

## Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan plateau

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### ABSTRACT

Intensive studies reveal that there is much uncertainty regarding how ecosystem and soil respiration will respond to warming and grazing, especially in the alpine meadow ecosystem. We conducted a first of its kind field-manipulative warming and grazing experiment in an alpine meadow on the Tibetan plateau to determine the effects of warming and grazing on ecosystem and soil respiration for 3-years, from 2006 to 2008. Generally, warming and grazing did not affect seasonal average ecosystem respiration ( $R_e$ ), and there was no interaction between grazing and warming. However, they significantly affected the  $R_e$  early in the growing season and by the end of the growing season. Warming significantly increased seasonal average soil respiration ( $R_s$ ) by 9.2%, whereas the difference mainly resulted from data gathered early in the growing season, before June 2007. Positive correlations between soil temperature and  $R_e$  and  $R_s$  were observed, and soil temperature explained 63–83% of seasonal  $R_e$  variations during the 3-year study and 19–34% of  $R_s$  variations in 2007. Seasonal  $R_e$  in 2008 and  $R_s$  in 2007 were slightly negatively correlated to soil moisture, but interannual average  $R_e$  decreased with a decrease in precipitation for all treatments. Warming and grazing reduced the  $Q_{10}$  value of  $R_e$  in 2007 and 2008 but did not affect the  $Q_{10}$  value of  $R_s$ . The  $Q_{10}$  values of  $R_s$  were much lower than the  $Q_{10}$  values of  $R_e$  in 2007. These results suggest that grazing may reduce the temperature sensitivity of  $R_e$  and that  $R_e$  was mainly controlled by soil temperature rather than moisture which varied with timescale in the alpine meadow.

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### 1. Introduction

Global mean temperature has increased by 0.76 °C since 1850 and is predicted to rise an additional 1.8–4.0 °C by the end of this century (IPCC, 2007). Elevated global mean temperature can substantially impact the global carbon (C) budget, leading to positive or negative feedbacks to global climate change (Luo et al., 2001; Rustad et al., 2001; Melillo et al., 2002). Recent micrometeorological tower observations by the Eddy covariance method in the Tibetan plateau have demonstrated that different ecosystems were weak carbon sinks with great yearly variation (Kato et al., 2004, 2006; Zhao et al. 2006). It is plausible that strong sensitivity of ecosystem respiration ( $R_e$ ) to temperature

change is the primary cause of the interannual variation in NEE (Nakano et al., 2008; Zhang et al., 2009). Many ecosystem-warming experiments in field scales have studied the effects of the potential increase in temperature on ecosystem carbon exchange (Luo et al., 2001; Bergner et al., 2004; Zhou et al., 2007; Bronson et al., 2008; Kimball and Conley, 2010; Amthor et al., 2010). As  $R_e$  is one of the largest gross fluxes in the annual C budget, small imbalances in photosynthesis and respiration can lead to significant interannual variation in atmospheric  $CO_2$  (Cox et al., 2000; Janssens et al., 2001; Griffis et al., 2004; Grogan and Jonasson, 2005; Trumbore, 2006; Oberbauer et al., 2007). To our knowledge, few studies report responses of ecosystem carbon change to ecosystem warming under controlled warming and grazing conditions. Therefore, information about how  $R_e$  and soil respiration ( $R_s$ ) will respond to climate warming and grazing in the alpine ecosystem of the Tibetan plateau is still rudimentary.

As the largest grassland unit on the Eurasian continent, the Tibetan plateau is mostly situated at 3500 m or more above sea

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level (a.s.l.), and it covers an area of approximately 2.5 million km<sup>2</sup> (Zheng et al., 2000). The Tibetan plateau is experiencing climatic warming and the region is predicted to experience “much greater than average” increases in surface temperatures in the future (IPCC, 2007). Moreover, the Tibetan plateau is one of the areas most sensitive to global climate change (Liu and Chen, 2000). Grazing is one of the most prevalent land uses in the region. Grazing can lead very quickly to changes in nutrient pools and fluxes (Ross et al., 1999; Augustine and Frank, 2001), vegetation cover, and plant community composition in grasslands (Oba et al., 2001; Wang et al., 2003; Klein et al., 2004, 2007), and changes in soil temperature (Hu et al., 2010; Luo et al., 2010), which affect Re (Ma et al., 2006; Lin et al., 2009) and Rs (Cao et al., 2004; Polley et al., 2008). The responses of respiration to warming and grazing are significantly different among different ecosystems with respect to vegetation types and climate conditions. This underscores the need to understand the relative importance of specific factors to Re and Rs at different spatial and temporal scales (Rustad et al., 2001). Therefore, accurate predictions of future climate changes in carbon exchange in the Tibetan plateau strongly depend on the feedbacks of terrestrial ecosystems to grazing as the climate warms, in particular the effects of warming on Re and Rs in the warmer world.

Historical meteorological records and climate model predictions have shown greater increases in daily minimum than maximum temperature and subsequent declining diurnal temperature ranges (Karl et al., 1991; Easterling et al., 1997; Stone and Weaver, 2002; Vose et al., 2005). However, underlying mechanisms for the differential responses of Re and Rs to asymmetrical diurnal warming and their consequent influence on terrestrial ecosystem C cycling remain elusive. To contribute to our understanding of C cycling, and especially to the role of the alpine ecosystem in global CO<sub>2</sub> budgets in future warming conditions, a study was conducted in an alpine meadow on the Tibetan plateau with controlled asymmetrical warming (warmed 1.2 °C during daytime/1.7 °C at nighttime) and moderate grazing on the field scale (Kimball et al., 2008; Luo et al., 2010). The warming manipulations were intended to mimic as closely as possible anticipated major environmental changes at the site by the year 2075. The objectives of this study were to (1) examine the effect of ecosystem warming and grazing on Re and Rs at different timescales (i.e., daily, monthly, seasonally, and interannually) during the growing seasons; (2) examine the relationship between Re and Rs and environmental variables (i.e., soil temperature, soil moisture, and precipitation) and plant biomass; and (3) compare the temperature sensitivity of Re and Rs under different treatments in the alpine meadow region.

## 2. Materials and methods

### 2.1. Controlled warming-grazing experiment

A detailed description of the experimental site, the design of the controlled warming with grazing experiment heated by the free-air temperature enhancement system (FATE), and measurements of soil temperature and soil moisture can be found in Zhao and Zhou (1999), Kimball et al. (2008), and Luo et al. (2010). In brief, in May 2006 eight hexagonal arrays of Mor FTE (1000 W, 240 V) infrared heaters were deployed over vegetation canopy that had previously been heavily grazed by sheep during cool seasons from October to May of prior years at the Haibei Alpine Meadow Ecosystem Research Station, with eight dummy arrays over reference plots. The heaters were controlled using the proportional-integral-derivative-output (PID) control system so as to ensure constant warming between heated and reference plots. The setpoint differences of the vegetation canopy between heated and corresponding reference plots were 1.2 °C during daytime and 1.7 °C at night during the growing season (from May to September). During the

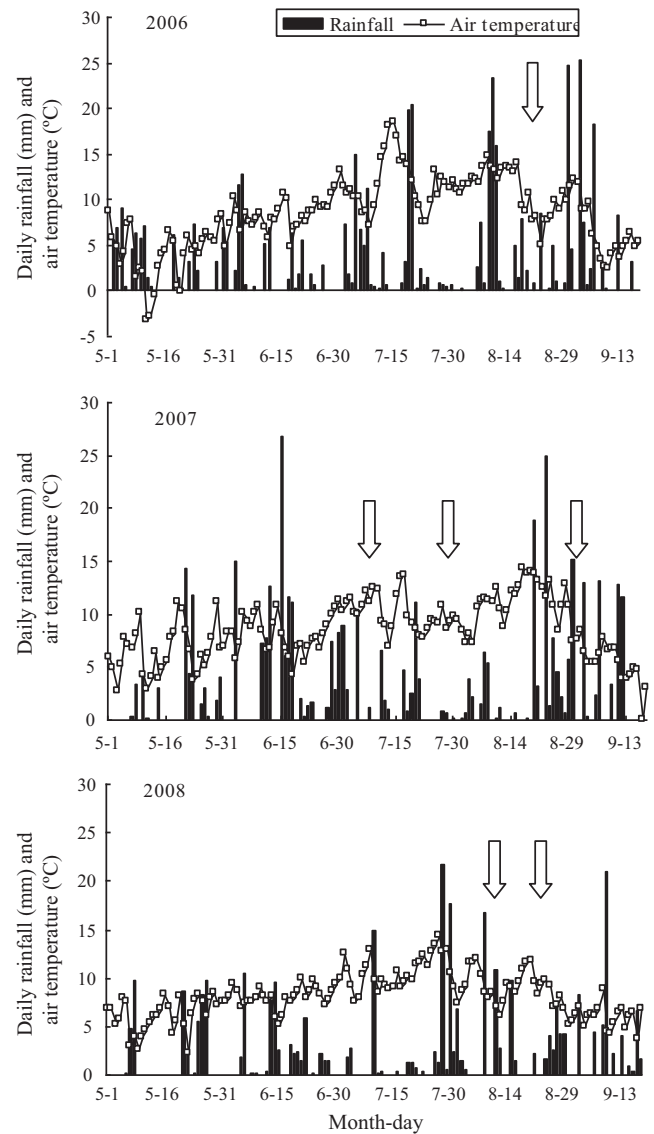
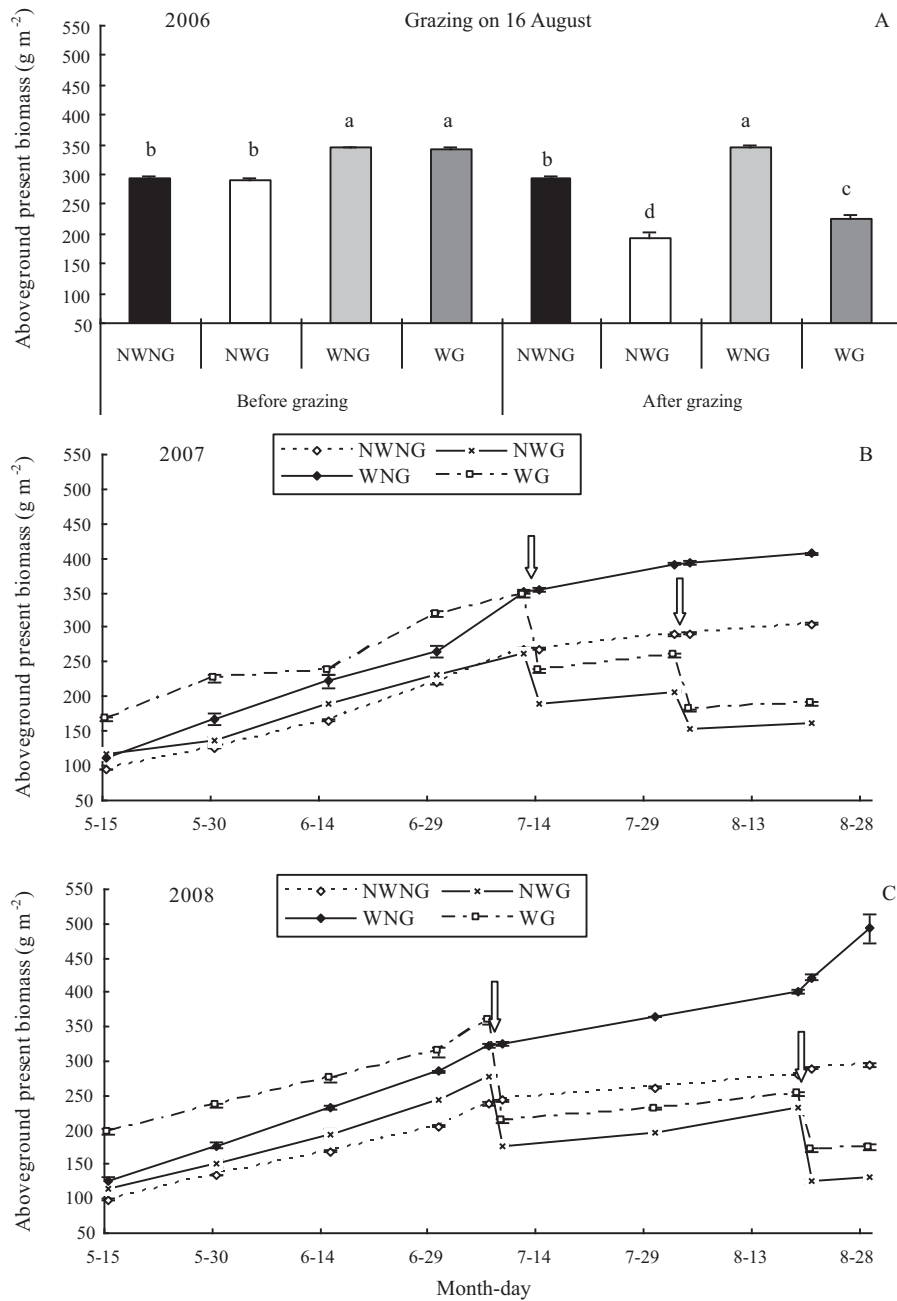


Fig. 1. Distributions of rainfall, air temperature, and grazing time during growing seasons from 2006 to 2008.  $\square$  means grazing time in the figures.

no-growing season (from October to April), because some infrared thermometers were not working, the power outputs of the heaters were manually set at 1500 W per plot. A two factorial design (warming and grazing) was used with four replicates of each of four treatments: no-warming with no-grazing (NWNNG), no-warming with grazing (NNG), 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. One adult Tibetan sheep was fenced in the grazing plots on the morning of 17 August 2006 for approximately 2 h. The canopy height was about 8–9 cm before grazing and 4–5 cm after grazing. The stocking rate roughly corresponded to a moderate stocking rate in the region. Similarly, 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 in 2007, and 8 July and 20 August in 2008. Mean temperature and total rainfall during the growing seasons from 1 May to 20 September in 2006, 2007, and 2008 were 8.4, 8.5, and 8.1 °C, and 449.2, 397.6, and 339.4 mm, respectively. The seasonal rainfall distribution and grazing time are shown in Fig. 1.

At 50 cm inside the edge of each plot, type-K thermocouples (Campbell Scientific, Logan, Utah, U.S.A) were used to automatically measure soil temperature at depths of 5, 10, and 20 cm every 1 min;



**Fig. 2.** Aboveground present biomass in warming and grazing (WG), warming without grazing (WNG), no warming with grazing (NWG), and no warming with no grazing (NWNG) in 2006, 2007, and 2008. Different letters mean significant difference at 0.05 level. → means grazing time in the figures. Mean  $\pm$  SE is shown in the figure.

15 min averages were stored. Soil moisture at depths of 10, 20, 30, and 40 cm was manually measured through a tube in the ground down to a 40 cm depth using a frequency domain reflectometer (FDR; Model Diviner-2000, Sentek Pty Ltd., Australia) at 8:00, 14:00, and 20:00 every day. The soil moisture was expressed as a volume percentage (%) or mm/10 cm. All data were collected from 26 May 2006 to 30 April 2008. The effects of warming and grazing on soil temperature and soil moisture during the experiment were reported before (Hu et al., 2010; Luo et al., 2010).

## 2.2. Estimation of aboveground live present biomass (APB) and belowground biomass

We used a non-destructive sampling method to estimate APB (Klein et al. 2007). The mean height and mean cover of the veg-

etation canopy were measured using a 100 cm  $\times$  100 cm quadrat divided into 400 5 cm  $\times$  5 cm squares. We also conducted this process off-plot from 2006 to 2008 on no-grazing and grazing fields, after which we harvested, dried, separated, and weighed the vegetation for which we had recorded mean height and coverage. The equations that were used to simulate aboveground live present biomass (APB) are:  $APB = -5.7575 + 0.0839C + 5.6656H$  ( $R^2 = 0.84$ ,  $n = 210$ ,  $P < 0.001$  (the  $P$ -value indicates the significance of the test. That  $P$ -value is below 0.05 means the correlation is not a coincidence), where  $C$  was the total canopy cover and  $H$  was mean canopy height in the community. We used a soil-drill sampler with a 4-cm diameter to take 0–10, 10–20, and 20–40 cm soil samples by the end of August each year. These root samples were immediately washed, dried at 80 °C, and weighed.

### 2.3. Measurement of $R_e$ and $R_s$

During the growing seasons, the  $R_e$  was measured every 3–5 days depending on weather conditions in 2006 and every 7–10 days from May to September in 2007 and 2008 using opaque, static, manual stainless steel chambers (Lin et al., 2009). The dimension (40 cm × 40 cm × 40 cm) and architecture of the chambers were the same as those reported by Ma et al. (2006). The fluxes of  $CO_2$  between 9:00 and 11:00 a.m. local time represent one-day average flux according to the diurnal gas flux variation measurement (data not shown). Chambers were closed for half an hour and gas samples (100 ml) were collected every 10 min using plastic syringes. Gas samples of  $CO_2$  concentrations were analyzed with gas chromatography (HP Series 4890D, Hewlett Packard, USA) within 24 h following gas sampling. The gas chromatography configurations for analyzing concentrations of  $CO_2$  and the methods of calculating each gas flux were the same as those described by Song et al. (2003).

$R_s$  was measured every 7–10 days from July to September only during the growing season in 2007 by using opaque, static, manual stainless steel chambers. By the end of April 2007, 16 collars were vertically inserted into the soil to a depth of 5 cm. The aboveground vegetation in these collars was removed thereafter and also a day prior to every respiration measurement campaign. Soil respiration rates were measured at the same time as measurements of  $R_e$ .

### 2.4. Data analysis

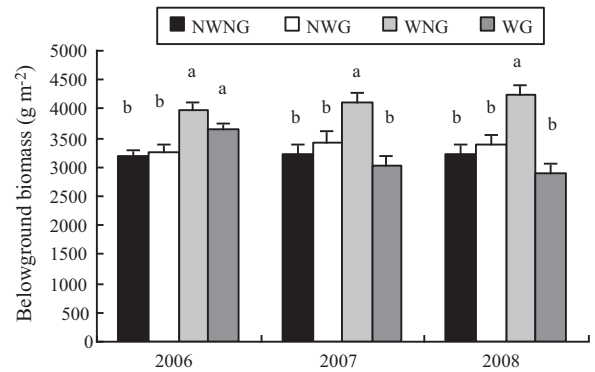
General linear model-repeated measures define factors (SPSS 13.0, SPSS Inc., Chicago, IL, USA) with warming and grazing as the main (between-subject) factors and with sampling date as the within-subject factor including interactions, was applied to test the effects of the main factors on APB and  $R_e/R_s$  (repeated-measures) by sampling date. Multi-comparison of least standard difference (LSD) was conducted for all measured variables within each sampling date using a two-way ANOVA (general linear model-univariate in SPSS) with APB or  $R_e/R_s$  as the dependent variable and warming and grazing as the fixed factors. Because no-grazing treatment was applied on all plots before 16 August 2006, the data during the growing season before and after 16 August 2006 were analyzed separately. The influence of warming and grazing on mean monthly, and seasonal  $R_e/R_s$  during growing seasons were investigated using a two-way ANOVA, in which warming and grazing were crossed (Hu et al., 2010).

Simple correlation and stepwise regression analysis were performed to test the possible dependency of respiration on soil moisture. We assessed the sensitivity of respiration to soil temperature at the depth of 5 cm by fitting exponential functions to the data from individual treatments during the growing season. A respiration quotient ( $Q_{10}$ ) described the change in fluxes over a 10 °C increase in soil temperature and is used to denote the derived temperature sensitivity of respiration. The methods of calculating  $Q_{10}$  were described in detail by Zhou et al. (2007). All significances mentioned in the text were at the 0.05 level.

## 3. Results

### 3.1. Aboveground live present biomass (APB) and belowground biomass

Warming significantly increased APB regardless of grazing, and grazing significantly decreased APB in 2006 (Fig. 2A). In particular, both warming and previous grazing treatments enhanced APB ( $P < 0.05$ ) before the first grazing on 13 July 2007 (Fig. 2B) and 8 July 2008 (Fig. 2C), whereas grazing significantly reduced APB immediately after grazing (Fig. 2B and C). There were no interac-



**Fig. 3.** Belowground biomass in different treatments in 2006, 2007, and 2008. Different letters mean significant difference at 0.05 level. Mean ± SE is shown in the figure.

tions between warming and grazing on APB ( $P > 0.05$ ). Warming significantly increased belowground biomass from 0 to 40 cm in 2006, whereas only warming with no grazing (WNG) significantly enhanced belowground biomass from 0 to 40 cm depth in 2007 and 2008 compared with other treatments (Fig. 3).

### 3.2. Ecosystem respiration ( $R_e$ )

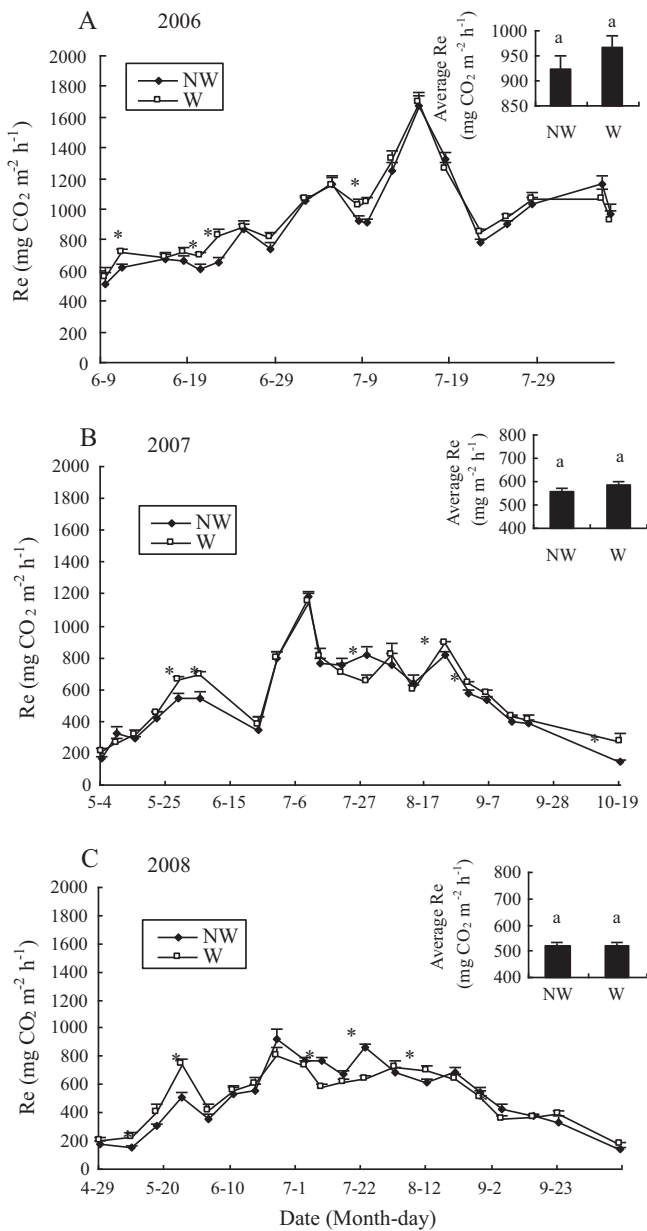
Generally, the effects of warming and grazing on  $R_e$  varied with sampling date and year, and there was no interaction between warming and grazing (Table 1). For example, warming significantly increased  $R_e$  in 5 out of 28 samples in 2006 (Fig. 4A), in 5 out of 20 samples in 2007 (Fig. 4B), and in 2 out of 20 samples in 2008 (Fig. 4C). However, sometimes warming significantly decreased  $R_e$ , as in July 2007 and especially in July 2008 during a drought (Fig. 4B and C). Thus, warming did not significantly affect seasonal average  $R_e$  during the growing seasons during the 3-year experimental period (Fig. 4). Similarly, although grazing did not significantly affect the seasonal mean  $R_e$  during the growing seasons in 2007 and 2008 (Fig. 5B and C), grazing significantly increased  $R_e$  in 6 out of 20

**Table 1**

Ecosystem respiration ( $R_e$ ) from repeated-measure (ANOVA) using year and sampling date as repeated-measures, conducted separately before and after grazing in 2006, and 2007–2008.  $F$  and  $P$  mean  $F$  value of ANOVA result and statistical significant, respectively.

Year	Period	Model	$F$	$P$	
2006	Before grazing	Warming (W)	1.47	0.246	
		Date (D)	113.99	<0.001	
		W × D	1.55	0.068	
		W	3.63	0.081	
		After grazing	Grazing (G)	36.86	<0.001
			W × G	2.55	0.137
	D		235.79	<0.001	
	W × D		4.09	<0.001	
	G × D		3.63	0.002	
	W × G × D		1.31	0.252	
	2007–2008	W	0.44	0.519	
		G	2.30	0.155	
W × G		0.30	0.595		
Year (Y)		21.90	<0.001		
W × Y		1.35	0.269		
G × Y		1.20	0.295		
W × G × Y		1.22	0.291		
D		147.10	<0.001		
W × D		4.08	<0.001		
G × D		2.98	<0.001		
W × G × D		0.89	0.592		
Y × D		17.99	<0.001		
W × Y × D	2.47	<0.001			
G × Y × D	1.37	0.144			
W × G × Y × D	0.77	0.740			

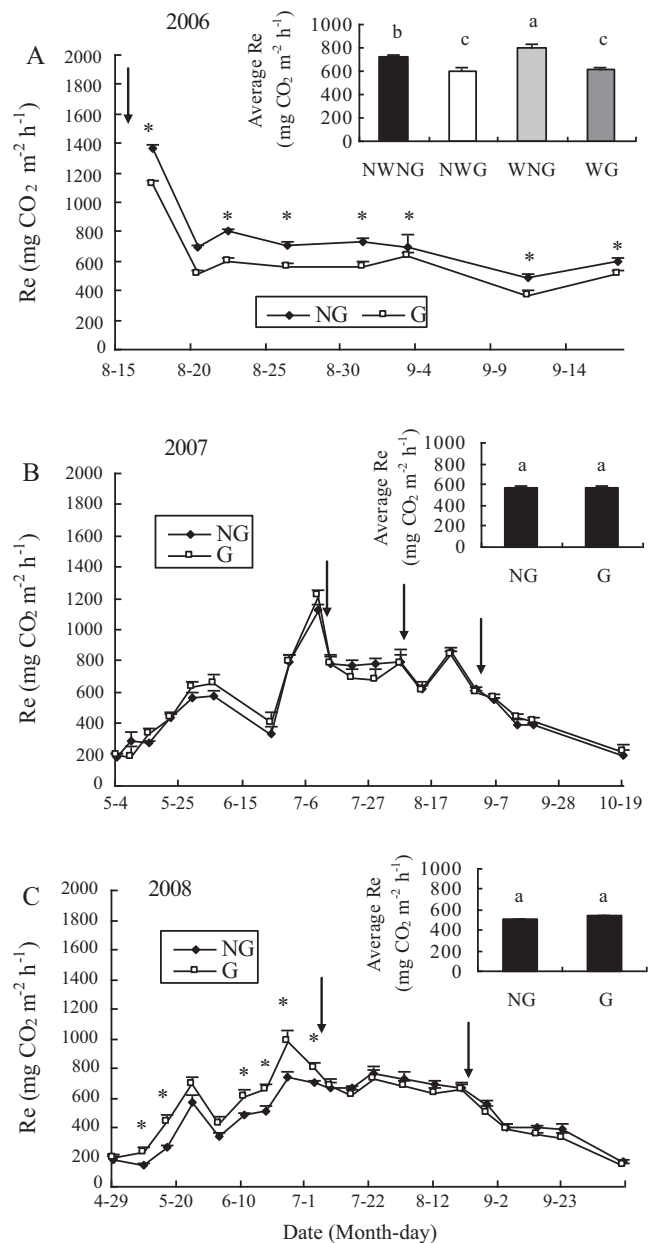




**Fig. 4.** Re in warming (W) and no warming (NW) plot during the growing time in 2006, 2007, and 2008. The panel is seasonal average Re. Different letters mean significant difference at 0.05 level. \*Significant difference between W and NW. Mean  $\pm$  SE is shown in the figure.

samples in 2008 (Fig. 5C). However, grazing significantly decreased average Re by approximately 20%, and WNG significantly increased average Re by 12.4% compared with NWNG from 17 August to 17 September in 2006 (Fig. 5A), and there was no interaction between warming and grazing during the period.

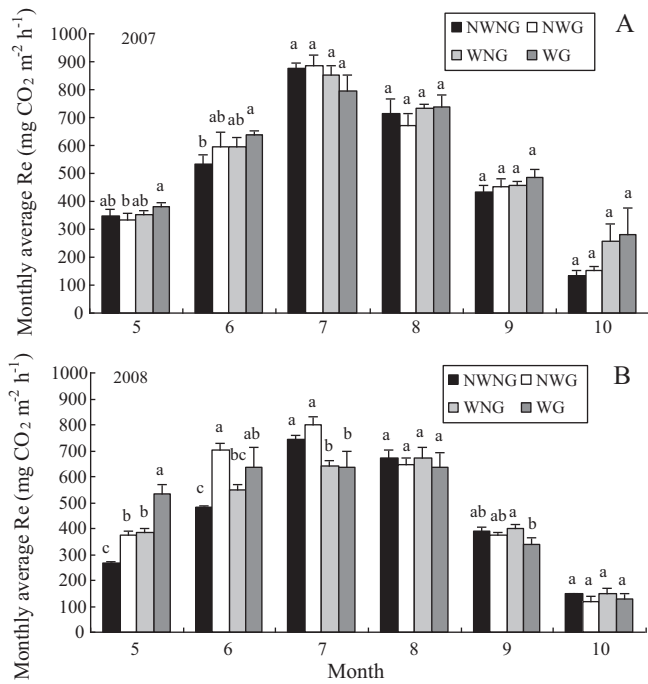
The effects of warming and grazing on Re varied with month, and warming or grazing modified the response of monthly Re to grazing or warming in 2007 and 2008 (Fig. 6A and B). For example, only WG significantly increased Re by 14.5% compared with NWG in May 2007, and by 19.8% compared with NWNG in June 2007, respectively (Fig. 6A). Warming regardless of grazing significantly enhanced Re by 41.6–43.1% in May and decreased Re by 16.5–25.9% in July 2008 (Fig. 6B). Grazing showed a trend ( $P=0.086$ ) to increase seasonal average Re by 9.3% during the growing season in 2008. Moreover, grazing enhanced monthly average Re by 31.3% ( $P<0.001$ ) in May and 32.1% ( $P<0.001$ ) in June 2008, whereas WG



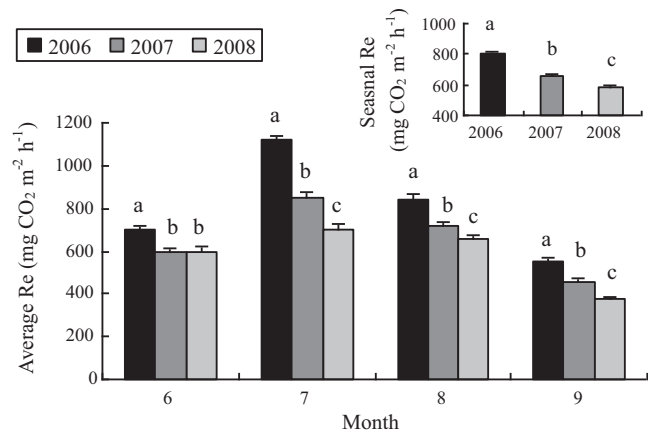
**Fig. 5.** Re in grazing (G) and no grazing (NG) plot during the growing time in 2006, 2007, and 2008. The panel in (A) is average Re for four treatments after grazing in 2006. The panel in (B and C) is seasonal average Re in G in an NG plot. Different letters mean significant difference at 0.05 level. \*Significant difference between G and NG. Mean  $\pm$  SE is shown in the figure.

decreased monthly average Re by 17.6% compared with WNG in September 2008 (Fig. 6B).

To investigate the annual variation in average Re during the growing seasons, we calculated the total average values and pooled all data for all treatments because there was no significant difference in seasonal mean Re among the different treatments. Total monthly and seasonal average Re during the growing seasons in 2006, 2007, and 2008 showed significant differences (Fig. 7) due to different climate conditions, and, especially, different precipitation levels (Fig. 1). The Re was the greatest in 2006, probably because the rainfall was normal in 2006, whereas the experimental site experienced a light drought in 2007 and a heavy drought in 2008. On the other hand, 2006 was the first experimental year when grazing occurred only once, on 16 August, which allowed for higher aboveground biomass before grazing.



**Fig. 6.** Monthly mean of Re in different treatments in 2007 and 2008. Different letters mean significant difference at 0.05 level. Mean ± SE is shown in the figure.



**Fig. 7.** The total average values pooled all data for all treatments in 2006, 2007, and 2008. The panel is seasonal average Re in 2006, 2007, and 2008. Different letters mean significant difference at 0.05 level. Mean ± SE is shown in the figure.

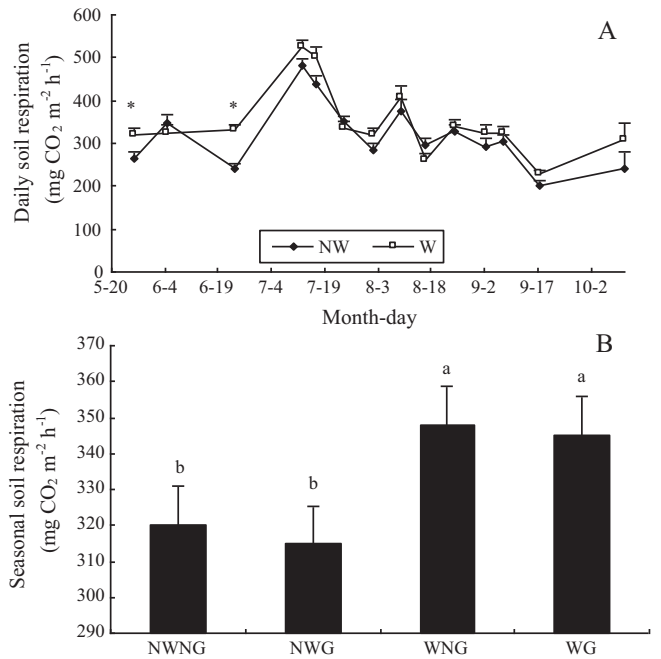
3.3. Soil respiration (Rs)

The impact of warming on Rs varied with sampling date or month (Table 2 and Fig. 8). Generally, although warming obviously increased seasonal average Rs by 9.2% during the growing season

**Table 2**

Soil respiration (Rs) from repeated-measure ANOVAs using sample date as repeated-measures in 2007. F and P mean F value of ANOVA result and statistical significant, respectively.

Model	F	P
Warming (W)	7.55	0.018
Grazing (G)	0.15	0.706
W × G	0.02	0.896
Sample date (D)	34.88	0.000
W × D	1.93	0.108
G × D	1.69	0.156
W × G × D	1.11	0.362



**Fig. 8.** Rs (A) in warming (W) and no warming (NW) plot and monthly average Rs (B) for four treatments during the growing time in 2007. Different letters mean significant difference at 0.05 level. \*Significant difference between W and NW. Mean ± SE is shown in the figure.

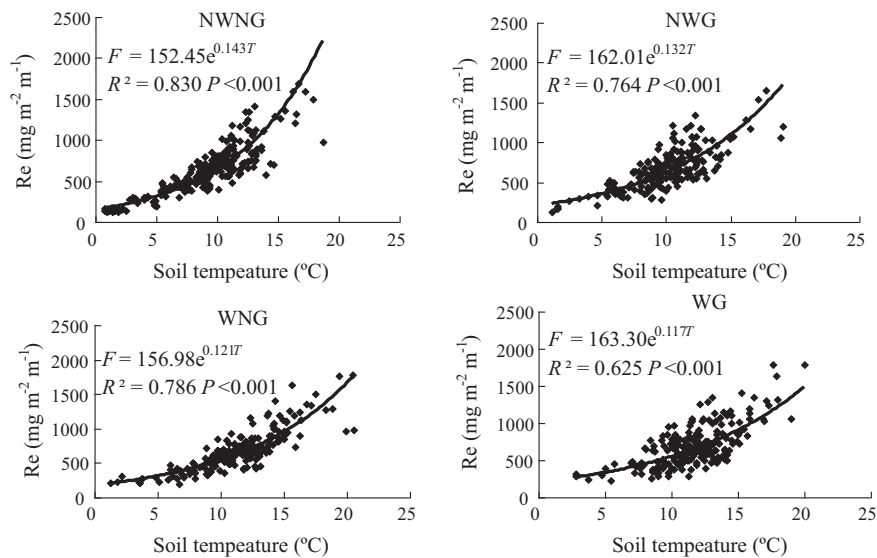
in 2007, it only increased monthly average Rs by 29.5% and 23.4% in May and June, respectively (Fig. 8). These results indicate that the difference between warming and no warming mainly resulted from data collected early in the growing season due to lower background soil temperature. No significant effect of grazing on Rs during the growing season was found, and there was also no significant interaction between warming and grazing (Table 2).

There was seasonal variation in the Rs/Re ratio in the meadow during the growing season in 2007. The Rs/Re ratio in NWNG reached a maximum of about 0.57 in the early growing season (in May and June), gradually decreased to about 0.47 in July and August, and then increased again to about 0.54 at the end of growing season (September and October). Generally, seasonal average Rs amounted to 52.6% (ranged 50.2–55.2%) of Re for all treatments throughout the growing season in 2007, and there was no significant difference among treatments ( $P > 0.05$ ).

3.4. Factors affecting Re and Rs

Re increased exponentially with soil temperature at 5 and 10 cm depths (soil temperature at 5 cm depth explained more variation in Re than at 10 cm depth (data not shown). Soil temperature at 5 cm depth explained 83.0, 76.3, 78.6, and 62.5% of the seasonal Re variation for NWNG, NWG, WNG, and WG, respectively, across the growing seasons of the three-year period (Fig. 9). Seasonal variation in Re showed no significant relationship to soil moisture in 2006 and 2007, whereas Re was negatively correlated to soil moisture, and soil moisture explained 12.5% of Re variation based on a linear model ( $P = 0.001$ ), when all data from all treatments was pooled in 2008. These results show that the Re may be mainly controlled by soil temperature rather than soil moisture in the alpine meadow.  $Q_{10}$  values were almost the same for all treatments in 2006, whereas the  $Q_{10}$  value was the highest for NWNG and the lowest for WG in 2007 and 2008 (Table 3). Moreover, both warming and grazing reduced the  $Q_{10}$  values in 2007 and 2008 (Table 3).

The relationships between soil temperature and Rs during the growing season were significantly positive, whereas soil tempera-



**Fig. 9.** Exponential relationships between ecosystem respiration (Re) and soil temperature during the growing seasons in different treatments across three years.

**Table 3**

$Q_{10}$  values of ecosystem respiration from 2006 to 2008 and soil respiration in 2007 during the growing seasons in warming and grazing (WG), warming without grazing (WNG), grazing without warming (NWG), and no warming and no grazing (NWNG).

Treatment	Ecosystem respiration			Soil respiration
	2006	2007	2008	2007
NWNG	3.11	4.34	5.64	1.43
NWG	3.09	3.71	4.78	1.54
WNG	2.91	2.92	4.34	1.50
WG	3.13	2.41	3.73	1.37

ture could account for only 18.8–33.8% of seasonal Rs variation for all treatments in 2007 (Table 4). In particular, negative linear correlations between soil moisture and Rs during the growing season were detected, and soil moisture could explain 10.0–22.1% of Rs variation in 2007 (Table 4). There was no obvious difference in the temperature sensitivity of Rs (i.e.,  $Q_{10}$ ) among the four treatments in 2007 (Table 3).

Although simple relationships were significant between APB and Re and Rs before the middle of July, stepwise regression analysis showed that there were no significant relationships between Re and Rs and APB ( $P > 0.05$ ) in 2007 and 2008, indicating that increased temperature induced and increase in APB, which coincided with trends of Re and Rs before grazing. However, in 2006, APB on 16 August after grazing could explain 41–68% of the vari-

**Table 4**

Regression models for the relationship between soil respiration ( $F$ ), soil temperature ( $T$ ) and soil moisture ( $M$ ) in different treatments in 2007.  $a$ ,  $b$  are significant coefficients.  $R^2$ ,  $P$  stand for determination coefficient and statistical significant, respectively.

$F = ae^{bT}$	$a$	$b$	$R^2$	$P$
NWNG	215.78	0.036	0.188	0.008
NWG	184.73	0.043	0.338	<0.001
WNG	201.03	0.040	0.204	0.006
WG	214.41	0.032	0.191	0.008
$F = aM + b$	$a$	$b$	$R^2$	$P$
NWNG	-5.053	459.89	0.143	0.008
NWG	-4.701	429.88	0.100	0.029
WNG	-5.624	479.12	0.177	0.003
WG	-6.676	500.28	0.221	0.001

ations in Re from 20 August to 17 September. There were no significant relationships between seasonal average Re and Rs and belowground biomass by the end of August each year ( $P > 0.05$ ) (data not shown).

## 4. Discussion

### 4.1. Temporal variation of Re and Rs in the alpine meadow

Spatially, Re is divided into aboveground (canopy respiration) and belowground (Rs) components. Aboveground respiration may be assumed to be largely autotrophic, but Rs combines plant root respiration (autotrophic) with heterotrophic respiration of substrates ranging from fresh plant litter to C inherited from parent rocks, and integrates production from the surface to depths of many meters (Trumbore, 2006). Controls on the balance between photosynthesis and respiration vary with timescale. On seasonal to interannual timescales, the phenology of plants, the supply of decomposable litter or exudates, and weather conditions like drought create temporary C storage or loss (Sacks et al., 2006; Scott-Denton et al., 2005; Borken et al., 2006; Davidson et al., 2006). Generally, in our study seasonal trends in Re and Rs were similar to previous reports at the same study site (Cao et al., 2004; Kato et al., 2006; Hu et al., 2009). Our study showed that seasonal variations in Re and Rs were considerably controlled by soil temperature, and peaks of Re and Rs were in July (Figs. 4 and 5). However, the interannual variations in Re during the growing seasons were strongly related to precipitation in the alpine meadow, indicating that drought reduced annual Re (Fig. 7), which was consistent with other research (Flanagan et al., 2002; Gaumont-Guay et al., 2006; Xia et al., 2009). For example, rainfall was 339 mm during the growing season in 2008, which was lower by about 25% than in 2006, and average Re was lower by about 28% in 2008 than in 2006. However, decreased rainfall during the growing season did not decrease plant primary production (Figs. 2 and 3), suggesting that interannual drought may mainly decrease Rs. Controversy exists as to the relative importance of changes in autotrophic and heterotrophic respiration components with short-term and long-term variation in climate (Davidson et al., 2000; Giardina and Ryan, 2000). Usually, heterotrophic respiration is more variable than autotrophic respiration; in particular, summer drought causes a drop in heterotrophic respiration in forests, mostly due to the reduction of

decomposition in the very dry litter layer (Trumbore, 2006). However, Boriken et al. (2006) also observed a decline in autotrophically respired CO<sub>2</sub> in a simulated drought experiment. For a short time, even APB could explain on average 50% of Re variations after grazing in 2006 in our study. The contribution of the seasonal average Rs to Re in 2007 was about 53%, which was close to the value in a Douglas-fir ecosystem (Jassal et al., 2007), and warming and grazing did not significantly affect the seasonal average of ratios of Rs to Re.

#### 4.2. Warming effects

Recently, some studies showed that warming had no effect on Re throughout the growing season in temperate grasslands (De Boeck et al., 2007; Xia et al. 2009), whereas other studies demonstrated that warming obviously stimulated Re in Arctic Tundra (Hobbie and Chapin, 1998; Grogan and Chapin, 2000). Therefore, the responses of Re to climate warming are ecosystem-dependent (Welker et al., 2004; Oberbauer et al., 2007). In our study, warming did not significantly affect seasonal Re in both wetter year (2006) and the drier years of 2007 and 2008 (Fig. 4). However, after 16 August 2006, WNG significantly increased Re by 12.4% compared with NWNG; there was no significant difference between NWG and WG (Fig. 3A), suggesting that grazing modified the response of Re to warming in 2006. Probably WNG increased APB (Fig. 2A) and belowground biomass (Fig. 3), which increased autotrophic respiration compared with NWNG. However, compared with NWG, WG decreased average soil moisture at 10 cm by 15% after 16 August 2006, which resulted in the tradeoff of the positive effect of increased APB and belowground biomass (Figs. 2A and 3) with the negative effect of decreased soil moisture on Re.

We found that warming increased Re early in the growing season (i.e., before June) during the 3-year experimental period (Figs. 3A and 6), whereas warming reduced Re in July, especially in the heavy drought year of 2008 (Fig. 6). Re is composed of autotrophic respiration and heterotrophic respiration, and the amount of plant aboveground biomass is a good proxy for estimating total autotrophic and heterotrophic activity (Flanagan and Johnson, 2005). The warming plot had an earlier grass shoot and more biomass than did the no warming plot (Fig. 2), thus greater Re for warming treatments resulted from both increases in autotrophic and heterotrophic respiration compared with no warming treatments early in the growing seasons (Fig. 8). During July in 2007 and especially in 2008, lower rainfall (Fig. 1) strengthened the effect of warming on soil moisture (Luo et al., 2010; Hu et al., 2010). Drought can lead to a transient reduction in Re (Griffis et al., 2004). However, warming-induced drought in July 2007 did not reduce Rs (Fig. 8). Thus, decreased Re could result from a decline in the aboveground autotrophic respiration, suggesting that aboveground autotrophic respiration may be more sensitive to warming than soil respiration in our study during periods of drought.

Many studies reported that elevated temperatures increased soil CO<sub>2</sub> flux (Rustad et al., 2001; Melillo et al., 2002; Emmett et al., 2004; Bergner et al., 2004; Slaney et al., 2007; Zhou et al., 2007; Bronson et al., 2008) because warming increased soil and litter decomposition (Bronson et al., 2008; Luo et al., 2010). Although warming increased seasonal Rs during the growing season in 2007 in our study, it did not affect Rs after June (Fig. 8A). These results suggested that the advance of the growing season and lower background temperature may contribute to greater Rs for the warming treatments early in the growing season in the alpine region (Bergner et al., 2004). However, some studies observed a declining trend in warming stimulation of soil CO<sub>2</sub> efflux (Rustad et al., 2001; Bronson et al., 2008). Thus, the long accepted relationship between soil temperature and Rs was questioned (Luo et al., 2001).

#### 4.3. Grazing effect

Many studies showed that there was a significant correlation between annual Rs and Re and GPP (Janssens et al., 2001; Mahecha et al., 2010; Migliavacca et al., 2011) and many studies found that clipping or grazing decreased Rs (Bremer et al., 1998; Johnson and Matchett, 2001; Wan and Luo, 2003; Cao et al., 2004) and Re (Susiluoto et al., 2008), but some studies found that grazing can enhance Rs (Frank, 2002) and Re (Bergner et al., 2004; Owensby et al., 2006; Polley et al., 2008). However, Bahn et al. (2006) found that clipping increased soil and root respiration by increasing soil temperature. Actually, when corrected for temperature effects, clipping decreased Rs by 20–50% (Bahn et al., 2006). Therefore, the effects of grazing on Rs and Re are complex and depend on grazing intensity and history (Cao et al., 2004). In our study, except for the first year (2006), grazing did not have detectable impacts on seasonal Rs in 2007 and Re in 2007 and 2008. This finding could be attributed to the following: (1) grazing reduced aboveground (Fig. 2) and belowground biomasses, especially for WG vs. WNG (Fig. 3), which decreased plant autotrophic respiration (Cao et al., 2004; Raiesi and Asadi, 2006) (2) soil respiration and most of its components depend directly on the input of carbon from living plants (Moyano et al., 2008). So, grazing reduced microbial respiration by reducing the input of labile C to soil (Raiesi and Asadi, 2006; Polley et al., 2008); and (3) grazing increased soil temperature (Luo et al., 2010; Hu et al., 2010), which increased Rs (Bahn et al., 2006). Therefore, the net effects of grazing on Rs and Re will be determined by the balance of negative and positive effects of grazing on ecosystem respiration processes (Zhou et al., 2007). In the short time, root respiration was little affected by clipping, suggesting that carbohydrate reserves sustained root metabolism for several days and that microbial respiration strongly responded to short-term changes in assimilate supply (Bahn et al., 2006). Therefore, in our study, with the first period of grazing on 16 August, reduced aboveground autotrophic respiration may have overridden the increased heterotrophic respiration by elevating soil temperature, which resulted in reduced Re in 2006. Conversely, in 2007 and 2008, grazing did not immediately reduce Re (Fig. 5) even though about 20–25% of aboveground biomasses were removed each time, suggesting that the contribution of reduced aboveground autotrophic respiration to total Re was small. For example, the average ratio of seasonal Rs and Re during the growing season in 2007 was about 58%, i.e., given that about 40% of the total Re derived from aboveground autotrophic respiration, the contribution of aboveground autotrophic respiration through 20–25% aboveground biomass removed by grazing was only approximately 10% of the total Re. On the other hand, Bahn et al. (2006) found that 75% of the reduced respiration can be recovered within 8 days after grazing.

#### 4.4. Temperature sensitivity of ecosystem and soil respirations

Although many environmental factors affect the biological and physical processes controlling ecosystem respiration rates, respiration rates are mainly related to soil temperature and moisture (Nakano et al., 2008). Consistent with previous results at the same site (Kato et al., 2006; Hu et al., 2009), the Re fluxes in 2008 and Rs fluxes in 2007 showed significant negative correlation with soil moisture in our study. In contrast to some recent findings in arid or semi-arid ecosystems (Chimner and Welker, 2005; Nakano et al., 2008), soil temperature may be more important to determine Re due to high soil moisture during the growing season in the alpine meadow (Zhao et al., 2006).

Q<sub>10</sub> is considered one of the most important parameters used to assess the temperature sensitivity of both soil and ecosystem respiration (Raich and Schlesinger, 1992; Boone et al., 1998; Zhou et al.,



2007). The  $Q_{10}$  values for Re (ranged 2.4–5.6) in our study were close to the range reported by previous studies in the alpine region (i.e., 1.3–4.6) (Zhao et al., 2006; Hirota et al., 2006; Nakano et al., 2008). Many studies found that the temperature sensitivity of respiration declines with increasing temperature (Kirschbaum, 1995; Griffin et al., 2002; Zhou et al., 2007; Nakano et al., 2008; Bronson et al., 2008). In our study, we also found that  $Q_{10}$  values of Re decreased as the growing season progressed (i.e., the average  $Q_{10}$  values of Re were 3.42, 2.04, 2.00, 2.25, and 1.57 in May, June, July, August, and September, respectively, for all treatments during the 3-year experimental period). However, inconsistent with previous reports (Reichstein et al., 2002; Flanagan and Johnson, 2005), in our study  $Q_{10}$  values of Re increased with a decrease in soil moisture (Table 3). For example, the  $Q_{10}$  value of Re was the smallest in 2006 and the largest in 2008 for NWNG (Table 3). Wen et al. (2006) also reported that wet soil conditions (i.e., soil water content exceeds the optimal moisture condition for ecosystem respiration) can decrease the temperature sensitivity of Re.

In our study, grazing and warming decreased the  $Q_{10}$  values of Re (Table 3) by increasing soil temperature, with lower soil moisture in 2007 and 2008 (Luo et al., 2010; Hu et al., 2010). However, it is difficult to separate the interaction between increases in soil temperature and reductions in soil moisture for their effects on  $Q_{10}$  (Xu and Qi, 2001). Removal of plants by grazing or clipping significantly reduced the temperature sensitivity of Re (Table 3), suggesting that respiration derived from recent plant carbon fixation was more temperature sensitive than respiration from bulk soil organic matter carbon stores (Grogan and Jonasson, 2005).

$Q_{10}$  values of Rs ranged between 1.4 and 1.5 in 2007 in our study, which was lower than the global average value (i.e., ranged 1.3–3.3) (Raich and Schlesinger, 1992; Raich and Potter, 1995; Tjoelker et al., 2001). Inconsistent with previous reports (Wan et al., 2002; Zhou et al., 2007), warming and grazing did not affect  $Q_{10}$  values of Rs in 2007 (Table 3). Our results supported the previous conclusion that Re was more sensitive than Rs to changes in temperature and soil water content (Jassal et al., 2007), suggesting that aboveground autotrophic respiration may be more sensitive to temperature change compared with Rs.

## 5. Conclusions

Generally, although warming increased seasonal Rs in 2007, it did not affect seasonal average Re during the 3-year experimental period. Therefore, warming (i.e., WNG) maybe increase the carbon sink capacity of the alpine ecosystem during the growing season because WNG increased net primary production compared with NWNG. Both seasonal Rs and Re in 2007 and 2008 were not affected by grazing. The interannual variability of Re during the growing season was related to fluctuations in precipitation, whereas seasonal variability of Re depended mainly on soil temperature. Warming and grazing decreased  $Q_{10}$  values of Re and had little impact on  $Q_{10}$  values of Rs, suggesting that warming and grazing may reduce the temperature sensitivity of Re and that aboveground autotrophic respiration maybe more sensitive to temperature change compared with Rs. This may account for that an over prediction of carbon respired may result for a warmer climate in the future in the alpine meadow on the Tibetan plateau, if we use current Re models. This study implicated that future warming would not stimulate Re (i.e., positive feedback) at all time in the alpine meadow on the Tibetan plateau, which may be due to the difference of the response level and mechanism between alpine meadow and arctic tundra. To understand response of Re/Rs to warming and grazing in no-growing seasons, future study should be focused on the investi-

gation on Re/Rs in no-growing seasons, especially during the period of snow melting and soil thawing.

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