

Interactive effects of grazing and global change factors on soil and ecosystem respiration in grassland ecosystems: A global synthesis

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Abstract

1. As the key carbon (C) fluxes between biosphere and atmosphere, soil respiration (R_s) and ecosystem respiration (R_e) play vital roles in regulating global C balance and climate-biosphere feedback in the Earth system. Despite the fact that numerous manipulative studies and a few meta-analyses have been conducted to examine the responses of R_s and its components (i.e. autotrophic [R_a] and heterotrophic respiration [R_h]) as well as R_e to grazing (G) or global change factors, the interactive effects between grazing and global change factors remain poorly understood.
2. Here, we performed a comprehensive meta-analysis of manipulative experiments with both grazing and global change factors to quantify their individual and interactive effects on R_s and its components as well as R_e .
3. Our results showed that grazing and drought significantly decreased R_s by 12.35% and 20.95%, respectively, whereas warming (W), nitrogen addition (N) and increased precipitation (P) stimulated it by 2.12%, 5.49% and 13.44%, respectively. Similarly, grazing, warming, nitrogen addition and increased precipitation increased R_e by 7.21%, 4.94%, 48.45% and 21.57%, respectively, while drought decreased it by 16.86%. However, the combinations of grazing with warming (GW), nitrogen addition (GN) and increased precipitation (GP) exhibited non-significant effects on R_s . More importantly, additive interactions between grazing and global change factors exhibited a substantial predominance on R_s , R_a , R_h and R_e rather than synergistic and antagonistic ones.
4. *Synthesis and applications.* Our findings highlight the crucial importance of the interactive effects between grazing and global change factors on soil respiration (R_s) and ecosystem respiration (R_e). Therefore, incorporating this key influence on ecosystem processes into Earth system models (ESMs) could better improve the prediction of climate-biosphere feedbacks and develop sustainable strategies for grassland management in the Anthropocene.

KEYWORDS

additive effect, drought, grazing, increased precipitation, meta-analysis, nitrogen addition, warming

1 | INTRODUCTION

Across the globe, grasslands occupy more than 40% of the world's ice-free land area (Hufkens et al., 2016) and account for 10%–30% of the global soil organic carbon (SOC, Ramankutty, Evan, Monfreda, & Foley, 2008). Currently, a majority of grasslands are experiencing simultaneous changes in human disturbance (e.g. grazing) and global climate change, which may impose profound effects on ecosystem services and functions by altering the biogeochemical cycle, especially carbon (C) cycle (Wilson, Strickland, Hutchings, Bianchi, & Flory, 2018; Zhu, Chiariello, Tobeck, Fukami, & Field, 2016). The altered C cycle may lead to a positive or negative climate-biosphere feedback, which in turn amplify or diminish their net effects on ecosystem biodiversity and stability (Zhou, Zhou, He, et al., 2017). Understanding the C dynamic of grasslands in response to human disturbance and climate change is thus crucial for better predicting future global C balance and developing sustainable strategies for grassland management (Chapin, Matson, & Mooney, 2002; McSherry & Ritchie, 2013; Zhou, Luo, Chen, et al., 2019).

Soil respiration (R_s) represents CO_2 flux released from the soil surface to atmosphere, which includes autotrophic respiration (R_a) by alive roots and their symbionts (Luo & Zhou, 2006; Zhou, Zhou, Zhang, et al., 2017) and microbial respiration (R_h) during organic matter and litter decomposition (Bond-Lamberty & Thomson, 2010). As the second largest C flux between the atmosphere and terrestrial ecosystem with a range from 68 to 98 Pg C/year, R_s is nearly 10 times higher than CO_2 emission from fossil fuel combustion (Bond-Lamberty & Thomson, 2010; Luo & Zhou, 2006). Ecosystem respiration (R_e) is the summed respiration from above-ground plants, below-ground roots and microbes, releasing nearly 120 Pg C/year to atmosphere (Beer et al., 2010; Luo & Zhou, 2006). Therefore, even small changes in R_s and R_e can have great potential to increase or decrease atmospheric C concentration and then influence C cycle feedbacks to climate change (IPCC, 2013).

Over past decades, a large number of ecosystem-level studies have been conducted to examine the responses of R_s and R_e to grazing or single global change factors (e.g. warming, drought or increased precipitation) in grasslands (Bagchi & Ritchie, 2010; Zavaleta, Shaw, Chiariello, Mooney, & Field, 2003). Several synthesized studies have been carried out to investigate the central tendency of R_s and/or R_e in response to grazing or single global change factors from diverse results at the global scale (Liu et al., 2016; Zhou et al., 2016). For example, Zhou, Zhou, He, et al. (2017) suggested that grazing increased R_s by 4.25% across all available field studies. N addition would lead to a significant stimulation in R_s by 7.84%, although R_a and R_h showed the opposite response directions (Zhou et al., 2014). Likewise, increased precipitation had been found to lead to a greater increase in R_s in arid areas, and the stimulated rates may decrease with increasing climate humidity (Liu et al., 2016). Warming stimulated R_s by 12% at the early stages, but the simulation would be offset by the adverse effects of microbial acclimation and warming-induced drought over time (Wang et al., 2014). Recently, numerous studies have

investigated the responses of R_s and/or R_e to grazing combined with global change factors, but showed contradictory results with increase (Zhu et al., 2015), decrease (Lin et al., 2011) and no effect (Sharkhuu et al., 2016). However, the general pattern about effects of grazing combined with global change factors on R_s and R_e remain elusive, although it is vital to assess the climate-biosphere feedbacks and develop ecosystem C sequestration strategies in the future (McSherry & Ritchie, 2013; Zhou, Luo, Chen, Hu, et al., 2019). These knowledge gaps will largely limit our ability to incorporate these potential effects into regional and global models for future global C prediction.

Grazing accompanying with single or multiple global change factors (e.g. warming, nitrogen addition, drought) may interactively (i.e. additive, synergistic or antagonistic) affect R_s and its components as well as R_e in grassland ecosystems (Zavaleta et al., 2003; Zhou et al., 2016). Although numerous grazing or single global change experiments had been conducted, multifactor studies with both grazing and global change factors were limited by methodological difficulties, cost and ecosystem diversity (Zhou et al., 2014). On the other hand, previous studies mainly focused on interactions among different global change factors, rather than them in combination with human disturbances such as grazing (Yue et al., 2017). However, grazing may have a dominant role in governing C cycling than global change factors, due to the stronger effects on plant community structure, soil microenvironment and soil microbial diversity in grassland ecosystems (Frank & Groffman, 1998; Zhou, Luo, Chen, Hu, et al., 2019). Whether the interactive effects between grazing and global change factors on C cycling is the same or not as those among multiple global change factors is an unsolved but vital issue to predict future C dynamic in grasslands. Therefore, it is necessary to compile all available data to probe the interactions between grazing and global change factors on R_s and its components as well as R_e , which could improve our understanding of climate-C cycle feedback in grassland ecosystems.

Here, we used a meta-analysis approach to examine how grazing and global change factors singly and interactively affect R_s , R_a , R_h and R_e . Specifically, our objectives were to (a) examine effects of grazing, global change factors and the combination of grazing and global change on R_s and its components as well as R_e ; and (b) investigate the overall interactive effects between grazing and global change factors (including additive, synergistic or antagonistic) on R_s and its components as well as R_e across all available studies.

2 | MATERIALS AND METHODS

2.1 | Data collection

Peer-reviewed papers regarding soil respiration (R_s) and its components (i.e. autotrophic [R_a] and heterotrophic respiration [R_h]) as well as ecosystem respiration (R_e) under grazing combined with global change factors (e.g. nitrogen addition, warming, drought) were searched from Google Scholar and Web of Science (1900–2018). To minimize publication bias, we used five criteria to select papers:

(a) At least a full-factorial experiment was designed to examine the effects of grazing combined with global change factors on R_s , R_a , R_h and/or R_e ; (b) The selected variables (e.g. R_s , R_a , R_h , R_e) of the control and treatment groups had the same spatial and temporal scales; (c) Plots for the control and treatment groups had the similar climate conditions, dominant species compositions, soil parameters and ecosystem type at the beginning of studies; (d) Mean values and standard deviation/error as well as sample size of concerned variables (e.g. R_s , R_a , R_h and R_e) in both control and treatment pairs could be obtained from digitized graphs, tables and/or texts of selected papers; (e) The manipulative methods of warming, nitrogen addition, irrigation or drought were clearly recorded, and experimental length were more than one growing season. Finally, 48 published papers (of more than 2000) with 259 pairs, were selected, among which 184 addressed R_s , and 75 pairs were R_e (See Appendix Text S1 and Figure S1 in Supporting Information). Here G is grazing, W is warming, N is nitrogen addition, P is increased precipitation and D is drought. The number of studies for the combinations of grazing with warming (GW), nitrogen addition (GN) and increased precipitation (GP) were 13, 9 and 4 respectively. Note that there were no available data from studies of grazing combined with elevated CO_2 (GE) and drought (GD).

Meanwhile, we also extracted the related C variables (below-ground plant carbon pool [BPCP], gross ecosystem productivity [GEP], net ecosystem exchange [NEE]) and environmental factors (i.e. mean annual temperature [MAT], mean annual precipitation [MAP] and latitude) into our compiled database. Environmental variables included MAP ranging from 94 to 930 mm, MAT ranging from -3.8 to $26.2^\circ C$ and latitude ranging from $30.9^\circ N$ to $50.1^\circ N$ (See Figure S1). Experimental duration ranging from 0.4 to 31 years. The C pools from below-ground parts (i.e. BPCP) was transformed by plant C content or plant biomass as Zhou, Luo, Chen, Hu, et al. (2019). If climate information were unavailable, we used site Geographical coordinates information to extract them from the global climate database (www.worldClim.com).

2.2 | Data analysis

2.2.1 | Individual and combined effects

The individual effect of grazing and single global change factor and combined effects of two factors (e.g. grazing + warming, GW) were calculated by the methods described as Hedges & Olkin (1985) and Luo, Hui & Zhang (2006). Specifically, lnRR, natural logarithm of response ratio, was used to calculate the magnitude of the effects of concerned treatments as below:

$$\text{LnRR} = \ln \left(\frac{X_t}{X_c} \right) \quad (1)$$

where X_c and X_t were the mean values of control and treatment pairs respectively. The detailed calculation of the weight (w) and variance

(v) of each RR as well as weighted LnRR (LnRR_{++}) were described as Zhou et al. (2014). Here, the combined effects were lnRR between the observed results with two factors (e.g. grazing + warming, GW; warming + N addition, WN) and the control.

2.2.2 | Interactive effects

In this study, the interactive effect is the simultaneous effect of two or more independent factors on concerned variables (e.g. R_s , R_a , R_h or R_e), in which their joint effect is markedly less or greater than the sum of parts, including antagonistic, synergistic and additive interactions (Zhou et al., 2016). Hedge's d was applied here to evaluate the interaction effect size of two individual pairs of treatments on the concerned variables using the method described as Gurevitch and Hedges (2001) and Zhou, Luo, Chen, Hu, et al. (2019). The main effects and their interactions between A and B were calculated using Equations 2–4 respectively.

$$d_A = \frac{(\overline{X_A} + \overline{X_{AB}}) - (\overline{X_B} + \overline{X_C})}{2s} J(m) \quad (2)$$

$$d_B = \frac{(\overline{X_B} + \overline{X_{AB}}) - (\overline{X_A} + \overline{X_C})}{2s} J(m) \quad (3)$$

$$d_I = \frac{(\overline{X_{AB}} - \overline{X_A}) - (\overline{X_B} - \overline{X_C})}{2s} J(m) \quad (4)$$

where $\overline{X_A}$, $\overline{X_B}$, $\overline{X_C}$ and $\overline{X_{AB}}$ are means of a variable in A and B treatments, and their combined pairs respectively; degree of freedom (m) and the pooled standard deviation (s) were calculated by following equations.

$$s = \sqrt{\frac{(n_C - 1)(s_C)^2 + (n_A - 1)(s_A)^2 + (n_B - 1)(s_B)^2 + (n_{AB} - 1)(s_{AB})^2}{n_C + n_A + n_B + n_{AB} - 4}} \quad (5)$$

$$m = n_C + n_A + n_B + n_{AB} - 4 \quad (6)$$

$$J(m) = 1 - \frac{3}{4m - 1} \quad (7)$$

where n_C , n_A , n_B and n_{AB} were sample numbers of control, A and B treatments as well as their combinations (A + B) and s_C , s_A , s_B and s_{AB} were the standard deviations of the treatments of control, A and B as well as their combinations, respectively; The detailed calculation of variance (v_2) of main effects and interactions (d_A , d_B and d_I) as well as weighted mean (d_{++}) were described as Zhou et al. (2016).

The 95% confidence interval (CI) of d_{++} and RR_{++} were calculated as $d_{++} \pm C_{\alpha/2 \times S}(d_{++})$ and $\text{RR}_{++} \pm C_{\alpha/2 \times S}(\text{RR}_{++})$ when the sampling number was more than 20. $C_{\alpha/2}$ is the two-tailed critical value of

the standard normal distribution (Zhou, Luo, Chen, Hu, et al., 2019). Otherwise, we used a bootstrapping method to resample data based on 5,000 iterations, which was consistent with the calculation of CI of individual and combined effect of concerned treatments. Interactions between two treatments were classified into three types, that are, synergistic, antagonistic and additive according to the above calculations (Crain, Kroeker, & Halpern, 2008). Specifically, the interaction was recognized as additive when 95% CI overlapped with 0. For factor groups whose individual effects were either both negative or exhibit opposite directions, the interactions <0 were classified as synergistic and >0 were antagonistic (Crain et al., 2008).

To reduce large uncertainty induced by the limited sample sizes, we mainly described and discussed those with at least 10 numbers for grazing and/or global change factors. We performed Pearson correlation analyses to explore the relationships between $RR(R_s)$ and environmental factors (i.e. MAP and MAT) under grazing, single global change factors (e.g. nitrogen addition, increased precipitation) and their combinations (e.g. GP and GN). All figures were mapped with SigmaPlot software (version 10.0; Systat Software Inc., CA, USA).

3 | RESULTS

3.1 | Individual effects of grazing and single global change factors and their combined effects on R_s and R_e

Across all the multifactor studies, grazing and drought significantly decreased R_s by 12.35% and 20.95%, respectively, while warming, nitrogen addition and increased precipitation stimulated it by 2.12%, 5.49% and 13.44% respectively (Figure 1a; Table 1). Similar to R_s , warming, nitrogen addition, and increased precipitation also stimulated R_e by 4.94%, 48.45% and 21.57%, respectively, while drought decreased it by 16.86%. Among these global change drivers, nitrogen addition showed the largest enhancing effect on R_e compared to other factors (Figure 1b; Table 1). In contrast, grazing exerted positive effects on R_e by 7.21%. Meanwhile, grazing decreased R_a by 15.58%, but nitrogen addition increased it by 15.20% and increased precipitation had insignificant effects on R_a (Figure 1c). R_h were significantly reduced by grazing (-20.49%), warming (-10.99%) and drought (-12.54%), but were stimulated by nitrogen addition (+14.68%) and increased precipitation (+23.38%, Figure 1d; Table 1).

The combined effects of the multiple factors were significant on R_s for warming + increased precipitation (WP, +42.49%) and warming + drought (WD, -8.05%), but grazing + warming (GW), grazing + increased precipitation (GP), grazing + nitrogen addition (GN), warming + nitrogen addition (WN) and increased precipitation + nitrogen addition (PN) did not significantly affect R_s . The GN also increased R_a by 12.24% but decreased R_h by 15.88%. Similar to R_s , GP exhibited non-significant effects on R_a and R_h . R_h was stimulated by WP with an increase of 21.63%, but significantly decreased by GN (-15.88%, Figure 1d). The responses of R_e to two-driver pairs were significantly stimulated by GN (+20.88%), WN (+52.04%), WP (+34.31%) and PN (+57.66%), but decreased it by WD (-10.51%, Table 1).

3.2 | Interactive effects of multiple factors on R_s and R_e

Across all the two-factor pairs, additive interactions showed the substantial predominance on R_s , R_a , R_h and R_e compared with synergistic and antagonistic interactions (Figure 2). This general pattern remained similar for each of those two-factor combinations when the sample size was more than eight (Figure 3). Specifically, the interactions in GP, WN and WD on R_s were synergistic with the stimulated effects, whereas the interactions in GW and WP on R_s were additive with the insignificant effects. The interactive effect of GN, GP and WP on R_h was additive except for WD, showing a synergistic interaction with significantly positive effects (Figure 3). Although antagonistic effects for the interaction of GN and WN (both $n = 6$) on R_e were observed, an additive interaction still exhibited a substantial predominance as shown by the frequency distribution and individual observations of GW, WP and WD on R_e .

3.3 | Regulation of biomes and environmental factors on R_s and R_e

Soil respiration was significantly correlated with BPCP but with different slopes in response to single and combined factors compared with those in the controls. Specifically, the significant relationships between SCP and BPCP under grazing (G), all single global change factor treatments (GC) and grazing activities combined with the global change factors (G + GC), were smaller than those under the control (Figure 4a-c). In addition, no correlation between BPCP and R_s under both multiple global change factors (GC + GC) and the control were observed probably due to the limited numbers of samples (Figure 4d).

Similarly, both $RR(R_s)$ and $RR(R_h)$ exhibited significant positive correlations with $RR(R_s)$ but with different slopes under G, GC, G + GC and GC + GC (Figure 5a,b). $RR(R_e)$ in response to G, GC, G + GC and GC + GC increased with GEP, with the largest increase under GC ($p < 0.05$, Figure 5c). Furthermore, $RR(R_e)$ exhibited significantly positive correlations with NEE under G, GC and GC + GC, but no significant correlation was found under G + GC (Figure 5d).

Our meta-analysis also showed that the $RR(R_s)$ induced by grazing and its combination with nitrogen addition (GN) exhibited significant positive correlation with MAP, while $RR(R_s)$ under grazing had no correlation with MAP (Figure 6a-c). The grazing-induced $RR(R_s)$ and its combinations with increased precipitation were positively correlated with MAT, despite that non-significant correlation between $RR(R_s)$ and MAT under increased precipitation alone was found (Figure 6d-f).

4 | DISCUSSION

4.1 | Individual effect of grazing or single-global climate change factor

Grazing by domestic livestock and global change factors (e.g. warming, nitrogen addition and drought) are the two most important

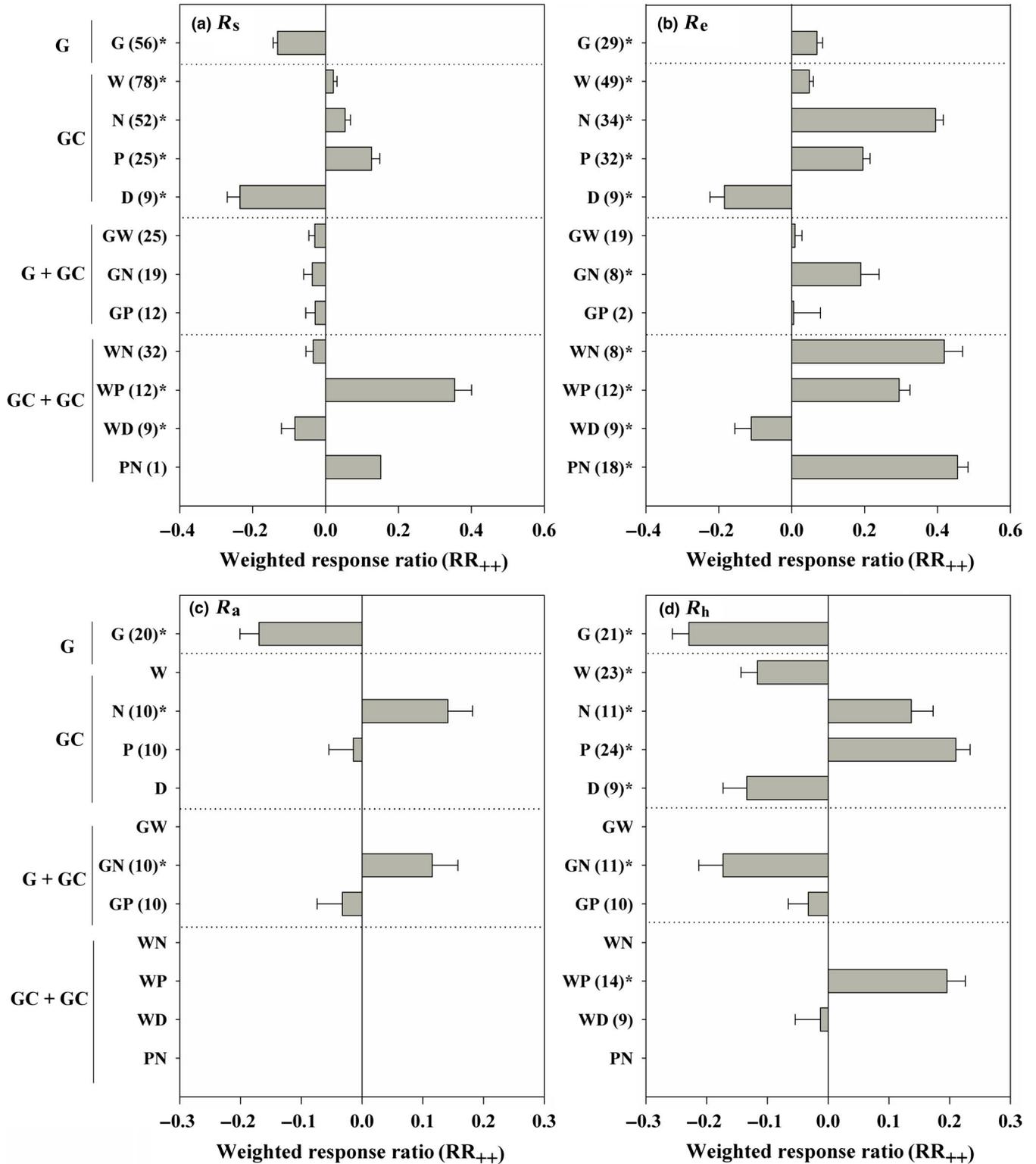


FIGURE 1 Weighted response ratio (RR₊₊) of soil respiration (R_s , a), ecosystem respiration (R_e , b), autotrophic respiration (R_a , c) and heterotrophic respiration (R_h , d) to the effects of single factor and two combined factors. Bars represent 95% confidence intervals. The vertical line was drawn at RR₊₊ = 0. G, W, N, P and D represent grazing, warming, nitrogen addition, increased precipitation and drought respectively. G, grazing; GC, all single-global climate change factor treatments; G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors

factors that significantly affect the C cycle in grassland ecosystems (McSherry & Ritchie, 2013; Yuan & Chen, 2015). Using a meta-analysis approach, we found that grazing significantly decreased

soil respiration (R_s) and its components (i.e. autotrophic respiration, R_a and heterotrophic respiration, R_h , Figure 1). The decreased C fluxes may be attributed to the decreased above-below-ground

TABLE 1 Percentage of concerted variables is represented as the mean \pm 95% confidence intervals

	R_s		R_a		R_h		R_e	
	Change value		Change value		Change value		Change value	
	$(e^{RR_{++}} - 1) \times 100\%$	<i>n</i>						
G	-12.35 \pm 1.24*	56	-15.58 \pm 3.20*	20	-20.49 \pm 2.76*	21	7.21 \pm 1.53*	29
W	2.12 \pm 1.03*	78	—	—	-10.99 \pm 2.74*	23	4.94 \pm 1.14*	49
N	5.49 \pm 1.51*	52	15.20 \pm 4.13*	10	14.68 \pm 3.66*	11	48.45 \pm 2.11*	34
P	13.44 \pm 2.30*	25	-1.43 \pm 4.09	10	23.38 \pm 2.37*	24	21.57 \pm 2.01*	32
D	-20.95 \pm 3.52*	9	—	—	-12.54 \pm 3.96*	9	-16.86 \pm 4.04*	9
GW	-2.88 \pm 1.71	25	—	—	—	—	0.93 \pm 1.94	19
GN	-3.57 \pm 2.40	19	12.24 \pm 4.31*	10	-15.88 \pm 4.07*	11	20.88 \pm 5.15*	8
GP	-2.84 \pm 2.61	12	-3.19 \pm 4.23	10	-3.22 \pm 3.34	10	0.56 \pm 7.63	2
WN	-3.32 \pm 2.05	32	—	—	—	—	52.04 \pm 5.11*	8
WP	42.49 \pm 4.78*	12	—	—	21.63 \pm 3.06*	14	34.31 \pm 2.98*	12
WD	-8.05 \pm 3.78*	9	—	—	-1.25 \pm 4.24	9	-10.51 \pm 4.62*	9
PN	16.37	1	—	—	—	—	57.67 \pm 2.92*	18

Abbreviations: R_a , autotrophic respiration; R_e , ecosystem respiration; R_h , heterotrophic respiration; R_s , soil respiration.

* $p < 0.05$.

biomass and substrate availability as well as microbial community induced by livestock grazing (Frank & Groffman, 1998; Mcsherry & Ritchie, 2013). Specifically, grazing-induced plant damage and removal would decrease photosynthetically fixed C inputs to roots, resulting in lower root biomass and root exudates (Bagchi & Ritchie, 2010; Mcsherry & Ritchie, 2013). In contrast, grazing significantly increased R_e largely due to the fact that most of those studies with R_e data had light grazing with low plant damage and removal (Figure 1b). Light grazing-induced over-enhancement in photosynthetic rates and biomass may increase plant C pools and R_s in those experiments (i.e. intermediate disturbance hypothesis, Sasaki et al., 2009), leading to increased R_e in response to grazing (Zhou, Zhou, He, et al., 2017).

Meanwhile, R_s increased significantly by warming, nitrogen addition and increased precipitation (Figure 1a), with the largest stimulation by increased precipitation. It has been shown that increased precipitation would stimulate productivity and net ecosystem CO_2 exchange (NEE) through enhancing nitrogen-use efficiency (NUE) and water-use efficiency (WUE), especially in arid and semi-arid grasslands (Flanagan, Wever, & Carlson, 2002; Liu et al., 2016). The increased precipitation thus greatly accelerates soil C turnover, causing larger stimulation on R_s in arid grassland ecosystems than other biomes (Liu et al., 2016). In contrast, drought significantly decreased R_s , which was similar to the results from Werner, Savage, Davidson, and Trumbore (2006) and Liu et al. (2016). The increased water stress induced by drought may decrease photosynthetic C, substrate availability (e.g. carbohydrate, humic acids), and microbial activity, further impeding root and microbial respiration and then R_s (Davidson, Samanta, Caramori, & Savage, 2012; Fuchslueger, Bahn, Fritz, Hasibeder, & Richter, 2014; Zhou, Wan, & Luo, 2007).

4.2 | Combined and interactive effects of grazing and global change factors

Predicting future climate-biosphere feedback in global grasslands requires the knowledge of the combined and interactive effects of grazing and climate change factors on C fluxes (Zhou, Luo, Chen, Hu, et al., 2019). In this study, we found that grazing significantly decreased R_s , but the negative effect was largely alleviated by the positive effect from warming, nitrogen addition and increased precipitation (Figure 1a). Grazing-induced decrease in soil moisture, nitrogen availability, soil microbial diversities and activities would inhibit plant growth and soil microbe decomposition and then R_s (McSherry & Ritchie, 2013). However, grazing associated with nitrogen addition (GN) or increased precipitation (GP) is likely to lead to an increase in soil nitrogen or moisture content, respectively, causing positive effects on plant growth and microbial activity (Zhou, Luo, Chen, Hu, et al., 2019). Warming-induced changes in plant phenology and increase in soil N availability would stimulate plant net primary productivity (NPP) and microbial activity (Liu et al., 2016; Sherry et al., 2007). Therefore, grazing in combination with warming (GW) would also enhance plant growth and microbial activity, largely alleviating the negative effects on R_s by grazing alone.

The combination of different global change factors also influenced the biogeochemical cycles of C in grassland ecosystems. Our meta-analysis found that the combinations of warming + increased precipitation (WP) significantly increased R_s , whereas warming + drought (WD) decreased it (Figure 1a). These results indicated that each global change factor may exhibit diverse influences on R_s when combined together. The positive effects of warming on R_s seemed to be strengthened by increased precipitation, resulting in the positive effects of WP on R_s . This is because both warming and increased precipitation would

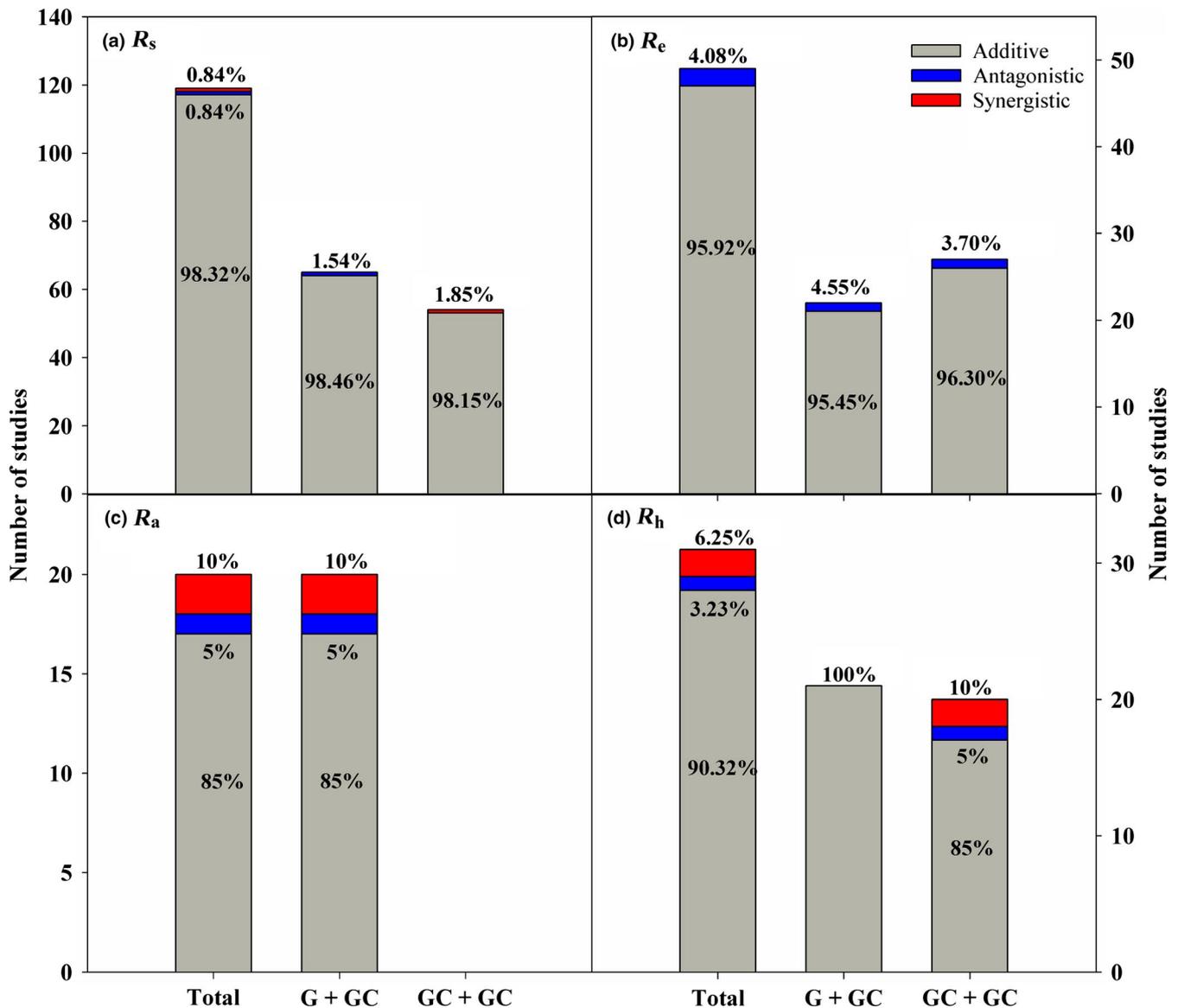


FIGURE 2 Frequency distribution of interaction types in individual studies with two-factorial designs for soil respiration (R_s , a), ecosystem respiration (R_e , b), autotrophic respiration (R_a , c) and heterotrophic respiration (R_h , d) in single factor and combined studies. G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors

stimulate plant growth to a greater extent compared with those in the control (Liu et al., 2016), resulting in positive effects on leaf and stem respiration and then R_e (Zhou et al., 2018). However, the greatly negative effects of drought on R_s would be intensified by the water stress induced by warming, leading to limited root growth and microbial decomposition for soil organic matter, which significantly decreased R_s and R_e (Liu et al., 2016; Sheik et al., 2011).

Interactive effects between grazing and global change factors on C cycling are critical for improving Earth system models to better predict grassland dynamics (Crain et al., 2008; Zavaleta et al., 2003). Our results showed that additive interaction between grazing and global change factors were generally common on R_s , R_a , R_h and R_e , rather than synergistic or antagonistic ones, which were similar to the experimental results of multiple climate change factors from Yuan and Chen (2015), Zhou et al. (2016) and Yue et al.

(2017). Nevertheless, the non-additive interaction (synergistic vs. antagonistic) between grazing and global change drivers on R_s and R_a should not be negligible when separately considering the different combinations (i.e. GN with antagonistic for R_s , GP with synergistic for R_s and R_a). Meanwhile, the interactions between warming and drought also exhibited a significantly synergistic influence on R_s and R_h , Leuzinger et al. (2011) and Dieleman et al. (2012) also suggested that the interactions between multiple global change drivers seemed to be more antagonistic. These differences may result from the differences in the concerned variables and combined group of driving factors (Zhou, Zhou, He, et al., 2017). Taken together, the interactions between human activity and climate change factors may show differential effects on diverse variables in grassland ecosystems.

Specifically, antagonistic interaction on R_s mainly occurred in combinations of grazing and nitrogen addition in grasslands under a

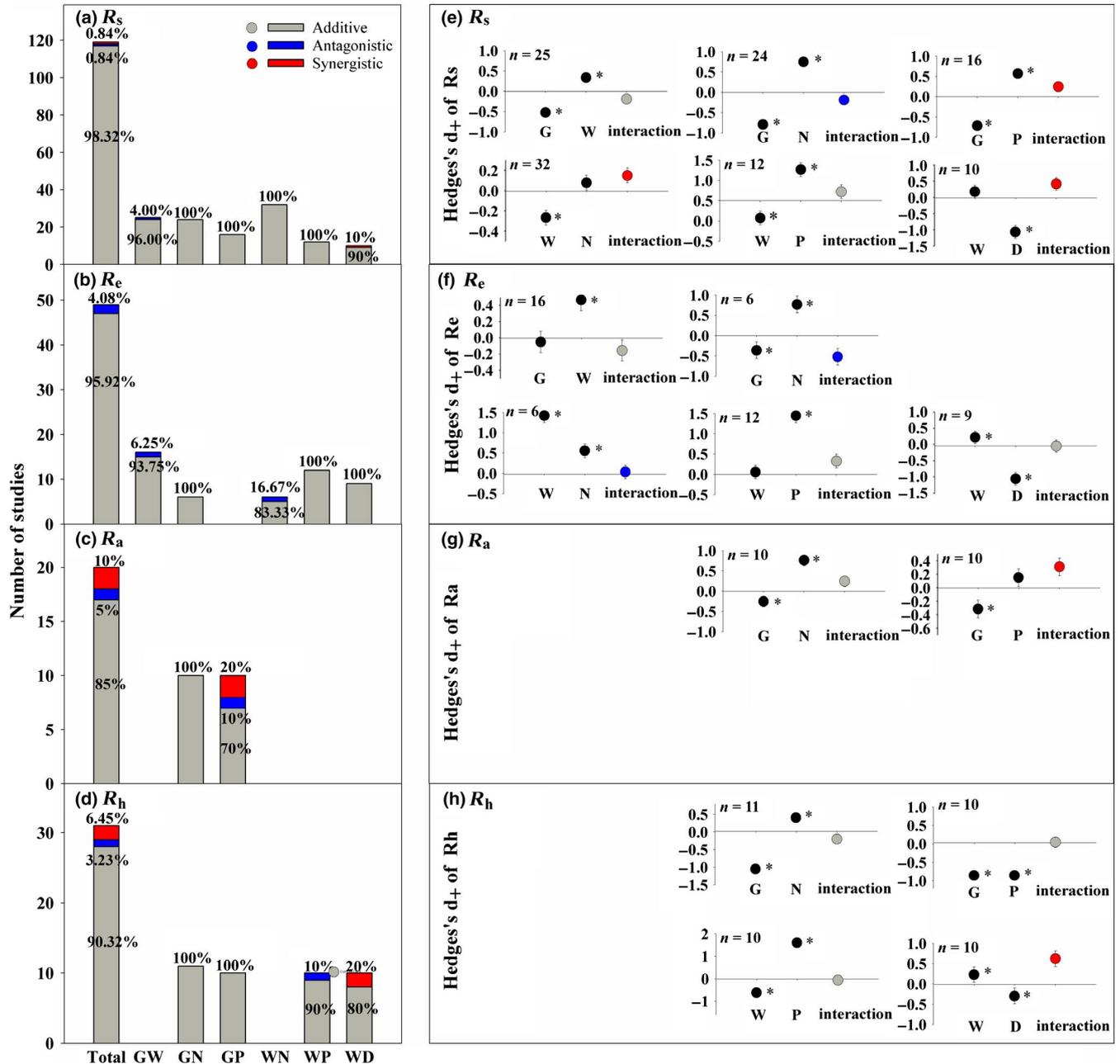


FIGURE 3 Frequency distribution of interaction types in individual studies with two-factorial designs for soil respiration (R_s , a), ecosystem respiration (R_e , b), autotrophic respiration (R_a , c) and heterotrophic respiration (R_h , d) in single factor and combined studies. G, W, N, P and D represent grazing, warming, N fertilization, increased precipitation and drought respectively. Asterisk in panel e, f, g and h indicated statistical significance ($p < 0.05$)

nitrogen limiting condition (Liu & Greaver, 2010; Niu et al., 2016), which could result from the stronger negative effect of grazing on nitrogen addition-induced increase in R_s . These changes may be attributed to the fact that plant damage and removal induced by grazing are likely to decrease the photosynthetically fixed C inputs to root, resulting in lower root biomass and BPCP (Frank & Groffman, 1998). R_a under GN exhibited similar positive responses to these under nitrogen addition alone, which could be ascribed to the greater proportion of newly assimilated C with larger root/shoot ratio in water-limited grasslands in response to nitrogen addition (Mokany, Raison, & Prokushkin, 2006). It has been shown that decreased C inputs induced by grazing may have

a significant negative effect on soil microbial biomass and soil C, which could further decrease the respiration from microbes (R_h , Mcsherry & Ritchie, 2013). Although nitrogen addition may stimulate microbial decomposition, this positive effect could be largely offset because grazing would largely decrease soil microbial diversity and soil organic matter decomposition when combined with grazing, leading to reduced R_h (McSherry & Ritchie, 2013). Therefore, the opposite responses of R_a and R_h lead to the overall non-significant GN effect on R_s .

Our results also indicated that the grazing combined with increased precipitation (GP) exhibited a synergistic interaction on R_s and R_a (Figures 1 and 3). The decreased soil moisture induced by grazing due

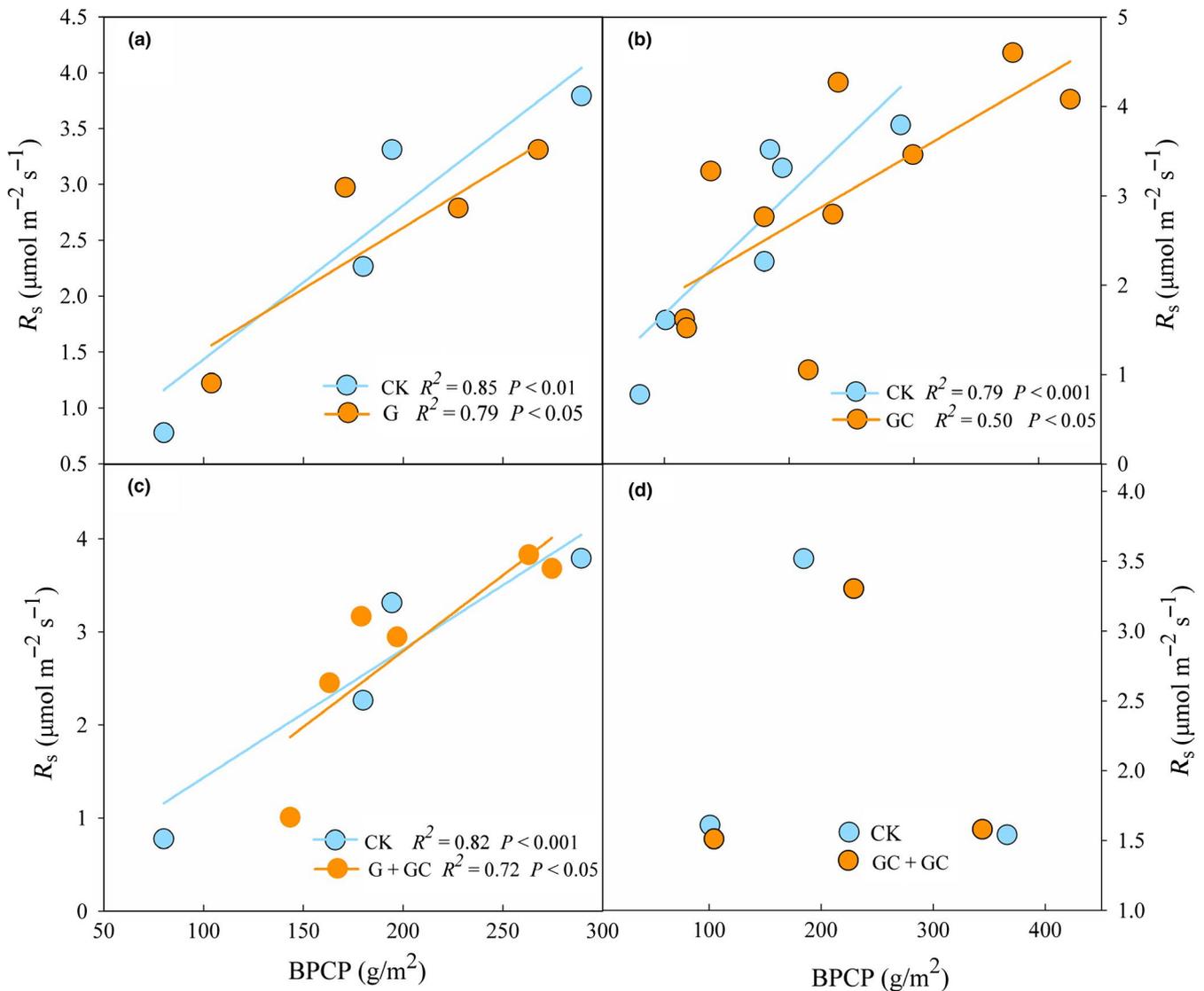


FIGURE 4 Observed soil respirations as a function of below-ground plant carbon pool (BPCP) in single and combined factors studies. G, grazing; GC, all single-global climate change factor treatments; G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors

to faster soil evaporation with poor ground cover may cause negative effects on root turnover and growth, but this effect could be largely relieved by increased precipitation in arid/semi-arid grasslands (Chapin et al., 2002; Liu et al., 2016). Therefore, the combined effects of grazing and increased precipitation in arid/semi-arid grasslands may exhibit neutral effects on R_s . Similar to R_s , the grazing combined with nitrogen addition showed antagonistic interaction on R_g , but significantly stimulated it in grassland ecosystems (Figures 1 and 3). These changes may be attributed to the antagonistic effects on NEE and GEP induced by GN (Zhou et al., 2014; Sharkhuu et al., 2016).

4.3 | Regulating mechanisms of environmental factors

Environment factors (e.g. MAP and MAT) have been widely demonstrated to affect plant performance and C cycling in response to grazing and/or global change factors (Chapin et al., 2002; Luo & Zhou,

2006). Our results showed that $RR(R_s)$ led to a significant positive linear correlation with MAP under nitrogen addition, which was consistent with the results from Zhou et al. (2014). Nitrogen-induced increase in R_s may be strongly stimulated as a result of higher plant productivity and microbial diversity in wetter than drier climates (Chapin et al., 2002; McSherry & Ritchie, 2013; Zhou et al., 2014). Microbial activity in humid regions is also more susceptible to nitrogen addition than those in arid areas, which largely increased microbial carbon-use efficiency (CUE) in soils (Manzoni, Taylor, Richter, Porporato, & Ågren, 2012; Niu et al., 2016). The combined effects of GN on R_s also exhibited a positive correlation with MAP, with the similar regression slope with those only under nitrogen addition. These results suggested that nitrogen addition played the important role in the responses of R_s to GN with increasing MAP compared to grazing.

Interestingly, the combined effects of GP on R_s exhibited a significant positive correlation with MAT, although negative correlation between $RR(R_s)$ and MAT under grazing was observed. Tropical and

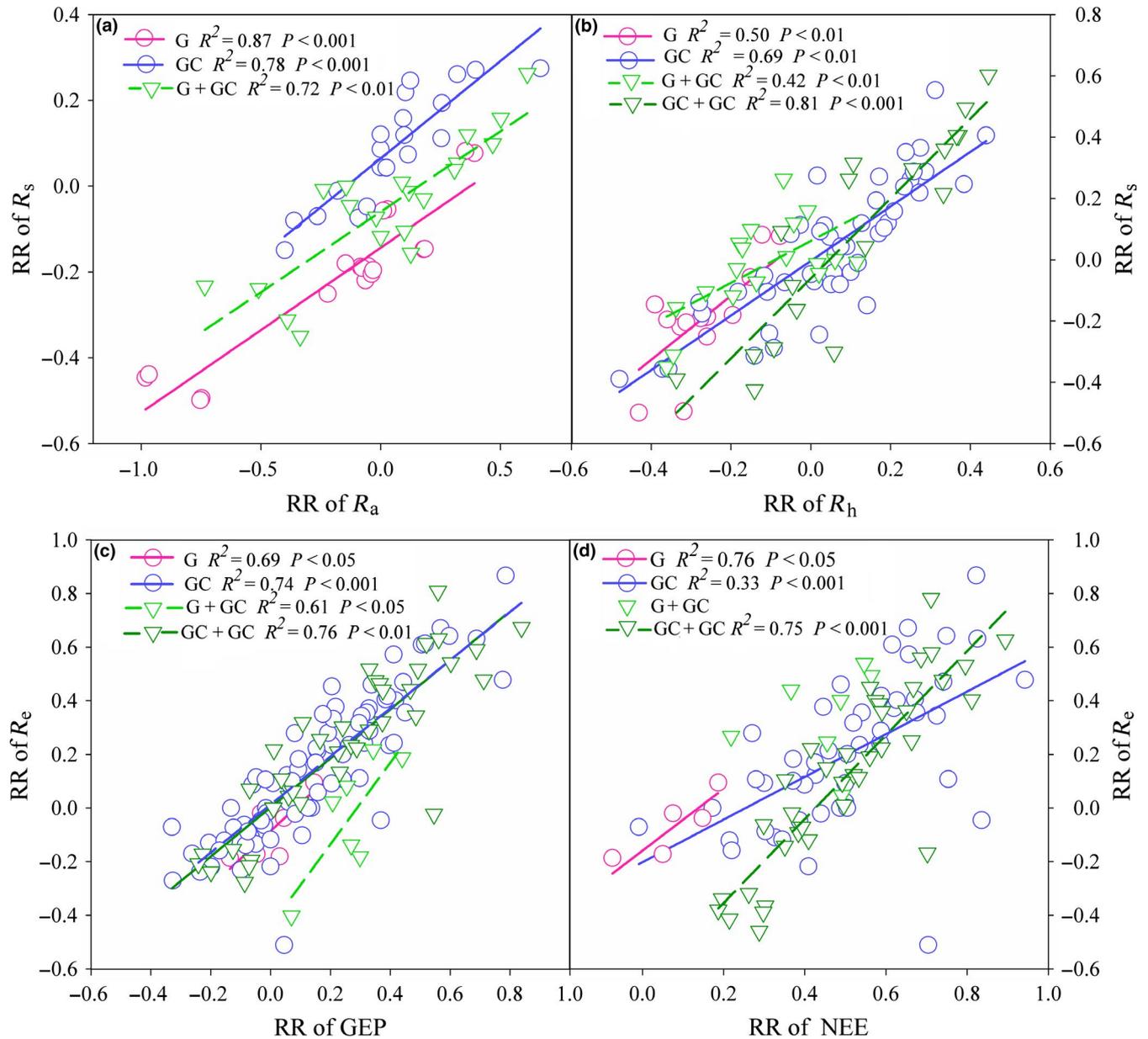


FIGURE 5 Correlations of the response ratios (RR) of soil respiration (R_s) with RRs of its two components, autotrophic respiration (R_a) and heterotrophic respiration (R_h) in single factor and combined studies (a, b). Correlations of the RRs of ecosystems respiration (R_e) with RRs of gross ecosystem productivity (GEP, c) and net ecosystem exchange (NEE, d) in single factor and combined studies. G, grazing; GC, all single-global climate change factor treatments; G + GC, grazing combined with a global climate change factor; GC + GC, two combined global climate change factors

temperate grassland usually have higher MAT and stronger evaporation than those in boreal ones with lower MAT (Chapin et al., 2002). Grazing-induced degradation and desertification may decrease ground cover as well as soil infiltrability, which largely lower soil moisture to depress plant root and microbial activity (Zhou, Zhou, He, et al., 2017). However, RR (R_s) showed a significant linear positive correlation with MAT under GP, largely resulting from an increase in water availability induced by increased precipitation, which largely stimulated plant growth and microbial activities respectively (Chapin et al., 2002). In addition, due to the antagonistic interaction between grazing and increased precipitation, plants can obtain more C allocation to roots as well as soil C accumulation under GP, which could significantly

contribute to increasing R_a and then R_s (Liu et al., 2016; Zhou et al., 2016).

4.4 | Guidelines for future grassland management and model development

Understanding the individual and interactive effects of livestock grazing and global change factors could help us to better predict climate-C cycle feedback in the Anthropocene (McSherry & Ritchie, 2013; Zhou, Luo, Chen, Hu, et al., 2019). In this study, we found that grazing, global climate change and their combinations significantly affected soil and ecosystem respiration (R_s and R_e) in grassland

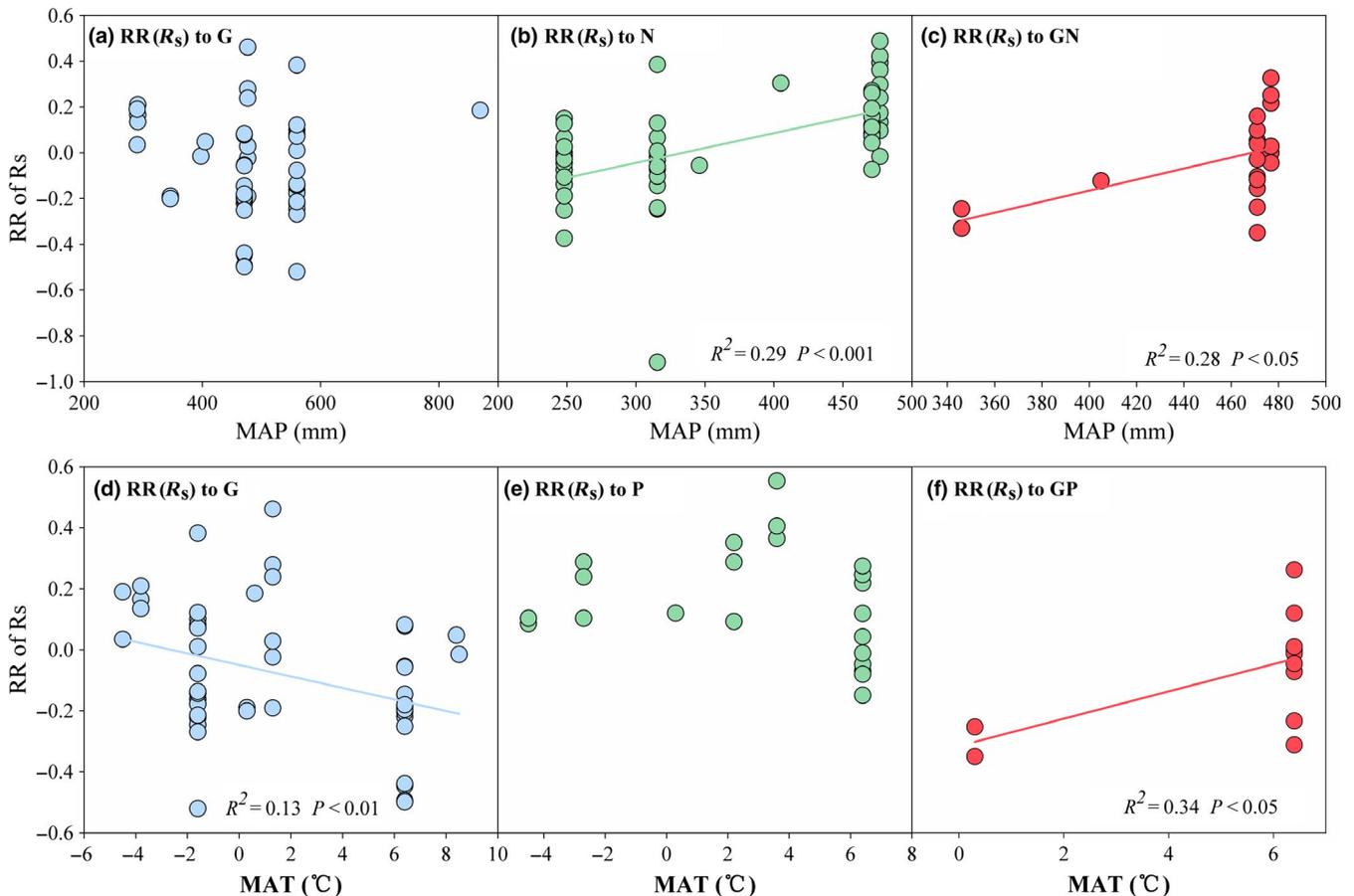


FIGURE 6 Effects of mean annual precipitation (MAP) and mean annual temperature (MAT) on the response ratios of soil respiration [RR(R_s)] to grazing (a, d), nitrogen addition (b), the combined treatments of G and N (GN, c), increased precipitation (e) and the combined treatments of G and P (GP, f). The black dots mean the observations and the grey shaded areas represent 95% confidence intervals

ecosystems. Our results help understand how grazing and global change factors interactively affected R_s and R_e at the global scale, which may offer some guidelines for future grassland management and model development.

First, our results showed that grazing significantly decreased R_s , but this negative effect was largely alleviated when combined with some global change factors (e.g. GW, GN, GP). These results indicated that increased temperature, nitrogen addition and irrigation could be used as an ecological measure to decrease soil C loss for the regions where it suffered overgrazing. Meanwhile, our studies mainly focused on the effects of two factors on R_s and R_e . However, Leuzinger et al. (2011) demonstrated that the response of R_s may decline with the increasing number of global change factors in terrestrial ecosystems. How and to what extent the effects of grazing combined with more global change factors (at least two) on R_s and R_e is still a knowledge gap to be solved in the future. In addition, the majority of studies included in our dataset were distributed in eastern Asia (especially in China and Mongolia, Figure S1). Therefore, more studies from other regions (e.g. Africa, Australia and Europe) should be preferentially conducted to develop a more comprehensive understanding of how grazing and global climate change factors influence the C cycling in grasslands.

Second, our results showed that additive interactions exhibited predominance on R_s and R_e compared with antagonistic and synergistic interactions, but grazing in combination with global change factors (G + GC) showed that three types of interactions were all important for R_s (e.g. GN for antagonistic, GW for additive, GP for synergistic, Figure 3e). However, most of the current land surface models usually do not differentiate the effects of diverse factors on R_s and R_e (Bond-Lamberty & Thomson, 2010), which may impede us to fully understand the C cycle feedback to climate warming to some degree. Hence, there is a need to incorporate interactive effects into land surface models treating with different multiple driving factors for better predicting grassland C cycle feedbacks to human disturbance and global change.

Third, environmental factors (both MAP and MAT) may be crucial in evaluating the responses of R_s to different driving factors, as the effects of grazing, global change factors and their combinations on R_s will largely change over environmental transects (Manzoni et al., 2012; McSherry & Ritchie, 2013; Zhou et al., 2014). Our meta-analysis found that the response ratios of R_s to grazing in warmer areas was clearly lower than those in the lower ones (Figure 6), suggesting that sensitivity of RR(R_s) to grazing varied with MAT. These results demonstrated the importance of decreasing grazing frequency and

intensity in colder regions compared to that in warmer ones, which may contribute to increased soil C sequestration in ecological fragile areas. Meanwhile, we also found that the significant correlation between RR (R_s) and MAT and MAP in response to GP and GN (Figure 6), indicating the necessity of conducting transect studies of experimental G + GC along the MAT and/or MAP gradients to carefully examine the effects of G + GC on C fluxes. These results of environmental transect experiments could thus be incorporated into future modelling prediction to better simulate C cycling in grassland ecosystems.

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AUTHORS' CONTRIBUTIONS

G.Z., Q.L. and Y.C. collected data, conducted data analysis and wrote the manuscript. X.Z. and G.Z. conceived, designed and oversaw the research. All authors discussed and revised the manuscript together.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.qm064b0> (Zhou, Luo, Chen, Hu, et al., 2019).

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