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Effects of whole-soil warming on ecosystem carbon fluxes in an alpine grassland

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Abstract

Background: Global warming impacts ecosystem carbon exchange, thus altering the carbon sink capacity of terrestrial ecosystems. However, the response of ecosystem carbon fluxes to whole-soil-profile warming remains unclear.

Methods: We first investigated the effect of whole-soil warming on ecosystem carbon fluxes in an alpine grassland ecosystem on the Qinghai-Tibet Plateau. We also compiled a database of 48 articles to examine the general patterns of experimental warming effects on these fluxes using a global meta-analysis.

Results: Our results showed that whole-soil warming elevated gross ecosystem productivity (GEP) by 14% and ecosystem respiration (ER) by 11%, but had a minor impact on net ecosystem carbon exchange (NEE) in the alpine grassland. In the meta-analysis, warming also enhanced GEP (10%–11%) and ER (13%), but did not alter NEE. Warming-induced shifts in plant community and extension of growing season may be the main reasons for the higher GEP and ER under warming, and the offset of both fluxes likely caused the minor response of NEE to warming.

Conclusions: More attention should be paid to the long-term response of ecosystem carbon fluxes to whole-soil or whole-ecosystem warming throughout the year. These novel findings may help us better predict and mitigate future climate-carbon feedback under realistic warming scenarios.

KEYWORDS

ecosystem respiration, gross ecosystem productivity, meta-analysis, net ecosystem carbon exchange, whole-soil warming

INTRODUCTION

Currently, the Earth is experiencing global changes characterized by climate warming, primarily due to the emission of greenhouse gases caused by human activities. Global surface temperatures have already risen by 1.1°C since the late 19th century (1850–1900), and are projected to rise by as much as 4°C by the late 21st century under a very-high emissions scenario (SSP5-8.5, IPCC, 2023). In terrestrial ecosystems, ecosystem carbon exchange plays a vital role in the global carbon cycle and is highly responsive to climate warming (Heimann & Reichstein, 2008; Song et al., 2019). Global warming significantly alters the carbon budget and balance determined by ecosystem carbon fluxes in terrestrial ecosystems (Houghton, 2007; Melillo et al., 2011; Tang et al., 2022), and these processes will in turn impact the carbon-climate feedback (Luo, 2007; Schimel et al., 2001). This indicates that climate warming could result in either positive feedback (exacerbating global warming) or negative feedback (mitigating global warming) (Chapin et al., 2008; Field et al., 2007). Consequently, numerous field warming experiments have been conducted to investigate the response of ecosystem carbon fluxes to warming across various global ecosystems (Niu et al., 2013; Oechel et al., 2000; Quan et al., 2019). Furthermore, both IPCC model projections and experimental observations show that the surface and deep soils have similar warming rates, with the same warming trend as the air (Hu & Feng, 2003; Soong et al., 2020). However, a knowledge gap persists regarding the influence of whole-soil warming on ecosystem carbon fluxes, despite existing studies about its impact on greenhouse gas emissions (CO_2, CH_4, and N_2O) (Chen, Han, Qin, et al., 2023, Chen et al., 2024; Nottingham et al., 2020; Soong et al., 2021). Therefore, examining the whole-soil warming effects on ecosystem carbon fluxes is essential for improving predictions of carbon-climate feedback under future realistic climate warming scenarios and aiding policymakers in developing effective climate mitigation strategies.

Ecosystem carbon fluxes include net ecosystem carbon exchange (NEE), gross ecosystem productivity (GEP), which represents the CO_2 fixed by plants via photosynthesis (carbon uptake), and ecosystem respiration (ER), which represents the CO_2 released via respiration in the ecosystem (carbon emission) (Ganjurjav et al., 2018; Verburg et al., 2004). The NEE is defined as the difference between GEP and ER, and it determines whether ecosystem function delivers net carbon sequestration (carbon sink) or net carbon release (carbon source), thereby indicating the potential ecosystem carbon sequestration capacity (Chapin et al., 2002; Wang et al., 2023; Zhou et al., 2018). These processes are influenced by plant growth, soil properties, and soil microbial activity, all of which respond to climate warming (Ganjurjav et al., 2022; Lv et al., 2020; Quan et al., 2024; Ravn et al., 2020). Temperature is a key factor influencing plant growth and, consequently, overall plant productivity (Khodorova & Boitel-Conti, 2013; Quan et al., 2024). Additionally, the ecosystem's primary productivity is also shaped by shifts in plant community composition and biodiversity, both of which are highly sensitive to climate warming (Ma et al., 2017; Quan et al., 2024). Elevated temperature also affects soil properties, such as soil moisture, gas diffusion, substrate quantity and quality, nutrient availability, and microbial community structure and physiological metabolism, thereby altering plant respiration, soil organic carbon (SOC) decomposition, and ultimately ER in response to warming (Chen, Han, Yuan, et al., 2023; Maes et al., 2024; Martins et al., 2017; Melillo et al., 2017). The trade-off between both processes determines the strength and direction of the NEE, and previous studies have found that warming promoted GEP and ER, resulting in variable NEE responses, from significant changes to no effect (Oberbauer et al., 2007; Sullivan et al., 2008). In one study, it was found that warming did not alter the GEP and ER, and therefore, the NEE was not significantly impacted by climate warming (Lu et al., 2013). Soil moisture also plays a critical role in modulating the response of NEE to climate warming. Rising temperatures often reduce soil water content, which in turn inhibits microbial activity and limits the potential increase in plant productivity driven by warming. Consequently, the NEE shift may depend on soil moisture availability, with sufficient soil moisture resulting in an increased NEE under warming treatment (Zhu et al., 2016). Furthermore, the effect of warming on the NEE is also related to the magnitude of temperature increase; low-level warming results in ecosystems acting as carbon sinks, and high-level warming turns them into carbon sources (Zhu et al., 2017). These inconsistent warming impacts on ecosystem carbon exchange therefore challenge our ability to predict and assess global carbon cycling accurately under future climate warming, particularly in determining whether ecosystems will shift between carbon sources and carbon sinks.

The Qinghai-Tibet Plateau, the third pole of the world, is the highest plateau in the world, with an average elevation of over 4000 m (Feng et al., 2020). It harbors vast SOC reserves, estimated at 7.4 Pg C in the top 1 m of soil (Yang et al., 2008). However, this region is warming at an accelerated rate of 0.3°C–0.4°C per decade, nearly twice the global average (Chen et al., 2015). This makes the plateau especially sensitive to climate warming and an ideal area to study the ecosystem carbon cycling under changing environmental conditions. Comprising nearly 60% of the plateau's area, alpine grassland is the most dominant ecosystem in this region, accounting for approximately 10% of China's total SOC storage (Yang et al., 2008). To explore the whole-soil warming effects, we established a whole-soil warming experiment in an alpine grassland ecosystem (Chen et al., 2024; Qin et al., 2023). This warming experiment heats the entire soil profile (down to 1 m) by 4°C, more realistically simulating a future warming scenario than previously implemented surface-soil warming, which missed the response of deeper soil horizons to warming (Chen et al., 2024). The experiment focuses on assessing the impacts of whole-soil warming on key ecosystem carbon exchange processes, including NEE, GEP, and ER. In addition, we also compiled a global database on ecosystem carbon fluxes to examine the general patterns of experimental warming effects on these fluxes, using a meta-analysis (a statistical method that could effectively understand a large number of independent results from various field warming experiments worldwide) (Chen et al., 2020; Lu et al., 2013; Song et al., 2019). This study aims to (a) provide the first direct measurements of whole-soil warming effects on ecosystem carbon fluxes (NEE, GEP, and ER) in an alpine grassland ecosystem, (b) identify the general response patterns of ecosystem carbon fluxes to warming based on surface-soil warming experiments globally, and (c) compare the findings from the whole-soil warming experiment with global trends derived from surface-soil warming studies. These efforts could offer valuable insights into the potential feedback mechanisms of carbon cycling under future climate scenarios.

MATERIALS AND METHODS

Study site

Our whole-soil field warming experiment was conducted at the National Field Observation Station of Haibei Alpine Meadow Ecosystem Research Station, located in Menyuan County, Qinghai Province, China (37°37′ N, 101°12′ E, and 3200 m a.s.l.) on the northeast Qinghai-Tibet Plateau. This region experiences a plateau continental climate with a short, warm growing season lasting from May to September (5 months) and a long, cold nongrowing season from October to April (7 months). The site has a mean annual temperature (MAT) of −1.1°C and a mean annual precipitation (MAP) of 485 mm, with over 80% of precipitation concentrated in the growing season. Alpine meadows, the dominant vegetation type in this region, make up nearly half of the Qinghai-Tibet Plateau's grassland area and account for 56% of its SOC storage (Yang et al., 2008). The plant community in an alpine meadow is primarily composed of *Kobresia humilis* (C.A. Mey. ex Trautv.) Serg., *Stipa aliena* Keng, *Elymus nutans* Griseb., *Carex przewalskii* T.V. Egorova, *Helictotrichon tibeticum* (Roshev.) Keng f., *Poa pratensis* L., *Tibetia himalaica* (Baker) H.P. Tsui, and other herbaceous plants (Liu et al., 2018). The soil in this area is classified as a Cryic Cambisol, with a loamy texture and a slightly alkaline pH of 7.6 (Chen et al., 2021). This field warming experiment, established before June 2018, was designed to preserve the natural temperature gradient of the ecosystem (Figure S1; Chen, Han, Qin, et al., 2023; Hicks Pries et al., 2017). This experiment has four blocks, and each block has a paired control plot and a warming (+4°C) plot. Thus, in total, there are four control plots and four warmed plots. For a more detailed description of this whole-soil field warming experiment, see Chen et al. (2024).

Ecosystem carbon fluxes

We monitored ecosystem carbon dioxide fluxes (NEE, GEP, and ER) using an infrared gas analyzer (IRGA; LI-6400, LiCor Inc.) paired with a transparent chamber (0.4 m × 0.4 m × 0.6 m). In July 2018, square collars (0.4 m × 0.4 m) with a groove were installed 10 cm depth into the soil across all eight plots. During measurements, the chamber was placed over the collar and sealed with water to prevent gas leakage. Inside the chamber, two small electric fans ran continuously to ensure even air mixing. Once a steady state was achieved, we recorded 13 consecutive CO_2 concentration measurements at 5-s intervals during a 60-s period. CO_2 concentration changes over time were used to calculate flux rates, determining net ecosystem CO_2 exchange (NEE). Positive NEE values indicated net carbon release, while negative NEE indicated net carbon uptake. Following NEE measurements, the chamber was ventilated and then covered with an opaque cloth to block light, allowing us to measure ER, which reflects CO_2 flux in the absence of photosynthesis. GEP was then calculated as the difference between NEE and ER (Niu et al., 2013). Ecosystem carbon fluxes were monitored every 2 weeks during the growing season (August 2018–September 2020), with measurements conducted between 09:00 a.m. and 12:00 noon on a total of 23 sampling dates.

Plant and soil properties

At the end of August 2019, after approximately 14 months of the contrasting warming and ambient treatments, plant and soil samples were collected from each plot. Aboveground biomass (AGB) was harvested from four 0.25 m × 0.25 m quadrats per plot, and oven-dried at 65°C until reaching a constant weight. Soil samples from 0 to 10 cm depth were obtained using a 5-cm diameter corer, with two cores taken from each plot. Fresh soil samples were transported to the laboratory within 24 h, stored at 4°C in cooler boxes packed with ice-bags. Visible stones were removed, and live roots were separated from the soil, which was then sieved through a 2 mm sieve. Belowground biomass (BGB) was determined by oven-drying living roots to constant weight at 65°C. Half of the sieved soil samples were air-dried to analyze carbon and nitrogen concentration, while the remaining soil samples were stored at 4°C for measurement of soil properties, available nutrients, and microbial biomass. As much as possible, analyses on stored soil were performed within 1 week. We determined soil pH, total SOC, total nitrogen (TN), ammonium nitrogen (NH_4^+-N), and nitrate nitrogen (NO_3^--N) by conventional methods (Chen et al., 2021). We also measured soil microbial biomass carbon (MBC) and nitrogen (MBN) by the chloroform-fumigation-extraction method (Vance et al., 1987).

Statistical analysis

All statistical analyses for this field warming experiment were conducted using R (version 4.3.0) (R Core Team, 2023). The daily soil temperature and soil moisture (water content) data detected by sensors and continuously recorded by data loggers were averaged to show the temporal patterns more clearly (Figures S2 and S3). To assess the effect of whole-soil warming and time (annual and total [3-year]) on ecosystem carbon fluxes (including NEE, ER, and GEP), a repeated measures analysis of variance (ANOVA) was performed using the *ezANOVA* function from the "ez" package. Then the Bonferroni test was applied, allowing us to examine the impact of warming treatments on mean ecosystem carbon fluxes. To further investigate the potential drivers of ecosystem carbon fluxes, we also determined the relationships between these fluxes and surface soil temperature and water content. We also constructed a Pearson correlation matrix to explore the associations between these fluxes and plant and soil properties, including AGB, BGB, soil pH, NH_4^+-N, NO_3^--N, SOC, TN, MBC, and MBN. Statistical significance between control and warming treatment is marked with asterisks ($^\dagger p < 0.10$, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $n = 4$) or labeled as nonsignificant (ns, $p > 0.10$).

Meta-analysis for the warming experiments

In this global-scale meta-analysis, we systematically reviewed all peer-reviewed publications before December 31, 2023 that investigated ecosystem carbon fluxes (NEE, ER, and GEP) under field warming experiments (none of which was a whole-soil warming experiment) across all terrestrial ecosystems (Figures S4 and S5). The literature search was conducted through multiple databases, including the Web of Science (https://www.webofscience.com), China National Knowledge Infrastructure (https://www.cnki.net), and Google Scholar (https://scholar.google.com). The search terms employed were: (a) "field experiment" or "manipulated experiment" (excluding laboratory incubation experiments), (b) "experimental warming" or "increased temperature" or "elevated temperature" or "enhanced temperature," (c) "net ecosystem production" or "net ecosystem exchange" or "NEE" or "NEP," (d) "gross ecosystem production" or "GEP," and (e) "ecosystem respiration" or "ER." To be included in the global-scale meta-analysis, studies had to meet the following criteria: (1) The study must have included both ambient treatment and experimental warming treatments. (2) The study must have reported at least one of the three fluxes (NEE, ER, and GEP). (3) The study must have reported, or allow for the calculation of, the means, standard deviations (SD) or standard errors (SE), and sample sizes for the relevant variables. (4) The warming method, warming magnitude, and warming duration of the field warming experiment must have been explicitly documented. (5) We only retained the data from ambient and warming treatments (Chen, Han, Qin, et al., 2023). (6) The ecosystem carbon fluxes (NEE, ER, and GEP) must have been measured over at least one growing season. Following the application of these inclusion criteria, a total of 43 studies (derived from 48 publications) were selected for inclusion in this meta-analysis (Figure S5).

To facilitate the understanding of results, we categorized ecosystems into three types: grassland, tundra, and wetland. Warming methods were classified into four categories: warming by open-top chamber (OTC), warming by infrared heater (IH), warming by greenhouse (GH), and other warming techniques, which included heating cables, horizontal curtains, translocation, and snow fences. Warming magnitudes (temperature increase level) were grouped into categories: <2°C and ≥2°C. Experimental durations in the field experiment were classified as <5 years, 5–10 years, and ≥10 years. In addition to three key variables, environmental factors associated with each warming experiment were also documented, including the geographic coordinates (longitude and latitude), altitude, MAT, and MAP. However, most articles did not provide the change of warming-induced soil moisture, so we obtained the aridity index (AI) at the site level according to latitude and longitude (Map of aridity, Food and Agriculture Organization of the United States). Additionally, relevant plant and soil properties were also recorded, following the same protocol as in our case study. In instances where different warming magnitudes were reported within a single study, each warming magnitude was treated as an independent observation. Furthermore, data from multiple years were included in this meta-analysis, rather than solely relying on the most recent observations, to maximize the number of observations. Ultimately, 208 individual observations (accessible via https://github.com/yancypku/W-NEE) were incorporated into this global-scale meta-analysis (Figure S5).

The effect size (log-response ratio method) was used to quantify the impacts of experimental warming on ecosystem carbon fluxes, as detailed in Chen et al. (2020). To assess the weighted effect size and 95% confidence interval (CI), we employed the *rma.mv* function from the "metafor" package in R, which applies random-effects models (the "study" was treated as a random factor). Warming effects are considered statistically significant if the 95% CI does not overlap zero. To examine the variability in effect sizes across different groups, we conducted a between-group heterogeneity (Q_B) test. A significant Q_B value ($p < 0.05$) indicated that the weighted effect sizes of a particular variable varied among the groups defined by ecosystem types, warming methods, warming magnitudes, and warming durations. The relative importance of each variable was assessed by summing the Akaike weights for all models that incorporated that predictor, as derived from mixed-effects meta-regression analyses (Chen et al., 2024). This was done using the "glmuti" package in R (Calcagno & Mazancourt, 2010). A threshold of 0.8 was applied to distinguish between important and nonessential predictors (Calcagno & Mazancourt, 2010; Terrer et al., 2016). Additionally, the relationships between the RR of ecosystem carbon fluxes with various factors, such as warming magnitude, warming duration, and MAT, were examined by regression analyses to explore the potential drivers. The data set and the list of publications in this global-scale meta-analysis are available at https://github.com/yancypku/W-NEE.

RESULTS

The responses of soil microclimates, plant, and soil properties to whole-soil warming

Seasonal fluctuations in soil temperature were observed across the soil profile at depths of 5, 10, 20, 30, 40, 60, 80, and 100 cm, with higher temperatures recorded during the growing season and lower temperatures during the nongrowing season (Figure S2). The soil temperature under the warming treatment had a higher value compared to the ambient treatment in all soil depths, especially for soil layers of 10–100 cm depth (Figure S2). However, the observed increase in surface soil (0–10 cm) over the 3-year study period was limited to an average of 2.55°C, falling short of the targeted 4°C increase across the entire soil profile (0–100 cm), despite the installation of two heating cable rings in the surface soil (Figure S1a). In contrast, soil temperature at depths of 10–100 cm achieved the targeted 4°C increase (Figure S1a). Soil water content exhibited a seasonal variation similar to that of soil temperature (Figure S3), yet no significant changes in either gravimetric water content, as measured through weighing during soil sampling, or volumetric water content, as measured continuously with sensors, were observed in response to whole-soil warming over the 3-year period (June 2018 to September 2020, Figures S1b and S3). Furthermore, neither plant nor soil properties showed significant alterations under the whole-soil warming treatment (Figure S6).

The responses of ecosystem carbon fluxes to whole-soil warming

The effects of whole-soil warming on ecosystem carbon fluxes were diverse over the 3 years (Figure 1). The fluxes of GEP and ER were changed by warming

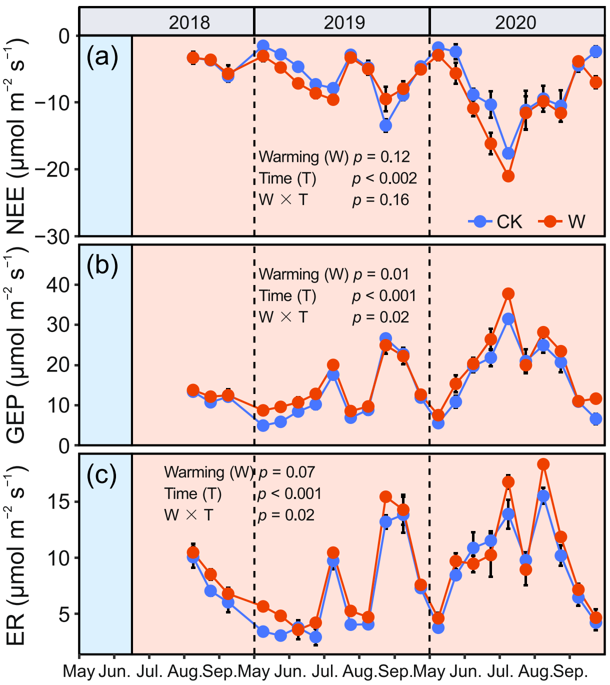

FIGURE 1 The temporal variations in ecosystem carbon fluxes were monitored under control (CK) and warming (W) treatments over 3 years (2018–2020, growing season) in the alpine grassland. (a) Net ecosystem carbon exchange (NEE), (b) gross ecosystem productivity (GEP), and (c) ecosystem respiration (ER). The light blue-shaded areas represent the pretreatment phase. Red corresponds to the warming treatment, and blue represents the control treatment. Data points are mean ± standard errors (n = 4).

(p = 0.01, p < 0.10), while NEE flux did not exhibit a significant response to warming treatment (Figure 1). All ecosystem carbon fluxes (NEE, ER and GEP) demonstrated significant temporal variation across the study period (p < 0.001, Figure 1). For the fluxes of GEP and ER, there was significant interaction between warming treatment and the year of measurement (p < 0.05), but there was no significant interaction for the flux of NEE (Figure 1). Despite these interactions, ecosystem carbon fluxes did not consistently respond to warming each year after the initiation of the whole-soil warming treatment (Figure S7). In 2018, no significant changes in any of the carbon fluxes were observed in response to warming (Figure S7a–c). In 2019, whole-soil warming increased GEP flux (p < 0.05) and ER flux (p < 0.10), while simultaneously decreasing NEE flux (p < 0.10) (Figure S7d–f). In 2020, whole-soil warming enhanced GEP flux (p < 0.10) and ER flux (p < 0.10) but had no significant effect on NEE flux (Figure S7g–i). Over the 3 years (2018–2020) period, the mean results indicated that whole-soil warming significantly increased GEP flux by 14% (p < 0.05), from 14.5 ± 0.40 μmol m^{-2} s^{-1} in ambient plots to 16.5 ± 0.39 μmol m^{-2} s^{-1} in warmed plots, and increased ER flux by 11% (p < 0.05), from 8.0 ± 0.38 μmol m^{-2} s^{-1} in ambient plots to 8.8 ± 0.16 μmol m^{-2} s^{-1} in warmed plots (Figure 2b,c). But, NEE flux remained unchanged by the warming treatment over the 3 years (−6.55 ± 0.59 μmol m^{-2} s^{-1} and −7.70 ± 0.23 μmol m^{-2} s^{-1} in ambient plots and warmed plots, respectively; Figure 2a). Correlation analyses revealed a significant negative correlation between NEE flux and both soil temperature and moisture (across plots and dates), whereas GEP and ER fluxes exhibited a significant positive correlation with soil temperature (Figure 3). However, no significant correlation was found between GEP and ER fluxes and soil moisture (Figure 3). With increasing soil temperature, the NEE flux was lower, but the fluxes of GEP and ER were higher (Figure 3).

Synthesis of experimental warming effects on ecosystem carbon fluxes

A total of 47 field warming experiments (none were whole-soil warming; our whole-soil warming experiment was not included) that met our data selection criteria were identified globally (Figure S4). These experiments were distributed across various ecosystems, with 33 located in grasslands, 13 in tundra, and 1 in a wetland (Figure S4). Specifically, out of the 208 observations, 164 were collected from grasslands, 38 from tundra, and only 6 from wetlands (Figure S5). Of these experiments, nearly 60% employed OTC for warming, while 29% utilized IH for warming, with relatively few employing other warming methods (Figure S6). Most field warming experiments (>80%) had a temperature increase level (warming magnitude) of less than 2°C, with the warming magnitude of other experiments being greater than 2°C (Figure S5). Furthermore, over 70% of the experiments had a warming duration of less than 5 years, with 23% lasting 5–10 years, and only a small proportion exceeding 10 years (Figure S5).

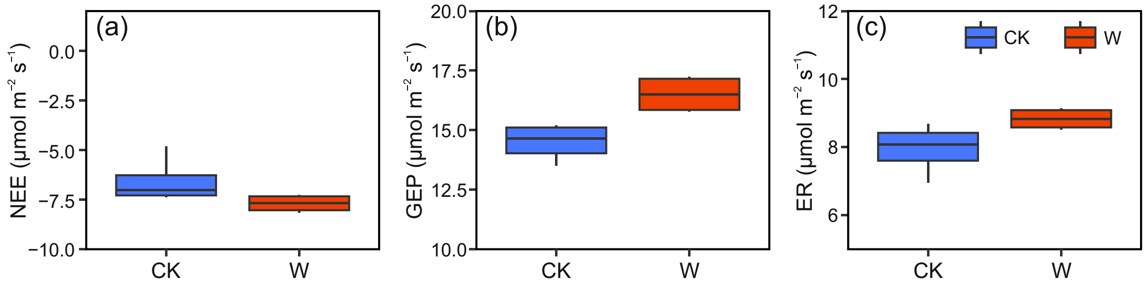

FIGURE 2 The three-year (2018–2020, growing season) averages of (a) net ecosystem carbon exchange (NEE), (b) gross ecosystem productivity (GEP), and (c) ecosystem respiration (ER) in the alpine grassland. Red denotes the warming (W) treatment, and blue represents the control (CK) treatment. Statistical significance between control and warming treatment is marked with asterisks ($^{\dagger}p < 0.10$, $^{*}p < 0.05$, $n = 4$) or labeled as non-significant (ns, $p > 0.10$).

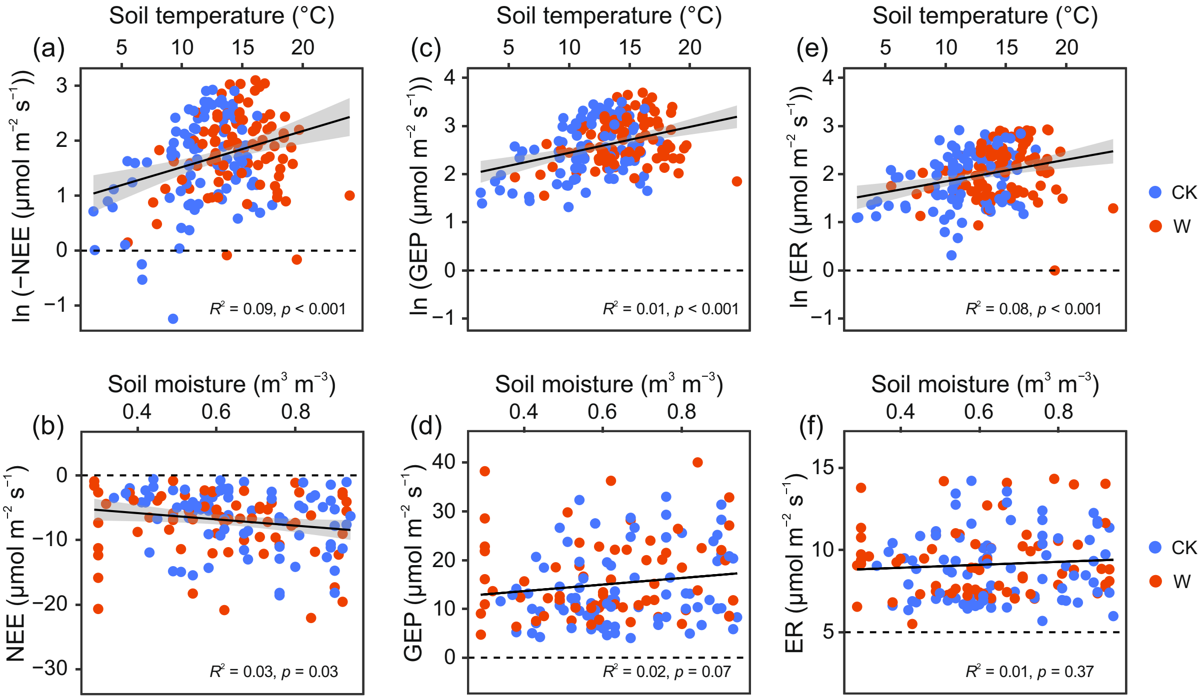

FIGURE 3 The three-year (2018–2020, growing season) relationships between ecosystem carbon fluxes—(a, b) net ecosystem carbon exchange (NEE), (c, d) gross ecosystem productivity (GEP), and (e, f) ecosystem respiration (ER)—and soil temperature (left panel: a, c, e), and soil moisture (right panel: b, d, f) at surface soil (0–10 cm) across plots and dates in the alpine grassland. Red denotes the warming (W) treatment, and blue represents the control (CK) treatment.

The effects of experimental warming on ecosystem carbon fluxes were highly variable (Figure 4 and Figure S8). Warming significantly increased ER by 13% (total data, $n = 206$, 95% CI: 6%−21%, $p < 0.05$, Figure 4a and Figure S8), whereas no significant effect on NEE was observed (total data, $n = 198$, 95% CI: −7% to 34%, Figure 4a and Figure S8). Interestingly, experimental warming tended to elevate GEP (total data, $n = 199$, 10%, 95% CI: −1% to 23%, $p < 0.10$, Figure 4a and Figure S8). For the results of paired data, warming significantly enhanced both GEP ($n = 196$, 11%, 95% CI: 1%–24%, $p < 0.05$) and ER ($n = 196$, 13%, 95% CI: 6%–22%, $p < 0.05$), but had no insignificant effect on NEE ($n = 196$, 95% CI: −35% to 31%, Figure 4b). For the related plant and soil properties, experimental warming significantly enhanced BGB by 8% (total data, $n = 23$, 95% CI: 1%–16%, $p < 0.05$), while warming did not change AGB, NH_4^+-N, NO_3^--N, SOC, TN, MBC, and MBN significantly (Figure S8). Ecosystem type and warming method did not significantly influence the responses of ecosystem carbon fluxes to warming (Figure S9). However, warming magnitude and duration were found to influence the response of GEP to warming, though they did not significantly affect NEE or ER (Figure S9). Model-averaged relative importance analyses indicated that both warming magnitude and duration could affect the GEP response (Figure S10b), while the response of ER was primarily influenced by warming duration (Figure S10c). Specially, warming of less than 2°C increased GEP, whereas warming exceeding 2°C resulted in a negative impact on GEP (Figure S9b). Experimental warming durations of more than 10 years of experimental warming enhanced GEP, but durations less than 10 years (both <5 years and 5–10 years) did not significantly alter GEP (Figure S9b). Conversely, warming durations of less than 5 years (<5 years) elevated ER, while warming durations

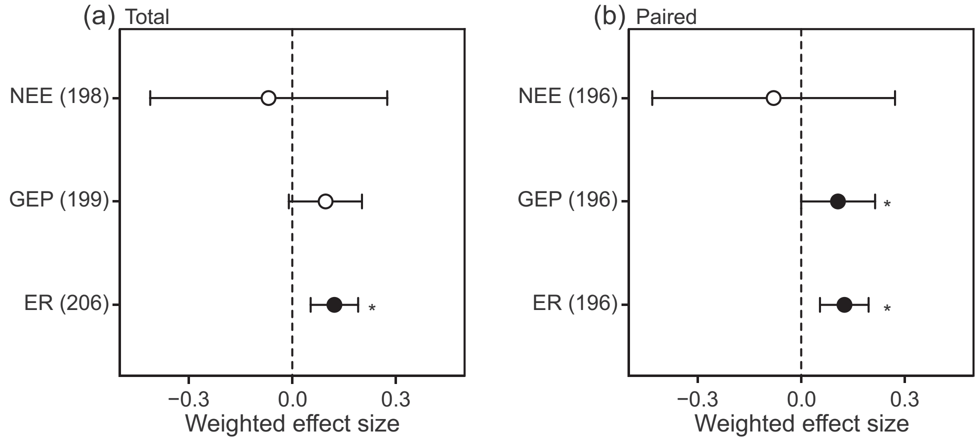

FIGURE 4 The experimental warming effects (none of which was a whole-soil warming experiment) on ecosystem carbon fluxes (net ecosystem carbon exchange [NEE], gross ecosystem productivity [GEP], and ecosystem respiration [ER]) across global terrestrial ecosystems (a, total data; b, paired data). Error bars represent 95% confidence intervals (CI), and the vertical dashed line indicates a weighted effect size of 0. Warming effects are considered statistically significant if the 95% CI does not overlap zero (marked with *). Sample sizes for each variable are provided in brackets.

of more than 5 years (5–10 years and >10 years) did not significantly influence ER (Figure S9c).

DISCUSSION

This study revealed that whole-soil warming led to a significant increase in GEP by 14% and ER by 11% (Figures 1 and 2). However, no significant effect was observed on NEE when averaged over the 3-year period (Figures 1 and 2). This finding aligns with the global results of the meta-analysis, which showed a 10% increase in GEP, a 13% increase in ER, and no change in NEE for total data; and an 11% increase in GEP, a 13% increase in ER, and no change in NEE for paired data (Figure 4a,b). Several whole-soil warming field experiments have been established in different ecosystems, such as temperate forests (Hicks Pries et al., 2017) and tropical forests (Nottingham et al., 2020), to assess soil carbon pool and flux responses to experimental warming. However, the responses of the ecosystem carbon exchange to whole-soil warming remain unknown. Many previous traditional near-soil surface warming experiments, which focus on warming only the top 0–20 cm of soil (but whole-soil warming experiments could heat the entire soil profile, including deep soils), have shown variable responses (Jia et al., 2019; Lv et al., 2020). For example, an IH-based warming experiment in an alpine meadow, which increased surface soil temperature by 1.5°C, demonstrated that warming during the growing season promoted both GEP and ER, but did not change NEE (Jia et al., 2019). Conversely, a nearby warming experiment using the same warming method found no response in ecosystem carbon fluxes to 1.8°C warming (Lv et al., 2020). Furthermore, a recent regional-scale meta-analysis also found no significant changes in ecosystem carbon fluxes in response to experimental warming (Chen et al., 2020). Consistent with the findings of our global meta-analysis, a previous global meta-analysis also reported that experimental warming increased GEP and ER by 16% and 6%, respectively, without altering NEE (Lu et al., 2013). Interestingly, the effects of whole-soil warming on ecosystem carbon fluxes were comparable to those observed in traditional near-soil surface warming experiments. However, whole-soil warming was found to significantly accelerate soil organic matter decomposition, leading to a substantial increase in soil-derived CO_2 flux (Chen et al., 2024).

There are several potential reasons for the observed response of GEP to warming. Elevated soil temperature may enhance the availability of substrates and nutrients, thereby simulating plant growth and promoting greater CO_2 fixation through photosynthesis, which in turn increases GEP (Lu et al., 2013). In addition, warming could also increase leaf temperature—especially in open-field environments—thereby directly enhancing photosynthetic rates, which may further contribute to increased GEP. However, our study found no significant changes in soil basic properties under whole-soil warming (Figure S4), and no significant correlations were identified between ecosystem carbon fluxes and these soil properties (Figure S11). Additionally, experimental warming may shift the plant community structure, promoting species with higher photosynthetic efficiency and enhancing ecosystem productivity (Liu et al., 2018; Quan et al., 2024). A previous study on plant community responses to whole-soil warming indicated no change in plant community diversity but a significant shift in species composition (Qin et al., 2023). Over 4 years, whole-soil warming increased the biomass of forbs, which have relatively high photosynthetic efficiency, and decreased the biomass of grasses, which have relatively low photosynthetic efficiency. This shift likely contributed to increased ecosystem productivity, even though total plant biomass remained unchanged (Qin et al., 2023). Moreover, the significant correlation between GEP and soil temperature suggested that GEP increases with increasing temperature (Figure 3c). Another reason contributing to the positive response of GEP to whole-soil warming may be the prolonged growing season, as increased soil temperatures lengthen the thaw season, thereby extending the growing season (Liu et al., 2021). Although warming significantly promoted GEP in both this whole-soil warming experiment and global meta-analysis of surface-warming experiments (Figures 2b and 4), the response of GEP to warming was influenced by both the magnitude and duration of warming in the meta-analysis (Figure S12c,d). A strong negative correlation was observed between the response ratio of GEP and warming magnitude, while the response ratio showed a significantly positive relationship with warming duration (Figure S12c,d). As the warming magnitude increased, the response ratio of GEP shifted from positive to negative, potentially due to soil drying induced by higher warming magnitudes (Reich et al., 2018). However, in this study, whole-soil warming did not change soil moisture (Figure S1b), so the significant increase in GEP remained stable over time. The relationship between the response ratio of GEP and warming duration requires further validation, as this study only examines the initial 3 years of the whole-soil warming experiment.

ER, representing ecosystem carbon emissions, plays a crucial role in the climate-carbon feedback (Ma et al., 2022). It was significantly elevated in both the whole-soil warming experiment and the global meta-analysis (all data and paired data from surface-warming experiments) (Figures 2c and 4). However, previous studies have also found that warming did not alter or even reduce ER (Fu et al., 2013; Lv et al., 2020). As a key component of ER, aboveground plant respiration plays a crucial role in shaping the overall strength of ER (Chen et al., 2020). Similar to GEP, ER showed a significant positive correlation with soil temperature, suggesting that experimental warming may promote the prolongation of the growing season, potentially increasing plant respiration (Chen et al., 2020; Liu et al., 2021). However, we did not directly measure the response of the plant's aboveground respiration to warming. In addition, the relationship between this increased ER with warming and the shifted plant functional groups (from grasses to forbs) is unclear. Therefore, these inferences require future validation. Soil respiration, which represents the second-largest terrestrial carbon flux, is another component of ER (Hicks Pries et al., 2017). It can be divided into plant root respiration (root-derived CO_2 efflux) and soil heterotrophic respiration (SOC-derived CO_2 efflux) (Chen et al., 2024; Hicks Pries et al., 2017). Although experimental warming increased belowground biomass in the global meta-analysis (Figure S8), potentially increasing root respiration, our previous study in this whole-soil warming experiment found that 4-year warming did not impact root respiration but significantly promoted SOC decomposition, leading to increased soil heterotrophic respiration (Chen et al., 2024). Besides providing more substrates and extending the growing season, warming also accelerated the physiological activity and turnover of soil microbes, resulting in higher SOC-derived CO_2 efflux (Chen et al., 2024). Thus, both plant respiration and soil heterotrophic respiration contribute to the overall response of ER to warming.

NEE, which represents the balance between GEP and ER, serves as a crucial indicator for measuring changes in ecosystem carbon sinks (Chapin et al., 2002). The negative NEE flux values observed in both ambient and warming treatment of the whole-soil warming experiment suggest that the alpine grassland ecosystem functions as a net carbon sink (Figures 1a and 2a). Our results indicated that whole-soil warming did not result in a significant change in NEE (Figure 2a), a result that aligned with conclusions of the global-scale meta-analysis (Figure 4). This insensitivity of NEE to experimental warming aligns with previous regional-scale meta-analysis (Chen et al., 2020), as well as results on the subarctic tundra ecosystem (Ylänne et al., 2015). The increased GEP induced by warming was offset by the increased ER, explaining why NEE showed a minor response to warming in both the whole-soil warming experiment and our global meta-analysis of surface-warming experiments (Figures 2 and 4). In addition, we found a close relationship between NEE and temperature across plots and dates (Figure 3a and Figure S12a), particularly that NEE flux would decrease markedly with increasing soil temperature (Figure 3a). In other words, experimental warming may help maintain the carbon sink function of the ecosystem (Gallego-Sala et al., 2018). Specifically, 3-year whole-soil warming tended to reduce NEE (14% increase in GEP vs. 11% increase in ER) in alpine grassland ecosystems (Figure 2). Soil moisture is another important factor affecting NEE, as indicated by the negative correlation between NEE and soil moisture (Figure 3b). However, in this study, whole-soil warming did not result in significant changes in soil moisture (Figure S1b). Overall, under the future warming scenarios, our findings suggest that warming may enhance the carbon sequestration function of grassland ecosystems.

Based on the results of this meta-analysis across the world, nearly 80% of the observations in our study were from grassland ecosystems, while carbon-rich tundra and wetland ecosystems were relatively unstudied (Figure S5). Among these findings, the ER response to warming varied across different ecosystems, whereas the responses of GEP and NEE exhibited no clear ecosystem-specific patterns (Figure S9). Yu et al. (2013) found that the response of ecosystem carbon fluxes was closely related to ecosystem types, with forest ecosystems typically exhibiting higher carbon sequestration capacities compared to grasslands. A recent regional-scale meta-analysis also indicated that the responses of GEP and ER to warming could be regulated by the ecosystem type (Chen et al., 2020). The responses of other important ecosystems to warming, such as forests and croplands, remain unclear. Further research is required to elucidate the response patterns of ecosystem carbon fluxes to climate warming across diverse ecosystem types. Moreover, the observations in our study were all from the Northern Hemisphere, highlighting the need to investigate how warming affects ecosystem carbon fluxes in Southern Hemisphere ecosystems (Figure S4). Our meta-analysis revealed that over 70% of field warming experiments had durations of less than 5 years, with durations over 10 years being very rare (Figure S5). The ecosystem carbon cycling could be significantly influenced by warming duration (Luo et al., 2011), and the responses of ecosystem carbon fluxes to warming varied across different sampling years (Figure S7). Specifically, warming duration influenced the response ratios of these fluxes (Figures S9 and S10). Jia et al. (2019) demonstrated that warming duration (3 vs. 5 years) significantly affected ecosystem carbon fluxes in an alpine meadow, with GEP and ER remaining unchanged after 3 years of warming but significantly elevated after 5 years of warming. Moreover, annual NEE data from 71 observational stations showed the decreasing trends from 2002 to 2017 (Li et al., 2021). However, our study only examined the first 3 years of whole-soil warming, and future research focusing on long-term warming effects is crucial for advancing our understanding of ecosystem carbon dynamics under ongoing climate change.

It is worth noting that two points require further consideration in future studies. First, the ecosystem carbon fluxes measured in our study were confined to the growing season. It remains unclear how these fluxes in the nongrowing season, as well as the annual total fluxes, respond to whole-soil warming. Continuous NEE from 2003 to 2012 in an alpine shrubland suggested that the absolute value of NEE during the nongrowing season could account for up to 53% of the NEE observed during the growing season. Notably, NEE in the nongrowing season was positive (a carbon source), whereas it was negative during the growing season (a carbon sink, Li et al., 2016). Moreover, these fluxes in our study were measured manually and sporadically. Thus, a combination of manual and automatic measurements (by chambers or eddy covariance towers) should be considered in future studies to continuously measure the response of these fluxes to climate change. In addition, it is worth noting that the response of ecosystem carbon fluxes to whole-soil warming was different at different stages of the growing season (Figure 1). Compared with other periods of the growing season, the impact of whole-soil warming on NEE and ER was more intense in the early stage of the growing season (Figure 1). However, the focus of our study is to compare the effect of whole-soil warming (case study) on ecosystem carbon fluxes with the overall effect of surface-soil warming (meta-analysis). Moreover, our data on ecosystem carbon fluxes only covered two complete growing seasons (the data on ecosystem carbon fluxes from 2018 was incomplete, with only three dates), and we need longer-term data to study the differences in the response of ecosystem carbon fluxes between different growing stages. Overall, once we have longer annual ecosystem carbon flux data, we could study the differences in carbon flux responses between the growing season and the nongrowing season, as well as the differences between different growth stages. Second, we did not warm the plant communities, despite considering the contribution of deep soils to overall ecosystem carbon fluxes that previous studies had ignored. Therefore, the absence of plant community responses to warming may underestimate or overestimate the response of these fluxes to whole-ecosystem warming (Liang et al., 2013). In conclusion, future studies should prioritize investigating the long-term, year-round response of ecosystem carbon dynamics to whole-soil or whole-ecosystem warming in fragile or carbon-rich ecosystems (especially in the Southern Hemisphere). Such studies would enhance the accuracy of ecosystem model predictions on terrestrial ecosystem carbon cycles under climate warming.

CONCLUSIONS

Overall, our study is the first we are aware of to determine the whole-soil warming effects on ecosystem carbon fluxes. Over 3 years, whole-soil warming elevated GEP and ER, but had no significant impact on NEE in an alpine grassland ecosystem on the Qinghai-Tibet Plateau. Similarly, warming-induced increases in both GEP and ER, with no change in NEE, were also observed in the global meta-analysis of surface-soil warming experiments. Warming-induced shifts in plant community and extended growing season may be the main reasons for the elevated GEP and ER under warming, but the offset between these fluxes led to a minor response of NEE to warming. Moreover, more attention should be paid to the long-term response patterns of ecosystem carbon dynamics throughout the year to whole-soil warming or whole-ecosystem warming, especially in fragile or carbon-rich ecosystems. This focus could help us evaluate and predict future climate-carbon feedback under realistic warming scenarios more accurately.

AUTHOR CONTRIBUTIONS

Ying Chen: Data curation; formal analysis; investigation; writing—original draft. **Mengguang Han**: Writing—review and editing. **Qi Shen**: Writing—review and editing. **Wenkuan Qin**: Data curation; formal analysis; investigation. **Zhenhua Zhang**: Resources; writing—review and editing. **Jin-Sheng He**: Resources; writing—review and editing. **Biao Zhu**: Conceptualization; funding acquisition; methodology; project administration; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at 10.6084/m9.figshare.27283083.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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