Agricultural and Forest Meteorology 214-215 (2015) 506–514

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Effects of warming, grazing/cutting and nitrogen fertilization on greenhouse gas fluxes during growing seasons in an alpine meadow on the Tibetan Plateau

Xiaoxue Zhu[a,d,1], Caiyun Luo[a,1], Shiping Wang[b,c,*], Zhenhua Zhang[a], Shujuan Cui[b,d], Xiaoying Bao[d], Lili Jiang[b], Yaoming Li[b], Xine Li[b], Qi Wang[b,d], Yang Zhou[b,d]

[a] Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China
[b] Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China
[c] CAS Center of Excellence in Tibetan Plateau Earth Science, Beijing 100101, China
[d] University of the Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Article history:
Received 29 November 2014
Received in revised form 1 September 2015
Accepted 14 September 2015

Keywords:
Carbon dioxide
Methane
Nitrous oxide
Climate change
Grazing
Nitrogen deposition

ABSTRACT

Increased nitrogen (N) deposition within the context of both warming and grazing is relevant to understand the response of greenhouse gases fluxes (GHG) (i.e. CO_2, CH_4 and N_2O fluxes) for alpine meadow ecosystems to projected changes in the environment. A previous controlled warming and grazing experiment only included no warming with no grazing (NWNG), no warming with grazing (NWG), warming with no grazing (WNG) and warming with grazing (WG) from 2006 to 2010. N fertilization was added to the experimental setup to determine the effects of warming, grazing and N fertilization on GHG fluxes in an alpine meadow on the Tibetan Plateau during the growing seasons from 2010 to 2012. Sheep grazing was utilized during the growing season from 2006 to 2010 and cutting was used as simulation of grazing during the non-growing seasons in 2011 and 2012. Warming significantly increased average seasonal CO_2 emission by 10%, and nitrogen addition increased average seasonal CH_4 uptake by 14% during the growing seasons in the dry years of 2011 and 2012. Warming increased average seasonal CH_4 uptake by 32–46% over the 3-year period, and grazing increased annual average N_2O emission by 62% only in 2010. N fertilization alone did not significantly affect CO_2 and N_2O fluxes during the experimental period. The interactive effects of warming, grazing/cutting and N fertilization effect on daily CH_4 or daily N_2O flux depended on sampling date. Ecosystem CO_2 emission was mainly affected by soil temperature and plant aboveground net primary production (ANPP), which explained about 55% and 18% of its variation. Soil moisture and ANPP could explain 17% and 8% of the variation of CH_4 uptake in the region. Our results suggest that the stimulating effect of warming on ecosystem respiration still occurs in 2011 and 2012 after warming for seven years. Moreover, our results imply that moderate grazing/cutting may be preferred compared with no grazing or no cutting because its negative effect on GHG fluxes was small, and interactive effect of warming, grazing/cutting and increased N deposition on GHG emission could be neglected in the alpine meadow.

1. Introduction

Fluctuations in greenhouse gas (GHG) concentrations in the atmosphere can lead to profound climatic and environmental changes (IPCC, 2013). Increasing GHG emissions are expected to raise global mean temperature by 2–7 °C by the end of this century (Allison et al., 2009). The United Nations Framework Convention on Climate Change (UNFCCC) was established to limit future climate change to a mean temperature not exceeding 2 °C above preindustrial times in 2012. This means that very significant cuts (>80%) in GHG emissions are needed, largely through reduced non-CO_2 emissions over the coming decades (Meinshausen et al., 2009). As the largest grassland unit on the Eurasian continent which covers an area of approximately 2.5 million km^2 (Zheng et al., 2000), the release of GHG such as carbon dioxide (CO_2), methane (CH_4),

* Corresponding author at: Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China.
E-mail address: wangsp@itpcas.ac.cn (S. Wang).
[1] These authors made equal contribution to this paper.

http://dx.doi.org/10.1016/j.agrformet.2015.09.008
0168-1923/

and nitrous oxide (N_2O) from alpine ecosystems has been the focus of biogeochemical research (Wang et al., 2009; Lin et al., 2009, 2011; Hu et al., 2010) due to its great potential contribution to feedbacks to global warming. Especially, anthropogenic N deposition can turn N-limited to N-saturated ecosystems, and threaten the 'health' of marine and terrestrial ecosystems (Galloway and Cowling, 2002; Liu et al., 2013a,b). China has become a region with the third highest rates of N deposition following America and Europe with significant increases also found in the Tibetan Plateau and the rates of N deposition will continue increasing in the coming decades due to economic development (Galloway and Cowling, 2002; Liu et al., 2013a,b). Therefore, accurate understanding of the effects of natural and anthropogenic factors on GHG fluxes are necessary for a more complete understanding of biosphere–atmosphere interactions under a future climate change.

The Tibetan Plateau provides an excellent natural laboratory for investigating the effects of climate change (i.e. warming), human activity (i.e. grazing) and N deposition on GHG fluxes. Historical climate records show that the Tibetan Plateau has experienced 'much greater than average' increases in surface temperatures (i.e., 0.32 °C per decade) (Liu and Chen, 2000; IPCC, 2013), and it likely will continue in the future. Warming is also predicted to increase N-deposition in high latitude and mountain regions because of increased precipitation (Hole and Engardt, 2008). In particular, the background of N deposition is low (i.e. total N deposition is 7.0–10.0 kg N ha^{-1} yr^{-1}) (Zou et al., 1986; Lü and Tian, 2007) and N atmospheric deposition rates will increase another two- or three-fold in the coming years (Galloway and Cowling, 2002). Moreover, previous results indicate that alpine steppe may be N-saturated above an average N load of 40 kg N ha^{-1} yr^{-1} in the terms of the responses of biotic characteristics (biomass N concentration, biomass N:P ratio, N-uptake efficiency and N-use efficiency) (Liu et al., 2013a,b). Meanwhile, grazing is a main land use in the region. Hence the study of the impacts of increased N deposition within the context of both warming and grazing is relevant to understand the response of GHG fluxes for the alpine meadow ecosystems to N deposition changes in this environment. In our previous studies we reported the effects of warming and grazing on ecosystem respiration (Lin et al., 2011), N_2O flux (Hu et al., 2010) and CH_4 flux (Lin et al., 2015) in the region from 2006 to 2008. The aim of this study was to determine the combined effects of enhanced N deposition, warming and grazing on GHG fluxes using the same manipulation experiment from 2010 to 2012 in the alpine meadow.

2. Materials and methods

2.1. Experimental site

Details of the experimental site and design of the warming and grazing were described by previous reports (Wang et al., 2012). In brief, the experiment was conducted at the Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), located at latitude 37°37′ N and longitude 101°12′ E. The mean elevation of the valley bottom is 3200 m. Mean temperature was 8.9, 8.1 and 8.3 °C and total rainfall was 412.6, 307.8 and 330.4 mm during the growing seasons from 1 May to 30 September in 2010, 2011 and 2012, respectively (Fig. S1). Compared to average rainfall during the growing season for 40-year in the region (i.e. approx. 450 mm), 2010 can be classified as an average year, whereas 2011 and 2012 were slightly drier, with 24% and 32% less rainfall than average, respectively. The plant community at the experimental site is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carex scabrirostris*, *Scirpus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Blysmus sinocompressus* and *Potentilla nivea*.

2.2. Controlled warming and grazing or cutting experiment

The design of the controlled warming (i.e. free-air temperature enhancement (FATE) system with infrared heaters) with grazing experiment was described previously by Kimball et al. (2008) and Wang et al. (2012). In brief, in May 2006 eight hexagonal arrays of Mor FTE (1000 W, 240 V) infrared heaters were deployed over the vegetation canopy that had previously been heavily grazed by sheep during the cool seasons from October to May of prior years at HBAMERS, with eight dummy arrays without heaters over reference plots. The heaters were controlled using the proportional-integral-derivative-outputs (PID) control system so as to ensure constant warming between heated and reference plots. The set point differences of the vegetation canopy between heated and corresponding reference plots were 1.2 °C during daytime and 1.7 °C at night in summer (Kimball et al., 2008). Warming was for a whole year before 2010, but it has been heating during the growing season from early of April to end of October since 2011 because warming in cold seasons had small effects on the alpine meadow based on ecosystem respiration due to too low environmental temperature (unpublished data). A two-way factorial design (warming and grazing) was used with four replicates of each of four treatments (Wang et al., 2012): no-warming with no-grazing (i.e. NWNG), no-warming with grazing (NWG), warming with no-grazing (WNG), and warming with grazing (WG). In total, 16 plots of 3-m diameter were fully randomized throughout the study site.

All experimental sheep were fenced into 3 additional 5 m × 5 m fenced plots for a day before the beginning of the grazing experiment to help them adapt to small plots. Two adult Tibetan sheep were fenced for approximately 1 h in each of the grazing plots on the mornings of 7 July and 23 August in 2010. The annual cumulative forage utilization rate during the growing season was 50–57.7% for NWG and WG treatments in 2010 (Wang et al., 2012). However, there was no grazing during growing seasons in 2011 and 2012, and grazing was replaced by cutting about 50% removal of litter biomass in October and next March each year. Because alpine meadows in the region are generally divided into two grazing seasons, i.e. warm season grazing from June to September and cold season grazing from October to May (Cui et al., 2014). Our previous results in the same experimental platform showed the effects of warming and grazing on GHG fluxes during the growing seasons (Lin et al., 2011, 2015; Hu et al., 2010), thus, here is that it was grazing during growing season as compared to winter grazing during the non-growing seasons.

2.3. Nitrogen (N) fertilization

A change in species composition under different treatments had been found before beginning the fertilization experiment in 2010 (Wang et al., 2012). In order to eliminate the mixed effect between species composition and N fertilization on ANPP and GHG fluxes, N fertilization and no-fertilization treatments using PVC tubes were conducted in each of the 16 plots for NWNG, NWG, WNG and WG treatments. Two PVC tubes (i.e. one for N fertilization (F) and another one for no-fertilization (NF) treatment in each plot) with an inner diameter of 30 cm were installed in each plot in early May 2010, i.e. in total 32 PVC tubes were used. The chambers were inserted into the soil to a depth of 40 cm, and only 5 cm protruded above the soil surface. Observed wet N deposition ranges from 7 kg N ha^{-1} yr^{-1} in Tibet Autonomous Region (on the western Tibetan Plateau) to 10.0 kg N ha^{-1} yr^{-1} in Qinghai Province (on the eastern Tibetan Plateau) (Zou et al., 1986; Lü and Tian, 2007).

Moreover, previous results indicated that alpine steppe might be N-saturated above an average N load of 40 kg N ha^{-1} yr^{-1} in the terms of the responses of biotic characteristics (biomass N concentration, biomass N:P ratio, N-uptake efficiency and N-use efficiency) (Liu et al., 2013a,b). Thus, in total, 3 fertilization events were performed, with 1, 1 and 2 g N m^{-2} (totally 40 kg N ha^{-1} yr^{-1}) on 7 and 24 July and 23 August in 2010 as NH_4NO_3–N applied uniformly as a solution, dissolved in 20 ml of deionised water, to the vegetation canopy. Similar, 4 fertilization events were performed with 1, 1, 1 and 2 g N m^{-2} (totally 50 kg N ha^{-1} yr^{-1}) as NH_4NO_3–N in the middle of May, June, July and August in 2011 and 2012. For the non-fertilized treatment, equal amounts of deionized water were applied. The plant community selected inside the PVC tubes was the same as that of the treated plot.

2.4. Soil temperature and soil moisture measurements

Soil temperature and soil moisture at 10 cm below the soil surface were monitored at each PVC tube when gas samples were collected. Soil temperature was measured using a digital temperature sensor (JM624 digital thermometer, Living-Jinming Ltd., China) and volumetric soil moisture was measured using a Time Domain Reflectometer (JS-TDR300, Meridian Measurement, USA). There was no monitoring in 2010 for the fertilization treatment.

2.5. Aboveground net primary production (ANPP)

In 2011 and 2012, maximum aboveground living present biomass (APB) was harvested inside the PVC tube of each plot in the mid of September 2011 and 2012, then dried at 65 °C for 48 h and weighed. The APB was used as ANPP because there was no grazing during the growing seasons.

2.6. GHG measurements

Details of measurements were reported by Lin et al. (2009, 2011, 2015) and Hu et al. (2010). In brief, during the growing seasons from 2010 to 2012, the GHG was measured every 7–10 days from 6 July in 2010, 21 June in 2011 and 13 May in 2012 to 31, 18 and 11 October in 2010, 2011 and 2012 respectively using opaque, static, manual stainless steel chambers (Lin et al., 2009). Hence the total samplings were 15, 18 and 16 times in 2010, 2011 and 2012, respectively. The dimension (40 cm × 40 cm × 40 cm) and architecture of the chambers were the same as those reported by Hu et al. (2010) and Lin et al. (2011, 2015). The PVC tubes with 30 cm diameter were the center of the basement of chamber, and the area of outside PVC tubes was covered by plastic which was inserted into soil about 5 cm surrounding the PVC tubes due to smaller area for the PVC tubes relative to the basement of the sampling chamber (Fig. S2). The GHG fluxes between 9:00 and 11:00 a.m. local time represent one-day average fluxes (Lin et al., 2009). Chambers were closed for half an hour and gas samples (100 ml) were collected every 10 min using plastic syringes. The mixing ratios of CH_4, CO_2, and N_2O were simultaneously analyzed within 24 h following gas sampling using a modified gas chromatograph (Agilent 6820, Agilent Co., Santa Clara, CA, USA) equipped with N_2 carrier gas, a flame ionization detector (FID) and an electron capture detector (ECD) (Wang and Wang, 2003).

The GHG fluxes were calculated as the following equation from Wang and Wang (2003): $F = \frac{M}{V_o}\frac{P}{P_o}\frac{T_o}{T}\frac{\Delta c}{\Delta t}H$, where: F is a GHG flux; $\Delta c/\Delta t$ is the slope of the linear regression for gas concentration gradient through time; M the molecular mass of each gas; P the atmospheric pressure; T the absolute temperature during sampling; V_o, T_o, and P_o are the gas mole volume, absolute air temperature, and atmospheric pressure under standard conditions, respectively; and H is the height of chamber during sampling.

2.7. Data analysis

Linear mixed models with repeated measurements was used for analysis of variance with SPSS version 22.0 (SPSS Inc. Chicago, USA) to test the effects of the main factors (i.e. warming, grazing/cutting and N application) on soil temperature and soil moisture at 10 cm depth, ANPP and GHG fluxes (repeated-measures) by sampling date. Type III sum of squares was adopted due to different samples sizes in 2011 and 2012. The data in 2010 was analyzed separately due to different warming and grazing patterns. For the warming and grazing experiment with a nested fertilization, plot (i.e. soil block) was taken as subject, warming, grazing and fertilization were between-subject factors, year, month and day were within-subject factors. Multi-comparison of least standard difference (LSD) was conducted for all measured variables within each sampling date and each soil depth using a two-way ANOVA. The influences of warming, grazing and fertilization on mean monthly, and seasonal GHG fluxes during growing seasons were investigated using a three-way ANOVA, in which warming, grazing and fertilization were crossed. Simple correlation analysis was performed to test the possible dependency of GHG on soil temperature, soil moisture and/or ANPP in 2011 and 2012. All significances mentioned in the text were at the 0.05 level.

3. Results

3.1. Soil temperature and soil moisture

Similar to previous reports before 2010 (Luo et al., 2010; Wang et al., 2012), soil temperature and soil moisture were significantly affected by warming and/or cutting, year, month and sampling date and interactions between warming and them during the growing season in 2011 and 2012 (Tables S1 and S2). Generally, warming reduced soil moisture by average 17% and 20% but increased soil temperature by 1.1 and 1.5 °C at 10 cm depth during the growing season in 2011 and 2012, respectively, and cutting only significantly increased soil temperature at 10 cm about 0.5 °C in 2012.

3.2. Aboveground net primary production (ANPP)

Although warming significantly increased ANPP and grazing did not affect it in 2010 (Wang et al., 2012), warming, cutting and fertilization alone did not significantly affect ANPP in 2011 and 2012. However, significant interactions were found between warming and year, between warming and cutting and between fertilization and year on ANPP (Table S3). For example, warming significantly increased ANPP by 12% only in 2012 (Fig. 1A), cutting increased ANPP by 18% only in 2011 (Fig. 1B) and fertilization increased ANPP by 4% only in 2012 (Fig. 1C).

3.3. GHG fluxes

Generally, GHG fluxes varied with treatment, sampling day and year (Figs. S3–S5). In 2010, only interactions between warming or grazing and sampling dates significantly affected CO_2 flux (Table S4). CH_4 flux was affected by warming alone and the interaction with warming, grazing, fertilization and sampling date; and N_2O flux was affected by grazing alone and the interaction between grazing and sampling date (Table S4). 6 out of 15 samplings for warming and 3 out of 15 samplings for grazing significantly affected CO_2 flux during the growing season of 2010 (Fig. S6). Especially, warming significantly increased CO_2 flux in September and October ($p < 0.05$) and it marginally decreased CO_2 flux in August ($p = 0.089$)

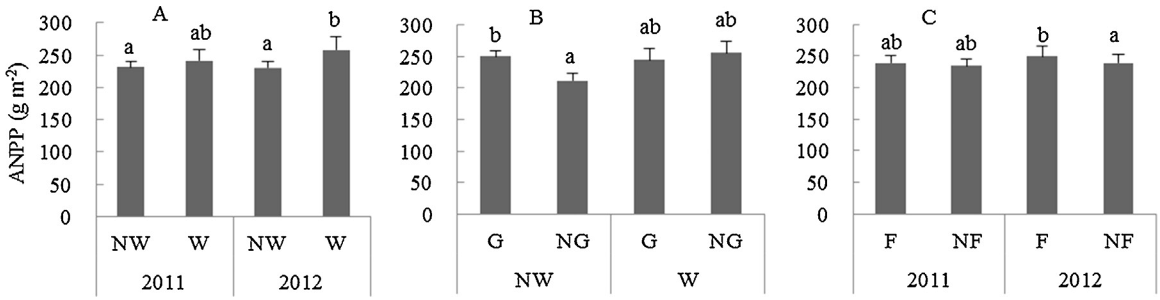

Fig. 1. Change of plant aboveground net primary production (ANPP) under different treatments. NW: no warming; W: warming; NG: no grazing; G: grazing; NF: no nitrogen fertilization; F: nitrogen fertilization. Data are averages of ANPP and standard error of the mean. Different letters represent were significant difference at $p < 0.05$.

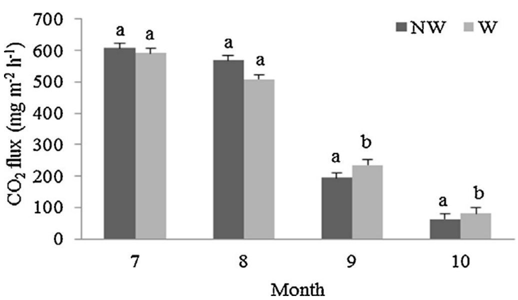

Fig. 2. Effect of warming on CO_2 flux under different months in 2010. NW: no warming; W: warming. Data are averages of CO_2 flux and standard error of the mean. Different letters represent were significant difference at $p < 0.05$.

compared with no warming (Fig. 2). Generally, fertilization alone did not significantly affect CH_4 flux (Fig. 3A), but warming alone average increased CH_4 uptake by 46% compared with no warming regardless of grazing and fertilization during the growing season (Fig. 3B). Although the effect of grazing on N_2O flux varied with sampling day (Fig. S7), grazing significantly increased N_2O emission by 62% compared with no grazing during the growing season regardless of warming and fertilization (Fig. 3C).

In 2011 and 2012, CO_2 flux was significantly affected by warming, year and sampling date (Table S5). Warming increased average CO_2 flux by 10% (Fig. 4A) and average seasonal CO_2 flux increased by 13% in 2012 compared with 2011 (Fig. 4B). CH_4 flux was affected by warming, fertilization and sampling dates and interaction between warming, cutting and sampling day (Table S5). Warming and fertilization alone significantly increased average CH_4 uptake by 32% and 14% (Fig. 5A and B), respectively, and average seasonal CH_4 uptake increased by 27% in 2012 compared with 2011 (Fig. 5C). Winter cutting significantly decreased CH_4 uptake only on 28 August in 2011 and increased it only on 30 June in 2012 under warming (Fig. S8). Warming, winter cutting and N fertilization alone did not significantly affect N_2O flux (Table S5), and the interactive effect between cutting and N fertilization on N_2O flux varied with year (Fig. 6).

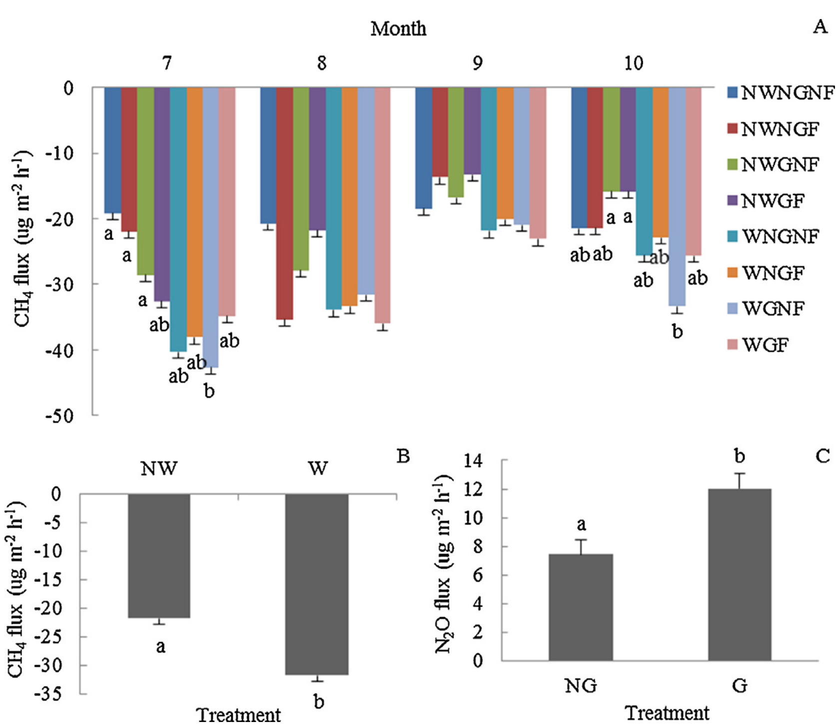

Fig. 3. Effects of warming, grazing and nitrogen fertilization on CH_4 (A and B) and N_2O (C) fluxes in 2010. NWNGNF: no warming, no grazing and no nitrogen (N) fertilization; NWNGF: no warming, no grazing and N fertilization; NWGNF: no warming, grazing and no N fertilization; NWGF: no warming, grazing and N fertilization; WNGNF: warming, no grazing and no N fertilization; WNGF: warming, no grazing and N fertilization; WGNF: warming, grazing and no N fertilization; WGF: warming, grazing and N fertilization; NW: no warming; W: warming; NG: no grazing; G: grazing. Data are averages of CH_4 (A and B) and N_2O fluxes and their standard errors of the mean. Different letters represent were significant difference at $p < 0.05$.

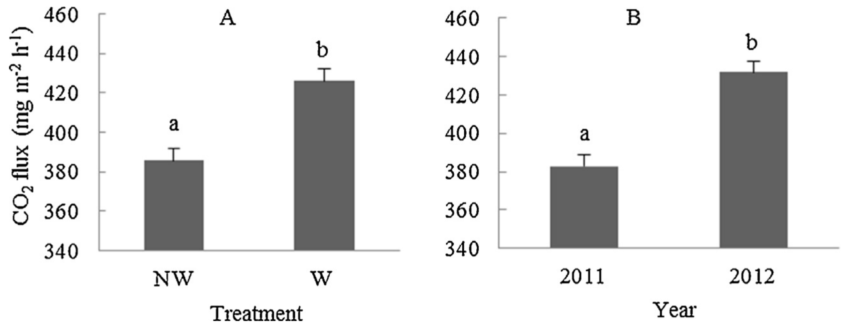

Fig. 4. Effect of warming on CO_2 flux in 2011 and 2012. NW: no warming; W: warming. Data are averages of CO_2 flux and standard error of the mean. Different letters represent were significant difference at $p < 0.05$. There were no significant differences among different treatments in 8 and 9 months in Fig. 3A.

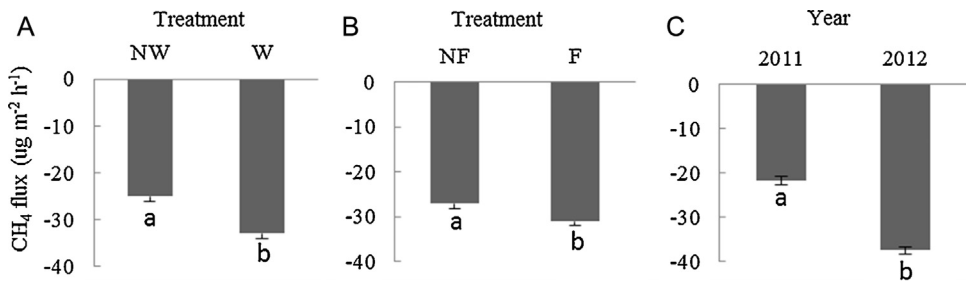

Fig. 5. Effects of warming and fertilization on CH_4 flux in 2011 and 2012. NW: no warming; W: warming. NF: no nitrogen (N) fertilization; F: N fertilization. Data are averages of CH_4 flux and standard error of the mean. Different letters represent were significant difference at $p < 0.05$.

3.4. *Relationships between GHG fluxes and soil temperature, soil moisture and ANPP*

Generally, CO_2 flux increased with soil temperature (Fig. 7A) and ANPP (Fig. 7B). Soil temperature and ANPP could explain about 55% and 18% of CO_2 flux variation, respectively. Significant positive and negative correlations were found between daily CH_4 flux and soil moisture (Fig. 7C) and between seasonal CH_4 flux and ANPP (Fig. 7D). Soil moisture and ANPP explained about 17% and 8% of daily CH_4 flux variation, respectively. There were no significant correlations between N_2O and soil temperature, soil moisture and ANPP (data not shown). Moreover, warming reduced the temperature sensitivity (i.e. exponential index) of CO_2 regardless of grazing and fertilization, but the effects of grazing and fertilization on it were small (Fig. S9). Warming enhanced the dependency (i.e. slopes of regression equations) of CH_4 flux on soil moisture under no fertilization regardless of grazing (Fig. S10A, B, E and F), but opposite trends were found for warming under fertilization regardless of grazing (Fig. S10C, D, G and H).

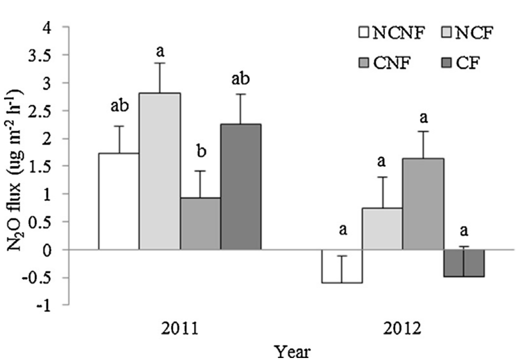

Fig. 6. Effect of different treatments on N_2O flux in 2011 and 2012. NCNF: no cutting and no nitrogen (N) fertilization; NCF: no cutting and N fertilization; CNF: cutting and no N fertilization; CF: cutting and N fertilization. Data are averages of N_2O flux and standard error of the mean. Different letters represent were significant difference at $p < 0.05$.

4. Discussion

4.1. *Effect of warming on GHG fluxes*

Consistent with previous results for first 3 years of warming from 2006 to 2008 (Lin et al., 2011), we found that warming still did not significantly affect CO_2 flux during the growing season in 2010 (Table S4). However, it significantly increased CO_2 flux during the growing seasons in 2011 and 2012 in our study (Table S5, Fig. 4A). Our result were obviously different from previous studies (Oechel et al., 2000; Luo et al., 2001; Rustad et al., 2001; Melillo et al., 2002; Eliasson et al., 2005; Bradford et al., 2008), which reported that the initially elevated rates of CO_2 flux in warmed soils returned to even lower CO_2 flux than those of the control soils over continuous warming time. This difference may be caused by the following. Firstly, soil substrate was not depleted because warming increased plant production (Fig. 2; Wang et al., 2012), litter decomposition (Luo et al., 2010) and soil dissolved organic carbon (DOC) (Luo et al., 2009; Rui et al., 2011) in the study. Secondly, the effect of temperature on CO_2 flux was over the effect of soil moisture in the region (Fig. 7A; Lin et al., 2011) although decrease in soil moisture concomitant with increase in temperature due to no significant correlation between CO_2 flux and soil moisture in our study, which was consistent with Lin et al. (2011). Probably indirectly because there were positive and negative correlations between soil temperature and soil moisture and plant production (Wang et al., 2012). Thirdly, there does not appear to be a temperature adaptation of soil microbial communities over warming time (Hartley et al., 2007, 2008, 2009). Warming significantly altered the functional structure of soil microbial community (Zhou et al., 2012), and could increase C-decomposition genes, such as cellulose and chitin-degradation genes (Yergeau et al., 2012; Zhou et al., 2012) because this presumably refers to the early period of this warming experiment.

Some researchers showed no effect of warming on CH_4 uptake for forests (Christensen et al., 1997; Rustad and Fernandez, 1998) and even decreases CH_4 uptake in a semiarid grassland (Blankinship

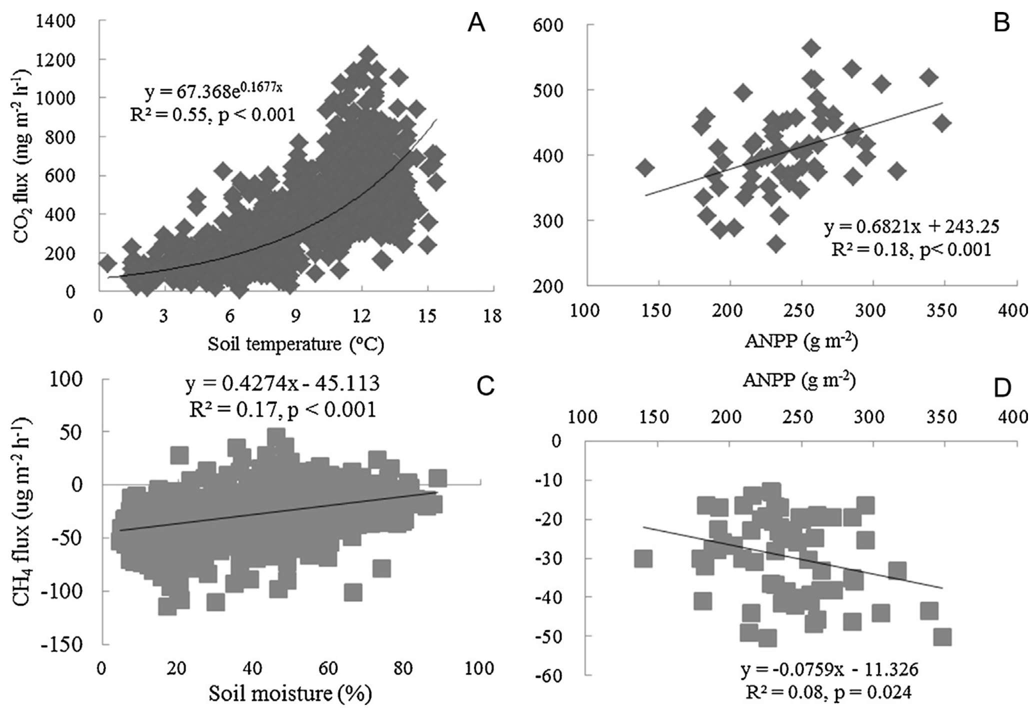

Fig. 7. Relationships between CO_2 and CH_4 fluxes and soil temperature (A), soil moisture (C) and plant aboveground net primary production (ANPP) (B and D).

et al., 2010a,b; Dijkstra et al., 2011). However, consistent with previous warming studies (Sjögersten and Wookey, 2002; Hart, 2006; Wang et al., 2009; Carter et al., 2011, 2012), warming significantly increased in CH_4 uptake rates in our study. Probably warming reduced soil moisture which was negatively correlated with CH_4 uptake rate (Fig. 7C), because CH_4 diffusion could be controlled by soil moisture in the alpine meadow (i.e. semi-humid soil) (Dunfield, 2007; Carter et al., 2011; Dijkstra et al., 2011). Meanwhile, Zheng et al. (2012) found that warming promoted the abundance of methanotrophs which could contribute to increased CH_4 uptake. Probably when fewer soil pores are water filled, more atmospheric CH_4 could reach methanotrophic microorganisms, which might respond positively to the temperature increase (Pearce and Clymo, 2001; Zhuang et al., 2007).

Nitrous oxide flux to the atmosphere is likely to increase under most scenarios of climate change (Dijkstra et al., 2012; Xu et al., 2012), whereas Carter et al. (2011) found that warming decreased N_2O flux or had no effect on N_2O fluxes (Carter et al., 2012). Our previous results showed that the effect of warming on N_2O flux varied with season and year (Hu et al., 2010). However, we found that warming did not significantly affect N_2O fluxes from 2010 to 2012 in the study (Tables S4 and S5). Probably the effects of increased soil temperature and decreased soil moisture on N_2O production processes were offset (Hu et al., 2010). Xu et al. (2003b) reported that denitrification was the main process for N_2O formation and could explain about 64–88% of the variation of total N_2O emission in the Inner Mongolia steppe. Lower soil moisture induced by warming probably increases O_2 diffusion within the soil which could lead to smaller anaerobic microsites and thereby decreased N_2O production via denitrification (Smith et al., 2013; Goldberg and Gebauer, 2009; Carter et al., 2012). However, there were no significant correlations between N_2O and soil temperature and soil moisture (data not shown) in our study, suggesting that other factors may affect N_2O production processes, such as soil N availability (Xu et al., 2003a,b; Ma et al., 2006; Lin et al., 2009). The N application rates to this low N system may be small, so N uptake by plants is perhaps more likely than N_2O emission, unless there might be optimal conditions as seen on the first measurement date (Fig. S5).

4.2. Effect of grazing/cutting on GHG fluxes

Many studies showed that grazing/cutting reduced CO_2 flux (Bergner et al., 2004; Owensby et al., 2006; Polley et al., 2008) or increased it (Bahn et al., 2006). Similar to previous results in the same experiment (Lin et al., 2011), we found that grazing/cutting alone did not significantly affect CO_2 flux during the growing seasons in our study (Tables S4 and S5). The net effects of grazing on it will be determined by the balance of negative and positive effects of grazing on ecosystem respiration processes (Zhou et al., 2007; Lin et al., 2011). For example, removal of plant biomass through grazing reduced plant autotrophic respiration (Raiesi and Asadi, 2006), but increased soil temperature which in turn increased soil respiration (Bahn et al., 2006). The small effect of winter cutting on CO_2 flux in 2011 and 2012 in our study was probably because winter cutting did not significantly affect plant production during the growing period in the region (Cui et al., 2014) and its effect on soil may be small due to freezing at that time.

Consistent with previous reports from the same experiment (Hu et al., 2010), grazing significantly increased N_2O flux during the growing season in 2010 (Table S1), but winter cutting alone did not affect it in 2011 and 2012 (Table S2). Meanwhile, there was a great difference in N_2O flux between 2010 (i.e. wetter year) and 2011 and 2012 (i.e. drier years). Previous studies showed that drier weather decreased N_2O production due to reduced denitrification (Smith et al., 2013; Goldberg and Gebauer, 2009; Carter et al., 2012). Although generally we found there were no significant correlation between N_2O flux and soil moisture in our study, greater N_2O flux was found on 6 July in 2010 which caused larger average seasonal N_2O flux relative to 2011 and 2012 because more rain fell during that period compared with 2011 and 2012 (Fig. S1). The result implies that winter mowing could have no effect on N_2O flux in the alpine meadow.

Grazing/cutting alone did not significantly affect CH_4 fluxes in our study (Tables S4 and S5), which is consistent with other results (Zhou et al., 2008; Chen et al., 2011). Some reports indicated that grazing reduced CH_4 flux (Liu et al., 2007; Saggar et al., 2007) due to trampling resulting in soil compaction may decrease O_2 diffusion into the soil and limiting CH_4 and O_2 availability for the oxidation process (Saggar et al., 2007; Liu et al., 2007). However, the trampling effect could be limited due to two times of grazing under the moderate grazing or winter cutting in our study. These conflicting responses of CH_4 uptake to grazing/cutting may be due to differences in grazing intensity and climate condition.

4.3. Effect of nitrogen fertilization on GHG fluxes

Previous studies showed that N fertilizer application depresses CO_2 flux (Ladd et al., 1994; Smolander et al., 1994; Ma et al., 1999; Micks et al., 2004; Al-Kaisi et al., 2008), whereas small increases or no effect were observed under N addition (Craine and Gelderman, 2011; Entry et al., 1996; Conti et al., 1997; Willson et al., 2001; Kaye et al., 2005; Zhang et al., 2007, 2012). In line with other observations (Micks et al., 2004; Jiang et al., 2010; Carter et al., 2012), we found that N addition did not alter CO_2 flux for 3-year in our study (Tables S1 and S2). The response of CO_2 flux to N addition may be related to soil N availability and amount of N addition (Carter et al., 2011). Our previous study indicated that warming did not significantly change soil N net mineralization rate in the alpine meadow and N could not limit plant production (Wang et al., 2012). Meanwhile, the annual N-application rates in our study were lower than other studies (Craine and Gelderman, 2011), which may limit impact on the N-status and associated processes because high N addition could remove N constraints on microbial metabolism and improve litter quality (Carter et al., 2012). Moreover, N addition may enhance plant respiration due to increase of N uptake (Jassal et al., 2011), but it also can reduce the microbial biomass and activity which may reduce soil respiration (Mo et al., 2008). Thus, the net effects of N addition on CO_2 flux may be offset by the opposite processes.

There was an inconsistent effect of N application on the sink strength of CH_4, including suppression (Bodelier and Laanbroek, 2004; Jiang et al., 2010) and little or no effect (Lessard et al., 1997) even to increased soil CH_4 oxidation (Bodelier and Laanbroek, 2004). These contradictory results suggest that the effects of increased N availability on CH_4 exchange are dependent on site specific properties (Carter et al., 2012). Our results indicated that there was no response of CH_4 uptake to N addition in the humid year (i.e. 2010) (Table S4), but it was increased by N addition during the drier years in 2011 and 2012 (Table S5 and Fig. 5B). Probably because the effect of N addition on it depends on the net effect between CH_4 oxidation (Chan and Parkin, 2001; Bodelier and Laanbroek, 2004; Menyailo et al., 2008) and production (Christopher and Lal, 2007) depending on soil moisture.

N fertilizer application can lead to substantial N_2O emission through nitrification-denitrification processes (Robertson and Vitousek, 2009). However, we found that N addition alone did not significantly affect N_2O flux during the experimental period (Tables S4 and S5), probably because denitrification could be limited by low temperature (Ambus et al., 2006; Curtis et al., 2006; Liu and Greaver, 2009) or low soil moisture in most sub-humid upland soils in the northern China (Ju et al., 2009) because reduced soil moisture decreased the N_2O efflux (Dobbie and Smith, 2003; Carter et al., 2012).

5. Conclusions

Warming significantly increased ecosystem respiration during the dry years in 2011 and 2012 and CH_4 uptake during the growing seasons over 3-year period. Grazing during the growing season in 2010 stimulated N_2O emission, but winter cutting did not significantly affect it in 2011 and 2012. N fertilization alone had no significantly effect on GHG fluxes and the interactive effect of warming, grazing/cutting and N fertilization on GHG fluxes was small. Therefore, our results suggest that increased N deposition could not affect GHG fluxes under future warming with grazing in the alpine region.

Acknowledgements

This work was supported by funding from the National Basic Research Program (2013CB956000), National Science Foundation of China (41230750 and 31272488) and Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB03030403). We are grateful to Dr. Andreas Wilkes for help with the language.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2015.09.008.

References

Al-Kaisi, M.M., Kruse, M.L., Sawyer, J.E., 2008. Effect of nitrogen fertilizer application on growing season soil carbon dioxide emission in a corn–soybean rotation. J. Environ. Qual. 37, 325–332.

Allison, I., Bindoff, N.L., Bindschadler, R., Cox, P., de Noblet-Ducoudre, N., England, M., Francis, J., Gruber, N., Haywood, A., Karoly, D., Kaser, G., Le Quere, C., Lenton, T., Mann, M., McNeil, B., Pitman, A., Rahmstorf, S., Rignot, E., Schellnhuber, H.J., Schneider, A., Sherwood, S., Somerville, R., Steffen, K., Steig, E., Visbeck, M., Weaver, A., 2009. The Copenhagen Diagnosis 2009 Updating the World on the Latest Climate Science. The University of New South Wales Climate Change Research Centre (CCRC), Sydney, Australia.

Ambus, P., Zechmeister-Boltenstern, S., Butterbach-Bahl, K., 2006. Sources of nitrous oxide emitted from European forest soils. Biogeosciences 3, 135–145.

Bahn, M., Knapp, M., Garajova, Z., Pfahringer, N., Cernusca, A., 2006. Root respiration in temperate mountain grasslands differing in land use. Global Change Biol. 12, 995–1006.

Bergner, B., Johnstone, J., Treseder, K.K., 2004. Experimental warming and burn severity alter soil CO_2 flux and soil functional groups in a recently burned boreal forest. Global Change Biol. 10, 1996–2004.

Blankinship, J.C., Brown, J.R., Dijkstra, P., Allwright, M.C., Hungate, B.A., 2010a. Response of terrestrial CH_4 uptake to interactive changes in precipitation and temperature along a climatic gradient. Ecosystems 13, 1157–1170.

Blankinship, J.C., Brown, J.R., Dijkstra, P., Hungate, B.A., 2010b. Effects of interactive global changes on methane uptake in an annual grassland. J. Geophys. Res. – Biogeosci. 115, G2.

Bodelier, P.L.E., Laanbroek, H.J., 2004. Nitrogen as a regulatory factor of methane oxidation in soils and sediments. FEMS Microbiol. Ecol. 47, 265–277.

Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E., Reynolds, J.F., Treseder, K.K., Wallenstein, M.D., 2008. Thermal adaptation of soil microbial respiration to elevated temperature. Ecol. Lett. 11, 1316–1327.

Carter, M.S., Larsen, K.S., Emmett, B., Estiarte, M., Field, C., Leith, I.D., Lund, M., Meijide, A., Mills, R.T.E., Niinemets, Ü., Peñuelas, J., Portillo-Estrada, M., Schmidt, I.K., Selsted, M.B., Sheppard, L.J., Sowerby, A., Tietema, A., Beier, C., 2012. Synthesizing greenhouse gas fluxes across nine European peatlands and shrublands – responses to climatic and environmental changes. Biogeosciences 9, 3739–3755.

Carter, M., Ambus, P., Albert, K.R., Larsen, K.S., Andersson, M., Prieme, A., van der Linden, L., Beier, C., 2011. Effects of elevated atmospheric CO_2, prolonged summer drought and temperature increase on N_2O and CH_4 fluxes in a temperate heathland. Soil Biol. Biochem. 43, 1660–1670.

Chan, A.S.K., Parkin, T.B., 2001. Effect of land use on methane flux from soil. J. Environ. Qual. 30, 786–797.

Chen, W.W., Wolf, B., Zheng, X.H., Yao, Z.S., Butterbach-Bahl, K., Bruggemann, N., Liu, C.Y., Han, S.H., Han, X.G., 2011. Annual methane uptake by temperate semiarid steppes as regulated by stocking rates, aboveground plant biomass and topsoil air permeability. Global Change Biol. 17, 2803–2816.

Christopher, S.F., Lal, R., 2007. Nitrogen management affects carbon sequestration in North American cropland soils. Crit. Rev. Plant Sci. 26, 45–64.

Craine, J.M., Gelderman, T.M., 2011. Soil moisture controls on temperature sensitivity of soil organic carbon decomposition for a mesic grassland. Soil Biol. Biochem. 43, 455–457.

Christensen, T.R., Michelsen, A., Jonasson, S., Schmidt, I.K., 1997. Carbon dioxide and methane exchange of a subarctic heath in response to climate change related environmental manipulations. Oikos 79, 34–44.

Conti, M.E., Arrigo, N.M., Marrelli, H.J., 1997. Relationship of soil carbon light fraction, microbial activity, humic acid production and nitrogen fertilization in the decaying process of corn stubble. Biol. Fertil. Soils 25, 75–78.

Cui, S.J., Zhu, X.X., Wang, S.P., Zhang, Z.H., Xu, B., Luo, C.Y., Zhao, L., Zhao, X.Q., 2014. Effects of seasonal grazing on soil respiration in alpine meadow on the Tibetan plateau. Soil Use Manag. 30, 435–443.

Curtis, C.J., Emmett, B.A., Reynolds, B., Shilland, J., 2006. How important is N_2O production in removing atmospherically deposited nitrogen from UK moorland catchments? Soil Biol. Biochem. 38, 2081–2091.

Dijkstra, F.A., Morgan, J.A., von Fischer, J.C., Follett, R.F., 2011. Elevated CO_2 and warming effects on CH_4 uptake in a semiarid grassland below optimum soil moisture. J. Geophys. Res. – Biogeosci. 116, G1.

Dijkstra, F.A., Prior, S.A., Runion, G.B., Torbert, H.A., Tian, H., Lu, C., Venterea, R.T., 2012. Effects of elevated carbon dioxide and increased temperature on methane and nitrous oxide fluxes: evidence from field experiments. Front. Ecol. Environ. 10, 520–527.

Dobbie, K.E., Smith, K.A., 2003. Impact of different forms of N fertilizer on N_2O emissions from intensive grassland. Nutr. Cycl. Agroecosyst. 67, 37–46.

Dunfield, P., 2007. The soil methane sink. In: Reay, D., Hewitt, C., Smith, K., Grace, J. (Eds.), Greenhouse Gas Sinks. CAB International, Oxfordshire, UK, pp. 152–170.

Eliasson, P.E., McMurtrie, R.E., Pepper, D.A., Strömgren, M., Linder, S., Ågren, G.I., 2005. The response of heterotrophic CO_2 flux to soil warming. Global Change Biol. 11, 167–181.

Entry, J.A., Mitchell, C.C., Backman, C.B., 1996. Influence of management practices on soil organic matter, microbial biomass, and cotton yield in Alabama "old rotation". Biol. Fertil. Soils 23, 353–358.

Galloway, J.N., Cowling, E.B., 2002. Reactive nitrogen and the world: 200 years of change. Ambio 31, 64–71.

Goldberg, S.D., Gebauer, G., 2009. N_2O and NO fluxes between a Norway spruce forest soil and atmosphere as affected by prolonged summer drought. Soil Biol. Biochem. 41, 1986–1995.

Hart, S.C., 2006. Potential impacts of climate change on nitrogen transformations and greenhouse gas fluxes in forests: a soil transfer study. Global Change Biol. 12, 1032–1046.

Hartley, I.P., Heinemeyer, A., Ineson, P., 2007. Effects of three years of soil warming and shading on the rate of soil respiration: substrate availability and not thermal acclimation mediates observed response. Global Change Biol. 13, 1761–1770.

Hartley, I.P., Hopkins, D.W., Garnett, M.H., Sommerkorn, M., Wookey, P.A., 2008. Soil microbial respiration in arctic soil does not acclimate to temperature. Ecol. Lett. 11, 1092–1100.

Hartley, I.P., Hopkins, D.W., Garnett, M.H., Sommerkorn, M., Wookey, P.A., 2009. No evidence for compensatory thermal adaptation of soil microbial respiration in the study of Bradford et al (2008). Ecol. Lett. 12, E12–E14.

Hole, L.R., Engardt, M., 2008. Climate change impact on atmospheric nitrogen deposition in northwestern Europe: a model study. Ambio 37, 9–17.

Hu, Y.G., Chang, X.F., Lin, X.W., Wang, W.F., Wang, S.P., Duan, J.C., Zhang, Z.H., Yang, X.X., Luo, C.Y., Xu, G.P., Zhao, X.Q., 2010. Effects of warming and grazing on N_2O fluxes in an alpine meadow ecosystem on the Tibetan plateau. Soil Biol. Biochem. 42, 944–952.

IPCC, 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp. 1535.

Jassal, R.S., Black, T.A., Ray, R., Ethier, G., 2011. Effect of nitrogen fertilization on soil CH_4 and N_2O fluxes, and soil and bole respiration. Geoderma 162, 182–186.

Jiang, C.M., Yu, G.R., Fang, H.J., Cao, G.M., Li, Y.N., 2010. Short-term effect of increasing nitrogen deposition on CO_2, CH_4 and N_2O fluxes in an alpine meadow on the Qinghai-Tibetan Plateau, China. Atmos. Environ. 44, 2920–2926.

Ju, X.T., Xing, G.X., Chen, X.P., Zhang, S.L., Zhang, L.J., Liu, X.J., Cui, Z.L., Yin, B., Christie, P., Zhu, Z.L., Zhang, F.S., 2009. Reducing environmental risk by improving N management in intensive Chinese agricultural systems. Proc. Natl. Acad. Sci. U.S.A. 106, 3041–3046.

Kaye, J.P., McCulley, R.L., Burke, I.C., 2005. Carbon fluxes, nitrogen cycling, and soil microbial communities in adjacent urban, native and agricultural ecosystems. Global Change Biol. 11, 575–587.

Kimball, B.K., Conley, M.M., Wang, S.P., Lin, X.W., Luo, C.Y., Morgan, J., Smith, D., 2008. Infrared heater arrays for warming ecosystem field plots. Global Change Biol. 14, 309–320.

Ladd, J.N., Amato, M., Li-Kai, Z., Schultz, J.E., 1994. Differential effects of rotation, plant residue, and nitrogen fertilizer on microbial biomass and organic matter in an Australian alfisol. Soil Biol. Biochem. 26, 821–831.

Lessard, R., Rochette, P., Gregorich, E.G., Desjardins, R.L., Pattey, E., 1997. CH_4 fluxes from a soil amended with dairy cattle manure and ammonium. Can. J. Soil Sci. 77, 179–186.

Lin, X.W., Wang, S.P., Ma, X.Z., Xu, G.P., Luo, C.Y., Li, Y.N., Jiang, G.M., Xie, Z.B., 2009. Fluxes of CO_2, CH_4, and N_2O in an alpine meadow affected by yak excreta during summer grazing periods on the Qinghai-Tibetan plateau. Soil Biol. Biochem. 41, 718–725.

Lin, X.W., Zhang, Z.H., Wang, S.P., Hu, Y.G., Xu, G.P., Luo, C.Y., Chang, X.F., Duan, J.C., Lin, Q.Y., Xu, B., Wang, Y.F., Zhao, X.Q., Xie, Z.B., 2011. Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan plateau. Agric. Forest Meteorol. 151, 792–802.

Lin, X.W., Wang, S.P., Hu, Y.G., Luo, C.Y., Zhang, Z.H., Niu, H.S., Xie, Z.B., 2015. Experimental warming increases seasonal methane uptake in an alpine meadow on the Tibetan plateau. Ecosystems 18, 274–286.

Liu, X.J., Zhang, Y., Han, W.X., Tang, A.H., Shen, J.L., Cui, Z.L., Vitousek, P., Erisman, J.W., Goulding, K., Christie, P., Fangmeier, A., Zhang, F.S., 2013a. Enhanced nitrogen deposition over China. Nature 494, 459–462.

Liu, L.L., Greaver, T.L., 2009. A review of nitrogen enrichment effects on three biogenic GHGs: the CO_2 sink may be largely offset by stimulated N_2O and CH_4 emission. Ecol. Lett. 12, 1103–1117.

Liu, C.Y., Holst, J., Bruggemann, N., Butterbach-Bahl, K., Yao, Z.S., Yue, J., Han, S.H., Han, X., Krummelbein, J., Horn, R., Zheng, X.H., 2007. Winter-grazing reduces methane uptake by soils of a typical semi-arid steppe in Inner Mongolia, China. Atmos. Environ. 41, 5948–5958.

Liu, X.D., Chen, B.D., 2000. Climatic warming in the Tibetan Plateau during recent decades. Int. J. Climatol. 20, 1729–1742.

Liu, Y.W., Xu, R., Xu, X.L., Wei, D., Wang, Y.H., Wang, Y.S., 2013b. Plant and soil responses of an alpine steppe on the Tibetan Plateau to multi-level nitrogen addition. Plant Soil 373, 515–529.

Lü, C.Q., Tian, H.Q., 2007. Spatial and temporal patterns of nitrogen deposition in China: synthesis of observational data. J. Geophys. Res., http://dx.doi.org/10.1029/2006.JD007990.

Luo, Y.Q., Wan, S.Q., Hui, D.F., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413, 622–625.

Luo, C.Y., Xu, G.P., Wang, Y.F., Wang, S.P., Lin, X.W., Hu, Y.G., Zhang, Z.H., Chang, X.F., Duan, J.C., Su, A.L., Zhao, X.Q., 2009. Effects of grazing and experimental warming on DOC concentrations in the soil solution on the Qinghai-Tibet Plateau. Soil Biol. Biochem. 41, 2493–2500.

Luo, C.Y., Xu, G.P., Chao, Z.G., Wang, S.P., Lin, X.W., Hu, Y.G., Zhang, Z.H., Duan, J.C., Chang, X.F., Su, A.L., Li, Y.N., Zhao, X.Q., Du, M.Y., Tang, Y.H., Kimball, B., 2010. Effect of warming and grazing on litter mass loss and temperature sensitivity of litter and dung mass loss on the Tibetan plateau. Global Change Biol. 16, 1606–1617.

Ma, B.L., Dwyer, L.M., Gregorich, E.G., 1999. Soil nitrogen amendment effects on seasonal nitrogen mineralization and nitrogen cycling in maize production. Agron. J. 91, 1003–1009.

Ma, X.Z., Wang, S.P., Wang, Y.F., Jiang, G.M., Nyren, P., 2006. Short-term effects of sheep excreta on carbon dioxide, nitrous oxide and methane fluxes in typical grassland of Inner Mongolia. N. Z. J. Agric. Res. 49, 285–297.

Meinshausen, M., Meinshausen, N., Hare, W., Raper, S.C.B., Frieler, K., Knutti, R., Frame, D.J., Allen, M.R., 2009. Greenhouse-gas emission targets for limiting global warming to 2 °C. Nature 458, 1158–1162.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon cycle feedbacks to the climate system. Science 298, 2173–2176.

Menyailo, O.V., Hungate, B.A., Abraham, W., Conrad, R., 2008. Changing land use reduces soil CH_4 uptake by altering biomass and activity but not composition of high-affinity methanotrophs. Global Change Biol. 14, 2405–2419.

Micks, P., Aber, J.D., Boone, R.D., Davidson, E.A., 2004. Short-term soil respiration and nitrogen immobilization response to nitrogen applications in control and nitrogen-enriched temperate forests. Forest Ecol. Manag. 196, 57–70.

Mo, J., Zhang, W., Zhu, W., Gundersen, P., Fang, Y., Li, D., Wang, H., 2008. Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. Glob Chang Biol. 14, 403–412.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L., Kane, D., 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature 406, 978–981.

Owensby, C.E., Ham, J.M., Auen, L.M., 2006. Fluxes of CO_2 from grazed and ungrazed tallgrass prairie. Rangel. Ecol. Manag. 59, 111–127.

Pearce, D.M.E., Clymo, R.S., 2001. Methane oxidation in a peatland core. Global Biogeochem. Cycles 15, 709–720.

Polley, H.W., Frank, A.B., Sanabria, J., Phillips, R.L., 2008. Interannual variability in carbon dioxide fluxes and flux–climate relationships on grazed and ungrazed northern mixed-grass prairie. Global Change Biol. 14, 1620–1632.

Raiesi, F., Asadi, E., 2006. Soil microbial activity and litter turnover in native grazed and ungrazed rangelands in a semiarid ecosystem. Biol. Fertil. Soils 43, 76–82.

Robertson, G.P., Vitousek, P.M., 2009. Nitrogen in agriculture: balancing the cost of an essential resource. Annu. Rev. Environ. Resour. 34, 97–125.

Rui, Y.C., Wang, S.P., Xu, Z.H., Wang, Y.F., Chen, C.R., Zhou, X.Q., Kang, X.M., Lu, S.B., Hu, Y.G., Lin, Q.Y., Luo, C.Y., 2011. Warming and grazing affect soil labile carbon and nitrogen pools differently in an alpine meadow of the Qinghai-Tibet Plateau in China. J. Soil Sediments 11, 903–914.

Rustad, L.E., Fernandez, I.J., 1998. Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce-fir forest soil in Maine USA. Global Change Biol. 4, 597–605.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., GCTE-NEWS, 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

Saggar, S., Hedley, C.B., Giltrap, D.L., Lambie, S.M., 2007. Measured and modelled estimates of nitrous oxide emission and methane consumption from a sheep-grazed pasture. Agric. Ecosyst. Environ. 122, 357–365.

Sjögersten, S., Wookey, P.A., 2002. Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra ecotone in the Fennoscandian mountains. Global Change Biol. 8, 885–894.

Smith, P., Haberl, H., Popp, A., Erb, K., Lauk, C., Harper, R., Tubiello, F.N., Pinto, A.S., Jafari, M., Sohi, S., Masera, O., Böttcher, H., Berndes, G., Bustamante, M., Ahammad, H., Clark, H., Dong, H., Elsiddig, E.A., Mbow, C., Ravindranath, N.H., Rice, C.W., Abad, C.R., Romanovskaya, A., Sperling, F., Herrero, M., House, J.I., Rose, S., 2013. How much land-based greenhouse gas mitigation can be achieved without compromising food security and environmental goals? Global Change Biol. 19, 2285–2302.

Smolander, A., Kurka, A., Kitunen, V., Malkonen, E., 1994. Microbial biomass C and N, and respiratory activity in soil of repeatedly limed and N- and P-fertilized Norway spruce stands. Soil Biol. Biochem. 26, 957–962.
Wang, S.P., Yang, X.X., Lin, X.W., Hu, Y.G., Luo, C.Y., Xu, G.P., Zhang, Z.H., Su, A.L., Chang, X.F., Chao, Z.G., Duan, J.C., 2009. Methane emission by plant communities in an alpine meadow on the Qinghai-Tibetan plateau – a new experimental study of alpine meadows and oat pasture. Biol. Lett. 5, 535–538.
Wang, S.P., Duan, J.C., Xu, G.P., Wang, Y.F., Zhang, Z.H., Rui, Y.C., Luo, C.Y., Xu, B., Zhu, X.X., Chang, X.F., Cui, X.Y., Niu, H.S., Zhao, X.Q., 2012. Effects of warming and grazing on soil N availability, species composition and ANPP in alpine meadow. Ecology 93, 2365–2376.
Wang, Y., Wang, Y., 2003. Quick measurement of CH_4, CO_2 and N_2O emission from a short-plant ecosystem. Adv. Atmos. Sci. 20, 842–844.
Willson, T.C., Paul, E.A., Harwood, R.R., 2001. Biologically active soil organic matter fractions in sustainable cropping systems. Appl. Soil Ecol. 16, 63–76.
Xu, R., Wang, M., Wang, Y., 2003a. Using a modified DNDC model to estimate N_2O fluxes from semi-arid grassland in China. Soil Biol. Biochem. 35, 615–620.
Xu, R., Wang, Y., Zheng, X., Ji, B., Wang, M., 2003b. A comparison between measured and modeled N_2O emissions from Inner Mongolian semi-arid grassland. Plant Soil 255, 513–528.
Xu, R., Prentice, I.C., Spahni, R., Niu, H.S., 2012. Modelling terrestrial nitrous oxide emissions and implications for climate feedback. New Phytol. 196, 472–488.
Yergeau, E., Bokhorst, S., Kang, S., Zhou, J.Z., Greer, C.W., Aerts, R., Kowalchuk, G.A., 2012. Shifts in soil microorganisms in response to warming are consistent across a range of Antarctic environments. ISME J. 6, 692–702.
Zhang, Z.H., Duan, J.C., Wang, S.P., Luo, C.Y., Chang, X.F., Zhu, X.X., Xu, B., Wang, W.Y., 2012. Effects of land use and management on ecosystem respiration in alpine meadow on the Tibetan plateau. Soil Tillage Res. 124, 161–169.
Zhang, L.H., Song, C.C., Zheng, X.H., Wang, D.X., Wang, Y.Y., 2007. Effects of nitrogen on the ecosystem respiration CH_4 and N_2O emissions to the atmosphere from the freshwater marshes in northeast China. Environ. Geol. 52, 529–539.
Zheng, D., Zhang, Q.S., Wu, S.H., 2000. Mountain Geoecology and Sustainable Development of the Tibetan Plateau. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 1–15.
Zheng, Y., Yang, W., Sun, X., Wang, S.P., Rui, Y.C., Luo, C.Y., Guo, L.D., 2012. Methanotrophic community structure and activity under warming and grazing of alpine meadow on the Tibetan Plateau. Appl. Microbiol. Biotechnol. 93, 2193–2203.
Zhou, J.Z., Xue, K., Xie, J.P., Deng, Y., Wu, L.Y., Cheng, X.L., Fei, S.F., Deng, S.P., He, Z.L., Van-Nostrand, J.D., Luo, Y.Q., 2012. Microbial mediation of carbon-cycle feedbacks to climate warming. Nat. Clim. Change 2, 106–110.
Zhou, X., Wan, S.Q., Luo, Y.Q., 2007. Source components and interannual variability of soil CO_2 efflux under experimental warming and cutting in a grassland ecosystem. Global Change Biol. 13, 761–775.
Zhou, X.Q., Wang, Y.F., Huang, X.Z., Hao, Y.B., Tian, J.Q., Wang, J.Z., 2008. Effects of grazing by sheep on the structure of methane-oxidizing bacterial community of steppe soil. Soil Biol. Biochem. 40, 258–261.
Zhuang, Q., Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Prinn, R.G., Steudler, P.A., Felzer, B.S., Hu, S., 2007. Net emission of CH_4 and CO_2 in Alaska: implications for the region's greenhouse gas budget. Ecol. Appl. 17, 203–212.
Zou, K.C., Zhang, J.X., Wang, Z.M., 1986. Study on nutrient concentrations in precipitation on Haibei Alpine Meadow Ecosystem. In: Haibei Alpine Meadow Ecosystem Research Station (Ed.), Alpine Biology, vol. 5. Science Press, Beijing, pp. 35–43.