

Linkages between grazing history and herbivore exclusion on decomposition rates in mineral soils of subalpine grasslands

Alan G. Haynes · Martin Schütz · Nina Buchmann ·
Deborah S. Page-Dumroese · Matt D. Busse · Anita C. Risch

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Abstract

Background & aims Herbivore-driven changes to soil properties can influence the decomposition rate of organic material and therefore soil carbon cycling within grassland ecosystems. We investigated how above-ground foraging mammalian and invertebrate herbivores affect mineral soil decomposition rates and associated soil properties in two subalpine vegetation types (short-grass and tall-grass) with different grazing histories. **Methods** Using exclosures with differing mesh sizes, we progressively excluded large, medium and small mammals

and invertebrates from the two vegetation types in the Swiss National Park (SNP). Mineral soil decomposition rates were assessed using the cotton cloth (standard substrate) method between May and September 2010.

Results Decomposition displayed strong spatio-temporal variability, best explained by soil temperature. Exclusion of large mammals increased decomposition rates, but further exclusion reduced decomposition rates again in the lightly grazed (tall-grass) vegetation. No difference among treatments was found in the heavily grazed (short-grass) vegetation. Heavily grazed areas had higher decomposition rates than the lightly grazed areas because of higher soil temperatures. Microbial biomass carbon and soil C:N ratio were also linked to spatio-temporal decomposition patterns, but not to grazing history.

Conclusions Despite altering some of the environmental controls of decomposition, cellulose decomposition rates in the SNP's subalpine grasslands appear to be mostly resistant to short-term herbivore exclusion.

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A. G. Haynes (✉) · M. Schütz · A. C. Risch
Swiss Federal Institute for Forest, Snow and Landscape
Research (WSL), Zürcherstrasse 111, 8903 Birmensdorf,
Switzerland
e-mail: alan.haynes@wsl.ch

A. C. Risch
e-mail: anita.risch@wsl.ch

N. Buchmann
Institute of Agricultural Sciences, ETH Zürich,
Universitätstrasse 2, 8092 Zürich, Switzerland

D. S. Page-Dumroese
USDA Forest Service, Rocky Mountain Research Station,
1221 South Main Street, Moscow, ID 83843, USA

M. D. Busse
USDA Forest Service, Pacific Southwest Research Station,
3644 Avtech Parkway, Redding, CA 96002, USA

Keywords Cotton decomposition rate · Soil temperature · Soil moisture · Microbial biomass carbon · C:N ratio · Soil carbon

Abbreviations

SNP	Swiss National Park
C	Carbon
N	Nitrogen
P	Phosphorus
OM	Organic matter
MBC	Microbial biomass carbon

PCA	Principal component analysis
PC	Principal component
PWP	Permanent wilting point
CTSL	Cotton tensile strength loss
CRR	Cotton rotting rate
q_{mic}	Microbial quotient (microbial C:soil C)

Introduction

The Earth's grassland soils store approximately 40 % of the world's soil carbon (C) and support a large community of herbivores, which are known to affect vegetation and ecosystem processes, including those that are linked to C cycling (White et al. 2000). By consuming plant material and therefore removing biomass, herbivory can result in both soil temperature and moisture changes (Archer and Detling 1986). Herbivores also translocate nutrients at a variety of spatial scales through excreta (Bakker et al. 2004), thereby producing heterogeneity in the abundance of soil nutrients and associated properties (e.g. nitrogen (N) mineralisation, microbial biomass). Faecal material, for instance, increases the availability of easily decomposable C (Piñeiro et al. 2010), while urine can increase N mineralisation and nitrification (Knapp et al. 1999). Such herbivore-driven changes in soil C and nutrient cycling can thus alter C turnover rates (Rossignol et al. 2011; Schmidt et al. 2011).

Over longer time frames, herbivores can also alter plant communities and plant tissue quality. Several studies have shown that productive areas intensively grazed by herbivores develop higher quality vegetation, while less productive, lightly grazed systems tend to be dominated by tougher, lower quality plant species (e.g. Bardgett and Wardle 2003; Wardle et al. 2004; Güsewell et al. 2005). These long-term effects are often a result of differences in ecosystem productivity caused by different nutrient cycling rates, with faster rates in productive compared to unproductive systems (Bardgett and Wardle 2003; Rossignol et al. 2011). In addition, herbivory affects plant tissue quality over short time frames: Grazing, for example, maintains enhanced leaf quality throughout the growing season at high but sustainable grazing intensities, while quality decreases towards the end of the growing season in systems with low grazing intensities (e.g. McNaughton 1979; Thiel-Egenter et al. 2007). Alterations in plant

quality as a result of herbivory ultimately feed back to belowground processes as higher quality litter might decompose much faster once returned to the soil. This was, for example, shown by Güsewell et al. (2005), who found that plant litter collected in long-term heavily grazed areas decomposed faster than litter collected in lightly grazed pastures.

Although the total herbivory at a site represents the combined activities of a diverse community of herbivores (Bardgett and Wardle 2003), only the effects of ungulates have been studied in relation to mineral soil OM turnover rates in grassland ecosystems (e.g. Shariff et al. 1994; Güsewell et al. 2005; Risch et al. 2007). However, several ecological processes linked to OM turnover (e.g. N mineralisation and availability) are affected by animals of different functional guilds and body size. For example, Bakker et al. (2004) found that N mineralisation rates were higher when cows (*Bos* spp.) were excluded from a grassland floodplain as the subsequent increase in vole (*Microtus arvalis*) population initiated a finer scale nutrient deposition. However, it is not known if, or to what extent, these smaller herbivores (e.g. lagomorphs, rodents, invertebrates) impact soil OM decomposition rates.

The Swiss National Park (SNP) features large (> 1 ha) homogeneous patches of two vegetation types that have developed on subalpine grasslands. Due to a combination of former land use and large herbivore grazing (mainly red deer [*Cervus elaphus* L.] and chamois [*Rupicapra rupicapra* L.]), high quality, heavily grazed vegetation has developed where cattle and sheep (*Ovis* spp.) rested during agricultural land use starting as early as the 14th century and ending with the foundation of the park in 1914 (Schütz et al. 2006). This vegetation type is typically grazed down to between 2 and 5 cm in height and is thus further referred to as short-grass vegetation. Where cattle formerly grazed but did not rest (resulting in net nutrient export), low quality, lightly grazed vegetation is predominant today (Schütz et al. 2006). This vegetation type is further referred to as tall-grass vegetation, as vegetation height frequently exceeds 20 cm. In addition to large grazers (red deer and chamois), these grasslands support a variety of other herbivores: medium sized mammals (marmots [*Marmota marmot* L.], mountain hare [*Lepus timidus* L.]), small mammals (e.g. *Clethrionomys* spp., *Microtus* spp., *Apodemus* spp.) and invertebrates (e.g. grasshoppers [Caelifera], cicadas [Cicadidae], caterpillars [Lepidoptera]), thus

enabling us to examine both the effect of progressive exclusion of functionally different herbivore guilds (using size-selective fences) and vegetation type featuring different grazing histories on cellulose decomposition in mineral soils.

The goal of our study was to assess how decomposition rates of a standard cellulose OM (cotton cloth) incubated in the mineral soil was altered when four groups of herbivores—large, medium and small mammals and invertebrates—were progressively excluded from short-grass and tall-grass vegetation of the SNP. We hypothesised that cellulose decomposition rates would be higher in soils of short- compared to tall-grass vegetation as C and nutrient cycling are generally faster in heavily grazed vegetation (Bardgett and Wardle 2003). Further, we expected decomposition rates to decrease with the progressive exclusion of herbivores in both vegetation types due to decreasing biomass consumption and resultant changes in soil temperature and moisture. We also expected that changes in microbial biomass carbon (MBC), microbial quotient (q_{mic}), soil C, N and P concentrations and soil C:N ratio due to exclusion would alter decomposition rates. By using a standard substrate (cotton cloth), OM quality was held constant and decomposition rates became a function of soil micro-climatic, chemical, biological, and physical properties.

Methods

Study region

Our study was conducted on subalpine grasslands of the SNP located in the eastern Swiss Alps between May and September 2010. Elevations within the SNP range from 1,350 to 3,170 m a.s.l., and yearly mean precipitation and temperature is 871 ± 156 mm and 0.6 ± 0.6 °C (average $\pm$ SD) measured at the Park's weather station in Buffalora (1,980 m a.s.l.) between 1960 and 2011 (MeteoSchweiz 2011). Two distinct vegetation types are currently found on the Park's subalpine grasslands: short-grass vegetation is dominated by red fescue (*Festuca rubra* L.), quaking grass (*Briza media* L.) and common bent grass (*Agrostis capillaris* L.), and tall-grass vegetation is dominated by evergreen sedge tussocks (*Carex sempervirens* Vill.) or mat grass (*Nardus stricta* L.; Schütz et al. 2006). Both vegetation types are found within the areas we used for the present

study. Herbivores grazing these grasslands were divided into four broad categories based on body size: large [red deer and chamois; 30–150 kg], medium [marmot and mountain hare; 3–6 kg], small vertebrate herbivores (small rodents; 30–100 g) and invertebrate herbivores (< 5 g).

Experimental design

Eighteen experimental sites were chosen across the SNP with nine being located on short-grass and nine on tall-grass vegetation (Appendix 1). Elevation differences between the 18 sites did not exceed 350 elevation meters and all sites were located on dolomite parent material (Appendix 1). Shortly after snowmelt in the spring of 2009, an enclosure network was established at each of the 18 sites. Each enclosure network consisted of five 2×3 m plots ("All" = no herbivores excluded; "Marmot/Mouse/Inv" = large vertebrates excluded; "Mouse/Inv" = large and medium vertebrates excluded; "Inv" = large, medium, and small vertebrates excluded; "None" = all herbivores excluded; see Appendix 2 for a schematic). The "All" plot allowed access to all animals while the remaining four plots were surrounded by a 2.1 m tall, 7×9 m electrified fence. Two centimetre wide electrified fencing bands (AGRARO Power fencing bands, Landi, Bern, Switzerland) were mounted at 0.7, 0.95, 1.2, 1.5 and 2.1 m height and powered by a solar panel connected to a 12 V battery (AGRARO Sunpower S250, Landi, Bern, Switzerland) to hinder large herbivores (red deer and chamois) from entering. We also mounted a fencing band at 0.5 m, but did not connect this to the power source to allow safe entrance for marmots and hare. One plot within this electrified enclosure remained unfenced to allow all animals except the large herbivores to graze ("Marmot/Mouse/Inv"), whilst the remaining three of the four plots were fenced with 1 m high enclosures of varying mesh size. One plot was surrounded by a 10×10 cm electric sheep-fence (AGRARO Weidezaunnetz, Landi, Bern, Switzerland) powered by the same solar panel as the 7×9 m fence excluded marmots and hare ("Mouse/Inv"). Small mammals were excluded using a galvanized metal mesh (Hortima AG, Hausen, Schweiz; mesh size 2×2 cm; "Inv"), while 1.5×2 mm mosquito mesh (Sala Ferramenta SA, Biasca, Switzerland) was used to exclude invertebrates ("None"). This enclosure plot was also covered with a roof consisting of mosquito mesh mounted on a wooden frame preventing invertebrates from jumping or crawling into the plot. Insecticide (Clean kill

original, Eco Belle GmbH, Waldshut-Tiengen, Germany) was sprayed on the “None” plot if needed to remove invertebrates that entered during data collection or emerged from the soil. Each of the 2×3 m plots were subdivided into six 1×1 m subplots. Subplots were used for different purposes (e.g. destructive vegetation and soil sampling, soil microclimate measurements, plant community composition and non-destructive biomass determination, decomposition) used throughout the entire experiment (see e.g. Risch et al. 2013). To avoid excessive damage from snow or avalanches, fence networks were removed at snowfall in October 2009 and reinstated immediately after snowmelt in May 2010.

Additional exclosures were placed outside the exclosure network at six locations for assessing the potential effects of the “None” exclosure on micro-climatic conditions. These exclosures were constructed from the same material as the “None” exclosures, but with a 20 cm wide strip of the material used for the “Inv” plots along the bottom of the eastern side (away from the prevailing weather front), allowing invertebrates to enter while still excluding anything larger (called “MCC”). Consequently, the construction assured a comparable microclimate to the “None” exclosure, but allowed invertebrates to forage. We were able to confirm that the exclusion of invertebrates affected aboveground biomass to a much greater extent than micro-climatic changes due to the installation of mosquito mesh roofs (Appendix 3): Exclusion of invertebrates and not the mosquito mesh roofs significantly increased aboveground biomass, maximum and mean vegetation height and, as a consequence, soil moisture. In contrast, UV radiation was the only parameter that was clearly and negatively influenced by the mosquito mesh roofs, apparently without major impacts on aboveground biomass.

Bi-weekly ungulate pellet counts (on two 4×25 m transects per fence; method adapted from Neff 1968) and grasshopper abundance (on ten 0.5×0.5 m quadrats per fence; method adapted from Gardiner et al. 2002; for details see Spalinger et al. 2012) showed that all sites were grazed by ungulates and invertebrates (Appendix 4). Marmot counts (conducted twice during the summer) indicated that they were also present at all sites (Appendix 4). Small mammal populations were not assessed at individual sites, and no attempt was made to quantify herbivore numbers within the individual exclosure networks. Game cameras (Moultrie 6MP Game Spy I-60 Infrared Digital Game Camera, Moultrie Feeders, Alabaster, AL, USA) were however used to ensure that herbivores were not deterred from

entering. Using this method, deer were observed nearby the exclosures, while marmots, hare and mice were observed within the exclosures. Biomass and biomass consumption values published by Risch et al. (2013) provide information on how much biomass has been consumed by each of our herbivore groups.

Decomposition

During the summer of 2010 (1 year after the fences were first erected), decomposition rates were estimated each month using the cotton cloth rotting method of Latter and Howson (1977) and Latter and Walton (1988). In each plot of the 18 sites (90 plots in total), three 20 cm wide×10 cm long sheets of 100 % unbleached cotton cloth (Daniel Jenny & Co., Haslen, Switzerland; specifications: American type SM 1/18", Warp: 34/1, Weft: 20/1, Weave plain, 29.5 picks cm⁻¹ warp, 22 picks cm⁻¹ weft, 237 g m⁻²) were inserted vertically into prepared slits in the soil to a depth of 10 cm ($n=270$ cotton strips for each monthly sample period). Each cloth was retrieved after 4 weeks and a new one inserted into the same slot. The soil on either side of the slot was then pressed back to together to ensure contact between the soil and the cloth.

To determine the change in tensile strength from insertion and extraction, five mechanical stress control cloths were inserted and immediately extracted. After removing the cloths from the soil, all excess soil was gently brushed from the cloths before they were air-dried at ambient humidity. This process was repeated each month between the end of May and the end of September resulting in four incubation periods (further referred to as month). A 20×1 cm strip containing 15 cotton threads running the length of the strip was prepared from the centre of each cloth. As the cloths were inserted width-ways into the soil, this 1 cm strip of cloth was approximately 5 cm beneath the soil surface during incubation. The strips were equilibrated at 50 % relative humidity and 20 °C for 48 h prior to tensile strength testing on a Scanpro Awetron TH-1 tensile strength tester (AB Lorentzen and Wettre, Kista, Sweden). Cloth strengths were then averaged per plot per month and tensile strength loss (CTSL) was calculated as

$$\text{CTSL} = \text{CTS}_{\text{control}} - \text{CTS}_{\text{final}}$$

where $\text{CTS}_{\text{control}}$ is the tensile strength of the control cloths and $\text{CTS}_{\text{final}}$ is the tensile strength of the incubated

cloths. The decay rate of cotton (cotton rotting rate; CRR) was then calculated according to Hill et al. (1985):

$$\text{CRR} = (\text{CTSL}/\text{CTS}_{\text{final}})^{1/3} \times (365/t)$$

where t is the incubation time in days. This function linearises the curvilinear response of tensile strength loss allowing for between site comparisons (Hill et al. 1985).

Soil properties

Soil moisture was measured in the top 12 cm of mineral soil using a Field-Scout TDR100 (Spectrum Technologies, Plainfield, IL, USA) and soil temperature with a waterproof digital thermometer (Barnstead International, Dubuque, IA, USA) every 2 weeks between late May and mid September in each plot. In September 2010, three 10 cm deep mineral soil samples were randomly collected from a 10×100 cm strip of clipped ground within each treatment plot using a 5 cm diameter×10 cm soil corer after removing the dense root layer (AMS Samplers, American Falls, ID, USA). All soil material was combined and analysed for C and N concentrations (Leco TruSpec Analyzer, Leco, St. Joseph, MI, USA), with subsequent calculation of C:N ratios for each plot. Soil P concentration was determined by the Olsen method for alkaline soil and analysed using the ascorbic acid colorimetric method (Kuo 1996). Three additional mineral soil samples were collected as described above, combined and immediately refrigerated prior to passing through a 2 mm sieve and being stored at 4 °C for microbial biomass carbon (MBC) analysis. Microbial biomass C was determined following the substrate-induced respiration procedure of Anderson and Domsch (1978). Soil MBC and C concentrations were also used to calculate the ratio of MBC to soil C (q_{mic}), which provides a measure C availability (Anderson and Domsch 1989). Soil physical characteristics (bulk density, field capacity, permanent wilting point [PWP] and texture [% clay and % sand]) were also determined using standard methods (g soil volume sample⁻¹, the pressure plate method of Klute (1986), and the hydrometer method of Gee and Bauder (1986), respectively) for each site.

Statistical analysis

A repeated measures ANOVA within a linear mixed model framework was used to test for seasonal differences on CRR (fixed effect: month; random effect: site). For this

purpose, CRR was log transformed to meet the normality criterion. Tukey's HSD test was then used to determine which months were significantly different from which others. Mixed models were conducted using the nlme package (Pinheiro et al. 2011) in R (R Development Core Team 2011).

Principle components analysis (PCA) was used to assess how CRR differed among herbivory treatments, vegetation type and site, with subsequent ANOVA performed on the PCA scores (fixed effects: treatment, vegetation type and site; site was included as a random effect when not included as a fixed effect). To assess how environmental factors affected decomposition rates, the environmental variables (soil temperature, soil moisture, MBC, soil C:N ratio, soil P, N and C concentration, q_{mic} , bulk density, texture [% clay and % sand], field capacity and PWP) and spatial variables (elevation, northing and easting) were then compared with principal components one and two (PCs) simultaneously using the envfit function in the vegan package (Oksanen et al. 2011) in R (R Development Core Team 2011). Envfit compares the ordination results with the environmental variables to find gradients through the points and assesses the significance of these gradients via permutation tests (we used 100,000 permutations). Spearman's ρ was used to assess whether average CRR was related to the environmental and spatial variables. Average CRR was considered the dependant variable and each environmental/spatial variable was the independent variable.

ANOVA within a linear mixed model framework was also used to test for differences in mean soil temperature, soil moisture, MBC, soil C:N ratio, soil N, P and C concentrations and q_{mic} among treatments and between vegetation types (fixed effects: treatment, vegetation type and the interaction between treatment and vegetation type; random effect: site). The significance of fixed effects was determined using Wald's χ^2 tests. A separate ANOVA was then performed for each vegetation type with treatment as the only fixed effect and site as a random effect. Significantly different treatments were then assessed with Tukey's HSD test.

Results

Environmental control of decomposition

Decomposition of cotton cloth was found to vary significantly in both time and space. Mineral soil cotton

rotting rate (CRR) was 9–10 % higher in August than in June and July for the short-grass vegetation, while in the tall-grass vegetation, CRR was 17–20 % higher in August and 9–11 % in September compared to June and July (Fig. 1; short-grass: $\chi^2=18.74$, $DF=3$, $P<0.001$; tall-grass: $\chi^2=32.07$, $DF=3$, $P<0.001$). Cotton rotting rate followed these temporal patterns on most plots, with a few exceptions that had high CRR in July. These plots were represented by high negative PC2 scores in the PCA (Fig. 2, Table 1). In general, the PCA revealed significantly positive correlation of average CRR with PC1 ($F_{1,85}=3317$, $P<0.001$, $R^2=0.975$), explaining 59 % of the variance in the data. Principal Component 2 explained a further 25 % of the variance, but did not significantly correlate with average CRR ($F_{1,85}=1.721$, $P=0.193$, $R^2=0.008$). Spatial variation in CRR among our 18 sites was similar to temporal variation among months. Cotton rotting rate was 24 % higher at the lower elevation, south-western sites compared with the higher elevation, north-eastern sites (Appendix 1, Figs. 2 and 3g; PC1: $F_{16,61}=6.58$, $P<0.001$, Fig. 3h; PC2: $F_{16,61}=2.36$, $P=0.004$, Fig. 3i, see also Table 2)

In general, PC1 was found to be significantly positively related to soil temperature, microbial biomass C (MBC) and q_{mic} (Fig. 2, Table 2). In contrast, we found

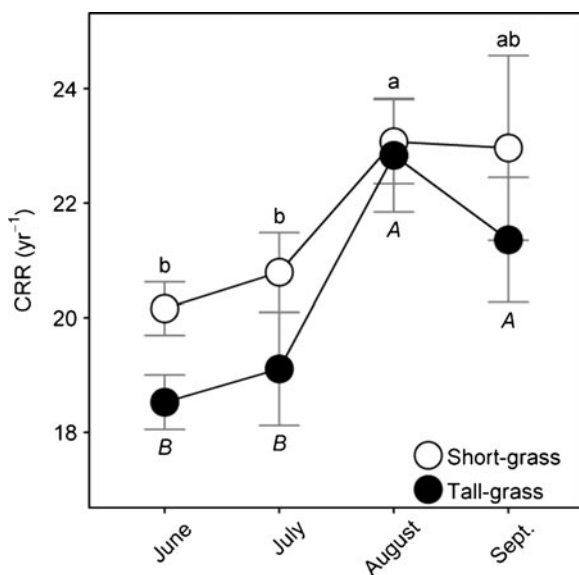


Fig. 1 Seasonal differences in cotton rotting rate (CRR) in the two vegetation types (mean $\pm$ SE, $n=45$). Capital letters denote statistically different values ($\alpha=0.05$), with different fonts for each vegetation type (lower case for short- and upper case for tall-grass vegetation)

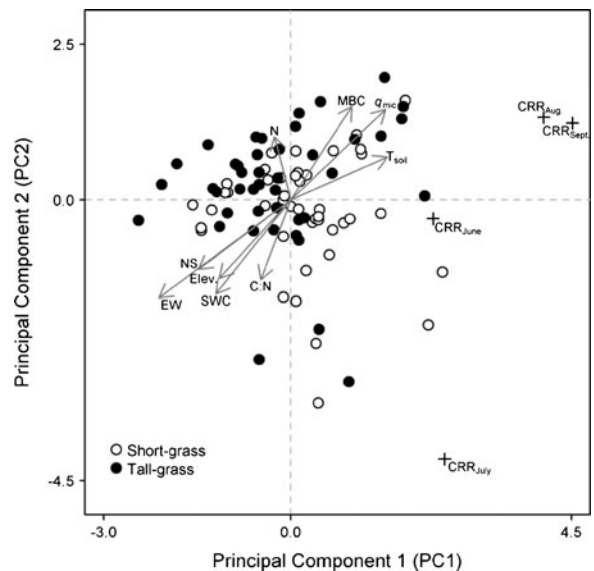


Fig. 2 Results of principal components analysis (PCA) of cotton rotting rate (CRR) in relation to environmental variables (grey arrows). Plus symbols represent the loadings of the monthly CRR measurements on the PCA axes. “ T_{soil} ” is soil temperature, “ SWC ” is soil moisture, “ MBC ” is microbial biomass carbon, “ $C:N$ ” is mineral soil C:N ratio, “ N ” is soil N concentration, “ $Elev$ ” is elevation, “ NS ” is the northing coordinate, “ EW ” is the easting coordinate and “ q_{mic} ” is the microbial quotient. Dashed horizontal and vertical lines are zero reference lines for the respective PC

negative relationships between PC1 scores and soil moisture. Soil C:N ratio and mineral soil N were positively related to PC1 and PC2, respectively (Fig. 2), but neither parameter significantly explained average CRR (Table 2). Mineral soil C and P, soil moisture retention (field capacity and PWP) and soil texture (% clay and % sand) did not significantly correlate with PCA scores (Fig. 2, Table 2). Spatial (inter-site) variability in soil temperature was up to 5.5 °C, while differences amongst months were smaller than 2.6 °C. Inter-site variability in soil moisture was as large as 24.9 % and up to 21.0 % over time.

Effects of grazing history and herbivore exclusion on soil properties and decomposition

Soil temperature was affected by grazing history as it was found to be on average 1.3 °C higher in the short-grass vegetation than the tall-grass vegetation ($\chi^2=4.39$, $DF=1$, $P=0.036$). Herbivore exclusion also altered soil temperature (Fig. 4a). Soil temperature decreased on average by 1.2 °C when all herbivores were excluded from either vegetation type (short-grass: $\chi^2=$

Table 1 Principle component loadings, eigenvalues and percentage of explained variance for principal components one and two

	PC1	PC2
CRR in June	2.28	−0.30
CRR in July	2.46	−4.15
CRR in August	4.05	1.32
CRR in September	4.51	1.23
Eigenvalue	45.30	19.43
Explained variance (%)	59.38	25.47
Cum. explained variance (%)	59.38	84.85

19.42, $DF=4$, $P<0.001$; tall-grass: $\chi^2=49.2$, $DF=4$, $P<0.001$). Conversely, soil moisture did not differ between the two vegetation types (Fig. 4b; $\chi^2=0.01$, $DF=1$, $P=0.93$), but it increased by 22 % when all

herbivores were excluded from the short-grass vegetation (Fig. 4b; $\chi^2=15.70$, $DF=4$, $P=0.003$). No effect of herbivore exclusion on soil moisture was found for the tall-grass vegetation ($\chi^2=5.39$, $DF=4$, $P=0.25$). Neither grazing history nor experimental herbivore exclusion significantly affected any of the other soil parameters measured, such as MBC (Fig. 4c), q_{mic} , concentrations of soil C, N and P as well as soil C:N ratio (Fig. 4d; all P -values >0.05).

We found that decomposition-rate patterns differed between the two vegetation types, with generally higher CRR in the short-grass compared to the tall-grass vegetation (PC1: $F_{1,61}=9.61$, $P=0.003$, Fig. 3b; PC2: $F_{1,61}=11.97$, $P=0.001$, Fig. 3c). However, against our expectations, we found no evidence of herbivore removal significantly affecting decomposition rates in short-grass vegetation (Fig. 3d; PC1: $F_{4,61}=1.38$,

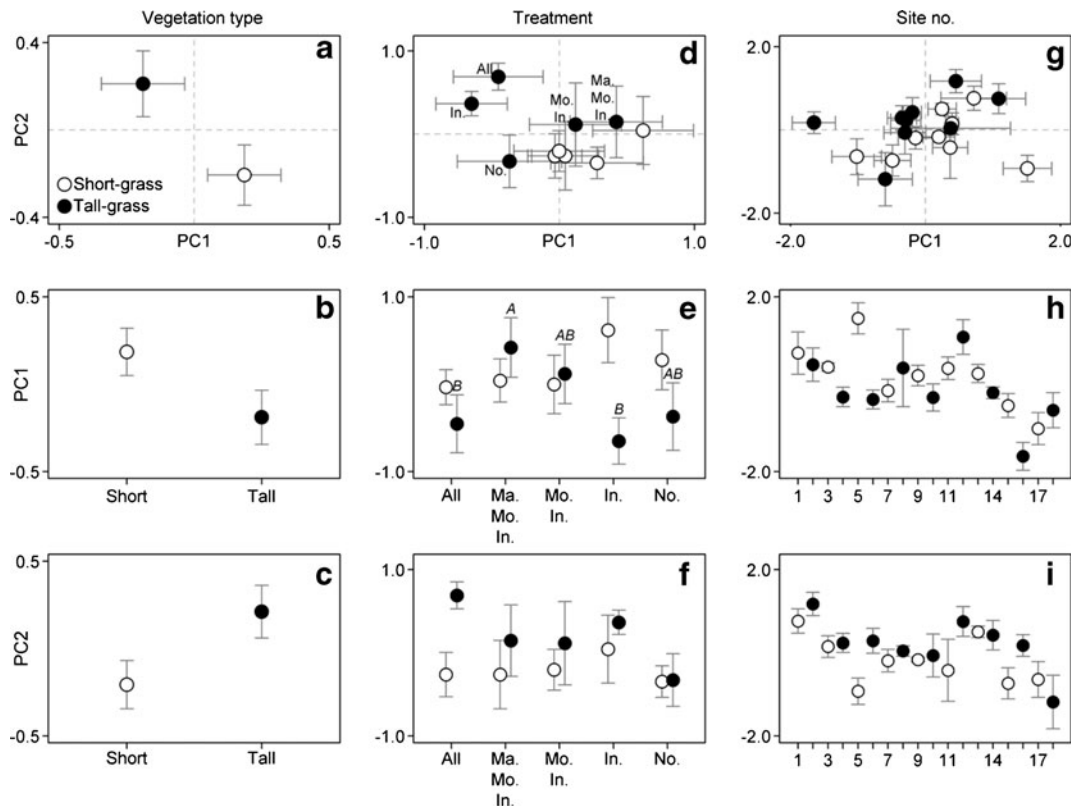


Fig. 3 Mean ($\pm$ SE) principal component (PC) scores of **a** vegetation type centroids; **b** vegetation scores on PC1; **c** vegetation scores on PC2; **d** treatment centroids; **e** treatment scores on PC1; **f** treatment scores on PC2; **g** site centroids; **h** site scores on PC1; **i** site scores on PC2. In **a**, **d** and **g**, dashed horizontal and vertical lines are zero reference lines for the respective PC.

Treatment abbreviations: “Ma.” – marmots; “Mo.” – Mouse; “In.” – Invertebrates; “No.” – None. In **d**, individual treatments are not indicated for short-grass as there was no effect of herbivore removal on patterns of decomposition. In **e**, uppercase italicised letters represent statistically different groups in the tall-grass vegetation

Table 2 Correlations between soil and spatial parameters and PCA and average CRR results

	PCA results				Average CRR	
	PC1	PC2	r^2	$P(>r)$	ρ	P
Soil temperature (°C)	0.914	0.407	0.181	< 0.001	0.395	<0.001
Soil moisture (%)	−0.624	−0.782	0.235	< 0.001	−0.227	0.035
Soil MBC (mg kg ^{−1})	0.547	0.837	0.202	< 0.001	0.216	0.045
q_{mic}	0.723	0.691	0.279	< 0.001	0.318	0.003
Mineral soil C (%)	−0.251	−0.111	0.040	0.182	−0.294	0.235
Mineral soil N (%)	−0.251	0.968	0.694	0.049	−0.086	0.430
Mineral soil C:N ratio	−0.353	−0.936	0.119	0.005	−0.062	0.569
Mineral soil P (%)	0.216	0.976	0.003	0.974	−0.068	0.533
Soil bulk density (kg m ^{−3}) ^a	0.095	0.996	0.063	0.065	0.030	0.908
Soil field capacity (%) ^a	−0.951	0.308	0.023	0.397	−0.196	0.449
Soil PWP (%) ^a	−0.921	−0.389	0.029	0.307	−0.113	0.666
Soil clay content (%) ^a	0.515	0.857	0.044	0.167	0.402	0.096
Soil sand content (%) ^a	−0.932	−0.362	0.023	0.404	−0.383	0.116
Elevation (m a.s.l.) ^a	−0.673	−0.739	0.183	< 0.001	−0.521	0.028
Nothing (NS) ^a	−0.799	−0.602	0.217	< 0.001	−0.517	0.030
Easting (EW) ^a	−0.803	−0.596	0.439	< 0.001	−0.598	0.010

PC1 and PC2 values are the correlations between the PC and the variable; PCA r^2 is the squared correlation coefficient of each soil variable with its most significant gradient through the PCA results, providing a measure of goodness-of-fit; $P(>r)$ is the proportion of times that randomised data fit as well or better than the real data, based on 100,000 permutations. ρ is Spearman's rank correlation coefficient. q_{mic} is the microbial quotient—the ratio of microbial C to soil C

^aSite averages used for Spearman's rank correlation

$P=0.25$, Fig. 3e; PC2: $F_{4,61}=1.29$, $P=0.29$, Fig. 3f). In contrast, exclusion of ungulates increased decomposition rates but further exclusion reduced them in the tall-grass vegetation (PC1: $F_{4,30}=4.02$, $P=0.01$, Fig. 3e; $F_{4,31}=1.65$, $P=0.19$, Fig. 3f).

Discussion

Environmental control of decomposition

We found that decomposition rates vary substantially both spatially and temporally as also shown in other studies (French 1988; Ineson et al. 1988; Aerts 1997; Piñeiro et al. 2010; Conant et al. 2011). This was not surprising in a mountainous area with high seasonality and abrupt changes in elevation over short horizontal distances resulting in distinct spatio-temporal patterns in air temperature and precipitation (Robinson 2002). Air temperature/precipitation and, accordingly, soil temperature/soil moisture are reported to be among

the most important environmental factors controlling decomposition worldwide (French 1988; Ineson et al. 1988; Epstein et al. 2002; Cornelissen et al. 2007; Piñeiro et al. 2010). It has been shown that both soil temperature and soil moisture can have positive, negative, or contrasting impacts on decomposition depending on whether the ecosystem is temperature limited (e.g. boreal and mountainous ecosystems), water limited (e.g. arid ecosystems) or both (Piñeiro et al. 2010). Soil temperature and moisture are also known to interact with one another—wet soils (high moisture content) are usually cooler than dry soils. Indeed, moisture induced reductions in soil temperature might have negative impacts on decomposition in temperature limited ecosystems (Cornelissen et al. 2007; Piñeiro et al. 2010). This latter process likely explains the spatio-temporal patterns in decomposition found in our study. Early in the vegetation period (June and July), soils were water saturated and, thus, generally cold, which limited decomposition rates. In late summer, higher soil temperatures combined with lower soil

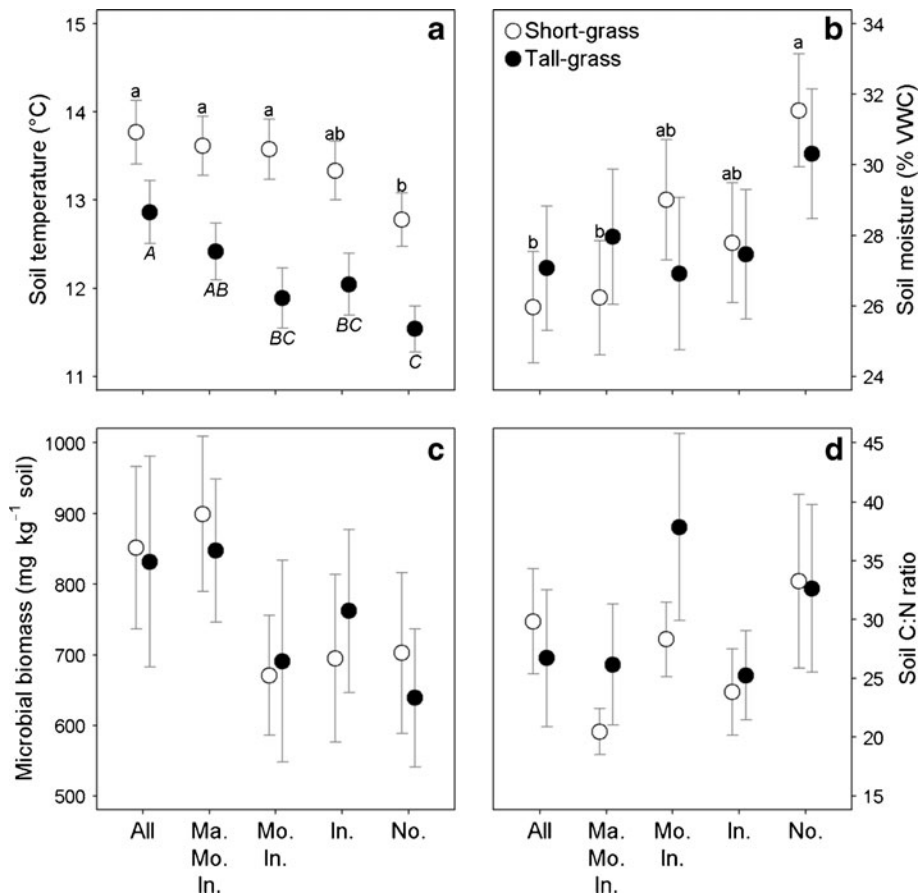


Fig. 4 Effects of herbivore exclusion on soil properties: **a** soil temperature (°C); **b** soil moisture (% volumetric water content [VWC]); **c** microbial biomass C (mg kg⁻¹ soil); and **d** soil C:N ratio (mean $\pm$ SE). Treatment abbreviations: “Ma.” – marmots;

“Mo.” – Mouse; “In.” – Invertebrates; “No.” – None. Letters denote statistically different values ($\alpha=0.05$; lower case for short- and upper case for tall-grass vegetation)

moisture lead to enhanced decomposition rates. Similarly, lower-elevation study sites in the south-western part of our study area (slightly higher air and soil temperatures, lower precipitation and soil moisture) exhibited higher decomposition rates than the higher-elevation sites in the north-eastern part. Congruent decomposition patterns were reported by Drewnik (2006) working in the Carpathian Mountains. He found that decomposition of cellulose filter paper decreased with altitude, noting a positive effect of air temperature on decomposition rates. In contrast to our findings, Withington and Sanford (2007) reported unchanged or increasing cotton cloth decomposition with increasing elevation in the Colorado Front Range. Their decomposition rates were positively related to soil moisture, indicating that precipitation increased

with elevation. Thus, in contrast to our study, their system was likely moisture-limited.

Besides soil microclimate, MBC had a positive, and soil C:N ratio a negative effect on CRR across the landscape. However, these findings are inherently linked to soil microclimatic parameters as microbial population sizes are closely linked to soil temperature/moisture regimes (Fisk et al. 1998). Other studies have reported both positive and negative effects of MBC and C:N ratio, respectively, on decomposition of non-standard OM substrates in field experiments (Pastor et al. 1988; Sowerby et al. 2000; Sistla et al. 2012), thus supporting our findings. Further, we detected no relationship between average CRR and soil N, C and P concentrations (Table 2), although the PCA results suggest variation in the parameters controlling CRR among months. Although soil N is

often considered to limit decomposition processes (Harmon et al. 1986; Robinson et al. 1995; Anderson and Hetherington 1999; Hobbie 2000), substantial variation in its effect is known to exist (Fog 1988). We found no evidence of soil P limiting average CRR, which is similar to what Aerts et al. (2003) and Güsewell et al. (2005) reported from grasslands in the Netherlands and the Swiss Alps, respectively. In contrast, Latter and Harrison (1988) reported a positive influence of soil P on cellulose decomposition. Soil C concentration has also been reported to be weakly positively related to cellulose decomposition (Schmidt and Ruschmeyer 1958).

Effects of grazing history and herbivore exclusion on soil properties

We found both long-term (grazing history) and short-term (herbivore exclusion) herbivory effects on soil temperature. Soil temperature was lower in historically lightly grazed tall-grass vegetation with more above-ground standing biomass compared to short-grass vegetation with reduced biomass (high consumption rates). In addition, soil temperature decreased with progressive exclusion of herbivores in both vegetation types, accompanied by a concomitant increase in aboveground standing biomass due to reduced herbivory (see also Risch et al. 2013). Thus, both the long- and short-term herbivore effects on soil temperature seem to be of an indirect nature, originating from taller and denser growing vegetation decreasing the radiant heating of the soil (Singer and Harter 1996). Lower soil temperatures caused by increasing standing biomass likely also reduced evapotranspiration (Archer and Detling 1986; Aerts 1997). Soil moisture generally showed opposing patterns to soil temperature with high soil moisture at low soil temperatures related to low herbivory and thus high standing biomass. However, soil moisture was only significantly influenced by herbivore exclusion in the short-grass vegetation.

Neither long-term grazing history nor short-term herbivore exclusion affected MBC, soil C:N ratio, soil N, C or P concentrations. The latter is somewhat surprising as Schütz et al. (2006) reported higher P concentrations in soils of short-grass vegetation in a well-studied region of the SNP—where we also established sites—compared to the concentrations in soils of tall-grass vegetation. Yet, this discrepancy likely can be explained with a much higher variability in former land use, and therefore P input (cf. Schütz et al. 2006), when considering

locations spread across the SNP rather than one particular grassland. Similar to our results, Wesche et al. (2010) found no effect of approximately 6 years of herbivore exclusion on soil C and N concentrations, but detected weak evidence for higher P concentrations under exclusion conditions—thus, the opposite of what we would have expected. They suggested that overgrazing at open sites led to depletion of soil P. Indeed, manual defoliation has been suggested to decrease soil P concentrations by reducing the availability of soil C for microbial activity (Shand et al. 1994).

Effect of grazing history on decomposition

Consistent with our hypothesis (Bardgett and Wardle 2003; Wardle et al. 2004), we found that decomposition rates were higher in the heavily grazed short-grass vegetation than in the lightly grazed tall-grass vegetation. There are a number of potential causes explaining these findings that partially have already been discussed above. Briefly, although not evident in our data, the long-term grazing activities of ungulates were reported to have caused increased soil P concentrations in the short-grass vegetation compared to the tall-grass vegetation (Schütz et al. 2006) due to excrement input, potentially resulting in higher nutrient availability in the short-grass vegetation. Grazing induced alterations in plant, and thus litter, N concentration could also have influenced the soil N availability as litter of a better quality is returned to the soil (Bardgett and Wardle 2003). Unpublished results from our study showed that shoot quality (in terms of N and fibre concentrations) is indeed higher in the short-grass compared to the tall-grass vegetation. Most likely, however, soil moisture and temperature are driving the differences in decomposition rates in our two grassland types as soils of the heavily grazed vegetation were warmer than those of the lightly grazed vegetation due to less shading by the vegetation.

Effect of progressive herbivore exclusion on decomposition

The exclusion of different herbivore guilds had no effects on decomposition rates in the short-grass vegetation. Large mammal exclusion increased, but further herbivore exclusion reduced decomposition rates in the tall-grass vegetation. This was rather surprising as we expected our treatments to lead to more distinct changes

in the short- compared to the tall-grass vegetation. The differences in CRR detected in the tall-grass vegetation could be due to herbivory having negative effects on ecosystem processes in lightly grazed or infertile systems as plant metabolism, C utilisation and exudation are reduced (Wardle et al. 2004; but see Paterson et al. (2003), Hamilton et al. (2008), Gavrichkova et al. (2010), Hafner et al. (2012) for examples from more frequently/systematically grazed systems where defoliation results in increased root exudation). Excluding the largest herbivores released the system from these negative impacts, which could explain why we found highest CRR in those plots. Indeed, decomposition rates were positively related to C availability (q_{mic}), although q_{mic} did not differ among treatments implying that C availability was unaffected by herbivore exclusion (Anderson and Domsch 1989). Reasons for finding lowest CRR in the plots where only invertebrates could access could be related to increases in invertebrate population size, total consumption or both as a response to reduced competition with other herbivores and therefore grazing pressure similarly to the one when all herbivores are present. Indeed, Risch et al. (2013) showed that ungulates and invertebrates consume similar quantities of biomass.

Explaining the lack of differences in CRR in the short-grass vegetation seems to be more complex, but could be related to a combination of the following four mechanisms:

- 1) Herbivore exclusion is known to reduce plant quality in heavily grazed ecosystems, which should eventually reduce decomposition rates (Wardle et al. 2002; Bardgett and Wardle 2003). However, higher availability of plant litter (more standing dead plant material) can stimulate microbial activity and biomass (Plante and Parton 2007) and could therefore offset any reduction in decomposition resulting from reduced quality.
- 2) Long-term excrement input into our grasslands (for details see Schütz et al. 2006) increased soil substrate availability such that the short-term exclusion of herbivores and its associated reductions in excrement input are irrelevant for substrate availability.
- 3) The short-term (two summer) exclusion of herbivores influenced both soil temperature and soil moisture. It is thus possible that changes in soil temperature and moisture nullified each other.

- 4) Two growing seasons of herbivore exclusion were too short to allow the microbial decomposer communities to adapt to the new conditions in this vegetation type. This is supported by our MBC data, which shows a slight, but not yet significant decrease with the progressive exclusion of herbivores. Similar to MBC, consistent changes to the microbial community structure may require longer time frames than the one we allowed to develop. Gutknecht et al. (2012), for instance, reported considerably higher inter-annual variation in microbial community composition over 6 years rather than finding consistent directional shifts in community composition due to microclimate-altering treatments. Similarly, differences in the soil microbial community structure were detected between 2009 and 2010, but herbivore exclusion or vegetation type did not affect the microbial community composition in a study conducted at our sites (Hodel 2011).

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