Increased CO_2 emissions surpass reductions of non-CO_2 emissions more under higher experimental warming in an alpine meadow

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HIGHLIGHTS

- Warming induced increase in CH_4 uptake and decrease in N_2O emissions
- Warming induced increase in CO_2 emissions dominant total greenhouse gas balance.
- Higher warming induces a significantly positive feedback to climate system.
- Warming-induced CO_2 emissions were most significant in non-growing season.

GRAPHICAL ABSTRACT
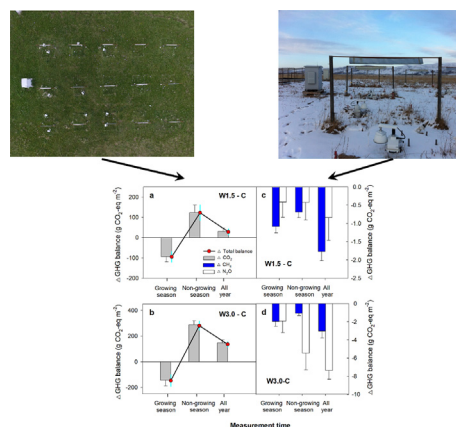
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ABSTRACT

It is well documented that warming can accelerate greenhouse gas (GHG) emissions, further inducing a positive feedback and reinforcing future climate warming. However, how different kinds of GHGs respond to various warming magnitudes remains largely unclear, especially in the cold regions that are more sensitive to climate warming. Here, we concurrently measured carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) fluxes and their total balance in an alpine meadow in response to three levels of warming (ambient, +1.5 °C, +3.0 °C). We found warming-induced increases in CH_4 uptake, decreases in N_2O emissions and increases in CO_2 emissions at the annual basis. Expressed as CO_2-equivalents with a global warming potential of 100 years (GWP100), the enhancement of CH_4 uptake and reduction of N_2O emissions offset only 9% of the warming-induced increase in CO_2 emissions for 1.5 °C warming, and only 7% for 3.0 °C warming. CO_2 emissions were strongly stimulated, leading to a significantly positive feedback to climate system, for 3.0 °C warming but less for 1.5 °C warming. The warming with 3.0 °C altered the total GHG balance mainly by stimulating CO_2 emissions in the non-growing

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Non-growing season
Warming magnitude

season due to warmer soil temperatures, longer unfrozen period, and increased soil water content. The findings provide an empirical evidence that warming beyond global 2 °C target can trigger a positive GHG-climate feedback and highlight the contribution from non-growing season to this positive feedback loop in cold ecosystems.

1. Introduction

The internationally agreed target for avoiding dangerous climate change is a global warming limitation of 2 °C above pre-industrial levels (Rogelj et al., 2016). Three principal greenhouse gases (GHG), CO_2, CH_4 and N_2O, contribute nearly 90% of the forcing to anthropogenic climate warming (IPCC, 2013). Warming may induce positive or negative climate feedbacks by altering ecosystem GHG sources and sinks. Although the sign and magnitude of GHG-climate feedbacks differ among ecosystems and remain poorly characterized, several lines of evidence indicate that cold ecosystems (e.g. ecosystems with mean annual temperature always below 0 °C) should experience an increase of GHG emissions in response to warming (Abbott and Jones, 2015; Wilson et al., 2016; Voigt et al., 2017b; Knoblauch et al., 2018; Voigt et al., 2019), resulting in a net positive feedback (Crowther et al., 2016; Commane et al., 2017; Jeong et al., 2018). Such a strong positive GHG-climate feedback could accelerate the rate of climate change, and would require more efforts to reduce anthropogenic GHG emissions in order to meet a given climate target (Gasser et al., 2018).

To characterize how GHG emissions change in response to warming, many warming experiments have been conducted in cold ecosystems (e.g., tundra, alpine grassland), but most of them have focused solely on the response of CO_2 fluxes (Oechel et al., 2000; Li et al., 2017; Mauritz et al., 2017; Wang et al., 2019b) and less measured concurrent changes of other critical greenhouse gases such as CH_4 and N_2O that also dramatically influence climate conditions (Zhu et al., 2015; Zhao et al., 2017; Chen et al., 2017; Voigt et al., 2017a). CH_4 and N_2O have a 28-times and 298-times greater warming potential than CO_2, respectively, based on a 100-years horizon (IPCC, 2013). Terrestrial ecosystems are globally a net sink of atmospheric CO_2 that captured about 29% of anthropogenic emissions during the last decade (Keenan et al., 2016). Yet, this global CO_2 uptake by terrestrial ecosystems could potentially be offset globally by CH_4 and N_2O emissions (Tian et al., 2016). As such, predicting future climate change feedbacks will necessitate that we understand the relative contribution of changes in these different greenhouse gases over the rest of the century.

Most of previous warming experiments largely perform a single warming level to investigate the differences of GHG between warming and control. How warming magnitude affects GHG fluxes is still limited. Low- and high-level warming can induce different changes in soil temperature, soil water content (Quan et al., 2019; Wang et al., 2020), soil nutrient availability, and vegetation coverage and composition (Chen et al., 2019), which may give rise to differential responses of GHG fluxes to varying warming magnitudes. In an alpine meadow, 2 °C warming decreased ecosystem carbon sink and the effect was insignificant, but 4 °C warming shifted the ecosystem from a net carbon sink to a net carbon source (Zhu et al., 2016). Although such limited study is useful to understanding the seemingly contrasting responses of CO_2 fluxes to warming magnitudes, few studies have compared responses of GHGs, especially CH_4 and NO_2 fluxes, to different warming levels in the field.

Our current understanding of GHG fluxes in response to warming is dominantly limited to measurements obtained during the growing season (Voigt et al., 2017b), mostly due to difficulties in conducting fieldwork in long and severe winter, especially in cold regions. Yet, the greatest impacts of warming are likely to occur in the non-growing season, when plant uptake is negligible and the activity of microorganisms – and thus GHG fluxes – are sensitive to elevated temperature and non-frozen conditions (Zona et al., 2016). Warming during the snow-covered season has been found to enhance GHG exchange through changing soil gases diffusivity (Wilson et al., 2017), increasing microbial activity and altering microbial metabolism (Xue et al., 2016; Feng et al., 2017; Segura et al., 2017), which results in a higher temperature sensitivity and increased GHG emissions to warming (Mastepanov et al., 2008; Koven et al., 2017; Voigt et al., 2017b; Wagner-Riddle et al., 2017).

In summary the three main limitations of ecosystem warming experiments as a tool to quantify the response of GHG emissions to warming in relation to climate targets are: 1) non-CO_2 gas fluxes are very rarely measured and a total GHG balance is still lacking in cold ecosystems, 2) a single warming level is widely applied, usually larger than projected for low warming climate scenarios, thus being less relevant to the goals of the Paris Agreement on Climate, and 3) non-growing season fluxes are rarely measured.

To address these critical research gaps, we set up a new warming experiment in an alpine meadow of the Qinghai-Tibetan Plateau (QTP). We measured all GHG fluxes for a low-level warming (+1.5 °C) (W1.5), a high-level warming (+3.0 °C) (W3.0) against the control treatment at ambient temperature (C). The results allow us to characterize temperature sensitivity of year-round net GHG balance (both losses and gains to the ecosystem). The chosen alpine meadow at high altitude (ca. 3500–4500 m) is representative of a large area of 504,000 km² of cold grasslands ecosystems in the QTP (Ding et al., 2016), which can be used as a test bed for the response of this important ecosystem to warming. Abundant light and precipitation during the growing season can favor plant growth and increase plant productivity, while low temperature in winter strongly limits soil organic matter decomposition. The studied site has high soil carbon and nitrogen density compared to temperate and tropical grasslands in China (Yang et al., 2007; Tang et al., 2018). It has experienced more rapid climate warming than the global average, and mean annual temperature is predicted to increase by 1.5 °C in 2049 and by 2.9 °C at the end of this century compared to the 2000s (Liu et al., 2009), twice the globe average (Piao et al., 2010).

We measured GHG fluxes using opaque chambers all year-round from August 2015 to August 2016. The research questions addressed with these data are (a) what are the differences in the warming responses of CO_2 versus CH_4 and N_2O fluxes, (b) what is the short-term sensitivity of annual GHG fluxes to different warming levels, and (c) what are the differences in the warming responses of GHG fluxes between the growing season and non-growing season.

2. Material and methods

2.1. Study site

The study site (32°48′ N and 102°33′ E; 3500 m a.s.l) was located in Sichuan Province, southwest China and belonged to eastern Qinghai-Tibetan Plateau (Fig. 1a). The climate is continental monsoon-affected. The multiple-year averaged annual precipitation is 750 mm (1961–2017), with approximately 80% occurring from May to September. The mean annual temperature in this region is 1.5 °C.

Alpine meadow is the dominant vegetation type in this region, which covers 27% of the total area (Ding et al., 2016). The vegetation cover typically dominates by *Deschampsia caespitosa*, *Poa pratensis*, *Elymus nutans*, *Agrostis hugoniana*, *Kobresia setchwanensis*, *Oxytropis kansuensis*, *Vicia sepium* and *Potentilla anserina*. The soil is classified as
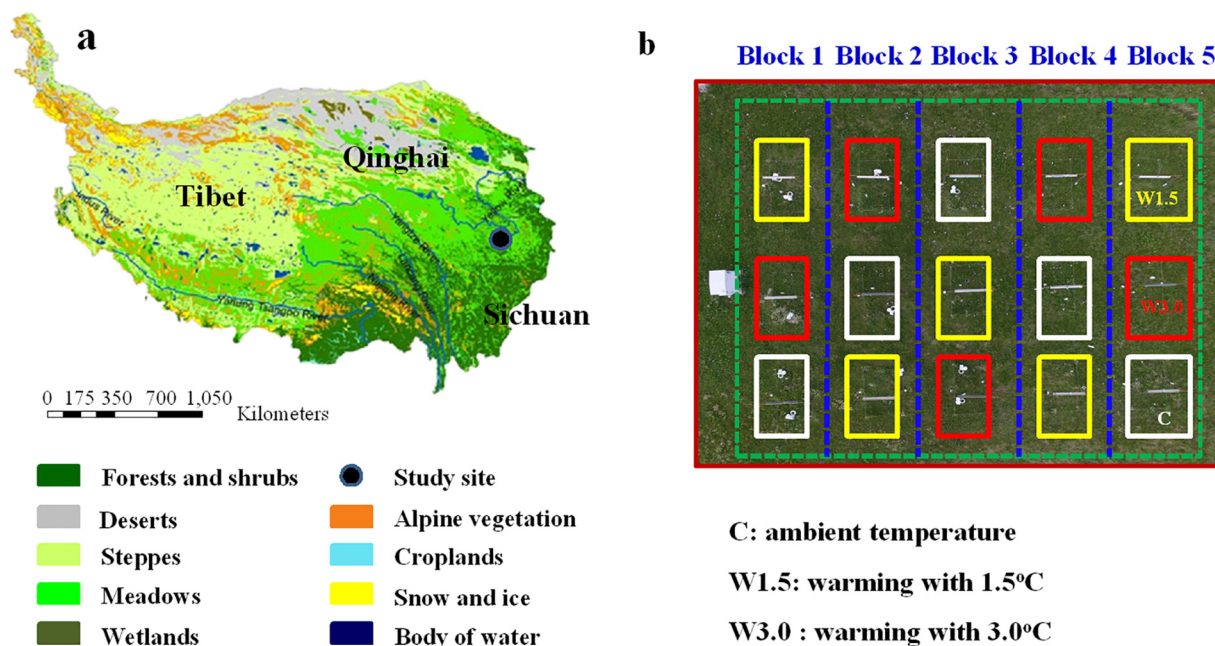
Fig. 1. Study site at the alpine meadow (a) and the schematic diagram of experimental warming design (b).

Cryumbrept according to the U.S. Soil Taxonomy (Shi et al., 2015). Topsoil (0–10 cm) organic carbon is 39 g kg^{-1}, the total nitrogen is 3.1 g kg^{-1} and soil pH value is 6.0 ± 0.1 (Table S1). More detailed description of the study site can be found in elsewhere (Quan et al., 2019).

2.2. Experimental design

The study was implemented as a randomized complete block design. We set up five blocks to replicate each treatment (Fig. 1b) with 3×2 m plots laid out in each of five blocks. Each block was randomly assigned to three warming treatments: ambient temperature (C), low-level warming (W1.5) and high-level warming (W3.0). Two adjacent plots were 3 m apart. The warming plots were heated since June 2014 by infrared radiators with the size of 165×15 cm (Kalglo Electronics Inc., Bethlehem, Pennsylvania, USA) installed 1.5 m off the ground and located in the center of each plot. According to a similar heating experiment in another Tibetan alpine meadow (Liu et al., 2019), the radiation output of the heaters for 1.5 °C warming was set at 1000 W while the radiation output of the heaters for 3.0 °C warming was set at 2000 W. In each ambient temperature plot, to simulate the (small) shading effect of the heaters, a dummy heater with no electrical power output was installed.

2.3. Measurement of ecosystem carbon fluxes using eddy covariance

Net ecosystem exchange (NEE), gross primary production (GPP), and ecosystem respiration (ER) were measured at 30-min intervals using eddy covariance method (Fig. S1a) near the experimental plots from August 2015 to August 2016. The eddy covariance system was installed 2 m off the alpine meadow ground with homogeneous vegetation and soil conditions throughout a patch of 1 km in all directions (Chen et al., 2020). The eddy covariance raw data were quality controlled after data collection using EddyPro 6.2.0 software (LI-COR). Detailed data corrections can be found in the previous study (Zhao et al., 2019).

When the data gaps of NEE were less than 2 h during the growing season daytime, we used linear interpolation method to fill missing NEE. The data gaps with larger blocks of missing data were extrapolated

based on the rectangular hyperbolic regression of daytime NEE against photosynthetic photon flux density (Falge et al., 2001). The missing data of NEE at nighttime were filled by exponential regression of nighttime CO_2 flux with the friction velocity >0.1 m/s against air temperature (Lloyd and Taylor, 1994). GPP was estimated by subtracting NEE from ER. At nighttime, ER was equal to NEE, while at daytime, ER was interpolated by using the exponential regression of NEE at nighttime against the air temperature.

Based on the dynamics of GPP (Fig. S2c) and previous studies in this area (Zhu et al., 2015; Lv et al., 2020), we characterized the non-growing season as the number of days with no-GPP to last from November 2015 to April 2016 with snow-covered landscape, and the remaining observation period as the growing season. In order to make comparisons among treatments more standardized, we defined the same length of growing season for all the three treatments. Previous study suggests that warming may extend the length of growing season (Richardson et al., 2018). We also evaluated the potential impact of warming-induced changes in the growing season length on GHG fluxes (Fig. S11).

2.4. Measurement of carbon dioxide exchange with warming treatments

In each temperature treatment, ecosystem respiration (ER) was measured using automatic opaque chambers at 30-min intervals from August 2015 to August 2016 (Fig. S1c). The missing data due to instrument failures accounted for 6% of year-around data, and were gap filled by the correlation between ER and soil temperature (Fig. 6a). During the non-growing season, carbon dioxide exchange (NEE) is equal to ER, thus daily ER was calculated for the determination of non-growing season cumulative NEE fluxes. In the growing season, daily NEE with warming treatments was extrapolated from daily ER measured by the opaque chambers, based on the relationship between daily ER and daily NEE measured by static transparent chambers (Fig. S5). By using static transparent chambers (Fig. S1b), NEE was measured using LI-6400XT (LI-COR Inc., Lincoln, NE, USA). The detailed description of this method can be found in the previous study (Niu et al., 2013). We measured NEE twice per month between 9:00 and 12:00 local time on sunny days for all treatments from May to October (Fig. S3). Daily NEE

were calibrated as the ratio of daily average value to daytime (9:00–12:00) average value (Wang et al., 2017) based on the diurnal patterns of NEE measured by eddy covariance (Figs. S1a, S4).

2.5. Measurement of methane and nitrous oxide fluxes with warming treatments

In each warming treatment, CH_4 and N_2O fluxes were measured simultaneously with ER using the opaque chambers at 30-min intervals from August 2015 to August 2016 (Fig. S1c). Each chamber is consisted of near infrared laser CO_2/CH_4 analyzer (type: 915-0011) and middle infrared laser N_2O analyzer (type: 913-0014) (Los Gatos Research Inc., San Jose, CA, USA). The missing data of CH_4 and N_2O fluxes accounted for 8% of year-round data, which were gap filled with the linear interpolation method as most data gaps were less than 2 h. Daily CH_4 and N_2O fluxes were calculated and summed for the determination of seasonal and annual cumulative fluxes.

2.6. Seasonal and annual total balance of greenhouse gas fluxes

For the chamber measurements of ER, CH_4, and N_2O fluxes, we randomly selected three replicates from five blocks for each gas measurement due to limited number of chambers. Seasonal cumulative fluxes of NEE, CH_4, and N_2O were obtained by summing up the daily fluxes in the growing and non-growing season, respectively. The annual cumulative gas fluxes were calculated by adding growing and non-growing season cumulative fluxes.

We calculated seasonal and annual total balance of three GHGs (CO_2, CH_4, and N_2O) using global warming potential approach (Tian et al., 2016). We applied a global warming potential for a 100-year horizon (GWP100) with 28 for CH_4 and 298 for N_2O, and without consideration of carbon-climate feedbacks to calculate the total GHG balance (Voigt et al., 2017b).

2.7. Soil microclimate, soil properties, above-and below-ground plant production

In each warming treatment, soil temperature (°C) and soil water content (%, vol) at 10 cm depth were measured by ECH_2O 5TE sensors (Decagon Devices, Pullman, Washington, USA), which can provide continuous measurements. Soil temperature and moisture were logged at 30-min intervals by the Decagon's Em50 data logger.

Five soil samples were collected from 0 to 10 cm in each plot at the end of the experiment in August 2016, mixed to form one composite sample, then passed through a 2-mm mesh sieve and divided into two parts. One part was air-dried to determine soil organic C (SOC) concentration, soil total N (TN) concentration and pH. Another part was stored in 4 °C before measuring soil available N (NH_4^+–N and NO_3^-–N) and microbial biomass. The dried soil subsamples were treated with 1 M HCl at room temperature for 24 h to eliminate the total inorganic C. Then, SOC and TN were analyzed with Vario EL III elemental analyzer (Elementar Analysensystem GmbH, Hanau, Germany). Soil pH was determined by a glass electrode in a 1:2.5 soil-to-water ratio. Soil available N was measured using a continuous-flow auto-analyzer (AA3, Seal Analytical, Germany). Soil microbial biomass C (MBC) and N (MBN) were measured using the chloroform fumigation extraction method (Vance et al., 1987).

All living plants were clipped at the ground level in a 0.5×0.5 m quadrat within each plot, in mid-August 2016 when plant biomass peaked. All plants were oven-dried at 65 °C for 48 h and weighed as aboveground net primary production (ANPP). Root in-growth cores were used to estimate belowground net primary production (BNPP), and the detailed measurement of BNPP can be found in the previous study (Wang et al., 2019a).

2.8. Statistical analyses

All statistical analyses were applied using R3.4.2 (R Core Team, 2016). Prior to the statistical tests, all variables were checked with histograms, density, and Q-Q plots. Shapiro-Wilk normality test was applied to inspect the normality of all variables, in combination with the Levene's test of the homogeneity of variances. The one-way analysis of variance (ANOVA) followed by Tukey's multiple comparisons were used to test the effects of warming treatments on seasonal and annual cumulative GHG fluxes.

Linear mixed-effect models were performed using the R package *lme4* (Bates et al., 2015) to analyze the effects of temperature treatments on average fluxes of daily ER, NEE, CH_4 and N_2O, as well as edaphic and plant variables. Warming treatment was treated as fixed effect, and block was set as random effect. The model was fitted using restricted maximum likelihood estimation, and model validation was assessed by graphically checking residuals. The homoscedasticity of model residuals was inspected by plotting residuals against fitted values. Tukey's HSD tests were further applied to multiple comparisons of the variables, with the function "glht" in the *multcomp* package.

We also examined the relationships between GHG (ER, CH_4, N_2O) fluxes and soil temperature and soil water content. Furthermore, a pairwise correlation analysis was performed using the *corrplot* package to example the correlations of daily GHG fluxes with other abiotic and biotic factors (e.g. SOC, TN, C:N ratio, NH_4^+–N, NO_3^-–N, pH, MBC, MBN, ANPP, and BNPP) at the plot level. The significance was set at $\alpha = 0.05$ throughout the whole statistical analyses.

3. Results

3.1. Abiotic and biotic factors

During the study period, warming increased soil temperature on average by 1.6 °C and 3.0 °C for W1.5 and W3.0 treatment, respectively (all $P < 0.05$, Fig. 2b and Table S1). In response to warming, soil water content decreased on average by 3% in the W1.5 treatment and 7% in the W3.0 treatment (all $P < 0.05$, Fig. 2c and Table S1). Warming did not significantly alter soil properties except soil NO_3^-–N, which decreased under warming ($P < 0.05$, Fig. S6b). Further, soil microbial biomass was not responsive to warming ($P > 0.05$). Warming did not significantly affect ANPP, and only W1.5 significantly increased BNPP (Table S1).

3.2. Warming effects on average fluxes of GHGs

Ecosystem respiration (ER) showed a clear seasonal pattern, with high CO_2 emissions in the growing season and low rates in the non-growing season (Fig. 2d). The ecosystem was a net sink of CH_4 fluxes, which had high uptake rate in the growing season and low value in the non-growing season (Fig. 2e). N_2O fluxes presented no strong seasonal pattern although the ecosystem switched between sink and source of N_2O (Fig. 2f).

Warming did not significantly affect the mean rates of ER, net CO_2 exchange (NEE), CH_4, and N_2O in the growing season, whereas W3.0 treatment significantly increased ER in the non-growing season (warmed: 211 mg CO_2 m^{-2} h^{-1}; control: 145 mg CO_2 m^{-2} h^{-1}) and decreased non-growing season N_2O emissions (warmed: 1.8 μg N_2O m^{-2} h^{-1}; control: 6.6 μg N_2O m^{-2} h^{-1}) as shown in Fig. 3 and Table S2.

3.3. Warming effects on cumulative fluxes of GHGs

On the annual basis, the control plots were net sinks for CO_2 (-79.3 ± 36.3 g CO_2 m^{-2} yr^{-1}, mean ± SE) and CH_4 (-266.3 ± 50.3 mg CH_4 m^{-2} yr^{-1}) but a net source for N_2O (48.7 ± 9.7 mg N_2O m^{-2} yr^{-1}) (Fig. 4). Under the control conditions, cumulative CO_2 emissions in the non-growing season (630.4 ± 66.0 g CO_2 m^{-2})
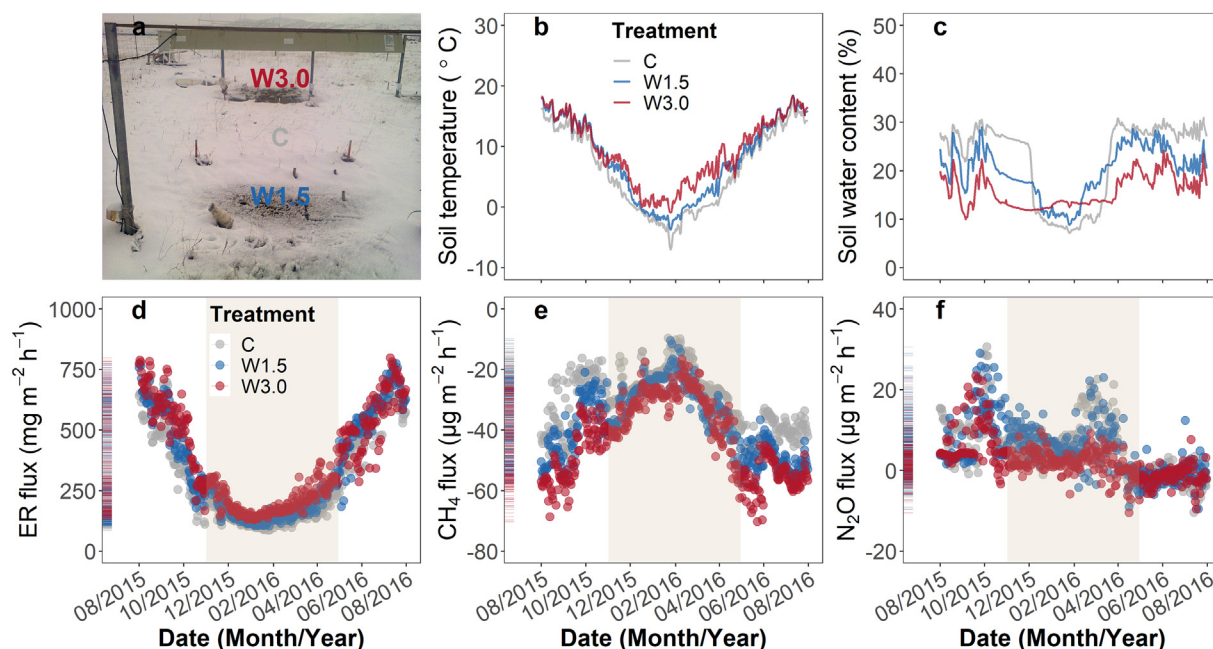
Fig. 2. Experimental plots in the snow-cover season (a), soil temperature (b) and soil moisture (c) at 10 cm depth. Mean fluxes of ecosystem respiration (ER, d), methane (CH₄, e), and nitrous oxide (N₂O, f) using opaque chambers. The colored bands along the Y axes represent value distributions by treatments. C: ambient temperature, W1.5: warming with 1.5 °C above ambient temperature, W3.0: warming with 3.0 °C above ambient temperature. Shade areas represent the duration of non-growing season. Positive and negative values are net release and uptake on greenhouse gas fluxes, respectively.
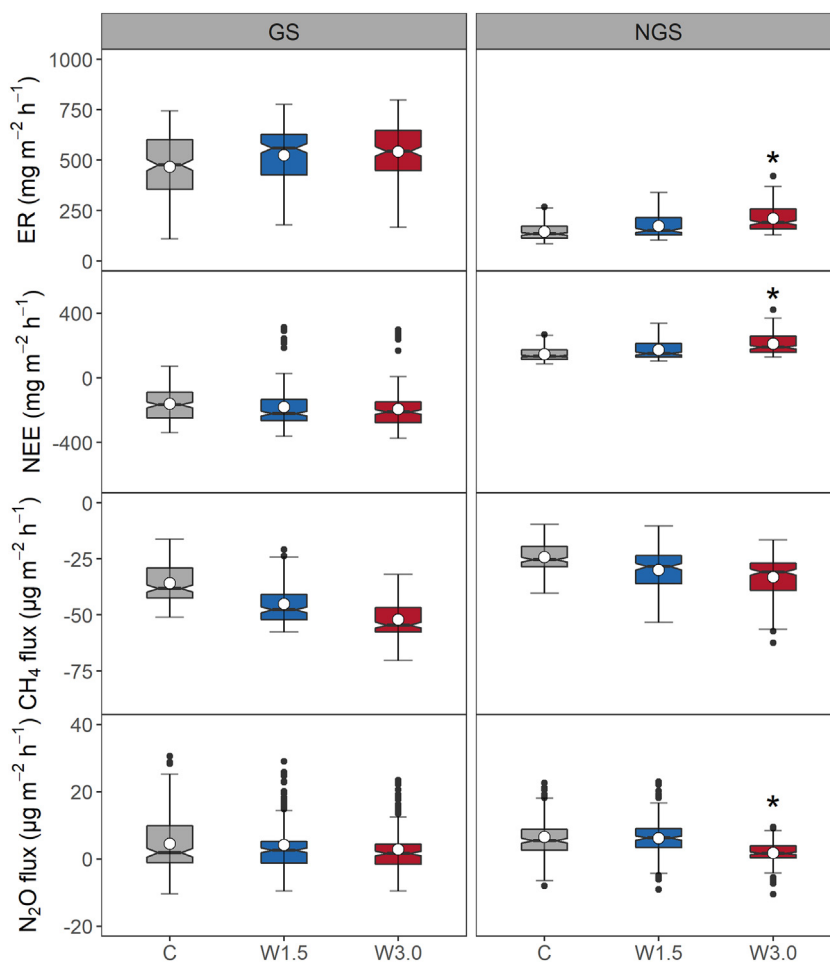
Fig. 3. The effect of warming on average fluxes of ecosystem respiration (ER), net ecosystem exchange (NEE), methane (CH₄), and nitrous oxide (N₂O) in growing season (GS) and non-growing season (NGS). C: control, W1.5: warming with 1.5 °C above ambient temperature, W3.0: warming with 3.0 °C above ambient temperature. "*" indicates significant difference (P < 0.05) from the control conditions.
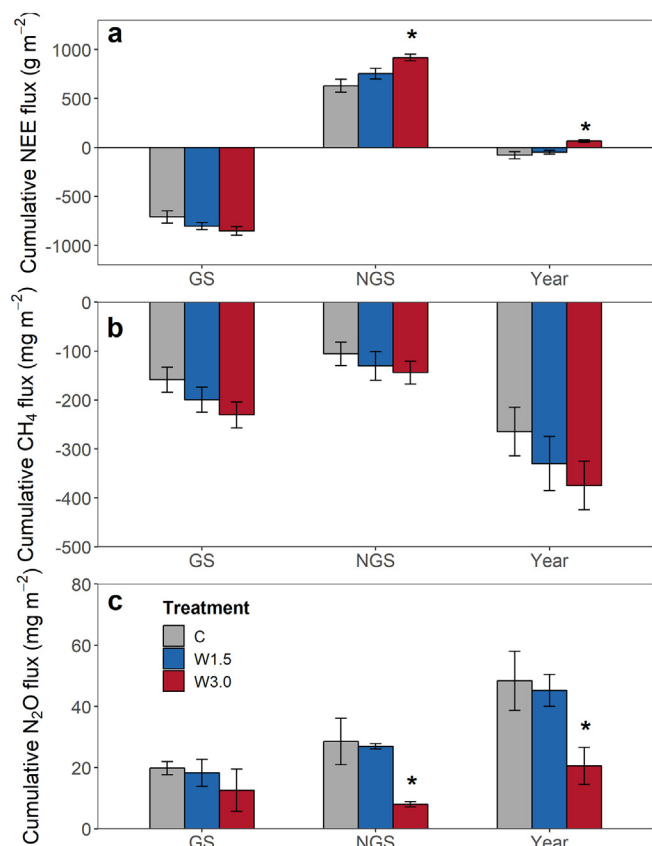
Fig. 4. Seasonal and annual cumulative fluxes (mean $\pm$ SE) of net ecosystem exchange (NEE, a), methane (CH_4, b), and nitrous oxide (N_2O, c). * on the top of error bars represent significant difference between the control and warmed plots at $P < 0.05$. C: ambient temperature, W1.5: warming with 1.5 °C above ambient temperature, W3.0: warming with 3.0 °C above ambient temperature.

Fig. 5. Seasonal and annual total balance of three greenhouse gases in equivalents under different warming treatments. * on the top of error bars represent significant difference between the control and warmed plots at $P < 0.05$. C: ambient temperature, W1.5: warming with 1.5 °C above ambient temperature, W3.0: warming with 3.0 °C above ambient temperature.
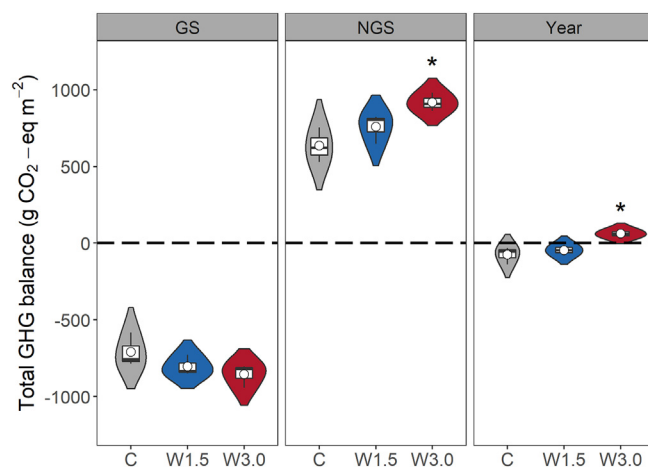
difference between W3.0 and the control was significant ($P = 0.019$, Fig. 4a and Table 1). The annual CH_4 uptake increased by 23% for W1.5 and by 40% for W3.0 (Fig. 4b and Table 1), although the differences between warming and the control were not significant (all $P > 0.05$). Warming decreased annual N_2O emissions by 7% in the W1.5 treatment and the difference between W1.5 and the control was not significant ($P = 0.788$, Fig. 4c and Table 1). The annual N_2O emissions was significantly decreased by 58% in the W3.0 treatment ($P = 0.044$). No evidence of a significant warming effect on the cumulative fluxes of any gases was detected in the growing season (all $P > 0.05$), but W3.0 significantly increased CO_2 emissions and decreased N_2O emissions in the non-growing season (all $P < 0.05$, Fig. 4a, c).

3.4. Total balance of GHG fluxes

Using a 100-year warming potential for CH_4 uptake and N_2O emissions (expressed as CO_2-equivalents, CO_2eqs), we infer a net GHG sink under ambient conditions, with an annual balance of -73.9 ± 32.3 g CO_2-eq m^{-2} yr^{-1} (Fig. 5, Table 1). While CO_2 fluxes dominated the annual total balance of all three GHG fluxes, the annual cumulative CH_4 uptake (-7.5 ± 1.4 g CO_2-eq m^{-2} yr^{-1}) increased the CO_2-eq sink by 10%, whereas the annual cumulative N_2O emissions (12.9 ± 2.6 g CO_2-eq m^{-2} yr^{-1}) offset 17% of the annual CO_2-eq sink (Table 1).

was lower than the cumulative uptake in the growing season (-709.7 ± 63.7 g CO_2 m^{-2}) (Fig. 4a and Table 1). The non-growing season cumulative CH_4 uptake (-105.7 ± 24 mg CH_4 m^{-2}) accounted for 40% of its annual total accumulated flux (Fig. 4b), while cumulative N_2O emissions in the non-growing season (28.5 ± 7.5 mg N_2O m^{-2}) contributed to 59% of its annual budget (Fig. 4c).

Compared to the control, the annual CO_2 sink decreased by 39% for W1.5, although the difference between these two treatments was not significant ($P = 0.496$). The ecosystem was switched from a net sink to a net source of CO_2 for W3.0 (66.9 ± 13.2 g CO_2 m^{-2} yr^{-1}), and the

Table 1
Seasonal and annual balance of CO_2, CH_4 and N_2O (mean $\pm$ SE) in CO_2-equivalents under different warming treatments. C: ambient temperature, W1.5: warming with 1.5 °C above ambient temperature, W3.0: warming with 3.0 °C above ambient temperature. The values in the brackets represent the percentage contribution of each gas to the total greenhouse gas balance. Positive and negative values are net release and uptake on greenhouse gas fluxes, respectively. Different letters in the same row indicate significant differences among warming treatments ($P < 0.05$).

	Fluxes	C	W1.5	W3.0	Change with warming	
					W1.5-C	W3.0-C
Growing season	CO_2 (g CO_2 m^{-2})	-709.7 ± 63.7 (100.1%)	-802.8 ± 37.3 (99.9%)	-851.6 ± 44.1 (99.6%)	-93.1	-141.9
	CH_4 (g CO_2-eq m^{-2})	-4.5 ± 0.7 (0.6%)	-5.6 ± 0.7 (0.7%)	-6.5 ± 0.7 (0.8%)	-1.1	-2.0
	N_2O (g CO_2-eq m^{-2})	5.3 ± 0.6 (-0.7%)	4.9 ± 1.1 (-0.6%)	3.3 ± 1.8 (-0.4%)	-0.4	-2.0
	Total GHG balance	-708.9 ± 63.2 a	-803.5 ± 37.8 a	-854.8 ± 43.0 a	-94.6	-145.9
Non-growing season	CO_2 (g CO_2 m^{-2})	630.4 ± 66.0 (99.3%)	754.3 ± 55.3 (99.5%)	918.5 ± 34.9 (100.2%)	$+123.9$	$+288.1$
	CH_4 (g CO_2-eq m^{-2})	-3.0 ± 0.7 (-0.5%)	-3.6 ± 0.8 (-0.4%)	-4.0 ± 0.7 (-0.4%)	-0.6	-1.0
	N_2O (g CO_2-eq m^{-2})	7.6 ± 2.0 (1.2%)	7.1 ± 1.6 (0.9%)	2.1 ± 0.2 (0.2%)	-0.5	-5.5
	Total GHG balance	635.0 ± 68.2 a	757.8 ± 56.1 a	916.6 ± 34.0 b	$+122.8$	$+281.6$
Year	CO_2 (g CO_2 m^{-2})	-79.3 ± 36.3 (107.3%)	-48.5 ± 19.5 (106.1%)	66.9 ± 13.2 (108.3%)	$+30.8$	$+146.2$
	CH_4 (g CO_2-eq m^{-2})	-7.5 ± 1.4 (10.1%)	-9.2 ± 1.5 (20.1%)	-10.5 ± 1.4 (-17.0%)	-1.7	-3.0
	N_2O (g CO_2-eq m^{-2})	12.9 ± 2.6 (-17.4%)	12.0 ± 1.4 (-26.3%)	5.4 ± 1.6 (8.7%)	-0.9	-7.5
	Total GHG balance	-73.9 ± 32.3 a	-45.7 ± 20.3 a	61.8 ± 13.1 b	$+28.2$	$+135.7$

The ecosystem was found to be a weaker sink of GHGs (-45.7 ± 20.3 g CO_2-eq m^{-2} yr^{-1}) for W1.5 compared to the control, although the difference between these treatments was not significant ($P = 0.501$). The ecosystem was found to switch to a significant GHG source of 61.8 ± 13.1 g CO_2-eq m^{-2} yr^{-1} ($P = 0.038$) for W3.0 compared to the control. The largest effect of W3.0 treatment on the annual total GHG balance was mainly attributed to changes in the non-growing season rather than that in the growing season (Fig. 5). CH_4 and N_2O cumulative uptake enhancement or emission reductions contributed relatively less than CO_2 to the total balance of GHGs (Table 1). The reductions of CH_4 and N_2O (CO_2eqs) offset only 9% of the warming-induced increase in CO_2 emissions in W1.5, against only 7% in W3.0. Thus, W3.0 treatment inducing net GHG source was mainly due to the increase in CO_2 emissions in the non-growing season (Fig. S7).

3.5. Factors regulating GHG fluxes

Ecosystem respiration (ER) increased exponentially with soil temperature (ST), with a temperature sensitivity (the factor by which the increase in the CO_2 emissions for a 10 °C increase in temperature, Q_{10}) of 2.8 (Fig. 6a). ER also showed a quadratic relationship with soil water content (SWC) (Fig. 6b), with a peak when SWC was approximately 20–25%. The CH_4 uptake rate increased with ST ($Q_{10} = 1.5$), and reached a maximum peak at intermediate SWC of approximately 21% (Fig. 6c, d). The mean N_2O flux showed significant but weak correlations with ST and SWC (Fig. 6e, f). Pairwise correlation analysis also

showed that N_2O flux presented a significantly positive correlation with either soil NH_4^+–N or NO_3^-–N (Fig. S8).

4. Discussion

This study provides in situ evidence that warming-induced increase in CO_2 emissions exceeds the enhancement of CH_4 uptake and reduction of N_2O emissions in this relatively cold ecosystem. CO_2 fluxes dominate the total GHG balance, resulting in a significantly positive feedback to climate system, for 3.0 °C warming but less for 1.5 °C warming. Results from this field study also show that warming has no significant effect on net CO_2 exchange in the growing season, although 1.5 °C warming and 3.0 °C warming increase NEE by 13% and 20%, respectively compared to the control. We show however that CO_2 emissions are more stimulated by 3.0 °C warming compared to the control and 1.5 °C warming during the non-growing season, a response that has not been characterized in most previous studies.

4.1. Warming effects on greenhouse gas fluxes and total GHG balance

On the annual basis, warming increased CH_4 uptake and decreased N_2O emissions (Fig. 4 and Table 1), but these effects were surpassed by warming-induced increase in CO_2 emissions (Table 1). This explains why the ecosystem switched to a net GHG source for W3.0, but remained a GHG sink for W1.5 (Fig. 5), which suggests a strong positive feedback of GHG fluxes under high-level warming for the studied site.
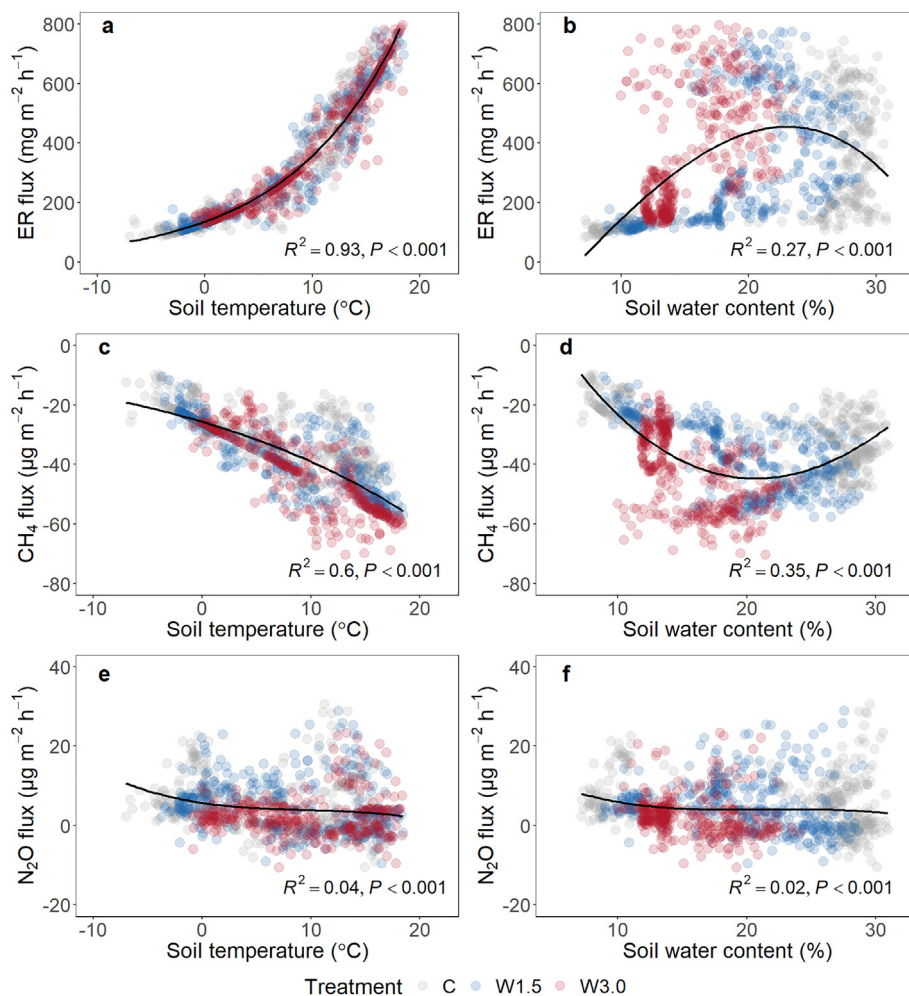
Fig. 6. Soil temperature (°C) and soil water content (v/v, %) at 10 cm depth in relation to daily mean fluxes of ecosystem respiration (ER, a, b), methane (CH_4, c, d), and nitrous oxide (N_2O, e, f) using opaque chambers across different warming treatments. C: ambient temperature, W1.5: warming with 1.5 °C above ambient temperature, W3.0: warming with 3.0 °C above ambient temperature.

The findings are consistent with a previous study in the Arctic showing that CO_2 fluxes dominated the total GHG balance in a subarctic tundra and that warming shifted the net GHG budget toward a net source of CO_2 equivalents in vegetated tundra surfaces (Voigt et al., 2017b). Our observed warming-induced stimulation of CO_2 emissions is also in line with previous studies (Dorrepaal et al., 2009; Schädel et al., 2016; Melillo et al., 2017), especially at high-latitude and high-altitude regions with large stocks of soil organic carbon (Crowther et al., 2016). Soil temperature exhibited the strongest positive effect on CO_2 release (Fig. 6a). CO_2 emissions were expected to increase by a factor of 2.8 for a 10 °C warming, which is similar to other cold areas, but higher than temperate and warm regions (Koven et al., 2017).

Although the response of CO_2 fluxes dominated the annual total balance of all three GHGs, CH_4 uptake and N_2O emissions still played an important role. CH_4 uptake, expressed as CO_2 equivalents, increased by 10% of the CO_2-eq sink and N_2O decreased 17% of the CO_2-eq sink under ambient conditions (Table 1). This indicates that an overall budget of three gases in combination is crucial to accurately evaluate the net GHG balance of ecosystems (Tian et al., 2016).

Warming increased CH_4 uptake was closely correlated with soil temperature and soil water content (Fig. 6c, d). It has reported that warming-induced increase in soil temperature directly enhances methanotrophic and decreases methanogen abundance (Zheng et al., 2012; Peltoniemi et al., 2016), thus resulting in an enhancement of soil CH_4 uptake. Furthermore, a lower soil water content was found under warming, which could have decreased anaerobic conditions by increasing air permeability and O_2 diffusion in the soil (Chen et al., 2017), favoring microbial oxidation of CH_4 in the soil profile (Dijkstra et al., 2013). Warming decreased annual N_2O emissions, likely related to changes in N-substrate availability (Xue et al., 2016; Dawes et al., 2017). The N_2O production is mainly determined by nitrification and denitrification processes occurring simultaneously (Butterbach-Bahl et al., 2013). We found that soil mineral nitrogen decreased by 24–34% in the warming plots (Fig. S6), probably due to plant growth leading to greater nitrogen uptake. Therefore, a decreased N-substrate availability for nitrification and denitrification could be one reason for limiting N_2O emissions under warming.

4.2. Non-growing season CO_2 emissions dominate warming response of total GHG balance

The annual net CO_2 balance depends on the balance between uptake by the vegetation in the growing season and release in the non-growing season (Schuur et al., 2013). Changes in CO_2 uptake under warming were extensively addressed in previous field experiments and global meta-analysis (Niu et al., 2011; Natali et al., 2014; Wang et al., 2019b). However, whether and how warming affects CO_2 loss in the non-growing season remains highly uncertain (Webb et al., 2016). A recent study across the circum-Arctic region has concluded that winter CO_2 release is larger previously thought before and may be outpacing CO_2 uptake in the growing season (Natali et al., 2019). As the average global temperature continues to rise in the foreseeable future, it is urgent to understand the sensitivity of CO_2 loss to warming during the non-growing season. Our field experiment showed that CO_2 uptake was not significantly responsive to warming (Fig. 4). In contrast, we found a significant increase of CO_2 emissions in the non-growing season for W3.0 compared to the control and W1.5, whereas previous studies were found to be too scarce to characterize this non-growing season response. Our results for the non-growing season agree with the limited evidence for an Alaska tundra where warming significantly increased the rates of CO_2 release during the winter time and triggered a positive feedback to climate system on the annual basis (Xue et al., 2016). Recent evidence from observation, in situ measurements, and modeling all have also demonstrated that warm winters can cause high CO_2 loss to either neutralize the positive effect of warming on the annual net CO_2

balance or induce a positive ecosystem-climate feedback (Liu et al., 2020; Sanders-DeMott et al., 2020).

Warming-induced stimulation of CO_2 release in the non-growing season could be mainly due to warmer soil temperatures, longer unfrozen period, and increased soil water content compared to the control conditions. CO_2 emissions can occur at temperatures as low as −20 °C in Arctic regions (Natali et al., 2019), as long as soil water is unfrozen and carbon is available to microbial decomposition (Segura et al., 2017). In our analysis, warming delayed the onset of soil freezing and advanced the timing of thawing in the subsequent spring (Fig. 2b), both of which stimulated CO_2 release in periods when most biota would be otherwise inactive. Specifically, in comparing with the control, the duration of soil frozen period was shortened by 32 days for W1.5. W3.0 treatment nearly made the soil unfrozen, thus almost suppressing the frozen duration (Fig. 2b, c). The duration of unfrozen days explained 81% of changes in the CO_2 emissions during the non-growing season (Fig. S9). Generally, soil freezing keeps CO_2 emissions low by reducing microbial biomass and enzyme activities (Davidson and Janssens, 2006; Sorensen et al., 2016), decreasing live root biomass (Reinmann and Templer, 2015), and slowing gas diffusion under reduced water content (Elberling and Brandt, 2003). Thawing of frozen soil stimulates CO_2 emissions due to increased microbial degradation and root decomposition (Schuur et al., 2008). Although warming did not affect soil microbial biomass in summer, we may have found a big influence of warming on soil microbial biomass in winter, contributing to the large increase in CO_2 emissions in the non-growing season. Warming also decreased snow thickness (Fig. S10) and increased soil water content in severe cold period (Fig. 2c), which makes soil substrate and enzymes more accessible to sustain microbial decomposition of soil carbon (Segura et al., 2017). The melted snow cover and thus removal of the insulating layer due to warming have resulted in more soil warming in the non-growing season than the growing season and contributed most to the increased CO_2 emissions. Furthermore, the underlying mechanisms such as warming induced changes in freeze-thaw cycles that may influence CO_2 release also deserve further investigations (Wang et al., 2020). Compared with 1.5 °C warming, overall, the nearly unfrozen soil under 3.0 °C warming caused larger contribution of CO_2 emissions in non-growing season and thus resulted in a positive feedback to climate warming.

When the growing-season length was extended by 5 days for W1.5 and 10 days for W3.0 according to a recent study on phenology changes of alpine meadow under warming (Suonan et al., 2017), the warming effects on GHGs did not change compared with those using the same growing-season duration (Fig. S11), partly due to that the GHG fluxes were small during the transition between growing and non-growing seasons. As such, these results highlight the importance of understanding non-growing season carbon fluxes in order to generate a mechanistic understanding of changes in soil carbon dynamics. This level of understanding is critical to guide modeling efforts to accurately reflect the land carbon-climate feedback over the rest of the century (Schuur et al., 2015; Zona et al., 2016; Commane et al., 2017).

4.3. Implications and limitations

The 2 °C warming target of the Paris Agreement on Climate refers to the global average temperature (Meinshausen et al., 2009), although there are some differences between IPCC reports on whether land and ocean or land only temperature should be considered (Millar et al., 2017), the QTP region warms two times faster than the rest of the globe. A global warming of 1.5 °C is equivalent to a regional warming of 3 °C and a global warming of 2 °C to a regional warming of 4 °C in the QTP. Thus, our results suggest that even a 1.5 °C warming could turn the QTP cold grasslands into a net GHG source and contribute to a positive GHG-climate feedback. Our results are limited to a one-year observation and the long-term response of QTP cold grasslands is unknown as on longer time scales, soil carbon decomposition and non-

CO_2 gases fluxes will depend on plant and microbial N availability, soil moisture and microbial activity and the balance between growing and non-growing seasons GHG fluxes will further change over time. Our results still indicate a fast response of QTP grasslands to warming, suggesting that the occurrence of extremely warm winters can strongly affect their GHG balance. Although the extrapolation of NEE from the measurements of ER in the growing season may report some uncertainties, this will not alter the conclusion that the higher warming induces a stronger positive feedback to climate system by stimulating the measurements of CO_2 emissions in the non-growing season.

5. Conclusions

In summary, this study contributes to filling a critical knowledge gap in our understanding of the impact of warming magnitude on ecosystem feedback and highlights the contribution of non-growing season to the positive GHG-climate feedback loop. Our results strongly suggest that keeping warming below the proposed 2 °C globally is essential not only for economic and social reason, but also for ecosystem security and alleviating this positive feedback.

Data availability statement

All data needed to evaluate the conclusion in the paper are present in the paper and/or the Supporting Information. Additional data related to this paper may be requested from corresponding author.

CRediT authorship contribution statement

Jinsong Wang: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Project administration. **Quan Quan:** Formal analysis, Investigation. **Weinan Chen:** Software, Formal analysis, Investigation. **Dashuan Tian:** Software, Formal analysis, Investigation. **Philippe Ciais:** Validation, Writing – review & editing, Supervision. **Thomas W. Crowther:** Validation, Writing – review & editing, Supervision. **Michelle C. Mack:** Validation, Writing – review & editing, Supervision. **Benjamin Poulter:** Validation, Writing – review & editing, Supervision. **Hanqin Tian:** Validation, Writing – review & editing, Supervision. **Yiqi Luo:** Validation, Writing – review & editing, Supervision. **Xuefa Wen:** Methodology, Validation, Writing – review & editing, Supervision. **Guirui Yu:** Validation, Writing – review & editing, Supervision. **Shuli Niu:** Conceptualization, Methodology, Validation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.144559.

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