Effects of Grazing on Ecosystem CO_2 Exchange in a Meadow Grassland on the Tibetan Plateau During the Growing Season

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Abstract Effects of human activity on ecosystem carbon fluxes (e.g., net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), and gross ecosystem exchange (GEE)) are crucial for projecting future uptake of CO_2 in terrestrial ecosystems. However, how ecosystem that carbon fluxes respond to grazing exclusion is still under debate. In this study, a field experiment was conducted to study the effects of grazing exclusion on R_{eco}, NEE, and GEE with three treatments (free-range grazing (FG) and grazing exclusion for 3 and 5 years (GE3 and GE5, respectively)) in a meadow grassland on the Tibetan Plateau. Our results show that grazing exclusion significantly increased NEE by 47.37 and 15.84 %, and R_{eco} by 33.14 and 4.29 % under GE3 and GE5 plots, respectively, although carbon sinks occurred in all plots during the growing season, with values of 192.11, 283.12, and 222.54 g C m^{-2} for FG, GE3, and GE5, respectively. Interestingly, grazing exclusion increased temperature sensitivity (Q_{10}) of R_{eco} with larger increases at the beginning and end of growing season (i.e., May and October, respectively). Soil temperature and soil moisture were key factors on controlling the diurnal and seasonal variations of R_{eco}, NEE, and GEE, with soil temperature having a stronger influence. Therefore, the combined effects of grazing and temperature suggest that grazing should be taken into consideration in assessing global warming effects on grassland ecosystem CO_2 exchange.

Introduction

Grasslands cover ~ 40 % of the earth's terrestrial surface, which play an important role in the global carbon cycle (Glenn et al. 1993). Currently, many studies have focused on the carbon balance of grasslands, especially with the increasing awareness about global atmospheric CO_2 concentration and its influences on climate and vegetation (Hunt et al. 2004; Melillo et al. 2002). Grassland management strategies affect ecosystem CO_2 exchange (Sjoegersten et al. 2012), nutrient cycling, and even regional climate (Del Grosso 2010). Indeed, interactions and feedbacks between grasslands and climate change will regulate the underlying mechanisms of ecosystem CO_2 exchange. Effects of management practices on grassland ecosystem CO_2 exchange are thus needed to develop optimal strategies for mitigating the effects of climate change and adapting to unavoidable changes in climate.

Grazing exclusion has been widely considered as a simple, effective method for restoring degraded grasslands (Shrestha and Stahl 2008). Many studies have investigated the effects of grazing exclusion on carbon cycles through actual grazing and simulated grazing (Chen et al. 2012; LeCain et al. 2002; Lin et al. 2011; Scott et al. 2004).

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Grazing can lead to changes in nutrient pools and fluxes (Augustine and Frank 2001; Chen et al. 2012; Morris and Jensen 1998; Patra et al. 2007), vegetation coverage (Susiluoto et al. 2008), community composition (Augustine and Frank 2001; LeCain et al. 2002), and soil temperature and moisture (Klein et al. 2004). Moreover, grazing can also alter the exchange rate and temperature sensitivity of ecosystem respiration (R_{eco}) and soil respiration (Augustine and Frank 2001; Bahn et al. 2006; LeCain et al. 2002; Mahecha et al. 2010; Migliavacca et al. 2011), and net ecosystem exchange (NEE, Wang et al. 2011).

Ecosystem CO_2 exchange is driven by photosynthesis as well as plant and soil respiration. Since carbon is more concentrated in plants and soils than in the atmosphere, small changes in ecosystem CO_2 exchange can lead to significant impacts on carbon budgets (Cox et al. 2000; Janssens et al. 2001; Oberbauer et al. 2007). Many processes can potentially affect ecosystem CO_2 exchange and then carbon fluxes between the earth and atmosphere. Modeling studies generally indicate that soil temperature and moisture are two of the most important factors influencing ecosystem CO_2 exchange (Friedlingstein et al. 2006). Although the research community has reached a consensus that grazing will lead to a warmer and drier microclimate (Klein et al. 2005; Zhang et al. 2012b), the effects of grazing exclusion on ecosystem CO_2 exchange are still diverse (Fu et al. 2013; Lin et al. 2011; Morris and Jensen 1998; Polley et al. 2008; Shen et al. 2013; Wang et al. 2011; Wei et al. 2012). These could be attributed to the following explanations: (a) different grassland ecosystems may respond asymmetrically to grazing, (b) grazing history and intensity diversely affect ecosystem carbon processes, (c) different components of the ecosystem may have distinct responses to grazing, and (d) the effects of grazing are combined with and influenced by other biotic and abiotic factors.

Another important issue in the system is temperature sensitivity of R_{eco} under grazing regimes. Some studies found that grazing and simulated grazing decreased the temperature sensitivity of R_{eco} (Lin et al. 2011; Shen et al. 2013), while grazing also increased the temperature sensitivity of R_{eco} (Fu et al. 2013). This disparity likely stems from the different substrate recalcitrances of the study regions combined with local variations in soil temperature and moisture (Lin et al. 2011; Zhou et al. 2009). In addition, recent model results have demonstrated that temperature sensitivity could be related to NEE and ecosystem productivity (Matthews et al. 2007). It is thus imperative to conduct experiments that investigate the whole ecosystem response to grazing exclusion. As the temperature sensitivity of R_{eco} is an important parameter in global climate change models, understanding the temperature sensitivity and seasonality in R_{eco} could lead to major improvements.

At 3,000 m or more above sea level, the Qinghai-Tibet plateau is often called the "earth's third pole," and it is the highest unique territorial unit in the world. Model projections showed that Tibetan climate is expected to become warmer and drier in the future if the levels of the greenhouse gases continue to increase (Callaway et al. 2002). As a result of its high-altitude climate, Tibetan grassland ecosystems are more sensitive to management strategies, including grazing and grazing exclusion, than many other areas (Cao et al. 2004). Climate change and grassland management are likely to affect the Tibetan Plateau grasslands in the future. In fact, the Tibetan and Mongolian Plateaus together play an important role in regional climate because they are a major influence on the East Asia summer monsoon system. Understanding ecosystem CO_2 exchange of this region is therefore critical not only for developing accurate and predictive global carbon cycle models but also for providing information to decision makers concerned with future climate.

The majority of grazing studies have used harvest techniques in the field and laboratory as the means of assessing grazing effects. Although there have been numerous studies that have examined ecosystem responses—including CO_2 exchange—to grazing and grazing exclusion in grasslands worldwide, little information on the grasslands of the Qinghai Tibetan Plateau is available. In particular, diurnal and seasonal variations in CO_2 exchange and the effects of grazing on the ecosystem carbon cycle are not well studied. In this study, we conducted a manipulative field experiment in a meadow grassland on the Tibetan Plateau to investigate the effects of grazing and grazing exclusion on ecosystem CO_2 exchange. Our aims were (1) to characterize the diurnal and seasonal variability in NEE, GEE, and R_{eco}, (2) to investigate how NEE, GEE, and R_{eco} respond to biotic and abiotic factors, and (3) to determine how grazing and grazing exclusion affect the temperature sensitivity of R_{eco} and the carbon budget of the region.

Materials and Methods

Study Site

This study was conducted at the Haibei Grassland Ecological Monitoring Station of the China Meteorological Administration. The site is in the meadow grasslands on the Tibetan Plateau in Xihai, Haiyan County, Qinghai Province, China (100°51′E, 36°57′N, 3,140 m) with a typical plateau-continental climate. The average annual precipitation from 1976 to 2010 was 398.2 mm, and 85 % of the rainfall was concentrated in the growing season (May to October), resulting in the rain and heat in the same period. The average annual evaporation from 1976 to 2010 was

1,455.8 mm (CAWS600-B, AG1-1, DT50), and the annual averaged air temperature was 0.8 °C. The monthly mean air temperature ranged from 13.4 °C in July to −14.2 °C in January (CAWS600-B, HMP45D, DT50). These data were acquired from Haibei Grassland Ecological Monitoring Station of the China Meteorological Administration.

The study site has a sandy-loam soil according to the Chinese soil classification system. The vegetation is typical of a meadow grassland, and it is dominated by *Stipa sareptana var. krylovii*, *Stipa purpurea*, *Koeleria cristata*, *Poa crymophila*, *Kobresia humilis*, *Artemisia scoparia*, *Aster tataricus*, *Medicago ruthenica*, etc. We define the growing season as the period from 20 April to 20 October (175 days); this is based on long-term observations of phenology and plant growth traits made by the Weather Haibei Livestock Experiment Station, China Meteorological Administration (Wei et al. 2008).

Experimental Design

Three 200 m × 200 m plots were selected for this study in April 2012. These were designated as follows: grazing exclusion for 5 years (GE5, fenced in October, 2007), grazing exclusion for 3 years (GE3, fenced in October, 2009), and open to free-range grazing (FG). There was a 10-m-wide buffer zone on each of the four sides of each plot, and each plot was subdivided into six subplots (90 m × 60 m). We selected one Section (1 m × 1 m) in the center of each subplot, so there were six replicates for each plot. Before grazing exclusion, all areas were freely grazed as winter pasture, and after grazing exclusion, the livestock was completely excluded from the GE3 and GE5 plots with fencing. The stocking density of the grazing animals in the FG plot was 0.5 yak and 2.5 sheep per hectare. We measured NEE and R_{eco} diurnally and seasonally throughout the 2012 growing season. In late August, we measured vegetative coverage, aboveground biomass (AGB), and belowground biomass (BGB).

NEE Measurements

Ecosystem carbon fluxes were measured twice a month at 3-h intervals. We first measured NEE with a 0.125 m^3 transparent cubic chamber (0.5 m on each side) attached to an infrared gas analyzer (LI-8100, LI-COR, Inc., Lincoln, NE, USA) that covered all the vegetation inside an aluminum frame. The chamber was placed onto and sealed to an aluminum frame that had been inserted 2–3 cm into the soil to provide a flat base between the soil surface and the chamber. One chamber was in each subplot. All the chambers were the same size, so we had six chambers in each plot. Previous studies have found that this static-chamber method can be successfully used to evaluate subplot-level CO_2 fluxes in grassland ecosystems (Niu et al. 2008; Xia et al. 2009a).

Glass was used for the chamber walls, which allows >90 % of photosynthetically active radiation to pass into the chamber (Xia et al. 2009b). Two small fans were used to mix the air inside the chamber during the measurements. Consecutive recordings of CO_2 concentrations were taken during a 120-s period after 10–30 s, which allowed for steady-state conditions to be reached within the chambers (Niu et al. 2008). Increases in air temperature within the chamber during the measuring period were less than 0.2 °C. Changes in CO_2 mixing ratios were within ~ 10 μmol mol^{-1} of the ambient concentrations, and those changes were too small to significantly alter stomatal conductance, canopy photosynthesis, or soil respiration (Huxman et al. 2004; Xia et al. 2009b).

After making a NEE measurement, the chamber was vented, replaced on the frame, and covered with an opaque cloth. Typically, 30 s after the chamber was covered, CO_2 began increasing and quickly reached a steady sate (Niu et al. 2008). The CO_2 exchange, which was measured when light was eliminated in this way, was recorded as R_{eco}. We measured R_{eco} from 08:00 to 20:00 (at 08:00, 11:00, 14:00, and 17:00 Beijing time) and NEE both during the day and night (at 08:00, 11:00, 14:00, 17:00, 20:00, 23:00, 02:00, and 05:00). The NEE values at night were equal to those of R_{eco}.

GEE was calculated as the difference between NEE and R_{eco}. Positive NEE values thus represent net carbon releases from the ecosystem, while negative values represent net carbon uptake (Niu et al. 2010). Net ecosystem productivity (NEP), R_{eco}, and gross ecosystem productivity (GEP) were calculated by multiplying the daily-integrated values of NEE, R_{eco}, and GEE by the number of days since the last measurements were made (Wan et al. 2009; Xia et al. 2009a). We collected data to characterize seasonal variations at least twice a month at two-week intervals from May to October. Samplings for studies of diurnal cycles were made at 3-h intervals from 08:00 to 08:00 the next day on clear sunny days for each of the three treatments. All terminology and abbreviations used here were adopted from a previous publication (Chapin et al. 2006).

Plant Biomass

A 1 m × 1 m frame with 100 equally distributed grids (0.1 m × 0.1 m) was placed above the vegetation canopy for measurements of plant biomass. Aboveground biomass was measured by clipping vegetation samples from 0.5 × 0.5 m sections (adjacent to the aluminum frame) of the grids on May 15, June 25, and August 20. Belowground biomass was measured in soil samples taken from the 0.5 × 0.5 m subgrids at depths of 0–5, 5–10, 10–20, and 20–40 cm. The roots were first washed and then oven dried at 65 °C for 72 h before being weighed.

Soil Temperature and Moisture

Soil temperature was measured using a thermocouple probe, while soil volumetric water content was measured using gypsum cast around two concentric stainless-steel electrodes (Delmhorst Instrument Co., Towaco, NJ, USA). These measurements were made at 10 cm, and the average soil temperature and soil moisture were Recorded every 5 mins from May to October with the use of HOBO data loggers (Onset Computer Company, Pocasset, MA, USA). The data were averaged to hourly and daily values for Figs. 1d–e and 3 showing soil temperature and soil moisture.

Data Analysis

Each of the six subplots for each treatment was considered an experimental unit, so replicate measurements were averaged by subplot for the data analysis. The statistical comparisons were performed in SPSS 13.0 for Microsoft Windows^{TM} using a one-way ANOVA for AGB, BGB, and canopy cover. Significant differences were evaluated at a confidence level of $P < 0.05$. Repeated measures analyses of variance were used to examine the effects of GE3 and GE5 on diurnal and seasonal variations in NEE, R_{eco}, and GEE (Niu et al. 2010). We evaluated the sensitivity of respiration to soil temperature at a depth of 10 cm by fitting an exponential function to the data from individual treatments during the growing season. The respiration quotient (Q_{10}) was calculated from the following equation:

$$R = ae^{bT},$$

where R is the rate of R_{eco}, T is the soil temperature in °C at a depth of 10 cm, a is the intercept of respiration when temperature is zero, and b is a constant that was used to calculate Q_{10} as follows:

$$Q_{10} = e^{10b}.$$

This method has been successfully used and validated in previous studies (Shi et al. 2012; Zhou et al. 2009).

Results

Variations in Biotic and Abiotic Factors

Precipitation in the study area occurs mainly from May to October, and about 60 % of the growing season precipitation falls in July and August. The maximum monthly precipitation during our study period was 280.5 mm in July (Fig. 1a). Evaporation averaged 4.89 mm day^{-1} during the growing season, and it exhibited similar patterns and variations with time to precipitation (Fig. 1b). Mean, maximum, and minimum air temperatures co-varied with
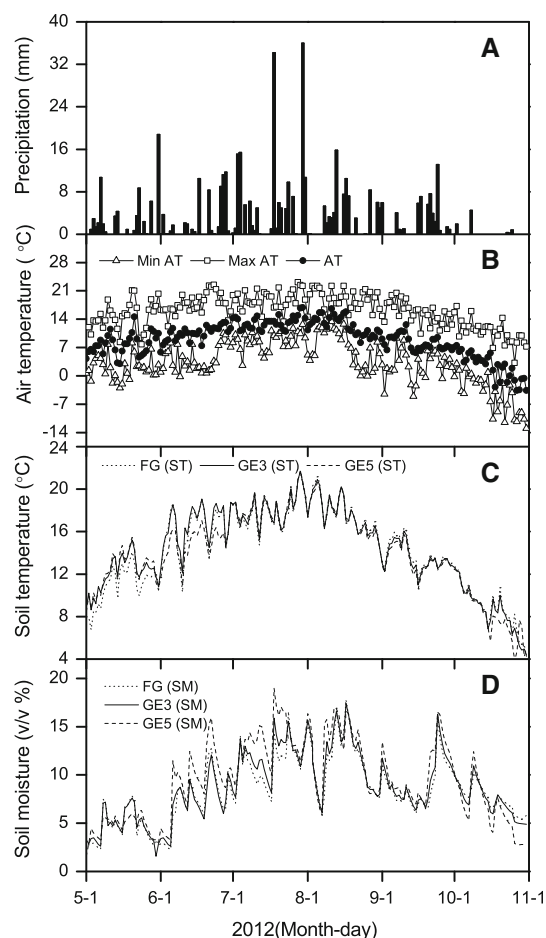

Fig. 1 a Precipitation, **b** mean (AT), maximum (Max AT), and minimum air temperature (Min AT) from May to October, **c** Soil temperature (ST) at 10 cm in the free-range grazing plot (FG, *dotted line*), grazing exclusion for 3 years (GE3, *solid line*) and 5 years (GE5, *dashed line*) plots, and **d** soil moisture (SM) at 10 cm in the FG (*dotted line*), GE3 (*solid line*), and GE5 (*dashed line*) plots

precipitation, which had their respective peak values of 13.29, 18.94, and 8.67 °C in July, respectively (Fig. 1c).

Soil temperature and moisture in all the plots were measured continuously at a depth of 10 cm, with the highest values at the period from mid-June to mid-August. Soil temperature followed the order of FG > GE3 > GE5, while soil moisture showed an opposite trend (Fig. 1d–e). The average soil temperatures during the entire growing season were 15.12 ± 1.76, 14.89 ± 1.77, and 14.74 ± 1.85 °C for FG, GE3, and GE5; soil moisture contents were 9.16 ± 1.42, 9.72 ± 1.48, and 10.03 ± 1.82 % for FG, GE3 and GE5, respectively.

AGB increased rapidly from early May to late July, and then increased only slightly until it reached a maximum of 295.36 and 316.6 g m^{-2} for GE3 and GE5 in August, respectively. Since livestock grazing occurred after July, the maximum AGB was 251.08 g m^{-2} in the FG plots in late July. Exclusion of livestock significantly increased
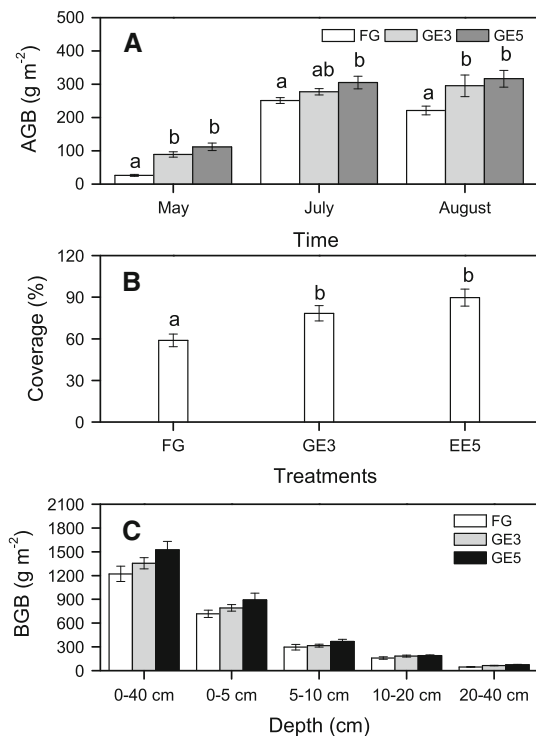
Fig. 2 Variations of **a** averaged aboveground biomass (AGB), **b** canopy cover, and **c** belowground biomass (BGB), and characteristics of their vertical distributions in FG, GE3, and GE5. *Vertical bars* indicate the standard errors of six subplots, *lowercase letters* denote the differences among FG, GE3, and GE5 ($P < 0.05$). (Canopy cover and BGB were measured in mid-August.)

AGB and canopy cover, which continued to increase with grazing exclusion time (Fig. 2a). Significant differences in AGB and plant canopy cover were found between the grazing exclusion and grazed sites (Fig. 2b, $P < 0.05$).

BGB also increased after the animals were excluded with continued grazing exclusion (from 1,220.47 in FG to 1,522.66 g m^{-2} in GE3). About 60 % of the total BGB was found in the 0–5 cm soil layer, and less than 5 % was found in the 20–40 cm soil layer (Fig. 2c). Grazing exclusion led to an increase in root biomass in the different soil layers and thus total BGB, but the vertical distribution of root biomass in different soil layers remained unchanged. The BGB:AGB ratios (R:S) were 5.52, 4.59, and 4.81 for FG, GE3, and GE5, respectively. No significant differences in BGB were found among FG, GE3, and GE5.

Diurnal and Seasonal Variations of NEE, R_{eco}, and GEE

The diurnal fluctuations of soil temperature and moisture at the 10-cm depth, NEE, NEE, and R_{eco} from May to October for the three treatments (FG, GE3, GE5) are presented in Fig. 3. The diurnal dynamics of NEE showed two peaks during peak growing season (June to September),

with the largest CO_2 assimilation rates at 11:00 and the largest CO_2 release rates at 20:00 (Beijing time). In contrast, R_{eco} showed a single peak at about 14:00.

Seasonal means of NEE, R_{eco}, and GEE were the highest in the middle of the growing season (late July or early August), and lower in the earlier and later growing season (Fig. 4). Grazing exclusion did not change the diurnal patterns in NEE, R_{eco}, and GEE, but it enhanced their peak values. When compared with FG, the maxima for NEE, R_{eco}, and GEE in GE3 increased by 28.52, 33.51, and 34.35 %, respectively; and the corresponding increases for GE5 were 14.23, 5.6, and 6.71 %, respectively. Grazing exclusion resulted in proportionately larger increases in GEE than in R_{eco} (Fig. 4). The ratios of R_{eco}: GEE during the growing season for FG, GE3, and GE5 were 0.76, 0.74, and 0.73, respectively.

Generally, grazing exclusion increased NEE, R_{eco}, and GEE. Table 1 presents the seasonally integrated values of these variables, referred to NEP, R_{eco}, and GEP. Compared with these values in the grazed plots (FG), NEP, R_{eco}, and GEP increased by 47.37, 33.14, and 36.55 % in GE3 and by 15.84, 4.29, and 7.06 % in GE5, respectively. All treatments (FG, GE3, and GE5) acted as carbon sinks during the growing season. The amount of carbon removed by livestock grazing during one growing season was about 91.00 g C m^{-2} compared with GE3 and 30.43 g C m^{-2} with GE5.

The mean values for both R_{eco} and GEE in GE3 and GE5 were significantly different from those in FG ($P < 0.001$ and $P = 0.001$ for R_{eco}, and $P < 0.001$ and $P = 0.011$ for GEE), but for NEE, the significant difference only occurred between GE3 and FG ($P = 0.038$, Table 2). The measuring data significantly affected the means of NEE, R_{eco}, and GEE ($P < 0.001$). There were significant interactions of measuring date and GE3 ($P < 0.001$) and of measuring date and GE5 ($P = 0.014$) for R_{eco} compared with the mean of FG (Table 2).

Factors Affecting R_{eco}, NEE, and GEE

R_{eco} at a depth of 10 cm increased exponentially with soil temperature. Indeed, soil temperature explained 59.5, 64.4, and 67.2 % of the seasonal variance in R_{eco} at FG, GE3, and GE5, respectively, throughout the growing season (Fig. 5a, d, g). In contrast, soil moisture only accounted for 37.1, 39.2, and 41.0 %, respectively, for the seasonal variations in R_{eco} (Fig. 6a, d, g).

Both NEE and GEE were also significantly and positively correlated with soil temperature during the growing season. Soil temperature accounted for 53.9, 53.2, and 55.1 % of the seasonal variation in NEE for FG, GE3, and GE5, respectively (Fig. 5b, e, h) and 41.2, 53.9, and 61.2 % in GEE (Fig. 5c, f, i). Soil moisture could explain
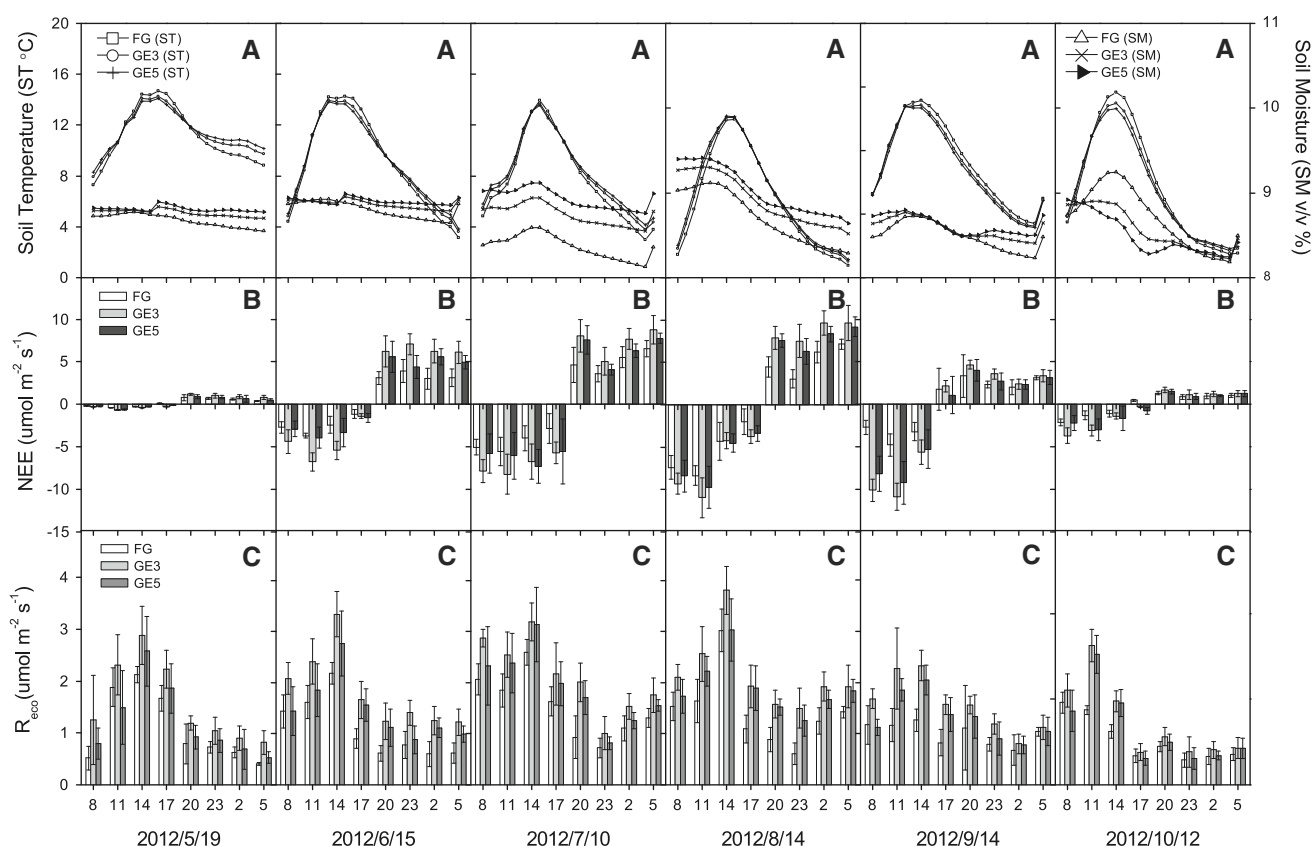
Fig. 3 Diurnal variations of soil temperature (ST) at the 10-cm depth in the free-range grazing site (FG, *open square* with *solid line*), grazing exclusion for 3 years (GE3, *open circle* with *solid line*) and 5 years sites (GE5, *plus* with *solid line*) and soil moisture (SM) at 10 cm in the FG (*open triangle* with *solid line*), GE3 (*cross* with *solid line*), and GE5 (*closed right pointing triangle* with *solid line*). Data are presented as 60-min averages. **b** Diurnal variations of net ecosystem exchange (NEE, mean ± standard error, SE) for FG (*open square*), GE3 (*light gray square*), and GE5 (*dark gray square*). **c** Diurnal variations of ecosystem respiration (R_{eco}, mean ± SE) for FG (*open square*), GE3 (*light gray square*), and GE5 (*dark gray square*). Data for NEE and R_{eco} are presented for 3 h intervals from 08:00 to 08:00 starting on May 19, 2012, June 15, 2012, July 10, 2012, August 14, 2012, September 14, 2012, and October 12, 2012

54.5, 59.1, and 62.9 % of the seasonal variation in NEE at FG, GE3, and GE5, respectively (Fig. 6b, e, h) and 33.9, 39.9, and 45.4 % in GEE (Fig. 6c, f, i).

During the growing season, the mean Q_{10} values were 2.55, 2.72, and 2.94 for FG, GE3, and GE5, respectively, which largely varied from 2.77 to 6.75 for GE5, 2.01 to 6.61 for GE3, and 2.51 to 4.53 for FG (Table 3). The Q_{10} values followed the order GE5 > GE3 > FG except for the FG Q_{10} values in July and September (Table 3). Grazing exclusion increased the Q_{10} values of R_{eco}, and the Q_{10} values were higher at the start and end of the growing season (May and October) than those during the peak growing season (June to September).

Discussion

Understanding the effects of grazing exclusion on ecosystem CO_2 exchange is important for the prediction of carbon dynamic to global climate change and human activities.

Our study showed that grazing exclusion significantly increased soil moisture, AGB, canopy cover, and decreased soil temperature. The diurnal and seasonal variations of R_{eco}, NEE, and GEE were controlled by soil temperature and soil moisture with stronger influence of soil temperature. The meadow grassland is a carbon sink during the growing season for all three treatments (FG, GE3, and GE5), while the longer grazing exclusion (GE5) decreased NEE, R_{eco}, and GEE compared with GE3. Interestingly, grazing exclusion increased temperature sensitivity (Q_{10}) of R_{eco} with larger increases at the beginning and end of the growing season (i.e., May and October), which resulted from a relatively lower temperature at that time.

Effects of Grazing Exclusion on Biotic and Abiotic Factors

Grazing can significantly affect biotic and abiotic factors in the grasslands and then contribute to ecosystem carbon
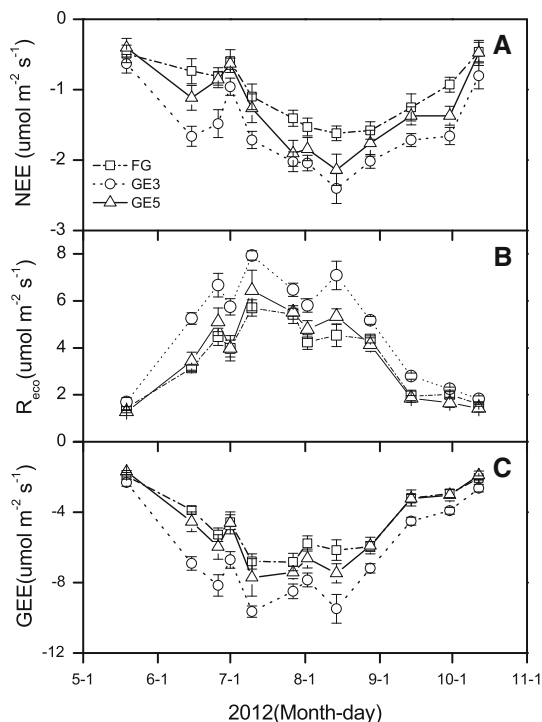
Fig. 4 Seasonal variations of net ecosystem exchange (NEE, **a**), ecosystem respiration (R_{eco}, **b**), and gross ecosystem exchange (GEE, **c**) for FG (*open square* with *dash-dotted line*), GE3 (*open circle* with *dotted line*), and GE5 (*open triangle* with *solid line*) from May to October. *Bars* represent standard error

Table 2 Results (*P* values) of two-way analyses of variances on the effects of grazing exclusion for 3 years (GE3), grazing exclusion for 5 years (GE5), measuring date (*D*), and their interactions on seasonal variation of net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), and gross ecosystem exchange (GEE)

Effect	NEE	R_{eco}	GEE
D	<0.001	<0.001	<0.001
GE3	0.038	<0.001	<0.001
GE5	0.122	<0.001	0.011
GE3 × D	0.068	<0.001	0.07
GE5 × D	0.08	0.014	0.104

cristata, and *Thinlea B1uegrass*) and canopy cover and thus AGB (unpublished data, Chen and Cao 2010–2013). Related research in this region has shown that the ratios of R:S in lightly and heavily grazed meadow grasslands were about 5 and 8, respectively (Cao et al. 2004), in agreement with our results.

Effects of Grazing Exclusion on R_{eco}, NEE, and GEE

Grazing exclusion (GE3 and GE5) significantly increased R_{eco}, NEE, and GEE relative to FG because exclusion promoted both carbon assimilation and release, although carbon sinks occurred at these three treatments during the growing season. Recent clipping and grazing studies have shown conflicting results on the responses of ecosystem carbon fluxes. For example, some studies have shown decreases in R_{eco} (Morris and Jensen 1998; Wang et al. 2011), while others found increases in R_{eco} (Li et al. 2006; Polley et al. 2008). Therefore, the response of R_{eco} to grazing is undoubtedly complex and ecosystem-dependent, which may be a function of grazing intensity and history (Cao et al. 2004).

Grazing may affect R_{eco} through at least four mechanisms: (1) an increase in soil temperature can stimulate R_{eco} (Jia et al. 2007); (2) inputs of urine and fecal material from animals could increase R_{eco}, because these wastes can stimulate plant growth, microbial activity and increase the levels of labile carbon and nitrogen (Jiang et al. 2012); (3) reduced AGB and BGB can have negative effects on R_{eco} (Morris and Jensen 1998); and (4) low organic matter in

dynamics (Kang et al. 2013; Sjoegersten et al. 2012). In our study, grazing exclusion (GE3 and GE5) significantly decreased soil temperature and increased soil moisture, AGB, and canopy cover compared to FG, while they did not significantly affect BGB (Fig. 2). The responses of soil temperature and moisture induced by grazing exclusion were consistent with the results from the previous study near our study site with warmer and drier conditions under high levels of grazing (Klein et al. 2005). However, grazing exclusion caused a greater increase in AGB compared with BGB, resulting in lower R:S ratio in grazing exclusion plots, which was consistent with previous results in the Tibet Plateau and other regions due to grazing and trampling by livestock (Taddese et al. 2007; Wu et al. 2013). Grazing exclusion also significantly increased the proportion of the dominant species (e.g., *Short Kobresia, Koeleria*

Table 1 Total growing season net ecosystem productivity (NEP), ecosystem respiration (R_{eco}), and gross ecosystem productivity (GEP) under free-range grazing (FG), grazing exclusion for 3 years (GE3) and for 5 years (GE5) in 2012 (mean ± standard error)

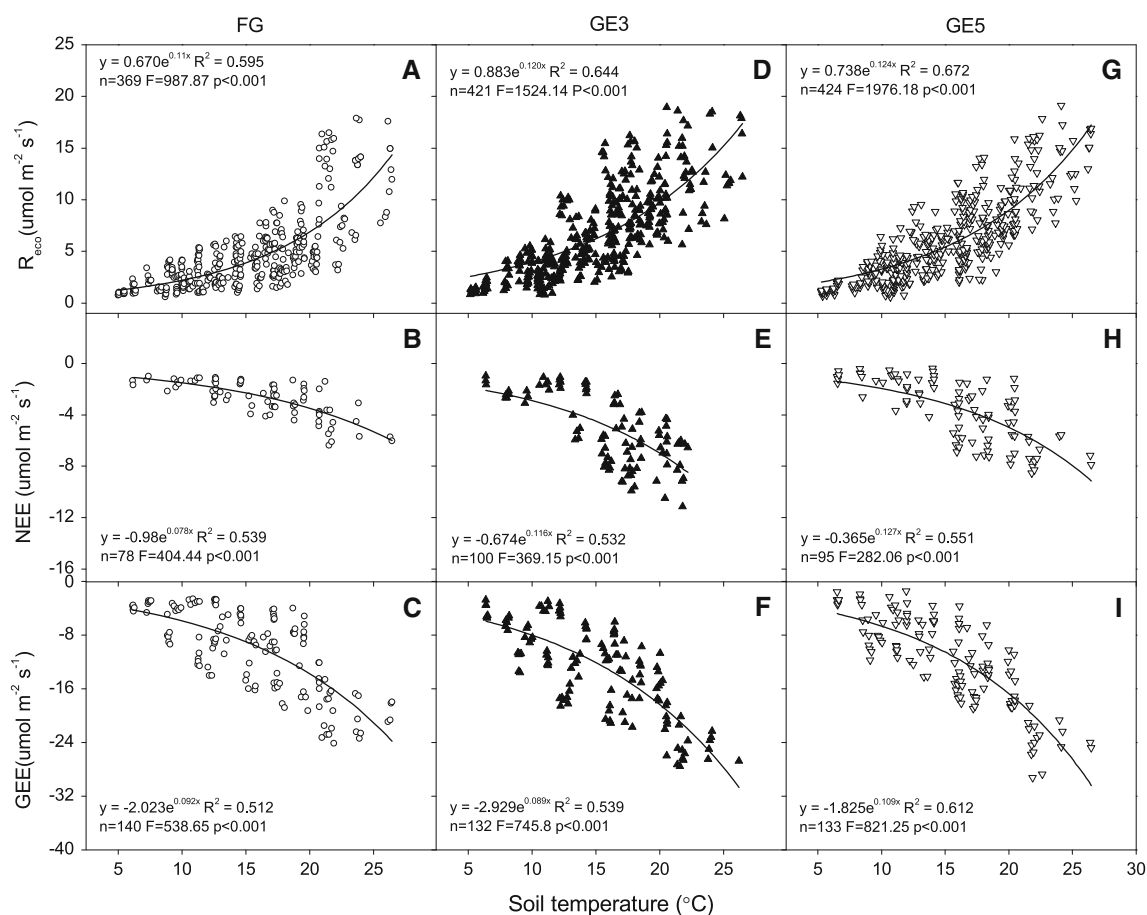|	FG	GE3	GE5
NEP (g C m^{-2})	−192.11 ± 5.97	−283.12 ± 7.73	−222.54 ± 9.54
R_{eco} (g C m^{-2})	610.20 ± 17.07	812.46 ± 18.57	636.41 ± 22.83
GEP (g C m^{-2})	−802.31 ± 11.12	−1,095.57 ± 10.84	−858.95 ± 13.29

Fig. 5 Exponential relationships of ecosystem respiration (R_{eco}), net ecosystem exchange (NEE), and gross ecosystem exchange (GEE) with soil temperature for free-range grazing site (FG, **a–c**), grazing exclusion for 3 years (GE3, **d–f**) and 5 years (GE5, **g–i**) plots during the growing season in 2012

grazing grasslands can reduce R_{eco} because respiration is sensitive to the input of carbon from living plants (Eriksen and Jensen 2001; Raiesi and Asadi 2006). In our study, the R_{eco} rates were higher in the grazing exclusion sites than in the grazed one (Fig. 4b), which reflects the balance between positive and negative effects on respiration. The combined effects of grazing exclusion on AGB, BGB, soil moisture, and residue input to soil on R_{eco} were greater than those caused by the increased temperature and the inputs of urine and fecal material from animals.

Factors that could affect NEE and GEE include AGB, BGB (Zhang et al. 2012b), soil temperature, soil moisture (Lin et al. 2011), canopy cover, community composition, and even soil nutrient concentrations (Chen et al. 2012). As almost all these factors can be influenced by grazing practices, the variations in NEE and GEE among different ecosystems could be related to grazing and management strategies (Cao et al. 2004). Consistent with previous studies in meadow grasslands (Kato et al. 2004; Lin et al. 2011), our results showed that grazing exclusion could

enhance NEE and GEE, which both followed the order GE3 > GE5 > FG (Fig. 4). The increases in NEE and GEE in response to grazing exclusion may result from at least three possible mechanisms. First, increases in AGB caused by grazing exclusion have been shown to increase both NEE and GEE (Kang et al. 2013; Liu et al. 2013). Second, grazing exclusion can alter community composition and structure (Ford et al. 2013; Mills and Adl 2011), particularly causing more stratified vegetative cover (Diaz Barradas et al. 2001; Niu et al. 2009). Indeed, some studies have shown that NEE and GEE can be significantly affected by canopy cover and community composition (Otieno et al. 2011; Soussana et al. 2012; Susiluoto et al. 2008). Our study also found that grazing exclusion significantly increased the canopy cover and AGB of dominant species (*Short Kobresia, Koeleria cristata,* and *Thinlea Bluegrass*) and thus stimulated NEE and GEE (unpublished data). Finally, grazing exclusion led to an apparent increase in soil moisture. The variations of soil moisture in our study can in fact explain the observed
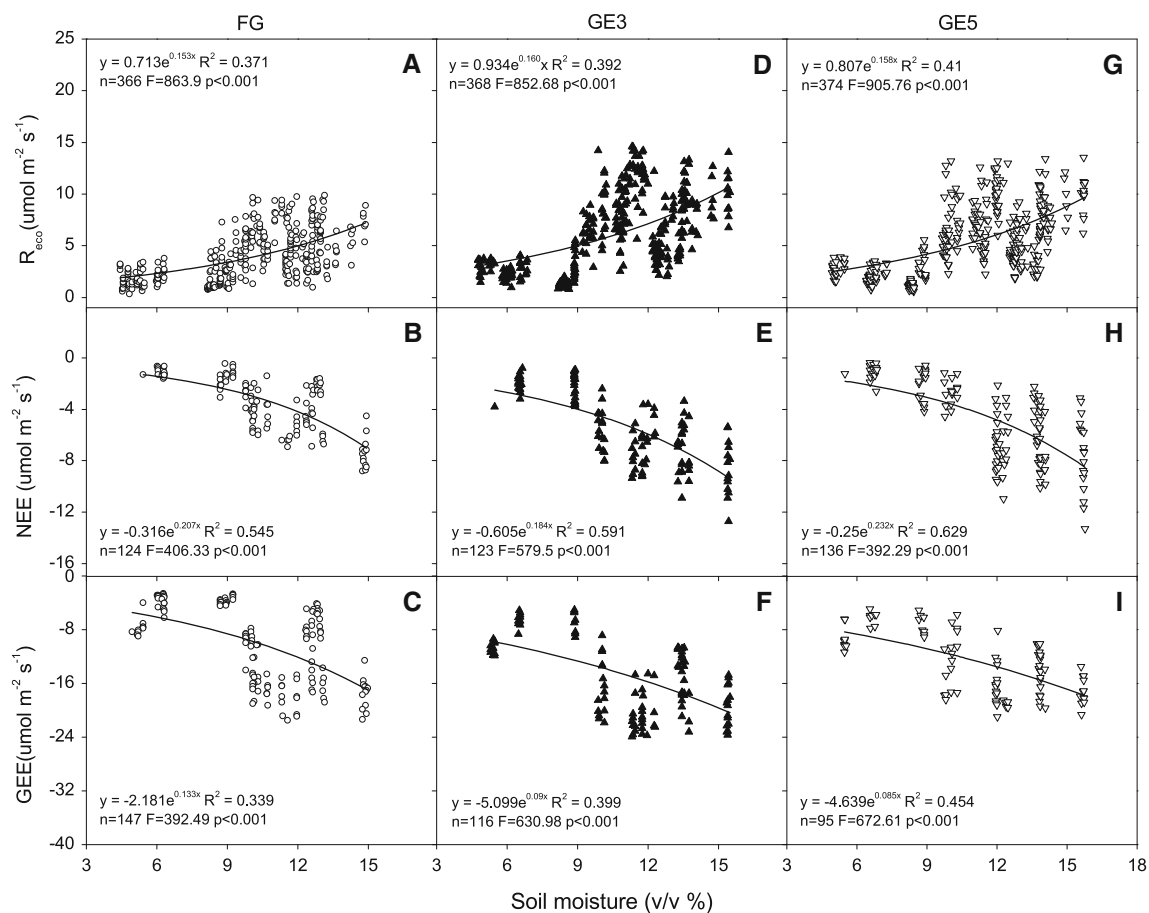
Fig. 6 Exponential relationships of ecosystem respiration (R_{eco}), net ecosystem exchange (NEE), and gross ecosystem exchange (GEE) with soil moisture for free-range grazing site (FG, **a–c**), grazing exclusion for 3 years (GE3, **d–f**) and 5 years (GE5, **g–i**) plots, respectively, during the growing season in 2012

Table 3 Growing season and monthly variations of Q_{10} values for free-range grazing (FG), grazing exclusion for 3 years (GE3), and grazing exclusion for 5 years (GE5)

Period	FG		GE3		GE5	
	Q_{10}	R^2*	Q_{10}	R^2	Q_{10}	R^2
Growing season	2.51	0.68	2.72	0.72	2.94	0.72
May	4.53	0.70	6.61	0.72	6.75	0.71
June	3.19	0.62	3.39	0.66	3.97	0.63
July	2.51	0.61	2.01	0.63	2.77	0.78
August	2.97	0.78	3.00	0.74	3.34	0.64
September	4.35	0.61	3.00	0.72	4.51	0.75
October	3.51	0.47	4.78	0.42	5.18	0.81

* R^2 is the coefficient of determination

greater variability in NEE and GEE in the fenced sites compared with the grazed one (54.5, 59.1, and 62.9 % of the seasonal NEE variation (Fig. 6b, e, h), and 33.9, 39.9, and 45.4 % of seasonal GEE variation for FG, GE3, and GE5 (Fig. 6c, f, i), respectively). The minor decrease in NEE, R_{eco}, and GEE in GE5 compared with GE3 may have

been caused both by a depletion of nutrients—that plot had smaller inputs nutrients from animals compared with GE3 and FG plots (Kang et al. 2013)—and higher residue accumulation which constrained decomposition and photosynthesis (shading effects on lower plants) (Walela et al. 2014).

Carbon sinks occurred in three treatments (FG, GE3, and GE5) during the growing season, and GE3 assimilated more carbon than GE5 relative to FG (Table 1). NEP, R_{eco}, and GEP were calculated by multiplying daily-integrated values of NEE, R_{eco}, and GEE by the number of days since the last measurements. We are aware that this method could lead to uncertainties resulting from rapidly changing environmental conditions and fluxes that would not be resolved with a non-continuous sampling design. Nevertheless, the values for NEP, R_{eco}, and GEP calculated by this method were similar to the results obtained by an eddy covariance method near our study site (Zhang et al. 2012a). Our approach also has been used successfully in previous studies (Wan et al. 2009; Xia et al. 2009a), suggesting that the uncertainties were not a major problem in this study.

Six subplots were selected for replicate measurements in our study to decrease the effects of subplot heterogeneity (including soil temperature, soil moisture, and vegetation cover) on ecosystem carbon fluxes (Scheiner 1998). This is important because the differences of ecosystem carbon fluxes in FG, GE3, and GE5 could then by attributed to variations in soil temperature and soil moisture (Figs. 5, 6). Additionally, it is worth mentioning that long-term observations would be useful in the future studies to clarify the effects of canopy cover, AGB, and BGB on R_s.

The static-chamber method used in our study is a relatively simple approach to measuring gas exchange, but previous studies have shown that it can be successfully used to evaluate subplot-level CO_2 fluxes in grassland ecosystems in Tibetan Plateau and other regions (Lin et al. 2011; Niu et al. 2008; Xia et al. 2009a). What is more, correlation analyses have shown that variations in microclimate (less than 0.2 °C in air temperature) and the build up or draw down of CO_2 (~ 10 μmol mol^{-1}) within the chamber during the measurement interval (less than 150 s) were typically too small to significantly alter stomatal conductance, canopy photosynthesis, or soil respiration (Huxman et al. 2004; Xia et al. 2009b).

The focus of our study was on the diurnal and seasonal variations in NEE, R_{eco}, and GEE, and we acknowledge that these results were limited to only 1 year of measurements. In a wetter or drier year, the results might be different (Scott et al. 2009). Nonetheless, 3-year variations in NEE, R_{eco}, and GEE were generally similar to our current results (unpublished data).

Effects of Soil Temperature and Soil Moisture on R_{eco}, NEE, and GEE

Although many environmental factors affect the biological and physical processes controlling ecosystem CO_2 exchange, changes in R_{eco}, NEE, and GEE are mainly driven by in variations in soil temperature and moisture (Zhou et al. 2009, 2007). Compared with grassland ecosystems in other arid and semi-arid regions constrained by soil moisture, such as Loess Plateau of China (Shi et al. 2011), R_{eco}, NEE, and GEE in our study area may be limited more by soil temperature than soil moisture. This is because precipitation on the Tibetan Plateau is concentrated during the growing season, and soil moisture in our study region is much higher than in the other arid and semi-arid regions. Indeed, fluctuations in diurnal temperatures in meadow grasslands appear to be the main environmental controls on R_{eco}, NEE, and GEE (Fig. 3). Previous studies have shown that aboveground respiration, photosynthesis, plant root respiration, and heterotrophic respiration were all sensitive to changes in soil temperature (Jia et al. 2013; Shi et al. 2012), so that soil temperature explained more of the

variance in R_{eco}, NEE, and GEE than soil moisture. The effects of grazing exclusion increased over time because changes in soil temperature and moisture explained increasing proportions of the variation in R_{eco}, NEE, and GEE (Figs. 5, 6), causing grazing exclusion areas to be more sensitive to environmental changes than grazed sites (Wang et al. 2011). We found the sustained high rates of NEE in July and August, which were consistent with previous results from the Tibetan Plateau (Kang et al. 2013; Kato et al. 2004) but different from semi-arid and arid grassland in other regions (Bell et al. 2012). These may result from moderate monsoon, which means relative high temperature and moisture during this same period in July and August.

Despite the numerous studies that have investigated the response of respiration to temperature, few ones have focused on how R_{eco} varied with temperature over seasonal scales. Q_{10} is considered as the most important parameter used to evaluate the sensitivity of R_{eco} to temperature (Zhou et al. 2010, 2006). In our study, grazing exclusion (GE3 and GE5) increased the Q_{10} values compared to FG (Table 3), which corroborate the implication that grazing exclusion sites were more sensitive to environmental changes than grazed sites. Higher Q_{10} values in grazing exclusion sites were consistent with previous results that removal of plants by grazing or mowing significantly decreased the temperature sensitivity of R_{eco} (Lin et al. 2011), since grazing increased soil temperature and higher temperature would result in lower temperature sensitivity of respiration (Craine et al. 2013; Tucker et al. 2013). The Q_{10} values of R_{eco} ranged from 2.01 to 6.75 from May to October, and the growing season averages were 2.55, 2.72, and 2.94 for FG, GE3, and GE5, respectively (Table 3). These results are comparable with findings of previous studies in meadow grasslands where Q_{10} ranged from 1.3 to 5.6 (Cao et al. 2004; Lin et al. 2011; Zhou et al. 2009). Interestingly, we found higher Q_{10} values at the start and end of the growing season (May and October) compared with the peak growing season (June to September) (Table 3). These findings are different from the results of previous studies that Q_{10} values of R_{eco} decreased as the growing season progressed (Lin et al. 2011). Different variations of soil temperature during growing seasons in the two studies may be the primary reason for the discrepancy of Q_{10} values. Soil temperature in the study of Lin et al. was still high in the September, and there were no data in the October, while both months in our study region had lower temperatures which resulted in higher Q_{10} values. Related results have proved that lower temperature would lead to higher Q_{10} values (Craine et al. 2013; Frey et al. 2013). The seasonal variation of Q_{10} values indicated that there might be some bias when calculating carbon flux by using constant Q_{10} values.

Conclusions

In the meadow grasslands on the Tibetan Plateau in Xihai, Haiyan County, Qinghai Province, China (100°51′E, 36°57′N, 3,140 m), as one of the main human activities in this remote area, grazing exclusion significantly decreased soil temperature while increased soil moisture, AGB, and canopy cover, and resulted in the stimulation of respiration rates (R_{eco}, NEE, and GEE), although it did not affect the seasonal and diurnal variations of R_{eco}, NEE, and GEP. Soil temperature and soil moisture were key factors in controlling the diurnal and seasonal variations of R_{eco}, NEE, and GEE, while soil temperature could explain more of the variance in these variables than soil moisture. There might be interactions between grazing and global climate change, since grazing enhanced carbon storage by stimulation of NEE, while warming promoted R_{eco}. Grazing exclusion increased Q_{10} values, which implied that grazing exclusion sites might more sensitive than grazing site to the climate change. Therefore, grazing and the concomitant variations of seasonal and monthly Q_{10} values should be taken into account in assessing carbon-climate feedbacks.

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