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Warm- and cold- season grazing affect soil respiration differently in alpine grasslands

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ABSTRACT

As a traditional practice in grasslands, grazing significantly affects soil respiration (R_s). To improve our understanding of grassland carbon cycling, it is critical to partition the responses of soil respiration to grazing into autotrophic (R_a) and heterotrophic (R_h) respiration. In addition, it remains unclear how grazing patterns, such as warm- and cold- season grazing, influence R_s and its components in alpine grasslands that are subject to increasing grazing pressure. Here, we conducted a six-year manipulative experiment combining with a meta-analysis, to investigate the responses of R_s and its components to moderate grazing in a Tibetan alpine grassland. Grazing patterns included warm-season grazing by sheep during the growing seasons of 2008 to 2010 and simulating cold-season grazing by clipping during the non-growing seasons of 2011 to 2013. Our results showed that warm-season grazing minimally affected R_s while cold-season grazing significantly increased R_s by 13.1%. This result was supported by a meta-analysis at seven grassland sites across the Tibetan Plateau. Further, we found that warm-season grazing did not affect R_a or R_h, whereas cold-season grazing enhanced R_a (23.2%) more than R_h (4.9%). Cold-season grazing affected R_s and R_a differently depending on interannual variation in climate conditions. A significant increase of 17.1% and 26.3%, respectively, was recorded in dry and cold years, but no change was recorded in wet and warm years. This study highlights the differential responses of R_s components to grazing, and suggests that different grazing patterns should be considered when evaluating future carbon cycles in grazing ecosystems on the Tibetan Plateau.

1. Introduction

Grazing is a common, traditional practice in natural grasslands, and it has a substantial influence on terrestrial carbon cycling process (McSherry and Ritchie, 2013; Schuman et al., 1999). Soil respiration (R_s) is the second largest carbon flux between soil and atmosphere, and encompasses autotrophic (R_a) and heterotrophic (R_h) respiration (Davidson and Janssens, 2006; Hanson et al., 2000; Kuzyakov, 2006). Previous studies have extensively explored the effect of grazing/clipping on R_s, with reported positive, neutral, and negative effects (Cui et al., 2014; Wan and Luo, 2003; Xu et al., 2015). However, few studies have partitioned the responses of R_s components, including R_a and R_h, to grazing, which constrains our understanding of the underlying mechanism for the controversial results obtained.

A number of studies have shown that the effects of grazing/clipping on R_s components are dependent on changes to plant properties and soil physical conditions (Bahn et al., 2006; Li and Sun, 2011; Wan and Luo, 2003). When considering plant properties, on one hand, grazing reduces photosynthate supply and above-ground litter by removing the above-ground part of plants, which might reduce R_a and R_h (Wan and Luo, 2003). On the other hand, grazing stimulates root growth (Cui et al., 2014; Hafner et al., 2012), thus increasing R_a and R_h. When considering soil physical conditions, grazing increases soil temperature (Li and Sun, 2011; Luo et al., 2010), which accelerates the decomposition of soil organic matter (Li et al., 2013) and improves the metabolic activity of plants (Melillo et al., 2011). However, grazing usually

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decreases soil moisture, which might inhibit R_h (Li et al., 2013). Hence, R_h and R_a might respond differently to the grazing-induced changes of plant properties and soil conditions. Assessing the direction and magnitude of their responses, along with identifying their drivers, will improve our understanding of carbon cycling processes.

The Tibetan Plateau covers approximately 370 million km^2 (Tang et al., 2009), with alpine grasslands covering approximately 62% of the total area (Zhang et al., 2007). Two types of grazing patterns are conducted in the Tibetan Plateau grasslands; namely, warm-season and cold-season grazing (Cui et al., 2014). Warm-season grazing is usually conducted from June to October during the growing season, whereas cold-season grazing is often conducted in the other months during the non-growing season. Warm-season grazing reduces the volume of living plants and cuts off the photosynthetic supply (Wan and Luo, 2003). Cold-season grazing removes standing litter and alleviates light limitation for plant growth (Zhu et al., 2015). The two grazing patterns might affect R_s in different directions and degrees. Until now, most studies have explored the response of R_s to either warm- or cold-season grazing in Tibetan alpine grasslands; however, it remains controversial how R_s components respond to the two grazing patterns (Chen et al., 2016; Cui et al., 2014; Lin et al., 2011). Moreover, few studies have explored interannual variation in how grazing affects R_s and its controls, because short-term studies have not captured the interannual dynamics (Chen et al., 2016; Fu et al., 2014). Here we used a long-term (6 years) manipulative experiment with two grazing patterns, combined with a meta-analysis, to (1) investigate the responses of R_s to the two grazing patterns, and further (2) partition the responses of R_s components.

2. Materials and methods

2.1. Study site

Our research site is located at the Haibei Alpine Grassland Ecosystem Research Station, which is located in the northeast of the Tibetan Plateau (37°36′E, 101°18′N) at an altitude of 3198 m (Fig. 1). Climatological data at this site from 1980 to 2014 shows that the mean annual air temperature was −1.1 °C, and that annual precipitation was 486 mm with 80% occurring during May to September. The alpine meadow is dominated by *Stipa aliena*, *Elymus nutans*, and *Kobresia humilis*. The averaged forage production was 344 g m^{-2} from 1980 to 2014. The soil is Mat Cry-gelic Cambisols according to the Chinese national soil survey classification system. The organic carbon density in the 0–10 cm layer is 63 g kg^{-1} (Lin et al., 2016).

2.2. Experimental design

In May 2006, a 27 m × 27 m area was fenced and divided into 16 plots separated by 3-m-wide buffer strips. Four treatments were applied to the 16 plots; namely, the control, warming, grazing, and a combination of warming and grazing. Four plots were used for each treatment. Considering that this research aimed to explore the effects of grazing on R_s, we only selected the treatments of control and grazing for analysis (warm-season grazing from 2008 to 2010 and cold-season grazing from 2011 to 2013). The control was set without grazing, warm-season grazing was carried out in July and August of every summer, and cold-season grazing was simulated by clipping vegetation from October of one year to March of the next year (Luo et al., 2009; Zhu et al., 2015). More specifically, for warm-season grazing, we fenced the sheep into three 5 m × 5 m plots one day before the grazing experiment started, to help the Tibetan sheep adapt to the small size of the plots. Two adult Tibetan sheep were fenced in the grazing plots for approximately 1 h on July 8 and August 20 in 2008, on July 9 and August 24 in 2009, and on July 7 and August 23 in 2010 (Lin et al., 2011). The exact length of grazing time depended on forage utilization. If forage utilization was below 50%, we grazed two sheep in the following day until the plant height was approximately half the initial height after grazing. For cold-season clipping, we clipped 50% of the litter biomass (Zhu et al., 2015). Forage utilization was set at 50%, because moderate grazing often uses nearly half of the forage production in the Tibetan Plateau grasslands (Cui et al., 2014; Dong et al., 2015; Gao et al., 2009).

2.3. Measurement of R_s and its components

We inserted polyvinyl chloride collars with a diameter of 20 cm (10 cm height) into a soil depth of 3 cm for measuring R_s, and inserted collars (65 cm height) into a soil depth of 60 cm for measuring R_h. The above-ground plants were removed in all collars. Compared to the collars for R_s, the deeper collars blocked the transportation of photosynthate from the plants outside the collars. Until R_h rate was no longer affected by dead roots and steady after six months (Wang et al., 2014), R_h was used for the analysis in this study. R_a was calculated by subtracting R_h from R_s.

From June 2008 to December 2013, R_s and R_h were both measured four or five times per month from May to September, and one time per month in the other months by using an automated chamber system (LI-8100; Li-Cor Inc., Lincoln, NE, USA). One day before conducting the measurement, we clipped the above-ground part of the plants inside the collars for R_s. All the measurements were done between 09:00 and 12:00 local time. To estimate annual emissions of R_s and its components, we first derived the daily R_s by calibrating the observed daytime value (09:00–12:00) based on the daily average value obtained from LI-8150 which automatically measured R_s and R_h once an hour in the control (Li-Cor Inc., Lincoln, NE, USA). Annual cumulative emissions were calculated by multiplying the time intervals by average daily fluxes between the two consecutive sampling dates (Wang et al., 2017).

2.4. Measurement of soil temperature and moisture

Soil temperature and moisture at the depth of 5 cm were obtained by using the temperature (LI-8100-203; Li-Cor Inc., Lincoln, NE, USA) and moisture sensors (Decagon Devices Inc., Pullman, WA, USA). Soil moisture was expressed as volumetric percentage (%).

2.5. Data collection

We conducted a meta-analysis to assess the grazing effect on R_s in the Tibetan Plateau grasslands. We used the Web of Science and China National Knowledge Infrastructure to search for all relevant literatures and dissertations. The results were filtered by the following conditions: 1. the studies were based on field experiments; and 2. the studies were located in an alpine meadow or alpine steppe on the Tibetan Plateau. For each study, we compiled the R_s data from the control and grazing treatments. To ensure the independence of the experiments, only the results in recent year were employed. Moreover, we separated grazing intensity into different levels (Gao et al., 2009). Moderate grazing intensity was defined as a forage utilization higher than 35%, but lower than 60%, or a grazing intensity between 4.2 sheep per hectare and 7.0 sheep per hectare. Heavy grazing intensity was defined as a forage utilization higher than 60% or a grazing intensity higher than 7.0 sheep per hectare (Dong et al., 2015; Gao et al., 2009). Based on the timing of grazing, we also separated grazing patterns into warm- and cold-season grazing.

2.6. Statistical analysis

A paired-*t* test was used to determine the differences in soil temperature and moisture at 5 cm depth, annual cumulative R_s and its components, and the ratio of R_h to R_s between the control and grazing treatments. We used linear regressions to examine how cold-season grazing effects varied with annual mean air temperature and annual

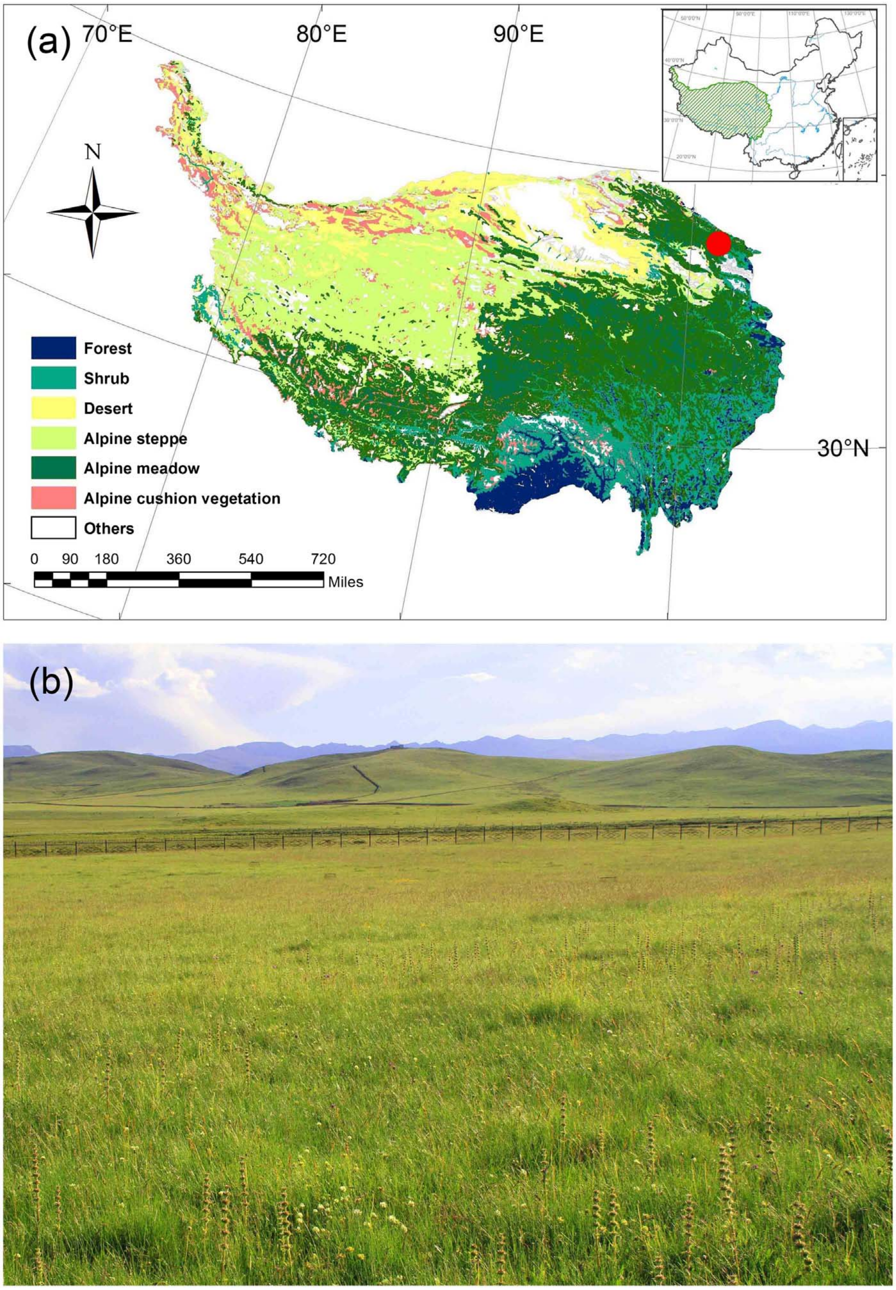

Fig. 1. Location **(a)** and landscape **(b)** of the field site on the Tibetan Plateau. Circle represents the location of the grazing experiment.

precipitation. All statistical analyses were conducted by using R 2.15.1 software (R Core Team, 2012).

The meta-analysis was used to evaluate the influence of grazing on R_s at a regional scale. The effect size was examined by the function $\mathrm{LnRR} = \mathrm{Ln}(X_T/X_C)$ (Hedges et al., 1999). LnRR refers to the natural logarithm of Response Ratio, and X_C and X_T refer to the R_s in the control and grazing treatments, respectively. Response ratios and bootstrapped 95% confidence intervals were calculated by Metawin (Sinauer Associates, Inc. Sunderland, MA, USA). If the bootstrapped 95% confidence interval did not overlap 1, then the grazing effect was considered significant.

3. Results

3.1. Grazing effects on environmental factors

Annual mean air temperatures were −0.8, −0.4, −0.3, −0.9, −1.2, and −1.1 °C from 2008 to 2013 (Fig. S1a), respectively. In 2012, the annual mean air temperature was lower than the long-term average value of −1.1 °C from 1980 to 2014. In other years, the annual mean air temperatures were higher than the long-term mean. In the meantime, annual precipitations were 429.9, 494.6, 493.3, 524.4, 352.6, and 403.4 mm from 2008 to 2013, respectively (Fig. S1b). Annual precipitations in 2008, 2012, and 2013 were lower than the long-term mean of 485.8 mm.

Soil temperature at 5 cm showed clear seasonal trends in both the control and grazing plots (Fig. S2a). Warm-season grazing significantly increased soil temperature by 1.1 °C over the experimental period of 2008–2010 (Fig. S1c; $P < 0.001$) while cold-season grazing significantly increased soil temperature by 0.7 °C across 2011–2013 ($P < 0.001$). Soil moisture at 5 cm depth fluctuated dramatically throughout the growing seasons (Fig. S2b). Compared to the control, warm-season grazing decreased soil moisture by 1.2% (Fig. S1d; $P < 0.001$), and cold-season grazing significantly decreased it by 1.1% ($P < 0.001$).

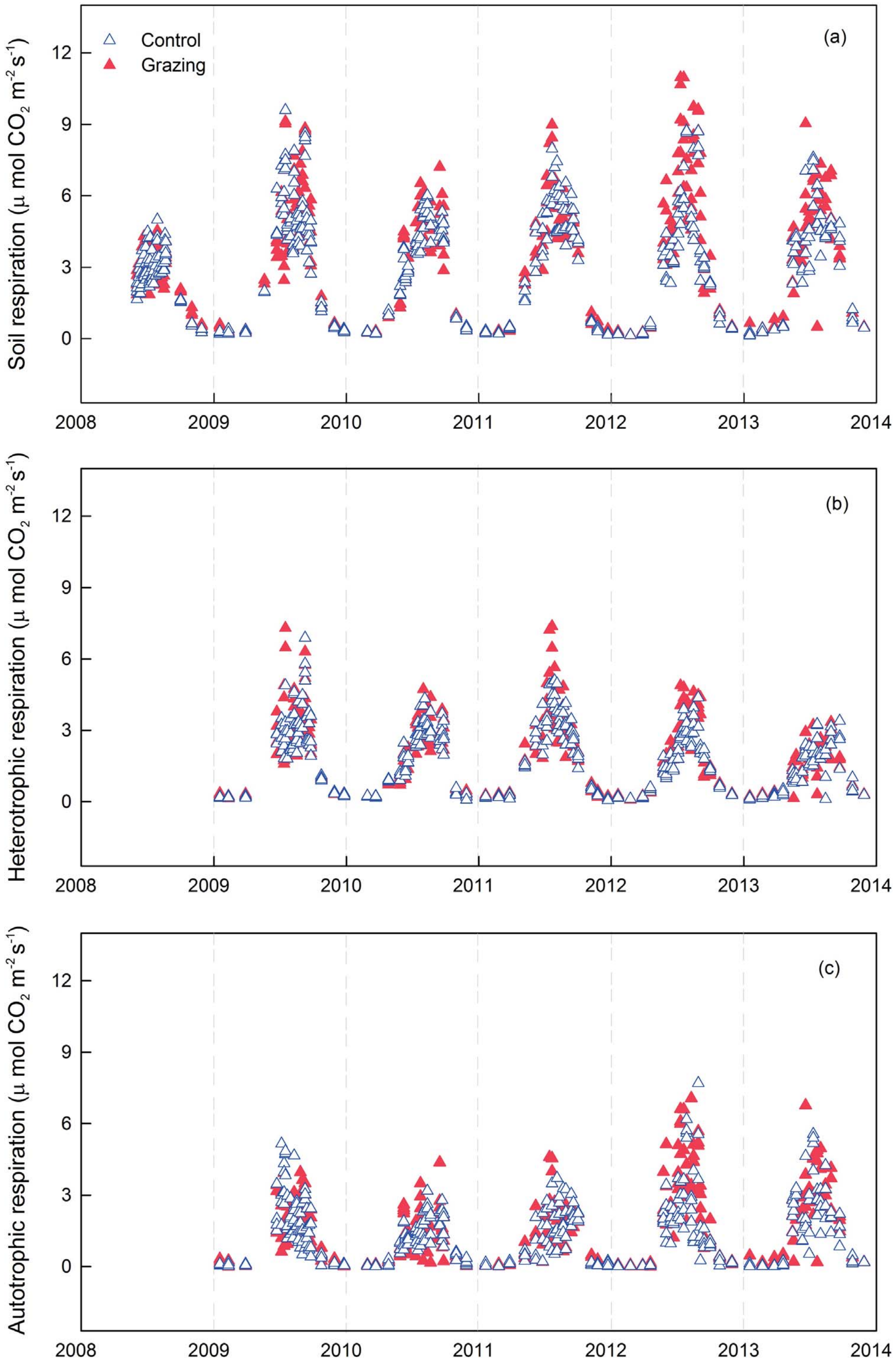

Fig. 2. Seasonal dynamics of soil respiration **(a)**, heterotrophic respiration **(b)** and autotrophic respiration **(c)** under the control and grazing treatments.

3.2. Grazing effects on R_s and its components

R_s and its components showed similar seasonal trends in both control and grazing plots (Fig. 2). During the experimental period, annual cumulative R_s fluctuated from 734.4 to 987.5 g C m^{-2} yr^{-1} (Table 1). Warm-season and cold-season grazing affected annual cumulative R_s and its components differently (Fig. 3). Warm-season grazing did not significantly affect R_s and its components, regardless of whether it was assessed for individual year or across all the experimental years (Fig. 3), and it did not change the ratio of R_h to R_s (Fig. 4a). In contrast, over the three experimental years of 2011 to 2013, cold-season grazing significantly increased R_s by 13.1% ($P < 0.001$), R_a by 23.2% ($P < 0.01$), and R_h by 4.9% (Fig. 3; $P = 0.12$), and considerably decreased the ratio of R_h to R_s (Fig. 4b; $P = 0.07$). The 21% of the increase in R_s was derived from R_h, whereas the other 79% was derived from R_a (Table 1). Clearly, the responses of R_s components to cold-season grazing exhibited a significant interannual variation (Fig. 3). Cold-season grazing significantly increased R_a in the dry and cold years of 2012 ($P < 0.05$) and 2013 ($P < 0.05$), and stimulated R_h in 2012 (Fig. 3b; $P < 0.05$). In the wet and warm year of 2011, cold-season grazing did not affect any of the R_s components.

Under both warm- and cold-season grazing conditions, positive

Table 1
Annual cumulative soil respiration (R_s) and contribution of heterotrophic respiration (R_h) under the control and grazing treatments. Values show means ± SE (n = 4). Different letters denote significance at $P < 0.05$.

Year	Treatment	Cumulative R_s (g C m^{-2} yr^{-1})	Contribution of R_h (%)
2009	Control	873.8 ± 23.1 a	60.7 ± 4.0
	Warm-season grazing	863.8 ± 24.1 a	63.9 ± 2.4
2010	Control	734.4 ± 15.4 a	63.6 ± 1.0
	Warm-season grazing	745.9 ± 11.3 a	64.6 ± 2.2
2011	Control	891.5 ± 49.2 a	67.9 ± 3.1
	Cold-season grazing	939.7 ± 16.3 a	66.0 ± 3.2
2012	Control	814.7 ± 27.7 b	52.0 ± 1.4
	Cold-season grazing	987.5 ± 12.4 a	47.5 ± 0.8
2013	Control	828.9 ± 22.1 b	45.7 ± 1.3
	Cold-season grazing	938.9 ± 24.3 a	41.2 ± 1.6

relationships between grazing-induced changes in R_s and changes in soil temperature were observed (Figs. S3a and b), but no correlations between the grazing-induced changes in R_s and changes in soil moisture were observed (Figs. S3c and d). Under cold-season grazing condition, significant negative relationships were found between grazing-induced changes in R_s and mean annual air temperature and annual precipitation (Fig. S4).

3.3. *Synthesis on the responses of R_s to grazing on the Tibetan Plateau*

To examine whether the observed trends of no effect of warm-season grazing on R_s, but an increase in R_s under cold-season grazing, were general patterns across Tibetan Plateau grasslands, we conducted a meta-analysis on the effect of different grazing patterns at seven sites across the plateau (Table S1). Overall, grazing did not affect R_s; however, the grazing effects varied with the intensity and pattern of grazing (Fig. 5). Moderate grazing significantly enhanced R_s, whereas heavy grazing did not significantly affect it (Fig. 5). Similar to the results obtained by our manipulative experiment, warm-season moderate grazing did not affect R_s while cold-season moderate grazing significantly increased R_s.

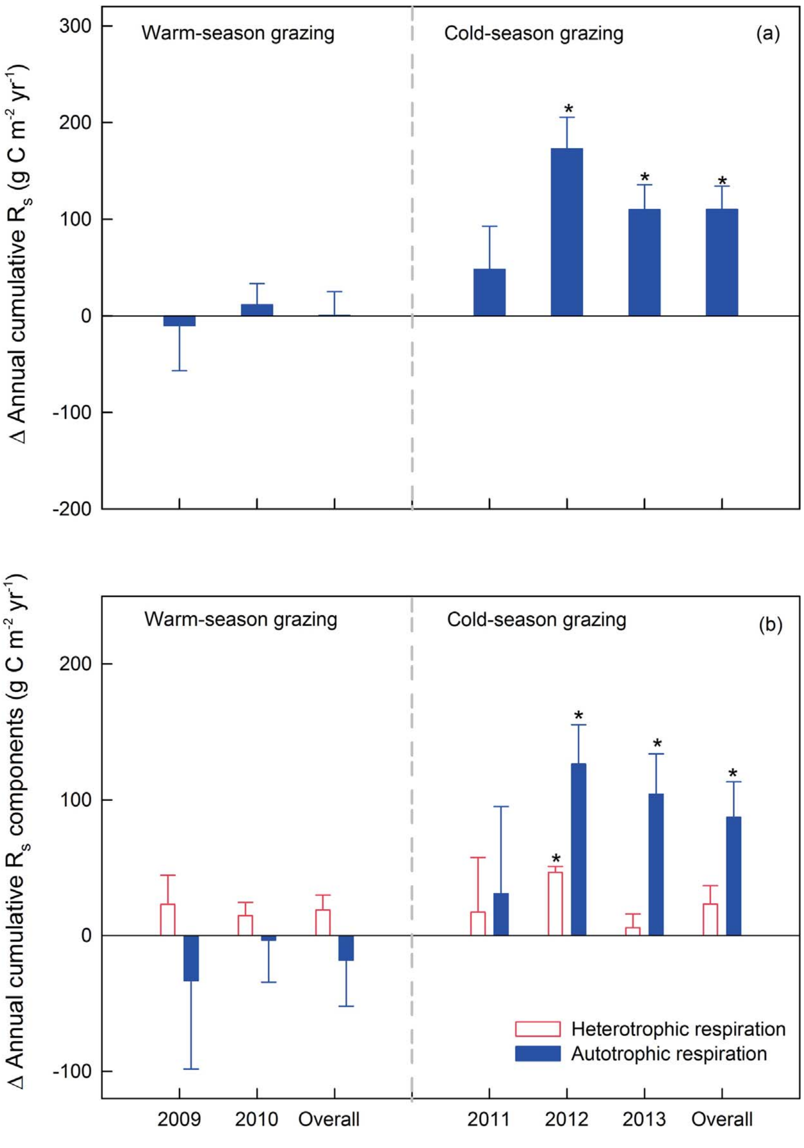

Fig. 3. Grazing-induced changes in annual cumulative soil respiration (R_s) **(a)** and its components **(b)** during 2009–2010 (warm-season grazing) and 2011–2013 (cold-season grazing). Bars show ± SE (n = 4). *: statistically significant at $P < 0.05$.

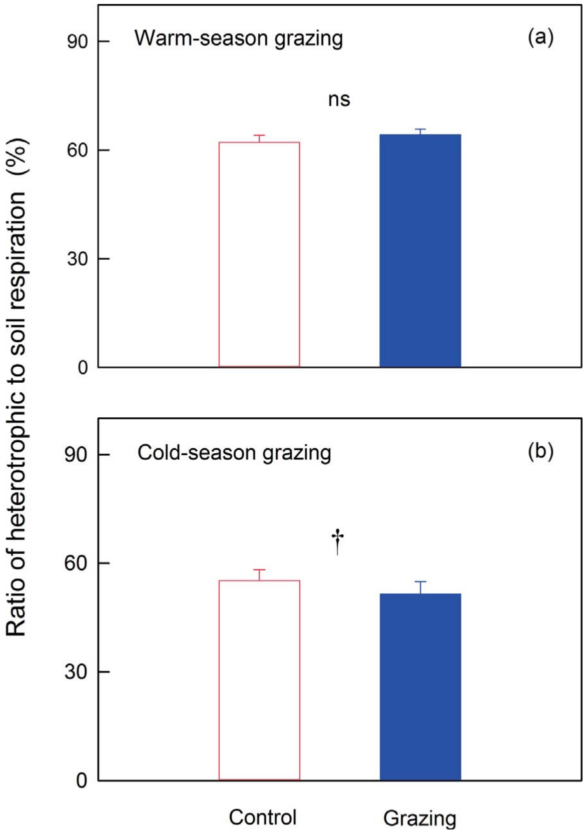

Fig. 4. Warm- **(a)** and cold-season **(b)** grazing effects on the ratio of heterotrophic respiration to soil respiration. Bars show ± SE ($n = 4$). ns and †: not statistically significant and statistically significant at $0.05 < P < 0.1$.

4. Discussion

4.1. R_s under different grazing patterns

Our experimental results showed that warm-season grazing did not affect R_s, which was further validated by the results of our meta-analysis across Tibetan grasslands. A previous study located at the same experimental site also found that warm-season grazing did not influence R_s from 2006 to 2008 (Lin et al., 2011). It has been reported that warm-season grazing reduces above-ground biomass (Lin et al., 2011), but stimulates below-ground biomass, in the Tibetan grasslands (Cui et al., 2014). Meanwhile, warm-season grazing significantly increased soil temperature in the present study. Therefore, the observed lack of change in R_s might be the result of the negative effect of reduced above-ground biomass being offset by the positive effect of increased root biomass and soil temperature under warm-season grazing condition.

Cold-season grazing significantly stimulated R_s, which is consistent with the results obtained from the meta-analysis of Tibetan grasslands. Cold-season grazing might remove standing litter, allowing more light to shine on the ground, thus favoring plant growth in the next year. This is supported by the observed increase in above-ground productivity at the same experimental platform in 2011 (Zhu et al., 2015). Simultaneously, cold-season grazing might increase root biomass in the Tibetan Plateau grasslands (Cui et al., 2014). Thus, the increase in substrates, as a result of increased above- and below-ground biomass, contributed to higher R_s in the current study. In addition, cold-season grazing led to a higher soil temperature, which can accelerate soil organic matter decomposition and thus increase R_s. Notably, our results showed that the two grazing patterns clearly affected R_s differently. Hence, improved regional mapping of grazing patterns is needed to improve estimates of the grazing effect on R_s in Tibetan alpine grasslands.

4.2. Greater effects of cold-season grazing on R_a than on R_h

The results of our manipulative experiment showed that cold-season grazing stimulated R_h, which might be explained in two ways. First, in the present study, cold-season grazing increased soil temperature by 0.7 °C, which might increase soil carbon dioxide emissions by stimulating microbial activity (Rustad et al., 2001) and increasing microbial biomass (Lu et al., 2013). Second, the shift in species composition might favor an increase in heterotrophic respiration. The increase in forb with a lower C: N ratio under simulated grazing condition, might alter the above-ground chemical properties of carbon input and produce more easily decomposable litter (Klein et al., 2007; Xu et al., 2015), thus contributing more microbial respiration. Third, the grazing-induced increase in root biomass might provide more root exudation and subsequently enhance R_h (Blagodatskaya et al., 2007, 2009; Cui et al., 2014). Meanwhile, cold-season grazing also increased R_a. This phenomenon is probably due to an increase in root biomass and soil temperature. Improved root biomass might produce more CO_2 from plant maintenance and growth respiration in Tibetan alpine grasslands (Cui et al., 2014; Geng et al., 2012; Hafner et al., 2012). Higher soil temperature leads to an increase in root physiological activity (Melillo et al., 2011), resulting in higher root respiration.

Interestingly, we found that cold-season grazing had a greater effect on R_a than on R_h. This phenomenon might be explained by the mutualistic interactions between plants and microbes (Hafner et al., 2012). Grazing causes the loss of nutrients by removing the above-ground part

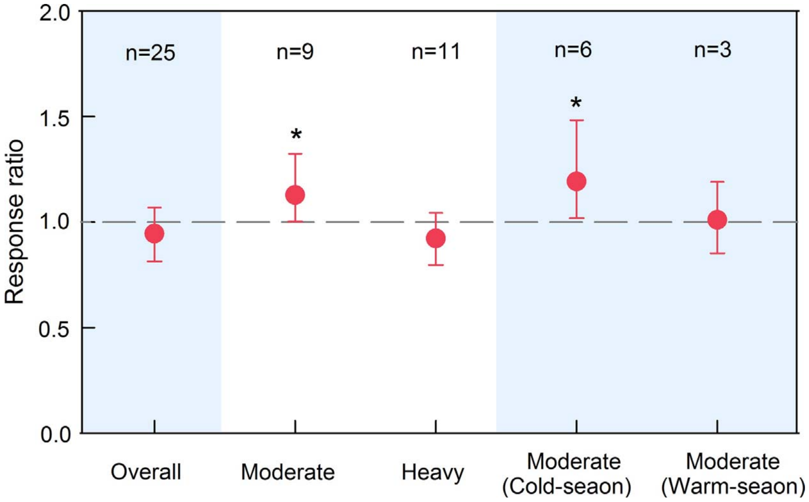

Fig. 5. Responses ratio of soil respiration to grazing across all Tibetan Plateau grassland sites. Moderate, moderate grazing intensity. Heavy, heavy grazing intensity. Warm-season moderate, warm-season moderate grazing intensity. Cold-season moderate, cold-season moderate grazing intensity. Error bars represent the 95% bootstrap confidence intervals of response ratio. The sample size for each variable is shown above the error bars.* denotes that the effect is considered significant.

of plants, which leads to nutritional stress for plants (Zhou et al., 2017). To alleviate nutrient limitation, plants allocate more biomass to the below-ground parts (i.e., roots) to access more nutrients (Chapin et al., 1987). This action increases the quantity and activity of soil microorganisms by enhancing root exudation (Blagodatskaya et al., 2009). In turn, the increased volume of soil microbes improves nutrient availability for plants. By this mechanism, the direct enhancement of R_a from the stimulated root biomass might outweigh the indirect increase of R_h from microbial activity depending on the stimulated root biomass.

4.3. *Interannual controls of cold-season grazing effect on R_s*

To date, most published studies have been conducted during the growing seasons and lasted for a short time (less than 3 years) in Tibetan alpine grasslands (Chen et al., 2016; Cui et al., 2014; Fu et al., 2014), and few studies have focused the interannual variations in grazing effects on R_s. In this current study, the observations of three whole years, including two drier and colder years (2012 and 2013) and one wetter and warmer year (2011), provided us with an opportunity to explore how the effects of cold-season grazing are influenced by interannual fluctuations in climate conditions. We found that grazing had a greater effect on R_s during the two cold years compared to the single warm year. This result is supported by the previous finding that ecological carbon processes are more sensitive to increased temperature in cold regions compared to warm regions (Crowther et al., 2016; Suh et al., 2009). It should be reasonable because the grazing-induced increase in soil temperature in colder years leads to a more effective relief of temperature constraints in the cold region. Moreover, we found that the grazing effect was greater in the two dry years compared to the single wet year. One possible explanation is a larger stimulation of root biomass induced by grazing in the dry year of 2012 compared to the wet year of 2011 (Luo et al., 2015). More root productivity might result in a higher increase in R_s. In short, this study showed that the grazing effect on R_s largely depends on the interannual variability of climate conditions, demonstrating the necessity of long-term study.

Of note, simulated grazing by clipping is different from the actual grazing activity of real sheep. For instance, hoof action is not accounted for when simply clipping vegetation. The absence of hoof action might cause the grazing effect on R_s to be underestimated, because trampling breaks down and decomposes litter (Naeth et al., 1991). However, this underestimation should not affect our general conclusions, because litter respiration only accounts for a small part of R_s in Tibetan Plateau grasslands (Zhang et al., 2003).

This study explored the responses of R_s and its components to different grazing patterns in an alpine grassland. Our results showed that warm-season grazing minimally affected R_s, whereas cold-season grazing stimulated it. These experimental results were supported by a meta-analysis results of seven Tibetan Plateau sites. Additionally, warm-season grazing had little effect on R_a and R_h, whereas cold-season grazing had greater effects on R_a than on R_h. This study suggests that R_s components respond differently to grazing. In conclusion, different grazing patterns should be incorporated into studies predicting how grazing affects R_s in Tibetan alpine grasslands.

Author contributions

Designed the experiments: J-SH SPW. Performed the experiments: HW HYL YHW ZRM WX ZHZ. Analyzed the data: HW HYL. All the authors contributed to writing and discussions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.07.041.

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