



Sustained increases in soil respiration accompany increased carbon input under long-term warming across global grasslands

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ABSTRACT

Respiratory effluxes of carbon (C) from the soil to the atmosphere are expected to rise with temperature, potentially intensifying future climate warming. However, whether and how this increase would be sustained under long-term warming is not well understood. Here, we combined a manipulation experiment in an alpine meadow with a global *meta-analysis* to explore the mechanisms underlying the long-term responses of soil respiration to climate warming. The results from the experiment in the alpine meadow showed that the warming-induced increase in net primary productivity (NPP, 23.6 %) explained 52 % of the increase in soil respiration across 6 years. In contrast, the warming-induced changes in soil moisture, soil temperature, microbial biomass C or nitrogen were not significantly correlated with soil respiration responses. Consistently, in the global *meta-analysis*, both soil respiration and NPP continually increased over the years by an average of 9.5 % and 15.9 %, respectively. The increases in soil respiration were also primarily correlated with the continued increases in NPP over this period. Notably, the sustained increase in soil respiration was mainly contributed by the response of autotrophic respiration, which was closely correlated with the sustained increase in belowground NPP under warming. The results from both our field experiment and *meta-analysis* suggest that the increased soil respiration under climate warming was at least partly from the stimulation of C input in grasslands. The simultaneous increases in soil respiration and NPP may counteract the expected positive terrestrial C-climate feedback and should be considered in land models to more accurately predict future climate change.

1. Introduction

Globally, the respiratory efflux of carbon (C) from soil is nearly ten times larger than anthropogenic emissions (Carey et al., 2016; Raich et al., 2002), contributing 10 % of global atmospheric carbon dioxide (CO₂) each year (Luo, 2007). Given such a great amount of C flux, a fractionally small change in soil respiration may have a dramatic effect on atmospheric CO₂ concentration and thus on Earth's climate (Bond-Lamberty et al., 2018; Yvon-Durocher et al., 2012). Therefore, it is

important to better understand the dynamics of soil respiration under climate change. Field experiments (Bradford et al., 2008; Zhou et al., 2010), modeling analyses (Luo, 2007; Raich et al., 2002), global *meta-analyses* (Lu et al., 2013; Wang et al., 2019) and fundamental biokinetics (Bond-Lamberty and Thomson, 2010; Davidson and Janssens, 2006) all suggest that soil respiration rates increase with climate warming, potentially leading to a positive feedback between the terrestrial C cycle and climate change. However, whether this stimulation is sustained under long-term warming is not well understood (Dacal et al., 2020;

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Zhou et al., 2007). The longest manipulative warming experiment (a 26-year soil warming experiment in a midlatitude hardwood forest) reported that the responses of soil respiration to warming showed a four-phase pattern, with phases of substantial soil C loss alternating with no detectable loss (Melillo et al., 2017), suggesting that warming-induced changes in soil respiration vary largely with warming duration. Therefore, it is critical to understand how soil respiration responds to long-term warming and its underlying mechanisms.

Grasslands cover nearly 40 % of the world's land surface (Liu et al., 2021) and store approximately 10 %–30 % of global soil C (Scurlock and Hall, 1998), but are highly vulnerable to climate change (Wang et al., 2019). Moreover, semiarid ecosystems and grasslands dominate the trend and interannual variability of the global terrestrial C sink, whose C balance is strongly associated with variations in both precipitation and temperature (Ahlstrom et al., 2015; Poulter et al., 2014). Therefore, it is critical to determine how soil respiration responds to climate warming in grasslands (Ahlstrom et al., 2015; Wang et al., 2019). Experimental warming studies have been extensively conducted in grasslands to explore soil respiration responses to elevated temperatures. However, the majority of these studies have typically lasted <3 years (Wang et al., 2019), and there is growing dispute about whether the increased soil respiration rate would last with long-term experimental warming (Luo et al., 2001; Peng et al., 2020; Xu et al., 2015). Multiple mechanisms have been proposed to explain the different responses of soil respiration to long-term warming, such as, the shift in plant community composition (Niu et al., 2013), the depletion of soil organic C (Davidson and Janssens, 2006), the thermal adaptation of microorganisms (Bradford et al., 2010), the reduced photosynthetic rates (Hogberg et al., 2001), and the reduction of soil moisture (Dominguez et al., 2017). Nevertheless, those mechanisms have been proposed in individual studies, the dominant mechanism underlying the long-term response of soil respiration to warming in global grasslands is still unclear. In addition, soil respiration is an integrated result of respiration associated with soil organic matter decomposition (heterotrophic respiration) and root activities (autotrophic respiration). Since the turnover times and controlling factors of plants and soil C pools are different, the response direction and magnitude of heterotrophic respiration and autotrophic respiration to climate warming may vary (Noh et al., 2016; Wang et al., 2014; Yan et al., 2022). Hence, without the separation of heterotrophic respiration and autotrophic respiration, soil respiration measurements alone provide little insight into ecosystem C cycling and insufficient evaluation of its response to future climate change.

Net primary productivity (NPP) is recognized as the key process and driving force of other C processes in ecosystems (Norby et al., 2002; Xu et al., 2012). Both field experiments and modeling studies have suggested that climatic change could alter the functioning of other ecosystem C processes via changes in NPP (Luo et al., 2009; Norby and Luo, 2004). For example, global warming is anticipated to significantly affect NPP by altering biogeochemical processes (Xu et al., 2012), and thus further influence aboveground and belowground C processes (Xu et al., 2015; Yan et al., 2021). Therefore, to reveal how NPP responds to global warming it is important to understand soil respiration responses. However, manipulative experiments in a range of biomes demonstrated that warming may have a variety of effects on NPP (Rustad et al., 2001), including positive (Wan et al., 2005), neutral (Liu et al., 2018; Xu et al., 2013) and negative (Klein et al., 2007) effects. The magnitudes and directions of NPP change under warming were primarily determined by the degree of water limitation (Gerten et al., 2008; Song et al., 2019) and nitrogen availability (Melillo et al., 2002). Moreover, as the primary driver of ecosystem C cycling (Hui and Jackson, 2006), any increase in NPP may accelerate soil respiration mainly by stimulating autotrophic respiration of plant roots. Concurrently, litter input rates are likely to increase as well, which would indirectly exacerbate the decomposition of soil microbes, and thus increase heterotrophic respiration (Rustad et al., 2001). A previous study conducted in forest reported that soil respiration would decrease approximately 54 % within two months if

assimilate flow to the root system is blocked (Hogberg et al., 2001), suggesting that the flux of instantaneous NPP to roots is a key driver of soil respiration (root respiration and rhizomicrobial respiration) (Meeran et al., 2021). This link is especially rapid and strong for grassland ecosystems (Kuzyakov and Gavrichkova, 2010). However, how NPP regulates soil respiration and its two components under long-term warming and related impacts on the global C cycle are poorly understood, which significantly slows progress in validating land models and projecting ecosystem functions under future climate change.

To reveal how soil respiration responses relate to NPP changes under long-term warming, we conducted two analyses: 1) a long-term field warming experiment (6 years) with three warming levels (control, +1.5 °C, +2.5 °C) on the Qinghai-Tibetan Plateau, which is one of the most sensitive and vulnerable areas to climate change; and 2) a global meta-analysis of 297 observations from 48 temperature manipulation studies in grasslands across the world. Specifically, we aimed to address the following questions: (1) How soil respiration and NPP respond to long-term warming? (2) How changes in NPP under long-term warming regulate the responses of soil respiration?

2. Materials and methods

2.1. Experimental study

2.1.1. Study area

The field experiment was conducted in an alpine meadow on the eastern Qinghai-Tibetan Plateau (32°48'N, 102°33'E, 3500 m a.s.l.). The mean annual temperature there is 1.5 °C with the monthly temperature ranging from −9.7 °C in January to 11.1 °C in July, while the mean annual precipitation is 747 mm with approximately 80 % occurring from May to September (the 1961–2013 average). The site was dominated by *Anemone rivularis*, *Potentilla anserina*, *Polygonum viviparum*, *Deschampsia caespitosa*, *Elymus nutans* and *Agrostis hugoniana*. The soil was classified as a Mat Gry-gelic Cambisol according to Chinese Soil Taxonomy Research. The soil pH is approximately 6.24, while the soil organic C and N contents are 37 g C kg^{−1} and 3.5 g N kg^{−1}, respectively.

2.1.2. Experimental design

A randomized complete block design with three warming levels and five replications was conducted in this study. Three 3 × 2 m plots laid out in each of five blocks were randomly assigned to the three treatments of the control, low-level warming (LW, +1.5 °C) and high-level warming (HW, +2.5 °C). The adjacent two plots were 3 m apart. Warming treatment was applied continuously since June 2014 in warming plots by 165 × 15 cm infrared radiators (MSR-2420, Kalglo Electronics Inc. Bethlehem, Pennsylvania, USA) suspended in the center and 1.5 m above the ground. A dummy heater with the same size and shape was suspended at the same height to simulate the shading effect in each control plot.

2.1.3. Soil respiration measurements

Soil respiration, heterotrophic respiration and autotrophic respiration were measured by using the surface and deep collar methods, which were commonly used in previous studies (Li et al. (2013); Luo et al., 2001; Zhou et al., 2007). Specifically, before the measurements were conducted, we installed two types of polyvinylchloride (PVC) collars (10.5 cm in diameter) in each plot in June 2014, with the surface PVC collars (5 cm in height and 10.5 cm in internal diameter) being permanently inserted 3 cm into the soil to measure soil respiration. Deep PVC tubes (40 cm in height and 10.5 cm in internal diameter) were also permanently inserted 38 cm into soil. After the deep collars were inserted into the soil, we removed the aboveground part of all plants in the collars to eliminate the C supply to roots. Plant regrowth was eliminated by periodically checking the collars and removing new plants once every few days. After several months of this operation, there were no plants growing within the collars. Thus, these deep PVC collars cut off

old plant roots and prevented new roots from growing inside the collar. Since plant roots were distributed mostly in the top 30 cm layer of the soil in this study area (Song et al. (2017)), the deep collars with 38 cm inserted into the soil were able to cut off all roots from growing into the collars. After one year, the remaining roots in deep collars were assumed to be totally dead. For the surface collars, the plants inside them were clipped at least one day before the soil respiration measurement to remove aboveground plant respiration while maintaining root respiration, which represented the total respiration. The autotrophic respiration was calculated by subtracting microbe respiration from total soil respiration.

Soil respiration and its components were measured twice a month between 10:00 and 15:00 (local time) during the growing season using an LI-COR 6400 portable photosynthesis system attached to the soil respiration chamber (LI-COR Inc., Lincoln, NE, USA).

2.1.4. Soil temperature and moisture measurements

Simultaneous with each measurement of soil respiration, soil temperature and soil moisture at a 10 cm depth in each plot were manually measured using portable time domain reflectometry equipment (TDR 100, Spectrum Technologies Inc., Chicago, USA) and LI-COR 6400 sensors, respectively.

2.1.5. NPP measurements

A frame of 0.1×1 m was randomly placed in each plot, and the aboveground living plants were clipped when biomass reached its peak in each growing season (in mid-August), which was similar to previous studies (Nippert et al., 2006; Wilcox et al., 2015; Zhang et al., 2019). All plants were oven-dried at 65°C for 48 h to a constant weight and weighed, which represents the aboveground net primary productivity (NPP). Since the species number in a frame size of 0.1×1 m can adequately represent the number of species in the plot in our field experiment (Quan et al., 2021; Song et al. (2017)), a frame size of 0.1×1 m for aboveground NPP estimation is reliable and representative. In contrast with other frame sizes (0.5×0.5 m or 1×1 m) used in previous studies (Li and Sun, 2011; Wang et al., 2016), clipping in the smaller frame minimizes the manual disturbance to plants, microbes and soil in the plots.

The belowground NPP was measured using the in-growth core method (Quan et al., 2020). More than 90 % of the plant roots were distributed within the top 20 cm of the soil, whereas nearly 100 % were within the top 40 cm as documented in previous studies (Quan et al., 2020; Song et al. (2017)). Thus, root sampling at 40 cm depth could well represent root productivity. One hole (40 cm in depth and 8 cm in diameter) was excavated in the soil in each plot at the end of the growing season in 2014. The soil samples were passed through a 1 mm mesh sieve, and the root material retained on the sieve was washed and oven-dried at 70°C to a constant weight, which represents the below-ground biomass in 2014. Subsequently, the soil sample without roots was placed back to refill the original holes. From 2015, the same procedure was repeated to collect the in-growth roots and estimate belowground NPP in each year. NPP was calculated by adding aboveground and belowground NPP. Detailed information on these measurements can be found in Yan et al., 2021.

2.1.6. MBC and MBN measurements

Soil microbial biomass was sampled from each plot in mid-August of each year. Five soil cores (6 cm in diameter, 10 cm in depth) from each plot were mixed into one composite sample, and passed through a 2 mm mesh. Subsequently, the soil sample was placed in a sterile plastic bag, sealed and transported to the laboratory for storage at 4°C . In this study, soil microbial biomass was measured by the fumigation-extraction method. Microbial biomass C (MBC) and microbial biomass N (MBN) were calculated as the difference in extractable C and N contents between fumigated and unfumigated samples, and the conversion factor was 0.45. All samples were measured within a week.

2.1.7. Soil C and N content measurements

Part of the soil sample mentioned above was air-dried to a constant weight in a greenhouse. The air-dried soil sample was ground using a ball mill. Subsequently, a 0.1 g ground soil sample was used to measure soil C and N contents (soil total organic C, TOC; soil total organic N, TON) within an elemental analyzer (Elementar vario EL cube, Germany).

2.1.8. Data analyses for the field experiment

Repeated-measures analysis of variance (ANOVA) was used to explore the effects of warming, year and their interaction on soil respiration, autotrophic respiration, heterotrophic respiration, NPP, aboveground NPP, belowground NPP, soil moisture, soil temperature, MBC and MBN among the different warming treatments. We set warming treatments and years as fixed effects, and set the block as a random effect. The warming effect on each variable was quantified by calculating the natural log of the response ratio. Linear regression was used to explore relationships between variables. Statistical analyses were conducted with R 3.5.2 (R Core Team, 2018). Origin 8.5 was used for plotting the data.

2.1.9. Meta-analysis

To further test whether the findings in the alpine meadow are applicable to other grasslands in the world, we analyzed the warming responses of soil respiration and NPP as well as their relationships across warming experiments conducted in grasslands at the global scale. Studies included in the meta-analysis (1900–2020) were collected by using the Web of Science (<http://apps.webofknowledge.com/>), Google Scholar (<http://scholar.google.com/>) and China National Knowledge Infrastructure (<http://www.cnki.net/>) for the following combinations of key words: (a) experimental warming (OR climate change OR elevated temperature) AND (b) soil respiration (OR carbon fluxes) AND (c) grassland (OR meadow OR steppe OR savanna OR pasture OR prairie). Papers screened in this meta-analysis were required to be based on the following criteria: (a) vegetation, soil and climatic parameters were presented for ambient and warming treatments; (b) results came from field experiments; (c) the variable of soil respiration was shown by its mean and sample size; (d) experimental method (warming magnitude, warming method and warming duration) had to be explicitly described as well; and (e) standard deviation (SD) or standard error (SE) were reported. Data shown in figures were extracted using GetData Graph Digitizer v.2.24 (<https://getdata-graph-digitizer.com/>). For studies with experimental factors other than warming, moreover, we only considered comparisons between treatments and controls that differed solely in warming (e.g., N loading vs N loading plus warming). Furthermore, most of the studies were collected from temperate and cold regions, while data from tropical and subtropical grasslands were missing because we did not find any relevant literature according to the key words. Overall, we established a global dataset composed of 297 observations from 48 temperature manipulation studies (Fig. S1), with warming magnitudes ranging from 0.5°C to 3.5°C , and experimental duration from 1 to 19 years. The mean annual temperature ranged from -4.5°C to 19.6°C , while the mean annual precipitation ranged from 150 mm to 1847 mm. Before conducting the meta-analysis, we have performed a heterogeneity test ($Q = 322.23$, $P = 0.000$) and analyzed the publication bias, and the results showed that our dataset met the requirement for further analysis.

The warming effect on each variable was quantified by calculating the natural log of the response ratio (LnRR), a metric commonly used in meta-analysis:

$$\text{LnRR} = \text{Ln}\left(\frac{x_t}{x_c}\right) = \text{Ln}(x_t) - \text{Ln}(x_c) \quad (1)$$

where x_t and x_c are the arithmetic mean values of variables in the experimental warming and ambient treatments, respectively. Linear regression was used to analyze the relationship between warming-

Table 1

Repeated measure ANOVA results (*F* values) on the effects of year, warming (W) and their interactions on soil moisture (SM), soil temperature (ST), soil respiration (Rs), net primary production (NPP), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN).

	SM	ST	Rs	NPP	MBC	MBN
Year	157.83***	21.06***	40.76***	19.48***	0.24	0.13
W	27.87***	53.05***	3.38 [^]	6.02*	1.67	1.87
Year*W	3.93*	1.12	3.43*	5.45*	1.75	1.87

[^], *, **, *** represents the statistical significance was at the level of $P < 0.1$, 0.05, 0.01, and 0.001, respectively.

induced changes in soil respiration and other variables.

3. Results

3.1. Soil property changes in the alpine meadow warming experiment

Warming significantly increased soil temperature by an average of 1.46 °C, 1.55 °C, 1.16 °C, 1.42 °C, 1.73 °C and 1.36 °C in 2015, 2016, 2017, 2018, 2019 and 2020, respectively with LW, while HW increased soil temperature by 2.31 °C, 2.25 °C, 2.06 °C, 2.51 °C, 2.70 °C and 2.42 °C in 2015, 2016, 2017, 2018, 2019 and 2020, respectively (Table 1; Fig. 1). Soil moisture exhibited pronounced interannual variations over the 6 years, and warming significantly decreased soil moisture by 4.86 %, 14.6 %, 10.16 %, 7.73 %, 8.91 %, and 11.45 % in 2015, 2016, 2017, 2018, 2019 and 2020, respectively, with LW, while HW decreased soil moisture by 25.14 %, 29.05 %, 14.67 %, 10.05 %, 15.18 %, 16.82 % in 2015, 2016, 2017, 2018, 2019 and 2020, respectively (Table 1; Fig. 1). Moreover, soil moisture in the first three years was significantly lower than that in the last three years, both in the control and warmed (LW and HW) plots (Fig. S2). Warming showed no

significant effects on MBC or MBN (Table 1). In addition, TOC and TON were negatively correlated with ANPP, MBC and MBN but positively correlated with ST, while MBC and MBN were positively correlated with ANPP (Fig. S5).

3.2. Effects of warming on soil respiration over time

Warming marginally changed soil respiration across years but with large interannual variations (Table 1 and Fig. S3). LW on average decreased soil respiration by 4.2 %, while HW increased soil respiration by 6.5 % over the 6 years. Specifically, in contrast with the control, LW decreased soil respiration by 18.5 %, 5.9 %, 15.2 %, 9.8 %, and 1.8 % in 2015, 2016, 2017, 2018 and 2019, respectively, but increased soil respiration by 25.6 % in 2020. HW decreased soil respiration by 6.3 %, 2.1 % and 10.4 % in 2015, 2016, and 2017, respectively, but increased soil respiration by 11.5 %, 10.9 % and 35.0 % in 2018, 2019 and 2020, respectively (Fig. 1). Moreover, warming on average significantly increased autotrophic respiration by 12.5 %, while heterotrophic respiration was not significantly changed under warming (Table S1 and Fig. 3). The regression analysis showed that warming-induced changes in soil respiration and autotrophic respiration were positively correlated with warming duration (Fig. 2a and Fig. 3).

3.3. Warming effects on NPP over time

Warming had significant impacts on NPP (Table 1), which also varied with time (Fig. 1). On average, over time, warming significantly increased NPP by 25.4 %, with LW and HW stimulating NPP by 18.8 % and 31.9 %, respectively (Fig. 1). Specifically, in contrast with the control, LW decreased NPP by 20.9 % in 2015 but increased NPP by 20.9 %, 45.7 %, 4.8 %, 12.1 % and 50.0 % in 2016, 2017, 2018, 2019 and 2020, respectively, while HW increased NPP by 9.3 %, 21.1 %, 50.3 %, 30.7 %, 13.7 % and 66.6 % in 2015, 2016, 2017, 2018, 2019 and 2020, respectively.

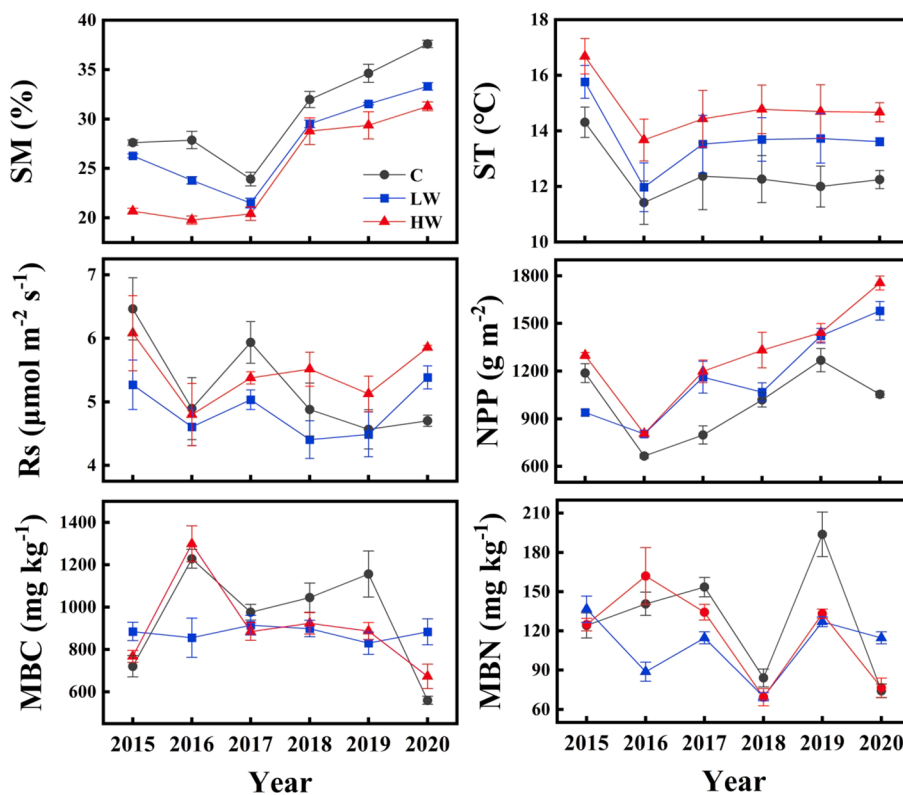


Fig. 1. Soil moisture (SM), soil temperature (ST), soil respiration (Rs), net primary production (NPP), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) under different warming treatments in an alpine meadow in different years. Error bars represent ± SE. C: control; LW: low-level warming (+1.5 °C); HW: high-level warming (+2.5 °C).

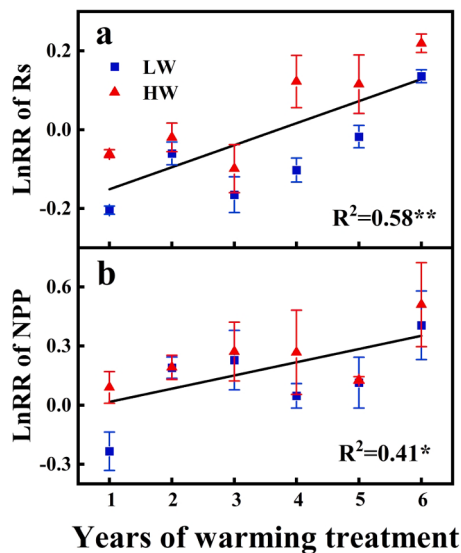


Fig. 2. Response ratio of (a) soil respiration (Rs) and (b) net primary production (NPP) over 6 years warming in the alpine meadow. Error bars represent $\pm$ SE. LW: low-level warming ($+1.5^\circ\text{C}$); HW: high-level warming ($+2.5^\circ\text{C}$). * , ** , *** represents the statistical significance was at the level of $P < 0.1$, 0.05 , 0.01 , and 0.001 , respectively.

2020, respectively (Fig. 1). Moreover, warming on average significantly increased belowground NPP by 46.2 %, while aboveground NPP was not significantly changed under warming (Table S1 and Fig. 3). The results also showed that the warming-induced changes in NPP and belowground NPP were positively correlated with the warming duration (Fig. 2b and 3).

3.4. Regulatory factors of soil respiration responses

Warming-induced changes in NPP were positively correlated with the responses of soil respiration (Fig. 4), which explained most (52 %) of the responses in soil respiration. The results also showed that the

responses of belowground NPP, TOC and TON to warming were positively correlated with the warming-induced changes in soil respiration, while warming-induced changes in soil temperature were marginally correlated with the responses of soil respiration. In contrast, warming-induced changes in soil respiration had no significant relationships with the changes in soil moisture, aboveground NPP, MBC or MBN (Fig. 4).

In addition, warming-induced changes in autotrophic respiration were positively correlated with warming-induced changes in soil temperature, NPP, belowground NPP, TOC and TON (Fig. 5), while warming responses of heterotrophic respiration were positively correlated with the responses of NPP and MBC (Fig. S4).

3.5. Global meta-analysis results

Considering the data of all grasslands that are involved in the meta-analysis, experimental warming generally stimulated both NPP and soil respiration over the experimental years. Across all studies, warming on average increased soil respiration by 9.5 %, with heterotrophic respiration and autotrophic respiration being increased by 12.1 % and 11.8 %, respectively. Warming increased NPP by 15.9 % and belowground NPP by 28.5 % but did not significantly change aboveground NPP. Moreover, warming decreased soil moisture by 10.7 % and increased soil temperature by 8.8 %. Global synthesis indicated that the response ratio of soil respiration, NPP, autotrophic respiration, aboveground NPP and belowground NPP linearly increased with warming duration from 1 to 19 years (Fig. 6 and Fig. S6).

In addition, the positive relationships between warming-induced changes in soil respiration and warming-induced changes in soil moisture, soil temperature, NPP, aboveground NPP, belowground NPP, MBC, MBN, TOC and TON were also detected (Fig. 7). Among them, the responses of NPP explained most of the responses of soil respiration (29 %), followed by MBC (17 %), MBN (16 %), soil temperature (9 %), TOC (7 %), TON (6 %) and soil moisture (3 %). The results also showed that warming-induced changes in autotrophic respiration were positively correlated with warming-induced changes in NPP and belowground NPP (Fig. S7), while warming-induced changes in heterotrophic respiration were positively correlated with warming responses of NPP,

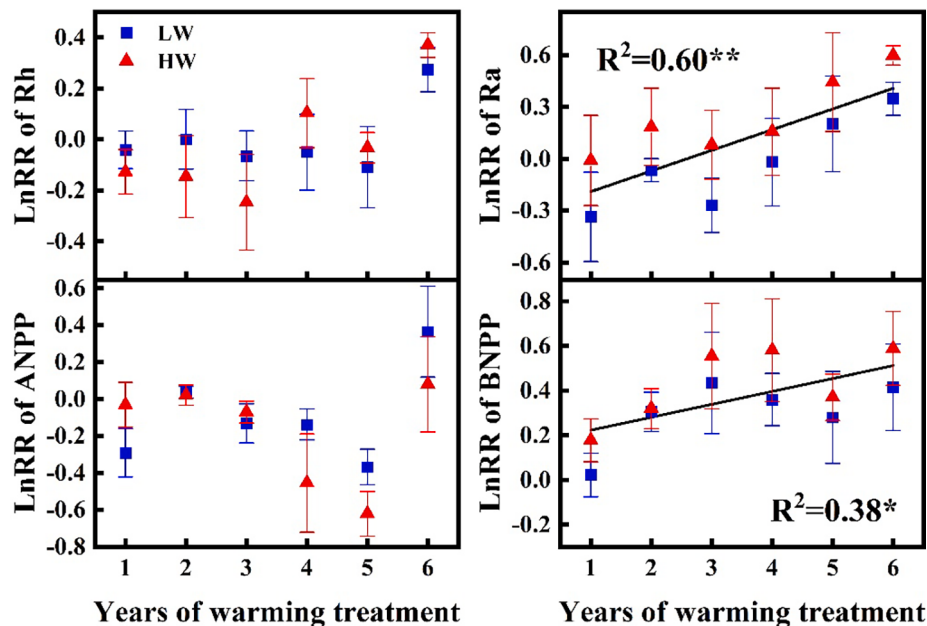


Fig. 3. Response ratio of heterotrophic respiration (Rh), autotrophic respiration (Ra), above-ground net primary production (ANPP) and below-ground net primary production (BNPP) over 6 years warming in the alpine meadow. Error bars represent $\pm$ SE. LW: low-level warming ($+1.5^\circ\text{C}$); HW: high-level warming ($+2.5^\circ\text{C}$). * , ** , *** represents the statistical significance was at the level of $P < 0.1$, 0.05 , 0.01 , and 0.001 , respectively.

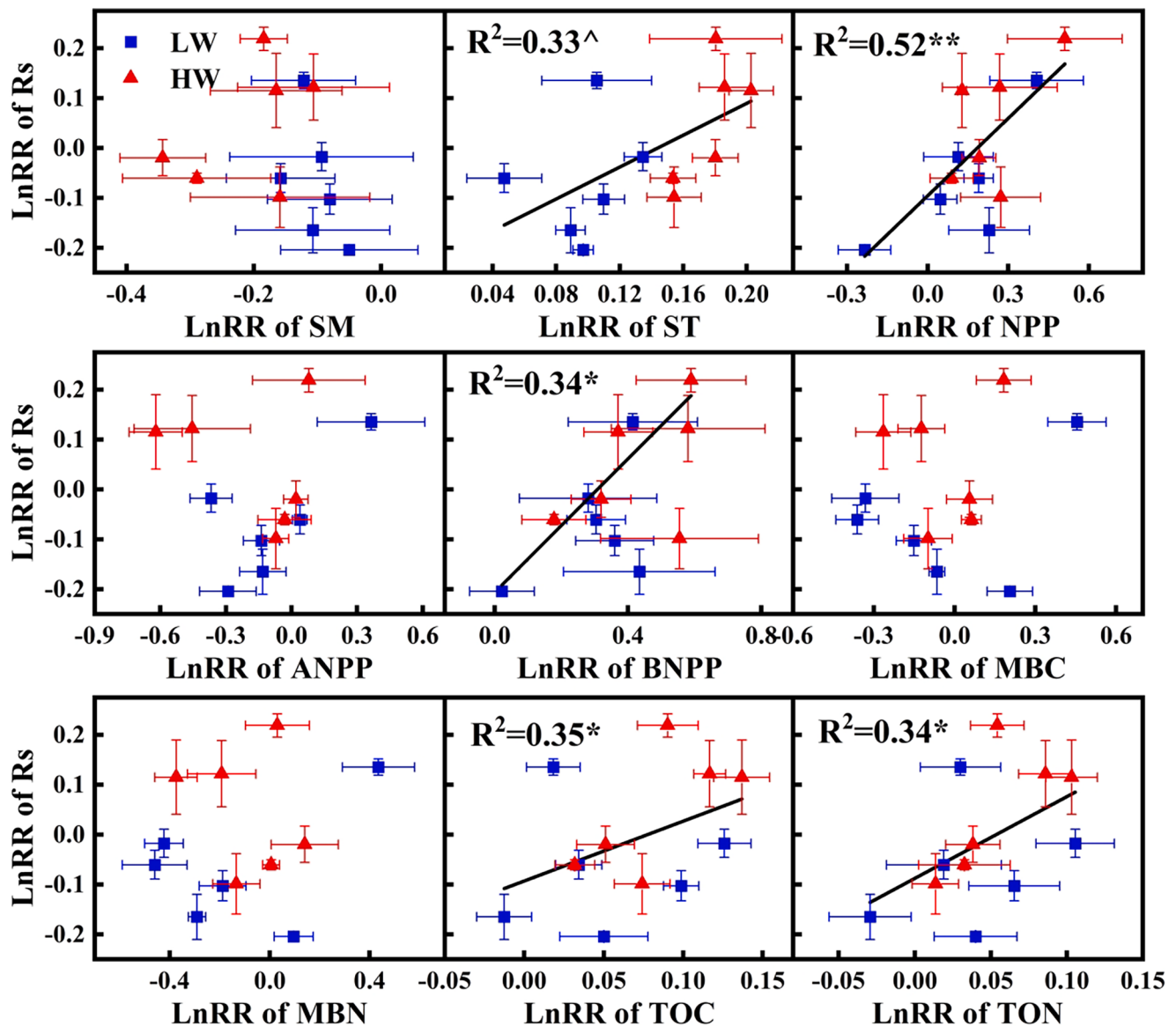


Fig. 4. Relationships of the response ratio of soil respiration (Rs) with warming-induced changes in soil moisture (SM), soil temperature (ST), net primary production (NPP), above-ground net primary production (ANPP), below-ground net primary production (BNPP), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), soil total carbon (TOC) and soil total nitrogen (TON) over the 6-year warming treatments. Error bars represent $\pm$ SE. LW: low-level warming ($+1.5$ °C); HW: high-level warming ($+2.5$ °C). ^, *, **, *** represents the statistical significance was at the level of $P < 0.1$, 0.05 , 0.01 , and 0.001 , respectively.

aboveground NPP, belowground NPP and MBC (Fig. S8).

4. Discussion

Based on a 6-year field warming experiment in an alpine meadow, we found that the responses of soil respiration to warming shifted from negative to positive and continually increased over the years. This indicates that conclusions based on short-term experiments may bias warming impacts in this ecosystem. The time-series of soil respiration responses was mainly due to the continuous stimulation of NPP over time. Consistently, we found that warming also continuously increased soil respiration and NPP in the global grasslands in the long-term when we synthesized results from 48 other warming experiments with the longest duration of 19 years. The responses of soil respiration were also positively correlated with warming-induced stimulation of NPP. These results suggest that the larger efflux of soil C under warming in grasslands is offset by the warming-induced increase in C assimilation and thus reduces the anticipated positive feedback between the terrestrial C

cycle and climate change.

5. Soil respiration responses to long-term warming

In the long-term warming experiment in the alpine meadow, the response of soil respiration to warming varied largely over the years (Fig. 1), with warming effects on soil respiration being continuously increasing (Fig. 2). The negative response in the first three years may be due to the lower soil moisture (Fig. 1 and Fig. S2). Some previous studies also demonstrated that the responses of soil C efflux to warming depend on soil moisture (Niu et al., 2008; Quan et al., 2019; Wang et al., 2020; Xu et al., 2015). Soil moisture could either offset or exacerbate direct warming effects on soil respiration. For example, warming could increase soil respiration by stimulating microbial activities (Bond-Lamberty et al., 2018), increasing the quantity and quality of soil organic matter (Melillo et al., 2017), shifting the microbial community toward more fungi (Wan et al., 2005), and increasing the allocation of photosynthate toward belowground (Yan et al., 2021). However, this

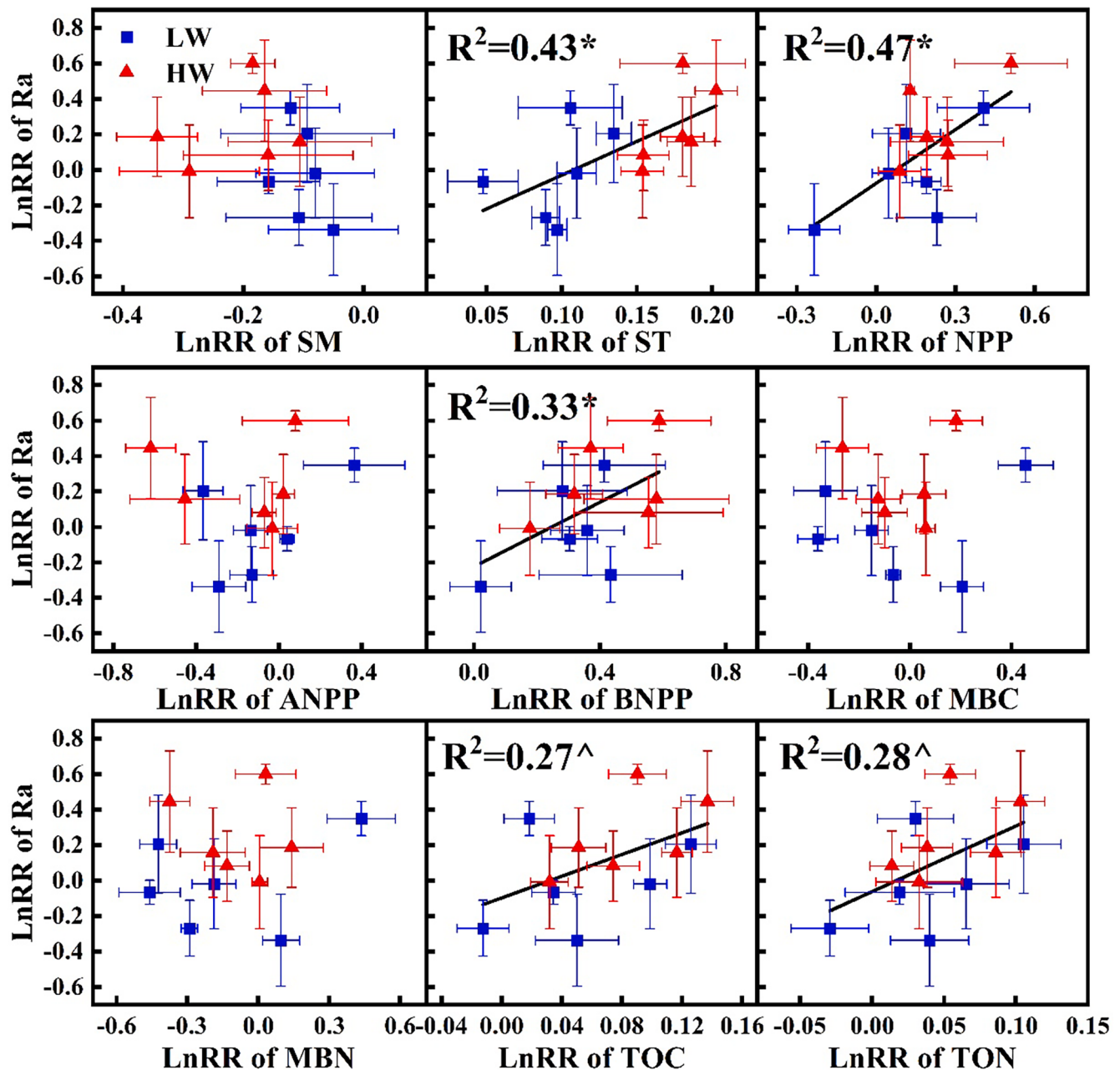


Fig. 5. Relationships of the response ratio of autotrophic respiration (Ra) with warming-induced changes in soil moisture (SM), soil temperature (ST), net primary production (NPP), above-ground net primary production (ANPP), below-ground net primary production (BNPP), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN) over the 6-year warming treatments. Error bars represent $\pm$ SE. LW: low-level warming ($+1.5$ °C); HW: high-level warming ($+2.5$ °C). ^, *, **, *** represents the statistical significance was at the level of $P < 0.1$, 0.05 , 0.01 , and 0.001 , respectively.

enhancement could be constrained by warming-induced soil water deficits (Niu et al., 2008; Wan et al., 2002; Wan et al., 2007). Hence, the lower soil moisture could offset the direct positive effects of warming on soil respiration. Under sufficient soil moisture conditions, these offset effects may not exist, so warming could stimulate soil respiration under sufficient soil moisture conditions. Moreover, the continued increase in soil respiration under warming was also observed in global synthesis over time (Fig. 5), which supports the similar findings in an alpine meadow and a tallgrass prairie (Peng et al., 2020; Xu et al., 2015), but extends to the global scale for the first time. These sustained increases in soil respiration under warming may be directly caused by the increased soil temperature (Figs. 4 and 7), which could stimulate higher activity of soil microorganisms (Melillo et al., 2002) and accelerate the metabolism of microbes and root exudation (Luo et al., 2009), as well as increase the

belowground C input (Figs. 4 and 7), and thus increasing heterotrophic respiration and autotrophic respiration. However, in this study, warming continuously stimulated autotrophic respiration but did not significantly change heterotrophic respiration over time, suggesting that the warming-induced sustained increase in soil respiration was mainly contributed by the warming responses of autotrophic respiration. The abundant C supply (Dacal et al., 2020; Melillo et al., 2002), stimulation of plant growth (Xu et al., 2015) and nitrogen mineralization and availability (Peng et al., 2020; Zhou et al., 2006) under warming also support the sustained increase in soil respiration.

Additionally, changes in temperature in global change experiments may trigger a hierarchy of mechanisms with a temporal pattern of responses beginning with small physiological and microenvironmental changes followed by large changes due to plant and microbial species

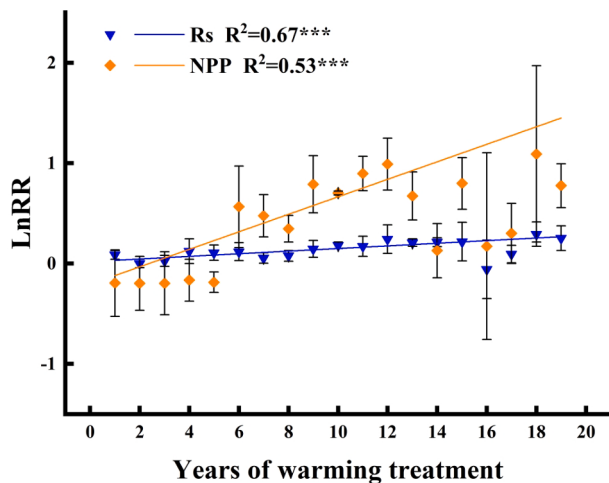


Fig. 6. Response ratio of soil respiration (Rs) and net primary production (NPP) over warming duration in world grasslands (data from the *meta-analysis*). Error bars represent 95% confidence intervals.

reorganization (Andresen et al., 2016; Melillo et al., 2017; Xu et al., 2015). The global *meta-analysis* results strongly support these mechanisms since warming-induced changes in soil respiration are positively correlated with changes in soil moisture, soil temperature, NPP, MBC, MBN, TOC and TON (Fig. 7). The continued increase in warming effects on soil respiration over time provides experimental evidence that soil respiration continues to rise under global warming in grasslands, and indicates the potential for intensifying global warming.

In contrast to our results, however, a previous field experiment showed that increases in soil respiration under warming diminished within a few years in a temperate forest (Melillo et al., 2002), mainly due to the substantial loss of soil C (1510 g C/m^{-2} (–|–), 17 %) across the full soil profile over the 26-year study (Melillo et al., 2017) and a reduction in microbial biomass (Bradford et al., 2008). However, our field experiment showed that warming increased SOC after 6 years of warming (Yan et al., unpublished), mainly attributed to the warming-induced increase in C input (Figs. 4 and 7) and the unchanged microbial biomass (Table 1 and Fig. 1), thereby continuously increasing soil respiration. Therefore, the difference in substrate availability to microbes under warming in these two ecosystems may explain the discrepancy, which suggests the importance of C input and availability on soil microbial-mediated C-cycle-climate feedbacks.

Our findings also implied that short-term responses of soil respiration to warming differ from long-term responses. Most published studies focus on soil respiration dynamics over short-term warming (Wang et al., 2019), making it difficult to gain insights into long-term soil respiration changes. The time-series intensified warming effects on grassland soil respiration indicate that previous assessments based on short-term experiments may underestimate the positive warming effects on soil C release. Hence, it is difficult to elucidate the soil C dynamics in the short-term duration of manipulative experiments (Lu et al., 2013). Moreover, without long-term observations, the complex mechanisms regulating the feedback between the terrestrial C cycle and climate change cannot be quantified, and models that incorporate the role of soil in C feedbacks to climate change cannot be tested (Melillo et al., 2017). Therefore, long-term manipulative experiments are urgently needed to better understand the responses of soil C to global warming (Andresen et al., 2016).

6. Increasing carbon input supports a sustained increase in soil respiration under long-term warming

A recent global *meta-analysis* across all grassland types demonstrated

that experimental warming stimulated NPP by an average of 15.4 % (Wang et al., 2019). By considering the temporal dynamics of the responses, we revealed that NPP continuously increased with warming over time at the alpine meadow site (Fig. 2). Consistently, the continued increase in NPP over time was also reported in alpine meadow and tallgrass prairie ecosystems (Luo et al., 2009; Quan et al., 2020; Wu et al., 2011; Xu et al., 2012; Xu et al., 2013). Furthermore, this pattern was revealed to be universal for all grasslands when we synthesized long-term NPP responses from 48 other warming experiments conducted in grasslands (Fig. 6). Moreover, in line with a previous global *meta-analysis* (Wu et al., 2011), experimental warming continuously increased belowground NPP but did not significantly change aboveground NPP over years, both in our field experiment and global synthesis, suggesting that the continuous increase in NPP under warming was mainly contributed by belowground NPP. These findings suggest that climate warming will increase grassland C uptake, especially the potential for additional soil C storage.

Warming may favor plant photosynthesis and growth by alleviating enzymatic limits on the biochemistry (Reich et al., 2018), and thus increasing the rates of CO_2 assimilation. Moreover, the stimulation of NPP under long-term warming may also be attributable to the enhancing N mineralization (Liu et al., 2017), changing plant species and functional type (Lin et al., 2010; Xu et al., 2015), increasing plant nutrient fixation and use efficiency (Chen et al., 2020; Rustad et al., 2001) and prolonging the growing season (Sherry et al., 2007). In contrast, NPP was reported to decrease under experimental warming in some ecosystems, such as semiarid and arid grasslands, which are primarily water-limited (Figure S9) (Harte and Shaw, 1995; Klein et al., 2007; Niu et al., 2008; Walker et al., 2006). Warming-induced atmospheric and soil water deficits can constrain the growth of plants and trigger their physiological responses to warming, generally suppressing plant physiological activity (Niu et al., 2008; Wang et al., 2019). In this study, however, the field experiment site and the collected studies, especially the long-term warming experiments, are mostly within the ecosystems with relatively more precipitation, such as alpine meadows and tallgrass prairies (Luo et al., 2009; Peng et al., 2020; Xu et al., 2015; Yan et al., 2021), and thus supporting the continuous increase in NPP under long-term warming. The difference in soil moisture between these ecosystems may cause this discrepancy, as warming could increase the grassland C assimilation rate in nonwater-limited habitats (Guo et al., 2018) but reduce plant productivity in arid regions (Klein et al., 2008). In addition, plant community structure shifts toward to high temperature and drought tolerance under long-term warming, such as C_4 species with higher water use efficiency than C_3 species increased under long-term warming in tallgrass prairie (Niu et al., 2013; Wan et al., 2005; Xu et al., 2015), thus supporting the sustained increase in NPP. Therefore, soil moisture should be considered as a key factor for the responses of NPP to global warming.

The positive relationship between the response of soil respiration and the warming-induced increase in NPP found in our field study in the alpine meadow (Fig. 4) is applicable to other grasslands around the world (Fig. 7). It has long been recognized that soil respiration positively correlates with ecosystem production across years (Raich and Schlesinger, 1992). Our results suggest that this mechanism holds true under long-term experimental warming. Greater plant productivity generally yields more roots and litter, and thus stimulates soil respiration by increasing autotrophic respiration (Fig. S5 and S8) from plant root physiological activities (Liu et al., 2017) and heterotrophic respiration (Fig. S6 and S9) from microbial decomposition (Xu et al., 2015). Increased NPP could also lead to a priming effect (Moore et al., 2020) and mobilization of protected soil C in metal-organic complexes (Keiluweit et al., 2015), leading to stimulation in soil respiration under warming (Pries et al., 2016). Moreover, as root respiration is a primary contributor to soil respiration (Zhou et al., 2007), the larger amount of photosynthetic C allocated to belowground under warming may stimulate soil respiration (Yan et al., 2021). Our results strongly support this

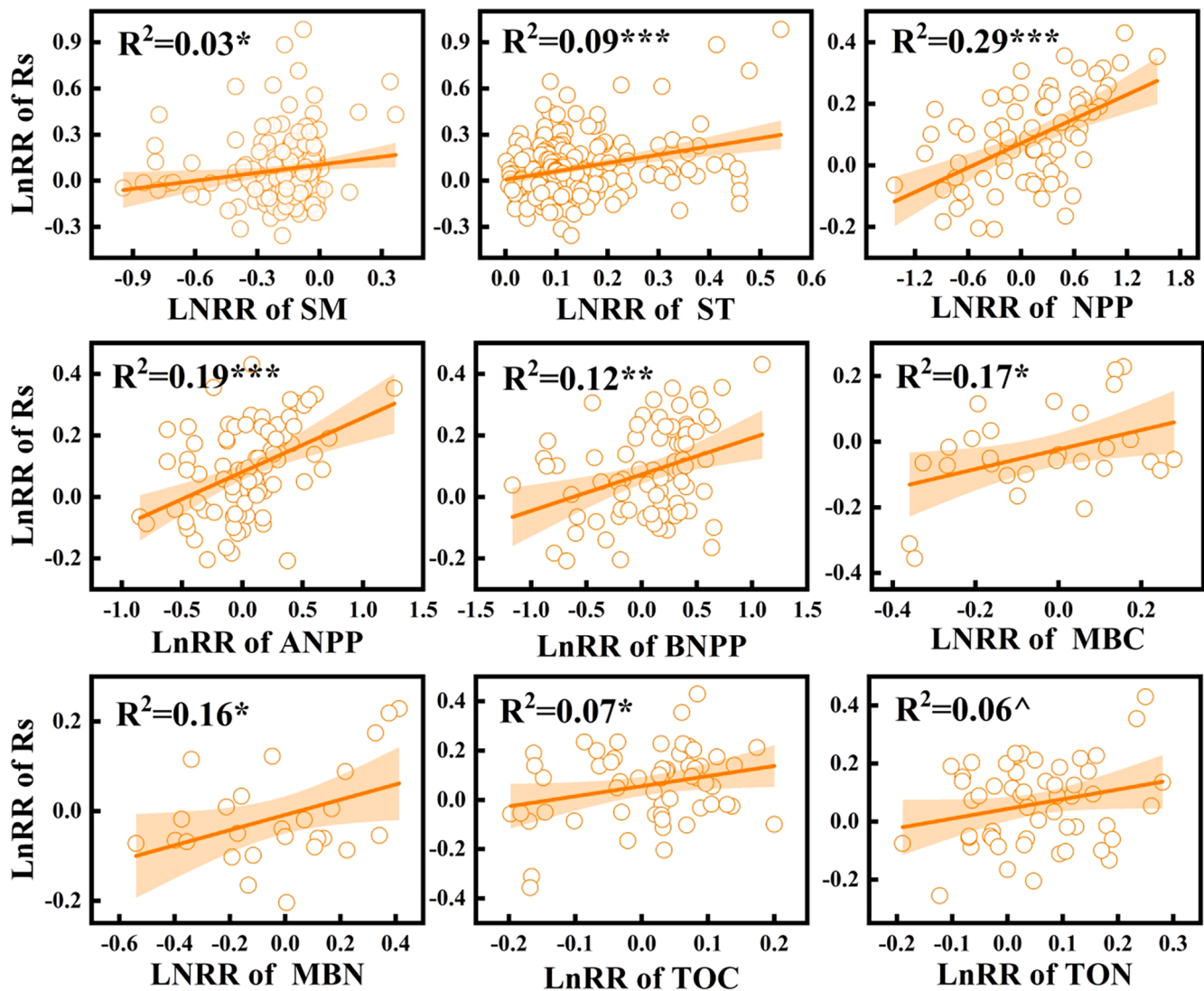


Fig. 7. Global synthesis of relationships between warming-induced changes in soil respiration (Rs) and warming-induced changes in soil moisture (SM), soil temperature (ST), net primary production (NPP), above-ground net primary production (ANPP), below-ground net primary production (BNPP), microbial biomass C (MBC), microbial biomass N (MBN), soil total carbon (TOC) and soil total nitrogen (TON) in grasslands over years (data from the *meta-analysis*). ^, *, **, *** represents the statistical significance was at the level of $P < 0.1$, 0.05, 0.01, and 0.001, respectively.

mechanism, since the sustained increase in soil respiration was mainly contributed by autotrophic respiration, which was closely correlated with the continuous increase in belowground NPP (Fig. 5 and Fig. S7). The synchronized responses of soil respiration and NPP suggest that warming-stimulated respiratory C release is primarily driven by increased C input from plant production. Hence, the temporal dynamics of soil respiration cannot be fully evaluated in isolation without considering plant interactions under long-term warming.

7. Implications

The time-series intensified warming effects on grassland soil respiration (Figs. 2 and 6) suggest that long-term warming could trigger a substantial loss of soil C. However, the simultaneous increases in NPP would offset the increases in soil C efflux, thus discounting the expected positive terrestrial C-climate feedback. In contrast, multiple previous studies on the responses of soil respiration to warming all suggest that the warming-induced stimulation of soil respiration would disappear in long-term warming due to the depletion of soil C (Dacal et al., 2020; Melillo et al., 2017; Peng et al., 2020). This discrepancy may be mainly

attributed to the fact that these studies ignored the critical role of plant community productivity in the regulation of ecosystem C-cycle feedback to climate warming. Notably, respiratory C release is tightly coupled with ecosystem C uptake (Figs. 4 and 7). The increase in C input potentially offset the soil C efflux from the sustained increase in soil respiration under long-term warming. Therefore, the C release from soil may be overestimated when the increase in C input is not considered under long-term warming in grasslands.

The linear correlation between the warming-induced changes in soil respiration and those of NPP suggests that experimental warming may accelerate ecosystem C cycling via stimulation of both C uptake and release without much impact on net ecosystem C storage in grassland. These results provide limited support for the positive C-climate feedback under future climate warming scenarios, as predicted by Earth System Models (ESMs) (Arora et al., 2020; Friedlingstein et al., 2006), and suggest that ESMs need to consider the increased C turnover rate. Moreover, most of the coupled C-climate models are primarily based on the kinetic sensitivity of C uptake and release processes to temperature (Cox et al., 2000; Friedlingstein et al., 2006). Our study indicates that except for C uptake and release kinetics, the regulation mechanisms via

changes in plant growth and community activity must be considered in future climate and ecosystem projections (Luo, 2007; Luo et al., 2009; Xu et al., 2015). To date, however, there is still limited understanding of changes in vegetation dynamics and ecosystem states under climate warming (Luo et al., 2014; Wenzel et al., 2014). Future observational and experimental research should focus on the less predictive components of terrestrial ecosystems to better understand, simulate and predict ecosystem C cycling in response to climate warming.

In summary, our results from the 6-year warming experiment and global meta-analysis all suggest that warming effects on soil respiration increased with warming duration, as did NPP. Warming-induced changes in soil respiration positively coupled with warming-induced increases in NPP. Notably, the sustained increase in soil respiration over the years was mainly contributed by autotrophic respiration, which was positively correlated with the continuous increase in belowground NPP. Our results, therefore, suggest that the continuous increase in soil respiration under warming, which may trigger a large efflux of soil C and a possible positive feedback between the terrestrial C cycle and climate change, is counteracted by the concomitant increase in NPP under global warming. Overall, our results highlight the need to incorporate the role of NPP in modeling soil CO₂ emissions, aiming to better forecast C cycling in grasslands and its feedback to climate warming.

Data accessibility statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2022.116157>.

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