Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau

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Abstract

Knowledge about the role of litter and dung decomposition in nutrient cycling and response to climate change and grazing in alpine ecosystems is still rudimentary. We conducted two separate studies to assess the relative role of warming and grazing on litter mass loss and on the temperature sensitivity of litter and dung mass loss. Experiments were conducted for 1–2 years under a controlled warming–grazing system and along an elevation gradient from 3200 to 3800 m. A free-air temperature enhancement system (FATE) using infrared heaters and grazing significantly increased soil temperatures (average 0.5–1.6 °C) from 0 to 40 cm depth, but neither warming nor grazing affected soil moisture except early in the growing seasons at 30 cm soil depth. Heaters caused greater soil warming at night-time compared with daytime, but grazing resulted in greater soil warming during daytime compared with night-time. Annual average values of the soil temperature at 5 cm were 3.2, 2.4 and 0.3 °C at 3200, 3600 and 3800 m, respectively. Neither warming nor grazing caused changes of litter quality for the first year of the controlled warming–grazing experiment. The effects of warming and grazing on litter mass losses were additive, increasing litter mass losses by about 19.3% and 8.3%, respectively, for the 2-year decomposition periods. The temperature sensitivity of litter mass losses was approximately 11% $°C^{-1}$ based on the controlled warming–grazing experiment. The annual cumulative litter mass loss was approximately 2.5 times that of dung along the elevation gradient. However, the temperature sensitivity (about 18% $°C^{-1}$) of the dung mass loss was about three times that of the litter mass loss. These results suggest greater warming at night-time compared with daytime may accelerate litter mass loss, and grazing will enhance carbon loss to atmosphere in the region through a decrease of litter biomass and an increase of dung production with an increase of stocking rate in future warmer conditions.

Keywords: alpine meadow, climate change, decomposition, dung, global change, grazing, infrared, litter, temperature sensitivity, warming

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Introduction

The decomposition of plant litter is a key component of the global carbon (C) budget (Raich & Schlesinger, 1992; Couteaux et al., 1995; Aerts, 1997, 2006; Robinson, 2002). Grasslands are one of the largest terrestrial ecosystems, and grazing is the main land-use on grasslands across the world. Climate change, especially warming, is predicted to affect most regions of the northern hemisphere and will be particularly pronounced at high northern latitudes during this century (ACIA, 2005; IPCC, 2007).

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Effects of warming and grazing on litter mass losses at the community scale may include four levels (Shariff *et al.*, 1994; Olofsson & Oksanen, 2002; Wang *et al.*, 2003; Aerts, 2006): (1) to alter rates of litter mass loss directly at very short time-scales through changes in soil temperature and soil moisture; (2) to decrease litter biomass and to increase excrement from grazing animals with the increase of grazing intensity at short time-scales; (3) to change plant litter quality indirectly at longer time-scales; and (4) to change indirectly long-term species composition and structure of decomposer and detritivore communities. Thus, any changes in factors that control litter mass losses may have important repercussions for the global C budget.

Climate warming will lead to increased litter mass losses and thus to a higher flux of carbon dioxide into the atmosphere (Meentemeyer, 1978; Berg *et al.*, 1993; Shaw & Harte, 2001; Liski *et al.*, 2003). These effects are likely to be most manifest in cold biomes (high-latitude and high-altitude sites) because here warming is predicted to be greatest, and decomposition in these regions is strongly temperature limited (Hobbie, 2000; Robinson, 2002; Aerts, 2006). Grazing influences the cycling of nutrients mainly in two ways: through transforming plants into urine and fecal material and by influencing litter mass losses (Hobbs, 1996; Bardgett *et al.*, 1998; Olofsson & Oksanen, 2002). The direct consumption of plants by herbivores normally enhances nutrient cycling, as the nutrient release from feces tends to be faster than the nutrient release from litter (Ruess & McNaughton, 1987; Ruess *et al.*, 1989; Hobbs, 1996). However, the direct effect of herbivores on nutrient cycling is not always positive as the release of nutrients from feces produced when grazers are facing nutrient shortage is slower than the release from plants and plant litter (Floate, 1970; Pastor *et al.*, 1993), because much of the nutrient content in the plant material is taken up by the herbivore during digestion (Pastor *et al.*, 1993).

The temperature sensitivity of soil C decomposition has recently received considerable attention (Giardina *et al.*, 2000; Melillo *et al.*, 2002; Fang *et al.*, 2005; Davidson & Janssens, 2006) because of its importance in the global C cycle and potential feedbacks to climate change (Davidson *et al.*, 2000; Mack *et al.*, 2004; Bellamy *et al.*, 2005; Knorr *et al.*, 2005). Some knowledge is also available on the potential responses of litter mass loss to climate warming (McTiernan *et al.*, 2003; Fierer *et al.*, 2005; Cornelissen *et al.*, 2007). However, to date, little is understood about the temperature sensitivity of dung mass loss under future warming conditions, even though in natural grazing ecosystems litter fall and herbivore dung are the two main processes by which minerals contained in the aboveground parts of plants are returned to the soil.

The largest grassland area on the Eurasian continent is the Tibetan plateau, which is mostly situated at 3500 m or more above sea level (a.s.l.) and which covers an area of approximately 2.5 million km^2 (Zheng *et al.*, 2000). Concurrent with climate changes, there have been profound changes in pastoral land-use dynamics on the plateau which have been resulting in increased grazing pressure on the alpine meadows (Duan *et al.*, 2005, 2006; Zhou *et al.*, 2005). In the plateau region, where open grazing by more than 13.3 million domestic yaks and 50 million sheep is practiced (Gerald *et al.*, 2003; Yao *et al.*, 2006), large amounts of animal excreta are directly deposited onto alpine grasslands. Understanding of the roles of litter and dung mass loss in nutrient cycling and their responses to climate warming and grazing in alpine ecosystems is still rudimentary. Moreover, because grazing decreases litter biomass but increases dung excreta of grazing animals, evaluation of the effects of grazing on C cycling and sequestration in grazing ecosystems under the future warmer conditions requires a better understanding of the temperature sensitivities of both litter and dung mass loss.

Temperature effects on litter mass loss are best studied by complementary approaches (Aerts, 2006). Although manipulative temperature experiments are limited in spatial and temporal scale and have potential artefacts, they have the advantage of a whole-ecosystem approach, factor separation, standardization and replication (Cornelissen *et al.*, 2001; Shaw & Harte, 2001). The method of using natural climatic gradients (McTiernan *et al.*, 2003; Kueppers *et al.*, 2004) has advantages over controlled laboratory or greenhouse studies (Hart & Perry, 1999; Shaver *et al.*, 2000) because ecosystem components that are subject to microenvironmental dynamics are hard, if not impossible, to replicate in the laboratory. Furthermore, the approach is relatively inexpensive and can be applied to a wider range of temperature differences than is possible when climate is manipulated using supplemental heating or cooling. On the other hand, there is no standardization or replication, and steering factors cannot be separated. However, in concert these temperature manipulation and climatic gradient approaches can be very powerful (Aerts, 2006).

This study examines the effects of warming and grazing on litter mass loss for a 2-year litter decomposition experiment in a controlled warming and grazing system described by Kimball *et al.* (2008) in an alpine meadow to elucidate the relative strengths of these controls over litter mass loss. At the same time, we conducted a litter and dung decomposition experiment along a mountain elevation gradient from 3200 to 3800 m over a broad range of temperature regimes to elucidate the relative temperature sensitivity of litter and dung mass losses in the region. This work seeks to explain how warming comparable to that expected

under global climate change influences mass losses directly through soil surface temperature and moisture changes, as well as indirectly through litter quality changes under warming and grazing. Also this study is unique in its exploration of the impact of climate change on the temperature sensitivity of litter and dung mass losses. The objectives were to determine: (1) how litter mass losses are controlled by soil microclimatic conditions and indirectly altered through changes in litter quality in the controlled warming–grazing experiment, and (2) what are the temperature sensitivities of mass losses of litter and yak dung along the elevation gradient.

Materials and methods

Experimental site

The experimental site is located at the Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), a facility run by the Northwest Institute of Plateau Biology, Chinese Academy of Sciences. HBAMERS is situated at latitude 37°37′N, longitude 101°12′E, and the mean elevation of the valley bottom is 3200 m. The station lies in the northeast of the Tibetan plateau in a large valley surrounded by the Qilian Mountains. The station experiences a typical plateau continental climate which is dominated by the southeast monsoon from May to September in summer and high pressure from Siberia in winter. Summers are short and cool, and winters are long and severely cold. Mean annual temperature is -2 °C, mean annual precipitation is 500 mm, over 80% of which falls during the summer monsoon season. A detailed site description can be found in Zhao & Zhou (1999).

Controlled warming–grazing experiment

The infrared heating system, herein called a free-air temperature enhancement (FATE), was described previously by Kimball *et al.* (2008). The setpoint differences between heated and corresponding reference plots were 1.2 °C during daytime and 1.7 °C at night in summer, which falls within limits of predicted temperature increases for this century (1.5–5 °C) (Houghton *et al.*, 2001). The canopy temperatures were measured with infrared thermometers every second, and the heaters were modulated at 1 s intervals [although the time-constant of the ceramic heating elements was about 6 min (Kimball *et al.*, 2008)]. Fifteen minute averages were output by the dataloggers. During winter from October to April, because some infrared thermometers were not working, the power outputs of the heaters were manually set at 1500 W plot^{-1}.

A two factorial design (warming and grazing) was used with four replicates of each of four treatments, i.e. no-warming with no-grazing (NWNG), no-warming with grazing (NWG), warming with no-grazing (WNG), and warming with grazing (WG). In total, 16 plots of 3 m diameter were used in a complete randomized block distribution in the field.

Initially, one adult Tibetan sheep was fenced in the grazing plots on the morning of 15 August 2006 for approximately 2 h. The canopy height was about 8–9 and 4–5 cm before and after grazing, respectively. Two adult Tibetan sheep were fenced for approximately 1 h in the grazing plots on the mornings of 12 July, 3 August and 12 September 2007. The canopy heights were about 6–7 and 3–4 cm before and after grazing, respectively. The canopy height of the vegetation was measured at 50 points within the plots before and after grazing, and the sheep were removed from the grazing plots when the canopy height was reduced to approximately half of the initial height. All experimental sheep were fenced into three additional 5 m × 5 m fenced plots for a day before the beginning of the grazing experiment to help them adapt to small plots.

At 50 cm inside the edge of each plot, type-K thermocouples were used to automatically measure soil temperature at depths of 5, 10 and 20 cm. All the thermocouples were connected to a CR1000 datalogger (Campbell Scientific, Logan, UT, USA). At the centres of all plots, temperature sensors (Model HMP45C_90 DTR500 Olar Radiation and Precipitation Shield, Vaisala, Finland) were also used to monitor air temperature at a height of 30 cm above the ground in 2008. The canopy height of the vegetation in August was about 15–20 cm. Soil and air temperatures were measured every 1 min, and 15 min averages were stored. The soil temperatures at 0 and 40 cm depth were manually monitored using mercury-in-glass thermometers under the shade of vegetation at 0 cm and with a tube in the ground down to 40 cm at 8:00, 14:00 and 20:00 hours every day.

Soil moisture at the depths of 10, 20, 30 and 40 cm was manually measured though a tube in the ground down to 40 cm depth using a frequency domain reflectometer (FDR; Model Diviner-2000, Sentek Pty Ltd., Stepney, Australia) at 8:00, 14:00 and 20:00 hours every day. The soil moisture was expressed as a volume percentage (%) or mm/10 cm.

Dung and litter sample collection

The plant community at the experimental site at 3200 m is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carex scabrirostris*, *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontop odiumnanum*, *Blvsmus sinocompressus*, *Potentilla nivea*, and *Dasiphora fruticosa*. We found that sheep dung is easily contaminated in the field, and it is difficult to collect enough within a short time, so we collected yak dung

samples for the dung decomposition experiment. After grazing at the study site, yaks were enclosed at night and fresh dung samples from 20 yaks were collected on 6 August 2006 from the corral the next morning. These samples were carefully mixed after collection. Eight fresh samples were immediately dried at 80 °C for measurement of dry matter (DM) and chemical components. Each fresh dung sample was weighed 125.6 g (dried weight at 80 °C was 22.2 g), and put into a sealed plastic bag to be carried to the field plots.

On 20 October 2006, litter samples were collected from two 10 cm × 10 cm squares in the controlled warming–grazing experiment. Meanwhile, mixed litter samples of the meadow community grazed by yaks near by the controlled warming–grazing experiment were also collected, air-dried and stored indoors until the beginning of the decomposition experiment.

Litter and dung decomposition

Near HBAMERS, three plots of 10 m × 20 m at the elevations of 3200, 3600 and 3800 m a.s.l. along the southern side of the Qilian Mountains were fenced in autumn 2005. Air-dried litter samples (20 g oven-dry mass) of mixed community litter samples collected from the meadow community grazed by yaks were placed in 10 cm × 20 cm litterbags constructed from 1 mm mesh nylon cloth. In total five litterbags containing the mixed community litter were put in each plot at the three sites at 3200, 3600 and 3800 m at spacings of 10–20 cm on 1 June 2007, and were taken back to the laboratory on 24 June 2008, to measure litter mass loss. Similarly, air-dried litter samples (20 g oven-dry mass) collected from the controlled warming–grazing experiment were put into the same size litterbags and placed back into their plots of origin. Because of a lack of litter material, two litterbags were put in each plot, and they were taken back to the laboratory on 20 October in 2007 and 2008, respectively, to measure litter decomposition rates.

The fresh dung samples were transferred to 0.5 mm mesh nylon bags in the field. In total, eight dung bags were placed in each plot from 3200 to 3800 m at spacings of 10–20 cm in fenced plots on 6 August 2006. They were taken back to the laboratory carefully and washed quickly using distilled water to remove the dust from the dung surface on 24 July 2007. There was almost no soil on the bottom surface of the nylon bags due to vegetation coverage being about 100% for all plots. To eliminate the effect of artificially constructed dung patches on plant communities in the small areas (about 7 m²) of the controlled warming–grazing experimental plots, we did not do dung decomposition experiment there.

All samples in each sampling period were dried at 80 °C to measure their mass loss, and then ground to pass through a 1 mm sieve to determine concentrations of C and nitrogen (N) using the methods described in AOAC (1984). Chemical compositions of litter and dung were measured by sequentially digesting material into fractions that corresponded with cellulose, hemicellulose, lignin and acid insoluble ash (Van Soest, 1963; Ryan *et al.*, 1990) on a forage fiber analyzer (ANKOM 200, Macedon, New York, NY, USA). All nutrient concentrations were calculated on the basis of organic matter (i.e. DM–acid insoluble ash).

Air and soil temperatures along the mountain elevation gradient

At the centre of each plot, weather stations (Onset Computer Corporation, Japan) were used to monitor air temperature at a height of 2 m above the ground and soil temperature at a depth of 5 cm. The sensors were connected to CR1000 dataloggers, air and soil temperatures were measured every 1 min, and then 15 min averages were stored and output.

Data calculation and analysis

For the controlled warming–grazing experiment, statistical significances of the impacts of warming and grazing treatments on soil temperature at different soil depths, air temperature and litter decomposition rates were determined by analysis of variance (ANOVA) of repeated-measures as described by Klein *et al.* (2007) using SPSS Version 12.0 (SPSS Inc., Chicago, IL, USA). One-way ANOVA and least significant difference (LSD) were used to assess the significance of the differences in litter and dung mass losses and in their temperature sensitivities due to the three temperature regimes associated with varying elevation above sea level.

The temperature sensitivity of decomposition rates was defined as the annual percentage decomposition (%) per 1 °C temperature difference. In order to define a consistent indicator of the temperature regimes across all the sites (warming–grazing experiment and elevation gradient experiment), we chose annual average soil temperature at 5 cm depth. Linear regression analysis was performed to test the dependency of the annual average percentage mass losses of litter and dung on the differences of annual average soil temperature at 5 cm depth among treatments or elevations. All significances mentioned in the text were at the 0.05 level.

Results

Soil temperature and soil moisture in the controlled warming–grazing experiment

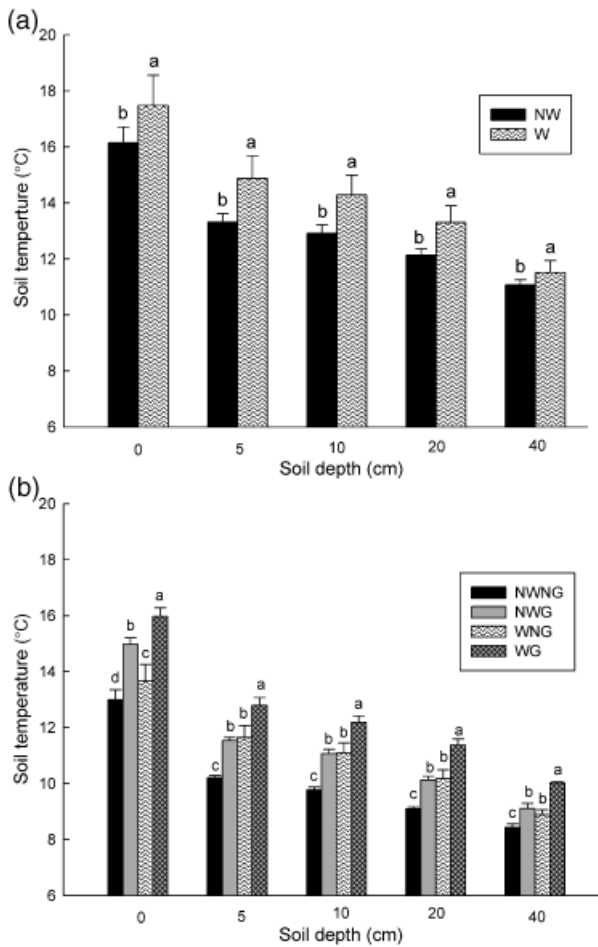Warming during the growing season in 2006 (Fig. 1a), and warming and grazing during the growing season in

Fig. 1 Average of the soil temperatures (mean ± SE) among treatments at different soil depths in 2006 (a) and 2007 (b).
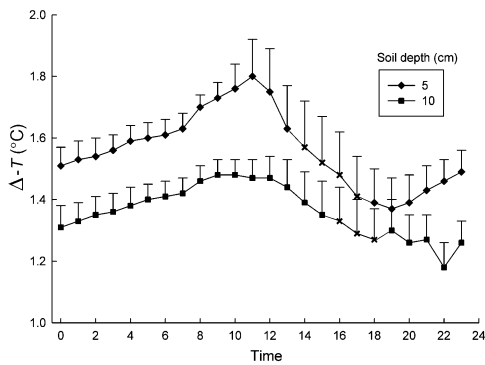

Fig. 2 Hourly soil temperature differences (mean ± SE) between warming and no-warming at 5 and 10 cm soil depths in 2006. Symbol of x in the figure means not significant at the 0.05 level.

Fig. 3 Hourly soil temperature differences (mean ± SE) among treatments at 5 cm (a) and 10 cm (b) soil depths in 2007. Symbol of x in the figure means not significant at 0.05 level. NWNG, no-warming with no-grazing; NWG, no-warming with grazing; WNG, warming with no-grazing; WG, warming with grazing.

40 cm soil depths were 0.8 and 1.3, 1.4 and 1.5, 1.2 and 1.4, 1.1 and 1.2, and 0.5 and 0.7 °C, in warmed plots compared with reference plots in 2006 and 2007, respectively. Grazing also increased average of soil temperatures by approximately 1.6, 1.3, 1.2, 1.2 and 0.9 °C at the 0, 5, 10, 20 cm at and 40 cm soil depths in 2007, respectively.

We also found that the hourly values of surface soil temperature differences between warmed and reference plots (5 and 10 cm) were statistically significant at night and in mornings but not afternoons at 14:00–17:00 hours (5 cm soil) or 17:00 and 18:00 hours (10 cm soil) for both years, respectively (Figs 2 and 3), indicating that variability was the greatest when air temperature and air turbulence were greatest. Moreover, with grazing, heater-induced increases in soil temperature were greater during the daytime than at night-time with a peak at noon in 2007 (Fig. 3) because grazing caused a greater soil temperature increase than warming did during

2007 (Fig. 1b) significantly increased soil temperatures for 0–40 cm soil depths, and no interaction between warming and grazing was detected in 2007. Mean seasonal soil temperature increases at the 0, 5, 10, 20 and
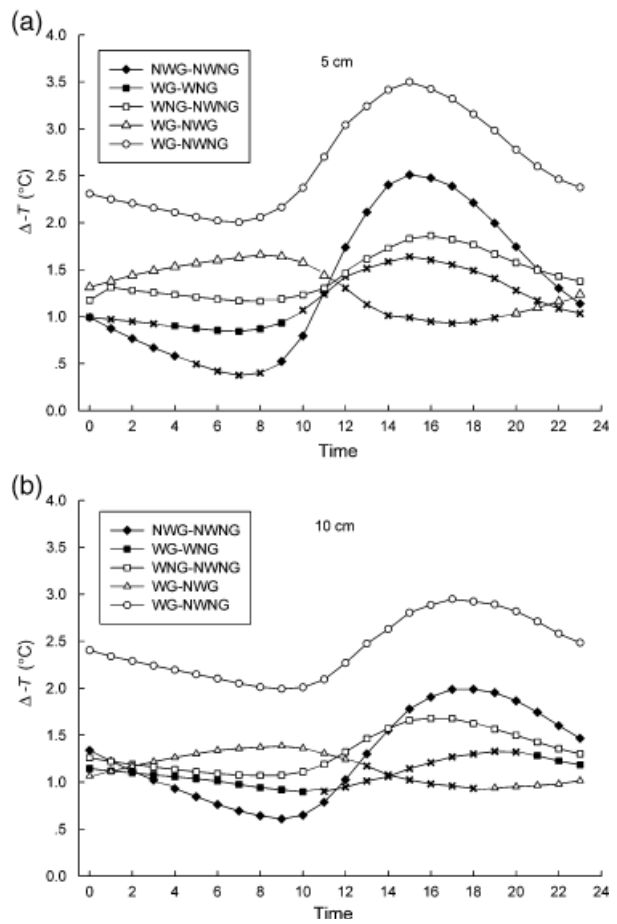
daytime (from 13 to 20 h). The effect decreased with soil depth increase. For example, soil temperature increased by nearly 3.5 °C at mid-day and 2.3 °C at midnight (difference of 1.2 °C) at 5 cm soil depth, whereas it increased by nearly 2.8 °C at mid-day and 2.4 °C at midnight (difference of 0.4 °C) at 10 cm soil depth (Fig. 3).

Soil moisture was mainly affected by day and month, and no significant differences were detected for indi-

Fig. 4 Differences in soil moisture at 30 cm in May and June (first-half of June) between treatments in 2007.

vidual warming or grazing treatments or their interactions for all soil depths in 2006 and 2007 (data not shown). However, in 2007 the effects of warming and grazing on soil moisture varied with day and month as well as soil depth. For example, in 2007, the differences in soil moisture at 30 cm in May and first-half of June were significant between WG and NWNG treatments, and the interaction of warming and grazing decreased the soil moisture by 14.4% and 17.7% in May and first-half of June, respectively, compared with NWNG treatment (Fig. 4).
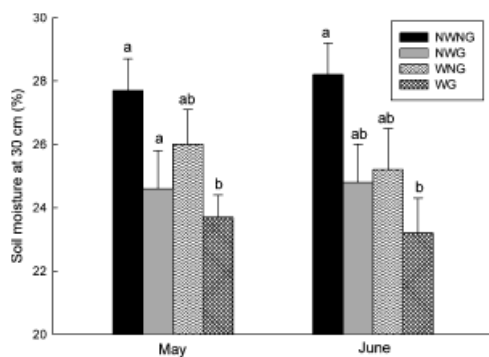
Air and soil temperatures along the elevation gradient

Along the elevation gradient annual air temperatures were 0.1, −1.2 and −2.2 °C at 3200, 3600 and 3800 m, respectively (data not shown). The soil temperature at 5 cm decreased with an increase in elevation, and annual average values over 2 years were 3.2, 2.4 and 0.3 °C at 3200, 3600 and 3800 m, respectively (Fig. 5). However, the patterns of soil temperature differences at 5 cm across elevations differed between the growing (May to October) and nongrowing seasons. For example, during the
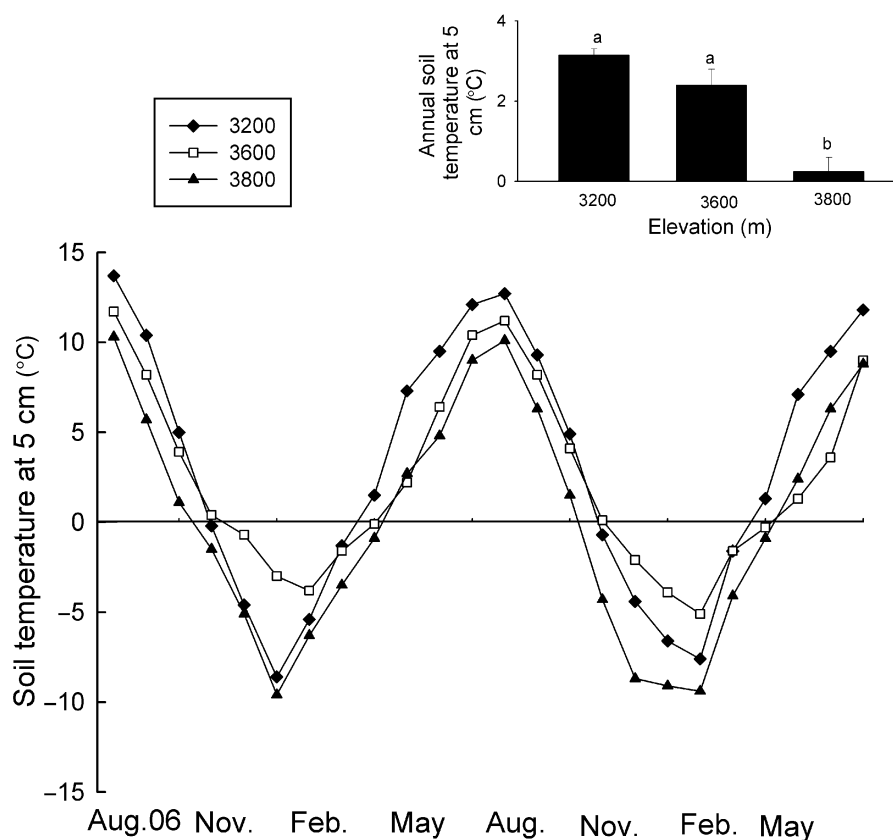
Fig. 5 Dynamics of soil temperature at 5 cm depth at different elevations above sea level (3200, 3600 and 3800 m) from August 2006 to July 2008. Panel on the right corner of the figure is the annual soil temperature at 5 cm depth at different elevations above sea level (3200, 3600 and 3800 m). Same letter means not significant at 0.05 level.
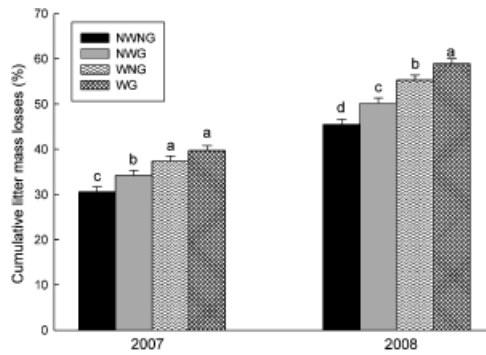
Fig. 6 Cumulative litter mass losses (%) under different treatments in 2007 and 2008. NWNG, no-warming with no-grazing; NWG, no-warming with grazing; WNG, warming with no-grazing; WG, warming with grazing. Different letters mean significant differences between treatments. Mean ± SE is shown in the figure.

growing seasons, the soil temperatures at 5 cm were 9.4, 6.7 and 5.8 °C at 3200, 3600 and 3800 m, respectively, whereas during the nongrowing season they were −3.2, −1.8 and −5.3 °C, respectively, indicating that during the nongrowing seasons, the average soil temperature at 5 cm was the highest at 3600 m because of temperature inversion at the foot of a mountain.

Litter mass losses in the controlled warming–grazing experiment

In the controlled warming–grazing experiment, neither warming nor grazing significantly affected initial litter qualities, including concentrations of C, N, hemicellulose, cellulose, lignin and C : N ratio in the litter in 2006 (data not shown). However, both warming ($F_{1, 12} = 95.974$, $P < 0.001$) and grazing ($F_{1, 12} = 19.534$, $P = 0.001$) significantly increased cumulative litter mass losses by 19.3% and 8.3%, respectively, but there was no significant interaction between warming and grazing ($F_{1, 12} = 0.359$, $P = 0.560$) over the 2-year decomposition period (Fig. 6). However, in 2007 warming (WNG + WG vs. NWNG + NWG) increased ($F_{1, 12} = 23.549$, $P < 0.001$) the average cumulative litter mass losses (19.0%; Fig. 6), NWG increased significantly the cumulative litter mass losses (11.8%; Fig. 6) and WG did not affect significantly the cumulative litter mass losses compared with NWNG, and there was an interactive effect between warming and grazing ($F_{1, 12} = 4.359$, $P = 0.036$) on the cumulative litter mass losses. In particular, there was no significant difference between the combined treatment effect (i.e. WG−NWNG) (9.1%) and the sum (10.4%) of the separate warming (i.e. WNG−NWNG) and grazing (i.e. NWG−NWNG) effects due to the lack of interaction between warming and grazing over the 2-year decomposition periods, indicating that the effects of
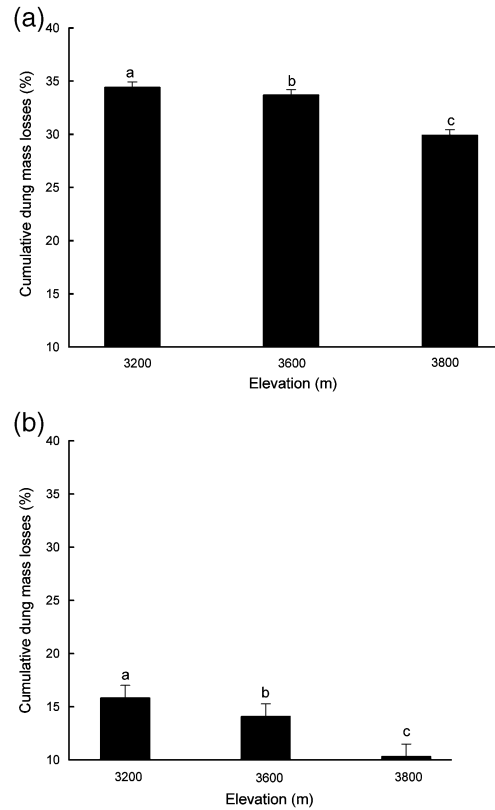

Fig. 7 Annual cumulative mass losses (%) of litter (a) and dung (b) along the elevation gradient.

Table 1 Initial chemical composition of litter and dung

	%C	%N	%HC.	%Cellu.	%Lig.	C : N	Lig : N
Litter*	28.6a	1.4a	19.2a	30.4a	5.8a	19.8b	4.0a
Litter†	29.6a	1.5a	20.3a	30.8a	4.1b	19.8b	2.7b
Dung	26.7a	1.2b	9.3b	16.1b	2.4c	23.1a	2.1b

*Litter, mixed litter of the community under free-grazing.
†Litter, mixed litter of the community under the controlled warming and grazing experiment. HC, hemicellulose; Cellu., cellulose; and Lig, lignin. Values followed by different letters for the same column means significant difference at 0.05 level.

warming and grazing on cumulative litter mass losses were additive.

Litter and dung mass losses along the elevation gradient

Annual mass losses of litter and dung decreased significantly with elevation increase (Fig. 7). Compared with annual mass losses at 3800 m, annual mass losses increased by 15.0% and 12.6% for litter, and 53.4% and 36.5% for dung at 3200 and 3600 m, respectively. The
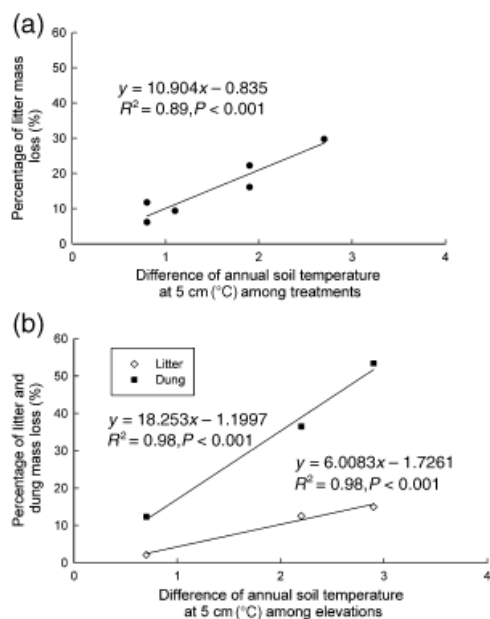
Fig. 8 Temperature sensitivities of annual litter and dung mass losses (% °C^{-1}) in the controlled warming and grazing experiment (a) and along the elevation gradient (b).

concentrations of N, hemicellulose, cellulose, lignin and lignin : N ratio in dung were significantly lower than that in litter, but the C : N ratio in dung was significantly higher than that in litter (Table 1). The average annual litter mass loss (32.7%) for the first-year decomposition period was approximately 2.5 times that of dung along the elevation gradient (Fig. 7a and b).

Temperature sensitivity of litter and dung mass losses

The slopes of the regression equations between the percentage mass losses and the differences of annual soil temperatures at 5 cm depth from different treatments or elevations reveal the temperature sensitivities of the litter and dung mass losses. Although the temperature sensitivity of the litter mass losses measured in the controlled warming and grazing experiment was greater than that measured along the elevation gradient (10.9% vs. 6.0% °C^{-1}), it was smaller than that of the dung mass losses (18.3% °C^{-1}) (Fig. 8), indicating that the dung mass loss is likely to be more sensitive to future warming.

Discussion

Effect of warming on litter mass loss

We noticed that during the first year, warming did not change litter quality of the alpine community. Therefore, the differences of litter mass losses between warming and no-warming treatments were caused directly by

environmental changes. Although soil moisture significantly influences litter mass loss (Robinson et al., 1995; Murphy et al., 1998), warming did not decrease the surface soil moisture significantly during the decomposition periods in our study except for May and early June (Fig. 4). Therefore, the differences in litter mass losses greatly depended on differences of soil temperature in our study which likely changed soil microbial activity (Davidson & Janssens, 2006).

Aerts (2006) reviewed the studies of global warming and litter mass loss in cold biomes and found that decomposition of plant litter is hierarchically controlled by the triad: climate > litter quality > soil organisms. The meta-analysis of experimental warming studies in cold biomes (34 site–species combinations) showed that warming resulted in slightly increased mass loss. However, this response was strongly dependent on the method used: i.e. open top chambers (OTCs) reduced mass losses (Sjögersten & Wookey, 2004), whereas heating lamps stimulated mass loss (Robinson et al., 1995; Rustad & Fernandez, 1998; Verburg et al., 1999; Shaw & Harte, 2001). The low responsiveness was mainly due to moisture-limited mass losses in the warming treatments, especially at mesic and xeric sites. At the wetter sites, this effect was very limited, and at mesic sites the positive effects of warming were balanced by the negative effects of drying, whereas at the xeric sites the drying effect dominated over the temperature effects (Murphy et al., 1998; Aerts, 2006). The negative effects of the OTC treatments suggest that the use of this method leads to stronger drought artefacts than when using heating lamps (Aerts, 2006). In a Rocky Mountain subalpine meadow ecosystem, summer soil-water content was significantly decreased by 25% with heater warming (Harte & Shaw, 1995). However, Wan et al. (2002) found that warming with heaters alone did not affect soil water contents, but clipping and interaction with warming decreased significantly soil water contents. In our study region, generally both warming with heaters in our study or OTC by Klein et al. (2005) and grazing in our study or clipping by Klein et al. (2005) alone did not significant affect soil moisture, but their interactions with day or month decreased significantly the soil moisture early in the growing season (May and early June) (Klein et al., 2005 and Fig. 4 in our study). Because in our study region 80% of annual precipitation occurs during the summer growing season (June–September), which is strongly influenced by the Asian monsoon, soil water contents were approximately 30–40% in the reference plots for all soil depths on a volumetric basis in our study. Therefore, the soil water content recharge through precipitation may have negated any more significant decreases in soil moisture with OTC (Klein et al., 2005) and FATE warming in the

region. Thus, litter mass loss with future climate warming likely will increase because there is sufficient soil moisture in the alpine meadow.

Latitudinal and altitudinal gradients can be considered as natural, long-term analogues for climate change (Aerts, 2006). This loss of litter mass as mediated by both temperature and moisture has been corroborated by natural gradient studies. Berg *et al.* (1993) showed that over a latitudinal gradient spanning from 70 to 31°N showed that average annual temperature explained 18% of the variance in annual mass loss of the Pinus litter, that total annual precipitation explained 30%, and that actual evapo-transpiration (AET) explained 50%, thereby indicating that temperature and moisture in combination are the most important climatic controls on litter decomposition rates. That soil moisture overrides the importance of temperature was also shown by Murphy *et al.* (1998). However, although we did not measure the soil moisture changes with elevation in our study, the temperature change explained about 98% of the variation of the litter and dung mass losses (Fig. 8b), indicating that temperature may be the key control factor for litter and dung mass loss under the wetter conditions (annual precipitation about 600 mm) in our region. Therefore, our study also clearly confirms that litter mass loss will increase in a warmer world if soil moisture is sufficiently high (Murphy *et al.*, 1998; Aerts, 2006).

Effect of grazing on litter mass loss

During the first year, grazing did not change the plant composition or litter quality of the alpine meadow community in the controlled warming–grazing experiment. This lack of response may have been due to the short duration of the grazing treatment. Klein *et al.* (2007, 2008) in our region and Post *et al.* (2008) in a tundra area observed that long-term grazing hinders the shift from graminoids to shrubs in the meadow communities. Also, the total cumulative grazing times in our study were about 4–8 h (2–4 h each year in 2007 and 2008) during the decomposition periods, so the disturbance by trampling and input of excrement from the grazing animals can be ignored. Therefore, similar to warming, the effect of grazing on litter mass loss mainly resulted from environmental change, especially from soil temperature increases because no significant difference of soil moisture between grazing and no-grazing treatments was observed in our study.

The temperature increase of the surface soil (0–20 cm) was almost the same (about average of 1.3–1.4 °C) for WNG (i.e. warming alone) and NWG (i.e. grazing alone) compared with NWNG during the growing seasons. Nevertheless, the former increased the litter mass losses

by approximately 21.5% and the latter by only about 10.4% because their warming patterns were different. In general, grazing resulted in a greater warming of surface soil than did infrared heating during daytime when solar radiation was strong due to shorter canopy height, but the warming of surface soil in the grazed plots at night time was generally less than that of the infrared heated plots (Fig. 3). For example, surface soil temperature (5 cm depth) of NWG did not significantly increase from 5:00 to 8:00 hours in the morning compared with NWNG, and WG did not significantly increase surface soil temperature (5–10 cm) from mid-day to afternoon compared with NWG (Fig. 3). Therefore, infrared warming usually decreased the diurnal temperature range but grazing increased the diurnal temperature range at the surface soil compared with reference plots (Fig. 3). These results suggest that the effects of temperature increase during the daytime on microbial activity may be relatively less than at night-time because higher background temperatures during daytime whereas at night temperatures were more often at or below freezing so that any warming above this threshold accelerated litter mass losses.

Although the effect of warming and grazing on litter mass losses was additive in our study, a number of studies shown that their effects on plant composition and litter quality (Klein *et al.*, 2007) and on the processes of ecosystem (Wan *et al.*, 2005) were not additive. Therefore, the effects of warming and grazing on C cycling remain a complex problem.

Temperature sensitivities of litter and dung mass losses

The temperature sensitivities of litter and dung mass losses will influence the rates of ecosystem C sequestration in a warmer world (Murphy *et al.*, 1998; Jones *et al.*, 2003; Fierer *et al.*, 2005; Davidson & Janssens, 2006). To date, the temperature sensitivity of dung mass loss has been overlooked, although dung mass is the same or more than litter biomass depending on stocking rates in a grazing ecosystem. Our study showed that the temperature sensitivity of annual dung mass loss increased by approximately 18% °C^{-1}, which was about three times that of litter across the elevation gradient (Fig. 8b). Probably the higher dung sensitivity resulted from two reasons. First, the differences in moisture concentration of litter and dung may have had an influence. For example, precipitation events may have kept the relatively bulky dung samples wetter longer, whereas the thin litter samples quickly dried at all elevations. Second, a difference of quality exits between litter and dung (Table 1). A number of studies have shown that litter nutrient concentration, fractions of stable C compounds (e.g. lignin), and C:N and lignin:N ratios are all variables that affect microbial

activity and litter decomposition rates (Melillo *et al.*, 1982; Taylor *et al.*, 1989; Running & Hunt, 1993; Parton *et al.*, 1994; Berg *et al.*, 1996; Murphy *et al.*, 1998). In our study, dung had lower N content and higher C:N ratio compared with that of litter (Table 1), indicating that its quality was lower (Eiland *et al.*, 2001). Fierer *et al.* (2005) found using a 53-day short-term litter incubation that, as decomposition progressed over time, the relative quality of the catabolized C substrates tended to decrease, while the temperature sensitivity of decomposition increased, suggesting that the temperature sensitivity of microbial decomposition is inversely related to litter C quality. Therefore, if more dung excreta is deposited on a meadow from grazing animals with an increase of stocking rate, more C could return more rapidly to the atmosphere from dung decomposition under the future warming. Thus, this finding makes a contribution to quantitative predictions of the effects of future warming on C cycling in grazing ecosystems.

Interestingly, we noticed that the temperature sensitivity of litter mass loss was significantly different between the controlled warming and grazing and the elevation gradient experiments (Fig. 8a and b) probably because of differences of litter quality and approaches used. First, we found that the litter used at the controlled warming–grazing experiment had significantly lower lignin concentration and lignin:N ratio compared with the litter used at the elevation gradient (Table 1). Second, at the controlled warming–grazing experiment, the differences among treatments were mainly caused by soil temperature differences and not changes of litter quality or soil moisture. Cornelissen *et al.* (2007) conducted their decomposition experiment by collecting leaf litter from the predominant species in 33 global change manipulation experiments in circum-arctic-alpine ecosystems (including the HBAMERL station where we did the experiments reported here) and then incubating them all simultaneously in two contrasting arctic zones (temperature difference of $3.7\,^{\circ}C$). They found that the litter decomposition rate was 42% faster in the warmer life zone compared with the colder life zone over 1–2 year, indicating that the temperature sensitivity was approximately $11\%\,^{\circ}C^{-1}$ after 1–2 years of incubation, which is almost the same as our result using the controlled warming and grazing experiment (Fig. 8a). However, the natural climate gradient could not separate the effects due to covarying temperature, precipitation, snow depth and radiation changes on litter mass losses. Although the approach has its disadvantage, it can be credibly used to evaluate the relative temperature sensitivities between different litters and dung because the environmental conditions will be the same at the same elevation gradient.

Conclusions

Warming and grazing both significantly increased litter mass losses on the Tibetan Plateau, and their individual effects on litter mass losses were additive. Greater warming at night-time compared with daytime resulted in faster litter mass losses. Although the dung mass loss was less compared with the litter mass loss, its temperature sensitivity was higher than that of litter mass loss. These results imply that grazing alone may cause slower C loss to atmosphere under no-warming conditions, whereas it may accelerate C loss to atmosphere under future warming conditions through litter and dung decomposition, especially with an increase in stocking rate. Although the approach of using a natural climate gradients can not separate the effects of temperature, precipitation, and other factors on litter and dung mass losses, the relative comparison of the temperature sensitivity of litter and dung mass losses should be credible. Therefore, our study on the temperature sensitivity of litter and dung mass losses has important implications for predictions about future contributions of alpine and possibly also other cold regions to C dynamics worldwide.

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