To investigate the impact of different herbivore groups on inflorescence number an exclosure experiment was conducted in which different groups of herbivores were selectively excluded on respect of their size. The plant individuals with inflorescences were counted on 8 dm^2 of every second subplot. On nutrient poor tall-grass vegetation, there was no significant impact of herbivores. This might be explained due to the fact that tall-grass communities consist mainly of tall growing graminoids which produce unpalatable and inconspicuous flowers. On short-grass vegetation on which large herbivores feed preferentially and which have a higher dynamic in vegetation changes, large animals like red deer and chamois reduced significantly the number of floral stems. Plots where all herbivores are excluded did not differ from plots with a high grazing pressure. This indicates that an intermediate herbivore pressure on short-grass vegetation might favour inflorescence production. Due to a lack of data of factors which also might influence the number of flowers the outcome of this study needs to be confirmed by further studies.

1. Introduction

1.1 Herbivory

On earth's surface, one third is covered by grassland (Lieth, 1978) on which a great range of vertebrate and invertebrate herbivores can feed. The global distribution of mammalian herbivores is under the control of the gradient of plant available water and the soil fertility. Herbivores can alter plant abundance, plant composition (Augustine and McNaughton, 2006), nitrogen availability (Cech *et al.*, 2008), N cycle rates, N fluxes (Singer and Schoenecker, 2003), leave litter availability, decomposition rates (Fornara and Du Toit, 2008), plant productivity, nutrient limitation and they can inhibit succession (Ritchie *et al.*, 1998). The effects of herbivory on vegetation may vary along ecosystems, between different seasons and may also depend on soil fertility, soil acidity, feeding behaviour (browsers vs. Grazers), on annual or daily migratory behaviour, moisture or disturbances, productivity, food chain complexity and abiotic constrains like fire or drought. (Oksanen *et al.*, 1981; Ritchie *et al.*, 1998; Singer and Schoenecker, 2003; Augustine and McNaughton, 2006; Cech *et al.*, 2008)

1.2 Herbivory on inflorescence

Herbivores also have might have an impact on plant propagation. It has been shown that ungulates feed selectively on the flowers and fruits. Therefore reproductive organs of plants are preferred to leaves (Hulber *et al.*, 2005). It is proposed that in alpine zones flowering inflorescence, fruits and seed of some plants have an especially high nutrient content (Jefferies *et al.*, 1994). Compared to graminoids, herbs are richer in nutrients (Blumer and Diemer, 1996) and provide in alpine environment big and colorful flowers. The inflorescences of grasses are rather inconspicuous (Körner, 1999). Not only pollinators are attracted but also predatory mammals (Hulber *et al.*, 2005). Latters foraging behaviour might be stimulated by the sensory traits like colour or odour (Black *et al.*, 1987) or just due to "rarity and novelty" of the food (NEWMAN *et al.*, 1992). A correlation between inflorescence size or number and the risk of browsing damage was shown (Ehrlen, 1997).
Grazing pressure and the resulting reduction of biomass is compensated by some plants by directing energy into compensatory growth of leaves. This might reduce the investments into the reproductive parts and therefore result in a lower number of inflorescence (Mulder and Harmsen, 1995). In experiments where inflorescence-feeding insects were excluded, retarded flowering, more seedlings and a higher number of flowering adults were observed (Louda

and Potvin, 1995). Simulated grazing by clipping parts of the plant also led to a lower production of flowering stems of a tall-grass (Bridle and Kirkpatrick, 2001).
The reaction of the plants can also be the opposite: in another experiment under cutting pressure some plant species produced a higher number of inflorescence compared to uncut plants (Leigh *et al.*, 1991). Deer browsed shrubs in a sand dune system in California showed significantly more inflorescence as when browsed, although there a significantly reduction of seed mass was found (Warner and Cushman, 2002).

The effect of herbivory on inflorescence of plants may depend on different factors, such as the plant composition and herbivore species. Large herbivores are pretended to have a higher grazing intensity than smaller vertebrate and invertebrate herbivores (Bakker *et al.*, 2004) and favour nutrient rich short-grass vegetation (Schutz *et al.*, 2003). But in alpine grasslands the effect of invertebrate herbivores like grasshoppers is thought to be higher as in lowland, they might remove 19 % to 30 % of the biomass (Blumer and Diemer, 1996) and therefore should not be neglected.
We conducted an exclosure experiment to evaluate the impact of different herbivores on inflorescence. In this study we wanted to test following hypotheses: (1) Big vertebrate herbivores such as red deer (*Cervus Elaphus L.*) or chamois (*Rupicapra rupicapra L.)* have the greatest negative effect on plant flowering: the larger the herbivores the larger its negative effect on inflorescence; (2) flowering stem number correlates negatively with grazing pressure.

2. Methods

2.1 Study site

The Swiss National Park was founded in 1914. The area of the Park formerly was used for agriculture and forestry. It ranges from 1700 to 3164 m a.s.l. It area of the park is 172 km^2. 86 km^2 of the area are covered by vegetation, thereof 50 are occupied by pine forests, 33 km^2 by alpine grassland and 3 km^2 by subalpine grasslands.
Due to formerly agriculture the subalpine grasslands consist of different mosaic patterns of soil nutrient content (Schutz *et al.*, 2003). Therefore two vegetation types are distinguished: nutrient rich short-grass communities and nutrient poor tall-grass communities (Risch *et al.*, 2008).

6 subalpine grassland were chosen as study sites. They range from 1960 to 2348 m a.s.l. Half of the fences are located on short-grass vegetation and tall-grass vegetation respectively.

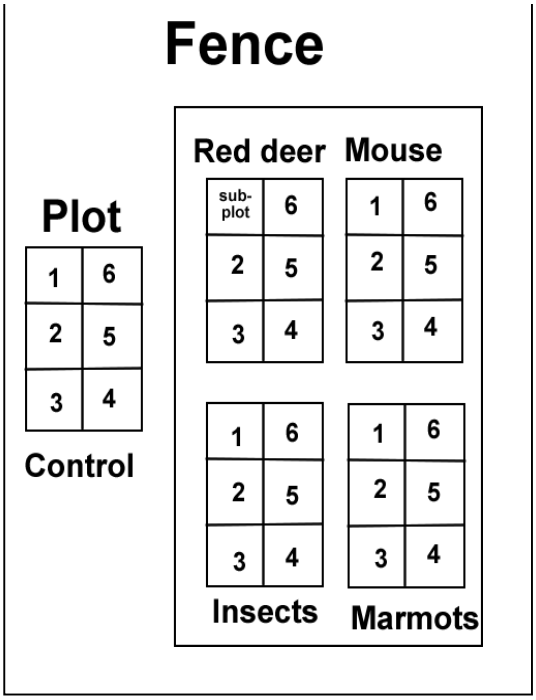
Table 1: The study sites are located in the subalpine level on dolomite bedrock. 9 fences are located on tall-grass, 9 on short-grass.

	Number of fences	Altitude	Latitude	Longitude
Val dal botsch	2	2065 - 2075	46°40'25.92"N	10°13'55.40"E
Grimmels	4	2015 - 2065	46°39'55.91"N	10°11'18.72"E
Minger	4	2090-2100	46°42'27.49"N	10°15'42.76"E
Margunet	2	2328-2348	46°40'29.30"N	10°14'39.55"E
Alp Stabelchod	4	1960 - 1975	46°39'49.64"N	10°14'30.07"E
Alp Stabelchod d.d	2	2125 - 2135	46°40'19.58"N	10°14'45.39"E

2.2 Fences

To investigate the effects of different herbivore groups, exclosure experiments were conducted. The herbivore groups were divided in respect of size and weight: Large vertebrates herbivores (< 10 kg; red deer and chamois), medium vertebrates (0.5 to 10 kg; marmots and hare), small rodents (10 to 500 g) and invertebrates (<10 g; e.g. Grasshoppers).

Figure 1: Schematic. One fence contains 5 plots. Every plot contains 6 subplots. “Mouse” plot means, that mice are the smallest excluded herbivore group.



The study sites were manipulated with different fences. The size of the meshes determined which groups of herbivores can enter the plot for foraging. One study site is called “fence” and contains 5 plots. Every plot contains 6 subplots. The “Control” plot is reachable for all herbivores. A large electrical fence surrounds the other 4 plots. The “Deer” Plot lies within this large fence. Therefore reed deer cannot enter this plot meanwhile all other herbivore groups can. The fence of the “Marmot” plot has even broader meshes and is also under voltage. In this way all marmots and hares are excluded but the rodents and insect still have access. The “Mouse” plot only provides food for insects. The “Insect” plot is totally surrounded of a very fine-

meshed net to exclude all kind of herbivores. To grant this effect the “Insect” plots frequently treated with insecticides.

Please note: “Mouse” plot means that mice are the smallest excluded herbivore group.

2.3Inflorescence count

To count the number of inflorescence eight rings with an area of 1 dm^2 (diameter = 11.2 cm; circumference = 35.45 cm) per ring where lain on the subplot. The constant order of the rings was foregoing randomly determined.

The plant individuals with inflorescence or a floral stems were counted. Just developing or already senescent reproductive parts where also included into the count. In fact we did not count the number of inflorescences but the number of individuals with inflorescences. Further, only the plant individuals which rooted in the ring area were counted. This procedure was conducted on the subplots 1, 3 and 5 on every plot. These counts were conducted between July and August.

Figure 2: The rings were put down in a random order.

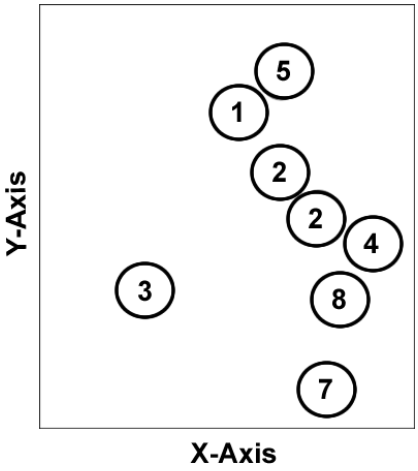


Table 3: coordinates of the rings.

Ring #	X-Axis (cm)	Y-Axis (cm)
1	54	76
2	75	49
3	27	32
4	88	45
5	64	84
6	66	61
7	76	8
8	80	31

2.4 Light

On every plot photosynthetically active radiation (PAR) and ultraviolet light were measured on the ground (0 cm) and 30 cm above the ground. These measurements were conducted five, respectively tree times with a time interval of at least two weeks.

3. Results

3.1 General (tall-grass and short-grass)

3.1.1 Light

All four light categories (PAR0, PAR30, UV0 and UV30) showed a significant difference between the “Insect plot” and the other plots (ANOVA). The statistical analysis was conducted for all fences without dividing short-grass fences from tall-grass fences.

Table 4: Measurment of photosynthetically active radiation [nm] and ultraviolet radiation [nm] measured direct on and 30 cm above the ground

	PAR0	PAR30	UV0	UV30
N of cases	90	90	90	90
Minimum	232.360	290.400	18.787	23.100
Maximum	1869.200	2019.520	150.970	148.740
Mean	1084.392	1186.807	79.963	90.323
Standard Dev	311.827	309.673	27.040	27.591
Variance	97236.153	95897.203	731.171	761.280

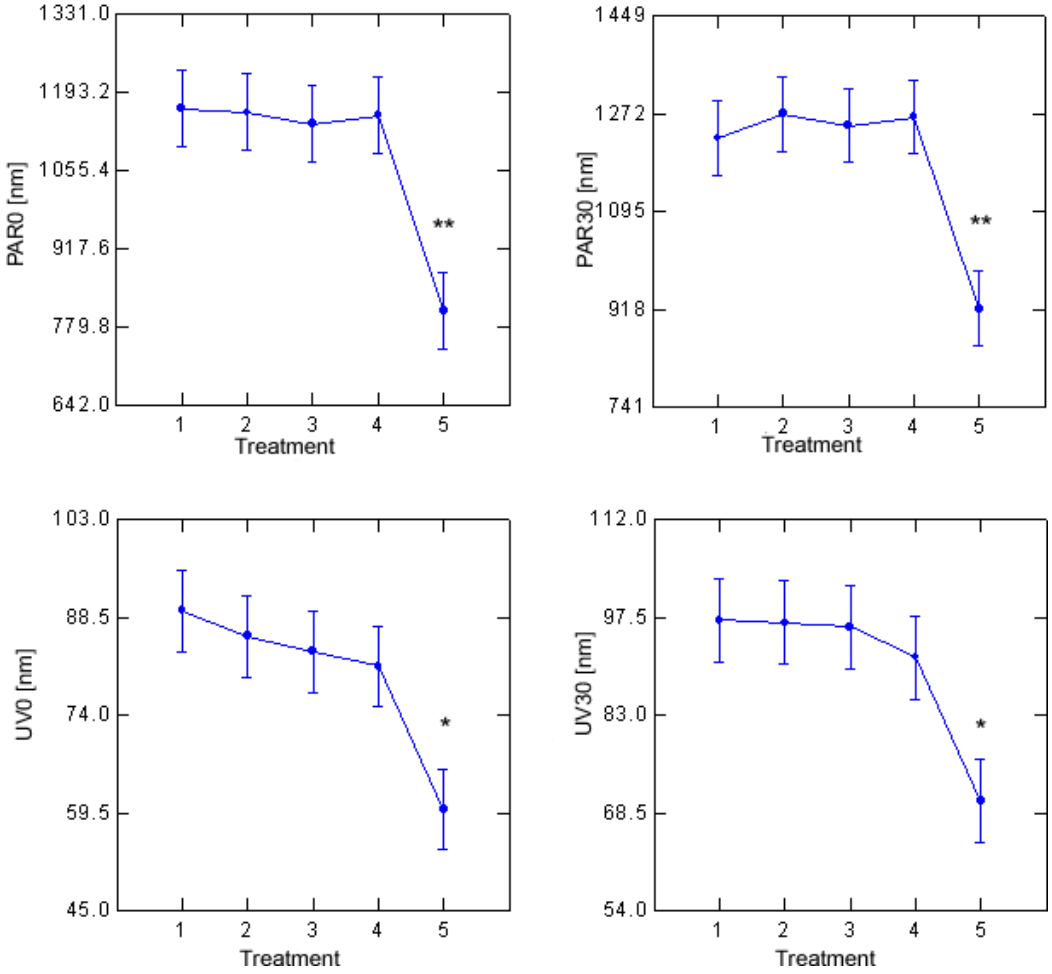
Table 5: Analysis of light values in the different plots (ANOVA)

	df	F-ratio	P
PAR0	4	5.221	0.001
PAR30	4	5.036	0.001
UV0	4	3.683	0.008
UV30	4	3.430	0.012

Table 6: Fisher's Least-Significant-Difference Test. Matrix of pairwise comparison probabilities, significance between “Insect” plot and other plots.

	Control	Deer / Chamois	Marmot / Hare	Mouse
PAR0	0.000	0.000	0.001	0.001
PAR30	0.002	0.000	0.001	0.000
UV0	0.001	0.003	0.007	0.015
UV30	0.003	0.003	0.004	0.017

Figure 2: Radiation in the "insect" plot differs significantly compared to the other plots.



Treatment: (1) Control; (2) Deer / Chamois; (3) Marmot / Hare; (4) Mouse; (5) Insect

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3.1.2 Inflorescence

For the inflorescence, the values (x) were transformed into value x' = LN(x+1).

Table 7: Overview of the inflorescence count.

	Control	Deer	Marmot	Mouse	Insect
N of cases	18	18	18	18	18
Minimum	0.900	1.100	1.040	0.930	1.100
Maximum	2.070	2.220	2.170	1.980	1.770
Mean	1.328	1.583	1.501	1.542	1.417
Standard Dev	0.331	0.297	0.316	0.313	0.224
Variance	0.110	0.088	0.100	0.098	0.050

There was no significant difference of inflorescence between the fences on tall-grass vegetation compared with fences on short-grass (p-value 0.145, ANOVA)

The number of inflorescent of every plot was compared with ANOVA. Due to the significant differences in aspect of ultraviolet and photosynthetically active radiation between the "insect" plot and the other plots the light values were included as covariates. For all four light

values a statistical significance was found, indicating that the effect of the difference in UV and PAR might outweigh the effect of the treatments, here the exclusion of herbivores.

Table 8: ANOVA with light as covariate without dividing short-grass and tall-grass vegetation. Significant influence of all four radiation values.

	df	F-ratio	P
Treatment	4	2.152	0.081
PAR0	1	7.830	0.006
Treatment	4	1.887	0.120
PAR30	1	7.552	0.007
Treatment	4	2.302	0.065
UV0	1	5.952	0.017
Treatment	4	2.112	0.086
UV30	1	5.286	0.024

3.2 Tall-Grass

In this section only fences put on tall-grass vegetation is analysed.

3.2.1 Light

Comparing PAR between the different plots showed no significant difference, neither for the UV radiation.

3.2.2 Inflorescence

Analyzing the data from the tall-grass plots, there was no significant difference between the different treatments (p-value 0.509, ANOVA). Adding light as covariates shows significant differences and therefore might explain the variations between the plots.

Table 9: ANOVA for tall-grass vegetation reveals radiation as a covariate with significant influence.

Source	df	F-ratio	P
Treatment	4	0.580	0.679
PAR0	1	4.051	0.051
Treatment	4	0.428	0.787
PAR30	1	6.840	0.013
Treatment	4	0.585	0.675
UV0	1	3.957	0.054
Treatment	4	0.568	0.687
UV30	1	4.303	0.045

Figure 3: Inflorescence numbers of the different tall-grass plots. There was no significant difference.

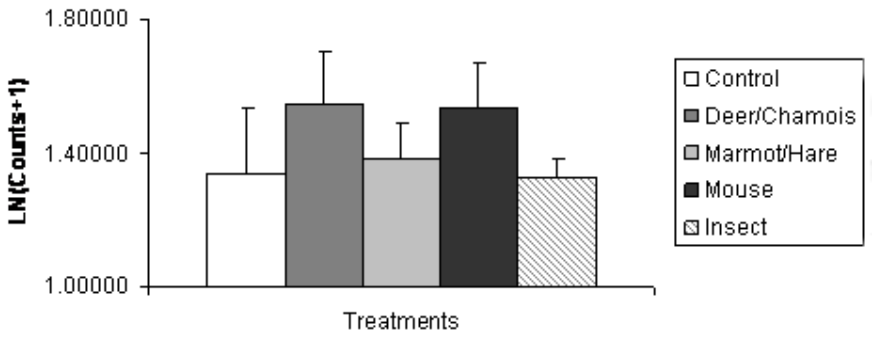

Table 10: Overview of inflorescence counts on tall-grass vegetation. Values were transformed into x' = LN(x+1)

	Control	Deer	Marmot	Mouse	Insect
N of cases	9	9	9	9	9
Minimum	0.900	1.100	1.040	0.930	1.100
Maximum	2.070	2.220	2.120	1.980	1.760
Mean	1.339	1.552	1.379	1.537	1.328
Standard Dev	0.437	0.386	0.328	0.369	0.234
Variance	0.191	0.149	0.107	0.137	0.055

3.3 Short-Grass

3.3.1.Light

Only considering short-grass fences, there were no significant differences of measured PAR and UV between the different plots.

3.3.2 Inflorescence

The inflorescences of the different plots were compared. There were significant differences between the control-plot and all the other plots, except the "insect"-plot (p-value 0.045, ANOVA). Adding light as covariates did not show any significance.

Figure 4: Inflorescence numbers of the short-grass plots. There was a significant difference between the control plot and the "Deer", "Marmot" and "Mouse" plot. There was no difference between the plot where all herbivores have access and where all herbivores were excluded.

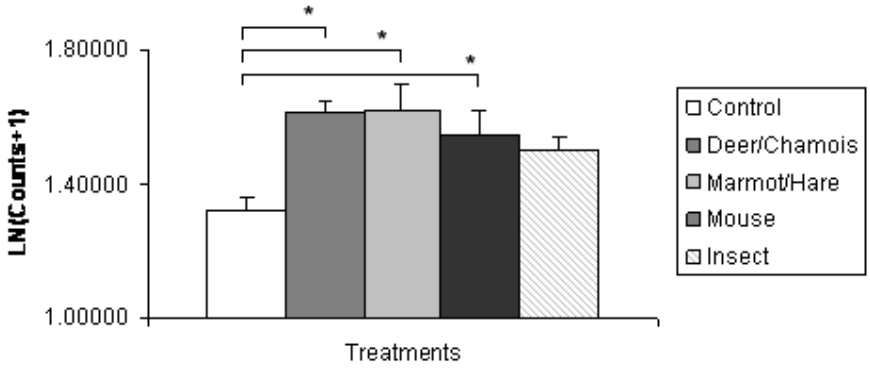

Table 11: Overview of inflorescence counts on short-grass vegetation. Values were transformed into x' = LN(x+1).

	Control	Deer	Marmot	Mouse	Insect
N of cases	9	9	9	9	9
Minimum	0.950	1.390	1.250	1.100	1.250
Maximum	1.570	1.980	2.170	1.850	1.770
Mean	1.318	1.613	1.622	1.547	1.506
Standard Dev	0.204	0.191	0.268	0.268	0.184
Variance	0.042	0.036	0.072	0.072	0.034

Table 12: ANOVA of inflorescence numbers of the plots with different herbivore pressures.

	df	F-ratio	P
Short-Grass	4	2.685	0.045

Table 13: Fisher's Least-Significant-Difference Test. Matrix of pairwise comparison probabilities.

	Control	Deer / Chamois	Marmot / Hare	Mouse
Deer / Chamois	0.008 *	1.000		
Marmot / Hare	0.007 *	0.934	1.000	
Mouse	0.038 *	0.535	0.482	1.000
Insect	0.086	0.318	0.280	0.702

4. Discussion

The outcome of the results partly contradicts our assumption. Surprisingly there was no significant difference in inflorescence number between the "control" plots were all herbivore group forage and the "insect" plots where all insects are excluded. This might partly been explained by the fact, that due do the fin red clamped around the plot there was significant

less ultraviolet and photosynthetically active radiation entering the plots. But this outcome has to be regarded differentiated.

Analysing the inflorescence number on tall-grass vegetation there was no difference between the different plots at all. This may indicate that on tall-grass vegetation herbivores do not have a significant impact on inflorescence number. Variation of floral numbers might be explained on tall-grass vegetation due to the experimental set up reducing radiation in the "insect" plots. Tall-grass vegetation is assumed to be nutrient poor with a high content of fibre and therefore less palatable (Bakker *et al.*, 1984) and is not favoured by large herbivores. Florisitc releves on tall-grass vegetation showed a high abundance of grasses like *Carex sempervirens* (own observation; data not yet available). Reproductive parts of grasses are assumed to be nutrient poor and inconspicuous therefore not attracting the attention of herbivores (Blumer and Diemer, 1996; Körner, 1999).

The results of the inflorescence count on short-grass communities provide another insight. This type of vegetation is assumed to be nutrient rich (Risch *et al.*, 2008) and having a higher dynamic in vegetation changes (Schutz *et al.*, 2003). There was a significant difference between the "Control" plot and the "deer", "marmot" and "mouse" plot. This indicates that the largest herbivore might have the largest impact on floral stem numbers.

Surprisingly there was no difference between the plot which all herbivores can enter and the plot where all herbivores are excluded. This is contradictory to the assumption that the less herbivore feeding on a plot the more inflorescence can be counted. This outcome also contradicts own observations made during fieldwork. Altough light showed no significant influence on inflorescence number on short-grass vegetation, the reduced radiation in the "insect" plot might explain partly this outcome.

Another possibility is to put this outcome under the light of floral compensation. In a study was shown that the absence from herbivores led to less inflorescence in some species (Leigh *et al.*, 1991; Warner and Cushman, 2002). One can hypothesize that the total absence of grazing pressure can lead to less flowering due to a lack of stimulation for floral stem production. The absence of herbivore disturbances might induce plants to invest more in their generative biomass. Subjectively a higher biomass was observed during fieldwork. The data about biomass still lack therefore a further analysis would be needed to confirm this prediction.

The intermediate disturbance theory predicts that a medium level of disturbance induces a higher floristic diversity (Grime, 1973a, b). The combination of grazing herbivores and high nutrient soil content might be such an intermediate disturbance leading to high dynamic in

vegetation change (Schutz *et al.*, 2003). One could argue that this dynamic not only is observed concerning changes in vegetation composition. There also in might be dynamic changes from reproductive to generative biomass production of plants therefore leading to a reduced flowering number due to absence of herbivory. Further one could argue that in the augmented inflorescence number are just found in the plots with intermediate grazing pressure.

There is still a lack of information about herbivore abundance around and within the plot. The conspicuous fences of the experimental set up could prevent medium and/or small vertebrates like marmots, hare or mice entering the plots. Therefore it is up to date not possible to distinguish the effects on short-grass vegetation of medium and small herbivores from the influence of insects which might rather not be influenced on their foraging behaviour due to the presence of the fenced plots.

Another critic is concerning the data collection. There was no differentiation between inflorescence of herbs and grasses. Variation of plant composition within the plots might also have an influence on the number of floral stems which might outweigh the effect of herbivores. For example: the presence of *Narduus stricta* which is a small grass with a high number of assumed unpalatable inflorescences might compensate the loss of flowers of herbs due to herbivory. Therefore for future analysis this differentiation should be included.

5. Conclusion

Herbivores seem not to have a significant impact on the number of inflorescence on nutrient poor tall-grass vegetation. This might be explained by the high abundance of grasses providing unpalatable flowering stems.

On nutrient rich short-grass vegetation only large herbivores seem to reduce significantly the number of inflorescence. But total absence of herbivores does not lead to a difference of floral stems as if large herbivores are present. This can be interpreted as a lack of disturbance. The highest number of floral stems are found where grazing pressure is not too strong and neither too weak.

Other factors as radiation, herbivore abundance around and within the fences and the plant composition are assumed also to have an influence on inflorescence production. Latter two factors were not included in this study and therefore their effects should be issue in future studies.

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