# Effects of grazing and soil micro-climate on decomposition rates in a spatio-temporally heterogeneous grassland

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**Abstract** Grazing and seasonal variation in precipitation and temperature are important controls of soil and plant processes in grasslands. As these ecosystems store up to 30% of the world's belowground carbon (C), it is important to understand how this variability affects mineral soil C pools/fluxes, and how C cycling might be affected by changes in precipitation and temperature, due to climate change. The aim of this study was to investigate the effects of grazing and differences in soil temperature and moisture on standard organic matter (OM) decomposition rates (cotton cloth) incubated in the top 10 cm soil of grasslands with variable topography in Yellowstone National Park (YNP) during the 2004 growing season. Grazing did not affect soil temperature, moisture, cotton cloth decomposition rates, soil bulk density, soil C and N concentrations, or soil C:N ratios. However, a large spatio-temporal variability in decomposition was observed: cotton cloth decomposition was positively related to soil moisture and soil C and N concentrations, and negatively to soil temperature. Highest decomposition rates were found in wetter slope bottom soils [season averages of decomposition given as rate of decomposition (cotton rotting rate=CRR)=23–26%] and lower rates in drier, hill-top soils (season averages, CRR=20%). Significantly higher decomposition rates were recorded in spring, early summer and early fall when soils were moist and cool (spring, CRR=25%; early summer, CRR=26%; fall, CRR=20%) compared to mid-summer (CRR=18%) when soils were dry and warm. Our findings suggest that climate-change related decreases in precipitation and increases in temperature predicted for North American grasslands would decrease soil OM decomposition in YNP, which contrasts the general assumption that increases in temperature would accelerate OM decomposition rates.

**Keywords** Cotton strip · Grazing · Heterogeneity · Soil moisture · Soil temperature · Standard organic material

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## Introduction

Grasslands are an important component of the global carbon (C) cycle, covering approximately one-third of

the earth's terrestrial surface area (Lieth 1978), and storing between 10 and 30% of the world's soil C (Anderson 1991; Eswaran et al. 1993). Recently, there has been considerable interest in understanding factors that control C cycling in grassland ecosystems, as changes in precipitation and temperature related to climate change may alter C pools. Soil C turnover rates are a function of organic matter (OM) quality and quantity and soil micro-climatic (temperature and moisture), physical, chemical (texture, pH, bulk density, C/nutrient concentrations) and biological (microbial biomass, composition, and diversity) properties (e.g., Epstein et al. 2002). The influence of soil temperature and moisture on OM and its decomposition will make soil C pools and processes sensitive to predicted future changes in climate (e.g., Jenkinson et al. 1991; Kirschbaum 1995; Bellamy et al. 2005). Large-scale evidence for this was recently provided by Bellamy et al. 2005, who proposed that climate change during a 25 year period (1978–2003) was responsible for soil C losses across England and Wales.

Many models that allow simulating the effect of climate and/or land use on grassland C dynamics have been developed during the past 60 years to better understand and predict changes in soil OM (for a recent overview see Shibu et al. 2006). As Smith et al. 1997 point out, such models embody our best understanding of soil C dynamics; however it is essential to evaluate them against field data. While considerable information on grassland C stores is available from soil surveys and inventories, field based data on decomposition rates mostly is from studies on turnover rates of surface litter (e.g., Shaw and Harte 2001; Koukoura et al. 2003; Smith and Bradford 2003). Considerably less information is available on OM decomposition in grassland soils.

Grassland is structurally and functionally heterogeneous habitat. Grassland soil temperature and moisture vary spatially, due to topo-edaphic gradients (e.g., Schimel et al. 1985; James et al. 2003), and temporally, due to seasonal changes in air temperature and precipitation (e.g., Lauenroth and Sala 1992; Briggs and Knapp 1995; Epstein et al. 2002; Knapp et al. 2002). These conditions create spatial variation in the amount (plant biomass) and quality (plant composition) of OM that is available to the soil decomposer food-web (e.g., Knapp et al. 1993; Briggs and Knapp 1995), and temporal

variation in the microclimatic conditions suitable for biological activity. Thus, OM decomposition rates should be expected to vary considerably within grasslands. Yet, little is known about the spatio-temporal variation of, and the controls on soil decomposition rates in grassland ecosystems (Homann and Grigal 1996; Murphy et al. 1998; Epstein et al. 2002).

Large herbivores also can affect OM decomposition in grassland ecosystems. Grazing can alter the soil microclimate (temperature and moisture) by increasing the radiant energy reaching the soil leading to higher soil temperatures, and by reducing the transpirational surface area of the vegetation, which reduces the rate of soil moisture loss (McNaughton 1984, 1985; Seastedt et al. 1988). Grazing has also been shown to enhance soil N availability (Shariff et al. 1994, McNaughton et al. 1997, Frank and Groffmann 1998, Johnson and Matchett 2001), which can lead to changes in soil biological properties (e.g., microbial biomass, composition). Further, it has been reported that grazing can increase the plant N content (McNaughton 1984, Coughenour 1991, Shariff et al. 1994), and therefore the quality of the OM entering the soil. Despite these many-fold ways grazing could influence OM decomposition in grassland soils, most studies have either focused on how herbivores affect surface litter decomposition rates (e.g., Olofsson and Oksanen 2002; Wardle et al. 2002) or assessed grassland-grazer interactions on ecosystem properties and OM decomposition through modeling approaches (recent review in Tietjen and Jeltsch 2007). We could only find two field studies that investigated the effect of herbivores on soil OM decomposition rates in grassland (Shariff et al. 1994; Güsewell et al. 2005). More information on how large grazers affect soil OM decomposition rates will be needed to comprehensively understand the impact of these animals on OM processes.

The objective of our study was to assess how grazing, soil moisture and soil temperature affect OM decomposition of a standard OM (cotton cloth) in grasslands of Yellowstone National Park (YNP). By using a standard organic substrate, OM quality is held constant (lignin content, C:N ratio, etc.) and decomposition becomes a function of soil micro-climatic, physical and chemical properties and the composition of the decomposer community (Berg 2000).

## Materials and methods

### Study area

The study was conducted on the northern winter range of Yellowstone National Park (YNP), located in the northwestern corner of Wyoming, USA (44°55′N to 45°10′ and 110°10′W to 110°50′W), and home to large migratory herds of elk (*Cervus elaphus* L.), bison (*Bison bison* L.), and pronghorn [*Antilocarpa americana* (Ord.)]. The northern winter range (~100,000 ha) is primarily comprised of grassland and shrub-grassland, and is inhabited by roughly 8,300 elks, 1,400 bison and 225 pronghorn (winter counts 2003/2004; Northern Yellowstone Cooperative Wildlife Working Group 1996–2004, P.J. White, R. Wallen personal communications). Elevations range from 1,600 to 2,200 m and the climate is fairly cool and dry, with mean annual temperatures and precipitation of 4.6°C and 379 mm, respectively (NOAA, weather data). Soils of the northern winter range are mostly derived from glacial till of andesitic and sedimentary origin laid down during the Pleistocene (Keefer 1987).

### Sampling design

We used three ungulate exclosures (100×200 m) that were established by the Park Service between 1958 and 1962 at Mammoth Hot Springs, Junction Butte and Lamar Valley. We established a total of five study sites at these three exclosures at locations where we could find good paired sites that included a wide range of topographic positions encompassing hill-top, slope and slope-bottoms. Two sites were located at the Mammoth exclosure (site 1, site 5), one at Junction Butte (site 2), and two at Lamar (site 3, site 5). The Mammoth and Lamar exclosures were approximately 48 km apart and the Junction Butte exclosure was roughly midway between those two. Elevation differences between the three exclosures did not exceed 250 m. The two study sites at the Mammoth and Lamar exclosures were separated by approximately 200 m and were considered spatially independent. The five sites varied in topography: sites 1 and 2 were located at dry hill tops, site 3 on a dry slope and sites 4 and 5 were located at relatively mesic slope bottoms. Detailed site descriptions are provided in

Table 1. Soils at all sites were classified as Mollisols according to the USDA keys to soil taxonomy (Soil Survey Staff 2003).

At each of the sites we established a set of paired plots (15×15 m) inside (ungrazed) and outside (grazed) the exclosure. The paired plots were established in grassland vegetation and had the same aspect, slope, and dominant plant species. Plots were located at least 5 m away from the fence to avoid a fence effect. Green and dead biomass were non-destructively measured in all the plots as described in detail by Risch and Frank 2006. Green biomass was considerably higher at sites 4 and 5 compared to the three other sites (Table 1), but did not differ in grazed and ungrazed grassland (Risch and Frank 2006). The percentage of vegetation cover at sites 1, 2 and 3 was approximately 50%, and over 90% at sites 4 and 5 (A. Risch, personal observation).

Ungulates were observed at each site throughout the 2004 sampling season (A. Risch, personal observations). Data on consumption rates of large ungulates are not available for the 2004 growing season. For the period 1999 to 2001, however, Frank (2007) reported that biomass consumed by large herbivores across topographically variable grassland averaged between 37±6 (mean±SE) and 60±16 g/m$^2$.

### Soil physical and chemical parameters: sampling and analyses

Five soil samples were randomly taken with a core sampler (core diameter, 2 cm) to a depth of 10 cm in each plot in July 2004, dried to constant weight at 60°C, passed through a 2 mm sieve and then analyzed for soil texture (hygrometer method) and soil pH (2:1 water-soil paste; Table 1). Five additional soil samples were randomly taken in each plot with a core sampler (core diameter 2 cm) to a depth of 10 cm in July 2004 after removing plant parts and surface plant litter ($O_i$ horizon). We decided to include the organic $O_e$ and $O_a$ horizons (if developed) in our 0–10 cm sampling depth, as they are an important factor in soil OM decomposition processes. Each of the soil samples was dried to constant weight at 60°C, passed through a 2 mm sieve, and analyzed for total C and nitrogen (N) with a CE Instruments NC 2100 soil analyzer (CE Elantech Inc., Lakewood NJ, USA). Sub-samples of each soil sample were further dried at 105°C to

**Table 1** Location, elevation, landscape position, soil type, soil texture, soil pH, and dominating plant species, amount of green and standing dead biomass of the five sites under study

| Site | Location | Elevation (m) | Landscape location | Soil Type | Soil Texture | pH | Dominant plant species | Green biomass (g m$^{-2}$) | Dead biomass (g m$^{-2}$) |
|------|----------|---------------|--------------------|-----------|--------------|----|------------------------|-----------------------------|-----------------------------|
| 1 | Mammoth Hot Springs | 1,900 | Hill top | Mollisol | Loamy sand | 6.8 | *Festuca idahoensis* Elmer | 53.4 | 6.4 |
| 2 | Junction Butte | 1,920 | Hill top | Mollisol | Loamy sand | 6.6 | *Festuca idahoensis* Elmer | 31.5 | 6.6 |
| 3 | Lamar Valley | 2,110 | Slope | Mollisol | Loamy sand | 7.2 | *Pseudoroegneria spicata* (Pursh) A. Löve | 39.4 | 11.7 |
| 4 | Lamar Valley | 2,100 | Slope bottom | Mollisol | Sandy loam | 7.2 | *Poa palustris* L. | 102.6 | 11.0 |
| 5 | Mammoth Hot Springs | 1,890 | Slope bottom | Mollisol | Loamy sand | 7.7 | *Poa pratensis* L. | 124.0 | 31.7 |

determine soil bulk densities, which were calculated based on the total dry weight and the volume of the sample. Soil temperature (10 cm depth) and moisture (0–10 cm depth) were measured with permanently installed sensors (Onset Computer, Bourne, MA, USA) in each grazed and ungrazed plot during the entire growing season.

Decomposition rates of standard material

We used a cotton strip assay (Latter and Howson 1977; Latter and Walton 1988) to assess the effect of grazing, soil moisture, and soil temperature on standard OM decomposition rates across the YNP landscape during the 2004 growing season. Cotton cloth tensile strength loss (CTSL) is a measure of decomposition, and can be used as an index to express the combined effect of soil microclimatic, physical, chemical and biological properties on OM decomposition (e.g., Latter and Walton 1988; Sagar 1988; Withington and Sanford 2007). Beginning in May 2004, five 20×10 cm sheets of 100% un-bleached cotton cloth obtained from Daniel Jenny & Co., Switzerland (specifications of cotton cloth: American Type SM 1/18″, Warp: 34/1, Weft: 20/1, Weave plain, 29.5 picks/cm warp, 22 picks/cm weft, 237 g/m$^2$) were inserted vertically into the soil of each plot by making a slit with a flat spade to a depth of 10 cm, inserting the cloth with the spade, and then pushing the slit closed with the spade to assure tight contact of cloth with soil. Deeper placement of the cloth than 10 cm was not possible due to the high rock content of the topsoil at most sites. The cloths were retrieved after one month and new sheets were installed and removed at monthly intervals from mid-May through mid-September (further referred to "May/June", "June/July", "July/August", "August/September" sampling periods). Five control cloths (same fabric as the incubated cloth) also were inserted at all the plots (grazed and ungrazed) each time a new set of cloths were incubated (monthly) and immediately removed in order to estimate CTSL from the insertion process.

After retrieval, the cloths were air-dried, the remaining soil gently removed, and 1 cm wide strips containing the same number of cotton threads were cut at the 4.5 to 5.5 cm soil depth. The strips were equilibrated at 50% relative humidity and 20°C for 48 h prior to strength testing on a Scanpro Awetron TH-1 tensile strength

tester (AB Lorentzen aand Wettre, Kista, Sweden). Cotton tensile strength loss was calculated as

$$CTSL = CTS_{control} - CTS_{final} \qquad (1)$$

where $CTS_{control}$ is the cotton tensile strength of the control cloth and $CTS_{final}$ the cotton tensile strength of the incubated sample. The rate of cotton decay (cotton rotting rate=CRR) was then calculated according to the function derived by Hill et al. 1985:

$$CRR = (CTSL/CTS_{final})^{1/3} * (365/t) \qquad (2)$$

where $t$ is the incubation period length in days. This function linearizes the curvilinear response for tensile strength loss, and allows between site comparisons (Hill et al. 1985).

Statistical analyses

Grazing effects on CRR, soil moisture, and soil temperature were analyzed with paired $t$-tests for each sampling period (May/June, June/July, July/August, August/September) separately. Grazing effects on bulk density, C and N concentrations, and C:N ratios of the top 10 cm soil also were analyzed with paired $t$-tests. To assess the relationships between soil microclimatic variables and CRR, we used linear regression analyses with soil moisture and soil temperature as independent, and CRR as the dependent variables. Data for soil moisture were arc-sine square root transformed in order to meet the normality assumption. Regression analysis also was used to assess the relationship between soil temperature and soil moisture, as well as between CRR and the amount of C and N stored in the soil. To analyze how CRR, soil moisture and soil temperature differed in space and time (between-site, between-month), we normalized the data using

$$y_{norm,i} = \frac{y_i}{\sqrt{\sum_{i=1}^{n} y_i^2}} \qquad (3)$$

to remove seasonal effects for between-site comparisons and spatial effects for between-month comparisons, respectively (where $y_i$ represent the non-normlized

(raw) data and $y_{norm,i}$ the normalized data; Quinn and Keough 2002). We then used the normalized data to perform a one-way analysis of variance, followed by a LSD post-hoc test for pairwise comparison (alpha-level=0.1) to assess how CRR, soil moisture and soil temperature changed across the landscape (site was independent, and normalized CRR, normalized soil moisture and normalized soil temperature were the dependent variables). To test how CRR, soil moisture and soil temperature changed over the course of the growing season, we used repeated-measure analyses of variance followed by a pairwise LSD post-hoc test (month was independent, and normalized CRR, normalized soil moisture and normalized soil temperature were the dependent variables).

## Results

### Grazing effects on decomposition of standard OM and soil properties

Long-term exclusion of large ungulates did not have any effect on CRR, soil moisture or soil temperature at any time of measurement throughout the 2004 growing season in YNP ($p$ values of $t$-tests for pairwise comparisons all > 0.05, $n$=5 for all tests). Because soil bulk density, soil C, N concentrations, and soil C:N ratios in 0–10 cm soil depth also did not differ between inside and outside of the exclosures ($p$ values of $t$-test for pairwise comparison all >0.05, $n$=5 for all tests), the data from grazed and ungrazed grassland plots were averaged for each site for further analyses (Table 2).

### Relationships between decomposition rates of standard OM and soil properties

Cotton cloth decomposition rates were significantly and positively correlated with soil moisture (Fig. 1a) and the 0–10 cm soil C ($p$=0.02, $n$=5) and N ($p$=0.02, $n$=5) contents. Soil moisture, C, and N content all co-varied with one another ($p$<0.001 for all comparisons). We also found a negative relationship between CRR and soil temperature (Fig. 1b), which was weakly negatively correlated (exponential decay function) with soil moisture (Fig. 1c). Temperature especially affected soil moisture at the dry, hill-top sites, while close to no effect of temperature was detected for the wetter, slope-bottom sites (Fig. 1c). No correlation was detected

**Table 2** Bulk density, C, N and C:N ratios for the top 10 cm of soil [after removing plant parts and surface plant litter (O_i horizon)]

| Site | Soil bulk density (Mg cm$^{-3}$) | | Soil C (%) | | Soil N (%) | | Soil C:N ratio | |
|---|---|---|---|---|---|---|---|---|
| | Ungrazed | Grazed | Ungrazed | Grazed | Ungrazed | Grazed | Ungrazed | Grazed |
| 1 | 1.2 (0.06) | 1.2 (0.02) | 4.7 (0.3) | 3.8 (0.3) | 0.40 (0.03) | 0.31 (0.03) | 11.5 (0.05) | 11.4 (0.28) |
| 2 | 1.1 (0.13) | 1.4 (0.05) | 3.0 (0.4) | 3.1 (0.4) | 0.25 (0.04) | 0.30 (0.03) | 12.0 (0.35) | 10.2 (0.15) |
| 3 | 0.9 (<0.01) | 1.0 (0.10) | 4.3 (0.5) | 4.3 (0.4) | 0.42 (0.04) | 0.42 (0.04) | 10.2 (0.17) | 10.2 (0.15) |
| 4 | 1.1 (0.04) | 1.0 (0.10) | 9.6 (0.4) | 9.5 (1.2) | 0.89 (0.03) | 0.82 (0.08) | 10.8 (0.23) | 11.5 (0.31) |
| 5 | 0.5 (0.13) | 0.7 (0.08) | 17.3 (0.4) | 20.0 (0.8) | 1.30 (0.04) | 1.60 (0.07) | 13.7 (0.08) | 12.3 (0.39) |

No variable was significantly different between grazed and ungrazed grassland ($p$ value $t$-test for pairwise comparison > 0.05). Standard errors in parentheses, $n=5$ for all variables. *1* Mammoth Hot Springs, hill-top; *2* Junction Butte, hill-top; *3* Lamar Valley, slope; *4* Lamar Valley, slope bottom; *5* Mammoth Hot Springs, slope bottom.

between soil temperature and soil C and N concentrations (C: $p=0.13$, $n=5$; N: $p=0.12$, $n=5$).

Spatio-temporal differences in decomposition rates of standard OM

Cotton cloth decomposition ($p<0.001$), soil moisture ($p<0.001$), and soil temperature ($p=0.002$) differed significantly across the landscape. Cotton cloth decomposition was fastest at site 5, where highest soil C and soil moisture values (20.3%) were found (Fig. 2a, site 5), compared to decomposition in hill-top and slope soils (sites 1, 2, 3), which had less C in the soil and were drier (4.7 to 7.0% moisture). Spatial differences in soil temperature were relatively small (13.9–16°C) compared to differences in soil moisture (4.7–20.3%). However, significantly higher soil temperatures were detected at the exposed hill-top site (site 1), which had sparse vegetation and was located at the lowest elevation compared to the other four sites.

We also detected significant differences in CRR ($p<0.001$), soil moisture ($p=0.004$), and soil temperature ($p=0.001$) over the course of the 2004 growing season. Cotton cloth decomposed fastest in

spring (May/June) and early summer (June/July, Fig. 2b), when soils were moist (11.0 and 10.1% across site averages) and cool (12 and 16°C). These decomposition values significantly differed from the much lower mid-summer (July/August) rates, when CRR was lowest due to warmer (18°C) and drier (7.9%) soils compared to spring and early summer conditions. In early fall (August/September), CRR was again significantly higher than in mid-summer (July/August: moisture 9%, temperature 13°C), but remained significantly below spring and early summer rates (Fig. 2b). Precipitation was higher in spring and fall, compared to mid-summer in both 2003 and 2004 (Fig. 3), and was similar to soil moisture trends observed during the 2004 growing season (data shown above).

## Discussion

### Grazing effects on standard OM decomposition

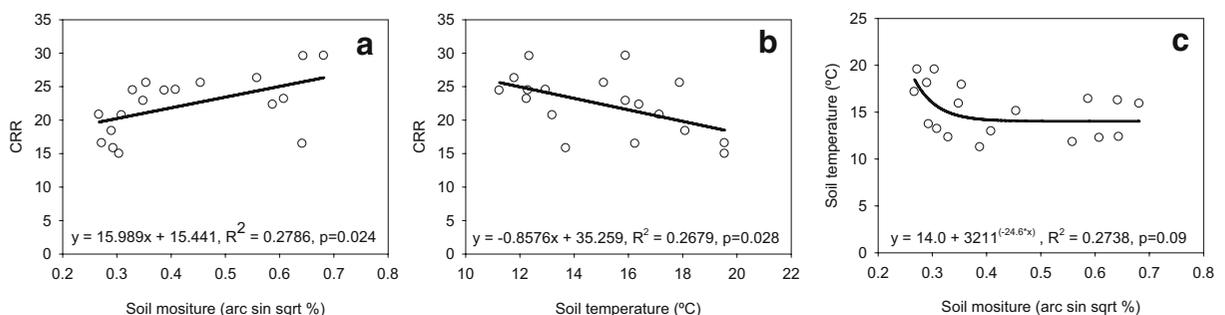Grazing did not affect CRR, soil moisture and soil temperature measured in YNP during the 2004



**Fig. 1** Changes in CRR (cotton rotting rate), soil moisture and soil temperature across the Yellowstone National Park landscape during the 2004 growing season: **a** relationship between CRR and soil moisture, **b** relationship between CRR and soil temperature, **c** relationship between soil moisture and soil temperature, $n=18$ for all three graphs
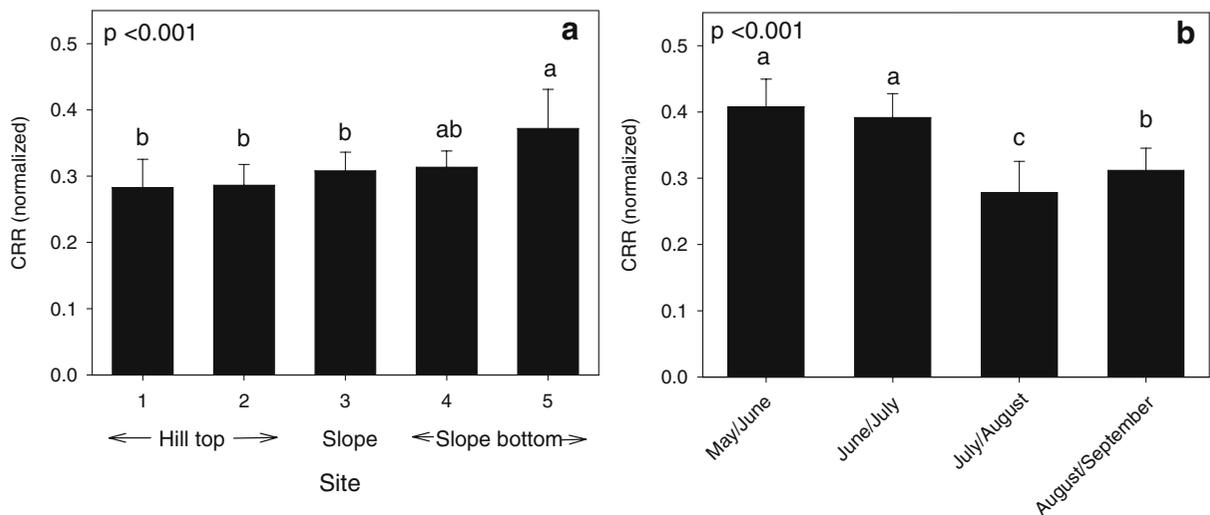
Fig. 2 Spatio-temporal variability in CRR (cotton rotting rate, normalized data): **a**) between-site differences (see Table 1) in CRR, and **b**) between-months differences in CRR. Different letters indicate significant differences between sites and months, respectively, based on a LSD test for pair-wise comparison (alpha-level=0.1). 1=Mammoth Hot Springs, hill-top; 2=Junction Butte, hill-top; 3=Lamar Valley, slope; 4=Lamar Valley, slope bottom; 5=Mammoth Hot Springs, slope bottom

growing season. Studies conducted in other ecosystems have reported that by removing transpirational, shade-casting plant surface area herbivores can increase soil moisture and temperature (McNaughton 1984, 1985; Seastedt et al. 1988), which should lead to higher decomposition rates in grazed compared to ungrazed grassland. The likely reason for not finding such grazing-related differences in soil microclimate and CRR in our study could be related to compensatory responses of the vegetation, resulting in the same amount of standing biomass inside and outside exclosures in 2004 (Risch and Frank 2006).

We could find only two studies that investigated the impact of grazing on OM turnover rates in grassland soils. Shariff et al. 1994 reported higher root decomposition under moderate livestock grazing in soils of a North Dakota (USA) prairie compared to heavy and ungrazed treatments. The opposite result was found by Güsewell et al. 2005, who reported higher plant litter decomposition rates in the soil of heavily grazed cattle pastures in southern Switzerland, as compared to pastures that were lightly grazed. However, both papers suggested that decomposition was controlled by changes in litter and/or root N concentrations under different grazing pressures, but they did not provide any information on soil moisture or soil temperature conditions. LeCain et al. 2000, 2002, in contrast, investigated how soil moisture changed under different grazing regimes; but did not

study decomposition processes. In these two studies, they found higher soil moisture in an ungrazed Wyoming, USA cattle pasture than in a grazed one (LeCain et al. 2000), and higher soil moisture in a heavily-grazed compared to a lightly-grazed pasture in Colorado, USA (LeCain et al. 2002). In Wyoming these results were attributed to a mulching effect by the accumulated litter and standing dead material inside the cattle exclosures, while in Colorado soil textures were different between the heavily- and lightly-grazed pasture. In a tall-grass prairie in Oklahoma (USA), Wan and Luo 2003 found significant short-term increases in soil temperature after simulating grazing by clipping as self-shading by the vegetation was reduced; but clipping did not consistently increase soil temperature and soil moisture over a one-year period (June 2001 to June 2002).

In our study, we also found no effect of large herbivores on soil bulk density, C and N concentrations or C:N ratios. These results are similar to findings by Raiesi and Asadi 2006, who reported no differences in soil bulk density or C and N concentrations (0–30 cm) in domestic livestock-grazed rangeland in Iran. Also Augustine and Frank 2001 did not find any consistent differences in soil C and N from grazed and ungrazed long-term grassland exclosures in Yellowstone National Park. In contrast, light grazing by cattle in the high-plain grasslands of Wyoming, USA increased C and N stored in the top

**Fig. 3** Monthly precipitation totals measured at the weather stations Mammoth Hot Springs, Tower Falls, and Lamar ranger station for the years 2003 and 2004 (NOAA, weather data). Lamar ranger station data is only collected during the winter months (November–April), therefore the May through October values are not available. Weather stations at Mammoth Hot Springs, Tower Falls, and Lamar Valley were within 2 km of the sites and therefore likely best reflect precipitation rates at sites 1/5, 2, and 3/4, respectively
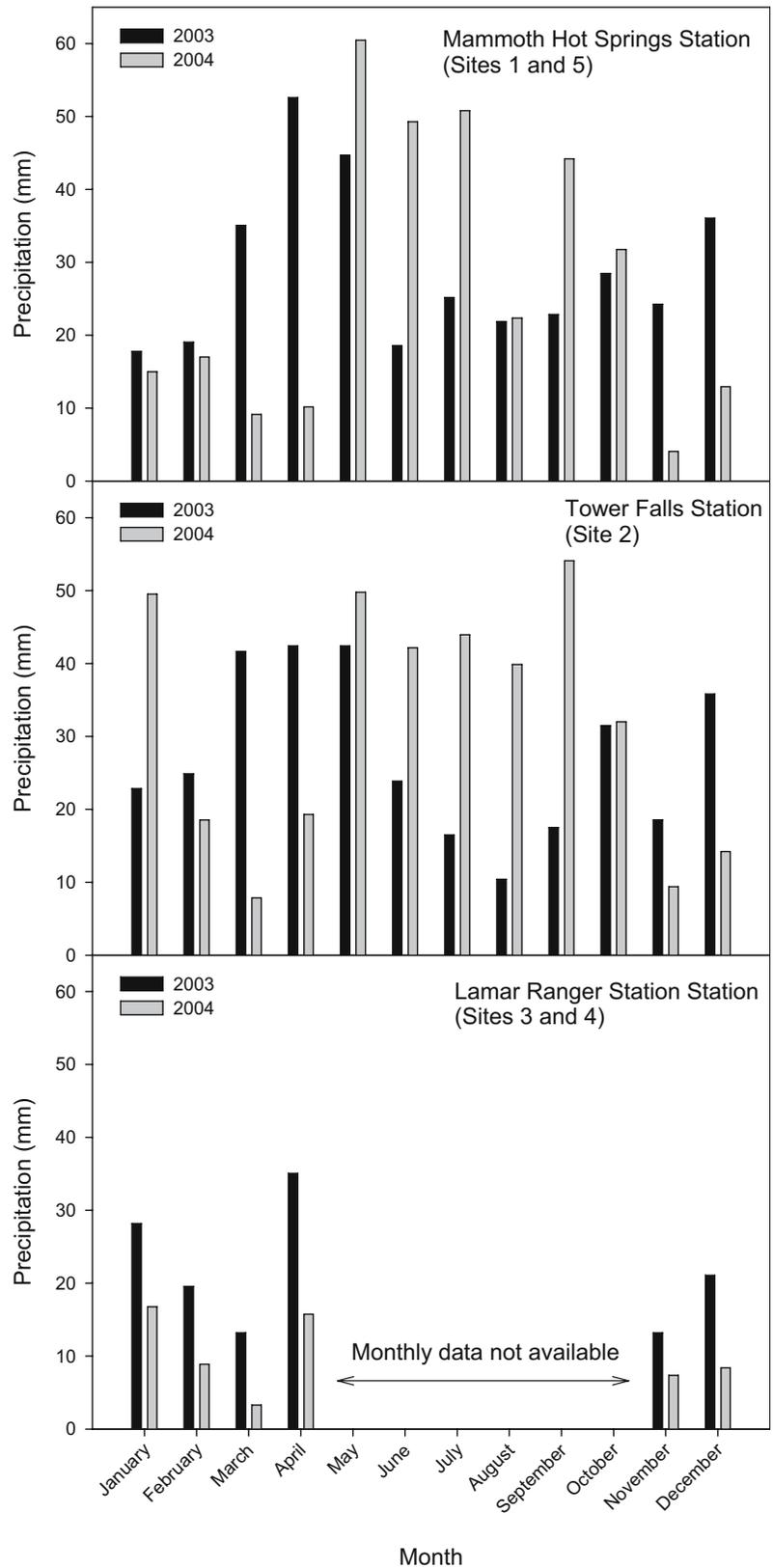
5 cm of soil compared to heavy or no grazing (Ganjegunte et al. 2005). Bison grazing in tall-grass prairie of Kansas, USA, also had a positive effect on soil N content (Johnson and Matchett 2001). Topography affected the impact of elk grazing in the Rocky Mountain National Park, Colorado, USA, where soil bulk density, soil C, N and nutrient concentrations were higher outside compared to inside the exclosures on slope bottoms, while no effects were detected on mid-slope and upland sites (Binkley et al. 2003).

Overall, the information available in the literature on how large herbivores influence soil properties shows that the effect of large mammals on these variables is highly dependent on the ecosystem studied and the grazing intensity that a particular ecosystem receives. As summarized in a recent review by Bardgett and Wardle 2003, positive effects of herbivory on soil biota and soil processes are generally found when soil fertility and grazing intensity are high within an ecosystem, while negative effects are to be expected in unproductive systems with low consumption rates.

Spatio-temporal differences in standard OM decomposition rates

Soil moisture and temperature have been shown to be drivers of soil C and N concentrations in grassland ecosystems and are generally included as interactive factors controlling decomposition rates in global C cycling models (see Shibu et al. 2006). Soil moisture, which seemed to be closely related to total amount of precipitation measured in YNP, was positively correlated to CRR in our study, while soil temperature had a negative effect. Soil temperature had a negative effect on soil moisture in the driest (hill-top) soils, where the cover of the vegetation was also lowest. There was no correlation between temperature and moisture for the wetter, slope-bottom soils. By inference then, the negative relationship between temperature and CRR may have been a function of temperature limiting soil moisture, the primary determinant of CRR in YNP, in dry grassland. Similar to our results, Homann and Grigal 1996 found a negative correlation between soil temperature and filter paper decomposition studied between May and July along transects containing abandoned field and prairie patches in Minnesota (USA). They attributed these results to a high inverse correlation between soil moisture and soil temperature,

but did not measure soil moisture levels. However, our results are in contrast to other studies conducted in mineral soil of forest, tundra and agricultural grassland ecosystems, where positive interactions between temperature and decomposition rates of standard OM material in mineral soil were found (e.g., Ineson et al. 1988; Hopkins et al. 1990; Jurgensen et al. 2006, Drewnik 2006, Withington and Sanford 2007). These latter studies were conducted in ecosystems where soil moisture was usually not limiting for OM decomposition, while in dry ecosystems, such as the grasslands in our study, changes in soil moisture likely were more important for an alteration of OM decomposition rates than temperature. Also, in a study that used a regional data set of aboveground primary production, soil organic C, soil texture, and climate to evaluate the environmental controls on decomposition rates throughout the US Great Plains, Epstein et al. 2002 suggested that temperature might be less important than moisture for OM decomposition in grassland ecosystems. They found a lack of correlation between air temperature and decomposition rates, which was modeled using net primary production and soil OM pools. Water was assumed to be the primary limiting factor in grassland ecosystems, although soil moisture data were not available. Similarly, Smith et al. 2005, when they modeled changes in soil organic C of European crop- and grasslands between 1990 and 2080, found that temperature only accelerated decomposition where soil moisture was not limiting.

In summary, our results showed that soil moisture was the primary control on cotton cloth decomposition in YNP grassland, with temperature only playing an indirect influence by modifying soil moisture levels at dry sites. We therefore would expect that climate change-related decreases in precipitation and increases in temperature predicted for water-limited ecosystems, such as grasslands of YNP (IPCC 2001), will lead to lower OM turnover rates and higher soil C storage. This scenario strongly contrasts the general assumption that increasing temperatures will lead to increases in OM decomposition (e.g., Kirschbaum 1995). Field studies such as the one we conducted in YNP are important to better understand the interactions between decomposition rates of OM material, soil temperature and soil moisture in grassland system and are needed if we were to better understand the effects of future climate change on their C sink-source relationships.

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