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Impacts of Different-Sized Herbivores on Root Biomass in Subalpine Grassland

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Abstract

Grassland ecosystems are the largest biome on Earth. Besides being a remarkable source of biodiversity, they provide important goods and services. Herbivores can strongly influence the function and structure of these ecosystems, namely altering biomass, woody and herbaceous plant diversity and soil characteristics. To identify the effects of grazing on belowground plant properties is valuable for the understanding of how sustainable a system is or how likely it is to change with altered grazing pressure. Although belowground biomass can be three to four times greater than aboveground biomass, belowground processes remain understudied in grasslands. Root biomass, length, elongation and distribution can be altered by regular defoliation, and its reduction can be connected with the intensity and frequency of defoliation. The present thesis focuses on the effects of grazing by different-sized herbivores on root biomass. It is part of a larger scope experiment sited in the Swiss National Park, in the south-eastern part of Switzerland. The exclusion of different-sized herbivores is an important aspect of this experiment, since the spatial and temporal scales at which plants and soil organisms operate change depending on the body size and life history of the organism concerned and the size of its habitat unit or domain. After the first year of the experiment, root biomass in tall-grass was significantly higher for the "Marmot, Mouse, Insect treatment", than for the "Insect" and the "None" treatment. Also for tall-grass and for the same year, a significant negative correlation was detected between root biomass and soil moisture. After the second year no significant findings were detected. These results suggest that further data should be gathered and other factors should be taken into account, given the complexity of the processes studied.

Keywords

Sub-alpine grassland, grazing, herbivore exclusion, root biomass.

1. Introduction

Grassland ecosystems represent about 40% of the world's total land area, providing important goods and services such as food, forage for livestock, biodiversity, carbon storage, tourism and recreation. Despite the most common use of grassland worldwide being the production of domestic livestock, a considerable number of wild herbivores depend on grasslands (Gibson 2009). Browsing and grazing herbivores can have a profound influence on the physiognomy, composition, and function of vegetation, exerting differential pressures on plant populations at different spatial and temporal scales (Schütz et al. 2003, Skarpe and Hester 2008). Through grazing herbivores can be important determinants of the spatial variability of their habitats, collecting nutrients that are diffusely distributed and concentrating them in urine and faecal patches (Frank 2006, Schütz et al. 2006). Bardgett and Wardle (2003) suggest a range of possible mechanisms through which herbivores can affect soil biota and ecosystem functioning. These effects can be positive, negative, or neutral depending on the balance of the different mechanisms. According to these authors, a combined aboveground-belowground approach is required due to the relevance of feedbacks taking place between herbivores, producers and decomposers. Since grazing is a combination of several factors simultaneously affecting plants and their environment it is intricate to predict and understand grazing effects (Mikola et al. 2009).

A major obstacle to understanding and generalizing plant functional response to grazing is the scarcity of comprehensive approaches coupling major functional processes (Leriche et al. 2001). Grazing implies multiple effects, making it difficult to transfer experiment findings to field conditions (Gao et al. 2008). Few grazing studies incorporating data on plant traits use an experimental approach because, among other aspects difficult to control and to measure, it is fairly complicated to quantify the effect of different herbivore densities (Evju et al. 2009). Dawson et al. (2000) conducted an experiment in a greenhouse on monocultures, enhancing the importance of considering intensity and frequency of defoliation when studying physiological responses to defoliation. They also pointed out the difficulty of making comparisons between studies where plants have been defoliated in different ways, as well as the need for an integrated approach in order to understand grazing effects. Grazing effects are also inseparable from herbivore body size. The minimum quality of food necessary for the survival of mammalain herbivores is connected to their body size (Illius and Gordon 1992). Herbivores differ in their physical capacity to eat, which includes bite size, grazing time, rumen

volume, etc., as well as in their ability to utilize a given feed and in their requirements for feed (Pearson and Ison 1987). Furthermore, the spatial and temporal scales at which plants and soil organisms operate change depending on the body size and life history of the organism concerned and the size of its habitat unit or domain (Bardgett et al. 2005). To assess the multiplicity of potential interactions taking place in a grassland ecosystem an experimental field design was set up in the Swiss National Park (SNP) to determine single and combined effects of four herbivore groups distinctly different in body size and foraging behaviour in two different vegetation types (short-grass characterized by high grazing pressure, and nutrient-poor tall-grass characterized by low grazing pressure). The present thesis is integrated in this experiment and focuses specifically on root biomass as a response to grazing.

Root biomass constitutes more than 60% of grassland living biomass with its extent being generally correlated with aboveground growth (root:shoot ratios can vary from 0.7:1 to 4:1). The majority of grass roots is located in the upper part of the soil. Root biomass generally increases over the course of the growing season if enough water is available. Environmental factors (fire, grazing, temperature and nutrients) as well as the amount and depth of soil moisture, soil type and light intensity on aboveground leaves affect root growth, morphology and functioning (Gibson 2009). Plants have intrinsic mechanisms that can increase their tolerance to herbivore damage, and which vary significantly among plant species and often include feedback loops between traits and events. Among these are the pre-existing high levels of carbon storage in roots for allocation of aboveground effects, and the ability to move carbon stocks from roots to shoots after damage (Strauss and Agrawal 1999). The effects of grazing on fine root growth and dynamics have been considered primary to comprehend herbivore interactions within carbon and nutrient cycling processes (Dawson et al. 2000) and there is some knowledge available on how grazers influence root biomass. However, little is known of how grazing by different herbivores affects root biomass and in such context this thesis gains much more importance. Johnson et al. (2001) drew attention to the fact that much of the evidence concerning the effects of grazing on root productivity comes from greenhouse pot experiments and short-term effects following clipping, and not from a consensus of field studies. They also cite nine field studies on root productivity, attributing the absence of a clear pattern of grazer effects to an obvious gap in the ability to predict the ecosystem consequences of grazers across a range of grassland ecosystems, and to the fact that this is an intriguing area of research. The fact that defoliation studies are mostly carried out using pot experiments,

while grazing studies focus on plants growing in the fields, may also contribute do discrepant outcomes (Mikola et al. 2009).

The objective of this study was to assess how the exclusion of different sized herbivores affects root biomass in two different grass types in the SNP. The results presented here focus on root biomass collected after the first and second seasons of herbivore exclusion. In addtion there was also an interest in assessing whether changes in soil moisture or soil temperature, as a result of grazing, were responsible for allterations in root biomass.

2. Methods and Material

2.1 Study site

The experiment took place on subalpine grasslands in the Swiss National Park (SNP), located in the south-eastern part of Switzerland. Founded in 1914 with the aims of total nature protection, research and information, the SNP covers an area of 170.3Km^2, 50 of which are forested and 3 covered with subalpine pastures. The elevation ranges between 1350 and 3170 a.s.l., the mean annual precipitation and temperature are 871 ± 156mm and 0.6 ± 0.6 °C (mean ± SD), respectively (Risch et al. 2008, MeteoSchweiz 2011). Because the SNP is one of the few areas that have not been directly influenced by human activity during most of the 20th century, it provides an exceptional opportunity to study the development of ecosystems in the absence of human intervention (Risch et al. 2009). The subalpine grasslands are characterized by large (> 1 ha) homogeneous patches of short and tall grass vegetation. Both vegetation types are grazed by wild ungulates, medium and small mammals as well as invertebrates, whereby considerably more intensive grazing is found in nutrient-rich short-grass (Schütz et al. 2003, 2006, Thiel-Egenter et al. 2007). Consequently, the average vegetation height of short-grass approximates 2 to 5 cm. Short-grass pastures are dominated by red fescue (*Festuca rubra* L.), perennial quaking grass (*Briza media* L.), and milfoil (*Achillea millefolium* L.). Tall-grass pastures, on the other hand, are composed mostly of evergreen sedge (*Carex sempervirens* Vill.), mat-grass (*Nardus stricta* L.) and Bellard's Kobresia (*Elyna myosuroides* (Vill.) Fritsch) (Risch et al. 2008).

2.2 Exclusion design

In total,18 sites (9 on short, 9 on tall-grass vegetation) on subalpine grasslands were selected. On each of the 18 sites an exclosure networtk with four different exclosure types was established. The "All" plot was accessible to all herbivores and was not fenced. A 2.1 m tall and 7 x 9 m sized fence constructed of 10 x 10 cm wooden posts and electrical equestrian tape (AGRARO ECO, Landi, Bern, Switzerland, 20 mm widths mounted at heights 0.7 m, 0.95 m, 1.2 m, 1.5 m and 2.1 m height) connected to solar powered voltage source (AGRARO Sunpower S250, Landi, Bern, Switzerland) sourrounded the other four plots and excluded large vertebrate herbivores (red deer, chamois). The "Marmot, Mouse, Insect" plot was not fenced additionally, i.e. only the large vertebrate herbivores were excluded while medium and small sized vertebrate as well as invertebrate herbivores had access. The "Mouse, Insect" plot was fenced with a 80cm high 5x5cm net and excluded large and medium sized vertebrate

herbivores. The "Insect" plot was surrounded by a 80cm high wire mesh of 1.5x1.5cm that excluded all vertebrate herbivores but not the invertebrates. The "None" plot excluded all aboveground herbivores, with a 80cm high mosquito screen (1x1mm net) at all four sides and top of the exclosure (Figure 1).
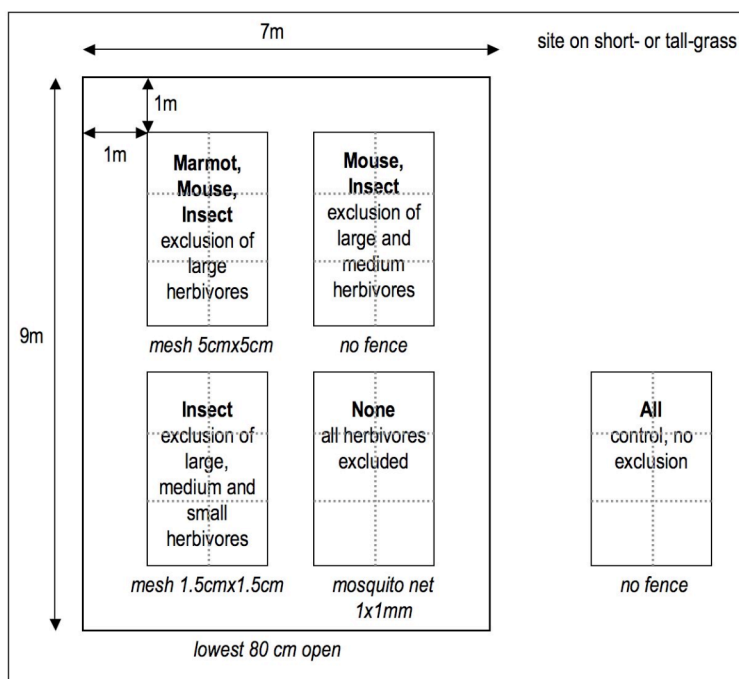

Figure 1: Scheme illustrating the exclusion design.

2.3 Field sampling and biomass estimation

Soil core samples (stander taper ST200, core diameter 2.2cm, Giddings Machine Company, Windsor, CO, USA) were collected in the fall of 2009 and 2010 (early September). Five samples (0-10 cm) were randomly collected in each treatment within a 10 cm x 100 cm strip where the vegetation had previously been clipped, adding up to a total of 450 soil samples each year (18 plots x 5 grazing treatments per plot x 5 samples per treatment). The samples were first dried at room temperature for a period of 48 hours and then fine roots were handpicked. Roots were dried for 24 hours at 65° C and weighed with a high-precision scale to determine their biomass. Soil temperature was measured with a water-proof digital thermometer (Barnstead International, Dubuque IA, USA) and moisture with a time domain reflectometer (Field-Scout TDR-100; Spectrum Technologies, Plainfield IL, USA). Both were collected by-weekly at all plots during both growing seasons. Root biomass data was made available by Bigna Stoffel.

2.4 Statistical data analyses

A Linear Mixed Model analysis was performed to understand how time of sampling, treatment and vegetatoin type affected root biomass. Grass type, year, treatment, "grass type x treatment", "grass type x year", "treatment x year" and "grass type x treatment x year" were used as fixed effects. "Fence (grass type)" was used as a random effect. Since only grass type ($F = 7.516$, df = 16, $p = 0.14$), year ($F = 63.903$, df = 144, $p = 0.00$), "grass type x treament" ($F = 3.931$, df = 144, $p = 0.005$) and "grass type x treatment x year" ($F = 2.688$, df = 144, Sig.= 0.034) were significant, the data analysis was split into two parts. In a first step, a linear mixed model was used to assess how root biomass differed between the two grass types in the two years, using grass type as a fixed effect. Therefore the data was analysed separately by year and, within each year for the two grass types. In a second step, a linear mixed model was used for each year, using treatment as a fixed effect. To meat the normality criteria the root biomass data was log-transformed.

In addition a correlation was made to investigate whether average growing season soil moisture and temperature could explain any of the differences in root biomass between the two years in the two vegetation types, using Spearman's Rho. All statistical analyses were conducted with IBM SPSS 19 (IBM Corporation, Route 100 Somers, NY 10589).

3. Results

Root biomass was different between the grass types in 2009 (F = 8.826, df = 88, p = 0.004; Figure 2), namely higher for tall-grass. The same finding was obtained for 2010 (F = 20.376, df = 88, p = 0.000; Figure 2). Root biomass was significantly negatively correlated with soil moisture for tall grass in 2009, according Spearman's Rho (Correlation coefficient = -0.385, p = 0.009).
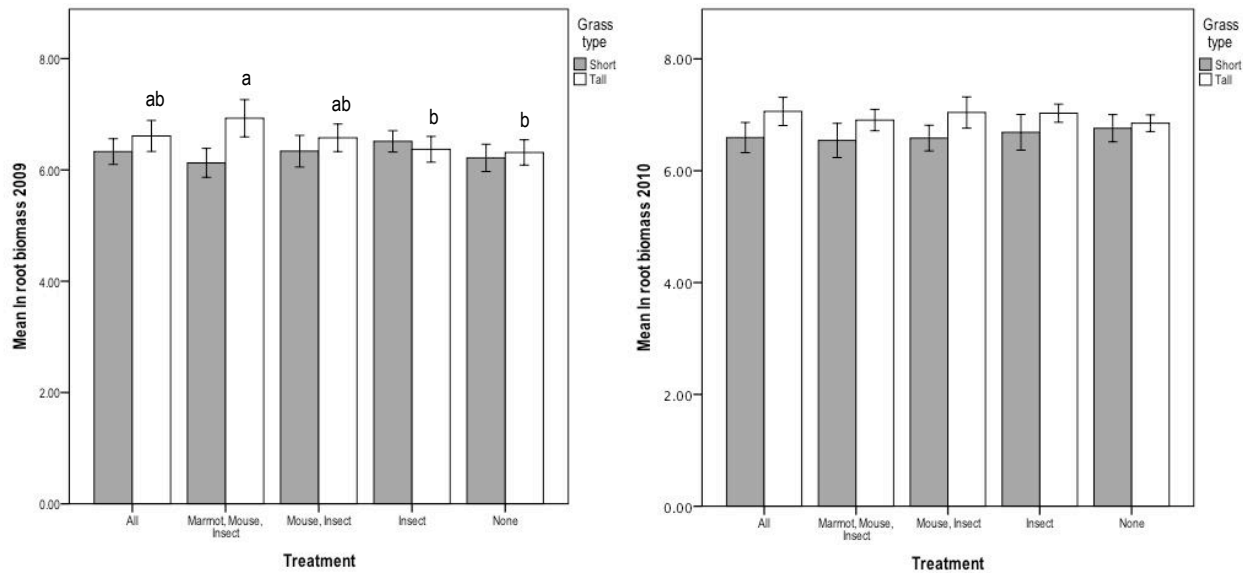
Figure 2: Bar graphs displaying mean ln root biomass for grass types and each year. Error bars represent +/- 2 SE.
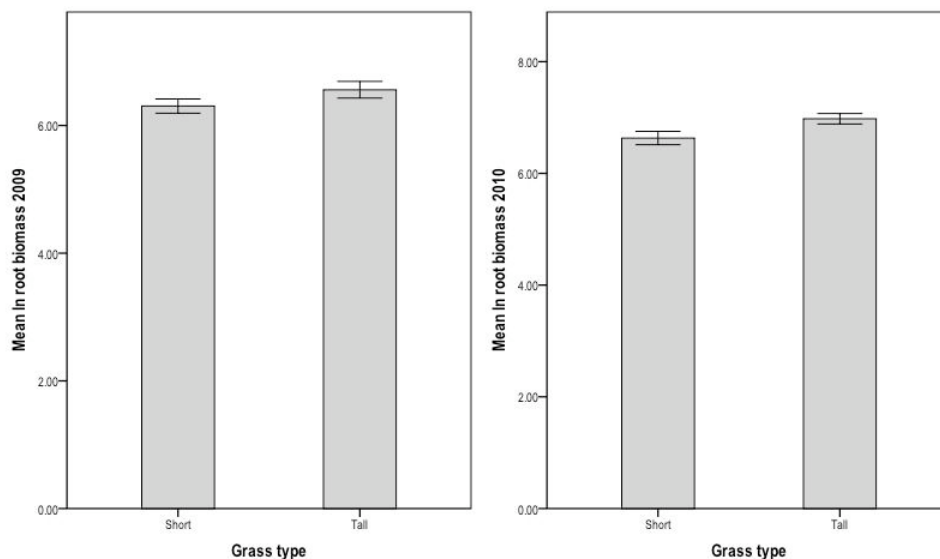
Figure 3: Bar graphs displaying mean ln root biomass for grass types, both years and for each treatment. Error bars represent +/- 2 SE.

Herbivore removal did not significantly alter root biomass in any of the two years of our study for short-grass (2009: F = 2.076, df = 32 , p = 0.107; 2010: F = 0.871, df = 32 , p = 0.492; Figure 3). In contrast, significant differences were found between the different treatments for the tall grass in 2009 (F = 5.713, df = 32, p = 0.001; Figure 3), namely significantly higher root biomass in the "Marmot, Mouse, Insect" treatment compared to the "Insect" and "None" treatments. In 2010, we could however no longer detect any grazer effect on root biomass (F = 0.895, df = 32, p = 0.478; Figure 3).

4. Discussion

After two years, it is a challenging task to yield clear conclusions from the experiment still taking place. This outcome is not unexpected when considering the myriad of interactions potentially occurring between various non-neglegible factors. What is known from the results is that, after the first year of the experiment (2009), root biomass was significantly higher for the "Marmot, Mouse, Insect" treatment compared to the "Insect" and the "None" treatment in tall-grass. Also for tall-grass and for the same year, a significant negative correlation was detected between root biomass and soil moisture. Since these results were not repeated in 2010, it's only possible to weave statements with some degree of assumption, since further knowledge derived from forthcoming data is necessary.

The exclusion of different-sized herbivores, as considered in the SNP experiment, takes into account a crucial contributor of the complexity of the interactions taking place in such studies. Bakker et al. (2004) emphasize the importance of herbivore type in the explanation of conflicting results on nutrient cycling in grasslands, concluding that different-sized herbivores have different effects on N cycling within the same habitat. In their experiment, three grazing treatments were set in the Junner Koeland area in The Netherlands, one with free access to cattle, rabbits and voles, another fencing off cattle and the third allowing only voles. The exclusion of large herbivores resulted in increased N annual mineralization under small herbivore grazing. The amount of roots decreased significantly after the cattle and rabbits were excluded. The vole number increased as a consequence of cattle exclusion, while rabbit grazing was facilitated by the presence of cattle. Since the proportion of the different-sized grazers was not taken into account for this thesis, nothing can be said about how they influnce each others' number. However, the higher amount of tall-grass root biomass detected in 2009 for medium-sized herbivores, when compared to the "All" treatment, could be linked to the large herbivores' influence on nutrient cycling. Bakker et al. (2009) discussed the influence of large herbivore grazing on smaller herbivores, pointing out that large mammalian herbivores may have considerable effects on grassland species composition, nutrient content and vegetation structure, as well as the degree of cover from predators; therefore changing the availability of food for small herbivores and their abundance. After seven years of cattle exclusion they concluded that, in productive grasslands, the abundance of small rodents is reduced due to grazing by large herbivores, while the number of rabbits and similar sized herbivores is facilitated. In the SNP experiment, it could be suggested that small-sized herbivores might

cause intermediate levels of disturbance (Grime 1973), therefore creating conditions for an increase in root biomass for the "Marmot, Mouse, Insect" treatment. Bagchi et al. (2006) associate the presence of small herbivores to the maintenance of diversity levels and ecosystem functioning, influencing plant diversity and dominance hierarchies either directly via defoliation or through indirect effects on plant-soil interactions.

Other studies focus on the exclusion of only one herbivore size, namely large. Within the realm of the most recent experiments measuring root biomass following large herbivore exclusion, namely the ones performed in the last decade, there are a few interesting examples worth discussing. Some of these experiments reported a reduction of root biomass due to grazing (Johnson et al. 2001, Chen et al. 2006, Gao et al. 2008, Klumpp et al. 2009 , Zhao et al. 2009, Shi et al. 2010), some an increase (Frank et al. 2002, Cui et al. 2005, Derner et al. 2006). There are also cases where grazing's influence on root biomass shifted in a relativley narrow time span (Mikola et al. 2009). It is important to remember that each experiment has its own context and, in the absence of a larger database, the simplistic agglutination of results discarding their spatial and temporal context, making direct comparisons with the SNP's experiment, is unreasonable.

Johnson et al. (2001) explored the roles of grazing and burning on root growth in experimental watersheds at Konza Prairie, Kansas. Grazing decreased root growth, specially in heavily grazed patches, and increased N cycling and availability. This implied, for these authors, that grazed plants were C-limited, with less C allocated to roots while shoots regrew. In the Mongolian grassland, Chen et al. (2006) obtained a model to study the root responses to grazing, under different conditions of stocking rates and precipitation. As a result from grazing, above and belowground biomass is reduced, leading to a smaller litter and nutrient input to the soil, and subsequent decrease of overall nutrient availability. Also in the Mongolian grassland, Gao et al. (2008) estimated root biomass for a period of three years in sites with different grazing intensity. A decrease of belowground biomass was observed with increasing grazing intensity, suggesting that the cause may be found in the reduced source size of C assimilating organs and the intensified re-translocation of root carbohydrates to shoot meristems. Klumpp et al. (2009) subjected grassland monoliths to different grazing intensities for a period of fourteen years. The shift to high disturbance lead to a decrease in root biomass. They concluded that grazing influences soil carbon storage by changing plant roots and their control over the soil microbial community and decomposition, subsequently enhancing decomposition and soil C

loss in more productive and disturbed grassland systems. Once again in Inner Mongolia, Zhao et al. (2009) looked at the effects of long-term grazing (>20 years) on *leymus chinensis* traits. Grazing significantly reduced the shoot and root/rhizome biomass. These studies, all implying root biomass decreases after grazing, present two possible processes triggered by grazing, one in which shoots increase as roots decrease and another in which shoots and roots both decrease. Dawson et al. (2000) mention that root growth reductions might aim to reduce belowground carbon demand in defoliated plants, permitting greater allocation of carbon to the shoot. Oba et al. (2000) explain the debate over the compensatory growth hypothesis, in which one school of thought defends the beneficial effects of herbivory, up to some minimum level. The opposing group identifies other factors, such as environmental conditions, more important than herbivory in demonstrating compensation. Biomass production alone might not sufficient proof. Without data regarding shoot biomass, which would clarify whether an increase in root biomass occurs with a decrease or an increase of shoot biomass, conjectures concerning the SNP experiment lack a solid foundation.

Other experiments report increases in root biomass, as a consequence of grazing inhibiting shoot growth. In 2002 Frank et al. compared aboveground and belowground production in grazed vs. ungrazed grassland in nine sites in Yellowstone National Park. According to their results, herbivory stimulated root production seven times more than shoot production, indicating a positive feedback on root growth. These authors make reference to other field studies which report the reduction, the absence of any effect and the increase of root biomass. Moreover, they alert towards the difficultiy of extrapolating previous field results, since biomass measurements ignore root turnover. Climate, namely temperature and precipitation, and consumers are indicated as the major determinants of primary production. As an explanation for ungulate facilitation of grassland whole-plant productivity, they mention the self-shading effects of tall, ungrazed vegetation; the long distance migration of native ungulates, which leads to short duration grazing peaks and sufficient recovery time for grazed plants; and the promotion of soil available nitrogen by grazers. According to the herbivore exclusion experiment carried out by Cui et al. (2005) in Inner Mongolia, compensatory growth was common in the grazed sites. In these, browsing removed most of the litter, making organic matter input dependent on root turnover and animal excreta. They assumed that root productivity and turnover were maintained or stimulated, since aboveground growth cannot increase or be maintained when root growth is inhibited. Derner et al. (2006) excluded herbivores in three different grass type sites in the North American Great Plains. The relative

proportion of fine root biomass was greater in grazed versus ungrazed sites, for the three grass types, although aboveground biomass was lower. Root turnover and rates of nutrient cycling processes is probably accelerated in grazed sites. Root biomass was redistributed into proportionally more fine roots in the 0-30cm soil depth. Larger root:shoot ratios for short-grass were attributed to enhanced root production in a water-limited environment and greater belowground constraints on soil-plant interactions. This could be an interesting point when looking at the negative correlation found between root biomass and soil moisture, for 2009 at the SNP. However, this result was only detected in tall-grass.

Further aspects seem to play a key role in the herbivore exclusion effects and should thus be taken into consideration. Plant traits for instance, since different species inherently possess lesser or better developed shoot and root systems. Evju et al. (2009) investigated the relationship between sheep selectivity, plant traits and species abundance in response to sheep grazing pressure. Species that were generally small and had a high root/shoot ratio increased in abundance at high grazing pressures, while species with small roots decreased. A high root/shoot ratio, which is connected to regrowth capacity, is a trait that reflects the plants' tolerance strategy. For these authors herbivore selectivity, plant tolerance and plant resistance are all connected to a range of morphological and physiological plant traits, which are helpful to the understanding of the mechanisms behind species' response to grazing. In two Yellowstone National Park grasslands, Frank et al. (2010) investigated the distribution of the roots of plant species. Root frequency was positively associated with shoot biomass among species, indicating the importance of large, well-proliferated root systems in the establishment of aboveground dominance.

Another undisputably relevant aspect is the spatial and temporal scales considered. When observing plant-herbivore studies, the effect of grazing is strongly dependent on the space and time scale considered (Brown and Allen 1989), among other reasons because the nutritional content of grass varies over complex spatial and temporal scales (Frank 2006). For three years Mikola et al. (2009) studied the potential plant defoliation, dung and urine return, and physical presence of animals to explain grazing effects in a cow pasture in Finland. Cow grazing increased root biomass in the first year, had an insignificant effect in the second year, and decreased root biomass in the third year. This shift from positive to negative effects might be attributed to soil compaction due to trampling leading to an increase root biomass in upper soil layer in grazed plots, and later to the colonization of control plots by plants with heavy

rhizomes. Defoliation and and physical presence of cows were responsible for the effects on root biomass, dung and urin return were not. This study is a good example of how relevant temporal scale can be; scale issues are principal to the study of herbivory impacts on plant community dynamics, and can also lie behind apparent controversies in the literature about herbivore influences on vegetation, therefore understanding their implications is fundamental (Hester et al. 2006). Kuijper et al. (2008) underlined the importance of experiments' time-scale in the study of the interactions between herbivores. Species that seem not to influence each other's abundance on a short time scale may facilitate one another when considering larger time-scales. Bardgett et al. (1998) include the effects on root morphology and biomass in the category of long-term interactions, stating that in the long-term aboveground herbivory can reduce root biomass and change the root morphology and architecture. Long-term approaches regarding plant community responses to herbivory are lacking, specially in colder regions where vegetation reacts slower to changing conditions (Eskelinen and Oksanen 2006). Since this thesis was written after the second year of the SNP's experiment, results most likely fail to properly address the middle and long-term effects of grazing on root biomass. Another problem related to time is the variation of temperature and moisture throughout the year and how it may affect root biomass. McNaughton et al. (1998) collected samples across the Serengeti on ten dates during an annual cycle, on a monthly basis during the rainy and early dry seasons and every two months during peak dry season. A pronounced minimum of root biomass took place in mid-wet season (February) and a maximum at the beginning of the dry season (June). Therefore the point in time in which sample collection took place at the SNP might have influenced the obtained values.

Spatial scale, as mentioned, is equally critical. The occurrence of forages with sufficient nutrient content and the spatiotemporal variation of vegetation productivity due to geographic gradients and production seasonality, can influence distribution and abundance of grazing animals (McNaughton et al. 1997). Hillebrand (2008) focused on the grazing-regulated spatial variability of peryphyton biomass, based on data derived from more than eight hundred experiments, concluding that grazers negatively affected its absolute variability. Such studies are only possible once a large database is available, which, in the case of root biomass, hasn't been achieved yet. Smaller spatial scales also seem to matter; Shi et al. (2010) excluded livestock for a period of seven years in an alpine meadow in the Qinghai-Tibetan Plateau. Exclusion significantly decreased bare ground cover, presumably due to the significant increase of aboveground live biomass, belowground root biomass and litter accumulation. In

combination with grazing intensity, slope influenced the degradation process of the meadow and the maintenance of forage production and biodiversity. While a flat valley can withstand low to moderate grazing intensities, a south-facing slope should be submitted to long and effective livestock exclusion. Jacobs and Naiman (2008) set up a three year herbivore-exclusion experiment in the semi-arid African savanna. Biomass of herbaceous plant species, in the presence of large herbivores, generally increased from the hillcrest to the lower and wetter riparian zone, with no change in species richness. Furthermore they mention that in ecosystems with an evolutionary history of grazing, grazing is considered to increase grass productivity and higher available water in riparian zones can enhance this effect. According to these authors, large herbivores are essential to the reduction of herbaceous competition and the maintenance of species diversity and ecosystem functioning in the studied ecosystems. However, Thiel-Egenter et al. (2007), whose experiment took place at the SNP, found lower aboveground net primary production in the grazing-adapted short-grass compared to the non-grazing adapted tall-grass. Although fence positions revealed no significant correlation with root biomass results in the SNP experiment, they should not be entirely discarded. For broader spatial scales results obtained for this experiment should account for spatial variability before being extrapolated for other sites. Since the response of grassland productivity to grazing may substantially vary between ecosystems, it's not feasible to foresee the potential effects of grazing on grassland processes in ecosystems where these interactions have not so far been studied (Thiel-Egenter et al. 2007).

The root-picking method is debatable and there are certainly advantages and disadvantages associated with this and other methods. Within the existing methods that measure root biomass and distribution (core method, ingrowth cores, monolith method, minirhizotrons, trench profile wall and core break methods), monolith and core methods have been verified to provide reliable estimations of root biomass and length density, in spite of destructive sampling and high labor requirement. Sample variance might be affected by soil sample size and sample position and a trade-off is always made between statistical precision and financial/time costs. The number of samples varies between ecosystems according to sample size, local vegetation heterogeneity and soil structure. Given the lack of a standard sampling strategy, sample schemes taken by different researchers differ, making it impossible to compare root biomass from different studies (Ping et al. 2010). In this thesis, the fact that the roots were hand-picked by different people during both years may have caused a bias in the results. Due to the representative amount of samples (450) and the time restraints inherent to a six months master

thesis, root picking by one single person was considered unreasonable. In addition, root extraction as well as the discrimination between actively growing roots and inactive or dead ones is difficult. Root biomass may be a poor indicator of belowground growth, given that root production and mortality take place simultaneously. Thus root growth dynamics should also be considered (Dawson et al. 2000).

5. Conclusion

An experiment such as the one conducted in the SNP is of great interest in the scope of comprehensive above and belowground approaches focusing on the effects of grazing by different-sized herbivores in grasslands. This thesis, because it was a six-month master thesis, focused solely on a specific aspect of this whirlpool of possible feedbacks, namely a feebly studied one – root biomass. It possesses value in itself but, more importantly, should be regarded as part of the the entire experiment, which ideally should incorporate an even larger temporal and spatial scale.

6. Acknowledgements

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Appendix A: Data

Table S1: Data collected after the first and second seasons following herbivore exclusion.

Grass type	Grassland	Fence	Treatment	Elevation (m)	North exposition (x° x`)	East exposition (x°x`)	Root biomass 2009 (g.m-2)	Root biomass 2010 (g.m-2)	Soil temperature 2009 (°C)	Soil moisture 2009 (%)	Soil temperature 2010 (°C)	Soil moisture 2010 (%)
Short	Stabelchod	1	All	1960	39.49	14.3	394.60	793.41	14.18	28.73	15.00	23.34
Short	Stabelchod	1	Marmot, Mouse, Insect	1960	39.49	14.3	436.69	772.26	14.64	26.60	14.84	24.09
Short	Stabelchod	1	Mouse, Insect	1960	39.49	14.3	557.70	839.50	14.58	35.73	14.63	24.00
Short	Stabelchod	1	Insect	1960	39.49	14.3	405.12	987.71	14.36	37.87	14.71	23.97
Short	Stabelchod	1	None	1960	39.49	14.3	431.43	792.30	13.66	29.80	13.20	26.60
Tall	Stabelchod	2	All	1960	39.49	14.3	1457.39	1258.56	12.95	24.60	12.91	20.54
Tall	Stabelchod	2	Marmot, Mouse, Insect	1960	39.49	14.3	883.90	1301.70	12.70	20.53	12.21	16.40
Tall	Stabelchod	2	Mouse, Insect	1960	39.49	14.3	1325.85	1110.19	12.60	21.00	11.70	15.54
Tall	Stabelchod	2	Insect	1960	39.49	14.3	878.64	1211.10	12.28	21.87	11.81	20.91
Tall	Stabelchod	2	None	1960	39.49	14.3	599.79	920.94	11.76	27.27	11.17	23.69
Short	Stabelchod	3	All	1960	39.49	14.3	584.01	662.93	14.04	26.07	14.73	21.14
Short	Stabelchod	3	Marmot, Mouse, Insect	1960	39.49	14.3	373.55	769.84	14.20	27.40	14.67	20.43
Short	Stabelchod	3	Mouse, Insect	1960	39.49	14.3	394.60	580.90	14.78	38.60	14.69	29.43
Short	Stabelchod	3	Insect	1960	39.49	14.3	683.97	713.44	14.50	31.33	15.44	17.74
Short	Stabelchod	3	None	1960	39.49	14.3	352.51	952.98	13.84	38.73	13.66	26.74
Tall	Stabelchod	4	All	1960	39.49	14.3	731.32	1591.55	12.88	37.93	12.14	22.94
Tall	Stabelchod	4	Marmot, Mouse, Insect	1960	39.49	14.3	1373.20	1013.23	13.06	25.60	11.80	22.23
Tall	Stabelchod	4	Mouse, Insect	1960	39.49	14.3	478.78	1407.56	12.58	23.53	12.29	18.80
Tall	Stabelchod	4	Insect	1960	39.49	14.3	694.49	1223.63	13.04	29.73	11.99	20.80
Tall	Stabelchod	4	None	1960	39.49	14.3	694.49	1096.04	12.60	28.27	11.91	20.60
Short	Stabelchoddadaint	5	All	2125	40.19	14.45	452.47	965.45	14.94	43.93	13.56	32.91
Short	Stabelchoddadaint	5	Marmot, Mouse, Insect	2125	40.19	14.45	320.94	961.72	13.34	32.73	12.30	25.69
Short	Stabelchoddadaint	5	Mouse, Insect	2125	40.19	14.45	278.85	703.91	14.20	55.73	12.56	34.77
Short	Stabelchoddadaint	5	Insect	2125	40.19	14.45	726.06	629.04	13.98	52.20	12.47	35.66
Short	Stabelchoddadaint	5	None	2125	40.19	14.45	810.24	519.71	14.28	43.53	12.41	32.11
Tall	Stabelchoddadaint	6	All	2125	40.19	14.45	1425.82	1227.83	15.68	16.87	13.73	16.14
Tall	Stabelchoddadaint	6	Marmot, Mouse, Insect	2125	40.19	14.45	2362.33	980.50	13.62	34.07	12.74	21.31
Tall	Stabelchoddadaint	6	Mouse, Insect	2125	40.19	14.45	999.65	838.32	13.68	21.67	12.73	18.74
Tall	Stabelchoddadaint	6	Insect	2125	40.19	14.45	915.47	991.92	13.22	19.53	12.60	16.31
Tall	Stabelchoddadaint	6	None	2125	40.19	14.45	894.42	1331.96	13.48	33.93	12.10	25.34

Grass type	Grassland	Fence	Treatment	Elevation (m)	North exposition (x° x`)	East exposition (x°x`)	Root biomass 2009 (g.m-2)	Root biomass 2010 (g.m-2)	Soil temperature 2009 (°C)	Soil moisture 2009 (%)	Soil temperature 2010 (°C)	Soil moisture 2010 (%)
Short	Margunet	7	All	2328	40.29	14.39	1157.49	1227.57	11.62	40.00	12.26	25.23
Short	Margunet	7	Marmot, Mouse, Insect	2328	40.29	14.39	720.80	891.16	12.78	36.47	12.41	32.51
Short	Margunet	7	Mouse, Insect	2328	40.29	14.39	1289.02	1332.48	11.96	45.27	11.53	32.63
Short	Margunet	7	Insect	2328	40.29	14.39	1068.05	1467.01	12.24	42.13	11.99	31.77
Short	Margunet	7	None	2328	40.29	14.39	705.02	1664.58	11.88	53.73	11.64	34.09
Tall	Margunet	8	All	2328	40.29	14.39	494.56	1410.88	12.36	53.33	11.54	32.69
Tall	Margunet	8	Marmot, Mouse, Insect	2328	40.29	14.39	2130.83	1011.75	11.64	54.60	10.81	33.14
Tall	Margunet	8	Mouse, Insect	2328	40.29	14.39	478.78	1159.23	11.22	53.93	10.13	33.66
Tall	Margunet	8	Insect	2328	40.29	14.39	363.03	911.21	10.94	55.07	10.11	40.91
Tall	Margunet	8	None	2328	40.29	14.39	284.11	902.05	11.54	54.20	10.43	36.89
Short	ValdalBotsch	9	All	2065	40.25	13.55	447.21	487.41	15.66	14.87	15.61	14.60
Short	ValdalBotsch	9	Marmot, Mouse, Insect	2065	40.25	13.55	310.42	387.44	15.34	31.13	14.23	22.91
Short	ValdalBotsch	9	Mouse, Insect	2065	40.25	13.55	815.50	691.50	15.98	16.00	15.34	17.09
Short	ValdalBotsch	9	Insect	2065	40.25	13.55	952.30	1306.70	15.30	19.53	14.93	20.37
Short	ValdalBotsch	9	None	2065	40.25	13.55	331.46	757.68	15.48	24.60	13.96	26.06
Tall	ValdalBotsch	10	All	2065	40.25	13.55	768.15	1050.95	13.88	15.33	13.74	17.43
Tall	ValdalBotsch	10	Marmot, Mouse, Insect	2065	40.25	13.55	794.46	961.56	14.04	18.07	13.70	23.09
Tall	ValdalBotsch	10	Mouse, Insect	2065	40.25	13.55	999.65	2044.50	12.86	22.00	13.19	23.60
Tall	ValdalBotsch	10	Insect	2065	40.25	13.55	804.98	1588.23	13.66	20.00	13.41	22.46
Tall	ValdalBotsch	10	None	2065	40.25	13.55	673.45	624.31	12.24	31.13	11.63	28.63
Short	Grimmels	11	All	2015	39.55	11.18	699.76	998.97	15.70	31.40	15.30	25.60
Short	Grimmels	11	Marmot, Mouse, Insect	2015	39.55	11.18	799.72	732.01	16.62	14.20	15.57	18.71
Short	Grimmels	11	Mouse, Insect	2015	39.55	11.18	568.22	624.41	16.18	17.67	15.47	22.26
Short	Grimmels	11	Insect	2015	39.55	11.18	573.48	1135.02	16.86	11.47	15.67	19.71
Short	Grimmels	11	None	2015	39.55	11.18	347.25	1272.71	15.84	19.67	14.77	28.29
Tall	Grimmels	12	All	2015	39.55	11.18	531.39	643.99	16.56	16.40	15.77	21.34
Tall	Grimmels	12	Marmot, Mouse, Insect	2015	39.55	11.18	778.68	1538.09	16.76	17.80	15.77	19.57
Tall	Grimmels	12	Mouse, Insect	2015	39.55	11.18	789.20	1387.67	15.88	20.87	14.40	15.26
Tall	Grimmels	12	Insect	2015	39.55	11.18	405.12	1547.35	16.84	17.80	15.86	19.97
Tall	Grimmels	12	None	2015	39.55	11.18	468.26	785.88	16.36	25.60	13.97	20.17
Short	Grimmels	13	All	2015	39.55	11.18	526.13	993.44	14.50	20.40	14.19	20.14
Short	Grimmels	13	Marmot, Mouse, Insect	2015	39.55	11.18	741.85	1504.69	15.48	22.47	14.67	22.14
Short	Grimmels	13	Mouse, Insect	2015	39.55	11.18	547.18	1106.77	15.32	20.67	14.39	22.20
Short	Grimmels	13	Insect	2015	39.55	11.18	673.45	825.92	14.40	19.93	13.57	21.77
Short	Grimmels	13	None	2015	39.55	11.18	847.07	850.49	14.08	28.87	13.89	29.14
Tall	Grimmels	14	All	2015	39.55	11.18	705.02	1972.78	13.56	29.47	13.56	27.06
Tall	Grimmels	14	Marmot, Mouse, Insect	2015	39.55	11.18	768.15	1070.42	12.42	24.67	12.44	21.77
Tall	Grimmels	14	Mouse, Insect	2015	39.55	11.18	668.19	849.60	12.16	22.20	11.90	19.43
Tall	Grimmels	14	Insect	2015	39.55	11.18	541.92	1266.35	11.48	22.07	11.24	21.49
Tall	Grimmels	14	None	2015	39.55	11.18	689.23	1160.91	12.36	26.87	11.47	25.46

Grass type	Grassland	Fence	Treatment	Elevation (m)	North exposition (x° x`)	East exposition (x°x`)	Root biomass 2009 (g.m-2)	Root biomass 2010 (g.m-2)	Soil temperature 2009 (°C)	Soil moisture 2009 (%)	Soil temperature 2010 (°C)	Soil moisture 2010 (%)
Short	Minger	15	All	2090	42.27	15.42	399.86	355.61	12.66	44.93	11.79	35.51
Short	Minger	15	Marmot, Mouse, Insect	2090	42.27	15.42	326.20	404.65	12.24	45.67	12.26	35.57
Short	Minger	15	Mouse, Insect	2090	42.27	15.42	562.96	453.05	13.96	43.80	13.36	32.00
Short	Minger	15	Insect	2090	42.27	15.42	536.65	533.66	12.68	45.40	11.49	40.37
Short	Minger	15	None	2090	42.27	15.42	484.04	876.90	12.28	41.27	10.44	42.91
Tall	Minger	16	All	2090	42.27	15.42	689.23	1316.75	11.80	40.27	11.24	41.51
Tall	Minger	16	Marmot, Mouse, Insect	2090	42.27	15.42	573.48	872.38	12.90	42.07	11.73	41.51
Tall	Minger	16	Mouse, Insect	2090	42.27	15.42	478.78	1750.76	13.14	38.53	10.94	49.71
Tall	Minger	16	Insect	2090	42.27	15.42	457.73	836.60	13.60	36.40	11.20	42.89
Tall	Minger	16	None	2090	42.27	15.42	447.21	883.64	13.94	24.13	11.19	36.40
Short	Minger	17	All	2090	42.27	15.42	689.23	553.39	13.94	22.93	14.47	22.97
Short	Minger	17	Marmot, Mouse, Insect	2090	42.27	15.42	389.34	416.17	14.16	19.33	14.10	21.37
Short	Minger	17	Mouse, Insect	2090	42.27	15.42	515.61	544.81	12.80	34.33	12.77	31.71
Short	Minger	17	Insect	2090	42.27	15.42	678.71	321.62	12.74	31.13	11.96	29.06
Short	Minger	17	None	2090	42.27	15.42	484.04	558.23	13.46	22.73	13.00	25.46
Tall	Minger	18	All	2090	42.27	15.42	463.00	645.09	13.96	32.87	13.24	34.51
Tall	Minger	18	Marmot, Mouse, Insect	2090	42.27	15.42	720.80	542.28	12.16	41.80	12.11	38.49
Tall	Minger	18	Mouse, Insect	2090	42.27	15.42	662.93	520.92	11.52	44.60	11.00	34.83
Tall	Minger	18	Insect	2090	42.27	15.42	484.04	848.49	12.46	44.93	11.81	30.74
Tall	Minger	18	None	2090	42.27	15.42	463.00	972.40	11.60	44.40	10.96	44.80

Appendix B: Result tables

Normality tests

Table S2: Tests of normality for root biomass and ln root biomass.

Tests of Normality

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	df	Sig.
Root biomass (g.m-2)	.100	180	.000	.920	180	.000
ln root biomass	.040	180	.200*	.992	180	**.408**

a. Lilliefors Significance Correction
*. This is a lower bound of the true significance.

Linear Mixed Model of the unsplit data

Table S3: Type III Tests of Fixed Effects using ln root biomass (g.m^{-2}) as the dependent variable.

Type III Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	16	14630.507	.000
Grass type	1	16	7.516	**.014**
Treatment	4	144	.845	.499
Year	1	144	63.903	**.000**
Grass type * Treatment	4	144	3.931	**.005**
Grass type * Year	1	144	.906	.343
Treatment * Year	4	144	1.413	.232
Grass type * Treatment * Year	4	144	2.688	**.034**

a. Dependent Variable: ln root biomass.

Correlation with abiotic factors

Table S4: Spearman's correlation coefficient for 2009.

Correlations

Grass type				Soil moisture 2009	Soil temperature 2009
Short	Spearman's rho	ln root biomass 2010	Correlation Coefficient	-.047	-.076
			Sig. (2-tailed)	.761	.621
			N	45	45
Tall	Spearman's rho	ln root biomass 2010	Correlation Coefficient	**-.385**[**]	.193
			Sig. (2-tailed)	.009	.204
			N	45	45

**. Correlation is significant at the 0.01 level (2-tailed).

Mixed Linear Model of the split data – grass type as a fixed effect

Table S5: Type III Tests of Fixed Effects for 2009.

Type III Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	88	22350.32	.000
Grass type	1	88	8.83	**.004**

a. Dependent Variable: ln root biomass 2009.

Table S6: Type III Tests of Fixed Effects for 2010.

Type III Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	88	31818.29	.000
Grass type	1	88	20.38	**.000**

a. Dependent Variable: ln root biomass 2010.

Mixed Linear Model of the split data - treatment as a fixed effect

Table S7: Type III Tests of Fixed Effects for 2009.

Type III Tests of Fixed Effects[a]

Grass type	Source	Numerator df	Denominator df	F	Sig.
Short	Intercept	1	8	5881.701	.000
	Treatment	4	32	2.076	.107
Tall	Intercept	1	8	4490.753	.000
	Treatment	4	32.000	5.713	**.001**

a. Dependent Variable: ln root biomass 2009.

Table S8: Pairwise Comparisons for tall grass, for 2009.

Pairwise Comparisons[b]

Grass type	(I) Treatment	(J) Treatment	Mean Difference (I-J)	Std. Error	df	Sig.[a]	95% Confidence Interval for Difference[a]	
							Lower Bound	Upper Bound
Tall	All	Marmot, Mouse, Insect	-.317	.143	32	.341	-.750	.115
		Mouse, Insect	.034	.143	32	1.000	-.398	.466
		Insect	.240	.143	32	1.000	-.192	.673
		None	.297	.143	32	.464	-.135	.729
	Marmot, Mouse, Insect	All	.317	.143	32	.341	-.115	.750
		Mouse, Insect	.351	.143	32	.199	-.081	.784
		Insect	.558*	.143	32	**.005**	.125	.990
		None	.614*	.143	32	**.002**	.182	1.047
	Mouse, Insect	All	-.034	.143	32	1.000	-.466	.398
		Marmot, Mouse, Insect	-.351	.143	32	.199	-.784	.081
		Insect	.206	.143	32	1.000	-.226	.639
		None	.263	.143	32	.759	-.169	.695
	Insect	All	-.240	.143	32	1.000	-.673	.192
		Marmot, Mouse, Insect	-.558*	.143	32	**.005**	-.990	-.125
		Mouse, Insect	-.206	.143	32	1.000	-.639	.226
		None	.057	.143	32	1.000	-.376	.489
	None	All	-.297	.143	32	.464	-.729	.135
		Marmot, Mouse, Insect	-.614*	.143	32	**.002**	-1.047	-.182
		Mouse, Insect	-.263	.143	32	.759	-.695	.169
		Insect	-.057	.143	32	1.000	-.489	.376

Based on estimated marginal means

a. Adjustment for multiple comparisons: Bonferroni.
*. The mean difference is significant at the .05 level.
b. Dependent Variable: ln root biomass 2009.

Table S9: Univariate tests for 2009.

Univariate Tests[a]

Grass type	Numerator df	Denominator df	F	Sig.
Short	4	32	2.076	.107
Tall	4	32	5.713	**.001**

The F tests the effect of Treatment. This test is based on the linearly independent pairwise comparisons among the estimated marginal means.

a. Dependent Variable: ln root biomass 2009.