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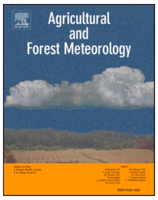

Effects of warming and clipping on CH_4 and N_2O fluxes in an alpine meadow

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ABSTRACT

Methane (CH_4) and nitrous oxide (N_2O) are two greenhouse gases with much more warming potential than carbon dioxide (CO_2). However, there have been less studies on their responses to climate warming and land use practices, such as hay harvest in grasslands. Especially, their fluxes are not well estimated during the nongrowing season. In this study, we investigated year-round (August 2015–August 2016) continuous measurements of CH_4 and N_2O fluxes in response to simulated warming, clipping (as a mimic of hay harvest), and their interaction in an alpine meadow on the Qinghai-Tibetan Plateau. Compared to the control, warming alone and in combination with clipping significantly increased CH_4 uptake by 42% and 51%, respectively, on the annual basis. Warming alone also significantly decreased year-round N_2O emission by 57% relative to that under control. However, clipping alone did not affect CH_4 and N_2O fluxes during the study period, and no significant interactive effect of clipping and warming was detected. Furthermore, warming had larger effects on CH_4 uptake but smaller effects on N_2O emission in the growing than nongrowing season. We also found that the responses in CH_4 and N_2O fluxes to different treatments were regulated by changes in soil temperature and moisture. Based on sustained global warming potential approach and expressed as CO_2-equvalents, the ecosystem switched from a net source of these two gases in the control (1.2 g CO_2-eq m^{-2}) to a net sink in warming (-11.3 g CO_2-eq m^{-2}) and its combination with clipping (-9.9 g CO_2-eq m^{-2}). The findings highlight the importance of understanding greenhouse gas fluxes in the nongrowing season and suggest the increase of CH_4 uptake and reduction in N_2O emission under climate warming will benefit ecosystem feedback and help mitigate climate change.

1. Introduction

Over the past century, we have witnessed the boom of greenhouse gas concentrations in the atmosphere, which contributes nearly 90% of anthropogenic climate warming (IPCC, 2007). A line of evidence suggests that warming can cause additional greenhouse gas emissions originating from terrestrial ecosystems (Stocker et al., 2013; Voigt et al., 2017a), inducing a positive feedback to climate system and accelerating the rate of global warming. So far most warming experiments have primarily focused on carbon dioxide (CO_2) fluxes (Crowther et al., 2016; Xue et al., 2016), and less attention has been paid to other pivotal gases such as methane (CH_4) and nitrous oxide (N_2O) (Dijkstra et al., 2012), although the global warming potential of CH_4 is 28 times and N_2O is 265 times larger than that of CO_2 based on the 100-year horizon (IPCC, 2013). Therefore, a comprehensive understanding of CH_4 and N_2O fluxes–more efficient in aggravating warming than CO_2 fluxes–would be crucial to assess feedbacks between the biosphere and atmosphere in a warming world.

CH_4 and N_2O exchanges with the atmosphere are the balance between their production and consumption, both of which are regulated by an array of abiotic and biotic factors, mainly including soil microclimate, substrate quantity and quality, gas diffusion, plant community composition, soil nutrient availability, and microbial activity (Livesley et al., 2011; Yang et al., 2018; Luan et al., 2019). Warming could directly

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and indirectly change these controlling factors, thereby influencing the magnitude and direction of CH_4 and N_2O fluxes. Atmospheric CH_4 uptake by grasslands, covering nearly one quarter of the global surface, is a prominent global sink of atmospheric CH_4 (Lin et al., 2015). Although some efforts have been made to quantify the effect of warming on CH_4 fluxes in grasslands, the results are disparate, including stimulation of CH_4 consumption (Zheng et al., 2012; Lin et al., 2015; Zhu et al., 2015), inhibition of CH_4 consumption (Dijkstra et al., 2013), and no change (Zhao et al., 2017; Wu et al., 2020). Results from manipulative experiments have also illustrated that warming can increase N_2O emission in grasslands (Cantarel et al., 2012; Chen et al., 2017a), possibly due to enhanced soil N cycling and microbial activity under elevated temperature (Shi et al., 2012; Bai et al., 2013). Due to warming induced soil drying and inhibited denitrification rate, in contrast, temperature increases have found to decrease N_2O emission (Hu et al., 2010). Meantime, the observations of experimental studies and meta-analysis also demonstrate that N_2O emission is not responsive to warming in grasslands (Zhu et al., 2015; Zhao et al., 2017; Li et al., 2020). The inconsistent and even contradictory findings could be largely ascribed to multiple processes controlling CH_4 and N_2O exchanges, thereby making it intractable to predict the fate of their atmospheric concentrations.

Clipping is one of the prevailing land use practices mimicking hay harvest in grasslands, and has a potential to considerably influence CH_4 and N_2O fluxes via directly reducing vegetation coverage and litter accumulation at the soil surface, changing soil microclimates, or indirectly affecting plant growth, soil C and N cycling, and soil microbial community (Niu et al., 2013; Zhang et al., 2015). Despite these processes appear to have substantial effects on CH_4 and N_2O exchanges, their influences are controversial and the underlying mechanisms remain elusive. For instance, clipping has enhanced CH_4 uptake and suppressed N_2O emission in a semi-arid grassland, largely due to clipping induced increase in soil temperature and decrease in soil inorganic N (Lu et al., 2015). In another semi-arid grassland, however, clipping has stimulated CH_4 uptake via affecting biotic factors such as plant aboveground net primary production and soil microbial biomass (Zhang et al., 2012). Furthermore, it is suggested that clipping has no effects on CH_4 and N_2O fluxes in an alpine meadow (Zhu et al., 2015). More importantly, although the previous studies have advanced our understanding of clipping effects on CH_4 and N_2O fluxes, the interactive effect of clipping with warming on CH_4 and N_2O exchanges is poorly understood and largely uncertain.

Another uncertainty is the seasonal variations of greenhouse gas fluxes. Our current understanding of greenhouse gas exchanges is mostly based on the field studies in growing season. However, few measurements have been conducted in nongrowing season, especially in cold ecosystems where soil microbial activity is sensitive to temperature increases (Sommerfeld et al., 1993; Zona et al., 2016; Natali et al., 2019), possibly resulting in the pulse of CH_4 and N_2O fluxes in winter time (Mastepanov et al., 2008; Wagner-Riddle et al., 2017). Therefore, the warming effects on CH_4 and N_2O fluxes in the nongrowing season could be larger than that during the growing season. For instance, elevated temperature has increased CH_4 uptake by 31%-39% in the growing season, but enhanced it by 162% in the winter period in an alpine meadow (Lin et al., 2015). Similarly, the positive warming effect on N_2O emission in the growing season is almost counteracted by the negative warming effect in the nongrowing season, giving rise to a neutral effect on N_2O emission based on annual scale in the same region (Hu et al., 2010). Collectively, the absence of cold season fluxes can induce large uncertainties in assessing annual budgets and evaluating the ecosystem-climate feedbacks (Treat et al., 2018).

In this study, the effects of warming and clipping and their interaction on year-round CH_4 and N_2O fluxes were investigated in an alpine meadow on the Qinghai-Tibetan Plateau, which is among the regions of the most sensitive to climate warming because the temperature in this area has increased at a rate of twice the global average (Chen et al., 2013). The alpine meadow is also one of important model systems for understanding the response of cold ecosystems to elevated temperature because of its high altitude and long winter time that have a high sensitivity to ongoing warming. The main purposes of this study are to investigate: (1) the effects of warming, clipping, and their interaction on CH_4 and N_2O fluxes; (2) the differences in the responses of CH_4 and N_2O fluxes between growing and nongrowing seasons; (3) the abiotic and biotic factors that regulate warming and clipping effects on CH_4 and N_2O exchanges in this alpine meadow.

2. Materials and methods

2.1. Study site

The study was conducted in the Institute of Qinghai-Tibetan Plateau (QTP) in Southwest Minzu University (32°48′ N and 102°33′ E; 3500 m a.s.l), which is located in Hongyuan County on the eastern edge of the QTP (Fig. S1a). The climate is continental monsoon-affected, with a mean annual precipitation of 750 mm, of which more than 80% distributes from May to September. The site has a mean annual temperature of 1.1°C. Soils are classified as Gelic Cambisols, with top soil (0-10 cm) organic carbon content of 39 g kg^{-1} and total nitrogen content of 3.1 g kg^{-1} (Table 1). This region has a typical vegetation type of alpine meadow, and the dominant species are composed of *Anemone rivularis, Deschampsia caespitosa, Kobresia setchwanensis*, and *Carex schneideri*. More detailed information on the study site can be found in the previous study (Quan et al., 2019).

2.2. Experimental design

The study was implemented as a randomized complete block design with five blocks as replicates. Two pairs of 3×2 m plots were established in each block. One plot was assigned as control, which was exposed to ambient conditions. The other plot was warmed continuously since June 2014 by 165×15 cm infrared radiators (MSR-2420, Kalglo Electronics Inc., Bethlehem, Pennsylvania, USA), which were suspended 1.5 m above the ground. The warming plot was set at an output power of around 2,000W and could increase soil temperature by an expectation of 3°C. In each control plot, a dummy heater was also installed with no power output to simulate the shading effect. The adjacent two plots were 3 m apart. As the infrared radiators primarily warming soil not the air (Kimball, 2005), we did not measure air temperature or plant surface temperature. From a similar warming experiment in another alpine meadow which reported that warming with infrared heaters increased air temperature by approximate 0.8°C on average at 30 cm above the soil surface (Liu et al., 2019), we estimated that our infrared radiators could increase air temperature by *c.* 0.8-1.0°C.

Each 3×2 m plot was divided into two 1.5×2 m subplots, of which one was unclipped and the other one was clipped at the soil surface in mid-August in each year since 2014. The clipped materials were taken away and not returned back from each subplot to mimic hay harvest, a commonly practiced land use in grasslands (Jia et al., 2012; Niu et al., 2013). Therefore, a total of four treatments were explored in this study: ambient temperature and unclipping (control, C), warming and unclipping (W), ambient temperature and clipping (CL), warming and clipping (WCL).

2.3. Measurement of CH_4 and N_2O fluxes

Three replicates for each treatment were randomly selected from five blocks to continuously measure CH_4 and N_2O fluxes between August 2015 and August 2016, using the automatic opaque chambers at 30-min intervals (Fig. S1b). Each chamber was equipped with near infrared laser CH_4 analyzer (type: 915-0011) and middle infrared laser N_2O analyzer (type: 913-0014) (Los Gatos Research Inc., San Jose, CA, USA) for flux monitoring. The chamber volume is 80 cm^3 and the lids down for 3 minutes for each measurement. The missing data of CH_4 and N_2O fluxes

Table 1
Abiotic and biotic factors under different treatments (Mean ± SE).

Treatment	ST	SM	SOC	TN	C:N ratio	NH_4^+–N	NO_3^-–N	pH	MBC	MBN	ANPP	BNPP
C	6.3±0.1a	23±1.1a	3.9±0.1a	0.31±0.01a	12.5±0.2a	19.0±4.9a	3.2±1.1a	6.05±0.14a	626±111a	44±18a	289±5a	376±21a
W	9.3±0.2b	16±0.6b	4.1±0.4a	0.33±0.03a	12.6±0.4a	13.4±2.8ab	1.1±0.8b	6.06±0.02a	791±124ab	71±10ab	281±18ab	433±42a
CL	6.4±0.2a	21±0.8c	3.7±0.5a	0.30±0.03a	12.4±0.3a	12.0±1.1ab	0.9±0.2b	6.10±0.06a	784±81ab	70±14ab	254±7bc	508±108a
WCL	9.9±0.2c	13±0.5d	3.7±0.3a	0.29±0.02a	12.6±0.3a	11.1±0.1b	0.8±0.1b	6.10±0.03a	850±45b	94±3b	230±7c	555±32a

Different letters in each column represent significant differences among treatments ($P<0.05$). ST: soil temperature (°C) at 10 cm depth; SM: soil moisture (%) at 10 cm depth; SOC: soil organic carbon content (%); TN: soil total nitrogen content (%); NH_4^+–N: soil ammonium nitrogen content (mg kg^{-1}); NO_3^-–N: soil nitrate nitrogen content (mg kg^{-1}); MBC: soil microbial biomass carbon (mg kg^{-1}); MBN: soil microbial biomass nitrogen (mg kg^{-1}); ANPP: aboveground net primary production (g m^{-2}); BNPP: belowground net primary production (g m^{-2}). C: control; W: warming; CL: clipping; WCL: warming and clipping.

due to instrument failures accounted for 8% of year-round data, which were gap filled with the linear interpolation method as most data gaps were less than two hours. Daily mean values of CH_4 and N_2O fluxes were calculated and summed for determination of cumulative fluxes in growing season (from May to October), nongrowing season (from November to April), and the whole study period. CO_2 flux was also monitored along with the measurement of CH_4 and N_2O fluxes. Since CO_2 fluxes have been widely studied, this study mainly focused on the annual CH_4 and N_2O fluxes that were always neglected in alpine grasslands in the previous studies.

2.4. Soil microclimate monitoring

In conjunction with measurement of CH_4 and N_2O fluxes, soil temperature (°C) and soil moisture (%, vol) at 10 cm, 20 cm, and 40 cm depth were continuously monitored in each treatment using ECH$_2$O 5TE sensors (Decagon Devices, Pullman, Washington, USA). Soil temperature and moisture were logged at 30-min intervals by the Decagon's Em50 data logger.

2.5. Soil sampling and analysis

Soil samples for measuring soil properties were collected at 0-10 cm depth in August 2016. Five soil cores (6 cm in diameter) were taken away from each subplot, mixed well to form one composite sample, and subsequently passed through a 2-mm mesh sieve and divided into two parts. One part was stored at 4°C prior to the analysis of soil inorganic N (ammonium, NH_4^+–N; nitrate, NO_3^-–N), microbial biomass C (MBC), and microbial biomass N (MBN). The other part was air-dried for determining soil organic C content (SOC), soil total N content (TN), C:N ratio and pH.

Total soil organic C and N contents were analyzed by Vario EL III elemental analyzer (Elementar Analysensystem GmbH, Hanau, Germany). Soil pH was measured with a glass electrode in a 1:2.5 soil-to-water ratio. The NH_4^+–N and NO_3^-–N concentrations were measured on 5g fresh soil samples, using a continuous-flow auto-analyzer (AA3, Seal Analytical, Germany). Soil MBC and MBN were determined using the chloroform direct-fumigation extraction method (Vance et al., 1987).

2.6. Plant sampling and analysis

Above-ground vegetation was sampled in a 0.5 × 0.5 m quadrat in each subplot in mid-August 2016 when biomass reached its peak. All plants in the quadrat were clipped at the soil surface. Live plants were oven-dried at 70°C for 48h and weighed as an estimate of aboveground net primary production (ANPP).

Root in-growth method was applied to evaluate belowground net primary production (BNPP). Specifically, two soil cores at 0-40 cm depth were collected in each subplot at end of growing season in 2015. The collected soils were passed through a 1-mm mesh sieve to remove visible roots, and the sampled soils without roots were then sealed in a 1-mm-poresize nylon mesh bag and refilled the original holes. At the end of the growing season in 2016, we harvested the root in-growth samples in the mesh bag and passed them through the 1-mm-mesh sieve. The sieved roots were collected and over-dried to a constant weight at 70°C to represent BNPP.

2.7. Data analysis

The statistical analyses were applied using R3.4.2 (R Core Team, 2018). Prior to statistical tests, all variables were checked using histograms, density, and Q-Q plots. First, linear mixed-effect models were performed using the R package *lme4* to test whether CH_4 and N_2O fluxes as well as environmental variables were affected by treatments. Warming, clipping, and their interaction were defined as fixed factors and the block was treated as a random factor in the models. Tukey tests were further applied for the comparison of differences among the four treatments, using the function “glht” in the *multcomp* package. Second, student’s *t*-test was applied to inspect if seasonal and annual cumulative fluxes differed significantly from the control. Moreover, based on the global warming potential approach (GWP) (IPCC, 2013), we also calculated net warming effect of seasonal and annual cumulative fluxes of CH_4 and N_2O combined, expressed as CO_2 equivalent under different treatments. As using GWP is criticized based on the fact that it measures the average forcing of a pulse over time rather than a sustained emission at a specific end-point in time (Neubauer and Megonigal, 2015), the sustained GWP over a 100-year time horizon (SGWP100, 45 for CH_4 and 270 for N_2O) was used in this study. Third, we investigated the relationships between gas fluxes and soil temperature and moisture at 10 cm depth. In addition, a pairwise correlation analysis was conducted using the *corrplot* package to example the effects of other environmental variables (SOC, TN, C:N ratio, NH_4^+–N, NO_3^-–N, pH, MBC, MBN, ANPP, and BNPP) on the annual averaged CH_4 and N_2O fluxes. In order to test whether the effect of a particular variable depended on the other variables, we also performed the partial correlation analysis in the *ppcor* package to evaluate the bivariate correlations between each gas flux and environmental variables using zero-order correlations and partial correlations (Pearson correlation) by controlling for one variable (Luo et al., 2017). The significance level was set at $\alpha < 0.05$ through the analysis.

3. Results

3.1. Treatment effects on abiotic and biotic factors

Soil temperature and moisture at 10 cm depth both showed clear seasonal patterns, with high values in growing season and low values in nongrowing season (Fig. 1a, b). Warming increased soil temperature by 3°C ($P<0.05$, Table 1), while clipping did not affect soil temperature during the study period ($P>0.05$). In response to warming, mean soil moisture decreased by approximately 7% ($P<0.05$, Table 1). Clipping significantly declined mean soil moisture by around 2% ($P<0.05$). The seasonal patterns of soil temperature and moisture at 20 cm and 40 cm depth were similar to those at 10 cm depth (Fig. S2). During the entire study period, warming increased soil temperature at 20 cm by 2.8°C and

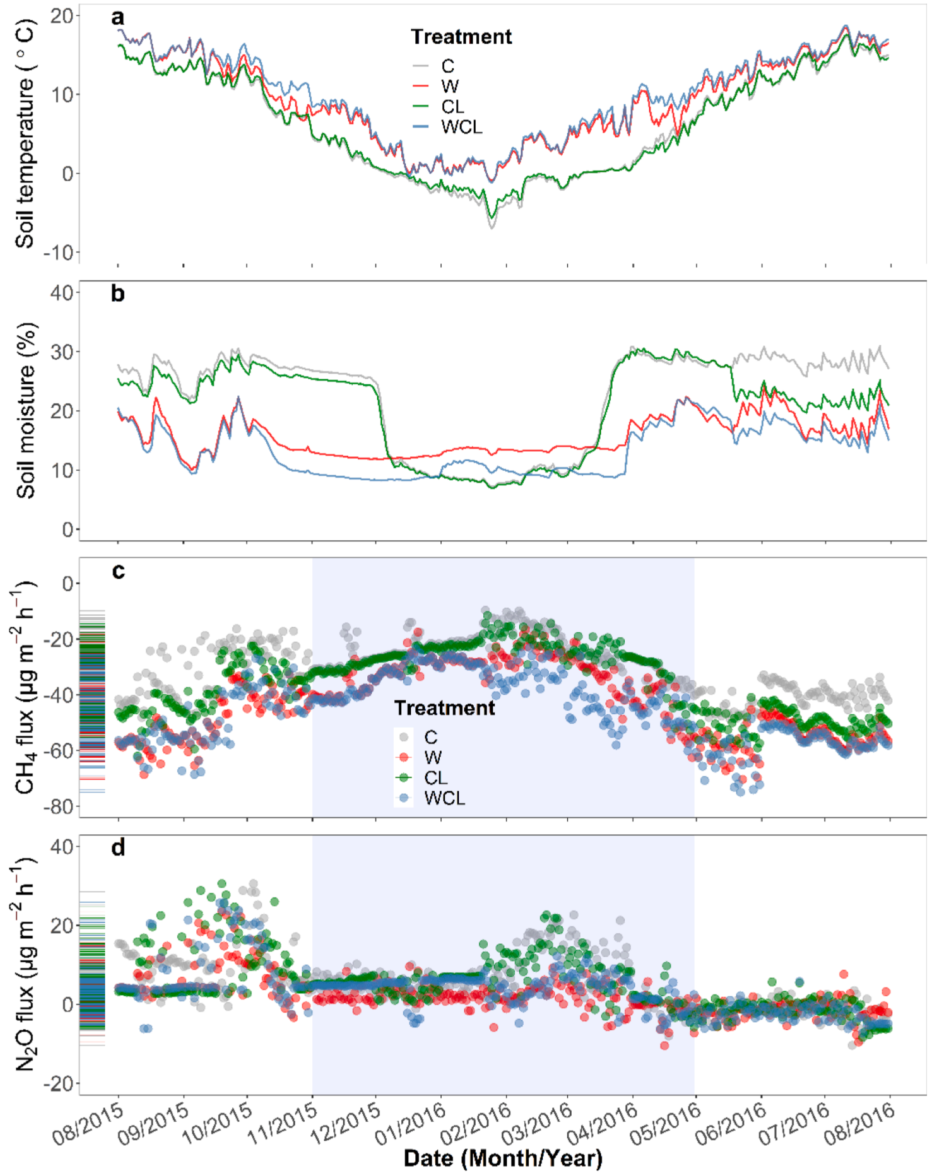

Fig. 1. Temporal variations of soil temperature at 10 cm depth (a), soil moisture at 10 cm depth (b), CH_4 fluxes (c) and N_2O fluxes (d) during the entire observation period. The blue shaded area indicates nongrowing season. The colored bands along the Y axes represent value distributions by treatments. C: control; W: warming; CL: clipping; WCL: warming and clipping.

40 cm by 2.2°C. Meantime, soil moisture decreased by 5% and 2% at 20 cm and 40 cm, respectively under warming treatment.

Soil organic C (SOC) and total N (TN) contents were not influenced by treatments ($P>0.05$, Table 1). Neither warming or clipping affected soil ammonium N ($P>0.05$), but warming and clipping both decreased soil nitrate N concentration ($P<0.05$). Soil pH was not altered by treatments ($P>0.05$). Although warming or clipping did not change microbial biomass C (MBC) and microbial biomass nitrogen (MBN) ($P>0.05$), the combined warming and clipping treatment (WCL) significantly increased them ($P<0.05$). Warming did not affect aboveground net primary production (ANPP) ($P>0.05$), but clipping and its association with warming significantly decreased it ($P<0.05$). Compared with the control, belowground net primary production (BNPP) was not changed by warming, clipping, or their combination ($P>0.05$).

3.2. Treatment effects on CH_4 and N_2O fluxes

CH_4 fluxes presented distinct seasonal patterns in different treatments, with high CH_4 uptake rates in growing season and low uptake rates in nongrowing season (Fig. 1c). However, N_2O fluxes showed no clear seasonal patterns in any treatments (Fig. 1d). Warming had a significant effect on CH_4 fluxes, but clipping did not affect them throughout the study period (Table 2). The combined warming and clipping treatment significantly increased the average CH_4 uptake across the year-round observation (Table 3). Furthermore, the significant warming effect on CH_4 fluxes was only found in growing season rather than in nongrowing season (Table 2). Specifically, both warming and its combination with clipping significantly increased the average CH_4 flux in the growing season (Table 3).

Warming exerted a significant effect on N_2O fluxes, but clipping did not impact them during the entire study period (Table 2). Warming alone significantly decreased the average N_2O emission on the annual basis (Table 3). Moreover, the significant warming effect on N_2O fluxes was only detected in nongrowing season, and the N_2O fluxes were not altered by any treatments in the growing season (Table 3).

3.3. Treatment effects on cumulative CH_4 and N_2O fluxes and their global warming potential

Under the control conditions, cumulative CH_4 uptake in the nongrowing season (–106 ± 16 mg CH_4 m^{-2}) accounted for 40% of annual cumulative flux (–264 ± 26 mg CH_4 m^{-2}), while cumulative N_2O emission in the nongrowing season (29 ± 8 mg N_2O m^{-2}) contributed to 59% of its annual budget (48 ± 10 mg N_2O m^{-2}) (Fig. 2). Compared to the control, warming alone and its combination with warming increased the cumulative CH_4 uptake by 42% and 51%, respectively during the entire study period ($P<0.05$, Fig. 2). Clipping alone had no significant effect on year-round cumulative CH_4 fluxes ($P>0.05$). In the growing season, the cumulative CH_4 uptake was enhanced by 45% and 49% for the warming treatment and warming in association with clipping, respectively ($P<0.05$). No evidence of treatment effects on the cumulative CH_4 uptake was detected in the nongrowing season. In contrast, cumulative N_2O fluxes were not affected by any treatments in the growing season ($P>0.05$, Fig. 2), but warming alone significantly decreased the cumulative N_2O emission by 72% relative to that under control in the nongrowing season, leading to a decrease of 57% in year-round cumulative N_2O emission as compared with the control.

Table 2
Results (P-values) of linear-mixed effect model on the effects of warming (W), clipping (CL), and their interactions (W×CL) on CH_4 and N_2O fluxes in growing season, nongrowing season, and year-round observation, respectively.

Source of variations	CH_4 fluxes (μg m^{-2} h^{-1})			N_2O fluxes (μg m^{-2} h^{-1})		
	GS	NGS	Year	GS	NGS	Year
W	**0.045**	0.197	**0.042**	0.133	**0.012**	**0.018**
CL	0.448	0.668	0.399	0.988	0.404	0.624
W×CL	0.573	0.887	0.782	0.964	0.309	0.524

GS: growing season; NGS: nongrowing season. The significant treatment effects were marked with bold.

Based on the sustained global warming potential approach (SGWP100) and expressed as CO_2-equivalents, the ecosystem was a net source of the balance of CH_4 and N_2O in the control (1.2 g CO_2-eq m^{-2}) during the study period (Fig. 3). Although clipping reduced a little net source of these two gases, the clipping effect was not significant ($P>0.05$). Compared with the control plots, warming alone and in interaction with clipping both switched the ecosystem from a net source to a net sink of these two gases, with net warming effect being –11.3 g CO_2-eq m^{-2} in warming and –9.9 g CO_2-eq m^{-2} in warming associated with clipping (Fig. 3). Similarly, in the growing season, the balance of these two gases was declined by 5.2 g CO_2-eq m^{-2} and 5.4 g CO_2-eq m^{-2} in warming alone and its combination with clipping, respectively relative to the control ($P<0.05$). Furthermore, only warming significantly decreased SGWP100 in the nongrowing season, largely due to the distinct decrease in N_2O emission and unaltered CH_4 uptake with elevated temperature in winter period (Fig. 2).

3.4. CH_4 and N_2O fluxes in relation to environmental variables

CH_4 uptake increased with soil temperature, explaining 63% variation of CH_4 uptake across treatments (Fig. 4a). CH_4 uptake also presented a quadratic relationship with soil moisture, with maximum CH_4 uptake rate at intermediate soil moisture of approximately 20% (Fig. 4b). N_2O fluxes showed a weak but significantly negative correlation with soil temperature (Fig. 4c). Similarly, there was a weakly quadratic relationship between N_2O fluxes and soil moisture (Fig. 4d).

The pairwise correlation analysis showed that neither CH_4 or N_2O fluxes significantly correlated with other environmental variables (SOC, TN, C:N ratio, NH_4^+–N, NO_3^-–N, pH, MBC, MBN, ANPP, and BNPP) (Fig. S3). When controlling the other environmental variables, the correlation coefficients of CH_4 and N_2O fluxes in relation to soil temperature and moisture did not change a lot (Fig. 5). However, when controlling the roles of soil temperature and moisture, the correlation coefficients decreased between most other factors and CH_4 and N_2O fluxes (Fig. S4), suggesting the variations of CH_4 and N_2O fluxes were primarily explained by soil temperature and moisture.

4. Discussion

4.1. Warming and clipping effects on CH_4 fluxes

This alpine meadow was a net sink of atmospheric CH_4 in both growing and nongrowing seasons under control conditions. The stimulated CH_4 uptake under elevated temperature is in agreement with results from other alpine meadows (Lin et al., 2015; Zhu et al., 2015; Chen et al., 2017a), but differs from previous field studies where decreased or unaltered CH_4 uptake was found in response to temperature increases (Dijkstra et al., 2011; Dijkstra et al., 2013; Zhao et al., 2017; Wu et al., 2020). Increased CH_4 consumption is likely attributed to the direct warming effect by changing soil temperature and the indirect warming effect by altering soil moisture (Fig. 4). The net CH_4 flux is determined by the balance between methanogenic and methanotrophic processes occurring simultaneously (Galbally et al., 2008). Here, higher soil temperature was found under warming treatment, and a significantly positive correlation was observed between CH_4 uptake and soil temperature, which agrees with the results from similar alpine meadow in this region (Wu et al., 2020). The increased soil temperature has found to directly enhance methanotrophic abundance and decrease methanogen abundance (Zheng et al., 2012; Peltoniemi et al., 2016), both of which can lead to a stimulation of CH_4 uptake.

Warming induced decrease in soil moisture could be another

Table 3
Average fluxes of CH_4 and N_2O in growing season, nongrowing season, and year-round observation under different treatments.

Treatment	CH_4 fluxes (μg m^{-2} h^{-1})			N_2O fluxes (μg m^{-2} h^{-1})		
	Growing season	Nongrowing season	Year	Growing season	Nongrowing season	Year
C	-35.95±0.65 a	-24.33±0.51 a	-30.18±0.51 a	4.49±0.58 a	6.57±0.44 a	5.52±0.37 a
W	-52.18±0.62 b	-33.15±0.65 a	-42.74±0.67 ab	2.85±0.46 a	1.84±0.23 b	2.35±0.26 b
CL	-44.28±0.62 ab	-26.37±0.53 a	-35.40±0.63 ab	4.44±0.62 a	6.35±0.39 a	5.39±0.37 ab
WCL	-53.46±0.70 b	-37.28±0.63 a	-45.44±0.63 b	2.88±0.58 a	3.88±0.27 ab	3.38±0.32 ab

C: control; W: warming; CL: clipping; WCL: warming and clipping. Different letters in each column represent significant differences among treatments ($P<0.05$).

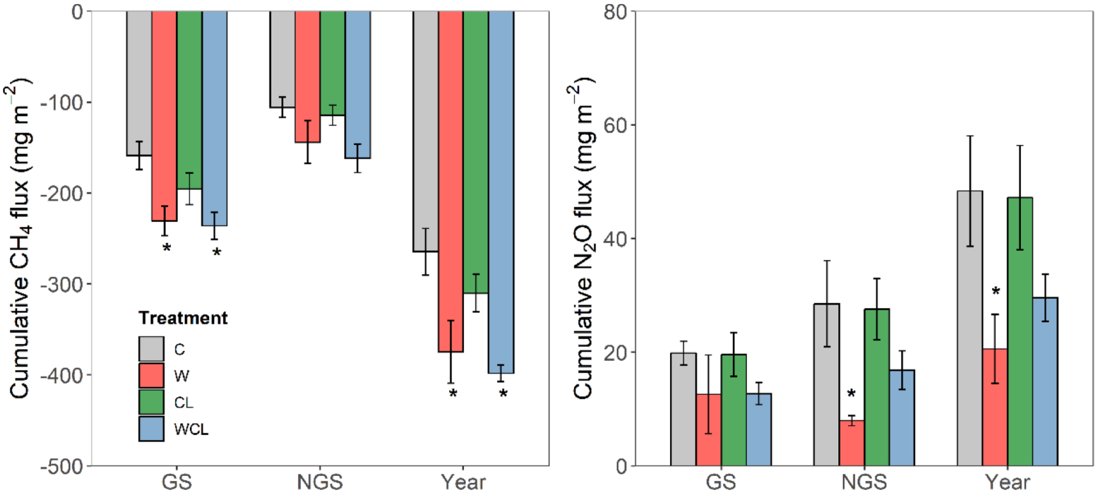

Fig. 2. Cumulative fluxes of CH_4 and N_2O under different treatments in growing season, nongrowing season, and year-round observation. C: control; W: warming; CL: clipping; WCL: warming and clipping. "*" represents significant differences ($P<0.05$) from the control conditions.

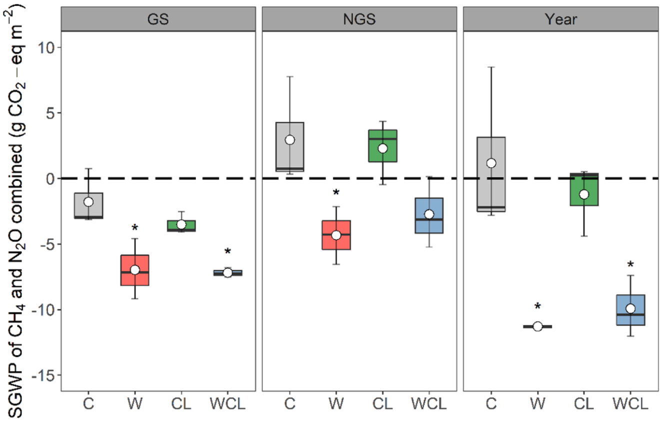

Fig. 3. Net balance of cumulative CH_4 and N_2O fluxes based on sustained global warming potential approach (45 for CH_4 and 270 for N_2O over a 100-year time horizon) under different treatments in growing season, nongrowing season, and year-round observation. The white point within the boxplots is the mean value of net warming effect. C: control; W: warming; CL: clipping; WCL: warming and clipping. "*" represents significant differences ($P<0.05$) from the control conditions.

mechanism for the positive effect of elevated temperature on CH_4 uptake. Soil moisture was significantly decreased by 7% under warming conditions (16 ± 0.6%), compared to the control (23 ± 1.1%) (Table 1). The CH_4 consumption presented a bell-shaped relationship with soil moisture with a maximum CH_4 uptake at approximately 20% of soil water content (Fig. 4b), which corroborates the results in semiarid grasslands (Dijkstra et al., 2011; Dijkstra et al., 2013). In mesic environments, CH_4 consumption by methanotrophic organisms is largely controlled by substrate (CH_4, O_2) diffusion (Lin et al., 2015). When soil moisture is high, CH_4 oxidation could be constrained by decreased soil air permeability and O_2 availability (Chen et al., 2017b). In our relatively wet soils, warming could change soil water-filled pore space and alleviate anaerobic conditions, which benefits CH_4 transporting from the atmosphere to soils. In addition, changes in soil moisture may have also decreased methanogenesis or enhanced the abundance of methanotrophs near the oxic interface (Zhang et al., 2019). Both of which could have increased microbial oxidation of CH_4, with a consequent stimulation of CH_4 uptake.

We found that other environmental variables did not correlate with CH_4 fluxes in this alpine meadow. The previous study has reported a negative relationship between soil NH_4^+–N and CH_4 oxidation because methanotrophic organisms switch to consume NH_4^+–N rather than oxidating CH_4 with increasing NH_4^+–N supply (Steinkamp et al., 2001). Some other studies have also stated that changes in biotic factors such as plant aboveground net primary production, belowground root biomass, and soil microbial biomass may also be responsible for warming effect on CH_4 consumption (Zhu et al., 2015; Chen et al., 2017b). However, elevated temperature did not significantly affect these abiotic and biotic factors in this study, which probably due to the short duration of the experiment. Furthermore, the roles of soil temperature and moisture on CH_4 uptake did not vary largely when controlling other environmental parameters (Fig. 5). Taken together, warming induced the increase in CH_4 uptake is mainly regulated by a combination of soil temperature and moisture. However, the long-term observations are still needed to test the effects of other environmental factors on the variations of CH_4 and N_2O fluxes.

We also demonstrated that clipping alone did not significantly affect CH_4 uptake (Fig. 2). The unchanged CH_4 fluxes under clipping alone is consistent with another comparable study (Zhu et al., 2015), but in contrast to the findings from studies in semiarid grasslands where clipping significantly increases CH_4 uptake (Zhang et al., 2012; Lu et al., 2015). Clipping induced increase in soil temperature dominantly

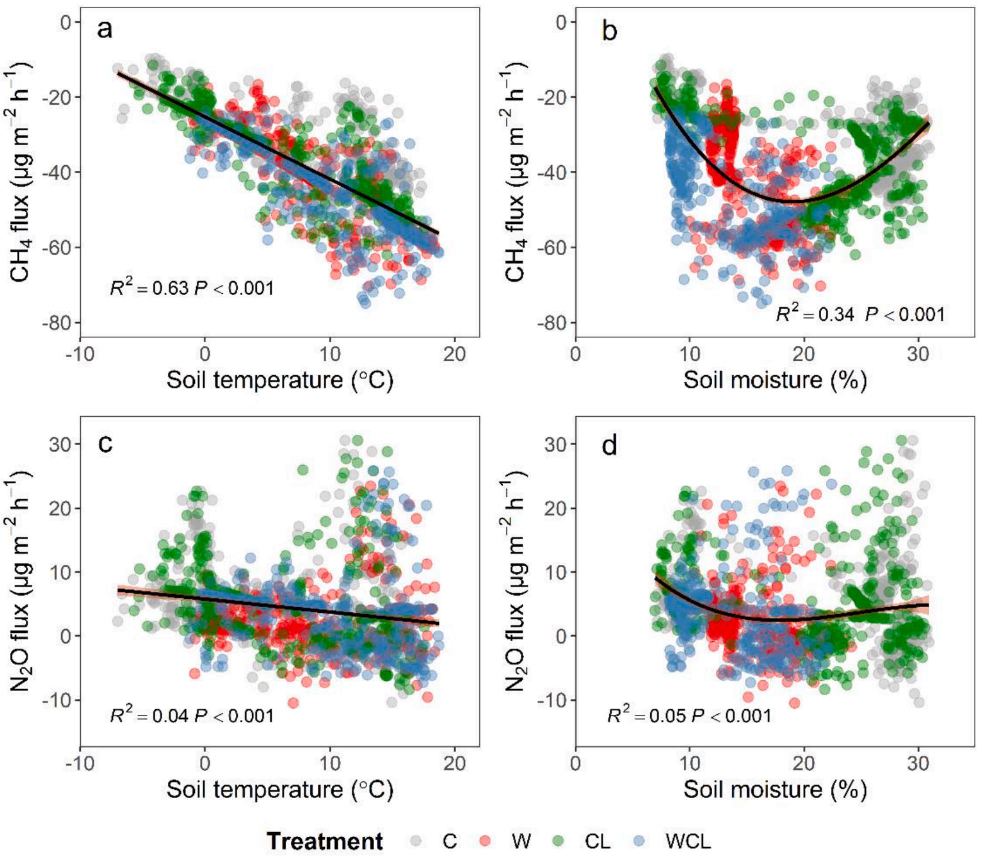

Fig. 4. CH_4 and N_2O fluxes in relation to soil temperature (a, c) and soil moisture (b, d) at 10 cm depth across different treatments throughout the entire study period. C: control; W: warming; CL: clipping; WCL: warming and clipping.

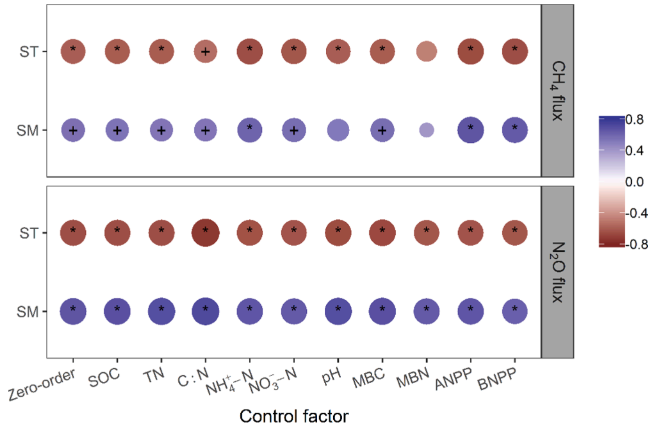

Fig. 5. Partial regression analysis of CH_4 and N_2O fluxes in relation to soil temperature (ST) and soil moisture (SM) after controlling each of other abiotic and biotic factors (SOC, TN, C:N ratio, NH_4^+-N, NO_3^--N, pH, MBC, MBN, ANPP, BNPP). SOC: soil organic carbon content; TN: soil total nitrogen content; C:N, the ratio of SOC to TN; NH_4^+-N: soil ammonium nitrogen content; NO_3^--N: soil nitrate nitrogen content; MBC: soil microbial biomass carbon; MBN: soil microbial biomass nitrogen; ANPP: aboveground net primary production; BNPP: belowground net primary production. $^*P<0.05$; $^+P<0.1$.

contributes to the enhancement of CH_4 oxidation in a semiarid grassland (Lu et al., 2015). However, no evidence of soil temperature increase was detected under clipping in this relatively wet ecosystem, which is likely due to that increasing solar radiation interception after aboveground biomass removing could be offset concurrently by energy consumption for enhancing soil water evaporation. Although the previous studies have demonstrated that the increase in CH_4 consumption can be attributed to the decrease in soil NH_4^+–N and the increase in soil microbial biomass (Zhang et al., 2012; Lu et al., 2015), we found clipping did not significantly change these factors (Table 1). Contrary to the clipping alone, clipping and warming in combination significantly stimulated CH_4 uptake (Fig. 3), which is likely due to a distinct increase in soil temperature and decrease in soil moisture as well as changes in soil inorganic N and soil microbial biomass.

4.2. *Warming and clipping effects on N_2O fluxes*

The positive values of averaged and cumulative N_2O fluxes in the control plots indicated that the alpine meadow soils were a net source of atmospheric N_2O, although production and uptake of N_2O occurred simultaneously (Fig. 1). This finding is consistent with results from studies in the same region (Zhu et al., 2015; Zhao et al., 2017). The decrease in N_2O emission with increasing temperature agrees with the previous studies (Hu et al., 2010; Carter et al., 2012), but opposites to others in which no change or increased N_2O emission in response to warming have been found (Zhu et al., 2015; Chen et al., 2017a; Cui et al., 2018; Li et al., 2020). N_2O production is mainly derived from soil nitrification and denitrification pathways, which are primarily governed by soil temperature, O_2 state in soils, soil water content, labile C, and available inorganic N (Weier et al., 1993). Elevated temperature induced decrease in soil NO_3^-–N largely due to increased plant uptake may result in a suppression of denitrification rate. Moreover, a bell-shaped relationship between N_2O fluxes and soil moisture was found in the present study (Fig. 4d). In water saturated soils, N_2O is mostly produced through denitrification, while well-aerated soils mainly produce N_2O from nitrification (Wrage et al., 2004). The reduced soil moisture under warming in this relatively wet soil probably have increased O_2 concentrations and led to partially aerobic microsites, thereby inhibiting N_2O production through denitrification (Brown et al., 2012; Carter et al., 2012).

Contrary to our expectation, we found N_2O fluxes were not responsive to clipping alone, which is in line with the finding of another study conducted also in the alpine meadow (Zhu et al., 2015). In temperate grasslands, in contrast, clipping has found to decrease N_2O emission due to increased soil temperature (Lu et al., 2015), decreased soil moisture, and substrates supplied to microbial nitrification and denitrification processes (Zhang et al., 2012). The unchanged N_2O fluxes under clipping alone in this study are explained from the following reasons. First, clipping caused no significant change in soil temperature, which may not largely promote microbial activities that control N_2O production and consumption. Second, although clipping significantly decreased soil moisture (Table 1), the relatively high soil water content in the clipping treatment (21 ± 0.8%) was still above the optimum soil moisture at which N_2O emission may be inhibited (Fig. 4d).

4.3. Growing season and nongrowing season responses

We found that CH_4 and N_2O fluxes in the nongrowing season were crucial to their annual budgets and warming responses of CH_4 and N_2O fluxes differed between growing and nongrowing seasons. Cumulative CH_4 uptake in the nongrowing season accounted for 40% of its annual budget in this study, which is higher than the previous result (27–29%) reported also in the alpine meadow (Lin et al., 2015). This suggests that year-round measurement of CH_4 is important. Further, we illustrated that the cumulative CH_4 uptake was not changed by treatments in the nongrowing season, but warming significantly stimulated CH_4 uptake in the growing season (Fig. 2). Under warming treatment, the larger increase in soil temperature in the nongrowing (4.3°C) than growing season (1.8°C) could potentially increase CH_4 uptake (Fig. 1a, Fig. 4a), but lower mean soil moisture relative to the control (14% vs.18%) may concurrently decrease CH_4 uptake (Fig. 4b), possibly resulting in a neutral effect of warming on CH_4 fluxes in the nongrowing season. Although the limited increase in soil temperature may have smaller impact on CH_4 uptake in the growing than nongrowing season, warming significantly decreased soil water content compared with the control (17% vs. 28%), which could enhance CH_4 diffusion into the soil and microbial consumption of CH_4.

In our study, the contribution of nongrowing season N_2O production to its annual flux (59%) was higher than the value reported in a similar alpine meadow (36–57%) (Hu et al., 2010). The high contribution of N_2O emission in the winter time could be mainly due to freeze-thawing events that may induce the pulse of N_2O release (Voigt et al., 2017b; Wagner-Riddle et al., 2017), through changes in soil cracking and soil gases diffusivity (Wilson et al., 2017), increase in microbial activity or change in microbial metabolism (Xue et al., 2016; Feng et al., 2017; Segura et al., 2017). Warming decreased N_2O fluxes mainly in the nongrowing season but not in the growing season (Fig. 2), which is like due to that warming stimulates root growth and increases NO_3^-–N uptake in the growing season (Table 1), then the decreased substrate supply for microbial nitrification and denitrification in the nongrowing season could be one reason for limiting N_2O emission. Overall, incorporating greenhouse gas fluxes in the cold season is urgent to reduce the uncertainty in assessing the feedback between land ecosystems and climate system.

When expressed in CO_2 equivalents, warming and its association with clipping both switched the ecosystem from a net source to a net sink of the balance between CH_4 and N_2O. Nevertheless, warming could also stimulate CO_2 emission (Crowther et al., 2016) that may offset the net sink of CH_4 and N_2O in combination. The annual cumulative CO_2 flux in this site was -79.3 g CO_2 m^{-2} in the control and 66.9 g CO_2 m^{-2} in the warming treatment (negative value represents CO_2 uptake and positive value indicates CO_2 emission) (unpublished data). Thus, when including CO_2 fluxes, warming shifted the ecosystem from a net sink (-78.1 g CO_2-eq m^{-2}) to a net source (55.6 g CO_2-eq m^{-2}) of these three gas fluxes in combination. 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.

Our results are limited to a one-year observation and the long-term response of CH_4 and N_2O fluxes is unknown. Over longer time scales, the gas fluxes will be influenced by changes in plant and microbial composition, nutrient availability and other regulation processes (Luan et al., 2019). Furthermore, the QTP area warms two times faster than the rest of the globe and CH_4 and N_2O fluxes will further change over time and with different warming degrees. Therefore, it is necessary to examine these responses across a wider biogeographic range, and for longer time-periods as well as with multiple warming levels in order to disentangle the ecological mechanisms governing CH_4 and N_2O responses to climate change and human activity. It is also noticeable that the warming treatment differences could be affected by potential differences in air temperature, plant surface temperature or soil temperatures along the soil profile. Thus, when interpreting the warming effects or comparing them among studies, we need to consider these different temperature variables.

5. Conclusions

To our knowledge, this study is one among the first investigating the effects of warming, clipping, and their interaction on CH_4 and N_2O fluxes over year-round. Warming significantly increased annual CH_4 uptake irrespective of clipping, but decreased N_2O emission on the annual basis. Clipping alone did not significantly affect either CH_4 or N_2O fluxes. Warming and clipping interaction was not detected in this study. Warming responses of CH_4 and N_2O fluxes differed between growing and nongrowing seasons, with significant warming effect on CH_4 uptake in the growing season and on N_2O emission in the nongrowing season. We also found that changes in soil temperature and soil moisture were primarily responsible for the variations in CH_4 and N_2O fluxes. In order to accurately assess and predict the ecosystem-climate feedbacks, the net balance of CH_4 and N_2O fluxes in conjunction with CO_2 flux is needed.

Author contributions

Shuli Niu and Jinsong Wang contributed to the preparation and design of the entire manuscript. Jinsong Wang, Quan Quan, Fangfang Ma, Weinan Chen, Song Wang, and Lu Yang collected the data. Jinsong Wang, Yiqi Luo, Dashuan Tian, and Shuli Niu analyzed the data and wrote the manuscript. All authors contributed to the drafts and revision and gave the final approval for publication.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108278.

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