Soil Biology and Biochemistry 168 (2022) 108616

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Response of grassland soil respiration to experimental warming: The long-term effects may be greater than we thought

Ziwei Chen [a,b,c,1], Dongsheng Zhao [a,*,1], Yu Zhu [a,b], Renduo Zhang [c], Caiyun Guo [d]

[a] Key Laboratory of Land Surface Pattern and Simulation, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, 100101, China
[b] College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, 100049, China
[c] Guangdong Provincial Key Laboratory of Environmental Pollution Control and Remediation Technology, School of Environmental Science and Engineering, Sun Yat-sen University, Guangzhou, 510006, China
[d] School of Civil Engineering, Changsha University, Changsha, 410022, China

ARTICLE INFO

Keywords:
Soil respiration
Grassland
Meta-analysis
Experimental warming
Three-phase pattern

ABSTRACT

Soil respiration (Rs) profoundly affects the global carbon cycle, and its response to climate warming in grasslands shows significant heterogeneity for poorly understood reasons. A meta-analysis was undertaken to evaluate the effects of warming (including the magnitude, methods, and duration of warming) and environmental factors (including climate, soils, and plants) on the response of Rs to warming in grasslands, using a global dataset of 168 independent measurements. Multi-model inference, an information-theoretical method for synthesizing results of multiple alternative models, was used to quantify the relative importance of the environmental factors. We found that the response of Rs to warming followed a three-phase pattern: Rs increased initially, then remained unchanged, and then increased again as the duration of warming increased. The long-term response was greater than the short-term response. The Rs response was also affected by the method of warming, with open-top chambers promoting Rs more than infrared heaters. The response of Rs to warming was also positively related to the magnitude of warming. Rs was greatly increased with warming in temperate grasslands compared with that in cold grasslands but did not change significantly in arid grasslands. According to multi-model inference, this can be attributable to differences in soil nutrients and the mean annual precipitation. Our findings suggest a greater long-term stimulation of Rs in a warming world than we previously thought, so short-term studies cannot provide a reliable scientific basis for carbon projections under long-term climate warming. Our results also demonstrate that the carbon released in cold grasslands could be overestimated if the water deficiency was not considered.

1. Introduction

Because soil respiration (Rs) provides the second-largest carbon flux in terrestrial ecosystems (Raich and Potter, 1995), a small change in Rs has a major effect on the CO_2 content of the atmosphere, potentially affecting climate change (IPCC, 2014; Melillo et al., 2017). The complexity and spatial heterogeneity of soil-based processes makes Rs a major source of uncertainty in modelling and projecting the global carbon budget (Bond-Lamberty and Thomson, 2010; Lavoie et al., 2015), and its response to warming remains poorly understood (Luo et al., 2001; Rustad et al., 2001; Carey et al., 2016; Zhou et al., 2016). Previous studies suggested that Rs in grasslands have the highest uncertainty among all biomes (Zhao et al., 2017; Warner et al., 2019). Grasslands are important components of terrestrial ecosystems, covering 31%–43% of the ice-free land globally and storing 28%–37% of soil organic carbon (White et al., 2000; Lal, 2004). Harsh environments and severe disturbance by human activities have rendered the soil carbon stock in grasslands highly sensitive to climate warming, which may have a significant effect on the global carbon budget (Wang and Fang, 2009; Stocker et al., 2013; Poulter et al., 2014). It is controversial whether grasslands will become carbon sources or carbon sinks under climate change; e.g., Dass et al. (2018) reported that grasslands will be more reliable carbon sinks than forests in a warmer world, while Chang et al. (2021) argued that grasslands are turning into carbon sources. Given the

* Corresponding author.
E-mail address: zhaods@igsnrr.ac.cn (D. Zhao).
[1] Note: Ziwei Chen and Dongsheng Zhao should be considered as co-first authors.

https://doi.org/10.1016/j.soilbio.2022.108616
Received 14 September 2021; Received in revised form 16 February 2022; Accepted 18 February 2022
Available online 12 March 2022

huge uncertainty of the response of grassland Rs to climate change, clarifying warming effect on grassland Rs is helpful to reduce the uncertainty of carbon cycle modelling in terrestrial ecosystems and provide more accurate projections.

The manipulative experiment is considered an indispensable method for the investigation of the Rs response to a warming world, since it effectively predicts the causal effects of climate change on soils (Yuan et al., 2017). Many such experiments have been conducted over recent decades to examine the responses of grassland Rs to climate warming, with inconsistent results. For example, a warming experiment conducted in the alpine meadow steppe on the Tibetan Plateau suggested that experimental warming significantly stimulated Rs (Peng et al., 2014). Another experiment in the Mongolian steppe showed a reduction in Rs with warming (Sharkhuu et al., 2016), whereas no significant effect of warming on Rs was observed on the Pannonian Plain (Lellei-Kovács et al., 2008). Such contradictory results have hampered us in clarifying the response of Rs to climatic warming on a global scale. The spatial heterogeneity of the Rs response may be related to environmental factors, including climatic, soil and plant (Wang et al., 2010, 2019b, 2019c; Reynolds et al., 2015; Li et al., 2020). Warming factors also contribute to this variability, including the magnitude of warming (Feng et al., 2017), the method of warming (Yan et al., 2020), and its duration (Yan et al., 2020).

Several meta-analyses of field studies of Rs have been undertaken. Wang et al. (2014) compared the differences in response to climate warming among Rs and its components: autotrophic respiration (Ra) and heterotrophic respiration (Rh). Zhou et al. (2016) analysed the effects of interactions between various factors, including warming, on global changes in Rs. Lu et al. (2013) investigated the impact of warming on various ecosystem carbon fluxes, including Rs. Song et al. (2019) summarized the effects of global change on ecosystem carbon cycling, including the effects of warming on Rs. Carey et al. (2016) evaluated the response of Rs to climate warming across biomes. These studies focused primarily on differences in the effects of warming on Rs across biome types (e.g., forest, grassland, farmland, and brush), and provided only an overall estimate of the Rs response of each biome. Despite the heterogeneity of Rs responses within a given biome, such as grassland, these studies did not consider such differences and their sources. Therefore, precisely quantifying the carbon budget of a terrestrial ecosystem and projecting the responses of its carbon cycle to future climatic warming remain challenging.

Although there have been previous meta-analytical studies of grassland Rs, they have not addressed the causes of these differences in the Rs response to warming. Wang et al. (2019b) mainly focused on the variations in the carbon flux in grasslands under the influence of climatic factors, but fewer than 10 observations for each climate type were made, resulting in the under-representation of their results. Zhou et al. (2019a, 2019b) attempted to quantify the Rs reactions to global change factors, including climatic warming and grazing, but overlooked the spatial variations in Rs, and therefore its heterogeneity. This lack of comprehensive studies limits our understanding of the differences in the Rs response to climatic warming in grasslands. Consequently, the effects of warming and environmental factors on the Rs response to experimental warming remain unresolved. It is not yet known whether the Rs response to warming has a global or regional pattern, or whether warming effects (specifically, the magnitude and duration of warming) are linear.

In this study, a comprehensive analysis of 168 independent measurements was undertaken to quantitatively evaluate the effects of warming on Rs in grasslands. Our aims were: (a) to quantify the response of Rs to experimental warming in grasslands; (b) to examine the effects of warming methodology and environmental factors on Rs response to warming; and (c) to clarify the mechanism of the Rs response to climatic warming.

2. Materials and methods

2.1. Data collection

To assess the effect of experimental warming on Rs in global grasslands, peer-reviewed publications during 2000–2019 were searched using the Web of Science (http://apps.webofknowledge.com) and China Knowledge Resource Integrated Database (http://www.cnki.net) using keywords: (a) soil respiration (OR carbon emission OR carbon exchange OR CO_2 fluxes); (b) experimental warming (OR elevated temperature); and (c) grasslands (OR pasture OR meadow OR prairie OR savanna OR steppe). Only studies meeting the following criteria were included in our meta-analysis: (a) field experiments; (b) studies including treatment with warming and control; and (c) studies providing the number of replicates, mean values, and standard deviations (or standard errors). Efforts were made to exclude duplicate results presented in multiple publications. Considering the independence assumption of meta-analysis, some researchers have advocated that each study should contain only one result (Vander Werf, 1992; Liao et al., 2008). However, in a specific study, the missing of information by exclusion of results may be a more serious problem than that resulting from violation of the independence assumption (Fu et al., 2015). There have been many meta-analyses including more than one result in a single study (Xia and Wan, 2008; Fu et al., 2015), with yearly results being incorporated in analyses in a study involving multi-year data (Ainsworth et al., 2003). Consequently, multiple years and multiple levels of warming magnitude at a single location were considered here as separate observations. Data from figures were acquired by GetData Graph Digitizer v. 2.26.

To reduce the risk of omitting some publications from our dataset, we checked a recently published global database for global-change manipulative experiments (Song et al., 2020) and added those studies that met our inclusion criteria but were not yet included in the dataset. Ultimately, a global Rs dataset was established with 168 independent measurements, covering the four regions of Asia, Europe, North America, and Oceania (Figure S1).

As well as Rs, the compiled dataset included related warming factors (the magnitude, method, and duration of warming) and environmental factors such as climate factors (mean annual air temperature [MAT] and mean annual precipitation [MAP]), soil factors (bulk density [bulk], sand content [sand], clay content [clay], organic carbon [OC], total nitrogen [TN], pH value measured in water [pH], and cation exchange capacity [CEC]), and plant factors (normalized difference vegetation index [NDVI], leaf area index [LAI], and gross primary productivity [GPP]). Because most studies did not provide all the required independent variables, missing data on climates, soils, and plants were obtained from global datasets and remote-sensing data based on site locations (Table S1). Changes in aboveground biomass (AGB) and belowground biomass (BGB) also were included in our dataset.

Based on the Koppen–Geiger world climate map, one of the most widely used climate classifications, grasslands were divided into three types: cold grasslands; temperate grasslands; and arid grasslands (Peel et al., 2007). Tropical grasslands were not included in this study because of the small sample size in the relevant studies. High-altitude grasslands were incorporated into cold grasslands. Descriptions and the defining criteria of these grasslands are shown in Table S2. To ensure the comparability of the soil environments, only topsoil data (0–20 cm) were used in the analysis, although a small number of studies recorded soil data for different depths.

2.2. Statistical analysis

To reflect the responses of grassland Rs to warming, response ratios (RR) were calculated (Hedges et al., 1999); i.e., the ratio of the mean value of Rs in a warming group ($\overline{X_t}$) to that in the control group ($\overline{X_c}$). The ln(RR) values were used to reduce bias, thus ensuring the normality of the sample distribution:

$$\ln(RR) = \ln(\overline{X}_t / \overline{X}_c) = \ln\overline{X}_t - \ln\overline{X}_c \tag{1}$$

with variance (v) of $\ln(RR)$ expressed as

$$v = \frac{S_t^2}{n_t \overline{X}_t^2} + \frac{S_c^2}{n_c \overline{X}_c^2} \tag{2}$$

where n_t and n_c are the sample sizes of warming and control groups, and S_t and S_c are the standard deviations of these groups, respectively. v and σ^2 were together used to estimate the weighting factor (w) for each $\ln(RR)$ value:

$$w = \frac{1}{v + \sigma^2} \tag{3}$$

where σ^2 is a value representing the between-study variance in the random-effects model. σ^2 was estimated with a restricted maximum likelihood method, which was considered as one of the best estimators of the between-study variance (Veroniki et al., 2016). The overall weighted-mean response ratio (RR_{++}) was computed for each $\ln(RR)$ and w value:

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{ki} w_{ij} \ln(RR)_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{ki} w_{ij}} \tag{4}$$

with the standard error:

$$\mathrm{SE}(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{ki} w_{ij}}} \tag{5}$$

where m is the number of groups (e.g., $m = 3$ when grouping by climate condition), and k_i is the number of replications in group i. If the 95% confidence interval ($CI_{95\%}$) did not overlap with zero, the effect of warming was considered significant ($p < 0.05$), with $CI_{95\%}$ estimated as:

$$CI_{95\%} = RR_{++} \pm 1.96 \;\; \mathrm{SE}(RR_{++}) \tag{6}$$

In addition to quantifying the warming effects of Rs, subgroup analyses and meta-regressions were performed to explore the roles of warming and environmental factors in regulating Rs. A Talwar robust regression method with an iteratively reweighted least squares algorithm was used in the meta-regression (Hinich and Talwar, 1975). The method was often used to minimize the impact of outliers on regression results (Baryamureeba, 2001; Kubínová and Nagy, 2018). Bootstrapped estimates of the slope of meta-regressions were provided to further verify the robustness of results (Crowther et al., 2016; Zhang et al., 2021). A given number of studies were randomly removed. The residual data were used for meta-regression to calculate the slope, and this was repeated 1,000 times. Although the uncertainty of the slope increased as more data were removed, estimates of the slope did not show statistically significant changes even after more than 70% of the data were removed (Figure S2, S3). A funnel plot (Egger et al., 1997) and fail-safe N (Rosenthal, 1978) were used to assess the risk of publication bias. This study lacked potential publication bias because the funnel plot was symmetric and the number of data points with high standard errors was small (Figure S4). Fail-safe N was estimated to be 8198, which is much greater than the 5k+10 threshold, where k is the number of observations, indicating that our results can be regarded as reliable estimates of true effects. Our meta-analysis was performed with OpenMEE, an open-source meta-analysis software the underlying architecture of which is based on the R programming language (Wallace et al., 2017).

The information–theoretic approach to model-based inference advocated by Burnham and Anderson (2002) was used to quantify the relative importance of environmental factors. This approach simultaneously examines several candidate models, weighting model estimates with the Akaike information criterion (Burnham and Anderson, 2002). The relative importance value of each predictor (i.e., the sum of the Akaike weights of the models containing the given predictor) indicates the overall support for that prediction among all models (Feng and Zhu, 2019). A critical value of 0.8 was set to distinguish between important and non-significant predictors (Terrer et al., 2016). Although multi-model inference is considered an excellent alternative to traditional null hypothesis testing (Grueber et al., 2011), it can have serious drawbacks when there is multicollinearity among the predictor variables in the candidate models (Cade, 2015). Unfortunately, there was obvious multicollinearity among the soil and vegetation variables, so before multi-model inference, a rotated principal components analysis (rPCA) using the variance maximizing method was conducted to reduce the number of correlated variables and thus minimize the effects of multicollinearity (Haaf et al., 2021). Ultimately, we obtained 3 rotated principal components with an eigenvalue of >1. According to their dominant loadings, they were interpreted as soil nutrients, plant productivity, and soil texture (Table S3). Due to the weak multicollinearity between MAT, MAP, and other environmental factors (all variance inflation factors were <5), we did not use MAT and MAP in the rPCA. Otherwise, it would be too difficult to interpret the generated rotated principal components. Three rotated principal components were regarded as important explaining variables for changes in Rs together with MAT and MAP. There was no significant multicollinearity among the above five variables. All multi-model inference was performed using R software v. 4.1.0.

3. Results

3.1. Effects of warming factors

The duration of the warming experiments performed in our study ranged from 1 to 13 years, with 77% of the experiments lasting no longer than 3 years (short-term studies) and only 23% of the studies being conducted for more than 3 years (long-term studies). Our result shows a nonlinear response of Rs with growing warming periods. The long-term studies showed greater uncertainty because of the small sample size, and the long-term effect of warming on Rs was stronger than the short-term effect (Fig. 1). With the growing duration of warming, Rs demonstrated a three-phase response pattern (Fig. 1). In the first year (Phase I), warming significantly stimulated Rs. However, the warming effect disappeared in the subsequent 2 years (Phase II). In the 4th year and thereafter (Phase III), the response of Rs became strong again and increased each year in general (except in the 8th and 9th years).

The warming methods in our dataset included open-top chambers (OTCs), infrared heaters (IRs), greenhouses, infrared reflectors, and heating cables. Among these warming methods, IRs (56%) and OTCs (33%) were used most frequently. The increase of Rs in OTCs was much greater than that with IRs (Fig. 2). Greenhouses and heating cables produced insignificant increases in Rs, and the large uncertainty could be attributed to their small sample sizes (Fig. 2). Infrared reflectors inhibited Rs, contrary to the effects of the other warming methods (Fig. 2).

Changes in Rs in response to warming showed a positive correlation with the magnitude of warming (Fig. 3). Rs increased by 4.8% for every 1 °C increase in soil temperature, indicating the continued increase in CO_2 emissions from soils in a warming world.

3.2. Effects of environmental factors

The warming response of Rs varied among climatic zones, although it showed a comprehensively positive global effect. Warming had no significant effect on Rs in arid grasslands (Fig. 4). Warming stimulated Rs more in temperate grasslands than in cold grasslands, with greater uncertainty (Fig. 4).

In addition to the effects of climatic zones, we conducted a robust meta-regression analysis of 12 environmental variables and the response

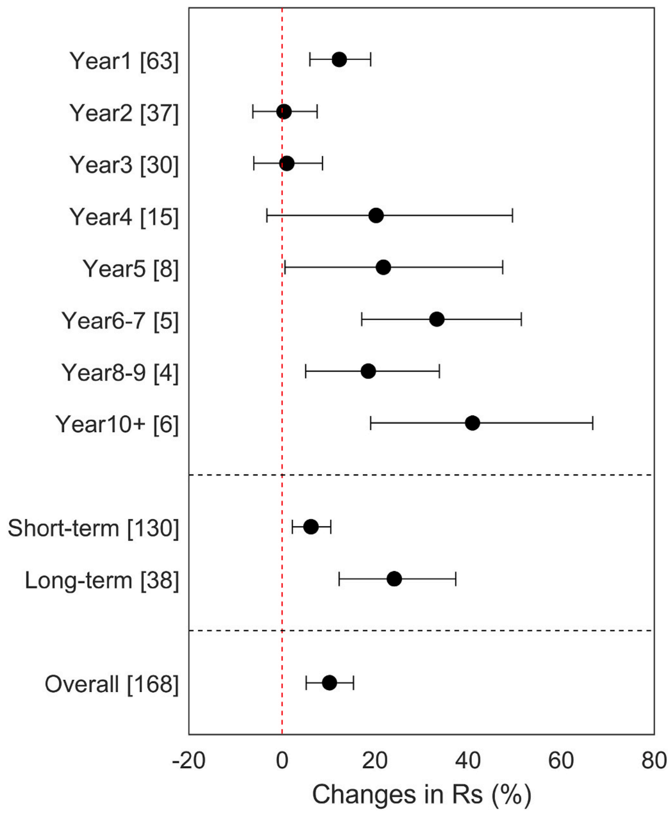

Fig. 1. Effects of the duration of warming on soil respiration (Rs). Dots with bars indicate the mean effects and 95% confidence intervals, respectively. Sample sizes are shown in square brackets. Short-term = 1–3 years of warming; Long-term = 4–13 years of warming.

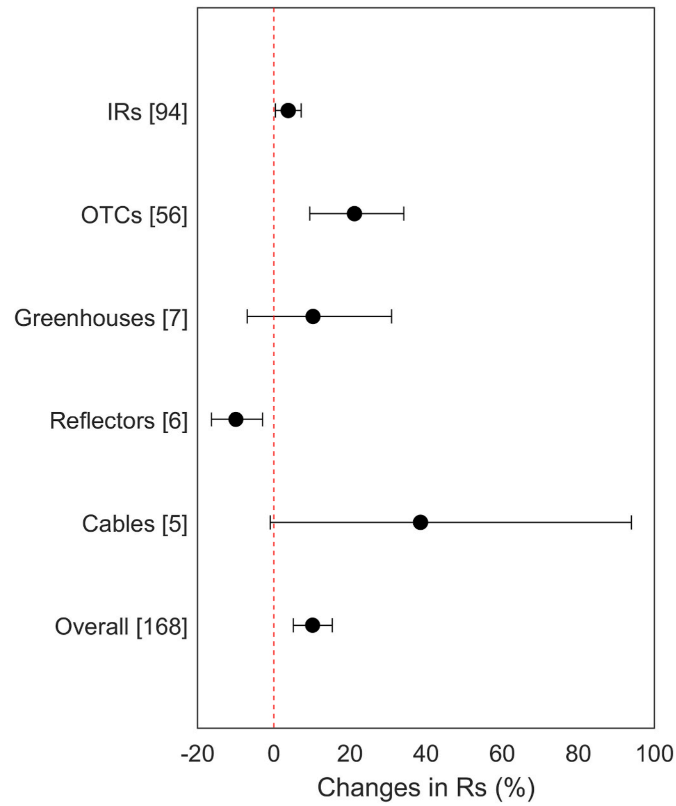

Fig. 2. Effects of the method of warming on soil respiration (Rs). Dots with bars indicate the mean effects and 95% confidence intervals, respectively. Sample sizes are shown in square brackets. IRs = infrared heaters; OTCs = open-top chambers; Reflectors = infrared reflectors; Cables = heating cables.

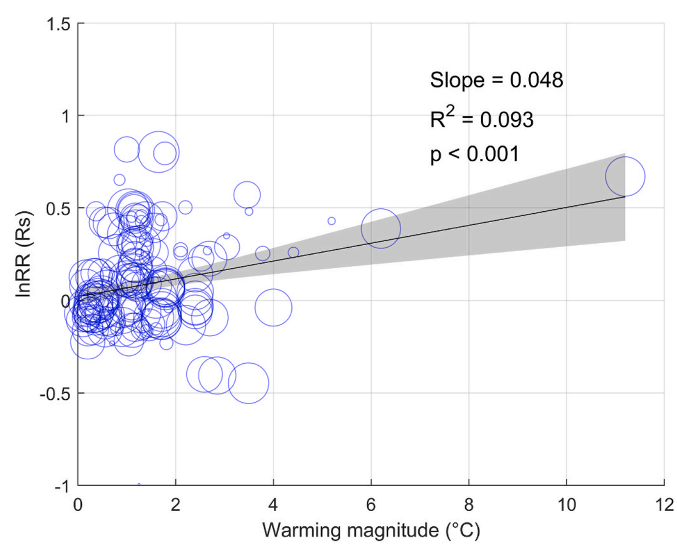

Fig. 3. Bubble plots of the robust meta-regression results between the response of soil respiration (Rs) to warming and the duration of warming. The shaded area represents the 95% confidence intervals.

of Rs to evaluate the effects of environmental factors on grassland Rs in the context of warming. The meta-regression results showed that the response of Rs to warming increased with increasing MAP, CEC, OC, and TN, whereas the effect declined with increasing soil bulk density, clay, and pH, implying that climate and soil are the critical predictors of changes in Rs (Fig. 5). None of the plant variables showed any significant correlation with the response of Rs (Fig. 5).

To test the effects of complex environments on Rs, we averaged the parameters for a series of candidate models that reflected different combinations of predictors and gave a relative importance value to each environmental parameter. Three rotated principal components from rPCA, i.e., soil nutrients, plant productivity, and soil texture, were included in the multi-model inference together with MAT and MAP. Finally, soil nutrients and MAP were both regarded as important variables with large effects on Rs, as their relative importance values were >0.8 (Table 1), and the coefficients were statistically significant. Specifically, the increase in Rs was stronger in fertile soil and with abundant precipitation. MAT, plant productivity and soil texture showed no significant effects on the response of Rs to warming (Table 1).

4. Discussion

4.1. Effects of warming factors

A 26-year soil-warming experiment at the Harvard Forest reported a four-phase pattern of Rs response to warming, with phases of massive soil carbon release alternating with phases of insignificant soil carbon loss (Melillo et al., 2017). Similarly, the present study indicates that with the growing duration of warming, the response of grassland Rs is nonlinear and could be divided into three phases in sequence. In Phase I (the first year of warming), Rs increased a lot, resulting in a rapid depletion of labile carbon pools in the soil and substantial loss of soil carbon (Hartley et al., 2007; Tucker et al., 2013). The large amount of decomposition of soil labile organic carbon in Phase I led to insufficient respiratory substrate supply (Hartley et al., 2007), and thus causing Rs to respond little during Phase II (the second and the third year of warming). The non-significant change in Rs during Phase II supports the results of Knorr et al. (2005). Assumed constant carbon input rates,

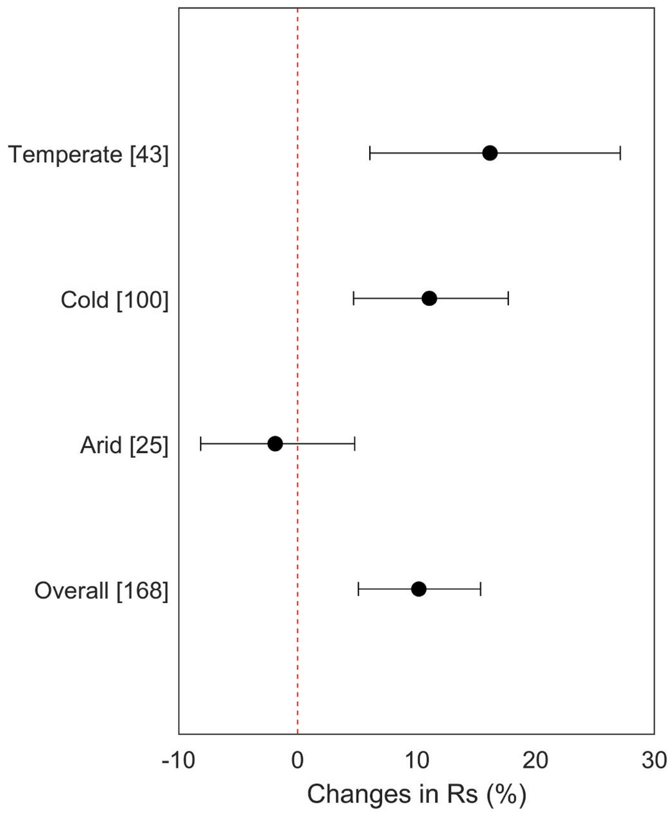

Fig. 4. Effects of climatic zones on soil respiration (Rs). Dots with bars indicate the mean effects and 95% confidence intervals, respectively. Sample sizes are shown in square brackets.

Knorr et al. (2005) argued that soil labile carbon pools would be close to a new equilibrium within the initial two years of warming. The non-significant effect in Phase II could also be partly attributed to the decreasing microbial biomass (Bradford et al., 2008; Tucker et al., 2013). In Phase III (the fourth year of warming and thereafter), Rs was increased again, and its responses became greater with the growing warming duration, suggesting that carbon release from soils will be accelerated in a long warming period. In this study, we found that increases in both AGB and BGB were greater with long-term warming than that with short-term warming (Figure S5), implying that the strong stimulation in Phase III can be attributed to the additional carbon input into soil. Long-term warming increases organic matter input into soil and the photosynthetic carbon allocated below ground, which offsets the warming-induced labile respiratory substrate consumption (Xu et al., 2015). The enhancement of the long-term response is also related to changes in microbial function, e.g., to increasing amounts of proteins used for microbial energy production and transformation (Liu et al., 2017) and increasing diversity within a potentially lignolytic bacterial community (Pold et al., 2015). Furthermore, it remains unknown

Table 1
Model-averaged estimates and relative importance values of environmental parameters.

	Estimates	$CI_{95\%}$ of estimates	Relative importance values
Soil nutrients	0.119***	[0.085, 0.152]	1.00
MAP	0.075**	[0.024, 0.126]	0.97
MAT	−0.026	[-0.085, 0.033]	0.36
Plant productivity	−0.016	[-0.064, 0.032]	0.32
Soil texture	0.000	[-0.047, 0.047]	0.27

***p <0.001, **p <0.01. CI95% = the 95% confidence interval; MAP = mean annual precipitation; MAT = mean annual air temperature. Soil nutrients, plant productivity, and soil texture are rotated principal components, and their loadings are shown in Table S3.

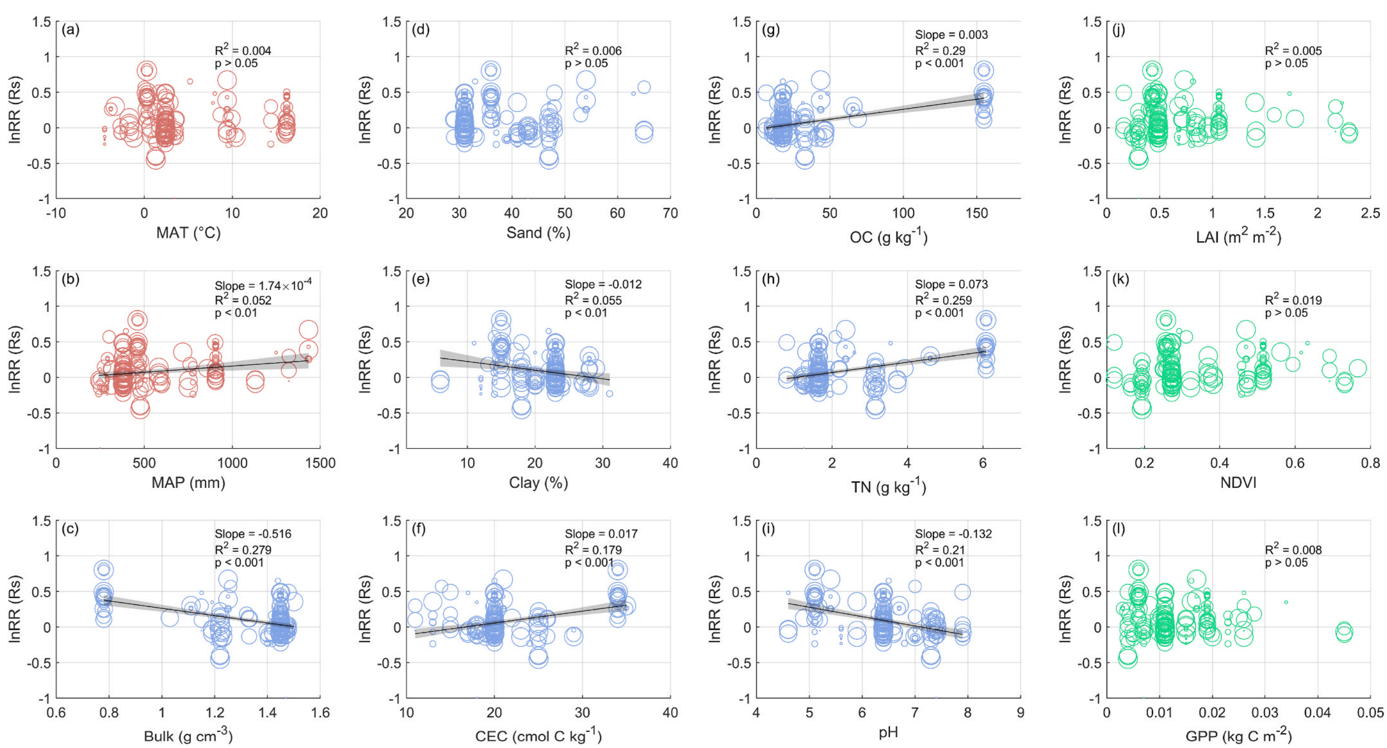

Fig. 5. Bubble plots of the robust meta-regression results between the response of soil respiration (Rs) to warming and MAT (a), MAP (b), bulk (c), sand (d), clay (e), CEC (f), OC (g), TN (h), pH (i), LAI (j), NDVI (k), GPP (l). The shaded area represents the 95% confidence intervals. MAT = mean annual air temperature; MAP = mean annual precipitation; Bulk = soil bulk density; CEC = cation exchange capacity; OC = soil organic carbon; TN = soil total nitrogen; LAI = leaf area index; NDVI = normalized difference vegetation index; GPP = gross primary productivity.

whether Rs will continue to increase with the longer warming duration or whether it will step into another phase where Rs remains constant as Melillo et al. (2017) reported. In this study, we found that Rs exhibits a nonlinear response to warming with the increasing duration of warming. Our results differed from previous meta-analyses which indicated that the stimulation of Rs may be weakened (Romero-Olivares et al., 2017; Wang et al., 2019b) or unaffected (Rustad et al., 2001; Lu et al., 2013) by longer warming periods. Short-term studies are unable to provide accurate projections for long-term warming, and long-term studies are needed to improve our understanding of the soil carbon cycle.

OTCs and IRs were used in most grassland warming experiments. We found that the positive Rs response to warming was much stronger for OTCs than for IRs, which is consistent with results of Wang et al. (2019b). The difference in the effects of warming methods cannot be attributed to a change in soil temperature because there was little difference between the magnitudes of warming with the two heating methods (Figure S6). The difference is likely to result from the asymmetrical diurnal warming effects of warming methods. The nocturnal warming induced by IRs was stronger than daytime warming, resulting in increased plant respiration and consumption of photosynthetic products (Wan et al., 2009). By contrast, the majority of OTCs-induced warming occurred during the day (Aronson and McNulty, 2009), with plant photosynthesis being promoted greatly (Wu et al., 2011). Therefore, plant growth for OTCs was promoted more than that for IRs (Figure S7). The large soil water loss due to direct heating of soil by IRs may also explain its slight warming effect (Yan et al., 2020), although OTCs are also assumed to affect wind flow and precipitation, thus reducing the soil water content (Aronson and McNulty, 2009). Inconsistent with OTCs and IRs, infrared reflectors reduced Rs. Infrared reflectors heat the soil by retaining day-time heat (Aronson and McNulty, 2009), with a subtle increase in soil temperature and limited direct stimulation of Rs (de Dato et al., 2010). Conversely, infrared reflectors strengthen the water limitation, which can account for the drop in Rs, because their curtains prevent rainwater entering the soil and inhibit steam condensation and dew formation (Lellei-Kovács et al., 2008), and warmer nights also lead to soil water loss. Heating cables showed no significant warming effect on Rs. However, we cannot rule out a possibility of a type II error, as all five observations showed that Rs increased with warming. Therefore, in follow-up studies, the sample size should be increased to reduce the estimating uncertainty. In brief, there are large differences in the effects of warming methods on Rs, so different warming experiments should only be combined with caution in future meta-analytical studies. To improve the comparability between studies, manipulative experiments should be carried out in accordance with standardized protocols in future studies. As the best method for replicating natural warming conditions (Aronson and McNulty, 2009), IRs are recommended for further use; heating cables are not recommended because of their strong disturbance to the soil (Aronson and McNulty, 2009).

Our findings support previous studies which showed that the increase in temperature correlates positively with the warming effect (Lu et al., 2013; Wang et al., 2014). Because Rs is a complex biochemical process, a first-order exponential equation (e.g., the Arrhenius equation) is usually used to describe the relationship between its components and soil temperature (Owen et al., 2000; Mikan et al., 2002), indicating the accelerated decomposition of litter and soil in a warming world (Bronson et al., 2008; Luo et al., 2010). Our findings suggest a positive feedback loop in global warming, with warming promoting soil carbon emissions, which in turn accelerate global warming. However, it should be noted that this study did not address one major concern about whether the temperature sensitivity of Rs (Q10) decreased with warming as proposed by Luo et al. (2001). As the majority of publications did not report Q10 values of the control and the warming groups, we cannot collect Q10 values and conduct a comprehensive analysis. Hence, further studies are needed to address this critical issue.

4.2. Effects of environmental factors

According to the Arrhenius equation, Rs is supposed to increase with rising temperature. However, the response of Rs to warming in this study varies among climatic conditions, with a lack of response in arid grasslands and greater stimulation in temperate grasslands than in cold regions. Nakagawa et al. (2017) emphasized that effect sizes and their uncertainties rather than statistical significance should be primarily focused on in meta-analyses. Despite the large overlap of 95% confidence intervals of Rs responses in cold and temperate grasslands, the difference between Rs responses has ecological significance. Our results signify that there exist environmental factors that limit the potential warming effect on Rs (as the Arrhenius equation indicates) in arid grasslands and cold grasslands. Both soil nutrients and MAP are significant limiting factors of Rs (Table 1), which means that these two environmental factors would be able to explain the spatial heterogeneity in the response of Rs to warming.

The lack of Rs response in arid grasslands could be attributed to the low MAP (Figure S8). MAP showed a significant positive linear relation with Rs responses (Fig. 5), and it was indicated as an important predictor of Rs in multi-model inference (Table 1). It has been reported that water plays a crucial role in regulating Rs in arid grasslands (Niu et al., 2008b). Warming-induced drought stress (Wertin et al., 2017) directly impairs the respiration of microbes and vegetation roots (Liu et al., 2002), which offsets the potential stimulating effect of warming on Rs. In response to water stress, stoma closure increases (Niu et al., 2008a), and the leaf area and photosynthetic pigments are both reduced (León-Sánchez et al., 2016). Soil drought also limits the efficiency of nitrogen utilization (Zhou and Shangguan, 2007), and thus obstructs the supply of respiratory substrates (Wan et al., 2007). Water shortage induced by warming is also likely to change the structure of soil microbial communities (Castro et al., 2010; Sheik et al., 2011) and to inhibit extracellular enzyme activity (Steinauer et al., 2015), thus restricting Rs.

Different from Wang et al. (2019b), this study found that the increment of Rs in cold grasslands was weaker than that in temperate grasslands. This means that environmental constraints of Rs in cold grasslands are stronger than in temperate grasslands. MAP in cold grasslands is much lower than that in temperate grasslands (Figure S8), which can account for the differences in the Rs response between cold and temperate grasslands. As in arid grasslands, a relatively lower MAP in cold grasslands implies that soil water loss caused by warming has a negative effect on Rs (Yan et al., 2020), partly offsetting the positive warming effect of Rs. In contrast, temperate grasslands, where MAP is high (Figure S8), have milder environmental conditions compared with the water-limited arid and cold grasslands. Therefore, among the climatic zones, Rs is more strongly stimulated in temperate grasslands, where the loss of soil water through warming does not limit Rs. Despite the water limitation of Rs in both cold and arid grasslands, Rs increased with warming in cold grasslands but hardly changed in arid grasslands. This should be attributed to differences in soil nutrients (particularly OC and TN). Because soil nutrients in cold grasslands are more abundant than that in arid grasslands (Figure S8), the restriction of soil nutrients on warming effects in cold grasslands is much weaker. Specifically, the large initial soil OC stock determines the great soil carbon loss potential (Crowther et al., 2016), and abundant TN would not limit the microbial decomposition of soil OC (Heimann and Reichstein, 2008). Warming also promotes the utilization of aged soil OC (Hopkins et al., 2012; Streit et al., 2014).

It was previously thought that the low temperature is a crucial limitation of Rs in cold grasslands, and warming would mitigate the low temperature limitation in cold grasslands and thus lead to a significant increase of Rs (Fahnestock et al., 1999; Dorrepaal et al., 2009). However, we were surprised to observe a non-significant correlation between MAT and Rs response (Fig. 5, Table 1). This suggested that the Rs response in cold grasslands is not directly controlled by MAT. Similar results have been observed before. Crowther et al. (2016) pointed out that MAT had no significant effect on soil C losses. Haaf et al. (2021) and Mahecha et al. (2010) respectively reported that the temperature sensitivity of Rs and ecosystem respiration was independent of MAT. They argued that the response of carbon fluxes to warming is controlled by changes in soil carbon pools and substrate availability, rather than by temperature itself. The regulation of soil nutrients on Rs response found in this study supports their statement.

In this study, Rs in cold grasslands changed less than previously observed. Several synthetic studies have provided estimates of the Rs response to warming in cold grasslands, but they are all higher than the estimates (10.5%) provided in this study. For example, Wang et al. (2019b) suggested that warming boosted Rs in cold grasslands by roughly 15%. Wang et al. (2019a) and Wang et al. (2014) reported a warming-induced stimulation of Rs in alpine grasslands by 13% and even over 50% respectively. It should be noted that these published results have much greater uncertainties than this study due to their small sample sizes. Given the adequate and representative sample size in this study, our finding should be more credible. One important reason is our result contained a larger number of studies conducted in high-altitude regions, particularly on the Qinghai-Tibet plateau and Inner Mongolia plateau in East Asia. MAP in these regions is lower than those in low-altitude cold grasslands located in the Americas and Europe (Fick and Hijmans, 2017). Since MAP is one of the crucial factors limiting Rs (Table 1), Rs in cold grasslands showed a stronger environmental constraint and thus a weaker increase compared with previous studies. The relatively lower Rs response in cold grasslands under inadequate water conditions observed in this study indicates that Crowther et al. (2016) may overestimate the soil carbon loss of cold grasslands under climate warming. In that study, soil carbon loss only depends on initial OC content and the intensity of warming, with the limiting effect of water being neglected.

Overall, both soil nutrients and MAP are critical factors limiting Rs. In temperate grasslands with weak environment restrictions, climatic warming directly increases basal Rs, and plants provide more respiratory substrates for soil microbes and roots. In cold grassland, although sufficient soil nutrients provide sufficient respiratory substrates for consumption under warming, the positive effect is limited by the water stress caused by warming. Warming may exacerbate water shortages in arid grasslands, where water stress may explain why Rs in arid grasslands changes little with warming.

4.3. Uncertainties and limitations

Due to the inherent limitations of the methodology, the effects of global warming on Rs may be more complex than indicated, with considerable uncertainties. To estimate the effects of climate warming on Rs more accurately and to develop more extensive knowledge of the mechanisms of the Rs response, four key issues must be addressed, as follows.

First, the compiled database used here was confined to the mid-latitudes of the Northern Hemisphere, with few data from other regions where there is a lack of funding support for warming experiments. The missing data induced bias, causing uncertainties in our findings. Manipulative studies are therefore encouraged in the southern hemisphere and tropical grasslands. Second, this study found that the response patterns for long- and short-term warming were inconsistent, but the sample size was much smaller for the former. The lack of comprehensive datasets for long-term studies limits the understanding of the long-term effect of climatic warming on Rs, with decades-long studies being needed. Third, present methods of separating Rs into Ra and Rh are defective and expensive (Wang et al., 2014), resulting in few studies reporting Ra and Rh, hindering clarification of mechanisms regulating Rs response to climate warming. More studies of Rs, Ra, and Rh are therefore needed to elucidate the Rs response to climate change. Fourth, few Rs studies reported data for soil microorganisms and related enzymes, possibly due to testing costs. This lack of data limited our ability to further explore the mechanisms of climate-warming effects on Rs. We advocate the inclusion of microbial factors in future studies.

5. Conclusion

In this study, we focused on the response of Rs to warming in grassland ecosystems based on an integrated analysis of 168 independent field measurements. We found that all warming factors affect the response of Rs to warming. Rs response shows a three-phase pattern with the duration of warming increased, and the long-term response of Rs may be much greater than is indicated in short-term studies. The nonlinear temporal effect on Rs suggests that the response of Rs to future warming could be greater than previously thought, and more long-term warming experiments and continuous carbon flux observations are needed to advance our understanding of the long-term response of Rs to future warming. The response of Rs differed under different warming methods, indicating that it is necessary to carry out manipulative warming experiments with standardized protocols to improve the comparability of results. The positive correlation between Rs responses and the magnitude of warming implies positive feedback of Rs on warming, i.e., warming-induced increasing CO_2 emissions into the atmosphere will contribute to global warming. We also found that the response of Rs also varies between climatic zones, and the spatial heterogeneity of the Rs response can be explained by differences in the distributions of water and soil nutrients. The relatively lower Rs response in cold grasslands suggests that warming effects could be overestimated if ignoring the water limitation. In conclusion, our findings reveal the heterogeneity of Rs response to climate warming in grasslands and its contributing factors, which may allow better modelling and simulation of the global carbon cycle in future studies.

Data availability statement

Dataset available via figshare https://doi.org/10.6084/m9.figshare.14216093.V5 (Chen et al., 2021).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to the scientists who contributed their data for this meta-analysis. This work was supported by projects of the National Key R&D Program of China (2017YFA0604803) and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDA20020202).

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.soilbio.2022.108616.

References

Ainsworth, E.A., Davey, P.A., Hymus, G.J., Osborne, C.P., Rogers, A., Blum, H., NÖSberger, J., Long, S.P., 2003. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with Lolium perenne grown for 10 years at two nitrogen fertilization levels under Free Air CO_2 Enrichment (FACE). Plant, Cell and Environment 26, 705–714.

Aronson, E.L., McNulty, S.G., 2009. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. Agricultural and Forest Meteorology 149, 1791–1799.

Baryamureeba, V., 2001. The impact of equal weighting of low- and high-confidence observations on robust linear regression computations. BIT Numerical Mathematics 41, 847–855.

Bond-Lamberty, B., Thomson, A., 2010. A global database of soil respiration data. Biogeosciences 7, 1915–1926.

Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E., Reynolds, J.F., Treseder, K.K., Wallenstein, M.D., 2008. Thermal adaptation of soil microbial respiration to elevated temperature. Ecology Letters 11, 1316–1327.
Bronson, D.R., Gower, S.T., Tanner, M., Linder, S., Van Herk, I., 2008. Response of soil surface CO_2 flux in a boreal forest to ecosystem warming. Global Change Biology 14, 856–867.
Burnham, K., Anderson, D., 2002. Model Selection and Multi-Model Inference: A Practical-Theoretical Approach.
Cade, B.S., 2015. Model averaging and muddled multimodel inferences. Ecology 96, 2370–2382.
Carey, J.C., Tang, J., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskel, M.A., Jiang, L., Machmuller, M.B., Mohan, J., Panetta, A.M., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgham, S., Collins, S.L., de Dato, G., Eddy, W.C., Enquist, B.J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Larsen, K.S., Luo, Y., Marhan, S., Melillo, J.M., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Rastetter, E., Reinmann, A.B., Reynolds, L.L., Schmidt, I.K., Shaver, G.R., Strong, A.L., Suseela, V., Tietema, A., 2016. Temperature response of soil respiration largely unaltered with experimental warming. Proceedings of the National Academy of Sciences 113, 13797–13802.
Castro, H.F., Classen, A.T., Austin, E.E., Norby, R.J., Schadt, C.W., 2010. Soil microbial community responses to multiple experimental climate change drivers. Applied and Environmental Microbiology 76, 999.
Chang, J., Ciais, P., Gasser, T., Smith, P., Herrero, M., Havlík, P., Obersteiner, M., Guenet, B., Goll, D.S., Li, W., Naipal, V., Peng, S., Qiu, C., Tian, H., Viovy, N., Yue, C., Zhu, D., 2021. Climate warming from managed grasslands cancels the cooling effect of carbon sinks in sparsely grazed and natural grasslands. Nature Communications 12, 118.
Chen, Z., Zhao, D., Zhu, Y., Zhang, R., Guo, C., 2021. CombinedDataset.xlsx (Figshare.
Crowther, T.W., Todd-Brown, K.E., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kroel-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Penuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming. Nature 540, 104–108.
Dass, P., Houlton, B.Z., Wang, Y., Warlind, D., 2018. Grasslands may be more reliable carbon sinks than forests in California. Environmental Research Letters 13, 074027.
de Dato, G.D., De Angelis, P., Sirca, C., Beier, C., 2010. Impact of drought and increasing temperatures on soil CO_2 emissions in a Mediterranean shrubland (gariga). Plant and Soil 327, 153–166.
Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V., Aerts, R., 2009. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460, 616–619.
Egger, M., Smith, G.D., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by a simple, graphical test. BMJ British Medical Journal 315, 629–634.
Fahnestock, J.T., Jones, M.H., Welker, J.M., 1999. Wintertime CO_2 efflux from Arctic soils: implications for annual carbon budgets. Global Biogeochemical Cycles 13, 775–779.
Feng, J., Wang, J., Ding, L., Yao, P., Qiao, M., Yao, S., 2017. Meta-analyses of the effects of major global change drivers on soil respiration across China. Atmospheric Environment 150, 181–186.
Feng, J., Zhu, B., 2019. A global meta-analysis of soil respiration and its components in response to phosphorus addition. Soil Biology and Biochemistry 135, 38–47.
Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315.
Fu, Z., Niu, S., Dukes, J.S., 2015. What have we learned from global change manipulative experiments in China? A meta-analysis. Scientific Reports 5, 12344.
Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24, 699–711.
Haaf, D., Six, J., Doetterl, S., 2021. Global patterns of geo-ecological controls on the response of soil respiration to warming. Nature Climate Change 11, 623–627.
Hartley, I.P., Heinemeyer, A., Ineson, P., 2007. Effects of three years of soil warming and shading on the rate of soil respiration: substrate availability and not thermal acclimation mediates observed response. Global Change Biology 13, 1761–1770.
Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.
Heimann, M., Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451, 289–292.
Hinich, M.J., Talwar, P.P., 1975. A simple method for robust regression. Journal of the American Statistical Association 70, 113–119.
Hopkins, F.M., Torn, M.S., Trumbore, S.E., 2012. Warming accelerates decomposition of decades-old carbon in forest soils. Proceedings of the National Academy of Sciences 109, E1753.
IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC.
Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. Nature 433, 298–301.
Kubínová, M., Nagy, J.G., 2018. Robust regression for mixed Poisson–Gaussian model. Numerical Algorithms 79, 825–851.
Lal, R., 2004. Soil carbon sequestration to mitigate climate change. Geoderma 123, 1–22.
Lavoie, M., Phillips, C.L., Risk, D., 2015. A practical approach for uncertainty quantification of high-frequency soil respiration using Forced Diffusion chambers. Journal of Geophysical Research: Biogeosciences 120, 128–146.
Lellei-Kovács, E., Kovács-Láng, E., Kalapos, T., Botta-Dukát, Z., Barabás, S., Beier, C., 2008. Experimental warming does not enhance soil respiration in a semiarid temperate forest-steppe ecosystem. Community Ecology 9, 29–37.
León-Sánchez, L., Nicolás, E., Nortes, P.A., Maestre, F.T., Querejeta, J.I., 2016. Photosynthesis and growth reduction with warming are driven by nonstomatal limitations in a Mediterranean semi-arid shrub. Ecology and Evolution 6, 2725–2738.
Li, J., Pei, J., Pendall, E., Fang, C., Nie, M., 2020. Spatial heterogeneity of temperature sensitivity of soil respiration: a global analysis of field observations. Soil Biology and Biochemistry 141, 107675.
Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J., Li, B., 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytologist 177, 706–714.
Liu, D., Keiblinger, K.M., Schindlbacher, A., Wegner, U., Sun, H., Fuchs, S., Lassek, C., Riedel, K., Zechmeister-Boltenstern, S., 2017. Microbial functionality as affected by experimental warming of a temperate mountain forest soil—a metaproteomics survey. Applied Soil Ecology 117–118, 196–202.
Liu, X., Wan, S., Su, B., Hui, D., Luo, Y., 2002. Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem. Plant and Soil 240, 213–223.
Lu, M., Zhou, X., Yang, Q., Li, H., Luo, Y., Fang, C., Chen, J., Yang, X., Li, B., 2013. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. Ecology 94, 726–738.
Luo, C., Xu, G., Chao, Z., Wang, S., Lin, X., Hu, Y., Zhang, Z., Duan, J., Chang, X., Su, A., Li, Y., Zhao, X., Du, M., Tang, Y., Kimball, B., 2010. Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau. Global Change Biology 16, 1606–1617.
Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413, 622–625.
Mahecha, M.D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S.I., Vargas, R., Ammann, C., Arain, M.A., Cescatti, A., Janssens, I.A., Migliavacca, M., Montagnani, L., Richardson, A.D., 2010. Global convergence in the temperature sensitivity of respiration at ecosystem level. Science 329, 838–840.
Melillo, J.M., Frey, S.D., DeAngelis, K.M., Werner, W.J., Bernard, M.J., Bowles, F.P., Pold, G., Knorr, M.A., Grandy, A.S., 2017. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. Science 358, 101–105.
Mikan, C.J., Schimel, J.P., Doyle, A.P., 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. Soil Biology and Biochemistry 34, 1785–1795.
Nakagawa, S., Noble, D.W.A., Senior, A.M., Lagisz, M., 2017. Meta-evaluation of meta-analysis: ten appraisal questions for biologists. BMC Biology 15, 18.
Niu, S., Li, Z., Xia, J., Han, Y., Wu, M., Wan, S., 2008a. Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China. Environmental and Experimental Botany 63, 91–101.
Niu, S., Wu, M., Han, Y., Xia, J., Li, L., Wan, S., 2008b. Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. New Phytologist 177, 209–219.
Owen, K.A., Everard, J.E., Beth, R.L., 2000. Response of Root Respiration to Changes in Temperature and its Relevance to Global Warming. New Phytologist, pp. 141–154.
Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11, 1633–1644.
Peng, F., You, Q., Xu, M., Guo, J., Wang, T., Xue, X., 2014. Effects of warming and clipping on ecosystem carbon fluxes across two hydrologically contrasting years in an alpine meadow of the Qinghai-Tibet Plateau. PLoS One 9, e109319.
Pold, G., Melillo, J.M., DeAngelis, K.M., 2015. Two decades of warming increases diversity of a potentially lignolytic bacterial community. Frontiers in Microbiology 6, 480.
Poulter, B., Frank, D., Ciais, P., Myneni, R.B., Andela, N., Bi, J., Broquet, G., Canadell, J.G., Chevallier, F., Liu, Y.Y., Running, S.W., Sitch, S., van der Werf, G.R., 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. Nature 509, 600.
Raich, J.W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. Global Biogeochemical Cycles 9, 23–36.
Reynolds, L.L., Johnson, B.R., Pfeifer-Meister, L., Bridgham, S.D., 2015. Soil respiration response to climate change in Pacific Northwest prairies is mediated by a regional Mediterranean climate gradient. Global Change Biology 21, 487–500.
Romero-Olivares, A.L., Allison, S.D., Treseder, K.K., 2017. Soil microbes and their response to experimental warming over time: a meta-analysis of field studies. Soil Biology and Biochemistry 107, 32–40.
Rosenthal, R., 1978. Combining results of individual studies. Psychological Bulletin 85, 185–193.
Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J., Gurevitch, J., Gcte, N., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.
Sharkhuu, A., Plante, A.F., Enkhmandal, O., Gonneau, C., Casper, B.B., Boldgiv, B., Petraitis, P.S., 2016. Soil and ecosystem respiration responses to grazing, watering and experimental warming chamber treatments across topographical gradients in northern Mongolia. Geoderma 269, 91–98.
Sheik, C.S., Beasley, W.H., Elshahed, M.S., Zhou, X., Luo, Y., Krumholz, L.R., 2011. Effect of warming and drought on grassland microbial communities. The ISME Journal 5, 1692–1700.
Song, J., Ru, J., Zheng, M., Wang, H., Fan, Y., Yue, X., Yu, K., Zhou, Z., Shao, P., Han, H., Lei, L., Zhang, Q., Li, X., Su, F., Zhang, K., Wan, S., 2020. A global database of plant

production and carbon exchange from global change manipulative experiments. Scientific Data 7, 323.

Song, J., Wan, S., Piao, S., Knapp, A.K., Classen, A.T., Vicca, S., Ciais, P., Hovenden, M.J., Leuzinger, S., Beier, C., Kardol, P., Xia, J., Liu, Q., Ru, J., Zhou, Z., Luo, Y., Guo, D., Adam Langley, J., Zscheischler, J., Dukes, J.S., Tang, J., Chen, J., Hofmockel, K.S., Kueppers, L.M., Rustad, L., Liu, L., Smith, M.D., Templer, P.H., Quinn Thomas, R., Norby, R.J., Phillips, R.P., Niu, S., Fatichi, S., Wang, Y., Shao, P., Han, H., Wang, D., Lei, L., Wang, J., Li, X., Zhang, Q., Li, X., Su, F., Liu, B., Yang, F., Ma, G., Li, G., Liu, Y., Liu, Y., Yang, Z., Zhang, K., Miao, Y., Hu, M., Yan, C., Zhang, A., Zhong, M., Hui, Y., Li, Y., Zheng, M., 2019. A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. Nature Ecology & Evolution 3, 1309–1320.

Steinauer, K., Tilman, D., Wragg, P.D., Cesarz, S., Cowles, J.M., Pritsch, K., 2015. Plant diversity effects on soil microbial functions and enzymes are stronger than warming in a grassland experiment. Ecology 96.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., 2013. Climate Change 2013: the Physical Science Basis. Cambridge University Press, Cambridge.

Streit, K., Hagedorn, F., Hiltbrunner, D., Portmann, M., Saurer, M., Buchmann, N., Wild, B., Richter, A., Wipf, S., Siegwolf, R.T.W., 2014. Soil warming alters microbial substrate use in alpine soils. Global Change Biology 20, 1327–1338.

Terrer, C., Vicca, S., Hungate, B.A., Phillips, R.P., Prentice, I.C., 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353, 72.

Tucker, C.L., Bell, J., Pendall, E., Ogle, K., 2013. Does declining carbon-use efficiency explain thermal acclimation of soil respiration with warming? Global Change Biology 19, 252–263.

Vander Werf, E., 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. Ecology 73, 1699–1705.

Veroniki, A.A., Jackson, D., Viechtbauer, W., Bender, R., Bowden, J., Knapp, G., Kuss, O., Higgins, J.P.T., Langan, D., Salanti, G., 2016. Methods to estimate the between-study variance and its uncertainty in meta-analysis. Research Synthesis Methods 7, 55–79.

Wallace, B.C., Lajeunesse, M.J., Dietz, G., Dahabreh, I.J., Trikalinos, T.A., Schmid, C.H., Gurevitch, J., 2017. OpenMEE: intuitive, open-source software for meta-analysis in ecology and evolutionary biology. Methods in Ecology and Evolution 8, 941–947.

Wan, S., Norby, R.J., Ledford, J., Weltzin, J.F., 2007. Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. Global Change Biology 13, 2411–2424.

Wan, S., Xia, J., Liu, W., Niu, S., 2009. Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. Ecology 90, 2700–2710.

Wang, G., Li, F., Peng, Y., Yu, J., Zhang, D., Yang, G., Fang, K., Wang, J., Mohammat, A., Zhou, G., Yang, Y., 2019a. Responses of soil respiration to experimental warming in an alpine steppe on the Tibetan Plateau. Environmental Research Letters 14, 094015.

Wang, N., Quesada, B., Xia, L., Butterbach-Bahl, K., Goodale, C.L., Kiese, R., 2019b. Effects of climate warming on carbon fluxes in grasslands- A global meta-analysis. Global Change Biology 25, 1839–1851.

Wang, Q., Zhao, X., Chen, L., Yang, Q., Chen, S., Zhang, W., 2019c. Global synthesis of temperature sensitivity of soil organic carbon decomposition: latitudinal patterns and mechanisms. Functional Ecology 33, 514–523.

Wang, W., Fang, J., 2009. Soil respiration and human effects on global grasslands. Global and Planetary Change 67, 20–28.

Wang, X., Liu, L., Piao, S., Janssens, I.A., Tang, J., Liu, W., Chi, Y., Wang, J., Xu, S., 2014. Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration. Global Change Biology 20, 3229–3237.

Wang, X., Piao, S., Ciais, P., Janssens, I.A., Reichstein, M., Peng, S., Wang, T., 2010. Are ecological gradients in seasonal Q10 of soil respiration explained by climate or by vegetation seasonality? Soil Biology and Biochemistry 42, 1728–1734.

Warner, D.L., Bond-Lamberty, B., Jian, J., Stell, E., Vargas, R., 2019. Spatial predictions and associated uncertainty of annual soil respiration at the global scale. Global Biogeochemical Cycles 33, 1733–1745.

Wertin, T.M., Belnap, J., Reed, S.C., 2017. Experimental warming in a dryland community reduced plant photosynthesis and soil CO_2 efflux although the relationship between the fluxes remained unchanged. Functional Ecology 31, 297–305.

White, R.P., Murray, S., Rohweder, M., 2000. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. World Resources Institute.

Wu, Z., Dijkstra, P., Koch, G.W., PeÑUelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology 17, 927–942.

Xia, J., Wan, S., 2008. Global response patterns of terrestrial plant species to nitrogen addition. New Phytologist 179, 428–439.

Xu, X., Shi, Z., Li, D., Zhou, X., Sherry, R.A., Luo, Y., 2015. Plant community structure regulates responses of prairie soil respiration to decadal experimental warming. Global Change Biology 21, 3846–3853.

Yan, C., Yuan, Z., Shi, X., Lock, T.R., Kallenbach, R.L., 2020. A global synthesis reveals more response sensitivity of soil carbon flux than pool to warming. Journal of Soils and Sediments 20, 1208–1221.

Yuan, Z.Y., Jiao, F., Shi, X.R., Sardans, J., Maestre, F.T., Delgado-Baquerizo, M., Reich, P. B., Penuelas, J., 2017. Experimental and observational studies find contrasting responses of soil nutrients to climate change. Elife 6.

Zhang, Z., Zhang, H., Cui, Z., Tao, F., Chen, Z., Chang, Y., Magliulo, V., Wohlfahrt, G., Zhao, D., 2021. Global consistency in response of terrestrial ecosystem respiration to temperature. Agricultural and Forest Meteorology 308–309, 108576.

Zhao, Z., Peng, C., Yang, Q., Meng, F.-R., Song, X., Chen, S., Epule, T.E., Li, P., Zhu, Q., 2017. Model prediction of biome-specific global soil respiration from 1960 to 2012. Earth's Future 5, 715–729.

Zhou, G., Luo, Q., Chen, Y., He, M., Zhou, L., Frank, D., He, Y., Fu, Y., Zhang, B., Zhou, X., 2019a. Effects of livestock grazing on grassland carbon storage and release override impacts associated with global climate change. Global Change Biology 25, 1119–1132.

Zhou, G., Luo, Q., Chen, Y., Hu, J., He, M., Gao, J., Zhou, L., Liu, H., Zhou, X., 2019b. Interactive effects of grazing and global change factors on soil and ecosystem respiration in grassland ecosystems: a global synthesis. Journal of Applied Ecology 56, 2007–2019.

Zhou, L., Zhou, X., Shao, J., Nie, Y., He, Y., Jiang, L., Wu, Z., Hosseini Bai, S., 2016. Interactive effects of global change factors on soil respiration and its components: a meta-analysis. Global Change Biology 22, 3157–3169.

Zhou, Z., Shangguan, Z., 2007. Vertical distribution of fine roots in relation to soil factors in Pinus tabulaeformis Carr. forest of the Loess Plateau of China. Plant and Soil 291, 119–129.