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Warming has a minor effect on surface soil organic carbon in alpine meadow ecosystems on the Qinghai–Tibetan Plateau

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Abstract

The alpine meadow ecosystem on the Qinghai–Tibetan Plateau (QTP) is very sensitive to warming and plays a key role in regulating global carbon (C) cycling. However, how warming affects the soil organic carbon (SOC) pool and related C inputs and outputs in alpine meadow ecosystems on the QTP remains unclear. Here, we combined two field experiments and a meta-analysis on field experiments to synthesize the responses of the SOC pool and related C cycling processes to warming in alpine meadow ecosystems on the QTP. We found that the SOC content of surface soil (0–10 cm) showed a minor response to warming, but plant respiration was accelerated by warming. In addition, the warming effect on SOC was not correlated with experimental and environmental variables, such as the method, magnitude and duration of warming, initial SOC content, mean annual temperature, and mean annual precipitation. We conclude that the surface SOC content is resistant to climate warming in alpine meadow ecosystems on the QTP.

KEYWORDS
alpine meadow, climate warming, meta-analysis, plant respiration, soil organic carbon, surface soil

1 | INTRODUCTION

Since the industrial revolution, global surface air temperature has increased by 0.8°C, which is mainly attributed to a large amount of fossil fuels have been burned by anthropogenic activities (IPCC, 2013). According to IPCC (2013), the global surface air temperature will increase by 1.1–4.8°C by the end of this century. This unprecedented climate warming will not only affect the adaptation strategies of aboveground vegetation (Lim et al., 2019; Liu et al., 2018; Rustad et al., 2001; Wang et al., 2020), but also profoundly regulate the belowground processes of terrestrial ecosystems (Carrillo et al., 2018; Chen et al., 2020; Hursh et al., 2017; Johnston & Sibly, 2018; Knorr et al., 2005; Wang, Dong, et al., 2014). Soil is the largest carbon pool in terrestrial ecosystems. Approximately 1500 Pg (10^{15} g) C is stored in soil (0–100 cm depth), which is about two times the size of the atmospheric carbon pool (760 Pg) and three times the size of the terrestrial plant carbon pool (500 Pg) (Lal, 2004; Schmidt et al., 2011). The annual flux of carbon out of soils is about 60–80 Pg and is six to eight times greater than the carbon emissions produced by human activities (Bond-Lamberty & Thomson, 2010; Schlesinger & Andrews, 2000). Thus, even a small change in the soil carbon pool (e.g., increased respiration from soil) could result in a large effect on the atmospheric carbon dioxide (CO_2) concentration, and further intensify global climate warming with positive feedbacks. Therefore, the response of SOC pool to warming plays a key role in the global C cycling (Nottingham et al., 2020).

There is considerable concern that warming will change the SOC pool and regulate ecosystem C cycles (Crowther et al., 2016; Melillo et al., 2017; Nottingham et al., 2020; Pries et al., 2017). Therefore, a large number of simulated warming experiments have been set up to investigate the responses of SOC content. These experiments have shown that soil C is vulnerable (Jia et al., 2019; Nottingham et al., 2020; Walker et al., 2018; Wu et al., 2017) or resistant (Sistla et al., 2013; Yuan et al., 2021; Yu et al., 2015) to climate warming in various ecosystems (e.g., alpine grassland, tropical forest, and arctic tundra). The inconsistent responses of SOC to warming are related to the differential responses of soil C inputs and outputs to warming, while the SOC pool is determined by C inputs from plant detritus (mainly from dead plant biomass) as well as C outputs from SOC decomposition caused by soil microbes (soil heterotrophic respiration) (Chen et al., 2020; Pries et al., 2017). For C inputs, the shifts in plant biomass could alter SOC pool. Climate warming could significantly affect vegetation photosynthesis, and aboveground and belowground net primary productivity (Dusenge et al., 2019; Loik et al., 2000; Wu et al., 2017). As a consequence, plant biomass (including aboveground and belowground biomass) is relatively sensitive to warming (Lin et al., 2010; Wang et al., 2020). However, the responses of plant biomass to warming can be positive (Day et al., 2008; Sardans et al., 2008), negative (Hollister & Flaherty, 2010; Zong et al., 2018), and neutral (Lim et al., 2019; Ma et al., 2017) in different studies. For C outputs, the SOC pool may be balanced by the C emission from soils through microbial decomposition. Moreover, soil respiration (including autotrophic respiration and heterotrophic respiration) is the second largest terrestrial C flux (Bond-Lamberty & Thomson, 2010). Therefore, the responses of soil microbial community to warming would regulate the SOC dynamics by microbial decomposition. In addition, the sum of aboveground plant respiration and belowground soil respiration is ecosystem respiration. Thus, these processes of C cycling together play a key role in regulating the SOC pool in response to warming (Carey et al., 2016; Haaf et al., 2021; Wang, Liu, et al., 2014).

The Qinghai–Tibetan Plateau (QTP) is the largest plateau in China and the highest plateau in the world with an average elevation more than 4000 m (Piao et al., 2019). It is called the “roof of the world” and “the third pole,” covering an area of approximately 2.5 million square kilometers. In the past 50 years, the QTP is one of the most remarkable areas of climate warming which had a double warming rate (0.3–0.4°C per decade) compared to global average, and its temperature will continue to increase in this century (Chen et al., 2015). The QTP stores a large amount of SOC with 7.4 Pg C in the top 1 m depth (Yang et al., 2008). Alpine meadow is one of two main vegetation types and stores more than 60% (4.7 Pg C in the top 1 m depth) of the total SOC on the QTP (Yang et al., 2008). Moreover, the alpine meadow ecosystem on the QTP is fragile and prone to degradation due to climate warming (Piao et al., 2019). Therefore, it is also a key area to study the responses of SOC to climate warming. As a consequence, many field warming experiments have been conducted in alpine meadow ecosystems on the QTP to study the effects of warming on terrestrial ecosystem processes, especially SOC dynamics (e.g., Chang et al., 2021; Jia et al., 2019; Li et al., 2020). Nonetheless, the general patterns of how climate warming affects the SOC pool and related C inputs and outputs in alpine meadow ecosystems on the QTP remain unclear.

In this study, we used two field warming experiments and a meta-analysis to investigate the mechanisms underlying the effects of warming on the SOC pool and related C inputs and outputs in alpine meadow ecosystems on the QTP. In the field warming experiments, we evaluated the responses of main variables related to the SOC pool to warming. These variables are related to inputs and outputs of C to/from soils, including aboveground biomass (AGB), belowground biomass (BGB), SOC, and microbial biomass carbon (MBC). Also, a meta-analysis was used to determine the effects of warming on variables related to soil C pools and fluxes (Rs, soil respiration; Rh, heterotrophic respiration; Ra, autotrophic respiration; ER, ecosystem respiration; ANPP, aboveground net primary productivity; BNPP, belowground net primary productivity). Therefore, results from this study combining field observations and meta-analysis could effectively improve the ability to predict the SOC dynamics under warming in the future. Specifically, the objectives of this study are to (1) explore the responses of the SOC pool and related C inputs and outputs (pools and fluxes) to warming; and (2) examine how environmental and experimental variables affect the responses of SOC to warming in alpine meadow ecosystems on the QTP.

2 | MATERIALS AND METHODS

To investigate the mechanisms underlying the effects of warming on SOC in alpine meadow ecosystems on the QTP, we used two field warming experiments and a meta-analysis (Table 1). First, we tested the response of SOC to multiple levels of warming by a 6-year field warming experiment (study 1). Then, to understand the response of SOC to long-term warming, we further used a 20-year field warming

TABLE 1 Summary of two field warming experiments and the meta-analysis related to warming experiments in alpine meadow ecosystems on the Qinghai–Tibetan Plateau. The “case” indicates a specific combination of method, magnitude, and duration of warming for the experiments in study 3

Study	Study type	Ecosystem	Soil layers (cm)	Magnitudes (°C)	Durations (year)	Number of cases
1	Case study	Alpine meadow	0–10	0.42/0.62/0.76/1.26	7	—
2	Case study	Alpine meadow	0–10	1.30–2.00	20	—
3	Meta-analysis	Alpine meadow	0–10	—	—	381

experiment (study 2). The two field warming experiments (study 1 and 2) were located about 200 m apart with similar climate and edaphic conditions (but slightly different plant community composition and biomass). Finally, to quantify the general patterns of how warming affects the SOC pool and related soil C inputs and outputs, we conducted a meta-analysis (study 3) to synthesize the responses of these variables to warming in multiple alpine meadow ecosystems across the QTP.

2.1 | Study site

The two field warming experiments were located at the Haibei National Field Research Station of Alpine Grassland Ecosystems (37°29′–37°45′N, 101°12′–101°23′E, 3250 m a.s.l.), northeast of the QTP, Menyuan county, Qinghai province, China. This area has a typical plateau continental climate with a long cold season (non-growing season, from October to April, 7 months) and a short warm season (growing season, from May to September, 5 months). The mean annual temperature (MAT) is −1.2°C, with the maximum temperature of 9.9°C in July and the minimum temperature of −15.2°C in January. The mean annual precipitation (MAP) is 489 mm, approximately 80% of which is concentrated in the growing season from May to September. Alpine meadow is the main vegetation type in this area. The area of alpine meadow accounts for more than 44% of the area of alpine grasslands, and its SOC storage accounts for 56% of the SOC storage of alpine grasslands on the whole QTP (Yang et al., 2008). The soil in the alpine meadow is classified as Mat-Cryic Cambisol (Hou et al., 2019). The alpine meadow is dominated by *Kobresia humilis*, *Stipa aliena*, *Elymus nutans*, and other herbaceous plants (Liu et al., 2018; Ma et al., 2017).

2.2 | Field experiments

2.2.1 | Study 1: Multi-level warming experiment

The multi-level warming experiment was established in the alpine meadow in July 2011, within a fenced 50 × 50 m^2 flat area. It consisted of 25 plots (2 m buffer zone between each plot), with five temperature treatments (ambient temperature and four year-round warming treatments from W1 to W4), and 5 replicates. These plots (unclipped and ungrazed) were distributed into the area which was divided into five columns and five rows using a random block design. Four types of open top chambers (OTC, conical, with same height 40 cm but different diameters) were constructed to simulate four levels of warming treatments. Both air temperature and soil temperature were increased by these four types of OTC treatments (W1–W4). Mean air temperature at 10 cm height aboveground was enhanced by 0.48, 0.60, 0.87 and 1.20°C in these plots, respectively. Mean soil temperature at 10 cm depth belowground was increased by 0.42, 0.62, 0.76, and 1.26°C in these plots, respectively (Figure S1). A complete description of this experimental design was described in Shi et al. (2017).

2.2.2 | Study 2: Long-term warming experiment

The long-term warming experiment was conducted in the alpine meadow in September 1997, within a fenced 30 × 30 m^2 flat area (with low grazing history). In this area, eight open top chambers (OTCs) were randomly placed to simulate warming treatments and outside of OTCs was considered as ambient treatments. Thus, there were two levels of warming treatments (ambient and warming treatments, eight replicates). Half of the warming and ambient plots had been clipped to simulate grazing until 2008, and all plots were not clipped since then. The OTCs were 1.5 m in diameter, 40 cm in height, and remained on the plots year-round. According to previous studies, the OTCs consistently elevated mean air temperature at 10 cm height aboveground by 1.0–2.0°C in the growing season, while also elevated mean soil temperature at 10 cm depth belowground by 1.3–2.0°C in the growing season (Table S1 and Figure S2) (Zhang et al., 2017). Klein et al. (2004) and Zhang et al. (2017) provided a detailed description of this warming experiment design.

2.3 | Plant and soil sampling and properties analysis

Aboveground biomass (0.5 × 0.5 m, randomly chosen within each plot) of 25 plots (ambient and four levels of warming treatments, five replicates) was harvested from study 1 in September 2017, oven-dried at 65°C to constant weight and weighed. In the meantime, surface soil samples (0–10 cm) near the plot center were collected using a soil corer (5 cm diameter) in study 1. In study 2, we chose five of the eight replicates which were well maintained (little damage to OTC fiberglass) for sampling. An earlier study (Yu et al., 2015) that sampled soils in all eight replicates in September 2013 reported no difference in SOC (0–10 cm) between ambient and warming treatments. The AGB of these 10 plots (five ambient and five warming) was harvested with the same method in study 1 in September 2017, oven-dried at 65°C to constant weight and weighed. Surface soil samples (0–10 cm) near the plot center were also collected using a soil corer (5 cm diameter) in study 2. In both studies, soil samples collected from three soil cores in one plot were mixed into one composite soil sample. All fresh soil samples were stored at 4°C using a closed cooler covered with ice-bags and taken back to the laboratory within 24 h. Visible stones were discarded and roots were picked when all soil samples were sieved through 2 mm sieve. Living roots were dried at 65°C to constant weight and weighed to obtain BGB.

The sieved soil samples were divided into two parts: air-dried for elemental analysis and stored at 4°C refrigerator for soil microbial biomass within 3 days. Gravimetric soil water content (SWC) was measured by calculating the mass loss with oven-drying at 105°C for 48 h. Air-dried soil samples were treated with 1 M hydrochloric acid (HCl) solution to remove the carbonate and then washed to neutral with deionized water several times. Soil organic carbon (SOC) concentration was then determined with an Elemental Analyzer (Elementar vario, Langenselbold, Germany). Soil MBC was measured by chloroform-fumigation-extraction method with the extraction efficiency coefficient 0.45 (Jenkinson et al., 2004; Vance et al., 1987).

All statistical analyses for field warming experiments were performed using the R platform [version 4.0.2] (R Development Core Team, 2020). The effects of different warming levels in the multi-level warming experiment (study 1) on all variables were determined by ANOVA with LSD test (Figure 1), while the effects of warming in the long-term warming experiment (study 2) on all variables were determined by students *t* test (Figure 2). Different lowercase letters indicate significant differences under different warming magnitudes in study 1 ($p < .05$). Asterisks indicate a statistically significant difference between warming and control treatment in study 2 (*$p < .05$, **$p < .01$, ***$p < .001$).

2.4 | Meta-analysis for warming experiments in alpine meadow ecosystems across the QTP

In this meta-analysis, we collected the peer-reviewed papers published before October 1, 2021 that studied the SOC pool and related C inputs and outputs under field warming experiments in alpine meadow ecosystems on the QTP, using the Web of science (https://apps.webofknowledge.com) and the China National Knowledge Infrastructure (CNKI, https://www.cnki.net). The key words used for the article selection were: (a) Tibetan Plateau or Qinghai–Tibet Plateau or Tibet Plateau, (b) field experiment or manipulated experiment, and (c) warming or increased temperature or elevated temperature. Articles selected for this meta-analysis had to meet the following criteria: (1) The experiment was conducted in alpine meadow ecosystems on the QTP. (2) At least one of the considered 10 variables (Figure 4) was reported. (3) Control and warming treatments had to occur in the same experiment. (4) The means, standard deviations (SD) or standard errors (SE), sample sizes of the selected variables were clearly reported or could be calculated from the data of publications. (5) The warming protocols (warming method, warming magnitude, and warming duration) were directly recorded. (6) We only included the results from the surface soil (0–10 cm) because very few studies sampled deeper soils. Finally, based on these criteria, 104 articles (listed in Table S2) and two field warming experiments (study 1 and 2) were included in this meta-analysis.

The "case" indicates a specific combination of method, magnitude, and duration of warming for the experiments. The results from different warming magnitudes in the same study were considered as independent cases. In addition, to include more data in this meta-analysis, the results from multifactor studies were also included, in which the warming effects can be obtained by comparing the difference between each pair of ambient treatment and manipulated treatment (e.g., fertilization vs. fertilization and warming, Chen et al., 2020). Warming methods were divided into open-top chamber (OTC) warming, infrared heater (IH) warming, and translocated (TL, from cold to warm area) warming. Experimental durations were divided into ≤5, 5–10, and 10–20 years (Figure 5). Also, we recorded a wide range of environmental variables related to warming experiments, including longitude, latitude, altitude, mean annual temperature (MAT), and mean annual precipitation (MAP). In the end, 44 sites (Figure S4) and 381 cases (Figure S2) were included in this study. The distribution of field warming experiments in alpine meadow ecosystems on the QTP was also made (Figures S4 and S5).

We quantified the effect size of warming on each variable by calculating the natural logarithm of response ratios (RR) (Hedges et al., 1999) (Equation 1):

$$RR = \ln\left(\overline{X}_T / \overline{X}_C\right) = \ln\left(\overline{X}_T\right) - \ln\left(\overline{X}_C\right), \qquad (1)$$

where $\overline{X}_T$ and $\overline{X}_C$ are the arithmetic mean values of variables in warming and control treatments, respectively.

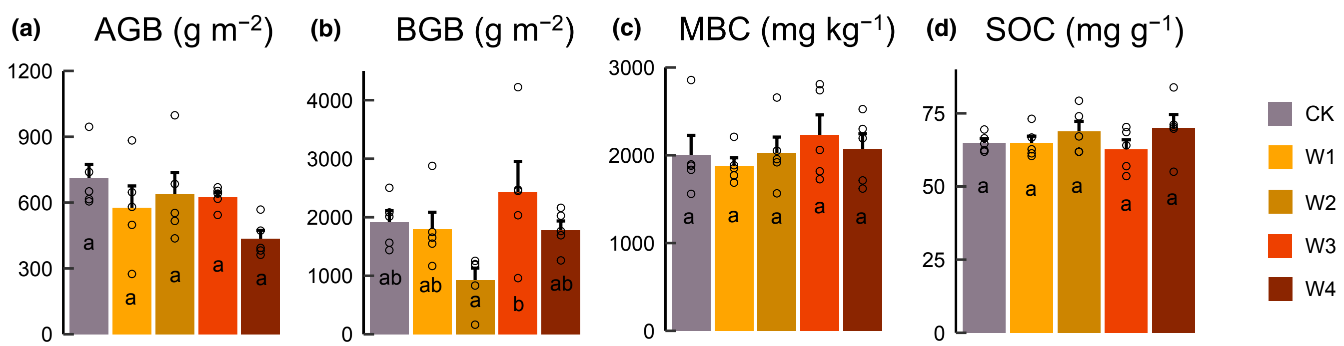

FIGURE 1 Effects of multi-level warming (CK, W1, W2, W3, and W4) on (a) aboveground biomass (AGB), (b) belowground biomass (BGB), (c) soil microbial biomass carbon (MBC), and (d) soil organic carbon (SOC) in the 6-year OTC warming experiment. Different colors mean different treatments. Bar values are the mean ± standard error. Different lowercase letters indicate significant differences under different warming magnitudes ($p < .05$) [Colour figure can be viewed at wileyonlinelibrary.com]

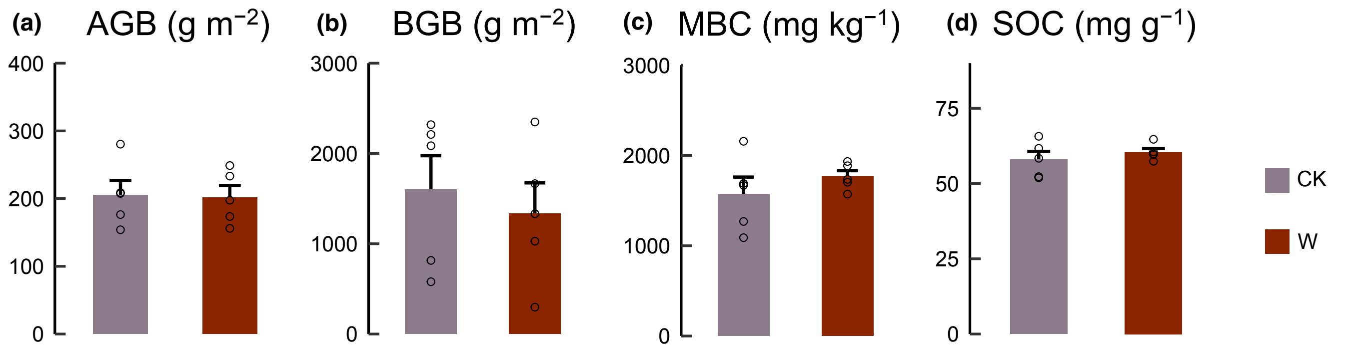

FIGURE 2 Effects of long-term warming (W) on (a) aboveground biomass (AGB), (b) belowground biomass (BGB), (c) soil microbial biomass carbon (MBC), and (d) soil organic carbon (SOC) in the 20-year OTC warming experiment. Different colors mean different treatments. Bar values are the mean ± standard error. Asterisks indicate statistically significant differences between warming and control treatment (*$p < .05$, **$p < .01$, ***$p < .001$) [Colour figure can be viewed at wileyonlinelibrary.com]

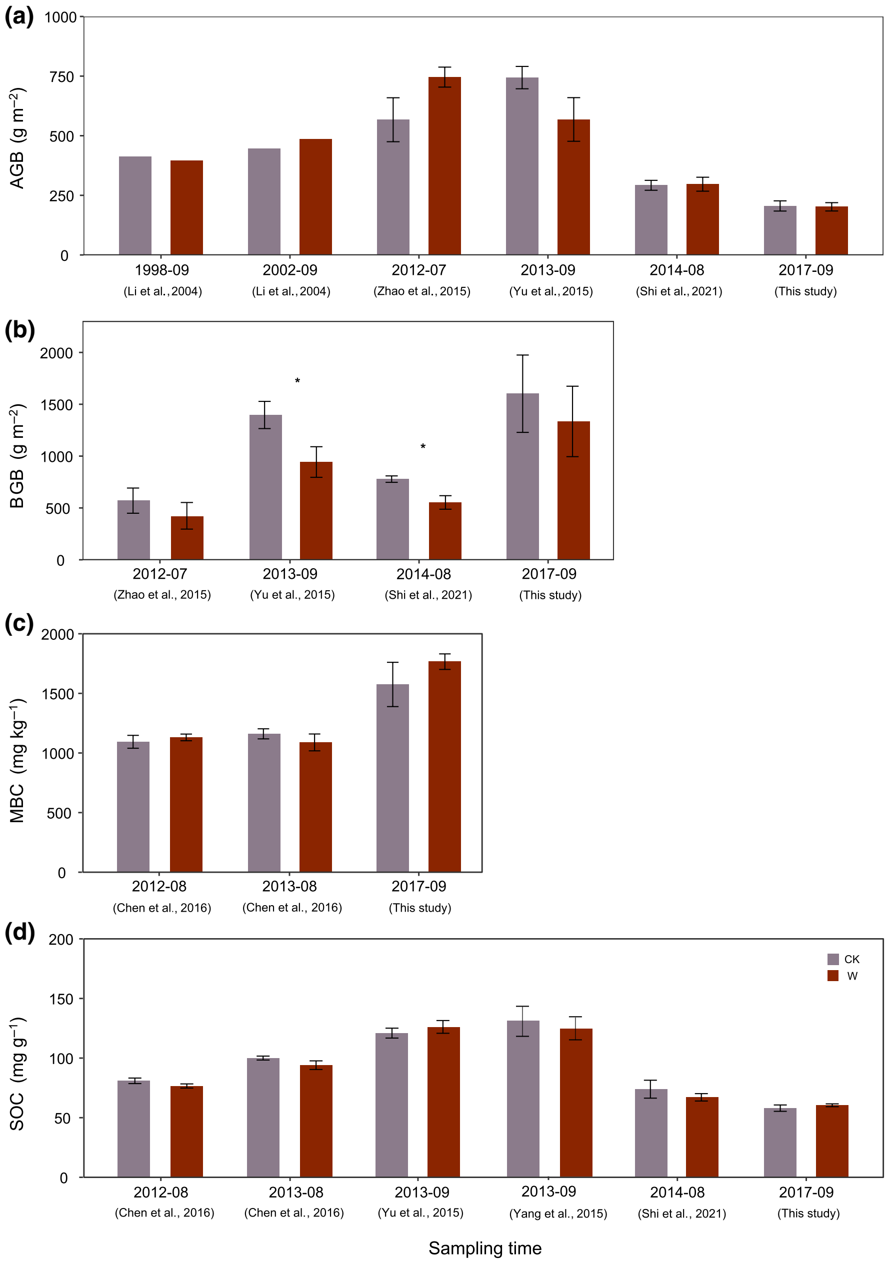

FIGURE 3 Effects of warming (W) on (a) aboveground biomass (AGB), (b) belowground biomass (BGB), (c) soil microbial biomass carbon (MBC), and (d) soil organic carbon (SOC) in the long-term OTC warming experiment. Although there were inter-annual fluctuations in the values of these four variables mainly due to different sampling and measurement methods, most of the effects of warming treatment were not significant. Parentheses below the sampling time indicate the source of the data (see Table S2 and reference list in the supplementary information). Different colors mean different treatments. Bar values are the mean ± standard error. Note that Li et al. (2004) only showed the mean value. Asterisks indicate statistically significant differences between warming and control treatment (*$p < .05$, **$p < .01$, ***$p < .001$) [Colour figure can be viewed at wileyonlinelibrary.com]

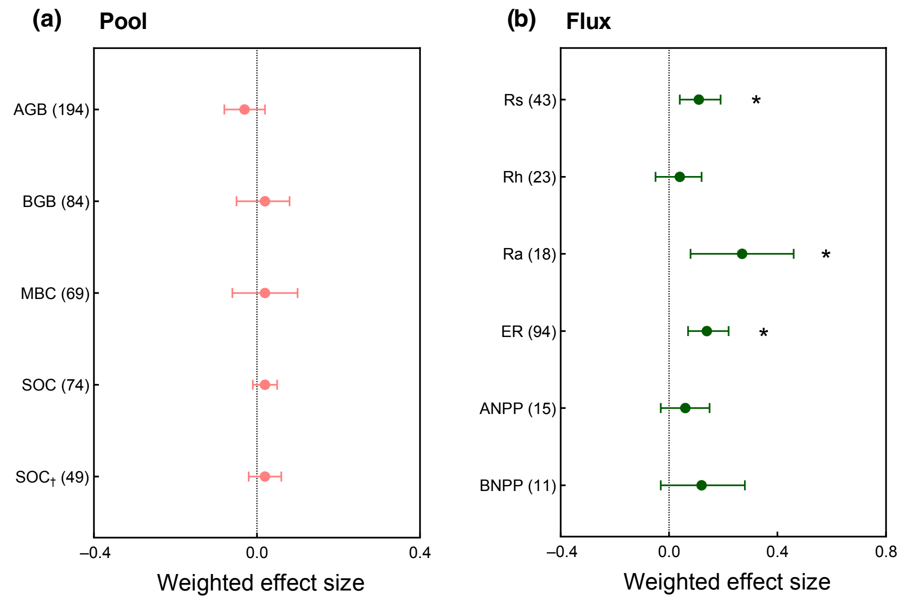

FIGURE 4 The responses of soil organic carbon (C) pool and related C (a) pools and (b) fluxes to warming in alpine meadow ecosystems on the Qinghai–Tibetan Plateau. AGB, aboveground biomass; ANPP, aboveground net primary productivity; BGB, belowground biomass; BNPP, belowground net primary productivity; ER, ecosystem respiration; MBC, microbial biomass carbon; Ra, soil autotrophic respiration; Rh, soil heterotrophic respiration; Rs, soil respiration; SOC, soil organic carbon. The "case" indicates a specific combination of method, magnitude, and duration of warming for the experiments. The cases of all variables except $SOC_{\dagger}$ were from all publications (multiple-sampling-year results), while the cases of $SOC_{\dagger}$ were only from most recent publications (latest-sampling-year results). Error bars represent 95% confidence intervals (CIs). The vertical dashed line represents the weighted effect size = 0. If the 95% CI did not overlap zero, the effect of warming was statistically significant (denoted by *). The sample size for each variable is in parentheses [Colour figure can be viewed at wileyonlinelibrary.com]

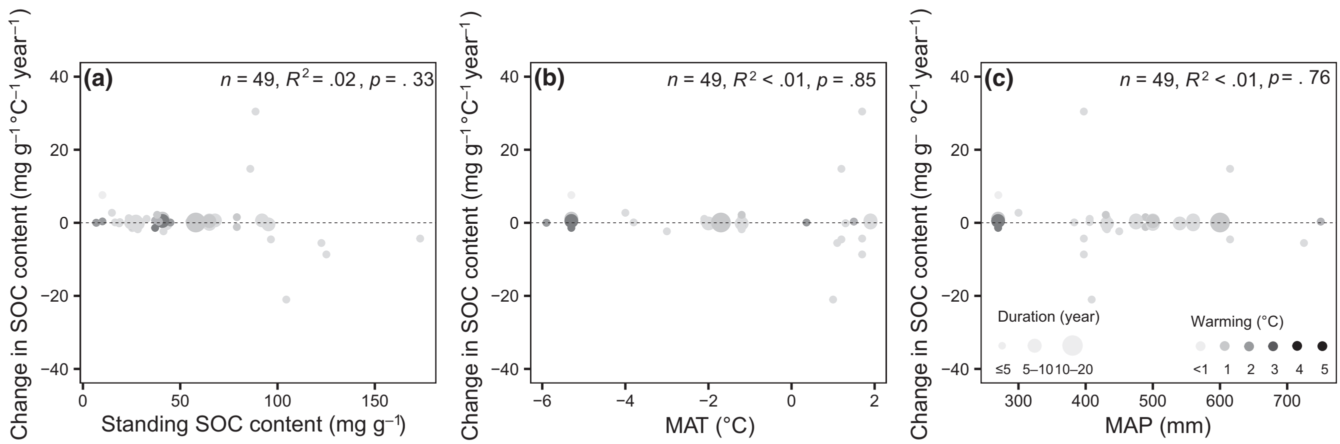

FIGURE 5 The relationships between warming-induced soil C loss (the SOC data were only from publications that contained latest-sampling-year results; $n = 49$) and environmental and soil variables (estimated using the mixed-effect model). Warming-induced changes in SOC content and standing SOC content (a), mean annual temperature (MAT, b), and mean annual precipitation (MAP, c). The size of each point means the warming duration of individual experiment, and the color of each point represents the warming magnitude of individual experiment

The variance (v) of each RR was calculated by Equation (2):

$$v = \frac{S_T^2}{N_T \overline{X}_T^2} + \frac{S_C^2}{N_C \overline{X}_C^2}, \quad (2)$$

where S_T and S_C are the standard deviations of means, N_T and N_C are the sample sizes, and $\overline{X}_T$ and $\overline{X}_C$ are the arithmetic mean values of variables in warming and control treatments, respectively.

The weighted effect size and 95% confidence interval (CI) were evaluated by random-effects model using the *rma* function from the R package "*metafor*" (Chen et al., 2020; Viechtbauer, 2010). The effects of warming were considered significant if the 95% CI did not overlap zero. Between-group heterogeneity test (Q_B) was used to examine whether different groups (e.g., warming methods) showed different responses under warming, and a significant Q_B ($p < .05$) indicated the weighted effect size differed among groups (Liu et al., 2016). The relative importance of predictors was expressed as the sum of Akaike weights for all models that included this predictor (based on mixed-effects meta-regression model), using the "*glmulti*" package in R (Calcagno & de Mazancourt, 2010). A cutoff of 0.8 was set to differentiate between nonessential and important predictors (Calcagno & de Mazancourt, 2010; Chen et al., 2020; Terrer et al., 2016). The regression analyses were used to determine the relationship between response ratios of warming and predictor variables. In addition, regression analyses were conducted to show the relationships between RR of SOC pool and RR of C inputs or outputs. Finally, we fitted linear mixed-effects models to evaluate soil C losses due to warming with environmental (MAT and MAP) and soil variables (standing SOC content) ($n = 49$, data from study 1 to –3, Figure 5). All statistical analyses were performed using the R platform [version 4.0.2] (R Development Core Team, 2020). The statistical significance was set at $p < .05$. The R script and database of study 3 (meta-analysis) were deposited at https://github.com/yancypku/meta-analysis.

3 | RESULTS

3.1 | Experimental warming effects on C pools and fluxes

In the multi-level warming experiment, AGB, soil MBC, and SOC were not significantly affected by different warming levels (W1–W4) under 6 years of warming ($p > .05$, Figure 1). The SOC content in control (CK), W1, W2, W3, and W4 treatments is 65.0, 64.9, 68.8, 62.7, and 70.0 mg g^{-1}, respectively (Figure 1d). In addition, BGB did not show significant difference between CK and warming treatments (W1–W4), while the value of BGB in W3 was significantly higher compared with W2 ($p < .05$, Figure 1b). Similarly, the effects of warming on AGB, BGB, soil MBC, and SOC were also not significant in the long-term warming experiment ($p > .05$, Figure 2). The SOC content in CK and warming treatment (W) was 58.0 and 60.4 mg g^{-1}, respectively (Figure 2d). Although there were inter-annual fluctuations in the values of these four variables (AGB, BGB, MBC, and SOC), the effects of warming on these variables were mostly not significant across various sampling years in the long-term warming experiment (Figure 3).

3.2 | Synthesis of warming effects on C pools and fluxes

Across all studies, the effects of warming on different processes related to the SOC pool were diverse (Figure 4 and Figure S6). The responses of AGB ($n = 194$), BGB ($n = 84$), and soil MBC ($n = 69$) to warming were not significant based on the multiple-year results (Figure 4a). Similarly, the responses of AGB ($n = 55$) and MBC ($n = 41$) to warming were not significant based on the latest-year results (Figure S6a), but warming significantly increased BGB by 13% based on the latest-year results ($n = 33$, 95% CI: 4%–23%, $p < .05$, Figure S6a). Moreover, no significant effects of warming on SOC were detected based on the multiple-year results ($n = 74$, 95% CI: −1% to 5%, Figure 4a) or the latest-year results ($n = 49$, 95% CI: −1% to 6%, Figure S6a). However, the effects of warming on variables of C fluxes were inconsistent (Figure 4b and Figure S6b). For the multiple-year results, warming had significantly positive effects on soil respiration (Rs) ($n = 43$, 12%, 95% CI: 4–21%, $p < .05$), soil autotrophic respiration (Ra) ($n = 18$, 31%, 95% CI: 8%–59%, $p < .05$), and ecosystem respiration (ER) ($n = 94$, 16%, 95% CI: 7%–24%, $p < .05$), while it had insignificant effects on soil heterotrophic respiration (Rh, $n = 23$), aboveground net primary productivity (ANPP, $n = 15$), and belowground net primary productivity (BNPP, $n = 11$) (Figure 4b). For the latest-year results, warming had significantly positive effects on Ra ($n = 4$, 59%, 95% CI: 30%–94%, $p < .05$) and ER ($n = 36$, 19%, 95% CI: 9%–31%, $p < .05$), while it had insignificant effects on Rs ($n = 16$), Rh ($n = 5$), ANPP ($n = 5$), and BNPP ($n = 3$) (Figure S6b).

Warming had insignificant effects on AGB, BGB, MBC, SOC, and Rh across all studies, and these effects were not dependent on the method of warming (Figures S7 and S8). However, the effect sizes of BGB and MBC had positive relationships with the magnitude of warming, while the effect size of BGB had a negative relationship with the duration of warming (Figure S9). For variables of C fluxes, warming significantly enhanced Rs ($n = 43$, 12%, 95% CI: 4%–21%, $p < .05$), and this effect of warming depended on the method of warming (Figure S8). Rs increased by 22% (95% CI: 7%–37%, $p < .05$) and 13% (95% CI: 3%–25%, $p < .05$) with OTC and infrared heater (IH), respectively, but it showed minimal response to warming with translocation (TL) (Figure S8a). Moreover, ER was also enhanced by warming (15%, 95% CI: 7%–24%, $p < .05$), and the response was dependent on the method of warming (Figure S8c). The response of ER to warming was significant in OTC warming experiments (15%, 95% CI: 6%–28%, $p < .05$), but not in IH warming experiments (Figure S8c). Additionally, the effect size of Rh had a significant negative relationship with the magnitude of warming, and the effect size of ER had a significant positive relationship with the magnitude of warming (Figure S10).

According to the results of model averaged of the summed Akaike weights (only using the latest-year results), the method of warming and the warming-induced change in soil water content (CSWC) could regulate the response of BGB to warming, while MAT and MAP could control the response of soil MBC to warming (Figure S11). The response of SOC to warming was similar to that of AGB and Rs in the results of model-averaged relative importance, and the warming method, magnitude and duration, and other environmental variables had no significant effects on the response of SOC to warming (Figures S11 and S12). The magnitude of warming and CSWC would alter the response of ER to warming (Figure S12). However, there were no significant relationships between the responses of BGB and MBC to warming with the warming method and other environmental variables (CSWC, MAT, and MAP) (Figure S13).

4 | DISCUSSION

According to the results of two field warming experiments in alpine meadow ecosystems on the QTP, warming had insignificant effects on the surface SOC pool and related variables (AGB, BGB, and MBC). Moreover, we analyzed a large number of field warming experiments with meta-analysis, and found that experimental warming had divergent effects on C fluxes in alpine meadow ecosystems on the QTP. Experimental warming did not alter AGB, BGB, and MBC, while enhanced Rs, Ra, and ER. Importantly, both the multiple-year results and the latest-year results clearly showed that the SOC pool had a minor response to experimental warming in alpine meadow ecosystems on the QTP, and experimental (warming method, magnitude, and duration) and environmental (MAT, MAP, altitude, and CSWC) variables did not significantly affect the response of SOC pool to experimental warming. Finally, there were no significant relationships between the warming-induced change in SOC content and the initial standing SOC content or climate (MAT and MAP) (Figure 5 and Figure S15). Overall, our study suggested that although plant respiration was accelerated by warming, the surface (0–10 cm) SOC stock was not significantly changed under warming in alpine meadow ecosystems on the QTP.

4.1 | Responses of C pools to warming

Experimental warming exhibited consistent insignificant effects on plant biomass (AGB and BGB) under different warming magnitudes in the 6-year multi-level warming experiment (study 1) and 20-year long-term warming experiment (study 2) (Figures 1 and 2), while experimental warming also showed insignificant effects on AGB and BGB in the meta-analysis (study 3) (Figure 4a). Temperature and SWC are key factors limiting plant growth in alpine ecosystems on the QTP with average altitude more than 4000 m (Yang et al., 2008). Hence, increased temperatures could stimulate plant photosynthesis and lead to higher plant biomass (Chen et al., 2020). However, no significant effects of warming on plant biomass (including AGB and BGB) were observed in alpine meadow ecosystems, which may be attributed to three possible reasons. First, experimental warming usually leads to both increased temperature and decreased moisture, which together may have a minor effect on plant growth. Furthermore, there was a negative relationship between warming-induced change of BGB and experimental duration (Figure S9f), which is likely caused by the shifted plant species composition and the adaptation of plant community to warming over time (Penuelas et al., 2007; Walker et al., 2006). Second, more than 70% of the warming experiments were low-intensity warming (<2°C), including the two field OTC warming experiments (study 1 and 2), which may not be high enough to alleviate the low temperature limitation of plant growth in alpine meadow ecosystems (Yuan et al., 2021). Indeed, the relationship between the effect size of BGB and the magnitude of warming suggested that the response of BGB would be positive and significant if warming is more than 2°C (Figure S9b). Third, the OTC warming treatment (more than 75% of all experiments) could slow the temperature exchange between the chamber room and the outside and reduce the daily variation in temperature, which could enhance plant respiration as shown by results of the meta-analysis (Figure 4b). Taken together, all these three reasons could contribute to explain the unchanged plant biomass under warming in alpine meadow ecosystems on the QTP.

The effect of warming on soil MBC was not detected in the two field experiments or in the meta-analysis. One possible reason is related to the unchanged plant biomass (aboveground and belowground) with warming. This result suggests that plant inputs to soil may not significantly change, and thus soil MBC may also remain unchanged under warming. Another possible reason is related to soil moisture and nutrient levels that also affect microbial community (Pec et al., 2021; Yang et al., 2019). Likely, the warming-induced lower soil moisture and the general low availability of soil nutrients (particularly N) in alpine meadow ecosystems pose significant limitation for microbial growth and reproduction under warming, thereby weakening the potential stimulatory effect of warming on soil MBC (Bragazza et al., 2013; Liu et al., 2017).

Both the two field experiments and the meta-analysis showed that warming had a minor effect on the surface (0–10 cm) SOC pool in alpine meadow ecosystems on the QTP (Figures 1–4). Moreover, the effect of warming on SOC was not changed by experimental or environmental variables (Figures S7d, S9, and S11d). Additionally, to verify the result from Crowther et al. (2016) that the effect of warming was contingent on the size of initial soil C stock, we also determined the relationships between warming-induced soil C loss and initial standing SOC content, MAT, and MAP. However, our results did not support their conclusion, because there were no significant relationships between the effect of warming on SOC content and the initial SOC content, MAT, and MAP (Figure 5 and Figure S15, using both multiple-year data and latest-year data) in alpine meadow ecosystems on the QTP. Our finding that experimental warming had a minor effect on SOC pool was consistent with previous studies using field-warming experiments (Chen et al., 2020; van Gestel et al., 2018; Yu et al., 2015) or long-term observations (Chen et al., 2017; Ding et al., 2017). Two possible mechanisms may explain the result that the SOC pool showed a minor response to warming in alpine meadow ecosystems on the QTP. First, it is relatively difficult to significantly change the vast soil carbon pool under relatively short-term warming (<5 year) and low-level warming (<2°C) given the large spatial heterogeneity in SOC pool among plots and the small effect of warming on SOC pool. Second, the unaltered inputs of C to soils from dead plant biomass (including AGB and BGB) and outputs of C from soils (indicated by unchanged Rh and MBC) under warming may together lead to undetectable changes in soil C pool (Figure 4).

4.2 | Responses of C fluxes to warming

Warming enhanced Ra and Rs by 31% and 12%, respectively, and it also increased ER by 16% in study 3 (Figure 4). Warming-induced increase trends in ANPP and BNPP (although not significant) may partly contribute to the stimulated Ra under warming (Figure 4b). Warming also enhanced aboveground plant respiration (increased Ra, Rs, and ER), while the insignificant response of Rh to warming may be attributed to the warming-induced decrease in SWC and the unchanged soil MBC. Experimental warming could enhance plant respiration (including aboveground and belowground), which is consistent with previous studies (Tiwari et al., 2021; Walker et al., 2016). Moreover, we found a significant negative correlation between the effect size of Rh and the magnitude of warming, but a significant positive correlation between the effect size of ER and the magnitude of warming (Figure S10). These results also suggested that experimental warming (particularly with high magnitude) would promote plant respiration (ER–Rh) in alpine meadow ecosystems on the QTP.

The objective of this study (study 1–3) was to investigate the overall effect of experimental warming on the SOC pool, as well as to elaborate the underlying mechanisms by studying the relevant C input–output variables. We found that most of the correlations among effect sizes of these variables were not significant, except for a positive correlation between the effect size of SOC and the effect size of MBC (Figure S14). Notably, the paired data between the effect size of SOC and those of Rs, Rh, Ra, ANPP, and BNPP were not enough to investigate their relationships (Figure S14). Therefore, more efforts should be invested to measure the C inputs and outputs to/from soil in addition to the SOC content in future warming experiments.

4.3 | Uncertainties and implications for future research

Most warming experiments in alpine meadow ecosystems on the QTP were warmed by OTC and IH technologies, which accounted for more than 95% of the total experiments (Figure S5). Additionally, our results suggested that the warming method of experiments could potentially affect the responses of ecosystem C processes to warming (Figures S7 and S8). However, these methods (OTC and IH warming) only increased the temperature of near-surface air and surface soil (<20 cm depth), while the deep soils store more than 50% SOC in the whole soil profile (Yang et al., 2008). Therefore, the contribution of deep soils to ecosystem C cycles is significant (Pries et al., 2017). Moreover, climate models also predict that the effects of future warming on deep soils and surface soils will be similar (Soong et al., 2021). Recent experimental and observational studies found interesting results of sensitive responses of SOC to warming in subsurface soils (>20 cm) in alpine grassland ecosystems on the QTP (Ding et al., 2017; Jia et al., 2019). On the other hand, about 75% of the warming experiments are performed by OTCs (Figure S5). However, there are some limitations in using OTC for warming experiments. The OTC created isolation between the inside and outside of the chamber, slowing down the temperature exchange and air flow between the inside and outside. This caused the temperature inside the chamber to rise, reducing the daily variation of temperature and lowering the moisture, resulting in a unique microclimate where the air composition and wind speed are not consistent with the outside (Yu et al., 2015). In addition, it would also partially block rainfall and snowfall, and impede biological dispersal. Therefore, these mixed effects make it more difficult to observe real ecosystem feedbacks to climate warming. Thus, to solve the above problems, the whole-soil warming technology (Pries et al., 2017) and the whole-ecosystem warming technology (Hanson et al., 2017) have received increasing attention in recent years. The whole-soil warming technology could warm not only surface soils but also deep soils (Nottingham et al., 2020; Pries et al., 2017). To increase the temperatures of the whole ecosystem including aboveground vegetation and soils across all layers, the whole-ecosystem warming technology is another method to better understand the responses of soil C stock (especially in deep soils) to experimental warming (Hanson et al., 2017).

According to our results of study 3, more than 75% of field warming experiments had an experimental duration <5 years (Figure S2). But the responses of some processes of ecosystem C cycling to warming had a positive relationship with experimental duration, suggesting that the warming effects on ecosystem C cycling may be regulated by long-term processes (Luo et al., 2011; Vicca et al., 2012). In this study, although the effects of warming on SOC from the 6-year multi-level warming experiment (study 1) were similar with those from the 20-year warming experiment (study 2), the effects of warming on BGB were slightly different between these two experiments (Figures 1 and 2). Therefore, long-term warming experiments should provide more accurate estimate of warming-induced changes in ecosystem C cycling. Additionally, the warming magnitude of experiments was another predictor to affect the responses of key C cycling processes to warming. Most field warming experiments (>70%) conducted in alpine meadow ecosystems on the QTP had low-level warming (<2°C). The global surface air temperature will increase by 1.1–4.8°C by the end of this century based on the report of IPCC (2013). As a result, we need to set up more field warming experiments with long-term plan and high-level warming (up to 4–5°C) to better predict the future responses of the SOC pool to warming in alpine meadow ecosystem on the QTP. Furthermore, future studies need to consider potential interactions and nonlinear relationships between the assessed predictor variables (which were not significant in this study).

Although a large number of field warming experiments have been carried out, different warming experiments had different warming designs (including warming method, magnitude, and duration of experiments) that may affect the responses of terrestrial ecosystem processes to experimental warming (Chen et al., 2020; Lu et al., 2013). Thus, the results from different field warming experiments were not directly comparable. Meanwhile, due to the spatial heterogeneity of ecosystems, the results of simulated warming experiments from a single site or a single ecosystem may have large uncertainty to extrapolate to other regions/ecosystems or validate ecosystem models. In the future, an important frontier is to adopt unified technologies (including the same method, magnitude, and duration of warming experiments), especially using the new generation of the whole-soil warming or whole-ecosystem warming technologies, to carry out global-scale coordinated distributed warming experiments across different ecosystem types and locations (Luo et al., 2011; Torn et al., 2015). Finally, we urgently need coordinated distributed experiments to investigate the impact of warming on whole-soil SOC content (Soong et al., 2021) as well as both C inputs and outputs to/from soil (Hanson et al., 2020), which can improve the prediction reliability of ecosystem models on SOC dynamics under warming.

5 | CONCLUSIONS

Experimental warming had divergent effects on the SOC pool and related C inputs and outputs in alpine meadow ecosystems on the QTP. Based on three complementary studies (including two field warming experiments and a meta-analysis on field warming experiments), the results showed that warming significantly increased soil respiration, soil autotrophic respiration, and ecosystem respiration, but did not significantly change aboveground and belowground plant biomass, surface soil (0–10 cm) MBC and SOC, soil heterotrophic respiration, aboveground and belowground net primary productivity. In addition, the effect of experimental warming on SOC pool was not correlated with experimental (e.g., the method, magnitude and duration of warming) and environmental (e.g., climate and elevation) variables. For example, there were no significant relationships between the effect of warming on SOC content and the initial SOC content, mean annual temperature, and mean annual precipitation. Taken together, this study provides evidence that although warming stimulates plant respiration, it has a minor effect on the surface soil carbon content in alpine meadow ecosystems on the QTP. In the future, coordinated distributed field warming experiments with new technologies (e.g., whole-soil and whole-ecosystem warming) are urgently needed to further study the responses of surface as well as deep soils to warming in alpine ecosystems on the QTP.

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CONFLICT OF 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 STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.16922791.v3

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