Grazing-induced changes in plant-soil feedback alter plant biomass allocation

G.F. (Ciska) Veen¹²³*, Saskia de Vries¹, Elisabeth S. Bakker⁴, Wim H. van der Putten²⁵, Han Olff³

¹ Community and Conservation Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC, Groningen, The Netherlands
² Department of Terrestrial Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB, Wageningen, The Netherlands
³ Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE901-83 Umeå, Sweden
⁴ Department of Aquatic Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB, Wageningen, The Netherlands
⁵ Laboratory of Nematology, Wageningen University and Research Centre, P.O. Box 8123, 6700 ES, Wageningen, The Netherlands

* Corresponding author
E-mail: ciska.veen@gmail.com

Running head: Vertebrate herbivores and plant-soil feedback
Abstract (248 words)

Large vertebrate herbivores, as well as plant-soil feedback interactions are important drivers of plant performance, plant community composition and vegetation dynamics in terrestrial ecosystems. However, it is poorly understood whether and how large vertebrate herbivores and plant-soil feedback effects interact. Here, we study the response of grassland plant species to grazing-induced legacy effects in the soil and we explore whether these plant responses can help us to understand long-term vegetation dynamics in the field.

In a greenhouse experiment we tested the response of four grassland plant species, *Agrostis capillaris* (L.), *Festuca rubra* (L.), *Holcus lanatus* (L.), and *Rumex acetosa* (L.), to field-conditioned soils from grazed and ungrazed grassland. We relate these responses to long-term vegetation data from a grassland exclosure experiment in the field.

In the greenhouse experiment, we found that total biomass production and biomass allocation to roots was higher in soils from grazed than from ungrazed plots. There were only few relationships between plant production in the greenhouse and the abundance of conspecifics in the field. Spatiotemporal patterns in plant community composition were more stable in grazed than ungrazed grassland plots, but were not related to plant-soil feedbacks effects and biomass allocation patterns.

We conclude that grazing-induced soil legacy effects mainly influenced plant biomass allocation patterns, but could not explain altered vegetation dynamics in grazed grasslands. Consequently, the direct effects of grazing on plant community composition (e.g. through modifying light competition or differences in grazing tolerance) appear to overrule indirect effects through changes in plant-soil feedback.
Introduction

In grasslands worldwide, aboveground vertebrate herbivores are key drivers of vegetation composition and dynamics (e.g. Hobbs 1996; Olff and Ritchie 1998; Bakker et al. 2006). At the same time feedback effects between plants and their biotic and abiotic soil environment influence plant performance and structure plant communities (e.g. Bever et al. 1997; van der Putten and Peters 1997; Ehrenfeld et al. 2005), and aboveground herbivory and plant-soil feedback interact with each other (Wardle et al. 2004). However, little is known on how grazing and plant-soil feedback may interact. Here, we study plant-soil feedback effects in grazed grassland in comparison with experimental plots within the grassland where grazers had been excluded.

It has long been recognized that large herbivores speed up or slow down soil nutrient cycling (Bardgett and Wardle 2003), which results in positive or negative feedback effects on plant performance (McNaughton et al. 1997; Ritchie et al. 1998; Hamilton and Frank 2001; Mikola et al. 2009; Medina-Roldan et al. 2012). Moreover, long-lasting changes in soil conditions by grazing and defoliation can modify plant competitive interactions (Medina-Roldan et al. 2012) and nutrient allocation and acquisition (Mikola et al. 2005; Sørensen et al. 2008; Mikola et al. 2009). These studies indicate that plants perform differently in soils from grazed and ungrazed grasslands. However, it is not well understood how grazing modifies the response of plant species to soils where conspecifics have been growing and how this affects long-
term vegetation dynamics. Many grassland plant species perform worse in soils conditioned by conspecific plants than in soils where heterospecific species have been dominant (Olff et al. 2000; Kulmatiski et al. 2008), due to the buildup of species-specific root herbivores and pathogens (van der Putten et al. 1993; Bever 2003).

The aim of our study was to investigate (1) whether plant-soil feedback effects differ between soils from grazed and ungrazed grasslands, (2) whether plant-soil feedback effects determined under controlled conditions are related to the abundance of conspecific plant species in the field in soils from grazed and ungrazed grasslands, and (3) whether spatiotemporal vegetation patterns of plant species in grazed and ungrazed grasslands may be explained by grazing-induced changes in plant-soil feedback.

Our first hypothesis was that herbivores alter plant performance via legacy effects in the soil. Herbivores may increase or reduce plant growth via changes in nutrient cycling (McNaughton et al. 1997; Hamilton and Frank 2001; Bardgett and Wardle 2003) and direct interactions between roots and soil organisms (Todd et al. 1992; Allsopp 1998; Mikola et al. 2009). Our second hypothesis was that plants build up species-specific negative plant-soil feedback (van der Putten et al. 1993; Bever et al. 1997; Bever 2003; Kulmatiski et al. 2008). As a result, plants will perform worse in soils where conspecific plants were abundant in the field (Mangan et al. 2010).

Finally, we hypothesized that spatiotemporal vegetation patterns become more dynamic if herbivores promote negative plant-soil feedback, because negative plant-soil feedback reduces the competitive ability of plants leading to increased species turnover (van der Putten and Peters 1997; Olff et al. 2000; Bever 2003; Revilla et al. 2013).
We tested the hypotheses by analyzing the responses of four grassland species in field-conditioned soils from grazed and ungrazed grassland plots under controlled greenhouse conditions. We then related this greenhouse response of plants to the past and present abundance of conspecifics in the field experiment. Finally, we explored whether these plant-soil feedback patterns could help in explaining spatiotemporal dynamics of plant species in a long-term grazing experiment in the field. In the discussion we propose mechanisms through which grazing may alter plant-soil feedback effects.

Methods

Study site

We performed our study in Junner Koeland, a 100-ha nature reserve along the river Overijsselse Vecht in the north-east of the Netherlands (52°32’N, 6°36’E). Our experiment was situated on a 50-ha floodplain, which used to be flooded regularly until canalization of the river Vecht (around 1910) and regulation of the water level. The Junner Koeland was common grazing land, used by farmers from the village Junne, and has been grazed extensively by livestock for centuries. Nowadays, it is managed as a nature reserve by the National Forestry Service (Staatsbosbeheer), and is grazed by cattle (Bos taurus (Bojanus, 1827)) from April till November at stocking rates of about 0.3 animals ha⁻¹. The most abundant wild larger vertebrate herbivores in the area are European rabbits (Oryctolagus caniculus (Linnaeus, 1758)) (Bakker et al. 2009). Dominant plant species in the grasslands are the graminoids Agrostis capillaris, Festuca rubra, Holcus lanatus, and Luzula campestris (L.). Frequently occurring dicots are Rumex acetosa and Trifolium repens (L.) (nomenclature follows van der Meijden 2005).
Field experiment

In 1994, we established a long-term exclosure experiment to study the plant community response to vertebrate grazing. We created 5 randomly established blocks, with 2 different grazing treatments per block. Each block contained a 12 m x 12 m chicken-wire fenced exclosure plot from which cattle and rabbits were excluded (“ungrazed”), and a plot of 12 m x 12 m to which all larger herbivores had free access (“grazed”). Within each plot 4 permanent subplots of 2 m x 2 m were established to record long-term vegetation responses to combined grazing by cattle and rabbits. All subplots were positioned at least 1 m from the fences to avoid edge effects. In each of the 2 m x 2 m subplots, we recorded plant species composition from 1995-2001 and from 2005-2008 at peak standing biomass (in July-August). We estimated cover of each plant species visually according to the decimal Londo scale (Londo 1976).

Greenhouse experiment

We grew four dominant plant species in undiluted field soil from the permanent subplots of the field experiment to determine their growth potential in field soil. We defined dominant plant species as species that across all years and plots had an average cover of >10% in at least one of the grazing treatments. We selected the grasses *Agrostis capillaris*, *Festuca rubra*, *Holcus lanatus* and the forb *Rumex acetosa*. *Agrostis* and *Festuca* are abundant in grazed plots, while *Holcus* and *Rumex* are abundant in ungrazed plots. Seeds of *Holcus* and *Rumex* were collected in the Junner Koeland area. Seeds of *Agrostis* and *Festuca* were purchased from the Cruydt-hoeck (Assen, The Netherlands). Seeds were germinated on sterile glass beads in plastic containers in the greenhouse three weeks prior to the start of the experiment.
In the fall of 2006 we collected approximately 6 kg of soil of the top 15 cm from each of the grazed and ungrazed 2 m x 2 m subplots from the Junner Koeland exclosure experiment using a soil core. In total we used 40 subplots (5 blocks x 2 grazing treatments x 4 subplots). We gently homogenized the 6 kg of soil per subplot, removed large roots and divided it over four 1500 ml pots, resulting in a total of 160 pots in the greenhouse experiment (40 subplots x 4 plant species). In each of these pots we planted four seedlings of each of the plant species in monoculture.

Pots were placed in the greenhouse at a day/night rhythm of 15/9h at temperatures of 21/15ºC respectively. Soil moisture content in all pots was kept constant at 25% w/w by watering 2-3 times per week using demineralized water. To account for possible light and temperature differences within the greenhouse the position of the pots was randomized once a week. Pots in the greenhouse were arranged in a randomized block design so that pots containing soil from the same subplot and block in the field were kept in one block in the greenhouse. The plants did not receive nutrients during the experiment, because this could modify the response of the plants to pure field soil.

After 12 weeks we harvested shoot biomass and used half of the soil from each pot to measure root biomass. Roots were washed with tap water. Shoot and root biomass were dried at 70ºC for 48 hours and weighed. Total root biomass per pot was calculated by multiplying by 2.

Data analysis

We determined the growth of each plant species in the greenhouse as total biomass (root + shoot biomass), shoot biomass and root biomass per pot. In addition, we
calculated the ratio shoot biomass/total biomass (shoot weight ratio; SWR), to
determine what proportion of the biomass was allocated aboveground.

For each of the four dominant plant species we calculated temporal stability in
the field as the average cover of a plant species over different years in an individual
plot divided by the standard deviation (Bezemer and van der Putten 2007). Spatial
stability in the field was calculated as the average cover of a plant species over the
four subplots within one grazing treatment within a block divided by the standard
deviation. This resulted in 5 replicate spatial stability measures per grazing treatment
for each year.

To test the influence of grazing treatment and plant species on biomass
production, SWR, and vegetation stability, we used general linear mixed models with
each of the respective measures as response variables. We used plant species and
grazing treatment as fixed factors and subplot and block as random factors. When
testing spatial stability we used block and year as a random factor.

For each of the plant species, we used a Pearson’s correlation analyses to
determine the relationship between greenhouse biomass production and field
abundance in the year previous to (2005) and the year of (2006) the greenhouse
experiment. A negative correlation between greenhouse biomass and field abundance
indicates a negative plant-soil feedback. When plants in the field build up species-
specific soil pathogens, plant performance in the greenhouse experiment will be
reduced. In contrast, a positive correlation indicates that species-specific soil
conditions favor plant growth. If plants in the field grow in spots where species-
specific biotic and abiotic conditions stimulate plant performance, conspecifics in the
greenhouse may also perform well. We test the year previous to the experiment to
account for legacy effects of plant species on soil conditions. P-values were corrected
using a sequential Bonferroni correction for multiple testing. $P$-values were ranked from largest to smallest and regarded significant when $P < \alpha/k$, where $\alpha$ is 0.05, and $k$ the rank of the $P$-value.

All data were analyzed using R, version 2.14. We implemented the lme4 package (Bates and Maechler 2009) for general linear mixed models. We used maximum likelihood estimation and determined effects of our fixed factors by comparing models with and without the variable of interest with a chi-square test statistic (Crawley 2007).

**Results**

*Plant biomass and root-shoot allocation*

Total plant biomass was higher in soils from grazed plots than in soils from ungrazed plots (Table 1). Shoot and root biomass responses to soils from grazed and ungrazed plots differed among plant species (Table 1). Shoot biomass was lower in soils from grazed plots for *Holcus* and *Rumex*, but not for *Agrostis* and *Festuca* (Fig 1a). Root biomass was higher in soils from grazed plots than from ungrazed plots for *Agrostis*, *Festuca* and *Holcus*, but not for *Rumex* (Fig 1b). Plant species allocated more biomass aboveground in soils from ungrazed plots than from grazed plots, indicated by a significantly higher SWR for all species (Table 1, Fig 1c). Total-, root- and shoot biomass, as well as the SWR, were different among plant species (Table 1, Fig 1).

*Relationship between plant biomass and field abundance*

Biomass production of *Holcus* in the greenhouse was positively related to the abundance in the field in 2005 in soils from grazed plots. It tended to be positively related to abundance in the field in 2006, while it tended to be negatively related to
field cover in ungrazed plots, but both relationships were not significant. Biomass of *Rumex* tended to be positively related to 2005-field cover in grazed plots only (Table 2).

**Temporal and spatial plant community stability**

In the field, the cover of the four dominant plant species changed over time (Fig 2). Both spatial and temporal stability were higher for *Agrostis* and *Festuca* than for *Holcus* and *Rumex* (Figs 3, 4). Grazing treatment affected the stability of these species differently (Table 4, Figs 3, 4). *Agrostis*, *Festuca* and *Rumex* were more stable over time under grazing by large herbivores, while the stability of *Holcus* was not different between grazed and ungrazed plant communities (Fig 3). Spatial stability of *Agrostis* and *Festuca* was higher in grazed than in ungrazed plots, while for *Holcus* and *Rumex* there was no difference between grazing treatments (Fig 4).

**Discussion**

**Plant biomass and root-shoot allocation**

In accordance with our first hypothesis we found that grazing-induced soil legacy effects altered plant growth. Plant biomass increased on soils with a grazing history, which is in line with many previous studies (McNaughton et al. 1997; Hamilton and Frank 2001; Mikola et al. 2009; Medina-Roldan et al. 2012). However, in our study this effect appeared very small for most of the plant species (Fig 1a, b) and hence may not be ecologically relevant for driving vegetation dynamics. The influence of grazing on plant biomass allocation patterns was more pronounced (Fig 1c). Previous work already showed that plants can allocate resources differently as a direct response to grazing (Holland et al. 1996) and that grazing-induced legacy effects in the soil can
increase nitrogen allocation (Mikola et al. 2005) and biomass allocation to shoots (Medina-Roldan et al. 2012). We now show that grazing-induced changes in soil properties can also feedback to increase biomass allocation to roots (Fig 1c).

We did not test how grazing altered plant-soil feedback effects on plant biomass allocation, but there are two potential mechanisms that may explain this effect. First, plant-soil feedback effects on biomass allocation can optimize the ability of plants to compete for limiting resources (te Beest et al. 2009). Indeed, we found increased biomass allocation to roots, which may enhance the competitive ability of plants for nutrients (Wilson 1988; Aerts et al. 1991; Casper and Jackson 1997) in soils from grazed plots where nitrogen mineralization has been shown to be slower (Bakker et al. 2004; Veen et al. 2010). At the same time, increased biomass allocation to shoots in soils from ungrazed plots increases the competitive abilities of plants for light, which may be a limiting factor under ungrazed conditions (Bakker and Olff 2003). Alternatively, reduced biomass allocation to roots may occur when belowground grazing and pathogen pressure is lower (Holah and Alexander 1999).

We did not find evidence for reduced belowground grazing pressure in our study system, as the abundance of plant-feeding nematodes was not different between grazed and ungrazed plots (Veen et al. 2010). Therefore, it appears that altered biomass allocation in response to grazing-induced soil legacy effects was mainly mediated via abiotic pathways. However, in order to fully understand what drives the altered biomass allocation in response to grazing-induced changes in soil conditions it will be necessary to quantify the contribution of soil biotic and abiotic factors to plant-soil feedback in more detail in future experiments.

Our greenhouse experiment lasted for 12 weeks, but we do not believe that this limited the potential of plant species to respond to grazing-induced soil legacy
effects (Fig 1 a, b). Most plant-soil feedback experiments that used field-conditioned soils had growing periods between 6 and 15 weeks and are able to detect strong plant-soil feedback effects (e.g. van der Putten et al. 1993; Bezemer et al. 2006; Mikola et al. 2009).

**Relationship between plant biomass and field abundance**

Although we expected to find negative plant-soil feedback effects for most of our species (Kulmatiski et al. 2008), we only found a tendency for a negative relation between greenhouse biomass and field abundance for *Holcus* in soils from ungrazed plots. In soils from grazed plots, *Holcus*, as well as *Rumex*, actually experienced a positive plant-soil feedback. These results show that grazing can alter the direction of plant-soil feedback. The negative plant-soil feedback effects on *Holcus* may play a role in ungrazed sites, because this species can become very abundant in the absence of grazing. Under such conditions species-specific root herbivores and pathogens may strongly increase and limit plant performance (van der Putten et al. 1993; Bever 2003). In contrast, positive feedback in grazed plots, where *Holcus* is not very abundant, may be explained by favorable biotic and abiotic soil conditions.

For most species we did not find a relationship between greenhouse biomass and field abundance. It is possible that these plant species were not inhibited or stimulated by species-specific soil biota. However, this was unexpected as many grassland species experience negative plant-soil feedback (Kulmatiski et al. 2008). The use of pure field soils in our greenhouse experiment may partly explain why relationships were not as strong as hypothesized. In such soils many factors, such as variation in abiotic soil properties (Bezemer et al. 2006; Manning et al. 2008; Harrison and Bardgett 2010; Schrama et al. 2013) and competitive interactions...
between plant species (Casper and Castelli 2007; Kardol et al. 2007; Medina-Roldan et al. 2012), have been proposed to interfere with the response of plant species to soil legacy effects (Brinkman et al. 2010). Moreover, we collected soils at the plot-scale, which may not concur with the landscape-scale of operation of large herbivores and with the individual plant scale at which plant-soil feedback effects operate. Finally, for *Festuca* and *Agrostis* we did not use seeds originating from the field site. The response of plant species to grazing-induced soil legacy effects might have been stronger when using seeds from the field plots, or when using transplants from grazed and ungrazed plots, as plants may genetically adapt to local environmental conditions (Linhart and Grant 1996). Indeed, previous studies found that genetically different populations of the same plant species respond differently to biotic legacy effects in the soil (Felker-Quinn et al. 2011).

**Temporal and spatial plant community stability**

We found that plant-soil feedbacks were not related to plant community stability. This is in contrast to our final hypothesis that negative plant-soil feedbacks increase vegetation dynamics, while positive plant-soil feedback increases vegetation stability (van der Putten and Peters 1997; Bever 2003; Revilla et al. 2013). Plant communities were more stable in grazed than in ungrazed grassland plots, whereas plant-soil feedback effects were generally not different between grazing treatments (Fig 1, Table 2). Only for *Holcus*, plant-soil feedback effects appeared to be more positive in soils from grazed plots (Table 2), but the stability of this species was not different between grazed and ungrazed plots (Fig 3, 4). Therefore, our results indicate that plant-soil feedback effects on plant community stability in grazed grasslands are being overridden by grazing of large herbivores (Veen and Olff 2011; Veen et al. 2012). For
moderate to high grazing intensity, foraging decisions of large herbivores result in a
homogeneous grazing pressure over large spatial scales (Ritchie and Olff 1999;
Haskell et al. 2002; Laca et al. 2010). Also, other factors, such as gap creation and
changes in soil abiotic properties through trampling may be important grazing-
induced drivers of vegetation dynamics (Medina-Roldan et al. 2012; Schrama et al.
2013).

We conclude that grazing-induced legacy effects in the soil enhanced plant biomass
allocation to roots, but had only minor impact on the strength and direction of plant-
soil feedback effects for most of the plant species. Moreover, plant-soil feedback
effects did not explain vegetation dynamics in grazed grassland. Therefore, the direct
effect of grazing on vegetation dynamics appeared more important than indirect
effects through changes in plant-soil feedback.

Acknowledgements

We would like to thank Maurits Gleichmann, Yzaak de Vries, Verena Cordlandwehr,
Harry Offringa and Carmen van der Veen for their help with collection of field data.
Thanks to Nelly Eck and Jacob Hogendorf for technical assistance in the laboratory
and greenhouse. We are grateful to the National Forest Service (Staatsbosbeheer) for
permission to perform our field work in the “Junner Koeland nature reserve”. This is
publication xxxx of the Netherlands Institute of Ecology.

References

allocation patterns and competitive ability. - Oecologia, 87: 551-559.


Table 1

Overview of general linear models testing the influence of grazing and plant species on total biomass, shoot biomass, root biomass and shoot weight ratio (SWR) for the four different plant species in the greenhouse experiment. Values in boldface represent significant effects at $P < 0.05$. Degrees of freedom are 1 for all the analyses of main factors and 3 for the analyses of two-way interaction effects.

<table>
<thead>
<tr>
<th></th>
<th>Grazing</th>
<th></th>
<th>Species</th>
<th></th>
<th>Two-way interaction</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\chi^2$</td>
<td>$P$</td>
<td>$\chi^2$</td>
<td>$P$</td>
<td>$\chi^2$</td>
<td>$P$</td>
</tr>
<tr>
<td>Total biomass</td>
<td>4.04</td>
<td>0.045</td>
<td>42.93</td>
<td>&lt;0.001</td>
<td>7.04</td>
<td>0.134</td>
</tr>
<tr>
<td>Shoot biomass</td>
<td>3.18</td>
<td>0.075</td>
<td>57.56</td>
<td>&lt;0.001</td>
<td>13.82</td>
<td>0.008</td>
</tr>
<tr>
<td>Root biomass</td>
<td>18.68</td>
<td>&lt;0.001</td>
<td>21.80</td>
<td>&lt;0.001</td>
<td>12.27</td>
<td>0.015</td>
</tr>
<tr>
<td>SWR</td>
<td>35.19</td>
<td>&lt;0.001</td>
<td>24.37</td>
<td>&lt;0.001</td>
<td>12.11</td>
<td>0.017</td>
</tr>
</tbody>
</table>
Table 2

Relationships between biomass production in the greenhouse and abundance of plant species in the field for all four plant species in the year before (2005) and the year of (2006) the experiment. $r =$ Pearson’s correlation coefficient, $P =$ $P$-value, df $=$ degrees of freedom. Values in boldface represent significant correlations at $P < 0.05/k$, where $k$ is the rank of the $P$-value (sequential Bonferroni correction). Correlations with $P < 0.10/k$ are displayed in italic.

<table>
<thead>
<tr>
<th></th>
<th>Ungrazed</th>
<th>Grazed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$P$</td>
</tr>
<tr>
<td>2005</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agrostis</td>
<td>0.47</td>
<td>0.035</td>
</tr>
<tr>
<td>Festuca</td>
<td>-0.22</td>
<td>0.366</td>
</tr>
<tr>
<td>Holcus</td>
<td>-0.62</td>
<td>0.003</td>
</tr>
<tr>
<td>Rumex</td>
<td>0.11</td>
<td>0.666</td>
</tr>
<tr>
<td>2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agrostis</td>
<td>0.10</td>
<td>0.666</td>
</tr>
<tr>
<td>Festuca</td>
<td>-0.01</td>
<td>0.965</td>
</tr>
<tr>
<td>Holcus</td>
<td>-0.61</td>
<td>0.004</td>
</tr>
<tr>
<td>Rumex</td>
<td>0.33</td>
<td>0.164</td>
</tr>
</tbody>
</table>
Table 3
Overview of general linear models testing the influence of grazing and plant species on temporal and spatial stability for the four different plant species in the field. Values in boldface represent significant differences between grazed and ungrazed treatments at $P < 0.05$. Degrees of freedom are 1 for all the analyses of main factors and 3 for the analyses of two-way interaction effects.

<table>
<thead>
<tr>
<th>Grazing</th>
<th>Species</th>
<th>Two-way interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\chi^2$</td>
<td>$P$</td>
</tr>
<tr>
<td>Temporal</td>
<td>26.91</td>
<td>$&lt;0.001$</td>
</tr>
<tr>
<td>Spatial</td>
<td>20.79</td>
<td>$&lt;0.001$</td>
</tr>
</tbody>
</table>
Figure legends

Fig 1. (a) Shoot biomass (BM) (g dry weight), (b) Root biomass (g dry weight) and (c) shoot weight ratio (SWR), expressed as the shoot biomass/total biomass, for the four plant species grown in the greenhouse in soils from grazed and ungrazed grassland communities (n = 5). Bars show mean values (±SE). Different letters indicate significant differences at $P < 0.05$.

Fig 2. Yearly cover (%) of four dominant plant species (three grasses *Agrostis capillaris*, *Festuca rubra* and *Holcus lanatus* and one herb *Rumex acetosa*) in the (a) ungrazed and (b) grazed treatments of the exclosure experiment in the field.

Fig 3. Temporal stability (average over all years/standard deviation over all years) for the four dominant plant species in the different grazing treatments of the exclosure experiment in the field. Bars show mean values (±SE). Different letters indicate significant differences at $P < 0.05$.

Fig 4. Spatial stability (average over plots within a year/standard deviation over plots within a year) for the four dominant plant species in the different grazing treatments of the exclosure experiment in the field: (a) *Agrostis capillaris*, (b) *Festuca rubra*, (c) *Holcus lanatus* and (d) *Rumex acetosa*. Dots show mean values (±SE).
Fig 1

(a) Shoot BM (gDW) for ungrazed and grazed conditions. Letters indicate significant differences.

(b) Root BM (gDW) for ungrazed and grazed conditions. Letters indicate significant differences.

(c) Shoot BM/Total BM (SWR) for different plant species: Agrostis, Festuca, Holcus, Rumex. Letters indicate significant differences.
Fig 2

(a) ungrazed
- Agrostis capillaris
- Festuca rubra
- Holcus lanatus
- Rumex acetosa

(b) grazed

Cover (%)
Year
Fig 4

(a) *Agrostis capillaris*
- ungrazed
- grazed

(b) *Festuca rubra*

(c) *Holcus lanatus*

(d) *Rumex acetosa*