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Responses of greenhouse gas fluxes to climate extremes in a semiarid grassland

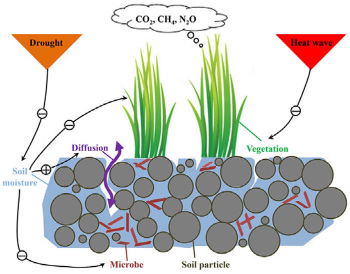
Linfeng Li [a], Wenyu Fan [a], Xiaoming Kang [b], Yanfen Wang [a], Xiaoyong Cui [a, **], Chengyuan Xu [c], Kevin L. Griffin [d], Yanbin Hao [a, *]

[a] College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China
[b] Institute of Wetland Research, Chinese Academy of Forestry, Beijing 100091, China
[c] School of Medical and Applied Sciences, Central Queensland University, Bundaberg, QLD 4670, Australia
[d] Department of Earth and Environmental Sciences, Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA

HIGHLIGHTS

- The magnitude and frequency of climate extremes are known to increase.
- Understanding the responses of GHG exchanges to climate extremes is vital to predicting future climate change.
- We performed climate extreme (extreme drought and heat wave) experiment to identify response amplitude.
- Climate extremes could change the budget of GHGs, and soil moisture is the critical mediating factor.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate extremes are expected to increase in frequency and intensity as a consequence of anthropogenic climate change attributed to the rise of atmospheric concentrations of greenhouse gases (GHGs). However, studies on the impacts of climate extremes on terrestrial ecosystems are limited. Here, we experimentally imposed extreme drought and a heat wave (~60-year recurrence) to investigate their effects on GHGs fluxes of a semiarid grassland in China. We estimated a 16% and 38% percent reduction in net ecosystem CO_2 uptake caused by the heat wave and drought respectively, but via different mechanisms. Drought reduced gross ecosystem productively (GEP) and to a lower extent ecosystem respiration (ER). By contrast, the simulated heat wave suppressed only GEP while ER remained stable. The climate extremes also created a legacy effect on GEP and NEE lasting until the end of the growing season, whereas ER recovered immediately. Although CH_4 and N_2O fluxes were unaffected by the heat wave, drought promoted CH_4 uptake and suppressed N_2O emission during the treatment period. The effect of drought on GHGs fluxes generally overwhelmed that of the heat wave treatment, and there were no interactive effects of these two types of climate extremes. Our results showed that responses of ecosystem GHGs exchange to climate extremes are strongly regulated by soil moisture status. In

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* Corresponding author.
** Corresponding author.
E-mail addresses: cuixy@ucas.ac.cn (X. Cui), ybhao@ucas.ac.cn (Y. Hao).

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conclusion, future amplification of climate extremes could decrease the sink for GHGs, especially CO_2, in this semiarid grasslands.

1. Introduction

Over the last century, average global temperatures have increased and precipitation patterns have changed. This trend is expected to continue as a result of increasing atmospheric concentrations of greenhouse gases (GHGs) from anthropogenic emissions (IPCC, 2014). Global climate change affects a range of biogeochemical processes, which feedback to determine the production and consumption of several important greenhouse gases including carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4) (Dalal and Allen, 2008). In general, warming and precipitation changes have different impacts on terrestrial CO_2, CH_4 and N_2O fluxes. On the one hand, warming and increased precipitation could facilitate plant photosynthesis and microbial activity, promoting the production and consumption of GHGs (Niu et al., 2008; Shi et al., 2012). On the other hand, drought or increased evaporation caused by warming can reduce soil moisture, thereby inhibiting plant photosynthesis and microbial activity, leading to lower emissions or consumption of GHGs (Hartmann and Niklaus, 2012; Shi et al., 2012). Consequently, the size of soil C and N pools and soil-to-atmosphere fluxes of C and N may be strongly affect by warming and changes in precipitation patterns (Bloor and Bardgett, 2012; Verburg et al., 2009).

Previous manipulative field experiments have promoted our understanding of the effects of global climate change on greenhouse gas exchanges (Dijkstra et al., 2012; Wu et al., 2011). However, most studies have focused on chronic environmental change rather than discrete climate extremes (Jentsch et al., 2007; Smith, 2011). Yet future climate extremes, such as severe drought and heat waves, have been projected to increase both in frequency and intensity (Dai, 2011; Hansen et al., 2012). Compared to the commonly studied mean changes in climate, climate extremes have shorter duration, and occur suddenly with a larger amplitude of climatic conditions. Thus, future alterations in the regime of climate extremes could have a large influence on the structure and function of ecosystems (Katz and Brown, 1992), not only accelerating change, but perhaps even altering the direction of such responses (Jentsch et al., 2007).

A number of studies have investigated how ecosystem processes and dynamics respond to expected changes in climate extremes (Fay et al., 2000; Hoover et al., 2014; Jentsch et al., 2007; Schwalm et al., 2012). Although many of these focus on atmosphere biosphere CO_2 exchange (Fay et al., 2008; Mirzaei et al., 2008), they report an inconsistent effect of climate extremes. For example, multiyear extreme drought reduced carbon uptake of multiple ecosystems in western North America (Schwalm et al., 2012). By contrast, higher carbon uptake was reported in an artificially assembled grassland system exposed to a continuous five-year extreme drought (Jentsch et al., 2011). The dissimilarities of responses between these studies may be partly attributed to ecosystem type, or be a result of the specific magnitude, duration, and timing of the climate extremes studied.

Studies on CH_4 and N_2O exchange between the atmosphere and the plant-soil system under climate extremes are more limited. Terrestrial ecosystems are important sources and sinks of CH_4 and N_2O, both of which are produced and consumed through biological processes including methanogenesis, CH_4 oxidation, nitrification and denitrification (Dalal and Allen, 2008). Extreme soil environments created by climate extremes can both directly and indirectly affect these processes (Bateman and Baggs, 2005; Borken et al., 2006). In addition, climate extremes could change plant community composition (Hoover et al., 2014), which also affects CH_4 and N_2O fluxes (Ward et al., 2013). However, there is still a large gap in our understanding of the impact of extreme climate events on fluxes of these two critical GHGs.

Semiarid and arid ecosystems are critically important to global GHGs emissions (Dalal and Allen, 2008). For example, they act as a significant sink of CH_4, accounting for up to 40% of global CH_4 soil consumption (Galbally et al., 2008). Located in both arid and semiarid regions, the Inner Mongolian temperate steppe is the major component of China's grassland ecosystems and predicted to be sensitive to climate change (Christensen et al., 2004). Significant changes in both temperature and precipitation have been reported in this area (IPCC, 2014) and models predict that future climate change will substantially alter the carbon sequestration in this grassland (Kang et al., 2011).

In this study, we performed a manipulative experiment in a semiarid steppe in order to explore how two types of extreme climate events, extreme drought and a heat wave, affect the uptake and emission of CO_2, CH_4 and N_2O. A full factorial design was used to examine the independent and interactive effects of drought and heat wave during a two-year period. Since this semiarid ecosystem is typically water limited, we predict that the water deficit would be aggravated by acute drought. Furthermore, a possible increase in evapotranspiration during a heat wave could further intensify the water stress and intensify the response to drought. Thus, we hypothesized that (1) both extreme drought and heat wave treatments will decrease CO_2 uptake, CH_4 uptake and N_2O emission; (2) due to the more direct impact on soil moisture, the effects of extreme drought would be greater than that of a heat wave (both manipulated to mimic a ~60-year recurrence scenario); and (3) the combined effect of extreme drought during a heat wave would be greater than the effect of either factor alone.

2. Materials and methods

2.1. Site description

This study was part of the Extreme Climate Events and Biodiversity II (ECEB-II) experiment at the Inner Mongolia Grassland Ecosystem Research Station in the Xilin River Basin (43°32′ N, 116°40′ E, 1200 m a.s.l), Inner Mongolia Autonomous region, China. Mean annual temperature is −0.48 °C and mean annual precipitation is 358 mm with 60–80% falling during the growing season from May to September. The experiment was established in a temperate steppe, dominated by *L. chinensis, Agropyron cristatum, Cleistogenes squarrosa,* and *Carex duriuscula,* that has not been grazed since 1979. The soil is classified as dark chestnut in Chinese soil classification or as Calcis-orthic Aridisol under US Soil Taxonomy classification, with 60% sand, 21% clay and 19% silt (Hao et al., 2013).

2.2. Experiment design

Extreme climate treatments were applied in a randomized block design with four replicates per treatment: extreme drought (D), heat wave (T), extreme drought and heat wave (TD) and ambient control conditions (C). The treatments were based on 58 years (1953–2010, the longest record period) of local weather data, which was analyzed for intensity of extreme climate events. Extreme drought, or the maximum number of consecutive days without rainfall, was defined as 30 days' rain-free period (Fig. S1). We calculated the 99th percentile of daily maximum temperature and used this temperature (38 °C, Fig. S1) to define the ~60 recurrence heat wave (De Boeck et al., 2010), which was recorded once in available temperature record and lasted 7 days (from July 13 to July 19 in 2000). Daily minimum temperature during that extreme heat wave only increased 1.2 °C compared to average daily minimum temperature in July 2000. This increment was much smaller than that of the daily maximum temperature (7.0 °C). Therefore, we deem that the heat wave in this area characterizes in large elevation of daily maximum temperature but little change of daily minimum temperature. Thus, extreme heat wave treatment in this study were set as maximum air temperatures around 38 °C during daytime (9:00–15:00 h) last for 7 days.

Treatments were randomly applied to 2 m × 2 m plots. A metal flashing was sunk to a depth of 40 cm around each plot and remained 10 cm above ground to prevent water exchange between the inside and the outside of the plot. The 9 m^2 (3 m × 3 m) rainout shelter, consisted of a steel frame supporting a transparent polyester fiber board with no obvious or significant shading effects, was used to induce drought by preventing rainfall into the plot. The shelter was a dual span (2.1 m and 1.8 m maximum and minimum heights, respectively) covered a central 2.0 m × 2.0 m core plot. Shelter sides and ends were kept open to maximize air movement and minimize temperature and relative humidity influences. Air temperature was not changed by the rainout shelter. Shelter roofs were sloped slightly towards a subtle topographic gradient to facilitate quick drainage of ambient rainfall. The extreme drought treatment was sustained for 30 days from July 20 to August 19 in both 2013 and 2014. Shelters were installed and covered the plots during the experimental drought period and then removed for the remainder of the year.

Heat wave treatments, from August 3 to August 9 in 2013 and from July 22 to July 28 in 2014, were applied with a transparent infrared lamp (2000 W, 220 V, 100 cm × 31.4 cm, PHILIPS) connected with a thermal resistance (CU 50, Micro Sensor Co., Ltd., China) to an intelligent temperature controller (XMT 7100, Huibang technology Co., Ltd., China). The air temperature was controlled by a single lamp suspended 1.5 m above the ground at the center of each plot. The treatment maintained air temperature at the canopy height >38 °C during the daytime, 09:00–15:00 h, for seven days from August 3 to August 9 in 2013 and from July 22 to July 28 in 2014. Warming started from 09:00 a.m., air temperature raised slowly as warming proceeded and maintained around 38 °C ultimately, then lasted till 15:00 p.m. Due to the limitation of infrastructure at the research station, the electric output could not provide sufficient power to run eight infrared lamps simultaneously, so asynchronous warming was used for T and TD treatment. After T treatment finished, infrared lamps were moved from T treatment plots to TD treatment plots. The TD treatment was warmed from August 10 to August 16 in 2013 and from July 30 to August 5 in 2014.

2.3. Soil water content, canopy temperature and soil temperature

During the experimental period, soil water content (SWC) of the 0–20 cm soil layer was measured in each plot with time domain reflectometry (TDR 300, Spectrum Technologies, Inc. CST, USA) inserted vertically into the soil profile. Soil temperature at the depth of 10 cm was measured by the soil thermometer (TL-883, Tonglixing technology Co., Ltd., China). Surface temperature of the vegetation was measured by plant canopy thermometer (ST-2955, Shanghai Sintek International Trade Co., Ltd., China). Here we report the temperatures from 10:00 to 15:00 coinciding specifically with the warming period when CO_2, CH_4 and N_2O fluxes were measured.

2.4. GHGs measurements

In May 2012, two square stainless steel frames (50 cm × 50 cm, 10 cm high) were inserted in each plot, with 3 cm extending aboveground. One frame has plane edge with air gasket and the other has water channel on the upper surface of the edge. The former was used to measured ecosystem CO_2 fluxes while the latter was used to measure CH_4 and N_2O fluxes.

Ecosystem CO_2 fluxes were measured with a transparent chamber (50 cm × 50 cm × 50 cm) placed on this frame and attached to an infrared gas analyzer (LI-840A, LI-COR Inc., Lincoln, NE, USA) with an air pump (6262-04, LI-COR Inc.), creating a closed loop. Sealing strips were glued on the bottom of the chamber to prevent leaking. During measurements two small fans mixed the chamber air and one probe monitored air temperature. CO_2 concentrations inside the chamber were recorded every second for 2 min and then used to calculate net ecosystem exchange (NEE). After each NEE measurement, the chamber was removed and vented, then returned to the frame, and covered by a reflective lightproof cloth to estimate as ecosystem respiration (ER). During CO_2 flux measurements, the change of air temperature in the chamber was negligible. CO_2 flux rates were calculated from the time-course of the CO_2 concentrations. Only the data of the middle 100 s (deleting first and last 10 s) were used. Gross ecosystem productivity (GEP) was calculated as the difference between NEE and ER (Chen et al., 2009).

A stainless steel static chamber (50 cm × 50 cm × 50 cm) was used to measure CH_4 and N_2O fluxes and the chamber was covered by thick foam plastics during gas collection for heat insulation. After placing of the chamber on the frame, gas samples were taken from the headspace after 0, 10, 20, 30, 40 min. These samples were subsequently analyzed for CH_4 and N_2O concentration on a gas chromatograph equipped with a flame ionization detector (CH_4) and an electron capture detector (N_2O) (Agilent 7890A GC System, Palo Alto, CA, USA). The CH_4 and N_2O fluxes were calculated as the slope of linear regressions from the measured gas concentrations with time (Liu et al., 2014).

Positive and negative GHGs flux values represent net ecosystem emission and uptake, respectively. GHGs usually measured and sampled in the morning (9:30–11:30 h) to enhance the comparability of data measuring in different days. Previous study at the same site suggested that the fluxes of ER, CH_4 and N_2O from 9:00 a.m. to 12:00 a.m. is a good representative of the daily average values in this grassland (Dong et al., 2000). Cumulative fluxes of GHGs produced/consumed over the measurement periods were calculated by multiplying the average flux measured on two consecutive dates by the time interval, and then summing the cumulative fluxes calculated for each time interval of the growing season. Notwithstanding that these calculated cumulative fluxes did not account variations during the measurement intervals and should not be regarded as precise quantifications of GHGs emissions of this grassland, this approach facilitates the comparison of relative changes of cumulative GHGs flux among treatments, where the systematic error produced by calculation was consistent.

2.5. Statistical analyses

A repeated measures ANOVA was used to test for the main effects of the heat wave and extreme drought treatments (both between-subjects factors), year (within-subjects factor), and their interactive effects on total GHGs flux and soil water content. Repeated measures ANOVA was further used to test for main effects of the heat wave and year (within-subjects factor) on surface temperature of the vegetation and soil temperature. Two-way ANOVA was used to test effects of heat wave, extreme drought and their interactive effects on cumulative GHG flux. Before conducting an ANOVA, the normality of error terms was evaluated using the Shapiro-Wilk test for goodness of fit, and homoscedasticity was evaluated using the Levene test for equality of variances. A post-hoc tests (Tukey's HSD) was used to test for differences in the average rates of NEE, ER, GEP, CH_4 and N_2O flux in each year. We used linear and quadratic regressions to correlate CO_2, CH_4, and N_2O flux to soil water content, air temperature and soil temperature by date and treatment. The level of significance for all statistical tests was set at $P = 0.05$. All statistical analyses were performed with R (version 3.0.2, R Development Core Team, 2013).

3. Results

3.1. Rainfall, temperature and soil water content

Rainfall during the growing season was 286.7 mm in 2013 and 255.5 mm in 2014, respectively, which are close to the long-tem mean (282 mm, during 1953–2010). Mean daily air temperature during the growing season (from May to September) was 15.3 °C and 15.1 °C, and the maximal mean daily temperature was 22.3 °C on 6 August in 2013 and 24.8 °C on 18 July in 2014, respectively. Maximum daily air temperature during the growing season was 32.6 °C, on 14 August 2013 and 36 °C on 27 July 2014 (Fig. 1).

The short-term heat wave treatment did not significantly affect SWC ($P = 0.075$), while the extreme drought treatment significantly reduced SWC during drought period ($P = 0.006$, Table 1). However, the difference of SWC disappeared soon after drought treatment finished. By contrast, extreme temperature plots did not significantly differ from the control plots in SWC during the treatment period. There were no significant warming × drought interactions in SWC. Heat wave treatment significantly increased surface temperature of the vegetation by 3.1 °C and 2.8 °C during the treatment period in 2013 and 2014, respectively ($P = 0.026$). Soil temperature also have raised 0.6 °C and 0.5 °C by the heat wave, but these changes were not statistically significant ($P = 0.161$, Fig. 2b and d).

3.2. Greenhouse gas fluxes

During the entire study period, under all treatments, the grassland ecosystem acted as a net sink for CO_2 and CH_4, but a net source for N_2O. Before the treatments began, there was no significant difference in GHG_S fluxes between treatment plots (Figs. 3 and 4). There was substantial interannual variation in ER, GEP, CH_4 and N_2O but not in NEE (Table 1).

Both heat wave and drought treatments significantly reduced ecosystem CO_2 uptake (leading to less negative NEE and decreased GEP) throughout the study periods (Table 1). In addition, the drought treatment reduced ER ($P < 0.001$, Table 1) while the heat wave treatment had no significant effect on ER (Fig. 3b and d). There were no significant interactive effects on CO_2 flux among the heat wave, drought and year during the measurement period ($P > 0.05$ for all, Table 1).

CH_4 uptake rates were promoted during the treatment periods (heat wave and drought), but neither treatment had a significant effect on CH_4 uptake across the two years, ($P = 0.132$ & 0.124 for heat wave and drought treatments respectively, Table 1). However, the stimulation of methane uptake was large during the early stage of the drought period (Fig. 4a). There was a significant interaction between drought and year ($P = 0.007$) with CH_4 uptake rates higher in 2013 than in 2014. During the period of drought in 2013, we observed V-shaped trend for CH_4 flux in the D treatment (Fig. 4a

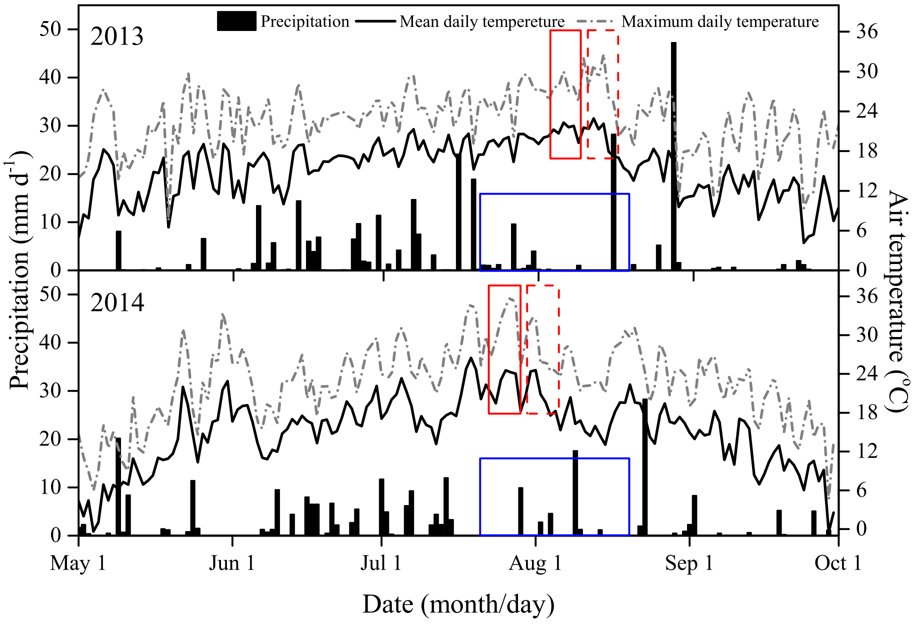

Fig. 1. Daily precipitation (bars) and air temperature (line) during the growing season in 2013 and 2014 over a semiarid grassland. Solid line indicates mean daily air temperature and short dash line indicates maximum daily air temperature. The blue box regions indicate the period of drought treatment and red box areas indicate the period of heat wave treatment, with the solid line red box showing treatment in heat wave plots and the dash line red box showing treatment heat wave combines with drought plots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Results (F values and *P* values) of repeated measures ANOVA on the effects of heat wave treatments, extreme drought treatments, year of treatment and their interactions on soil temperature (T_s), surface temperature of the vegetation (T_v), soil water content (*SWC*), net ecosystem exchange (*NEE*), ecosystem respiration (*ER*), gross ecosystem productivity (*GEP*), CH_4 flux and N_2O flux.

	T_s		T_v		*SWC*		*NEE*		*ER*		*GEP*		CH_4		N_2O	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
T	2.298	0.161	6.851	**0.026**	4.174	0.075	4.985	**0.050**	0.188	0.676	5.970	**0.040**	2.807	0.132	0.106	0.753
D	/	/	/	/	14.063	**0.006**	26.212	<**0.001**	29.009	<**0.001**	60.267	<**0.001**	2.955	0.124	12.733	**0.007**
Y	26.796	<**0.001**	71.719	<**0.001**	0.770	0.406	3.425	0.101	29.710	<**0.001**	9.772	**0.014**	135.588	<**0.001**	26.736	<**0.001**
T × D	/	/	/	/	0.655	0.442	0.003	0.955	0.705	0.425	0.217	0.654	0.314	0.590	0.006	0.941
T × Y	0.031	0.864	0.052	0.825	6.591	**0.033**	0.044	0.839	0.406	0.542	0.130	0.728	0.838	0.387	0.015	0.906
D × Y	/	/	/	/	3.268	0.108	2.746	0.136	0.794	0.399	1.151	0.315	34.173	<**0.001**	13.157	**0.007**
T × D × Y	/	/	/	/	0.131	0.727	0.471	0.512	0.322	0.586	0.148	0.711	7.054	**0.029**	0.039	0.848

T: Heat wave; D: Extreme drought; Y: Year.
P-values are in bold when $P < 0.05$.

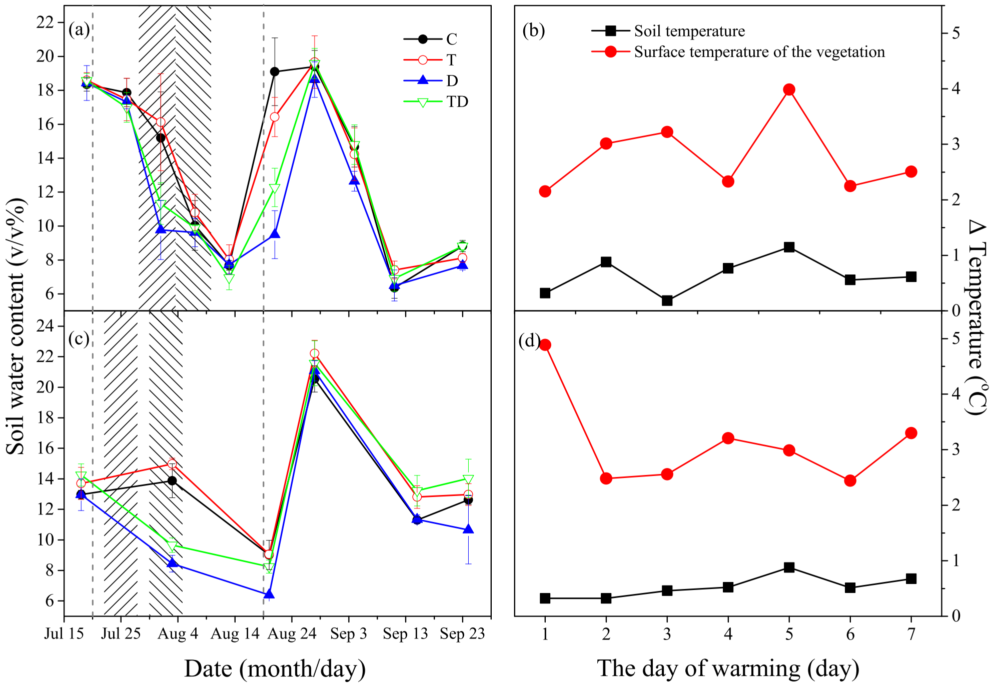

Fig. 2. Effect of heat wave and extreme drought on soil water content at 0–20 cm soil depth in 2013 (a) and 2014 (c). Effect of heat wave on the change of soil temperature and canopy temperature (the difference was calculated by the temperature in T treatment minus in the temperature C treatment) during warming period in 2013 (b) and 2014 (d). Treatments are C, ambient control; T, heat wave; D, extreme drought; TD, heat wave and extreme drought. The area between the two dashed lines indicate the period of drought and gridded areas indicate the period of heat wave, in which the upward sloping gridded area shows treatment in T plots, and the downward sloping area shows treatment in TD plots. Error bars indicate 1 SE.

and b).

The heat wave treatment had no significant effect on N_2O fluxes across two years ($P = 0.753$, Table 1). However, drought significantly affected N_2O flux and there was also a significant interannual difference ($P = 0.007$ for both the drought effect and the interaction of drought by year, Table 1). N_2O emission rates were higher in 2013 and lower in 2014 under drought than ambient conditions (Fig. 4c and d). It should be noted that N_2O fluxes of D and TD treatments on 26 August were obviously higher than any other days in 2013 (Fig. 4c) yet similar to N_2O fluxes of C and T treatments on 3 August in 2014 (Fig. 4d).

3.3. The cumulative GHGs fluxes

Over two years, the T, D, and TD treatments significantly decreased cumulative net ecosystem CO_2 uptake by 15.9%, 38.4% and 52.0%, respectively (all changes here and below refer to % of control plots, Table 2; Fig. 5a). Heat wave-induced reduction of cumulative net ecosystem CO_2 uptake showed a legacy effect, mainly occurring after the treatment finished (12.0% out of 15.9%). This is primarily attributable to the legacy in the response of cumulative GEP (−15.8%, mostly after treatment, Fig. 5c) since the influence of the heat wave treatment on ER was generally small (−3%, Fig. 5b). By contrast, under D and TD treatments, about half of the reduction in NEE and GEP occurred during the treatments and half after the treatments (Fig. 5c), while ER declined about 20% in both treatments, mainly during the treatment period (Fig. 5b).

The cumulative CH_4 uptake was 25.5%, 22.1% and 12.7% higher in the heat wave, drought and heat wave plus drought treatments, respectively, but the treatment effects were not significant (Fig. 5d; Table 2). The majority of cumulative CH_4 uptake increment occurred after treatment in T and TD plots, but during treatment in D plots. The D and TD treatments significantly decreased the cumulative N_2O emission by 50.9% and 49.5% compared to control

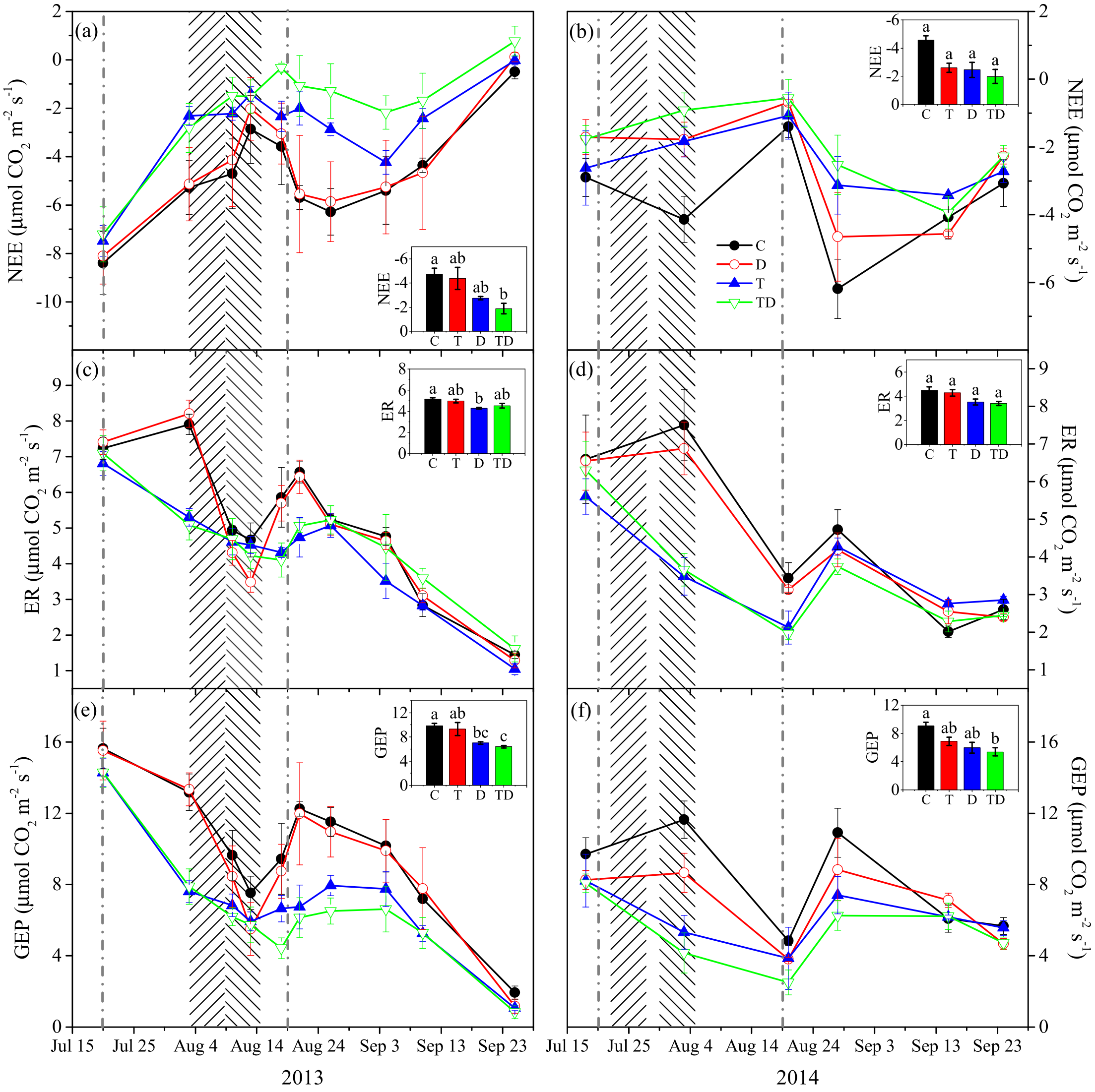

Fig. 3. Temporal dynamics and means of net ecosystem exchange (NEE) (a, b), ecosystem respiration (ER) (c, d), and gross ecosystem productivity (GEP) (e, f) in response to heat wave and extreme drought treatments during the measurement period in 2013 (a, c, e) and 2014 (b, d, f). Treatments are C, ambient control; T, heat wave; D, extreme drought; TD, heat wave and extreme drought. The regions between the two dash dot lines indicates the period of drought treatment and gridded areas indicate the period of the heat wave treatment, with the upward sloping grid showing treatment in T plots and the downward sloping area showing treatment TD plots. Negative values indicate the ecosystem absorbs CO_2 from the atmosphere (net sink), while positive values indicate the ecosystem emits CO_2 into the atmosphere (net source). Error bars indicate 1 SE.

plots, mostly during the treatments. By comparison the extreme heat wave treatment almost had no effect on cumulative N_2O emission (Fig. 5e).

3.4. *The relationship between GHGs fluxes and microclimate*

Irrespective of experimental treatment, the temporal variation in CO_2 flux could be largely explained by soil water content (Fig. 6a, c). NEE was negatively correlated with soil water content in the 0–20 cm soil layer (Fig. 6a), and ER was positively correlated (Fig. 6c). There was a significant quadratic relationship between NEE and air temperature and NEE reached its bottom at about 28 °C (Fig. 6b). Moreover, soil temperature was positively correlated with ER (Fig. 6d). CH_4 fluxes had a significant U-shaped relationship with soil water content with optimum SWC around 12% (Fig. 6e). However, there was no relationship between CH_4 and soil temperature (Fig. 6f). N_2O fluxes were not correlated with soil water content but positively related to soil temperature (Fig. 6g and h).

4. Discussion

4.1. *Response of GHGs to extreme drought*

Extreme drought decreased ecosystem carbon uptake in this semiarid grassland (Fig. 3a and b). The negative drought effect on NEE could be largely attributable to the lower soil water content (Fig. 6a), which imposed water stress on plants. Typically, when water stressed, plants close stomata to prevent water loss, but by doing so limit photosynthetic activity and diminish carbon uptake (Niu et al., 2008; Saleska et al., 1999). Drought may also cause increased plant root mortality. This leads to declines in dissolved organic carbon from root exudates and reduced microbial activity and soil respiratory CO_2 emission (Hagedorn and Joos, 2014; Sotta et al., 2007). Although ecosystem respiration was reduced by drought (Fig. 3c and d), drought generally reduced GEP more, resulting in lower net ecosystem CO_2 uptake. Thus our results are consistent with other studies finding that GEP was more sensitive to drought than ER (Hussain et al., 2011; Lund et al., 2012).

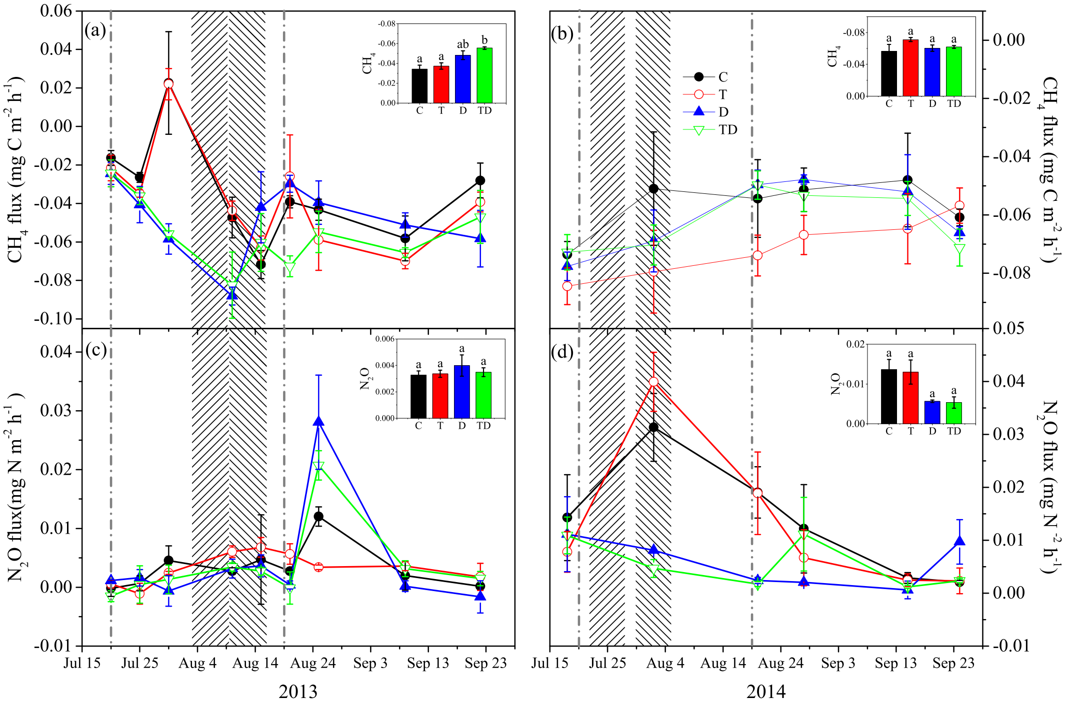

Fig. 4. Temporal dynamics and means of (a, b) methane flux rates and (c, d) nitrous oxide flux in response to extreme high temperature drought treatments during the measurement period in 2013 (a, c) and 2014 (b, d). Treatments are C, ambient control; T, heat wave; D, extreme drought; TD, heat wave and extreme drought. The area between the two dashed dot lines indicate the period of drought and gridded areas indicate the period of heat wave, in which the upward sloping gridded area shows treatment in T plots, and the downward sloping area shows treatment in TD plots. Negative values indicate sinks for CH_4 and N_2O while positive values indicate sources for CH_4 and N_2O. Error bars indicate 1 SE.

Table 2
Results (F values and *P* values) of two-way ANOVA on the effects of heat wave, extreme drought and their interactions on the total cumulative flux.

	Cumulative NEE		Cumulative ER		Cumulative GEP		Cumulative CH_4		Cumulative N_2O	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
T	5.641	**0.045**	0.067	0.802	5.920	**0.041**	0.666	0.438	0.001	0.985
D	35.988	**<0.001**	40.548	**<0.001**	83.991	**<0.001**	0.249	0.632	21.036	**0.002**
T × D	0.033	0.861	0.507	0.497	0.294	0.602	3.218	0.111	0.001	0.977

T: Heat wave; D: Extreme drought.
P-values are in bold when $P < 0.05$.

Globally, semiarid and arid ecosystems are a significant sink of CH_4, with an average CH_4 uptake rate of 6.5 ± 3.6 ng C m^{-2} s^{-1} and accounting up to 40% of the global CH_4 soil sink (Galbally et al., 2008). Furthermore, the local water regime is known to have an important role in CH_4 flux in the arid and semiarid environment (Dijkstra et al., 2011). We report a U-shaped relationship between soil water content and CH_4 flux with a tipping point of about 12% soil water content (Fig. 6e). This is similar to what Dijkstra et al. (2013) reported for a semiarid grassland in Wyoming, USA. CH_4 uptake is limited by diffusivity of CH_4 from the atmosphere into deeper soil profile, where the soil moisture is high. The observed decline of soil water content under the drought treatment may have enhanced soil aeration promoting CH_4 oxidation by methanotrophs (Fig. 2). However, excessively low soil moisture may restrain methanotrophs activity and reduce CH_4 uptake (von Fischer et al., 2009). The V-shaped trend for CH_4 flux observed during the period of drought in 2013 supported this mechanism (Fig. 4a). In 2014, soil water content before drought treatment started was close to the optimum (12%, Fig. 2c), and corresponded to the highest rates of CH_4 uptake. As the drought treatment progressed, activity of the methanotrophs was suppressed as SWC continued to decline. Thus the low soil moisture at the start of the experimental treatments in early 2014 appears to explain the continuous reduction CH_4 uptake that year (Fig. 4b). The observed annual variation of CH_4 fluxes indicated that the response to drought will vary depending on the antecedent weather and soil water content.

Past work shows that N_2O emission rates tend to decline under severe drought as decreased soil water content inhibits nitrification and denitrification (Hartmann and Niklaus, 2012). During the drought period, cumulative N_2O emissions were reduced by 43.1% compared to the ambient conditions (Fig. 5e). However, when the ecosystem received first rainfall pulse following the drought treatment, we observed an abnormally high pulse of N_2O emission in D and TD treatments in 2013 (Fig. 4c). Previous studies show that a single pulse of N_2O emission driven by a moderate rainfall event can account for as much as 15–90% of the total weekly production (Liu et al., 2014; Nobre et al., 2001). Soil rewetting following prolonged drought has also been found to account for 20–40% of the annual total N_2O emission in an acidic fen (Goldberg et al., 2010). In our study, the 2013 flux of N_2O was stimulated by rainfall following the drought period, and this effect was stronger in the drought treatment plots compared to the control plots (Fig. 4c). The stimulation was significant, increasing the flux of N_2O by a factor of 72

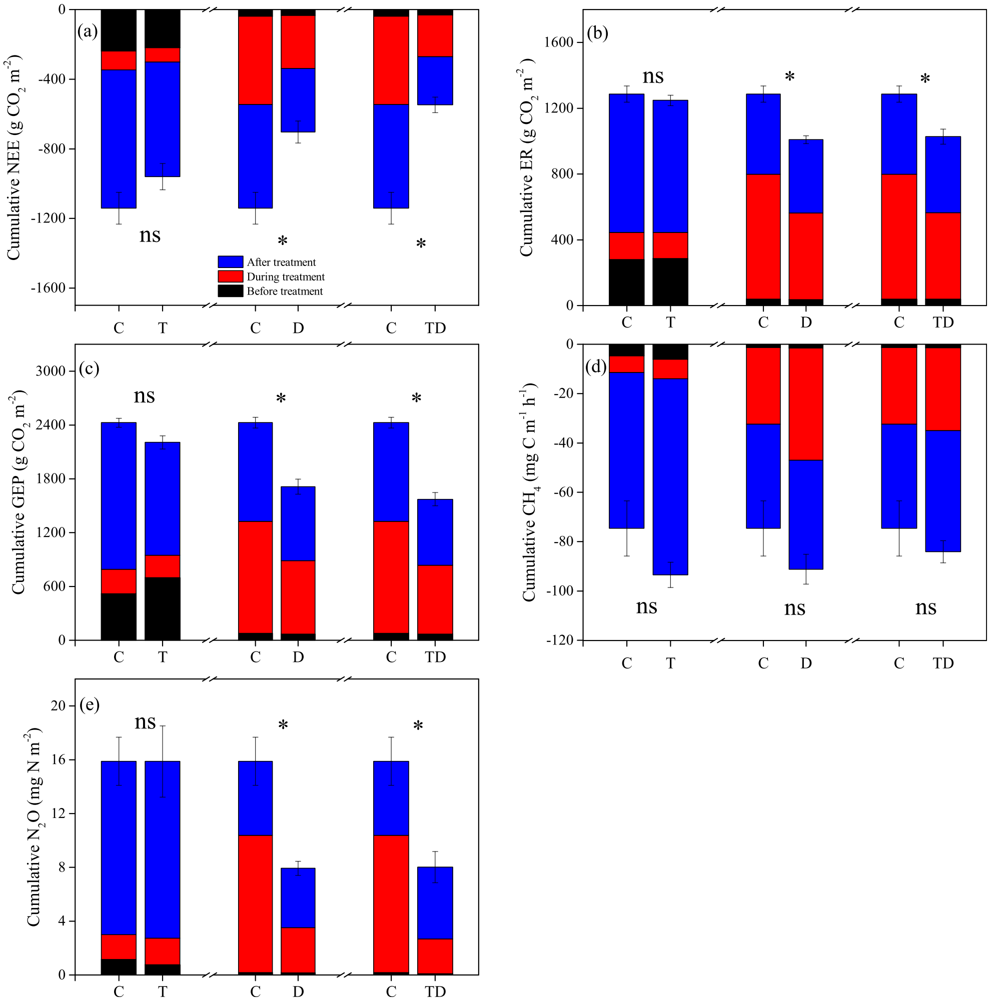

Fig. 5. The cumulative NEE (a), ER (b), GEP(c), CH_4 (d), N_2O (e) during the measure period. When compare ambient to climate extreme treatments, the cumulative flux was divide into before treatment period, during treatment period and after treatment period. The valves were the means of two years. Negative values indicate the ecosystem absorbs GHGs from the atmosphere (net sink), while positive values indicate the ecosystem emits GHGs into the atmosphere (net source). Error bars indicate 1 SE.

compared to that before the rain, and indicated that the extreme drought enhanced the sensitivity of N_2O flux to rainfall events. Drought may promote the accumulation of NH_4—N, NO_3—N and organic substrates derived from the dead microbial biomass caused by water deficiency. In addition, the consumption of NH_4—N and NO_3—N by plants and N loss by leaching tends to decrease under drought stress (Liu et al., 2014). As soils rewet, the surviving microbial community is revived and rapid consumption of the accumulated mineral N and organic substrates could contribute to the production of a N_2O pulse (Kim et al., 2010; Liu et al., 2014). However, the observed abnormal N_2O emission pulse in drought plots (D and TD) after drought did not appeared in 2014 (Fig. 4d). It may be again being that the antecedent conditions resulted in a more severe and longer period of soil drying prior to the induction of the drought treatment in 2014. The resulting severely low SWC may have pushed the system beyond the microbial tolerance and limited the recovering during soil rewetting. Overall, soil water status appears to have determined the response of N_2O emission to rainfall following the drought treatment.

4.2. *Response of GHGs to heat wave*

Models suggested that future climate warming will increase carbon sequestration (Piao et al., 2009). However, heat waves could lead to a comparably larger net carbon release or decrease in sink strength (Zscheischler et al., 2014). In our study, we observed that the capacity for CO_2 uptake was significantly decreased by the heat wave treatment. This may be attributed to reduced stomatal conductance, leaf water potential and photosynthetic N-use efficiency, leading to lower canopy photosynthesis (De Boeck et al., 2011; Wang et al., 2008). In addition, we also observed that the optimal air temperature for NEE was approximately 28 °C (Fig. 6b), which is in accordance with another study in the same ecosystem (Niu et al., 2008).

Long-term warming substantially increases soil temperature and this is expected to increase microbial activity, promoting production and consumption of GHGs (Dijkstra et al., 2011; Shi et al., 2012). In addition to the direct effects of heat stress on plants and soil, growing evidence suggested that the main effects of heat on ecosystems are indirect warming-induced drought effect (Niu et al., 2008; Saleska et al., 1999). However, in our study, soil temperature was not significantly altered by the short duration heat wave (Fig. 2b and d), which was similar to the observation in another heat wave experiment on herbaceous community (Wang et al., 2008), the same as soil water content (Fig. 2a and c). Thus, the addition of the heat wave treatment was unlikely to accelerate microbe activity by rising soil temperature or suppress microbe activity by dropping soil water content. As a result we found relatively stable ER, CH_4

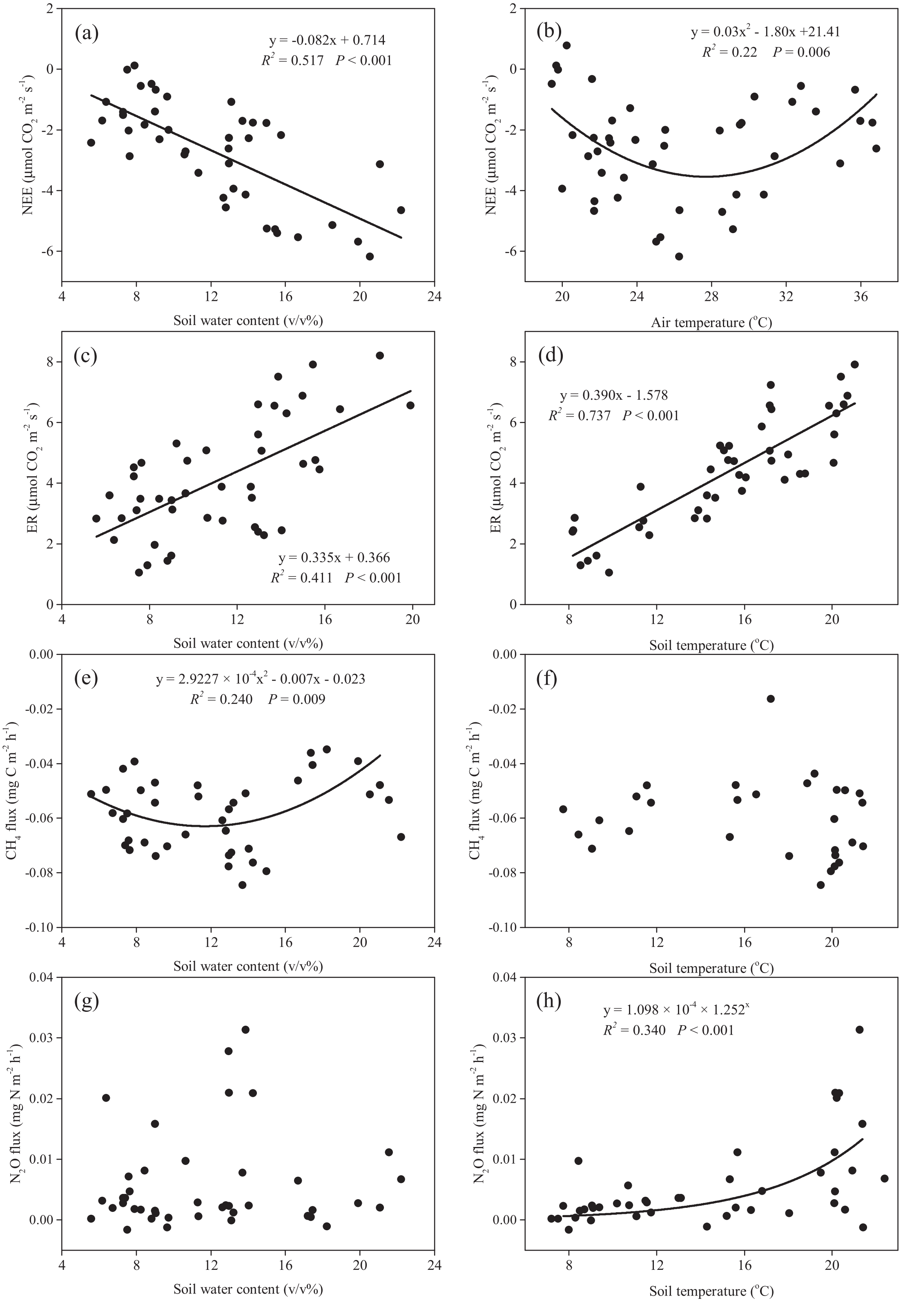

Fig. 6. Fluxes of NEE (a, b), ER (c, d), CH_4 (e, f) and N_2O (g, h) as a function of soil water content in 0–20 cm (a, c, e, g), air temperature (b) or soil temperature in 10 cm (d, f, h). Each data point is the average CO_2, CH_4 or N_2O flux, and average soil water content measured in the three replicates of each treatment at a specific data during measure period. Regression lines are only shown when significant ($P < 0.05$).

and N_2O fluxes for the duration of the heat wave. It is possible that a larger response would be found if the temperature was higher during the heat wave or the heat wave continued over a longer period of time.

4.3. Response of GHGs to combined extreme drought with heat wave

Often extreme drought is accompanied by a heat wave (Breshears et al., 2005). The two types of climates extremes may synergistically affect leaf and ecosystem processes (Reichstein et al., 2013). For example, drought drives stomatal closure of plants and reduce ecosystem evapotranspiration, thereby aggravating the effect of a heat wave (De Boeck et al., 2007). However, contrary to our hypothesis, no significant interactive effects of heat waves and droughts on GHGs fluxes were observed ($P > 0.05$ for all, Tables 1 and 2). Compared to the heat wave treatment, the extreme drought treatment exerted a significantly larger influence on measured GHGs fluxes (Fig. 5). The temporal dynamics of GHGs fluxes in the combined treatment were generally in accordance with the trend in drought treatment (Figs. 3 and 4). Our observations clearly demonstrate the predominant role of water availability in regulating ecosystem GHGs exchange in this semiarid grassland during the known ~60-year recurrence of extreme drought and high temperature events.

5. Conclusions

The goal of this study was to explore how fluxes of GHGs were affected by extreme climate events (~60-year recurrence drought and heat wave) in a semiarid grassland. In our experiment, a simulated heat wave weakened ecosystem CO_2 uptake, but ER, CH_4 and N_2O flux were little affected by this stress. Extreme drought treatments had a more dramatic effect, decreasing GEP and, to a lesser extent ER, leading to reduced net ecosystem CO_2 uptake. Drought also promoted CH_4 uptake and suppressed N_2O emission. These complex responses of GHG fluxes to drought and heat wave partially support our hypothesis (1). In general, the drought treatment had stronger impacts on GHGs fluxes than the heat wave treatment, supporting our hypothesis (2). This indicates that soil water content played a dominant role in regulating ecosystem level greenhouse gas exchange in this semiarid grassland. Importantly, there were no significant interactions between the heat wave and extreme drought treatments on GHGs fluxes, rejecting our hypothesis (3). Future climate extremes are likely to have significant effects on semiarid grasslands, altering carbon cycling and an establishing a variety of feedbacks to the climate system.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.atmosenv.2016.07.039.

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