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REGULAR ARTICLE

Precipitation determines the magnitude and direction of interannual responses of soil respiration to experimental warming

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Abstract
Background and aims Soil respiration (R_s) is expected to positively feedback to climate warming. The strength of this feedback is uncertain as numerous environmental factors, such as precipitation and soil moisture, can moderate the warming response of R_s.
Methods We combined seven-year R_s measurements in a warming experiment in the Tibetan alpine grassland

Yonghui Wang and Chao Song contributed equally to this work.

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with a meta-analysis on grassland warming experiments globally to investigate how precipitation and soil moisture influences the warming response of R_s. We further analyzed the warming responses of heterotrophic (R_h) and autotrophic (R_a) components of R_s.
Results Warming enhanced growing-season R_s in the wet years but decreased it in the dry years in the field experiment at the Tibetan grassland. Precipitation modulated the warming responses of growing-season R_s via R_h, but not R_a. Consistent with the field experiment, a positive relationship between precipitation and the warming response of growing-season R_s was also observed in the global-scale meta-analysis on grassland warming experiments.
Conclusions Precipitation influences the warming effects on R_s and could result in variation in warming response of R_s across years and experimental systems. Empirical functions provided by this study could be used to reduce the uncertainty in predicting R_s in a warmer future.

Keywords Climate changes · Heterotrophic respiration · Autotrophic respiration · Tibetan plateau · Grassland ecosystems · Climate-carbon model

Introduction

Soil respiration (R_s) is the soil-to-atmosphere CO_2 flux, composed of heterotrophic respiration of soil microbes (R_h) and autotrophic respiration of plant roots (R_a). R_s releases ~90 petagrams of carbon from soils to the atmosphere annually at the global scale, roughly nine times of the annual anthropogenic CO_2 emission (Bond-Lamberty and Thomson 2010; Schlesinger and Bernhardt 2013; Hashimoto et al. 2015). The global temperature has rapidly increased since the 1880s, with an average speed of 0.065 °C per decade (IPCC 2013). As a major CO_2 fluxes between terrestrial ecosystems and the atmosphere, R_s is expected to be stimulated by the pronounced climate warming because of the universally observed positive respiration–temperature relationship (Luo 2007; Bond-Lamberty and Thomson 2010; Allison et al. 2011; Yvon-Durocher et al. 2012; Melillo et al. 2017), potentially creating a positive climate–carbon cycle feedback (Xu et al. 2015; Melillo et al. 2017). However, the strength of this feedback is largely uncertain as the warming response of R_s varied considerably across time and ecosystems (Davidson and Janssens 2006; Luo et al. 2009; Liu et al. 2009; Subke and Bahn 2010; Suseela and Dukes 2013; Wang et al. 2014a). A potential reason is that a suite of factors beyond temperature, such as precipitation (Liu et al. 2009, 2016), soil moisture (Wan et al. 2005; Liu et al. 2009, 2016; Carey et al. 2016) and soil carbon substrate quality and quantity (Melillo et al. 2002, 2017; Xu et al. 2015), can control R_s and regulate its warming response. Thus, understanding the effects of these regulating factors is crucial for accurately predicting the climate–carbon feedback in a warmer future.

Among the myriad biotic and abiotic drivers of R_s, soil water availability is particularly important (Luo 2007; Liu et al. 2009; Suseela and Dukes 2013). This is because R_s is usually closely correlated with precipitation or soil moisture as evidenced in observational studies (Raich and Schlesinger 1992; Geng et al. 2012), manipulative experiments (Liu et al. 2009; Suseela and Dukes 2013), and meta-analysis (Liu et al. 2016). In addition, previous soil warming experiments have shown that increase in temperature usually leads to decrease in soil moisture, which can potentially offset the positive effect of higher temperature on R_s, and even results in a decrease in R_s (Luo 2007; Liu et al. 2009). Since reductions in soil moisture often accompany warming (Luo 2007; Carey et al. 2016; Liu et al. 2016, 2018) and climate warming is predicted to result in more extended and severe drought at the global scale (Dai 2013; Trenberth et al. 2014; Marvel et al. 2019), it is not realistic to only consider the effects of warming alone. Instead, considering how soil water availability influences the effects of warming on R_s is necessary and can improve our ability to accurately predict R_s under the ongoing climate warming.

Another challenge in reducing the uncertainty in the feedback between R_s and climate warming is the variation in the warming effects over time and in different ecosystems. The warming effects on R_s may change over time. For example, the response of R_s to warming can be determined by interannual or decadal variability in climate or warming-induced slow changes, e.g. consumption of available substrates (Melillo et al. 2002, 2017; Kuzyakov and Gavrichkova 2010) and reorganizations of plants and soil microbe communities (Xu et al. 2015; Melillo et al. 2017). Due to their long time scale, it is difficult to detect these changes in short-term experiments, which are prevalent in the literature (e.g. Liu et al. 2009; Lin et al. 2011; Suseela and Dukes 2013; Chen et al. 2016). Using long-term field experiments becomes necessary to describe the variability of warming effects over time. In addition to temporal variability, the effects of warming on R_s may also vary across experimental systems. For example, while experiments at some sites showed acclimation to warming (Luo et al. 2001; Atkin and Tjoelker 2003; Reynolds et al. 2015), other studies declared no evidence for acclimation (Hartley et al. 2008; Vicca et al. 2009; Jing et al. 2014). As a result, synthesizing findings from studies becomes necessary to reveal the general effects of warming amid its great cross-ecosystem variability.

In this study, we investigated how soil water availability modulates the effects of warming on R_s as changes in temperature are often concurrent with changes in soil water availability. We used soil moisture and precipitation as approximate index of soil water availability. To overcome the challenge of the across years and different experimental systems variation, we combined a seven-year in-situ warming experiment in the alpine grassland of the Tibetan Plateau and a global-scale meta-analysis on warming experiments in grassland ecosystems (including 10 individual experiments). We hypothesized that the across years and different experimental systems variation in warming response of R_s are associated with precipitation and soil moisture. We also analyzed the warming responses of the R_h and R_a and whether these responses are modified by precipitation in the in-situ warming experiment.

Materials and methods

Study site

We conducted an in-situ warming experiment in alpine grassland at the Haibei Alpine Grassland Ecosystem Research Station (Haibei Station, 101°12′E, 37°70′N, 3200 m a.s.l.), located in the north-eastern part of the Tibetan Plateau, China. This area has a continental monsoon climate, with a short and cool growing season (normally starts in mid-April and ends in late-October) and a long and cold non-growing season (Zhao and Zhou 1999; Wang et al. 2014b, 2018b) (Fig. 1). From 2007 to 2013, the mean annual air temperature ranged from −1.82 to −0.71 °C and the annual precipitation ranged from 350.6 to 501.3 mm, according to climatic data collected from a nearby weather station (see below for details about climatic data collection) (Table 1, Fig. 2). The soil developed is Mat-Gryic Cambisol (Chinese Soil Taxonomy Research Group 1995). Soil organic carbon content, bulk density, and pH are 63 g kg^{-1} soil, 0.8 g cm^{-3}, and 7.9 at 0–10 cm soil depth, respectively (Wang et al. 2014b, 2018b). At the experimental site, the plant community is dominated by *Kobresia humilis, Festuca ovina, Elymus nutans, Poa pratensis, Carex scabrirostris, Scripus distigmaticus, Gentiana straminea, Gentiana farreri, Leontop odiumnanum, Blvsmus sinocompressus, Potentilla nivea* and *Dasiphora fruticosa* (Luo et al. 2010). The mean aboveground net primary production was 372.2 g m^{-2} $year^{-1}$ (ranged from 300 to 450 g m^{-2} $year^{-1}$) (Wang et al. 2012, 2018b).

The in-situ warming experiment in the Tibetan alpine grassland

Our in-situ warming experiment was established in May 2006 using an infrared heating system for enhancing soil temperature (Kimball et al. 2008; Luo et al. 2010; Wang et al. 2012). Specifically, a 27 m × 27 m area was separated into four rows of 3-m width with 3 m in between. Each row was further separated into four circular plots of 3-m diameter with 3 m between adjacent circular plots. In each row, two out of four circular plots were randomly selected and arranged as a control plot and a warming plot. Then, a hexagonal array of six "dummy" heaters and a hexagonal array of six Mor FTE (1000 W, 240 V) infrared heaters were suspended ~1.5 m above control and warming plots, respectively, resulting in four replicates for both of control and warming treatments (Figure S1). These infrared heaters were controlled by a proportional-integral-derivative-output system with infrared thermometers. The heating system had spatially uniform effects on the canopy temperature (Kimball et al. 2008), and raised the soil temperature at 5 cm depth by 2.3 °C in the warming plots throughout the studied period (Fig. 3a). Further details on the design of our in-situ warming experiment and the infrared heating system can be found in previously published papers (Kimball et al. 2008; Luo et al. 2010; Wang et al. 2012).

Measurement of soil respiration in the in-situ warming experiment

We measured R_s in the control and heated plots from 2007 to 2013. Due to logistic constraints, the measurement protocol differed over time. But we calibrated

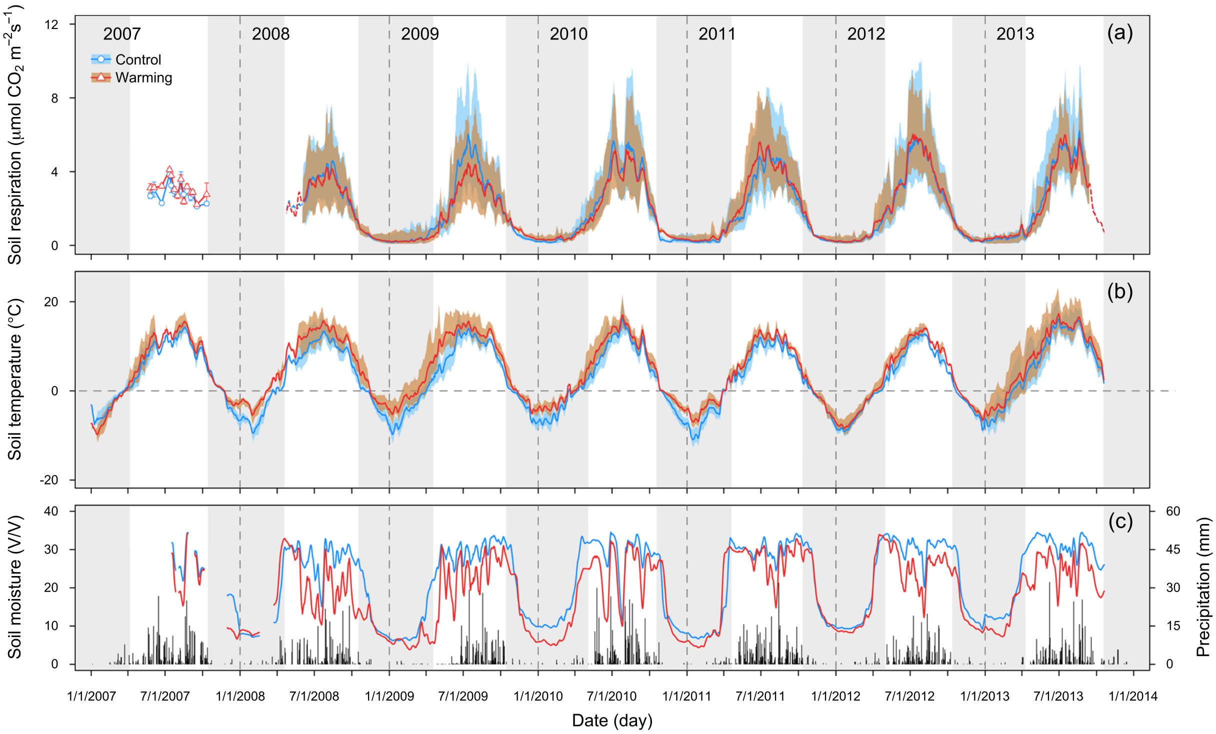


Fig. 1 Seasonal and annual variations in soil respiration (**a**), soil temperature at 5 cm depth (**b**), soil moisture at 5 cm depth and precipitation (**c**) in the in-situ warming experiment. Colored lines represent smoothed (7-days running mean) times series of soil respiration, soil temperature and moisture at 5 cm depth under control (blue) and warming (red) treatments. Times series of soil respiration and soil temperature also shown as colored areas between smoothed (7-days running mean) daily maximum and smoothed (7-days running mean) daily minimum values. The blank and shading periods represent growing seasons and non-growing seasons, respectively

different measurement protocols against each other to ensure consistency. Specifically, we used a static chamber to manually measure R_s in the growing season of 2007 in four replicated control and heated plots every two weeks (Lin et al. 2011) (Fig. 1a). From June 2008 to September 2013, we used a LI-8150 Multiplexer Automated Soil CO_2 Flux System to measure R_s hourly in four (from June 2008 to September 2013) or three (from October 2009 to September 2013) replicates of control and heated plots throughout the year and a LI-8100 Automated Soil CO_2 Flux System (Li-Cor Inc., Lincoln, NE, USA) to manually measure the R_s of the remained one replicate every week (from October 2009 to September 2013). To make sure that we can use the manually and automatically measured R_s data together, we calibrated the R_s measured manually to that measured automatically using their regression relationships (Figure S2-S3).

Table 1 Climate characteristics of the in-situ manipulative warming study site during the studied period. Data of air temperature and precipitation were collected from a nearby weather station (< 50 m, see Materials and Methods)

	2007	2008	2009	2010	2011	2012	2013
Overall							
Mean annual air temperature (°C)	−0.91	−0.71	−0.81	−0.83	−1.46	−1.82	−0.83
Annual precipitation (mm)	498.2	406.4	350.6	480.8	501.3	367.3	415.8
Growing season							
Mean air temperature (°C)	7.10	6.61	6.70	7.43	6.51	6.71	7.02
Precipitation (mm)	455.2	358.6	331.2	446.3	461.4	339.9	378.1

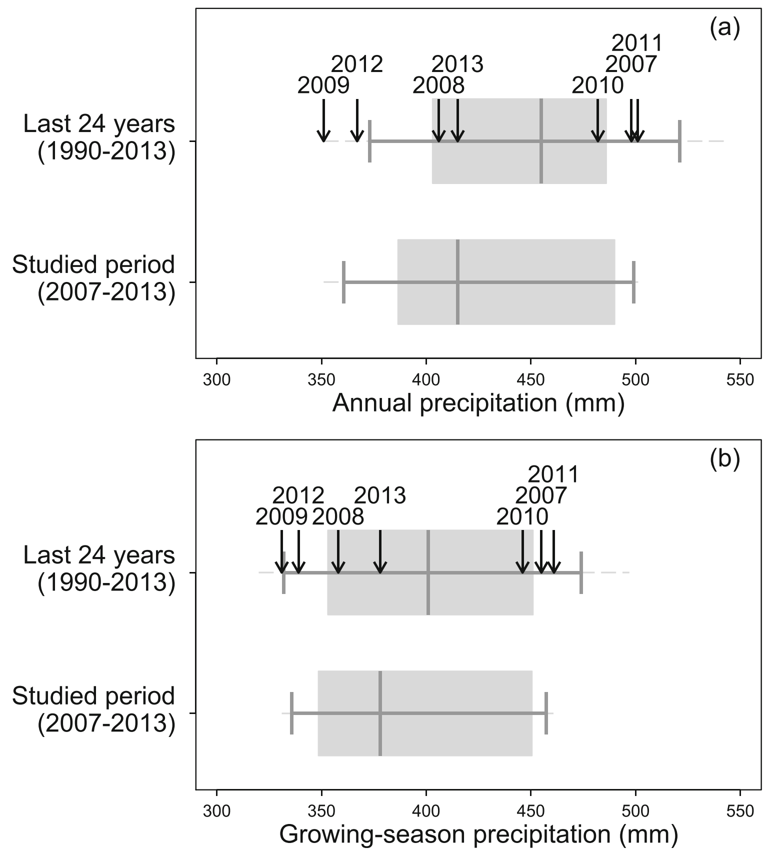


Fig. 2 Box plots of annual precipitation (**a**) and growing-season precipitation (**b**) in the study site of in-situ warming experiment during the past 24 years (1990–2013). The dashed grey lines represent the minimum and maximum precipitations. The box plots show the medians (vertical solid black lines in the grey box), inter-quartile ranges (grey box) and 10th and 90th percentiles (short black lines). Black arrows represent annual and growing-season precipitation over the seven years (from 2007 to 2013) of the in-situ warming experiment

In addition to the total R_s measurements, we used a deep-collar method to estimate the heterotrophic (R_h) and autotrophic (R_a) components of R_s. We installed polyvinyl chloride (PVC) collars (20 cm in diameter and 65 cm in height) to a depth of 60 cm in the plots to exclude organic matter input from plants in August 2008. The installation depth was effective because ~90% of the below-ground biomass is distributed in the top 20 cm (Liu et al. 2018). Soil respiration with collar installed is the R_h and the difference between respiration with and without the collar is the R_a. It is worth noting that the installation of collars resulted in an artificial increase in dead roots input into soils, causing a large contribution of R_h to R_s in the first year of installation (~90% in 2008). However, such a contribution rapidly declined to a relative stable level in the second year (~60% in 2009) (Figure S4) and remained at such a level (Wang et al. 2014b), suggesting that the experimental artifact of collar installation almost disappeared after two years. Thus, we only used data starting from 2010 to estimate R_h and R_a. Further details of the measurement protocols can also be found in our previous studies (Wang et al. 2014b, 2018b).

Hourly data on soil temperature and moisture (volumetric soil moisture, V/V%) at 5 cm depth (ST5 and SM5) in both control and warming plots were automatically collected through LI-8150-203 soil temperature probes and Decagon EC-5 Soil Moisture Sensors (Decagon Devices Inc., Pullman, WA, USA) attached to long-term chambers (Fig. 1b-c). We also collected hourly air temperature and daily precipitation data using an AWS310 Automatic Weather Station (Vaisala, Finland) from a nearby weather station (< 50 m).

Collection of R_s data from warming experiments in global grassland ecosystems

To investigate the influence of precipitation on the warming effects on R_s in grassland ecosystems globally, we collected R_s data from previously published warming experiments. Specifically, we collected peer-reviewed journal articles by searching Web of Science (2000–

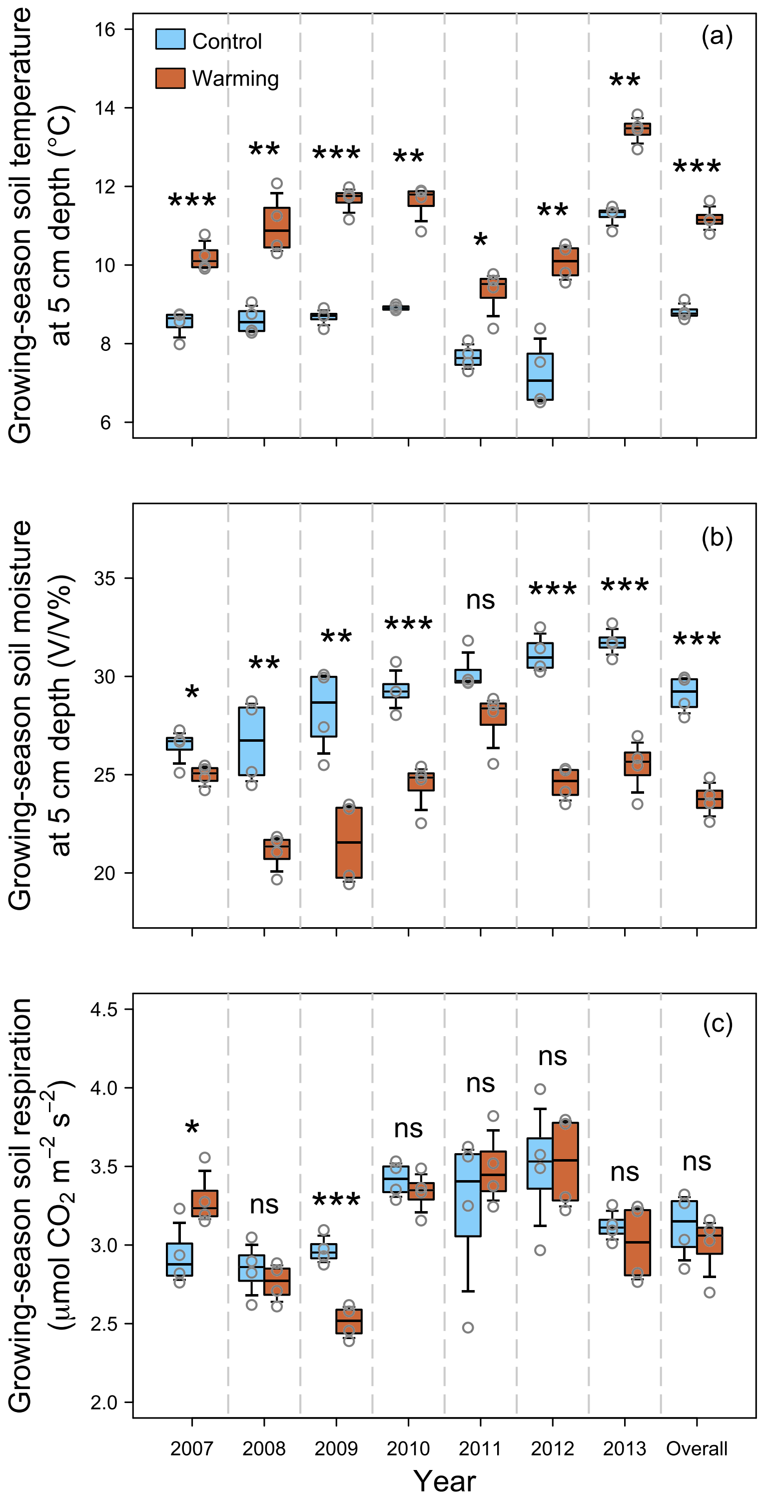


Fig. 3 Effects of warming on the growing-season soil temperature (**a**) and moisture (**b**) at 5 cm depth and the growing-season soil respiration (**c**) in the in-situ warming experiment. The box plots show the medians (solid black lines in the boxes), inter-quartile ranges (colored boxes) and 10th and 90th percentiles (short black lines). Grey cycles represent actual values. The effects of warming were analyzed using the linear mixed-effects model method, indicated by *** when $P < 0.001$, ** when $P < 0.01$, * when $P < 0.05$ and ns (not statistically significant) when $P > 0.10$

2016). We first searched papers containing soil respiration (or soil CO_2, soil carbon, carbon cycle, carbon processes, heterotrophic respiration, autotrophic respiration, and greenhouse gases) and warming (or heating, increasing temperature, elevated temperature, and climate changes) in the title resulting in 479 papers. Then, we screened and selected among these papers using the following criteria: (1) Warming experiment was conducted in grassland ecosystems, (2) soil temperature and moisture under control and warming treatments were reported and the effects of warming were provided or could be calculated from given results, (3) year- or site-specific growing-season precipitation was directly reported or could be calculated from reported daily or monthly precipitation, (4) the measurement of R_s was conducted no less than one growing season and (5) the effect of warming on R_s was provided or could be calculated from reported results. The screening resulted in 10 experiments suitable for the analysis (Table S1, Figure S5). Data of soil temperature and moisture, precipitation and R_s from these selected warming experiments were recorded when they are directly provided. We also used "Data Thief" software (http://datathief.org) to extract data from the figures if they were not directly reported. Specifically, we imported statistical graphics into the "Data Thief" software. Subsequently, focal variables, e.g. R_s, measured from different treatments or from different treatments within different periods were localized in "Data Thief". Then, their values were estimated based on the calibration of the vertical axis.

Statistical analysis

In this study, we focused on the effects of warming on R_s (and R_h or R_a) during the growing season because of the following two considerations. First, only growing seasons R_s data are available in many warming experiments (Liu et al. 2009; Lin et al. 2011; Chen et al. 2016), as cumulative R_s during this period contributed to the majority (80–90%) of annual total R_s (Suseela and Dukes 2013; Wang et al. 2014b) (Fig. 1a). Second, the growing-season R_s are more responsive to warming treatment (Xia et al. 2009; Liu et al. 2009; Garten Jr. et al. 2009; Lin et al. 2011; Suseela and Dukes 2013; Chen et al. 2016), while R_s during non-growing season is often not driven by temperature (Wang et al. 2014b). Referenced to our previous studies in this area, the growing season in our in-situ warming experiment was defined as the period in which seven-day smoothed daily mean air temperature is consecutively higher than 0 °C for 5 days (Wang et al. 2014b, 2018b) (Fig. 1).

In this meta-analysis, we chose data from published warming experiments based on the following criteria: (1) when R_s was measured only in the growing-season (for example see studies of (Liu et al. 2009; Lin et al. 2011; Chen et al. 2016)) or was measured throughout the year but separately reported the growing-season and non-growing-season R_s (for example see study of (Suseela and Dukes 2013)), the reported R_s or growing-season R_s were directly used, and (2) when R_s was measured throughout the year without separated into growing-season R_s and non-growing-season R_s, R_s during the period with daily mean temperature > 0 °C was used (for example see studies of (Zhou et al. 2007; Luo et al. 2009; Wang et al. 2011)). Here, defining growing season with daily mean temperature rather than seven-day smoothed daily mean temperature is because the temperature and R_s in these collected studies were usually measured with a low frequency (1–2 times per month in studies of (Zhou et al. 2007; Luo et al. 2009; Wang et al. 2011)). Although difference in definitions of growing season among these studies is a potential source of uncertainty in estimating the growing-season R_s, its effect is likely small because of the usually low R_s during the onset and end of the growing season (Suseela and Dukes 2013; Wang et al. 2014b).

We first analysed how warming treatment influenced growing-season mean ST5, SM5 and R_s (and R_h or R_a) in our warming experiment. Because precipitation varied across years, examining the warming effects over each year allowed us to gain quantitative insights on whether warming changed respiration and qualitative insights on when warming led to changes in respiration. Here, we employed linear mixed-effects model to analyze whether the warming treatment affected growing-season mean ST5, SM5 and R_s (and R_h or R_a). In the model, warming and date of measurement were treated as categorical fixed effects, and plot was treated as a random effect. We analysed data from each of the seven years separately as well as all seven years combined. Analyzing data from each year separately is equivalent to using all data together but allowing variance of random effects and residuals to vary across years. Since the variation among plots (Fig. 3) and variation of residual appear to differ across years, we believe our approach of separate analysis for each year is adequate. An alternative approach is to construct a model that explicitly model the interactive effects of temperature and moisture (see Appendix 1). While such model allows us to explicitly account for the effects of temperature and soil moisture, the model requires us to make assumptions about how temperature and moisture may influence soil respiration. In contrast, our approach of using treatment as categorical factor does not require any assumptions of the form of temperature and moisture effects. Given that our goal is to examine whether and when warming influences soil respiration, and that the results from the two approaches are consistent (see Appendix 1), we only present the results from the analysis using treatment as a factor.

For both the warming experiment and meta-analysis, we examined how precipitation or warming-induced changes in soil moisture influence the warming effects of R_s. To that end, we first quantified the responses of growing-season R_s and soil moisture to warming using the metric standardized change percentages (SCP). SCP is defined as the proportional changes in R_s or soil moisture in response to a 1 °C increase in temperature. This metric standardized the warming responses across experiments, as warming treatment did not always lead to the same amount of temperature increase (Wang et al. 2014a). Specifically, SCP was calculated as follows:

$$SCP = 100\% \times \frac{X_W - X_C}{X_C \times (T_W - T_C)} \tag{1}$$

where X_W and X_C are variables (e.g. R_s and SM5) in the warming and control treatments, respectively, and T_W and T_C are soil temperatures in warming and control treatments, respectively. We used linear regression to quantify how the SCP of R_s was related to growing-season precipitation and the SCP of the soil moisture. We chose linear regression based on visual inspection of the relationship between SCP of R_s on that of soil moisture and precipitation (see Appendix 2). For both meta-analysis and our experimental data, SCP of each plot was calculated using the growing-season average. Although it is possible to use high-frequency respiration and moisture data to explicitly model the interactive effects of temperature and moisture in our experiment (see Appendix 1–2), we chose to use the approach of the SCP metric. This is because high frequency data is not available and using the SCP metric allowed us to use a consistent statistical method for both our experiment and the meta-analysis.

All statistical analyses were performed and graphs were prepared using R 3.0.1 (R Core Team 2013). We fit linear mixed-effects models with the *lme4* package (Bates et al. 2014) and performed hypothesis testing with Satterthwaite adjustment of degrees of freedom using the *lmerTest* package (Kuznetsova et al. 2017). Hypothesis tests were considered statistically significant when the P value was < 0.05 or marginally significant when the P value < 0.10. We did not adjust P value for multiple comparisons when examining warming effects in each year for our warming experimental data. Thus, P value should only be viewed as the type I error rate for the single hypothesis tested. Datasets of our in-situ warming experiment and meta-analysis on global grasslands warming experiments, as well as the R code used for statistical analyses can be found in supporting information (Appendix 2).

Results

Effects of warming on soil temperature and moisture in the in-situ warming experiment

Precipitation varied considerably during the in-situ warming experiment. The range of annual precipitation during the experimental period represented 78% of that over the past 24 years (ranged between 351.3 and 543.0 mm from 1990 to 2013, Table 1, Fig. 2a). The annual growing-season precipitation ranged from 331.2 to 461.4 mm, representing 73% of its range (from 319.9 to 497.1 mm) over the past 24 years (Table 1, Fig. 2b). Although average growing-season precipitation and annual precipitation during the experiment were slightly lower than the average during 15 years prior to the experiment, the range overlaps and the means were not significantly different (Figure S6, Appendix 2).

The warming treatment significantly increased the growing-season mean ST5 by 2.3 °C (ranged from 1.6 °C to 3.0 °C for different years, $P < 0.05$ for all, Table 2, Fig. 3a, Appendix 2), but significantly decreased the growing-season mean SM5 by −4.9 V/V% over the 7-year study period ($F_{1,6} = 117.83$, $P < 0.05$, Table 2, Fig. 3a, Appendix 2). In addition, warming significantly reduced the growing-season mean SM5 in each year (ranged from −6.7 to −1.5 V/V% for different years, $P < 0.05$ for all, Table 2, Fig. 3b, Appendix 2), except for 2011 (−2.5 V/V%, $F_{1,5.48} = 2.48$, $P = 0.17$, Table 2, Fig. 3b, Appendix 2).

Effects of warming on R_s in the in-situ warming experiment

In the field experiment, growing-season mean R_s ranged from 2.85 to 3.51 μmol CO_2 m^{-2} s^{-1} for different years,

Table 2 Results (F-values) for effects of warming, measuring date and their interactions on soil temperature at 5 cm depth (ST5), soil moisture at 5 cm depth (SM5), soil respiration (R_s) and its heterotrophic (R_h) and autotrophic (R_a) components. The effects of warming were analyzed using the linear mixed-effects model method, indicated by *** when $P < 0.001$, ** when $P < 0.01$, * when $P < 0.05$ or # when $P < 0.10$. These results can also be found in supporting information (Appendix 2)

	ST5	SM5	R_s	R_h	R_a
2007					
Warming	40.92***	7.46*	6.62*		
Date	921.33***	60.34***	8.72***		
Warming:Date	2.21***	5.84***	0.96		
2008					
Warming	29.82**	21.62**	0.63		
Date	174.01***	35.60***	91.77***		
Warming:Date	2.85***	7.41***	2.08***		
2009					
Warming	205.02***	18.75**	41.62***		
Date	353.29***	65.78***	255.31***		
Warming:Date	20.07***	9.09***	11.10***		
2010					
Warming	24.79**	110.49***	0.50	3.66	3.38
Date	231.29***	47.89***	138.00***	16.06***	6.01***
Warming:Date	2.65***	5.53***	2.08***	3.22***	2.13*
2011					
Warming	6.17*	2.48	0.71	0.06	0.46
Date	119.41***	9.59***	98.72***	10.32***	4.86***
Warming:Date	0.81	3.05***	3.45***	2.25**	1.94*
2012					
Warming	33.49**	83.91***	0.04	5.13#	0.93
Date	145.36***	23.02***	94.99***	14.77***	6.31***
Warming:Date	1.55***	2.10***	1.16	2.72**	1.17
2013					
Warming	24.71**	68.87***	0.18	9.44*	0.79
Date	453.68***	50.60***	78.28***	19.25***	7.73***
Warming:Date	3.55***	10.42***	1.13	3.81***	3.48***
Overall					
Warming	407.33***	117.83***	0.86	3.61	1.98
Date	170.23***	32.06***	83.82***	8.33***	4.14***
Warming:Date	3.42***	5.33***	2.69***	1.73**	1.38*

with a cross-year mean of 3.15 μmol CO_2 m^{-2} s^{-1} over the studied period (Fig. 3c). The direction and magnitude of the warming effect on growing-season R_s varied considerably across years. Specifically, the warming treatment increased the growing-season mean R_s by 12.7% in 2007 ($F_{1,6} = 6.62$, $P = 0.04$, Table 2, Fig. 3c, Appendix 1–2), but reduced it by −15.3% in 2009 ($F_{1,6} = 41.62$, $P < 0.001$, Table 2, Fig. 3c, Appendix 1–2). In other years, warming in general led to slight decrease in R_s but may increase R_s slightly when soil moisture under warming treatment is higher. However, these effects were not statistically detectable (Table 2, Fig. 3c, Appendix 1–2). When integrated over the seven years of the experiment, warming led to slight decrease in R_s but such decrease was not statistically significant (−1.7%, $F_{1,6} = 0.86$, $P = 0.39$, Fig. 3c, Appendix 1–2).

Effects of warming on R_h and R_a in the in-situ warming experiment

During the in-situ warming experiment, year 2010 and 2011 are relatively wet and 2012 and 2013 are relatively dry based on historical records of growing-season precipitation in the last 24 years (Fig. 2). We found that the warming led to decreases in R_h in dry years (2012: −14.9%, $F_{1,7.99}$ = 5.13, $P = 0.053$; 2013: −13.1%, $F_{1,6.18}$ = 9.44, $P = 0.02$, Table 2, Fig. 4a, Appendix 2). During the two relatively wet years, warming led to a minor increase in R_h in 2011 and a decrease in R_h in 2010. The effects were not statistically significant in either years and the decrease in 2010 was of a smaller magnitude compared to the dry years (2010: −11.3%, $F_{1,6.01} = 3.66$, $P = 0.10$; 2011: 4.2%, $F_{1,6.61}$ = 0.06, $P =$ 0.81, Table 2, Fig. 4a, Appendix 2). In contrast, R_a was generally higher under the warming treatment although such effects were not statistically significant (Table 2, Fig. 4b, Appendix 2).

Precipitation and soil moisture regulate the response of R_s to warming

When examining the effects of precipitation and soil moisture on the warming response of R_s, we found that the SCP of growing-season R_s was positively related to the growing-season precipitation ($P = 0.04$, Fig. 5a, Appendix 2) and SCP of growing-season soil moisture ($P = 0.047$, Fig. 5b, Appendix 2) in our warming

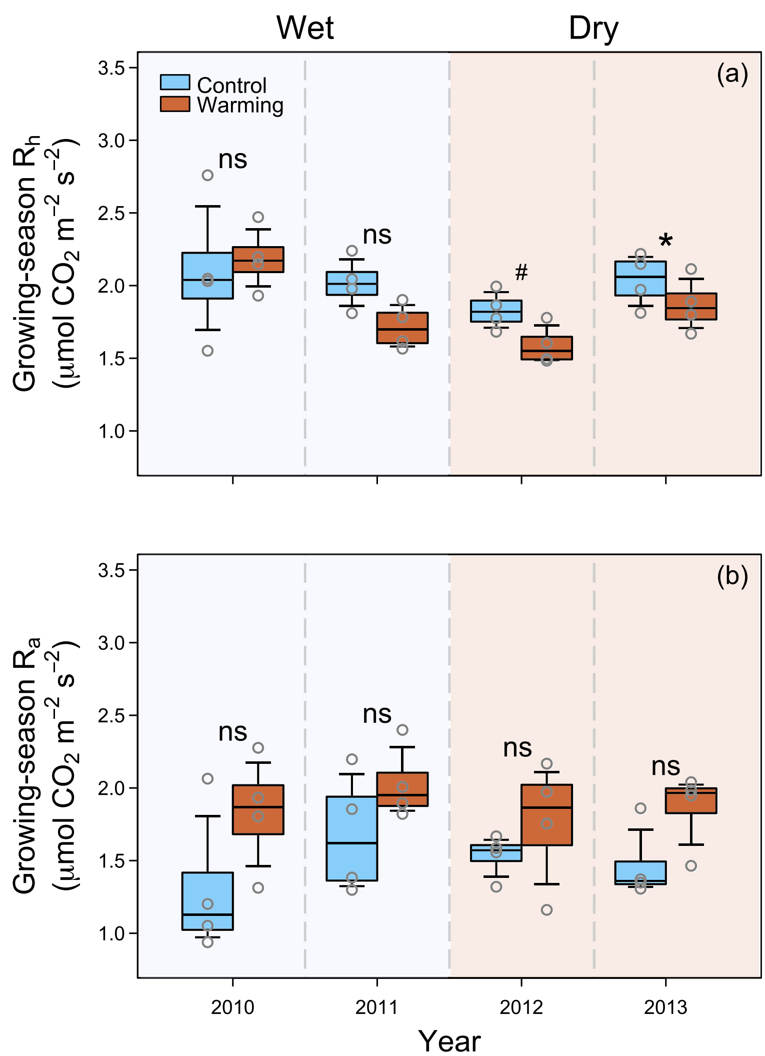
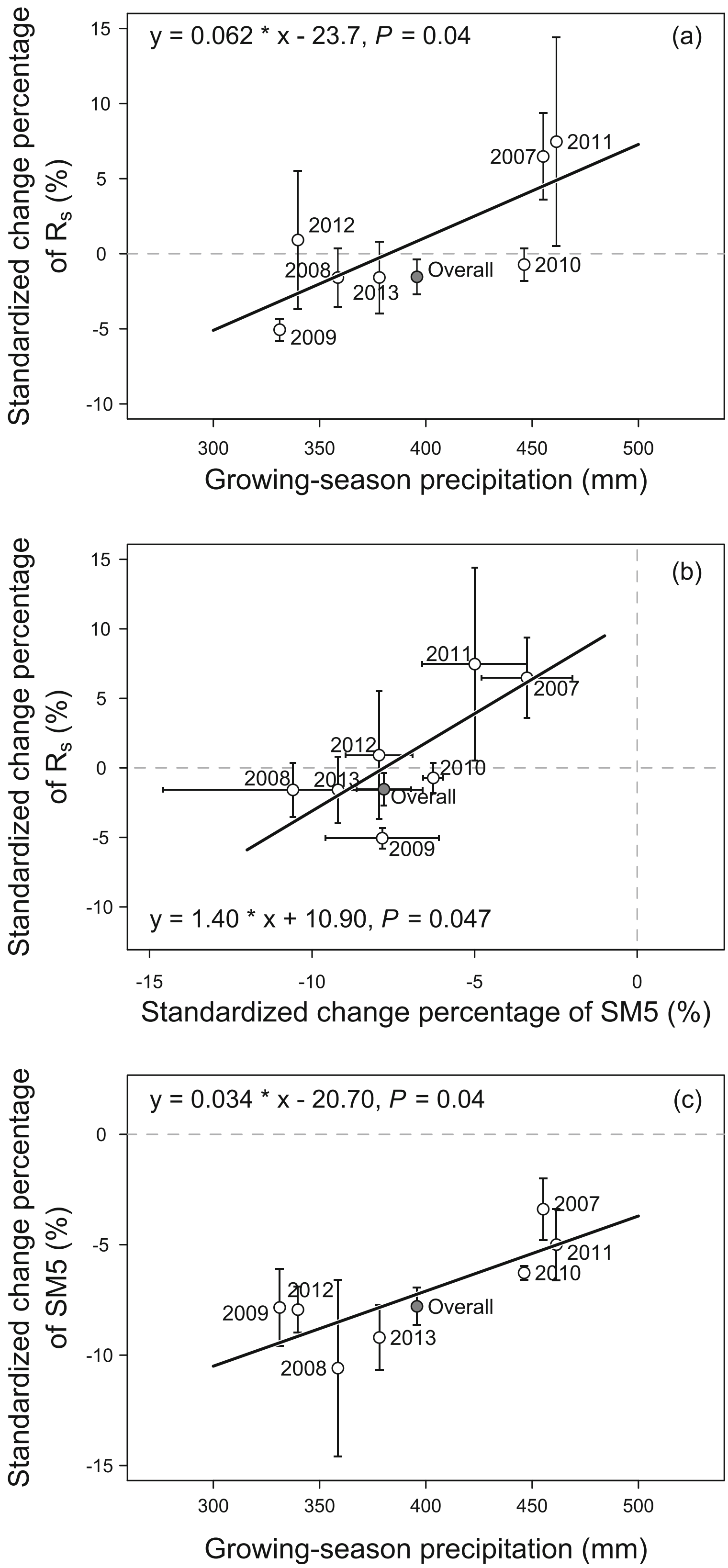


Fig. 4 Effects of warming on the growing-season heterotrophic (R_h, **a**) and autotrophic (R_a, **b**) respirations in the in-situ warming experiment. The box plots show the medians (solid black lines in the boxes), inter-quartile ranges (colored boxes) and 10th and 90th percentiles (short black lines). Grey cycles represent actual values. The effects of warming were analyzed using the linear mixed-effects model method, indicated by * when $P < 0.05$, # when $P < 0.10$ and ns (not statistically significant) when $P > 0.10$. Periods colored with blue and yellow represent dry and wet years, respectively (details can be found in Fig. 2)

Fig. 5 The standardized change percentage of soil respiration (R_s) in relation to the growing-season precipitation (**a**) and standardized change percentage of soil moisture at 5 cm depth (SM5, **b**) and the standardized change percentage of SM5 in relation to the growing-season precipitation (**c**) in the in-situ warming experiment. Vertical and horizontal bars represent the standard error of the means ($n = 4$ for both of the R_s and SM5). The result of linear regression was shown in each panel



experiment. These two relationships are consistent because SCP of growing-season soil moisture was positively related to the growing-season precipitation ($P = 0.04$, Fig. 5c, Appendix 2). Based on these linear regressions, we established two empirical equations to quantify the effects of precipitation and the SCP of soil moisture on the SCP of R_s within the growing season (Fig. 5a, b):

$$SCP\_R_s\ (\%) = 0.062 \times GSP\ (mm) - 23.7, \tag{2}$$

$$SCP\_R_s\ (\%) = 1.40 \times SCP\_SM\ (\%) + 10.9, \tag{3}$$

where SCP_R_s is standardized change percentage of growing-season R_s, GSP is growing-season precipitation, and SCP_SM is standardized change percentage of growing-season soil moisture. It is worth pointing out that soil moisture and precipitation are closely associated (see Appendix 2). Thus, the consistency of these two relationships was expected.

In the global scale meta-analysis of warming experiments in grassland ecosystems, the SCP of growing-season R_s was also positively associated with growing-season precipitation ($P = 0.03$, Fig. 6a, Appendix 2) and the SCP of growing-season soil moisture ($P = 0.047$, Fig. 6b, Appendix 2). Based on these results from the meta-analysis, effects of the precipitation and the SCP of soil moisture on SCP of R_s within the growing season can be quantified with the following equations (Fig. 6a, b):

$$SCP\_R_s\ (\%) = 0.015 \times GSP\ (mm) - 6.29 \tag{4}$$

$$SCP\_R_s\ (\%) = 0.699 \times SCP\_SM\ (\%) + 4.68 \tag{5}$$

Discussion

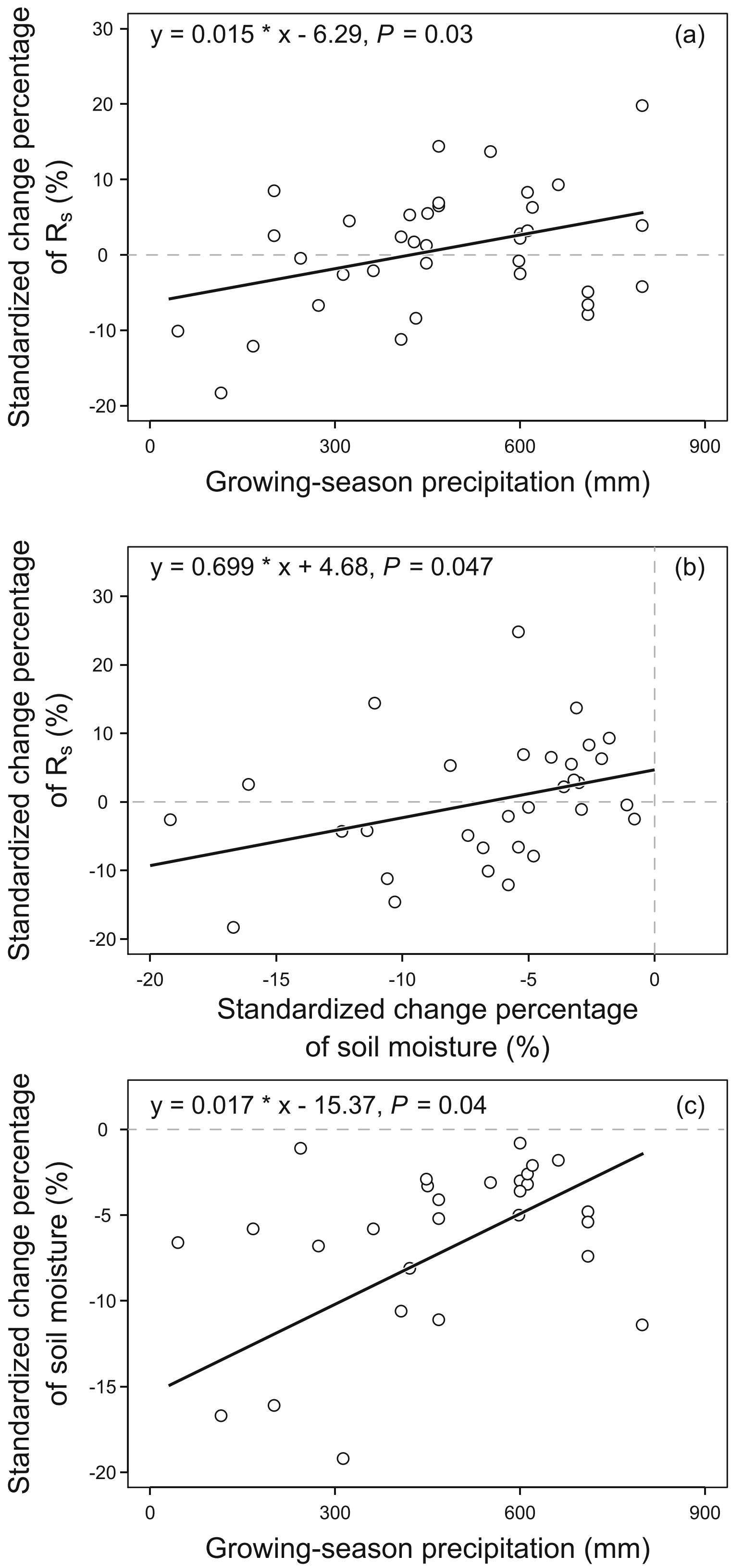
We combined a 7-year in-situ warming experiment and a global scale meta-analysis to investigate how precipitation and soil moisture regulate the warming responses of R_s. We found that, in the growing season, the warming responses of R_s, quantified by SCP, were positively affected by precipitation and soil moisture in both our long-term in-situ warming experiment and the meta-analysis. Furthermore, we found that precipitation and soil moisture influenced the warming responses of the growing-season R_h and R_a differently in the in-situ warming experiments. Although we likely had limited statistical power to detect the warming effects due to the low number of years sampled, we observed that warming usually led to decreases in growing-season R_h, particularly in dry years, growing-season R_a generally increases under warming. Taken together, these results suggest that precipitation and soil moisture may modulate the response of R_s to warming. Considering the concurrent changes in temperature and soil moisture is thus necessary for accurately predicting R_s in the future.

Precipitation and soil moisture regulated warming response of R_s

In our alpine grassland warming experiment, the effect of warming on growing-season R_s varied considerably across years. When combined over seven years, warming led to a slight but statistically non-significant decrease in R_s (Fig. 3c, Appendix 1–2). The temporal variation in the warming effects is likely driven by soil moisture (Fig. 3b and c, Appendix 1). Our findings are consistent with previous warming experiments (Wan et al. 2007; Liu et al. 2009; Suseela et al. 2012; Suseela and Dukes 2013) and recent global scale meta-analyses on warming experiments (Wang et al. 2014a; Carey et al. 2016). In general, the net effect of warming on R_s depends on the balance between the positive effect of high temperature and the negative effect of warming-induced drying (Luo 2007; Wan et al. 2007; Wang et al. 2014a; Carey et al. 2016). Our observations that warming consistently led to decreases in soil respiration particularly during dry years suggests that warming-induced drought may outweigh the positive effect of high temperature. However, when water availability is higher such as observed in 2007 and 2011 in our experiment, the positive effect of high temperature could be larger.

The global-scale meta-analysis of warming experiments in grassland ecosystems also showed significant influences of precipitation and soil moisture on the warming response of R_s during the growing season. This is consistent with the patterns found in the 7-year in-situ warming experiment. The significant effects of precipitation and soil moisture on the warming response of R_s suggest the net effect of warming is contingent on water availability in soil, as approximated by precipitation or soil moisture (Liu et al. 2009; Geng et al. 2012). While a consistent positive respiration–temperature relationship has been shown in syntheses when the temperature effect was isolated (Mahecha et al. 2010; Yvon-Durocher et al. 2012), using such relationship without considering the

Fig. 6 The standardized change percentage of soil respiration (R_s) in relation to the growing-season precipitation (**a**) and standardized change percentage of soil moisture (**b**) and the standardized change percentage of soil moisture in relation to the growing-season precipitation (**c**) in warming experiments of global grassland ecosystems. The result of linear regression was shown in each panel



negative effects of warming-induced drying in soil could lead to erroneous predictions.

Climate warming and changing precipitation regimes are the two most pronounced aspects of climate changes (Piao et al. 2010; IPCC 2013). Reductions in precipitation and soil moisture are predicted to occur concurrently with rising temperature (Dai 2013; Trenberth et al. 2014; Marvel et al. 2019). Our study shows that the effects of warming on growing-season R_s depend on water availability. Therefore, incorporating the effects of soil moisture or precipitation into the respiration–temperature relationship becomes necessary for an accurate prediction of soil carbon flux in a warming climate. For example, we did find a significant positive effect of warming on growing-season R_s in the in-situ warming experiment over the seven years of the experiment. In fact, average growing-season respiration over the seven years appeared to decrease slightly under the warming treatment. Given that the precipitation at the experimental site is close to the regional average (Tan et al. 2010; Shi et al. 2014; Ma et al. 2018) and annual precipitation has not changed significantly over the last few decades (Zhuang et al. 2010; Piao et al. 2010; Wang et al. 2018a), we predict no significant changes in growing-season R_s, in response to climate warming, even though temperature in the Tibet Plateau has increased significantly during the last decades at a rate twice of the global average (Hansen et al. 2010; You et al. 2010; Piao et al. 2010; Zhang et al. 2013).

Responses of R_h and R_a to warming

We found that R_h, and R_a, responded to the warming treatment differently. Although we could not always detect the effects statistically due to small sample size, growing-season R_h was generally lower under warming treatments, especially in dry years, and R_a was consistently higher under warming treatment over all seven years. We speculate that such differential responses of R_h and R_a are the results of different capacity to remain homeostasis by microbes and plants. Higher temperature facilitates the growth of soil microbes, potentially resulting in increased R_h (Sheik et al. 2011; Zhou et al. 2012). However, warming associated drying can limit the growth of soil microbes and therefore offset the positive effect of high temperature on R_h (Liu et al. 2009; Sheik et al. 2011). In addition, high temperature enhances the activities of extracellular enzymes activities and consequently decomposition of substrates and R_h (Davidson and Janssens 2006; Zhou et al. 2012; Chen et al. 2018). However, warming-induced drying limits diffusion of extracellular enzymes and decomposable substrates, reduces R_h (Davidson and Janssens 2006). Our previous 2-year (2009–2010) investigation in the same in-situ warming experiment showed that the soil microbial biomass carbon and nitrogen had not been affected by warming even in the year (2009) with the lowest precipitation during the studied period (2007–2013), and extracellular enzymes activities were also not significantly affected by warming (Jing et al. 2014).

In contrast, growing-season R_a may be less sensitive to the warming-induced decrease in water availability. This is consistent with a recent meta-analysis that showed a non-significant effect of warming on R_a in grassland ecosystems (Wang et al. 2014a). The non-significant warming effects on R_a may partly arise from a lack of statistical power because the uncertainty associated with R_a as a calculated quantity based on R_s and R_h is likely high. Nevertheless, we speculate that the capacity of maintaining homeostasis via physiological processes in plants could also be responsible. For example, plants can use groundwater in deep soils and adjust stomatal conductance when facing water stress (Jackson et al. 2000; Chaves et al. 2002). A previous study found that R_s is less sensitive to fluctuations of soil moisture in ecosystems dominated by deep-rooted plants than those dominated by shallow-rooted plants (Vargas et al. 2010). In addition to physiological mechanisms, plant community composition may also change and consequently influence its response to warming and the associated drying. For example, a 5-year warming experiment (Ma et al. 2017; Liu et al. 2018), near our experimental site (about 200 m) showed that warming by ~2 °C results in shallow-rooted species being replaced by deep-rooted species without significantly affecting the community net primary productivity (Liu et al. 2018). In summary, these physiological and community mechanisms might be plausible explanations for why warming effects on R_a may be generally less dependent on soil moisture.

Implications on the long-term response of R_s to climate warming

The response of growing-season R_s, the majority component of the annual total R_s, to warming varied considerably across years in the seven-year warming experiment, showing either positive, neutral, or even negative responses at a single site. Our analyses suggest that the interannual variability in water availability in soil may be responsible. This is supported by the observation that the warming effects tend to be positive and more pronounced in wet years than dry years. These results suggest that short-term experiments that are likely to miss the interannual variability in precipitation may provide a biased and imprecise prediction of the warming effects. In addition, the variability of warming effects on R_s has also been found to be associated with slow changes in the ecosystem. For example, a long-term (13 years) warming experiment in the tall grass prairie showed that warming led to a higher proportion of C_3 plants and more high-quality substrates for soil microbes and plant roots, resulting in an increase in R_s (Xu et al. 2015). A 26-years experiment in Harvard forest (Melillo et al. 2002, 2011, 2017) found that consumption of soil carbon pools (Melillo et al. 2002) and reorganization of soil microbial communities (Frey et al. 2008) regulated the response of R_s to warming, resulting in complex and highly variable responses of R_s to warming over time (Melillo et al. 2017). Together, the results from our long-term warming experiment and previous studies suggest that the effects of warming on R_s cannot be simply extrapolated from short term experiments, and the long-term responses of R_s to climate warming depends not only on temperature itself, but also on the interactions between temperature and other abiotic and biotic factors. Understanding the effects of biotic and abiotic drivers of R_s that change simultaneously with temperature is key for an accurate prediction of soil carbon flux in a warming climate.

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