

# **The influence of ungulates on above- and belowground biomass, seasonal production and decomposition in an exclosure experiment in the Swiss National Park**

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Anita Langenegger



Conducted at the Swiss Federal Research Institute WSL, Birmensdorf

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Referent: Dr. M. Schütz, WSL  
Koreferent: Dr. F. Filli, SNP

## Abstract

The influence of grazers on grassland ecosystems has been examined in various studies. However, the effect that grazing native ungulates can have seem to diverge between different ecosystems and different grazers. An overall experiment which investigates the influence of native grazers on grasslands in the Swiss National Park (SNP) is missing so far. Therefore, we conducted an exclosure experiment which analysed the influence of red deer (*Cervus elaphus* L.) on the parameters aboveground seasonal biomass production, standing crop, belowground biomass, soil moisture, soil temperature and soil activity in subalpine and alpine grasslands in the SNP. At eight sites, we compared data from inside the fence (grazing non-tolerant) and outside the fence (grazing tolerant) areas. Aboveground seasonal biomass production was investigated by comparing biomass production in grazing tolerant to biomass production in grazing non-tolerant areas under two different clipping treatments (early spring grazing treatment and repeated grazing treatment). The comparison of aboveground seasonal biomass production in grazing tolerant and grazing non-tolerant areas showed no difference, except at high consumption sites, where early spring grazing treatment caused vegetation to overcompensate. Repeated grazing treatment showed no effect in the grazing tolerant areas, but increased production significantly in the grazing non-tolerant areas. Standing crop, soil activity and soil moisture were significantly lower in grazing tolerant areas while soil temperature was higher. Belowground biomass production did not differ between grazing tolerant and grazing non-tolerant areas, but showed a significant relation to soil moisture.

## Introduction

Since traditional land use is no longer profitable in high elevation areas of the European Alps, more and more of the former agriculturally used land is being abandoned. Along with this process, native grazers are reintroduced to the ecosystems. As they have no natural enemies, their populations develop very well to an extent where it becomes questionable if the ecosystems can support the high numbers of grazers. It is therefore of great interest to know how land use abandonment and grazing ungulates affect vegetation cover and soil parameters. In this study, we examined the influence of red deer, *Cervus elaphus* L., on different parameters in an exclosure experiment in the Swiss National Park (SNP). The experiment included the following parameters: aboveground seasonal biomass production, standing crop, belowground biomass, soil moisture, soil temperature and soil activity.

Aboveground biomass production seems to be influenced positively by native herbivores (Frank and McNaughton 1993; Moss et al. 1991; Shariff et al. 1994; Singer and Schoenecker 2003). This might be the result of a positive feedback loop (Pandey and Singh 1992) which comes from an indirect herbivore effect on other trophic levels (McNaughton et al. 1988; Holland et al. 1992). According to Holland and Detling (1990) and Seagle and McNaughton (1992), the increased aboveground production in grazed ecosystems may result from nitrogen in ungulates excretions which is more readily available for plants than nitrogen in dead plant material. Oesterland and McNaughton (1988, 1991) and Polley and Detling (1990) found that a higher photosynthetic rate of grazed plants can lead to higher relative growth rates of grazed plants versus ungrazed plants. Shariff et al. (1994) indicate that an increase in soil mineralization rate could cause a higher aboveground net primary production in moderately grazed ecosystems. However, Coughener (1991) found no increase in productivity with elk grazing and Singer and Schoenecker (2003) and Moss et al. (1981) found a grazing caused reduction in aboveground production. In the SNP, a study on productivity in two different pastures (short-grass grazing tolerant, and tall-grass grazing non-tolerant) showed no difference in aboveground primary production, however under a long

term grazing influence, it showed a negative effect of herbivore impact on aboveground productivity (Egenter et al. (subm.)).

Different results were found on the influence of grazers on root development or belowground biomass. Coughener (1991) detected no effect of grazing on belowground biomass, whereas Jamison (1963), Johnson and Matchett (2001), Holland and Detling (1990), Holland et al. (1992), Davidson and Milthorpe (1966), Evans (1973a, b) and Hodgkinson and Baas Becking (1977) found that root growth was negatively affected by grazers. This might be the result of reduced C-allocation to belowground structures due to repeated grazing (Holland and Detling 1990). Some authors (Jaramillo and Detling 1988, Singer and Schoenecker 2003) found increased root growth in grazed ecosystems. Increased root growth in grazed ecosystems might be beneficial for grazed plants because it enhances the plants resistance to grazing and other disturbances (Jaramillo and Detling 1988, Stark and Grellman 2002). Risch et al. (2004) found that biomass in pastures with grazing animals was nearly all belowground, but that it did not change during succession from short grass pasture to stone pine forest in the SNP.

Water availability can limit growth and production in alpine plants and therefore probably influence spatial patterns of productivity (Billings and Bliss 1959, Peterson and Billings 1982, Isard 1986, Enquist and Ebersole 1994). Soil moisture was examined in former enclosure experiments by Stark and Grellman (2002) and by Frank and Mc Naughton (1993), who found higher soil moisture in grazed versus ungrazed areas. Higher soil moisture in grazed areas can be explained with lower transpiration rates because of less aboveground biomass (Mc Naughton 1985, Wraith et al. 1987). Coughener (1991) found no difference in soil moisture between enclosure and surroundings.

Standing crop has been found to be better developed in the absence of grazers (Coughener 1991, Detling 1988, Frank and McNaughton 1993, Singer 1995, Singer and Harter 1996, Singer and Schoenecker 2003). In the SNP, Holzgang (1997) found a higher phytomass dry weight in ungrazed versus grazed parts of the examined grasslands. The study of Egenter et al. (subm.) states that there was more aboveground biomass production in the tall-grass pasture where grazing was not too intensive and that standing crop was higher in ungrazed areas. Less developed standing crop in grazed ecosystems results in higher soil temperatures and irrigation rates (Knapp and Seastedt 1986, Ruess 1987, McNaughton et al. 1988) and therefore higher decomposition rates or soil activity in grazed versus ungrazed locations (Knapp and Seastedt 1986, Ruess 1987, McNaughton et al. 1988, Coughener 1991). The high soil activity in grazed ecosystems can also be explained with the higher C:N ratio which results from the grazers' excretions. The higher C:N ratios lead to higher decomposition rates (Seagle et al. 1992, Pastor et al. 1993).

The parameters investigated in our study seem to have shown controversial grazing effects in different ecosystems and under the pressure of different grazers so far (Stark and Grellman 2002, Moss et al. 1981). Apart from that, grazing habits and grazing intensity may have strong effects on the results of studies (Singer and Schoenecker 2003; Shariff et al. 1994; Bickley et al. 2002). To provide information about the development of abandoned grasslands in the SNP, it is important to investigate the influence of red deer grazing on the spot. Moreover, an investigation which compares our parameters inside and outside of permanent enclosures in an experiment in the SNP is missing completely. Therefore, we conducted a study in which data was collected from eight 15 year old enclosures and their references to approach the question of long-term red deer grazing influence on alpine and subalpine pastures in the SNP. According to former studies, we hypothesized that grazing

- increases aboveground seasonal biomass production
- reduces root development
- reduces standing crop and thus
- enhances soil moisture, soil temperature and consequently soil activity

## Methods

### Study site

The SNP is situated in the southeast of Switzerland in the canton of Grisons. The park has a size of 170 km<sup>2</sup>. Its elevation extends from 1500m.a.s.l. to 3170m.a.s.l. (Schütz et al. 2000). The vegetation cover is 50 km<sup>2</sup> woods, of which almost all is coniferous, 33 km<sup>2</sup> alpine and 3 km<sup>2</sup> subalpine grasslands (Schütz et al. 2003). Almost 50% of the park are not covered with vegetation and consist of debris, bare rock and high mountain region. The park is one of the few areas in Western Europe that have not been directly impacted by humans during most of the 20<sup>th</sup> century. It was founded in 1914, thus traditional land use already ceased 90 years ago. Before its foundation, distinct vegetation and nutrient patterns had developed as a result of the agricultural use. After the foundation of the park in the year 1914, all grazing, logging and hunting was stopped and former agriculturally managed subalpine grasslands were abandoned (Schütz et al. 2000). In addition to land use abandonment, red deer (*Cervus elaphus* L.), which was formerly extinct in Switzerland, was reintroduced to the country through migration shortly after the foundation of the National Park (Haller 2002). The distinct vegetation and nutrient patterns persisted until the numbers of red deer increased rapidly up to more than 2000 between 1940 and 1970 (Braun-Blanquet et al. 1931, Stüssi 1970, Pictet 1948, Achermann et al. 2000, Schloeth 1972).

Over the last two decades, about thirty permanently installed enclosures were built in the SNP. The initial aim was to examine the influence of ungulates on the development of forest and especially on forest rejuvenation. However, the enclosures also provide an ideal method to investigate ungulates influences on other parameters (Scheurer 1992), such as the ones examined in our study.

### Experimental design

We collected data from eight enclosure sites: Fuorn, Grimmels, La Schera, Alp Stabelchod, NP4, NP8, NP32, and Channels. They are situated in alpine or subalpine grasslands at an elevation of 1800 to 2240m.a.s.l. For detailed information, see Table.1.

Name	Characterization of location	Elevation (m.a.s.l.)	Size (mxm)
Fuorn	Subalpine pasture	1800	6 x 6
Grimmels	Forest clearing	2000	4 x 4
La Schera	Subalpine pasture	2135	4 x 4
Alp Stabelchod	Subalpine pasture	1908	4 x 4
NP4	At timberline on a meadow	2205	12 x 20
NP8	In forest	2238	12 x 20
NP32	Subalpine meadow	2130	12 x 20
Channels	Subalpine pasture	2140	12 x 25

Table.1 View of the permanent enclosures.

To find out about long term grazing influence on the parameters aboveground seasonal biomass production, standing crop, belowground biomass, soil moisture, soil temperature, and soil activity, we established plots, sensors or sample sites inside and outside the enclosures. In this way, we obtained information about the differences between grazing tolerant (samples from outside the enclosures) and grazing non-tolerant areas (samples from inside the enclosures). The sites are very different from each other, thus the collected data provided information for a large number of ecosystems. Red deer could be proved to be grazing at all sites because of evident grazing signs on plants, and deer pellets or tracks around the fences.

### Aboveground seasonal biomass production under different grazing treatments

Grazing influence on aboveground seasonal biomass production was estimated by using two different clipping treatments. On one side, we examined long term grazing influence on aboveground seasonal biomass production by comparing productivity in grazing tolerant and grazing non-tolerant areas. Aboveground seasonal biomass production was estimated on three replicates outside and inside the enclosure at all sites. All plots outside the enclosure were protected from grazing animals with the help of wire baskets. They had a size of 44 x 27 cm, which was also the size of the plots inside the fences. The vegetation of all plots was clipped down to 1.5 cm at the beginning of growing season, simulating early spring grazing by red deer (referred to as "early spring grazing treatment"). The vegetation of the plots was clipped again at the end of growing season (mid August). This would provide data to estimate aboveground seasonal biomass production in grazing tolerant (areas outside the enclosure that have been subject to grazing since red deer was reintroduced to the SNP) and grazing non-tolerant (areas inside the fences that have not been subject to grazing for the past 15 years) parts. Especially, it would provide information about the influence of early spring grazing on aboveground seasonal biomass production in grazing tolerant and grazing non-tolerant areas. On the other hand, we carried out an experiment with repeated clipping, which would provide information about perpetual grazing influence on productivity in grazing tolerant and grazing non-tolerant areas. Again, three plots were established inside, three outside each enclosure and the ones outside the enclosure were protected by the same wire baskets. The vegetation of all plots was clipped down to 1.5 cm at the beginning of growing season and again approximately every twenty days, resulting in four production intervals per site: "spring" from mid May to mid June, "early summer" from mid June to the beginning of July, "late summer" from the beginning of July to the end of July, "fall" from the end of July to mid August. The clipped material was collected and dried to constant weight at a permanent temperature of 105 °C. Adding up all four harvests and comparing it to aboveground seasonal biomass production from early spring grazing treatment (one harvest mid August), provided information about the influence of simulated red deer grazing intensity on productivity.

### Standing crop and consumption by red deer

Standing crop was estimated by establishing three replicates inside and outside the enclosure. The plots had a size of 44 x 27 cm, and outside the fence they were protected from grazing animals by wire baskets. To determine the amount of biomass consumed by red deer, we established a reference for each of the plots outside the fence. The difference between the reference and the protected plot showed how much vegetation red deer removed by grazing during the whole growing season. The vegetation of the six plots and the three references outside the fence were clipped at the end of growing season (end of August), the material was collected and dried to constant weight at 105°C.

### Soil temperature

Soil temperature was measured with loggers (Watchdog model 100) which recorded the current temperature at an interval of 60 minutes. We buried one logger outside and one inside the enclosure. The loggers were placed at a depth of 15 cm, 1 - 2 m away from the fence to prevent its influence. We were careful to completely close the holes so that no water or air could enter.

### Belowground biomass

Soil samples were taken in the beginning of July, three replicates outside and three inside the enclosure. This provided data to estimate the influence of grazers on root biomass. Soil samples were only taken to a depth of 20 cm because of the high rock content in the subsoil. Soil bulk density was estimated using the polyurethane foam technique of Page-Dumroese et al. (1999). After drying the soil for 48 hours at a temperature of 60 °C, it was crushed and stones and roots were separated from the rest by a 2 mm sieve. The roots were separated from the stones by manual work. Using a relatively big sieve prevented us from destroying

the roots while we crushed the soil samples. This method allowed us to extract belowground biomass without destroying or losing a significant part.

### Soil moisture

To approach the question of grazing red deer influence on soil moisture, we measured it with moisture sensors (Watchdog model 6450) which were hooked to a data logger (Watchdog model 425) that recorded at an interval of 60 minutes. The sensors were buried in the root penetrated soil at a depth of 10 - 20 cm. Soil moisture, again, was measured outside and inside the enclosure at a place approximately 1 m away from the fence to prevent its influence. The cables which connected the sensors to the logger were protected from rodents with plastic tubes. The measuring procedure provided a large set of data over the growing season 2004.

### Soil activity

To estimate the influence of red deer on soil activity, we used cotton strips. The strips had a size of 10 x 20 cm. Four strips were carefully buried on a line outside, four on a line inside the fence. An additional strip was buried and removed right away. It served as a reference. The strips were removed after approximately 20 days and dried in the air. Soil activity was determined by tearing apart the strips and measuring F(max) of the reference and the actual samples. The difference between the two provided data on soil activity.

### Statistical analyses

To test if a parameter was different in grazing tolerant and grazing non-tolerant areas over all sites, the test performed was an ANOVA. We also used an ANOVA to test if there was a difference between the enclosure sites. All data, except the one of soil moisture, soil temperature and soil activity, was ln-transformed for the analyses and the tests were performed using the SPSS software. The comparison of aboveground seasonal biomass production between early spring grazing treatment and repeated grazing treatment was performed with a T-Test. The comparison of the data from inside and of the data from outside each enclosure on its own was done with a Kruskal-Wallis Test (production "spring", production "early summer", production "late summer", and production "fall") or a T-Test (aboveground seasonal biomass production). Consumption by red deer and the difference between soil moisture of high and low consumption sites were also investigated with a T-Test. The relationship between belowground biomass and soil moisture was investigated with a Wilcoxon sign rank sum test.

## **Results**

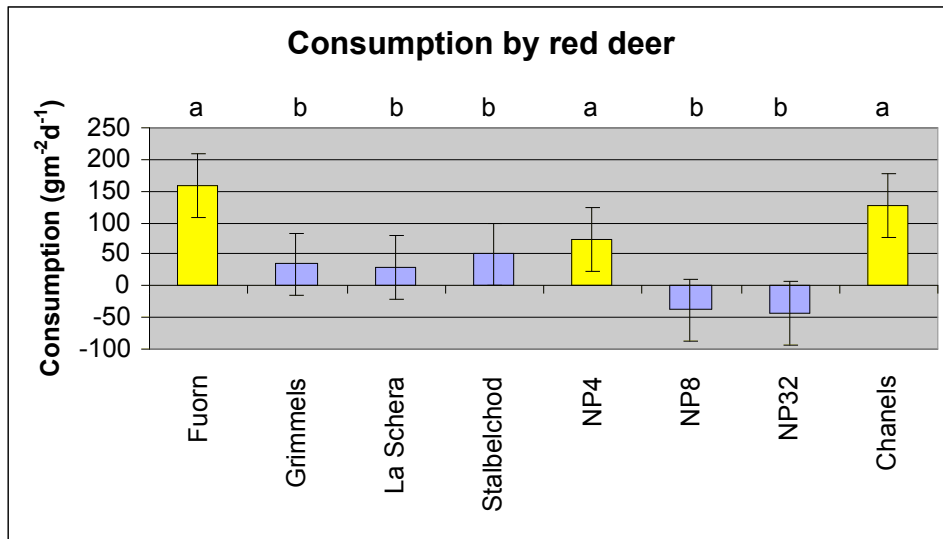
### Site effects

The eight sites we had selected were very different from each other as seen in the significant site effects in all the parameters we investigated: aboveground seasonal biomass production under early spring grazing treatment ( $P < 0.001$ ), aboveground seasonal biomass production under repeated grazing treatment (production "spring" ( $P = 0.003$ ), production "early summer" ( $P < 0.001$ ), production "late summer" ( $P = 0.012$ ), production "fall" ( $P = 0.024$ )), standing crop ( $P = 0.002$ ), belowground biomass ( $P = 0.001$ ), soil moisture ( $P < 0.001$ ), soil temperature ( $p < 0.001$ ), and soil activity ( $p < 0.001$ ).

### Standing crop and consumption

Standing crop was significantly lower in grazing tolerant versus grazing non-tolerant areas ( $P = 0.003$ ). In grazing tolerant areas, standing crop ranged from  $84 \text{ g m}^{-2}$  at Grimmels to  $232 \text{ g m}^{-2}$  at La Schera, and in grazing non-tolerant areas from  $150 \text{ g m}^{-2}$  at NP32 to  $318 \text{ g m}^{-2}$  at Chanel. Following standing crop, and, like we expected, soil temperature was significantly lower in grazing non-tolerant than in grazing tolerant areas ( $P < 0.001$ ). Biomass consumption by red deer differed very much between the sites. It was found to be much higher at Fuorn,

NP4 and Channels (Fig.1). The difference between these three and the other five sites was significant ( $P < 0.001$ ). At NP8 and NP32, we could not show any grazing impacts in the growing season of 2004, whereas at Fuorn, 158 g m<sup>-2</sup> aboveground biomass was consumed.



*Fig. 1* Biomass consumption by red deer during the growing season of 2004. a, b = pillars with the same letters are not significantly different at  $p=0.05$ .

#### Aboveground seasonal biomass production under different grazing treatments

The comparison of the aboveground seasonal biomass production under early spring grazing treatment in grazing tolerant and grazing non-tolerant areas showed no general effect over all enclosure sites. Aboveground seasonal biomass production ranged from 0.9 g m<sup>-2</sup> d<sup>-1</sup> at Grimmels to 2.5 g m<sup>-2</sup> d<sup>-1</sup> at NP4 in grazing tolerant and from 0.8 g m<sup>-2</sup> d<sup>-1</sup> at NP32 to 2.2 g m<sup>-2</sup> d<sup>-1</sup> at NP4 in grazing non-tolerant areas. Grimmels showed a higher aboveground seasonal biomass production in grazing non-tolerant areas ( $P=0.037$ ), and NP32 showed a higher aboveground seasonal biomass production in the grazing tolerant area ( $p=0.040$ ). However, early spring grazing treatment showed an effect at the high consumption sites, where aboveground seasonal biomass production was significantly higher in the grazing tolerant than in the grazing non-tolerant areas ( $P=0.011$ ). Otherwise, aboveground seasonal biomass production did not correlate with biomass consumption by ungulates.

Repeated grazing treatment compared to early spring grazing treatment showed no overall effect in the grazing tolerant areas outside the permanent enclosures, where aboveground seasonal biomass production under early spring grazing was equal to aboveground seasonal biomass production under repeated grazing treatment. However, the effect of repeated grazing treatment was visible in the grazing non-tolerant areas inside the fences, where it increased aboveground seasonal biomass production in six of the eight enclosures (all but Grimmels and NP8). Overall, the difference between aboveground seasonal biomass production under early spring grazing treatment and repeated grazing treatment in grazing non-tolerant areas was significant ( $p=0.024$ ) (Fig.2).

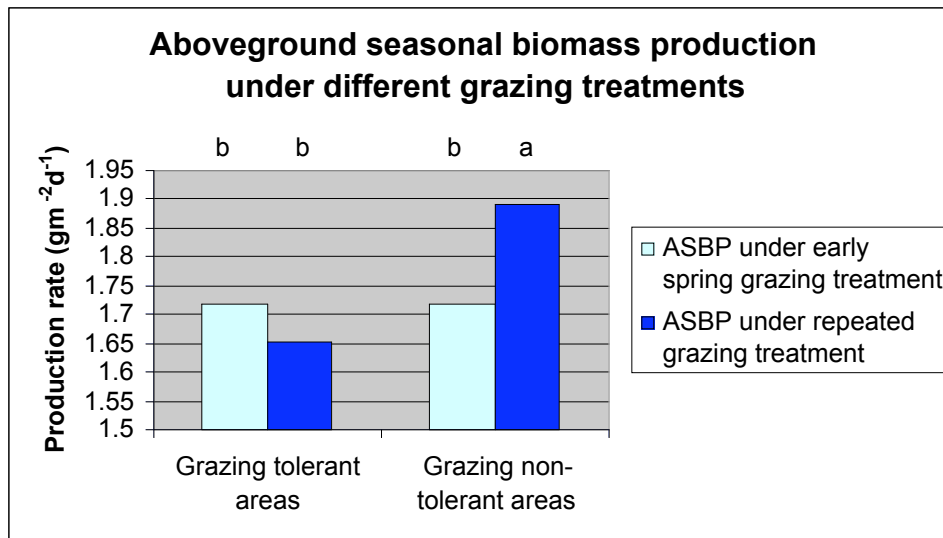


Fig. 2 Aboveground seasonal biomass production under early spring grazing treatment compared to aboveground seasonal biomass production under repeated grazing treatment.

However, aboveground biomass production showed different seasonal patterns in grazing tolerant and grazing non-tolerant areas under repeated grazing treatment (Fig.3).

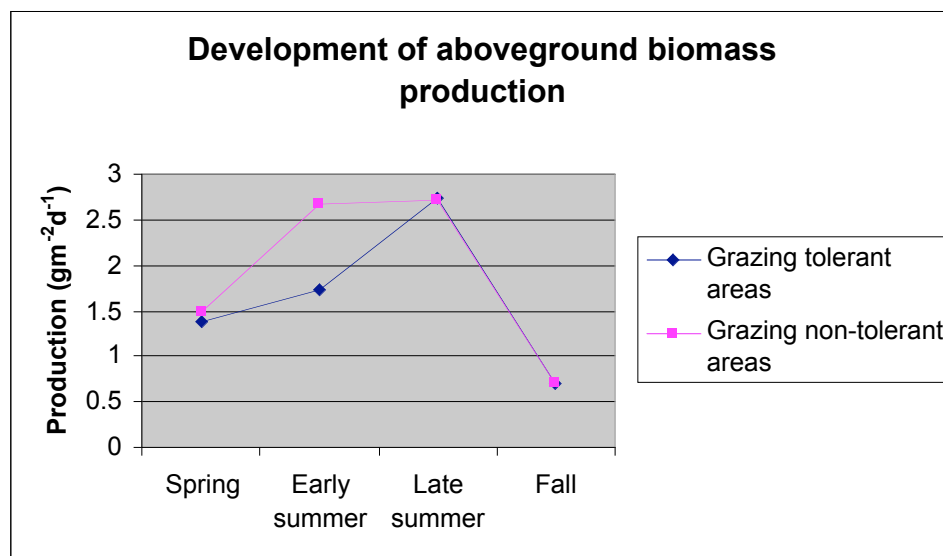


Fig. 3 Development of aboveground biomass production in the course of the growing season 2004.

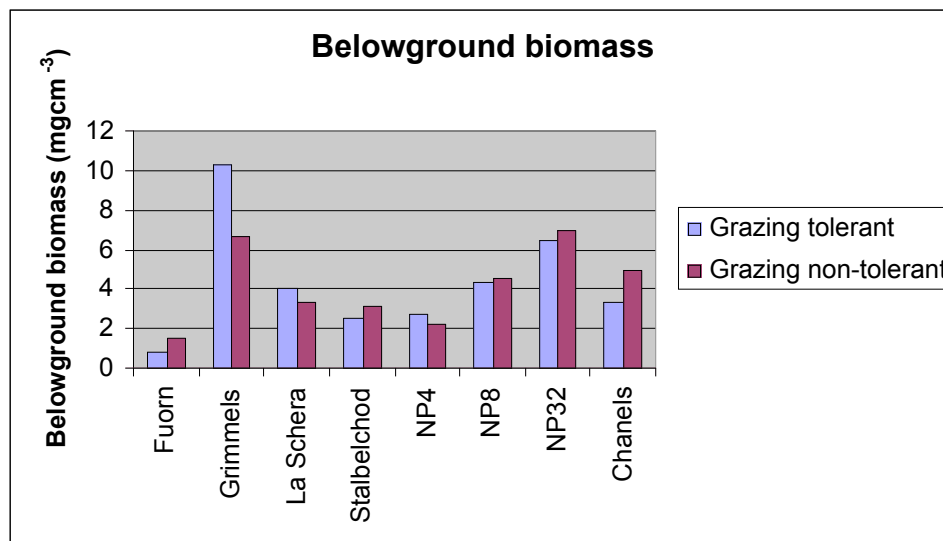
In spring, aboveground biomass production was similar in grazing tolerant and grazing non-tolerant areas, only Fuorn showed a significantly higher aboveground biomass production rate in grazing tolerant areas ( $P=0.049$ ). Aboveground biomass production rates were significantly higher in grazing non-tolerant compared to grazing tolerant areas in early summer ( $P=0.003$ ). In late summer, there was no difference in aboveground biomass production rates between grazing tolerant and grazing non-tolerant areas. Fuorn, Grimmels and NP8 showed a significantly higher aboveground biomass production rate in grazing tolerant areas, La Schera had a significantly higher aboveground biomass production rate in grazing non-tolerant areas (all  $P=0.049$ ). In fall, there was no difference in aboveground



biomass production rate between grazing tolerant and grazing non-tolerant areas, but aboveground biomass production rate was significantly higher in grazing tolerant than in grazing non-tolerant areas at site NP32 ( $P=0.049$ ). Aboveground biomass production rates were highest in late summer, where they ranged from  $1.7 \text{ g m}^{-2} \text{ d}^{-1}$  at Grimmels to  $3.6 \text{ g m}^{-2} \text{ d}^{-1}$  at NP32 in grazing tolerant, and from  $1.4 \text{ g m}^{-2} \text{ d}^{-1}$  at NP8 to  $4.1 \text{ g m}^{-2} \text{ d}^{-1}$  at NP4 in grazing non-tolerant areas.

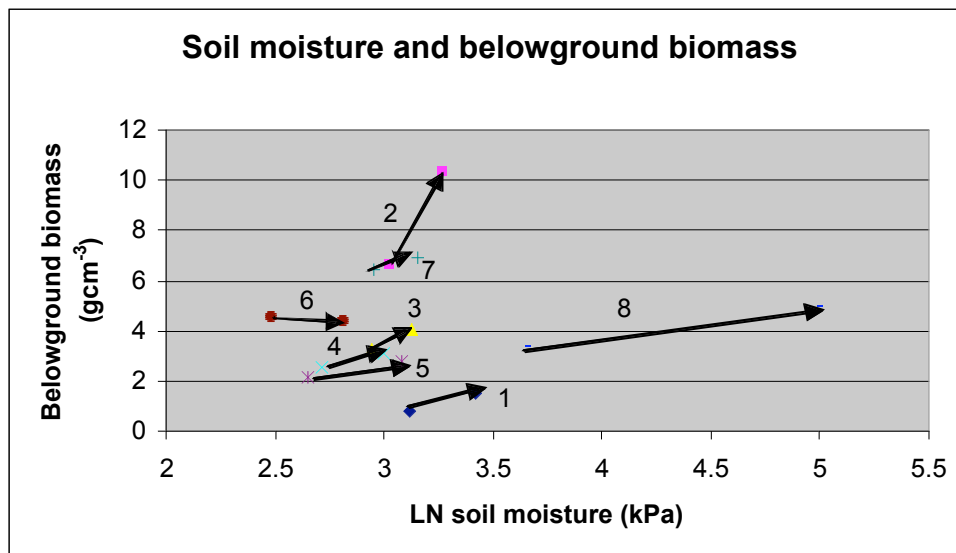
#### Belowground biomass

Belowground biomass ranged from  $0.7 \text{ mg cm}^{-3}$  at Fuorn to  $10.3 \text{ mg cm}^{-3}$  at Grimmels in grazing tolerant areas, and from  $1.5 \text{ mg cm}^{-3}$  at Fuorn to  $6.9 \text{ mg cm}^{-3}$  at NP32 in grazing non-tolerant areas. We found no overall relationship between belowground biomass and grazing tolerance, neither over all sites, nor for a single site (Fig.4).



*Fig.4* Belowground biomass. There was no significant overall difference between belowground biomass in grazing tolerant versus grazing non-tolerant areas.

We also tested if there was a significant difference between grazing tolerant and grazing non-tolerant areas at the high consumption exclosure sites, but there was none. However, we found that biomass between the high consumption sites Fuorn, NP4 and Chaneln was significantly higher than at the other sites ( $P<0.001$ ). The relationship between aboveground and belowground biomass in (SC/BB) grazing tolerant and grazing non-tolerant was not significant. There was a significant relationship between belowground biomass and soil moisture. In the area with higher soil moisture, belowground biomass was also higher at all sites but one (NP8) ( $P=0.05$ ) (Fig.5).



*Fig.5* Soil moisture and belowground biomass. Legend: 1= Fuorn, 2= Grimmels, 3= La Schera, 4= Alp Stabelchod, 5= NP4, 6= NP8, 7= NP32, 8= Chanel. In the area with higher soil moisture, belowground biomass was also higher. The interaction soil moisture and belowground biomass was significant. The only exception to this pattern was NP8, where soil moisture was higher outside the enclosure and belowground biomass was higher inside the enclosure.

### Soil activity

Even though standing crop was lower and soil temperature was higher in grazing tolerant areas like expected, we found soil activity to be lower in grazing tolerant than in grazing non-tolerant areas at all sites ( $p=0.007$ ). The effect of grazing on soil moisture over all sites was significant ( $P<0.001$ ) and soil moisture was, against our expectations, higher in grazing non-tolerant areas. Looking at each site, soil moisture was higher in grazing tolerant areas at Grimmels, La Schera, NP4 and NP8 (all  $P<0.001$ ). It was higher in grazing non-tolerant areas at Fuorn, Alp Stabelchod, NP32 and Chanel (all  $P<0.001$ ). Hence, even though we found higher standing crop and lower soil moisture in grazing non-tolerant areas, soil activity and soil moisture were, against our expectations, higher in these areas.

### **Discussion**

As all parameters showed significant site effects, our study sites are proved to not be equal. Thus, our results are valuable for various types of ecosystems within the SNP, which allows us to apply our conclusions on the entire park.

### Aboveground biomass

Aboveground biomass production changed in the course of the growing season. Even though the differences between grazing tolerant and grazing non-tolerant parts were only significant during the early summer, the development of aboveground biomass production in the course of the growing season was remarkable. Aboveground biomass production reached its peak during late summer (beginning of July to end of July) in grazing tolerant and grazing non-tolerant regimes. Moreover, after the peak in late summer, aboveground biomass production was the same in grazing tolerant and grazing non-tolerant areas. Before the peak, aboveground biomass production was lower in grazing tolerant areas. During early summer, aboveground biomass production in the grazing non-tolerant areas was already almost as high as in late summer, and it was significantly higher in the grazing non-tolerant than in grazing tolerant areas. This suggests a different development of aboveground biomass production in grazing tolerant versus grazing non-tolerant areas, with a higher

aboveground biomass production in grazing non-tolerant areas in the beginning of the growing season, then a peak in both with the same aboveground biomass production, followed by a decline in grazing tolerant and grazing non-tolerant areas. Our results coincide with the findings of Egenter et al. (subm.), who found different growth-patterns in grazing tolerant and grazing non-tolerant vegetation types. Egenter et al. found that aboveground biomass production in grazing tolerant and grazing non-tolerant grasslands was highest in the same clipping interval (mid June to mid July), and that aboveground biomass production in the grazing non-tolerant vegetation type ceased after the peak, while production in the grazing tolerant did not cease but decline. This growth pattern is very similar to the one we found, as we found the peaks in aboveground biomass production of both, grazing tolerant and grazing non-tolerant, in the same clipping interval and we found that after the peak, aboveground biomass production in both areas declined rapidly.

Like expected, standing crop was higher in the grazing non-tolerant areas. The difference between grazing tolerant and grazing non-tolerant areas was significant. Likewise, soil temperature was found to be higher in the in grazing tolerant areas. Our results coincide with our hypothesis. Therefore, we conclude that standing crop and soil temperature depend on grazing, and that grazing reduces standing crop and thus enhance soil temperature.

The influence of the two different clipping treatments varied between grazing tolerant and the grazing non-tolerant areas. In the eight grazing non-tolerant areas, grazing ungulates were excluded for 15 years. In five of the eight grazing tolerant areas, grazing pressure was proved to be moderate (Grimmels, La Schera, Alp Stabelchod, NP8, NP32, Chanel), whereas in the other eight, grazing pressure was high (Fuorn, Chanel, NP4). On one hand, experimental clipping simulated ungulate grazing early after snowmelt in spring (early spring grazing treatment), on the other hand, it simulated repeated ungulate grazing over the whole vegetation period (repeated grazing treatment).

The vegetation inside the exclosures, which had not been grazed in the past 15 years, showed overcompensatory growth under repeated grazing treatment compared to early spring grazing treatment. Jaramillo and Detling (1988) obtained the same result, as they found a higher percentage of biomass and N allocation to sheath and reproductive structures at the expense of belowground parts in grazing non-tolerant plants under simulated grazing pressure. However, we did not find differences in belowground biomass between grazing tolerant and grazing non-tolerant areas in our study. Since we found higher soil activity inside exclosures than outside, grazing doesn't seem to enhance but to reduce soil activity in the SNP. These results coincide with the decelerating nutrient cycle proposed by Ritchie et al. (1998). In the decelerating nutrient cycle, key forage plants decline and unpalatable plants with N poor tissues increase in grazed areas. This results in a decrease in litter N concentration, decelerating N-mineralization rates and N pool decline. Our results, therefore, coincide with the results of Singer and Schoenecker (2003), who found decelerating nutrient cycling in grazed short willow and aspen vegetation types in Rocky Mountain National Park. According to Singer and Schoenecker (2003), the substantial N losses in the Rocky Mountain National Park were due to within ecosystem climate changes or to a net movement of N from willow and aspen vegetation type. They also indicate that grazing in these vegetation types was very intensive, and that grazers had a relatively less important effect on rates of N processes compared to N processes in grazing non-tolerant vegetation types. Therefore, grazing probably did not affect nutrient cycling in a positive way in the Rocky Mountain National Park. In the model of De Mazancourt et al. (1998), grazing only accelerates nutrient cycling in ecosystems with large losses of the limiting nutrient during recycling of plant detritus, or where herbivores bring nutrients from outside the ecosystem. As soil activity in our study was found to be higher in ungrazed versus grazed areas, we must assume that grazing does not accelerate nutrient cycling in the SNP. Soil activity may also correlate positively with soil moisture, which was also significantly higher in grazing non-tolerant than in grazing tolerant areas in our study. This result coincides with the results of Epstein et al. (2002), who found that precipitation influenced decomposition rates in water

limited regions. Epstein et al. also compared the influence of temperature, soil texture and soil moisture on decomposition rates in the U.S. Great Plains, and found that the factor influencing decomposition rate most of all was soil moisture. With the available data, we could not explain the reasons for the decrease in soil activity through grazing at the examined enclosure sites. However, there are several ways in that grazing could decrease soil activity, such as too intensive grazing (Shariff et al. 1994), a net movement of N from the systems (Singer and Schoenecker 2003), a lack of nutrient import by ungulates to the grazed ecosystems (De Mazancourt et al. 1998), within ecosystem climate changes (Singer and Schoenecker 2003), or the higher soil moisture in the ungrazed areas (Epstein et al. 2002).

In the three grazing tolerant areas, where biomass consumption by ungulates was high and vegetation therefore adapted to heavy grazing pressure, vegetation overcompensated when grazing simulated early spring grazing. Overcompensatory growth as response to early spring grazing pressure in grazing-tolerant areas seems to be a reasonable strategy assuming that grazing patterns of ungulates may change in space and time. Frank and McNaughton (1993) suggest that native large herbivores stimulate aboveground seasonal biomass production when they graze grasslands early in the growing season, because they provide additional resources and let the plants time to recover until the end of growing season. Shariff et al. (1994) compared a moderate grazing treatment with a long term not grazed and a heavy grazing treatment, and found a higher decomposition rate in the moderate grazing treatment compared to the long term not grazed and the heavy grazing treatment. They suggest that the differences in soil N mineralization and immobilization rates may be due to changes in N concentration in litter and root substrates. N concentration in litter and root substrates increased during decomposition in the moderate grazing treatment, while it decreased or showed no change in the long term not grazed and in the heavy grazing treatment. Like this, the moderate grazing treatment increased the supply of N for plants, while the long term not grazed and the heavy grazing treatment did not. This indicates that moderate grazing may cause an accelerating nutrient cycle, while heavy or no grazing may not. As we found overcompensatory growth at the three high consumption sites, our results could support the accelerating nutrient cycle scenario of Ritchie et al. (1998). The accelerating nutrient cycle scenario suggests that plants react to grazing by faster nutrient uptake, higher growth rates and higher tissue concentration N, which results in higher litter quality. This, together with the deposition of excretions, leads to higher litter decomposition and higher mineralization rates. The resulting higher N availability to plants stimulates aboveground biomass production. For our study sites, Egenter et al. (subm.) found higher N concentration in leaf tissues of heavily grazed plants compared to moderately grazed plants and Achermann (2000) found a positive correlation between grazing intensity and the amount of excretions deposited. According to these results, we suggests that red deer cause an accelerating nutrient cycle in the three high consumption sites Fuorn, NP4 and Chanel.

### Belowground biomass

The differences in belowground biomass and the relation of aboveground and belowground biomass between grazing tolerant and grazing non-tolerant areas were not significant in our study. However, in the three sites with a high grazing pressure, belowground biomass was significantly lower compared to the five sites that were rarely grazed. Therefore, we conclude that grazing has a long-term effect on belowground biomass in the SNP. Since no differences between grazing non-tolerant and the grazing tolerant areas were recorded, it is likely that short-term effects of grazing pressure on belowground biomass are not important. However, belowground biomass was closely related to soil moisture in our study. Fisk et al. (1998) found similar results in a comparing study of dry, moist and wet tundra, where the production of foliage and roots was significantly correlated to soil moisture. Dwire et al. (2004) found that belowground biomass accounted for 68 - 81% of total biomass in wet and moist meadows, and the amount of belowground biomass was less high in dry meadows. Similar results have been found for a dry tropical savannah, where belowground net primary production was significantly related to rainfall (Pandey and Singh 1992). According to Pandey and Singh (1992), several studies have revealed a correlation between precipitation

and productivity in low rainfall areas. They also indicate that, because the root system occupies less soil space, root growth is further reduced by the unavailability of water. Because the climate in the SNP is characterized by low amounts of annual precipitation (925 +/- 162mm), and poorly developed soils (Risch 2004), we suggest that belowground biomass is as strongly influenced by the climate as by the grazing native ungulates. For more profound understanding, this topic must be subject to further investigations.

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