

Grazing exclusion reduced soil respiration but increased its temperature sensitivity in a Meadow Grassland on the Tibetan Plateau

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Abstract

Understanding anthropogenic influences on soil respiration (R_s) is critical for accurate predictions of soil carbon fluxes, but it is not known how R_s responds to grazing exclusion (GE). Here, we conducted a manipulative experiment in a meadow grassland on the Tibetan Plateau to investigate the effects of GE on R_s . The exclusion of livestock significantly increased soil moisture and above-ground biomass, but it decreased soil temperature, microbial biomass carbon (MBC), and R_s . Regression analysis indicated that the effects of GE on R_s were mainly due to changes in soil temperature, soil moisture, and MBC. Compared with the grazed blocks, GE significantly decreased soil carbon release by 23.6% over the growing season and 21.4% annually, but it increased the temperature sensitivity (Q_{10}) of R_s by 6.5% and 14.2% for the growing season and annually respectively. Therefore, GE may reduce the release of soil carbon from the Tibetan Plateau, but under future climate warming scenarios, the increases in Q_{10} induced by GE could lead to increased carbon emissions.

Introduction

Grassland management is a global concern because it not only affects local herders who depend on productive grasslands for their livelihoods but also the global population through significant feedbacks to climate change (Mcsherry and Ritchie 2013). Many grasslands around the world are currently experiencing unprecedented degradation as a result of enhanced human activities and poor grassland management practices (Milchunas and Lauenroth 1993; Su *et al.* 2005). Although the causes of grassland degradation are varied and not always known, overgrazing by livestock is commonly thought to be one of the most significant contributing factors (Li *et al.* 2013c). Degradation is itcqa a vague term (Harris 2010) which includes several possible problems, including reductions in forage production, expansion of sandy areas, and soil erosion (Liu *et al.* 2008; Wen *et al.* 2013). Currently, grazing exclusion (GE) is one restoration method that has been broadly applied, especially in China (Jing *et al.* 2013; Lu *et al.* 2013; Mcsherry and Ritchie 2013; Laurenson and Houlbrooke 2014; Chen *et al.* 2015). Despite its wide application, however, the effects and efficacy of this remediation technique on ecosystem functions remain unclear.

Soil respiration (R_s) is the largest flux of carbon exchange between the soil and the atmosphere, and even small fluctuations in R_s can result in significant variations in the soil carbon budget (Luo and Zhou 2006). There are also evidences suggesting that small increases in terrestrial R_s can result in significant higher atmospheric CO_2 concentration, and, ultimately, feedbacks to global climate change (Luo and Zhou 2006; Vargas *et al.* 2011). It also has been shown that the amount of carbon stored in grassland soils is influenced by grassland management practices, especially grazing (Conant *et al.* 2001; Maia *et al.* 2009; Mcsherry and Ritchie 2013; Cao *et al.* 2015). Therefore, understanding how GE affects R_s would significantly contribute to our knowledge of grassland soil carbon flux and inform grassland management techniques to combat climate change.

The underlying mechanisms affecting the responses of R_s to GE are still not fully understood, but is well-documented that R_s increases exponentially with soil temperature (Laganière *et al.* 2012; Suseela *et al.* 2012). Furthermore, GE has been found to significantly decrease soil temperature compared to grazed plots due to increased canopy coverage (Susiluoto *et al.* 2008; Schoenbach *et al.* 2012). In addition, GE can modify R_s by altering plant biomass accumulation; for example, one field experiment along a desert steppe in northern China showed that GE increased R_s in proportion to the increases in above-ground biomass (AGB) and below-ground biomass (BGB) (Hou *et al.* 2014). Soil microbial

activity also can be affected by GE through its effects on soil temperature and plant productivity (Lu *et al.* 2013; Nianpeng *et al.* 2013; Zou *et al.* 2013). Indeed, a related field experiment conducted on the Tibetan Plateau found that GE profoundly repressed abundances of genes involved in carbon-degradation due to a corresponding increases in AGB and soil substrate availability (Yang *et al.* 2013). R_s , especially heterotrophic respiration, is strongly associated with microbial communities and their activities (Suseela *et al.* 2012). Although these studies provide evidence that GE may have profound effects on R_s , our understanding of the responses of R_s to GE is still hampered by our poor knowledge regarding the driving mechanisms.

The temperature sensitivity of R_s as indicated by Q_{10} – as used here a measure of the rate of change in R_s as a consequence of raising the temperature by 10°C – links the response of R_s to global climate change (Zhou *et al.* 2007, 2009). Many current land-surface carbon-climate models are based on this parameter (Davidson *et al.* 2012; Suseela *et al.* 2012; Hamdi *et al.* 2013), but few studies have investigated the response of Q_{10} to GE, and the results to date have been inconclusive. One incubation experiment showed that GE decreased Q_{10} (Paz-Ferreiro *et al.* 2012) while another field study indicated that GE increased Q_{10} (Lin *et al.* 2011). Although the effects of GE on Q_{10} are still unclear, the conflicting results suggest that there may be interactive effects of climate warming and GE on R_s , and therefore, the effects of GE on Q_{10} should be incorporated into models of the effects of human activities on R_s . Indeed, understanding how Q_{10} responds to GE is a key to predicting the feedbacks between R_s to GE, but this is currently limited by the paucity of relevant studies.

As one of the highest and youngest Plateau in the world, the Tibetan Plateau extends over 2.5 million km^2 (Zhang and Welker 1996). The majority of the Plateau stands ≥ 3000 m above sea level, and this high elevation makes it particularly susceptible to disturbances caused by human activities. Covering an area of 1.2×10^6 km^2 and accounting for about 48% of the Plateau's land area (Hu *et al.* 2004), the alpine meadow grassland is one of the most widespread types of vegetation on the Plateau. The CO_2 exchange between the meadow grassland and the atmosphere has been the focus of carbon-flux research due to its critical effects on the East Asian summer monsoon (Risch and Frank 2010). Moreover, the Tibetan Plateau is currently experiencing an intensification of human activities, including grazing, and a relatively high temperature increase (IPCC, 2014), rendering the great quantities of soil carbon susceptible to release (Ward *et al.* 2014). The Chinese government is currently imposing GE in areas over one-third of the Tibetan Plateau (Cencetti

2011; Yu and Farrell 2013), but it is largely unknown how GE will affect the release of soil carbon.

To address these knowledge gaps, we conducted a field manipulation experiment in a meadow grassland on the Tibetan Plateau to investigate the effects of GE on R_s . Our aims were to (1) to determine how soil temperature, soil moisture, microbial biomass carbon (MBC), AGB, BGB and R_s respond to GE; (2) to explore the underlying mechanisms associated with the responses of R_s to GE; and (3) to evaluate the effects of GE on Q_{10} .

Materials and Methods

Study site

This study was conducted at the Haibei Grassland Ecological Monitoring Station of the China Meteorological Administration, which is in the town of Xihai, Haiyan County, Haibei Prefecture, Qinghai, China (100°51'E, 36°57'N, 3140 m). The study area has a typical plateau continental climate. The average annual precipitation from 1976 to 2010 was 398.2 mm, with 85% of the rainfall falling during the growing season from May to October. The average annual air temperature is 0.8°C, and the monthly mean air temperature ranges from 13.4 in July to -14.2°C in January. The study site has a sandy loam soil texture, and the soils were classified as mountain brown according to the Chinese soil classification system or as cambisols in the Food and Agriculture Organization classification scheme (Klein *et al.* 2005). The vegetation is typical meadow grassland dominated by *Stipa sareptana* var. *krylovii*, *Stipa purpurea*, *Koeleria cristata*, *Poa crymophila*, *Kobresia humilis*, *Artemisia scoparia*, *Aster tataricus*, and *Medicago ruthenica* (Fig. 1) (Chen *et al.* 2015).



Figure 1. The studied grassland on the Tibetan Plateau.

Experimental design

Twelve 60 m × 30 m blocks were selected for this study in April 2012. Six blocks were placed in a pasture that had been fenced in October 2007 to exclude grazing, and the other six blocks were in an adjacent free-grazing pasture. Buffer zones 5–10 m wide were set between adjacent blocks. Before GE, all blocks had been freely grazed as winter pasture which typically occurred from the end of September to early April. For the GE treatment, the livestock was completely excluded from six blocks. The stocking density of the animals in the grazing pasture was 0.5 yak and 2.5 sheep per hectare which is equivalent to 1.41 tropical livestock units ha⁻¹.

Soil respiration measurements

At the commencement of the field measurements, polyvinyl chloride collars (PVC, 20 cm in internal diameter and 5 cm in height) were randomly inserted 2–3 cm into the soil in each block to measure R_s . All above-ground plant material was removed before the PVC collars were inserted into the soil for both the grazing and GE treatments. After that, all living plants inside the PVC collars were clipped at least 1 day before R_s measurements in order to exclude plant respiration (Zhou *et al.* 2007), but the clipped plant material was left in the collars to decompose. During the growing season, variations of R_s were measured at least twice each month, and diurnal cycles of R_s were measured at 2-h intervals from 08:00 to 20:00 (i.e., 08:00, 10:00, 12:00, 14:00, 16:00, 18:00, and 20:00, local time). During the nongrowing season (NGS), measurements were collected once per day between 8:00 and 12:00 local time. Our data has shown that measurements taken between 8:00 and 12:00 are a good proxy for diurnal mean values (Chen *et al.*, 2015). A soil CO₂ Flux Chamber was attached to a gas analyzer (LI-8100; LI-COR, Inc., Lincoln, NE) for 2 min on each collar to measure R_s and then moved to the next collar. All measurements were carried out on sunny days.

Plant biomass

Above-ground biomass was determined by weighing all vegetation clipped from six 0.5 m × 0.5 m quadrats in each block. BGB was measured by collecting six replicate soil samples (4 cm in diameter) from depths of 0–40 cm. Our previous results showed that >95% of the total BGB is distributed in the upper 0–40 cm of the soils (Chen *et al.* 2015). Both above- and below-ground plant material was washed and then oven dried at 65°C for 72 h before being weighed. AGB and BGB were collected from

all 12 blocks on 14 May, 19 June, 9 July, 15 August, 8 September, and 14 October in 2012.

Soil sampling and microbial biomass carbon

Soil samples were collected at a depth of 0–10 cm at the same time as the BGB samples were collected. For each block, we removed surface litter and collected soil from 0 to 10 cm with the use of a soil auger (4 cm in diameter). Soil samples were cleaned of plant roots and large stones using a 2-mm sieve, and then all visible plant matter was manually removed from the sieved samples. The samples were then packed into a portable refrigerated box and transported to the laboratory where they were stored at 4°C and analyzed within 2 weeks.

Microbial biomass carbon was measured by the chloroform fumigation-extraction method (Brookes *et al.* 1985). Briefly, a 10 g moist soil field sample was fumigated with chloroform for 24 h and extracted with 0.5 mol·L⁻¹ K₂SO₄ in an end-to-end shaker for 1 h, then the supernatant was filtered. Meanwhile, a second 10 g moist soil sample was not fumigated but directly extracted as described above. The amounts of total carbon in the fumigated and un-fumigated soil extracts were determined using a TOC analyzer (Multi N/C 3100; Analytik, Jena, Germany). To account for incomplete extraction, we used an extraction efficiency factor of 0.45 following (Brookes *et al.* 1985). The MBC concentrations were calculated as the difference between fumigated and un-fumigated samples.

Soil temperature and moisture

Soil temperature and soil moisture were recorded with HOBO data loggers (Onset Computer Company, Pocasset, MA). Soil temperature was measured using a thermocouple probe while the soil moisture content was measured using gypsum cast around two concentric stainless-steel electrodes (Delmhorst Instrument Co., Towaco, NJ). Data loggers recorded average soil temperature and soil moisture every 5 min. Soil temperature was measured for the whole experimental period, which was from April 2012 to May 2013. Soil moisture data were unavailable during the NGS due to consistent freezing temperatures.

Data analysis

Monthly variations in R_s were calculated from the daily arithmetic mean values, which were the averages of all measurements made during the same day. Two-way analyses of variance (ANOVA) were applied to examine the

effects of GE, measuring date, and their interactions on R_s . One-way ANOVAs were used to compare the differences in AGB, BGB, MBC, and Q_{10} between the grazing and GE blocks. Significant differences were evaluated at a probability level of $P < 0.05$. Linear or exponential regression analyses was used to assess the influence of MBC, soil temperature, and soil water content on R_s . Multiple linear regression analysis was used to evaluate the overall effects of AGB, BGB, MBC, soil temperature, and soil moisture on R_s . The goodness of fit relative to the number of model parameters was evaluated by the Akaike information criterion (AIC). The model with the smallest AIC value is regarded as the most likely representation of the truth (Akaike 1974; Burnham and Anderson 2004). GE-induced variations in R_s refer to a calculation of R_s in the GE blocks minus the corresponding R_s value for the grazed blocks.

An exponential function was applied to assess temperature sensitivity of R_s by: $R = \alpha e^{bT}$. Where R is the R_s , T is the soil temperature, α is the intercept of respiration when the temperature is 0°C, and b is a constant that was used to calculate Q_{10} using the following function (Zhou *et al.* 2007): $Q_{10} = e^{10b}$. Carbon released from soil was calculated by multiplying daily values of R_s and the number of days between measurements (Niu *et al.* 2010).

Results

Variations in biotic and abiotic factors

Grazing exclusion significantly increased soil moisture, but GE decreased soil temperature relative to the grazed plots during the growing season (Fig. 2). The highest soil temperature and moisture readings occurred from mid-June to mid-August. The mean soil temperature during the growing season was 15.1 and 14.7°C for the grazing and GE blocks, respectively. The mean soil moisture during the growing season was 9.1% and 10.0% for grazing and GE respectively (Fig. 2). During the NGS, no significant difference between blocks was found for soil temperature.

Above-ground biomass increased rapidly from early May to late July when peak values of 251.08 g·m⁻² were recorded for the grazing block and 316.6 g·m⁻² for the GE block. Compared with the grazed blocks, GE significantly increased AGB during the growing season. Although BGB also increased from May to August, no significant GE effect was found for BGB (Fig. 3). Compared with grazing, GE significantly reduced MBC by 6.3%, 9.3%, 9.3%, and 4.6% in June, July, August, and September respectively (Fig. 4).

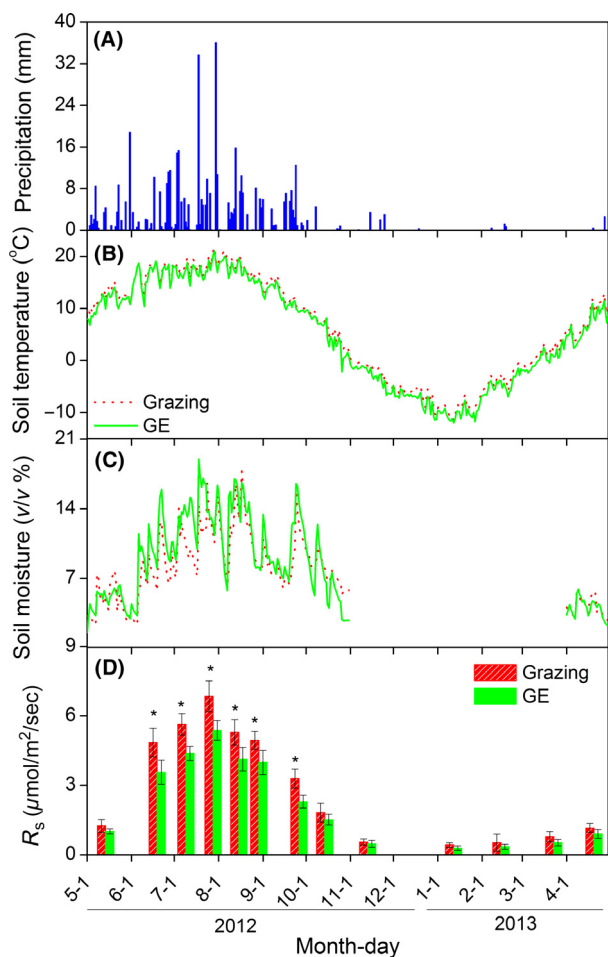


Figure 2. Annual variations of (A) precipitation, (B) soil temperature, (C) soil moisture, and (D) soil respiration (R_s) for the grazing and grazing exclusion (GE) treatments. Vertical bars indicate arithmetic means \pm standard errors for six replicates. Asterisks indicate significant differences for GE effects on R_s at a probability of $P < 0.05$.

Variations in soil respiration

The daily patterns of R_s during the growing season were similar between the grazing and GE blocks (Fig. 5), and for both blocks, the daily peak R_s values coincided with peaks in the daily soil temperatures. Over the longer term, R_s was highest during July and August (Fig. 2D), coincident with the highest soil temperature and moisture values. Annually, R_s ranged from 0.42 to 6.05 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ for the grazing block compared with 0.28 to 5.38 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ for the GE block. R_s varied less during the NGS, ranging from 0.42 to 1.16 and 0.28 to 0.90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ for grazing and GE blocks, respectively (Fig. 2D). Compared with grazing, GE significantly decreased R_s during the growing season as well as

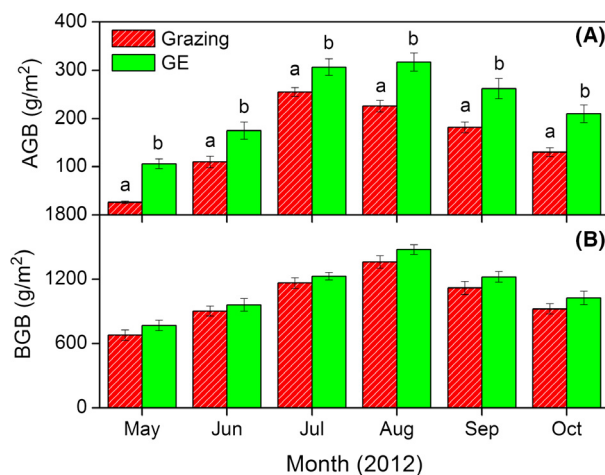


Figure 3. Variations of (A) above-ground biomass (AGB) and (B) below-ground biomass (BGB) for the grazing and grazing exclusion (GE) treatments. Vertical bars indicate arithmetic means \pm standard errors for six replicates; different lowercase letters indicate a significant difference between grazing and GE at a probability $P < 0.05$. No significant differences were found for BGB.

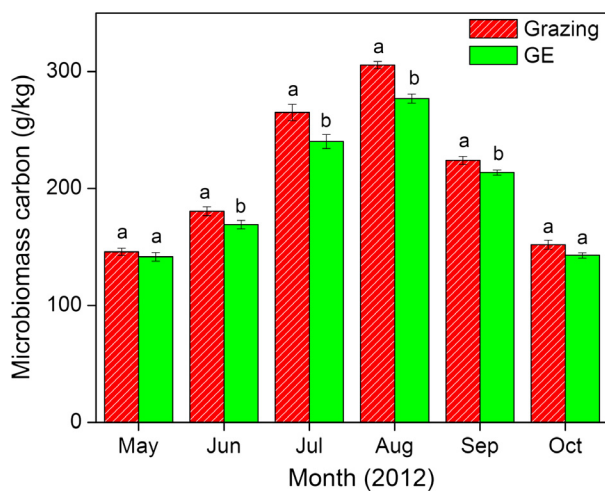


Figure 4. Variations of microbial biomass carbon (MBC) for grazing and grazing exclusion (GE) treatments. Vertical bars indicate arithmetic means \pm standard errors for six replicates; different lowercase letters indicate a significant difference between grazing and GE while the same letters indicate no statistical difference ($P < 0.05$).

annually (Table 1). Monthly differences in the mean R_s values were statistically significant, and there were significant interactive effects between GE and measurement date on R_s both during the growing season and annually (Table 1).

Grazing exclusion decreased the release of soil carbon by 21.40% annually and 23.36% during the growing sea-

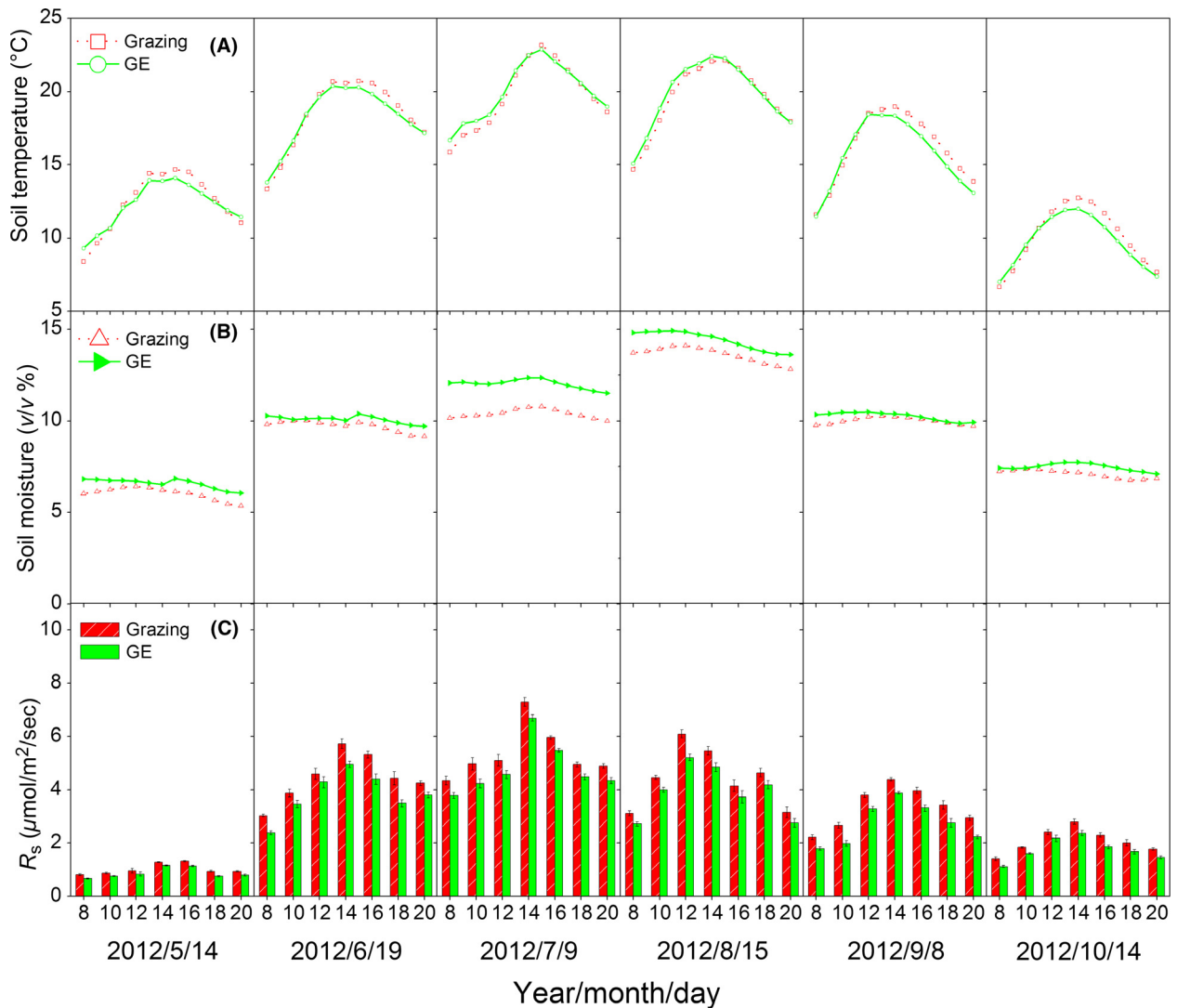


Figure 5. Daily variations of (A) soil temperature, (B) soil moisture at 10 cm depth, and (C) soil respiration (R_s) for grazing and grazing exclusion (GE) treatments during the growing season. Vertical bars show \pm standard errors for six replicates. Values in the x-axis indicate the hours.

Table 1. Results (P values) of two-way analyses of variance on the effects of grazing exclusion (GE), measuring date (D), and their interactions on soil respiration.

Effect	Growing season	Non-growing season	Annual
D	$P < 0.001$	0.461	$P < 0.001$
GE	0.015	0.655	0.034
$D \times GE$	$P < 0.001$	0.766	0.007

values in bold indicate significant difference.

son. Although there was no significant GE effect on R_s during the NGS, the proportion of carbon released by R_s during that period was 21.20% and 23.16% of annual totals for the grazing and GE blocks, respectively (Fig. 6).

Factors affecting soil respiration

R_s was significantly correlated with soil temperature and moisture during the growing season (Fig. 7 and Table 2), and regression analysis showed that changes in soil temperature accounted for 66.4% and 73.5% of the seasonal variations of R_s for grazed and GE blocks respectively. Soil moisture accounted for another 14.9% and 28.3% of the respective variance (Fig. 7). Pearson's correlation analysis showed that GE-induced reductions in R_s were mainly associated with co-occurring changes in MBC and soil temperature (Table 2); indeed, MBC alone accounted for 63.8% of the variations of R_s during the growing season (Fig. 8). In addition, our regression analysis showed that the best model for the effects of GE-induced

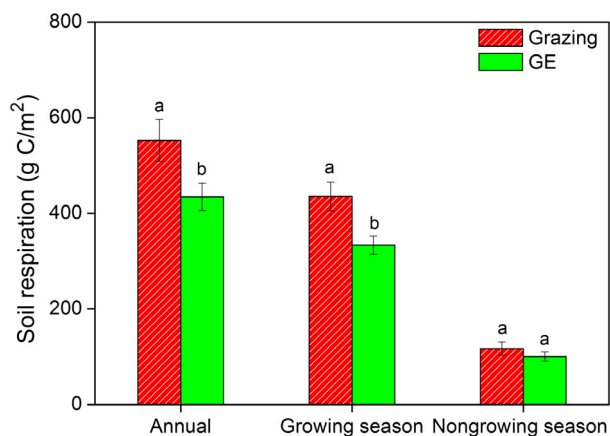


Figure 6. The amount of carbon released by soil respiration (R_s) annually and for the growing season and nongrowing season for the grazing and grazing exclusion (GE) treatments. Vertical bars indicate mean \pm standard errors for six replicates; different lowercase letters indicate a significant difference between grazing and GE while the same letters indicate no statistical difference ($P < 0.05$).

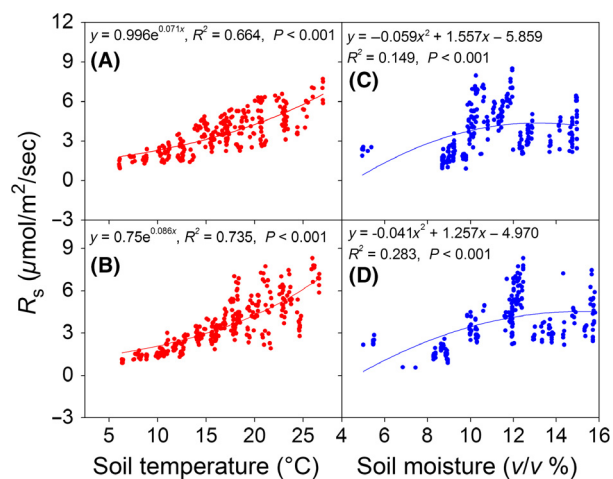


Figure 7. Relationships between soil temperature, soil moisture and soil respiration (R_s) for the grazed blocks (A and C) and the grazing exclusion (GE) blocks (B and D).

variations on R_s included soil temperature, soil moisture, and MBC as predictors (Table 3).

Temperature sensitivity of soil respiration

Q_{10} values were significantly higher for both the GE and grazing blocks during the growing season compared with the NGS (Table 4). During the former, Q_{10} values for all blocks ranged from 1.67 to 4.12, and higher values found at the start and end of the growing season compared with the peak growing season. During the NGS, Q_{10} values from all blocks ranged from 1.62 to 1.84. GE significantly increased Q_{10} values relative to grazing both during the

Table 2. Results (P value) of Pearson's correlation analyses of grazing exclusion induced variations in soil temperature (ST), soil moisture (SM), microbial biomass carbon (MBC), above-ground biomass (AGB), below-ground biomass (BGB) and soil respiration (R_s). Values in italic indicate negative correlation, values in bold indicate significant correlations at $P < 0.05$.

	ST	SM	MBC	AGB	BGB	R_s
ST	1.000					
SM	<i>0.704</i>	1.000				
MBC	0.426	<i>0.407</i>	1.000			
AGB	<i>0.511</i>	0.306	<i>0.914</i>	1.000		
BGB	<i>0.616</i>	0.714	<i>0.508</i>	0.709	1.000	
R_s	<0.001	0.521	0.006	0.897	0.687	1.000

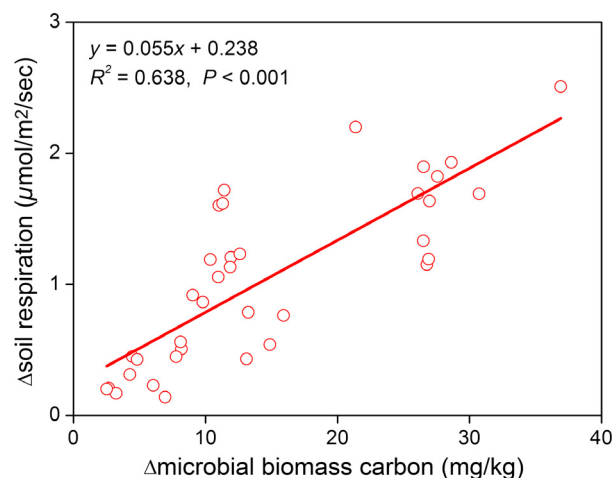


Figure 8. Relationship of grazing exclusion (GE) induced variations in soil respiration (R_s) and microbial biomass carbon (MBC). The data used are only for the growing season because MBC was measured only during that season.

Table 3. Multiple linear regression analysis of the interactive effects of grazing exclusion-induced changes in both biotic and abiotic exclusion-induced changes in soil respiration (R_s). Plus sign (+) indicates entered variables. Akaike information criterion (AIC). See Table 2 for other abbreviations.

Variable	ST	SM	MBC	AGB	BGB	R^2	P	AIC
R_s	+	+				0.378	<0.001	-25.800
R_s	+		+			0.508	<0.001	-34.268
R_s		+	+			0.234	n.s.	-18.304
R_s	+	+	+			0.538	<0.001	-34.514
R_s				+	+	0.005	n.s.	-8.904
R_s			+	+	+	0.202	n.s.	-14.841
R_s	+	+	+	+	+	0.542	<0.001	-30.843

growing season and annually. Significant differences between GE and grazing also were found during the start (May) and end (September and October) of the growing

Table 4. Temperature sensitivity of soil respiration for the grazing and grazing exclusion (GE) blocks.

Period	Grazing	GE
Annual	2.53 ± 0.25	2.89 ± 0.21
NGS	1.62 ± 0.11	1.84 ± 0.21
Growing season	3.25 ± 0.15	3.46 ± 0.13
May	3.53 ± 0.08	4.12 ± 0.26
June	2.59 ± 0.34	3.06 ± 0.40
July	1.67 ± 0.14	2.21 ± 0.48
August	2.30 ± 0.40	3.02 ± 0.52
September	2.36 ± 0.23	3.64 ± 0.17
October	2.80 ± 0.32	3.22 ± 0.30

Values are arithmetic mean ± standard error for six replicates. Bold values indicate a significant difference between grazing and GE ($P < 0.05$).

season, but there was no difference during the peak of the growing season (June, July, and August) or during the NGS (Table 4).

Discussion

Grazing exclusion effects on biotic and abiotic characteristics

Grazing exclusion can have significant effects on an ecosystem's biotic and abiotic characteristics, and these in turn can affect soil carbon fluxes (Mcsherry and Ritchie 2013). In our study, GE significantly decreased soil temperature but increased soil moisture during the growing season (Fig. 2), and these findings are consistent with previous studies in similar areas of the Tibetan Plateau (Cao *et al.* 2004; Klein *et al.* 2005). Increased canopy coverage (Chen *et al.* 2015) was likely to be the primary driver for the lower soil temperatures but higher soil moisture associated with GE. This was largely due to the higher canopy coverage resulting in lower soil surface irradiance and evaporation in the GE sites compared with these in grazing sites (Klein *et al.* 2005).

Grazing exclusion also resulted in significantly higher AGB but not BGB (Fig. 3). Variations of both AGB and BGB were within the ranges reported previously (Yang *et al.* 2009; Jing *et al.* 2013). Increased AGB was the most obvious result of excluding the livestock, and this also likely due to increases in the coverage of some perennial grass species (e.g., short *Kobresia* sp., *K. cristata*, and *Poa angustifolia* L, unpubl. data, J. Chen, X. Zhou, and J. Cao). Other possible explanations for the increased AGB under GE could be related to GE-induced changes in plant phenology (Han *et al.* 2015), enhanced soil nutrient cycles (Lu *et al.* 2015), or altered plant community (Kohyani *et al.* 2011). The nonsignifi-

cant response of BGB to GE is consistent with earlier short-term GE studies (Medina-Roldán *et al.* 2012; Koerner and Collins 2014). One possible explanation was that the short duration of GE in the current study was insufficient to have significant impacts on BGB, since positive responses were usually found in long-term GE studies (Cheng *et al.* 2011; Garcia-Pausas *et al.* 2011). The lack of significant increases in BGB to GE may also be related to the reduction in livestock excreta inputs and consequently altered nutrient cycles, a hypothesis with some support from other studies on the Tibetan Plateau (Fu *et al.* 2014) and Inner Mongolia (Liu *et al.* 2012).

Effects of grazing exclusion on soil respiration

Grazing exclusion significantly decreased R_s both during the growing season and annually (Table 1). GE-induced changes in soil temperature and moisture had significant impacts on R_s (Fig. 7, and Table 2), and this is consistent with results from other regions where reductions in R_s following GE were likely driven by changes in these variables (Paz-Ferreiro *et al.* 2012; Gong *et al.* 2014). A possible explanation for these findings is that virtually all biogeochemical processes associated with R_s are inextricably linked to soil temperature and moisture (Risch *et al.* 2013). The seasonal variations in R_s also followed the patterns of precipitation (Fig. 2), and the impacts of precipitation on R_s have been reported in previous interannual studies (Liu *et al.* 2009; Lu *et al.* 2015). Given the strong impacts of precipitation on R_s , future long-term studies should examine the interactive effects of precipitation and grazing on R_s .

Reductions in MBC are another factor that likely contributed to the lower R_s following GE (Fig. 8), and this was independent of the changes in soil temperature and moisture (Table 2). Previous studies have reported that R_s and MBC were closely related (Suseela *et al.* 2012; Peng *et al.* 2014), and this can be explained by the fact that soil heterotrophic respiration, which accounts for more than half of total R_s in most ecosystems, is mainly the result of microbial growth and decomposition (Tucker *et al.* 2013; Peng *et al.* 2014). Livestock excreta inputs might be a contributing factor to higher MBC in grazed blocks due to their critical roles in supplying labile substrates to fuel microbial growth and metabolic activities (Liu *et al.* 2012; Wang *et al.* 2013). Other studies also have found that MBC can be reduced as a result of depleted labile soil carbon (Song *et al.* 2012; Tucker *et al.* 2013). Our results suggest that grazing-mediated MBC plays important roles in controlling R_s on the Tibetan Plateau, but more research on the mechanisms of MBC variations are needed.

Studies conducted in temperate regions have shown that GE significantly increased R_s due to corresponding increases in plant productivity, litter accumulation, and litter decomposition (Su *et al.* 2005; Li *et al.* 2013b; Gong *et al.* 2014). However, multiple regression analysis in the current study showed that GE-induced variations on R_s were mainly due to changes in soil temperature, soil moisture, and MBC, but not correlated with GE-induced changes in AGB and BGB (Table 3). It is worth noting that GE-induced increases in AGB, BGB and litter accumulation are not necessarily accompanied by increases in litter decomposition (Lindsay and Cunningham 2009; Jing *et al.* 2013). Indeed, results of a recent study conducted near our study site showed that grazing increased litter decomposition by grazing-induced higher soil temperatures (Luo *et al.* 2010). Those findings were possibly related to the thermal constraints on the dynamics of carbon decomposition on the cold Tibetan Plateau where the large amounts of carbon stored in the soils may be particularly susceptible to changes in microclimate and MBC (Lin *et al.* 2011). Our results suggest that the effects of GE-induced changes in MBC and soil temperature and moisture on R_s may have overridden the effects of GE-induced higher plant productivity and possibly higher litter decomposition.

Soil respiration during the nongrowing season

We found no significant response of R_s to GE during the NGS, and this can be explained by the extremely low soil temperature and frozen soil water at our study site (Chen *et al.* 2015). That is, both microbial activities and root respiration are known to be affected by soil temperature and available soil moisture (Li *et al.* 2013a; Prem *et al.* 2014). This explanation is consistent with previous studies which showed that R_s during the NGS is consistently low due to the constraints on microbial and root activities (Pacaldo *et al.* 2013; Wang *et al.* 2014). However, our study did show that the amount of carbon released during the NGS could account for >20% of the annual total at both the grazed and GE blocks (Fig. 6). This finding runs counter to a previous hypothesis to the effect that R_s in winter should approach zero (Fahnestock *et al.* 1998), but it is consistent with some recent results showing that R_s during the NGS accounted for 14–30% of annual total R_s (Elberling 2007; Pacaldo *et al.* 2013). Our results suggest that carbon released during the NGS should be taken into consideration when calculating annual soil carbon flux on the Tibetan Plateau.

We further took the R_s during the NGS into consideration when calculating the annual carbon release. The GE-induced reductions on annual soil carbon release

remained significant, although GE had no significant impacts on the R_s during the NGS (Fig. 6). A previous study also showed that significantly more carbon was stored during the growing season in areas where livestock was excluded, and a more pronounced effect was seen after 3 year of GE compared with 5 year of exclusion (Chen *et al.* 2015). Those results—together with our new findings that GE significantly reduced soil carbon release both during the growing season and annually—indicate that GE may be an effective method for increasing carbon storage on the Tibetan Plateau.

Grazing exclusion effects on temperature sensitivity

Grazing exclusion significantly increased Q_{10} both during the growing season and annually (Table 2), and these increases in Q_{10} imply that the carbon stored in the soils of the Tibetan Plateau may be particularly vulnerable to the climate warming (Luo and Zhou 2006). Increases in Q_{10} induced by GE also have been reported for the Yellowstone National Park, and those effects were attributed to changes in the quality of soil organic carbon (SOC) (Chuckran and Frank 2013). The quality of SOC was not measured in the current study, and this limits our ability to fully explain the GE-induced variations in Q_{10} . Nevertheless, other studies have shown that Q_{10} is closely related to soil temperature and moisture (Lin *et al.* 2011; Chen *et al.* 2015), and therefore, it is possible that the GE-induced changes in soil microclimate also contributed to the relatively high Q_{10} values observed. Regardless of which explanation is correct, our results clearly demonstrate that the dynamics of carbon cycling in grazed and GE areas will differ if the climate changes. More specifically, GE blocks will be more susceptible to increased releases of soil carbon if the climate warms.

Grazing exclusion markedly increased Q_{10} during the start and end of the growing season (Table 2), and significantly higher values of Q_{10} were observed during those periods compared with the peak of the growing season. Our results are consistent with other studies which have shown that grazing decreased Q_{10} during the growing season (Lin *et al.* 2011) and that low Q_{10} values occur during the peak of the growing season (Chen *et al.* 2015). Previous research has shown that Q_{10} is regulated by both temperature and moisture, and higher temperatures and moisture would result in lower Q_{10} (Zhang *et al.* 2010). Therefore, the variations in soil temperature and moisture we observed during the growing season were likely the primary drivers for the monthly variations in Q_{10} . Given these results, one would predict that if the climate warms, GE will cause the largest quantities of carbon to be released at the start and end of the growing season.

No significant GE effect on Q_{10} was found during the NGS (Table 2) when Q_{10} values were lower than those during the growing season. These results appear to be at odds with previous studies which showed that higher Q_{10} values in temperate regions occurred during the NGS (Shi *et al.* 2012; You *et al.* 2013). However, these contrasting results might be explained by the extremely low temperatures and frozen soil water during the NGS on the Tibetan Plateau (Aanderud *et al.* 2013; Wang *et al.* 2014). In fact, recent studies have shown that in cold regions soil moisture—not soil temperature—may be the primary regulator of Q_{10} during the NGS (Aanderud *et al.* 2013; Chang *et al.* 2013; Wang *et al.* 2014). Indeed, it is possible that the low soil temperatures and frozen soil water during the NGS on the Tibetan Plateau inhibited soil microbial activity, thus reducing Q_{10} .

Conclusions

The extremely high elevation of the alpine grassland on the Tibetan Plateau makes it unusually vulnerable to human-induced disturbances. In this study, GE was found to significantly increase AGB and soil moisture but decrease soil temperature, MBC, and R_s . The GE-induced reductions in R_s were closely correlated with decreases in soil temperature and MBC. Compared with the grazed blocks, GE also significantly increased Q_{10} , which indicates that GE blocks may have a higher potential for carbon release under future global warming scenarios. Our results highlight the importance of including interactive effects of human activities and global climate change in models of soil carbon fluxes.

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Conflict of Interest

None declared.

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