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Heavy mowing enhances the effects of heat waves on grassland carbon and water fluxes

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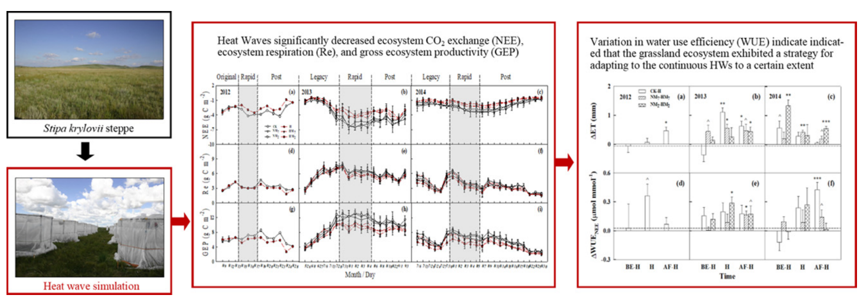
HIGHLIGHTS

- Heat waves (HWs) significantly decreased grassland NEE, Re, and GEP.
- The rapid, post, and legacy effects of HWs were defined and quantified.
- Continuous HWs over multiple years produced cumulative effects on reducing grassland NEE.
- Mowing increased the effects of HWs by extending the legacy effect.

GRAPHICAL ABSTRACT



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ABSTRACT

Heat waves (HWs) are a type of extreme weather event that is of growing concern in the scientific community. Yet field data based on sound experiment on the variation of ecosystem CO_2 levels under HWs remain rare. Additionally, ecosystems react to HWs and the coupled human activities (such as grazing in grasslands) are unknown. Thus, a 3-year field experiment was conducted to simulate HWs in conjunction with different mowing intensities that mimicking grazing in a *Stipa krylovii* steppe on the Mongolian Plateau. HWs significantly decreased ecosystem exchange (NEE) of CO_2, ecosystem respiration (Re) and gross ecosystem productivity (GEP) by 31%, 5% and 16%, respectively, over the three years. Continuous HWs over multiple years produced cumulative effects by reducing NEE at 20%, 34% and 40% in the first, second and third HW years, respectively. During three pre-defined three periods of HWs (during HW period, after HW period in the same year, and after HW period in the next year), variations in water use efficiency indicated that the grassland ecosystem exhibited a strategy for adapting to the continuous HWs to a certain extent, by adjusting community structure or increasing litter biomass. Finally, mowing increased the effects of HWs by extending the legacy effect, such that restoration of the grassland required a greater amount of time under the combination of HWs and mowing.

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1. Introduction

Heat waves (HWs) represent a typical extreme weather event and are of growing concern in the scientific community because the sudden increase in temperature associated with HWs can cause ecosystem functions to shift dramatically and rapidly (De Boeck et al., 2010; Meehl and Tebaldi, 2004). The frequency and intensity of HWs have increased significantly, affecting >73% of the global terrestrial area since the mid-20th century (IPCC, 2013; Perkins-Kirkpatrick et al., 2016). Over the long term, extreme weather events such as HWs can act as important drivers of species evolution because they may lead to the

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elimination of individuals that are not suited for the environment (Gutschick and BassiriRad, 2003; Li et al., 2017; Zinta et al., 2014).

The sudden high temperatures associated with HWs have a greater impact on plants than gradual temperature increases (Sanz-Lázaro, 2016; Xia et al., 2009). Recent studies showed that HWs can significantly alter plant photosynthesis and respiration (Ameye et al., 2012) as well as aboveground and belowground biomass accumulation (Qu et al., 2016), reduce CO_2 sequestration strength (Tatarinov et al., 2016), and alter the reallocation of CO_2 and nitrogen within an ecosystem (Li et al., 2017). High temperatures also up-regulate leaf-cooling transpiration, resulting in excessive heat damage and greater evapotranspiration (ET), which may lead to the occurrence of drought (Duan et al., 2016). Previous studies have to some extent revealed the degree of the hazardous effects caused by HWs in ecosystems and the possible underlying mechanisms, but the results appear inconsistent and unilateral (Tatarinov et al., 2016). In most HW studies, the degree of the effects of HWs on the CO_2 flux has been examined at an interannual scale (Ciais et al., 2005; Lei et al., 2015; Qu et al., 2016; Reichstein et al., 2007). Because thermal and hydrological conditions vary both seasonally and annually, HWs with similar intensities may produce very different effects on ecosystems, as hydrological and thermal conditions and plant growth status differ over time, suggesting that the impacts of HWs can on the ecosystem CO_2 flux be easily overestimated or underestimated (Reichstein et al., 2007). Unfortunately, previous studies addressing HWs have been based on laboratory tests and have involved different definitions of HWs compared with naturally occurring HW events (Ameye et al., 2012; Bauweraerts et al., 2013; De Boeck et al., 2011). Furthermore, most of these previous studies were conducted on single plants, rather than entire ecosystem. Within a community, however, plants may reduce the impact of HWs through interactions among microorganisms or plants by adjusting the composition and structure of these organisms (Jentsch et al., 2007). Additionally, most HW experiments focus on a single HW event, and even though multiple HW simulation experiments can be conducted in a period no longer than a single growing season, there is a lack of long-term observational experiments (Fitzgerald et al., 2016; Sanz-Lázaro, 2016).

Grassland ecosystems, which account for approximately 40% of the global land surface area (Imer et al., 2013; Jmo and Hall, 1998), play an essential role in global CO_2 cycling. For example, grassland soils hold large quantities of organic CO_2 and store approximately 28%–37% of global soil organic carbon (Lal, 2004). Grassland ecosystems are also more vulnerable to climate change than forest and cropland ecosystems (Reichstein et al., 2007; Imer et al., 2013). Unfortunately, reliable evidence regarding how grassland ecosystem CO_2 and water fluxes respond to HWs remains rare. Land-use change is another important factor that may fundamentally alter ecosystem CO_2 exchange and its response to climate change (Chen et al., 2015). For example, mowing and grazing are among the most prevalent land uses in global grassland landscapes (Shao et al., 2013) and have great potential to alter CO_2 fluxes and energy budgets by changing photosynthetic activity and stimulating compensatory growth (Han et al., 2014; Niu et al., 2013). Despite its importance, our knowledge of how grassland ecosystems respond to HWs in the face of these human disturbances based on sound experiments remains very limited.

A 3-year field experiment was conducted in this study to simulate HWs in conjunction with different mowing regimes to mimic human disturbance in a grassland ecosystem. Our study objectives were to: (1) quantify the independent and interactive contributions of multiple HWs and mowing treatments to net ecosystem CO_2 exchange (NEE), ecosystem respiration (Re) and gross ecosystem productivity (GEP); (2) explore the potential legacy effects of HWs under different mowing treatments; and (3) quantify the interactive effects of HWs and mowing on CO_2 and water fluxes and plant growth. We speculate that previous studies may have overvalued the effects of HWs on ecosystem CO_2 and water fluxes by neglecting the fact that ecosystem resistance and resilience to the HWs may be higher than individual plants. Additionally, we hypothesize that mowing may alleviate the effects of HWs because this activity could change the species composition and structure, which in turn will enhance the adaptability of the community through stimulating compensatory growth (e.g., more suitable to the hot and drought conditions).

2. Materials and methods

2.1. Study site

Our manipulative experiment was conducted in a semi-arid area in Duolun County (42°02′ N, 116°17′ E), Inner Mongolia, China. Mean annual precipitation is 385 mm in the region, while the average annual temperature is 2.1 °C, and the monthly mean temperatures ranges from −17.5 °C in January to 18.9 °C in July. The soils are classified as chestnut soils in the Chinese classification or Haplic Calcisols based on the FAO classification, containing 62.75 ± 0.04% sand, 20.30 ± 0.01% silt, and 16.95 ± 0.01% clay. The mean bulk density of the soils is 1.31 g cm^{-3}, and the pH is 7.12 ± 0.07. The plant community is dominated by perennial species, including *Stipa krylovii* Roshev, *Artemisia frigida* Willd., *Potentilla acaulis* L., *Cleistogenes squarrosa* (Trin.) Keng, *Allium bidentatum* Fisch. ex Prokh., and *Agropyron cristatum* (L.) Gaertn. The study site has been fenced to exclude grazing since 2001 (Shao et al., 2014). The 50-year historical records of nearby climatic data (1967–2016) from Duolun (Station#: 54208, 42°41′ N, 116°28′ E, 1245.4 m a.s.l.) were obtained from the China meteorological data-sharing service system (http://cdc.cma.gov.cn/) to determine the length and timing of HW treatment (Qu et al., 2016).

2.2. Experimental design

A full factorial experiment was designed with two factors: HW and mowing. The HW treatment included two levels: HW (H) or no HW (N). The mowing treatment included three levels: no mowing, light mowing (7 cm stubble, M_7) and heavy mowing (2 cm stubble, M_2). This experiment therefore yielded six treatments: CK (no heat + no mowing), H (heat + no mowing), NM_7 (no heat + 7 cm stubble), NM_2 (no heat + 2 cm stubble), HM_7 (heat + 7 cm stubble) and HM_2 (heat + 2 cm stubble). Each treatment was performed in four replicates, yielding a total of 24 plots (2 m × 2 m). We randomly allocated the treatments among the plots, which were laid out in total area of 308 m^2, with a 2-m buffer zone established between any two neighboring plots.

2.3. Heat wave treatment

Open-top chambers (OTCs) with a heater inside were constructed to simulate the effects of HWs (Fig. 1). The OTCs were octagonal in shape, with a diameter of 2.0 m and a height of 1.5 m, and were constructed using 6-inch steel tubes. During the HW treatment, the OTCs were covered with transparent PVC film. The light transmittance of the film was >90% based on measurements of photosynthetically active radiation (PAR) inside and outside the covered OCTs. A heater (20 cm × 15 cm × 15 cm) was hung inside each OTC at a height of 1.5 m and was powered at 3500 W. The OTCs were left open during the 5:00–6:00 h daily so that the internal and external environments of the OCTs remained consistent. Non-heated plots were also covered with a similar chamber to ensure comparable conditions.

According to the historical climate data for Duolun County, HWs usually occur in summers (Qu et al., 2016). Therefore, we started our heat simulation experiment during the same period. Dry sunny days were selected as heating periods following the natural occurrence of HWs. The experimental periods, intensity and duration of the simulated HWs also followed the changes in local historical conditions. The canopy temperature was increased by ~6–10 °C during the day and by ~4 °C at night. The HW treatments were carried out during three different

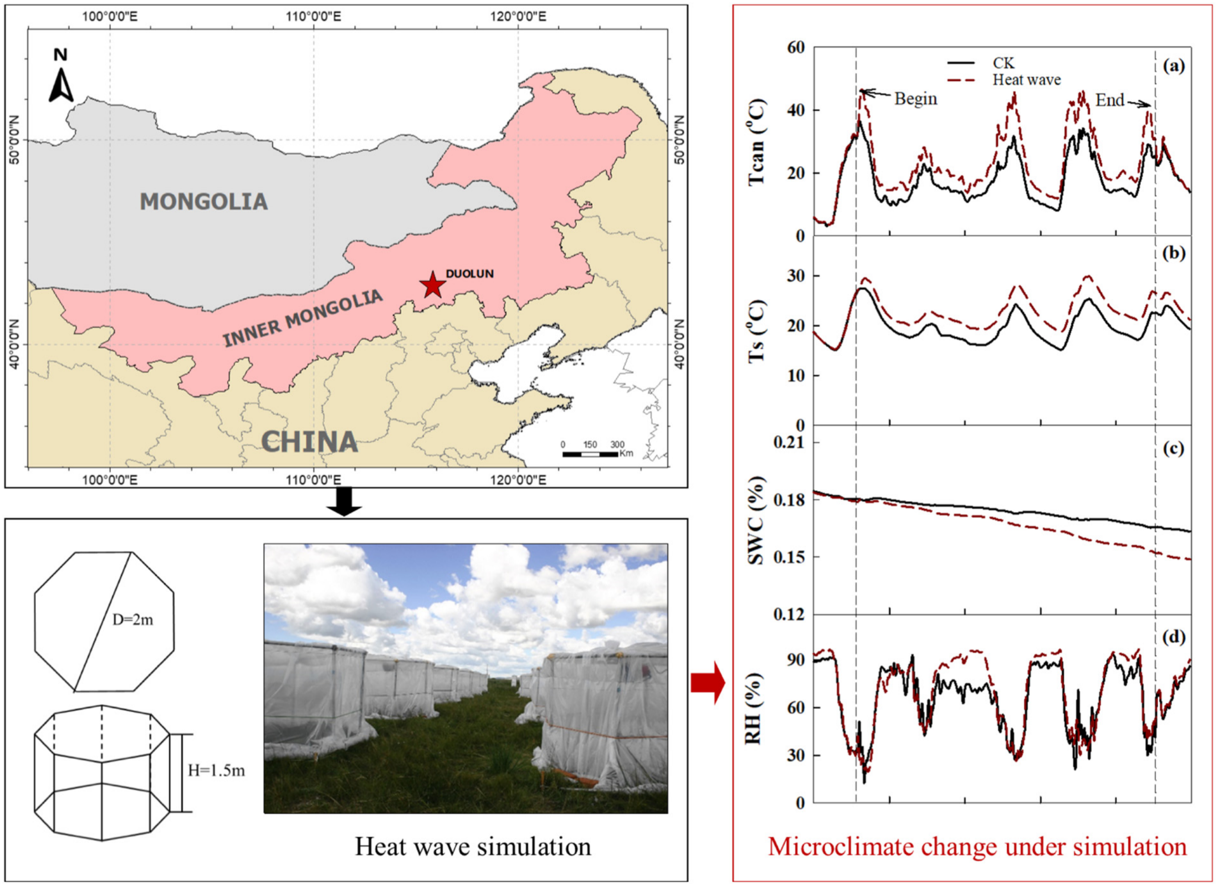

Fig. 1. Study site and layout in Duolun (top left), illustration of the field experiment in simulating heat wave (HW) (bottom left), and the changes in major microclimatic variables (right) at a *Stipa krylovii* steppe on the Mongolian Plateau in 2012. CK: no heat plots, Heat Wave: HWs plots. The length of heat waves are 3 days in 2012. T_{can}, canopy air temperature (a), T_s, soil temperature (b), SWC, soil water content (c) and RH, relative humidity (d). D, diameter and H, height. Dotted line indicates the beginning and ending of HW treatment.

periods: over 3 days in 2012, in a preliminary experiment, and over 5 days in 2013 and 2014.

2.4. Mowing treatment

Light and heavy mowing treatments were applied to simulate local grassland management practices (e.g., harvesting or grazing). In the light and heavy mowing treatments, 7 cm or 2 cm of stubble, respectively, was left intact by a field mower (Yard-man 160CC, USA). Mowing was conducted in the end of August, when local harvesting is normally performed.

2.5. Energy and microclimate measurements

An energy and microclimate measurement system was installed in the experimental plots to continuously measure PAR, net radiation (R_n), soil heat flux (G), soil water content (SWC), canopy air temperature (T_{can}), soil temperature (T_s), soil surface temperature (T_{sur}), air temperature (T_a), and air humidity (RH). PAR was measured with an LI-190SB (LI-COR, Lincoln, NE, USA). A total of twelve Q7.1 net radiometers (REBS, Seattle, WA, USA) were installed 0.5 m above the canopy to measure R_n. Six CS616 water content reflectometers (CSI, Campbell Scientific Inc., Logan, UT, USA) were installed at a depth of 0–30 cm; twenty four T_{can} probes (E-type thermocouples) manufactured by the authors were installed at a height of 20 cm, and fourth eight T_s probes (T-type thermocouples) were installed at depths of 2 cm and 6 cm; and two air temperature and RH probes (HMP45C, CSI) were installed at a height of 30 cm in the unmowed and heavy-mowed plots. Two AM25Ts (CSI) were used, and all of the measurements were recorded with a CR10X datalogger (CSI) every 20 s and averaged in 30 min intervals. The entire system was powered by a 20 W solar panel and a 12 V deep cycle marine battery.

2.6. Measurements of ecosystem gas exchange

Ecosystem gas exchange was measured with a transparent chamber (0.5 m × 0.5 m × 0.5 m) attached to an infrared gas analyzer (IRGA; LI-6400, LI-COR) on a frame member in each plot. During the measurements, the chambers were sealed along their lower edges. Two small fans ran continuously to mix the air inside the chambers during these measurements, and nine consecutive recordings of CO_2 and water vapor concentrations were taken at the base of each chamber at 10 s intervals during a 90 s period. CO_2 and water flux rates were determined from the temporal changes in the measured concentrations to calculate NEE and ET, according to method slightly modified from Steduto et al. (2002). Following the measurement of NEE, the chambers were vented, replaced on their bases, and covered with opaque cloth. After the CO_2 concentration in the chamber had reached a steady, increased level (usually 0.5 min after the chamber was covered), the CO_2 exchange measurements were repeated. Because the second set of measurements was taken under conditions with no light (i.e., no photosynthesis), the obtained values represented Re.

GEP was calculated as the difference between NEE and Re. Ecosystem water use efficiency (WUE) was calculated as NEE:ET. Positive and negative NEE values represent net CO_2 uptake or release in the ecosystem, respectively. Ecosystem gas exchange was measured from 9:00–11:00 h every three sunny days.

ΔNEE, ΔRe, ΔGEP, ΔET and ΔWUE were also calculated to measure the differences in NEE, Re, GEP, ET and WUE between the non-heated and heated plots under different mowing levels in different experiment

Table 1
Statistics of 50-year heat waves (HW) in Duolun at a *Stipa krylovii* steppe on the Mongolian Plateau from 1967 through 2016 (10 year interval).

	Hot day (day/10 yr)	Heat wave (times/10 yr)	Mean HW length (day)	Max HW length (day)	Times per month			
					May	June	July	August
1967–1976	130	3	5	5	–	1	1	1
1977–1986	112	3	7	10	–	–	3	–
1987–1996	115	4	6.8	8	–	–	3	1
1997–2006	213	11	7.7	12	1	2	7	1
2007–2016	195	11	7.7	14	–	2	6	3
Total	765	32	67.3	14	1	5	20	6

periods. The difference between the CK and H treatments reflects the HW effect without interference from human activity; for example, NM_7 minus HM_7 indicates the HW effect under harvest management, while NM_2 minus HM_2 represents the HW effect under grazing management.

2.7. Measurements of biomass

The peak aboveground biomass was estimated by harvesting the grass within an area of 0.15 m × 0.5 m in each plot in late August. After the aboveground plant residues were collected, one soil core (10 cm diameter) was collected from the 0–15 cm and 15–30 cm soil layers to estimate the belowground biomass in each plot. All of the cores were transported to the laboratory as soon as possible and were then carefully washed on a 60-mesh sieve to separate the roots from the soil. The plant samples and washed roots were oven dried at 65 °C for 72 h before weighing. The results were considered to represent the aboveground and belowground biomass for the current year.

2.8. Data analysis

Repeated-measures ANOVA (two way) was used to examine the HW and mowing effects on CO_2 and water fluxes over the growing season in 2012, 2013 and 2014. One-way ANOVA was employed to examine the statistical differences in the average CO_2 flux and biomass among the six treatments ($P < 0.05$, Duncan's Test). A paired-samples *t*-test was used to examine the statistical differences in microclimate, NEE, Re, GEP, ET and WUE during different HW periods. All statistical analyses were conducted with SPSS 22.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

3. Results

3.1. HW history and biomass

A total of 765 hot days and 32 HW events were identified in the historical local climate records (Table 1). HWs occurred primarily in May–August, with the majority occurring in July and August. During the last 50 years, only one HW occurred in June. However, four HWs occurred in June and one in May within the last decade. The longest duration of an individual HW was 14 days, which occurred in July 2010. Furthermore, 22 of the 32 HWs occurred within the last 20 years, accounting for 68.9% of all HWs of the past 50 years, which is equivalent to approximately one HW per year in recent years.

The aboveground biomass during the experimental period was also significantly affected by the HW and mowing treatments, showing a clear cumulative effect over the years (Table 2). In 2013, only the HW plus mowing treatment caused a significant difference in aboveground biomass and total biomass ($P < 0.05$), due mostly to differences in litter weight, but not in fresh and dry weight. In 2014, however, mowing alone caused a significant difference in aboveground biomass, with fresh, dry and litter weight all contributing to the difference. Additionally, there was a significant difference in litter weight between the CK and H treatment in 2013, but not in 2014.

3.2. CO_2 and water exchange

NEE was significantly reduced by the HW treatments beginning in the second year (2013), which made the greatest contribution to the significant change in GEP ($P < 0.05$) whereas the change in Re was insignificant (Table 3). However, mowing caused no significant changes in ecosystem CO_2 exchange; the interactive effect of the HW and mowing treatments was also insignificant ($P > 0.05$). When the study period was separated into three periods (before HWs (BE-H), during HWs (H) and after HWs (AF-H)) to examine the potential effects of the HW treatments, significant differences in NEE, Re and GEP were observed between the periods, with the exception of Re ($P < 0.05$) in 2012. The HW effects on NEE and GEP in 2013 also appeared to be dependent on the period ($P < 0.05$).

We considered three effects: instantaneous, immediately-post, and long term after each treatment. They represent the periods during, after in the same year, and after a HW period in the next year, respectively. HWs caused a rapid effect on NEE, which decreased significantly ($P < 0.05$) by 34.8%, 28.2% and 38.4%, while Re decreased by 8.6%, 5.4% and 10.9%, and GEP decreased by 20.3%, 14.5% and 22.5% in the unmowed, light-mowed and heavy-mowed plots, respectively (Fig. 2). HW caused the largest rapid effect in the unmowed plots in 2013, where NEE, Re and GEP decreased by 44.4%, 13.1%, and 27.9%, respectively (Table 4). However, the largest HW effect was observed in the heavy-mowed plots in 2014, where NEE, Re and GEP decreased by 43.6%, 12.2%, and 24.3%, respectively, while the unmowed plots showed the smallest decreases. Overall, the HWs caused a larger decrease in NEE than in Re, with NEE showing a 34.8% decrease, which was nearly 4 times of the decrease in Re, of 8.6%.

HWs also caused obvious post effects and legacy effects on CO_2 fluxes after the heat treatment (Table 4). We considered the ΔNEE value during the AF-H period as the HW post effect to measure the influence of HWs under different mowing conditions (Fig. 3). ΔNEE = 0

Table 2
Aboveground biomass (g m^{-2}, mean ± SE) under heat wave and mowing treatment at a *Stipa krylovii* steppe on the Mongolian Plateau in 2013 and 2014 ($n = 6$). Different letters indicate significant differences ($P < 0.05$, one-way ANOVA, Duncan test) among treatments. CK (no heat + unmowed), H (heat + unmowed), NM_7 (no heat + 7 cm stubble), HM_7 (heat + 7 cm stubble), NM_2 (no heat + 2 cm stubble) and HM_2 (heat + 2 cm stubble). Total: total aboveground biomass equal to the sum of dry weight and litter weight.

Year	Biomass	CK	H	NM_7	HM_7	NM_2	HM_2
2013	Fresh weight	648.22 ± 15.87a	512.13 ± 94.38a	545.20 ± 31.44a	543.45 ± 29.95a	544.25 ± 39.21a	480.45 ± 9.27a
	Dry weight	388.22 ± 21.86a	309.73 ± 66.89a	352.62 ± 29.94a	311.95 ± 51.44a	325.82 ± 26.16a	291.35 ± 38.37a
	Litter weight	135.61 ± 11.49b	169.33 ± 27.34a	99.02 ± 20.25b	100.83 ± 8.87b	37.16 ± 7.80c	36.12 ± 1.16c
	Total	523.44 ± 23.31a	479.06 ± 94.20ab	451.63 ± 11.47ab	412.78 ± 43.30ab	362.99 ± 26.93ab	327.47 ± 38.98b
2014	Fresh weight	471.43 ± 15.84ab	536.17 ± 89.50a	451.53 ± 18.78abc	434.43 ± 40.49bc	361.23 ± 18.97c	348.10 ± 26.41c
	Dry weight	357.40 ± 33.45a	368.53 ± 39.76a	314.23 ± 10.58abc	312.53 ± 35.64bc	262.63 ± 5.52c	262.47 ± 31.27c
	Litter weight	354.76 ± 9.33a	376.40 ± 29.89a	117.82 ± 7.25b	130.49 ± 43.77b	20.40 ± 1.80c	22.35 ± 4.93c
	Total	712.16 ± 25.46a	744.93 ± 53.30a	432.06 ± 15.22b	443.02 ± 62.43b	283.03 ± 7.10c	284.82 ± 35.46c

Table 3
The *P*-values resulted from a repeated-measurement ANOVA on the effects of HWs (H), mowing (M), sampling period (P, include three period, before, during and after HW) and their interactions on net ecosystem CO_2 exchange (NEE), ecosystem respiration (Re), gross ecosystem productivity (GEP), evapotranspiration (ET) and water use efficiency (WUE) during different experiment years (2012–2014).

Treat	NEE			Re			GEP			ET			WUE		
	2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014	2012	2013	2014
HW	0.379	**0.008**	**0.010**	0.831	0.310	0.467	0.610	**0.009**	**0.035**	0.718	**0.040**	0.051	0.431	0.136	**0.012**
M	–	0.955	0.760	–	0.878	0.721	–	0.863	0.683	–	0.539	0.646	–	0.943	**0.047**
HW × M	–	0.866	0.981	–	0.989	0.782	–	0.890	0.895	–	0.922	0.536	–	0.889	0.239
P	**0.000**	**0.000**	**0.001**	0.149	**0.000**	**0.000**	**0.011**	**0.000**	**0.000**	**0.010**	**0.034**	**0.000**	**0.000**	**0.000**	**0.000**
P × HW	0.661	**0.017**	0.127	0.846	0.405	0.759	0.959	**0.021**	0.193	0.872	0.851	0.384	0.458	0.590	0.117
P × M	–	0.933	0.906	–	0.308	0.683	–	0.758	0.874	–	0.685	0.787	–	0.979	0.931
P × HW × M	–	0.842	0.253	–	0.436	0.469	–	0.511	0.404	–	0.958	0.591	–	0.997	0.719

The bold numbers highlight the significance at $P < 0.05$.

indicates full restoration of the ecosystem following a HW. Our results showed that the recovery time was shortest in the unmowed plots (34 d), intermediate in the light-mowed plots (38 d), and the longest in the heavy-mowed plots (41 d). The ΔNEE, ΔRe and ΔGEP values obtained during the BE-H period indicate whether the legacy effects of HWs continue through to the following year (Fig. 4). Interestingly, there were no significant differences in ΔNEE, ΔRe and ΔGEP among the unmowed plots (Fig. 4b, e, h white boxes), but significant differences were observed in the light- and heavy-mowed plots ($P < 0.05$) in 2013 (Fig. 4b, e, h shadow boxes), suggesting that the HWs that occurred in 2012 produced no legacy effects under the unmowed treatment, whereas this was not the case for the light and heavy mowing treatments. In 2014, the third year of the experiment, significant differences in ΔNEE, ΔRe and ΔGEP caused by HWs remained in all mowed plots ($P < 0.05$, Fig. 4c, i), except for ΔRe under the light mowing treatment (Fig. 5f). The HW legacy effects on the ecosystem CO_2 exchange appeared to be the largest in heavy-mowed plots and the smallest in unmowed plots.

HWs caused substantial decreases in ecosystem ET and WUE, with significant decreases being observed in 2013 for ET and in 2014 for WUE ($P < 0.05$) (Table 3). ET decreased by 7.4%, 8.6% and 19.6%, whereas the WUE decreased by 12.3%, 6.1% and 3.8% in the unmowed, light-mowed and heavy-mowed plots, respectively, in 2014. The changes in ΔET and ΔWUE during the different HW periods (Fig. 5) revealed contrasting responses of ΔET and ΔWUE. For example, HWs caused a significant change in ΔWUE ($P < 0.001$) but had no significant influence in ΔET in 2014.

4. Discussion

4.1. HW simulation method and microclimate change

Rapid warming with drought, which is a major characteristic of HWs, was simulated properly in our experiments. Previous studies addressing HWs have indicated rapid warming in terms of canopy temperature, rather than air temperature, accompanied by water limitation (Bauweraerts et al., 2013; De Boeck et al., 2015; Ruehr et al., 2016). These studies indicated increases in T_{can} of 6–10 °C during the day and 4–6 °C during the night, which was well simulated in the present study (Fig. 1). Our results revealed obvious droughts following HW treatments (Fig. 1c), due to rapid water consumption and indicting a similar phenomenon to what occurs in natural HWs (Ameye et al., 2012; Bauweraerts et al., 2013; De Boeck et al., 2011). We chose late July as our HW treatment time because HWs occur mostly in July and August according to the 50-year local historical records (Table 1). The results also indicated an increase in the number of HWs during the last 20 years (1997–2016), with more than half of HWs occurring within these two decades.

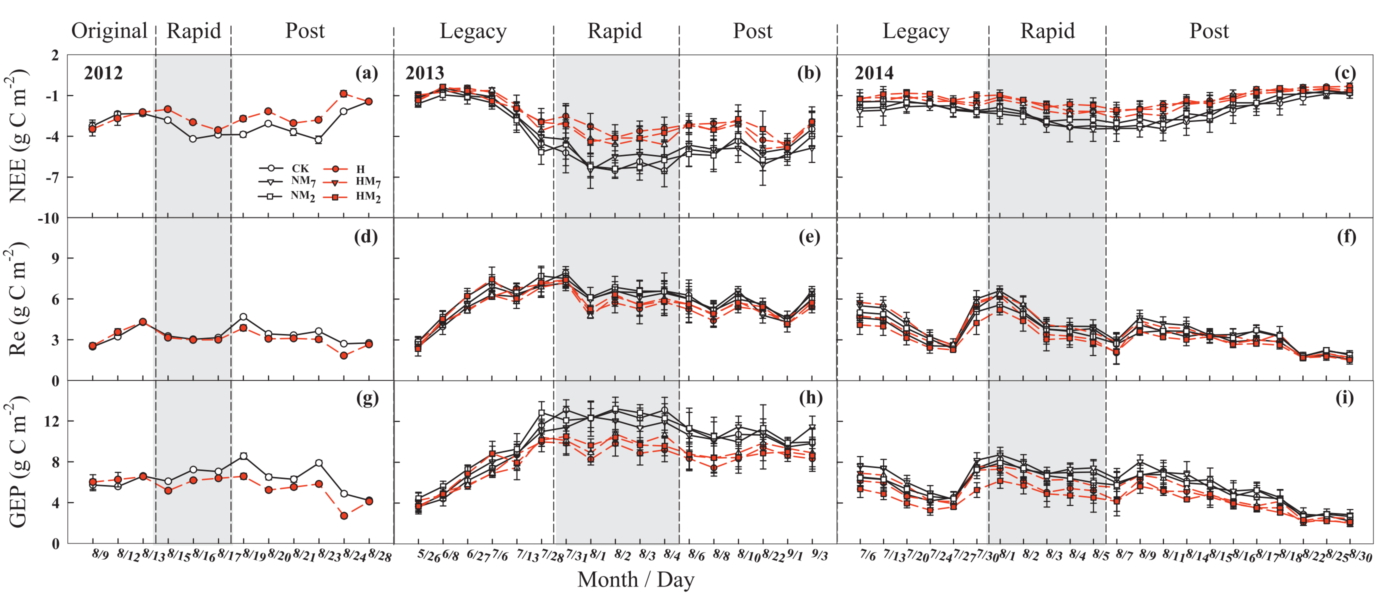

Fig. 2. Daily changes in: (a, b, c) net ecosystem exchange (NEE), (d, e, f) ecosystem respiration (Re), and (g, h, i) gross ecosystem productivity (GEP) under heat wave (HW) and mowing treatment at a *Stipa krylovii* steppe on the Mongolian Plateau during 2012–2014. Error bars indicate standard errors among the plots. Grey areas indicate the HW treatment periods. HW effects include rapid effect (during HW period), post effect (after HW period in the same year), and legacy effect (after HW period in the next year). CK (no heat + unmowed), H (heat + unmowed), NM_7 (no heat + 7 cm stubble), HM_7 (heat + 7 cm stubble), NM_2 (no heat + 2 cm stubble) and HM_2 (heat + 2 cm stubble).

Table 4
HW and mowing effects on net ecosystem exchange (NEE) of CO_2, ecosystem respiration (Re) and gross ecosystem productivity (GEP) during different experiment years (2012–2014). HW effects include rapid effect (during HW period), post effect (after HW period in the same year), and legacy effect (after HW period in the next year). Unmowed (include CK and H treatment), light-mowing (include NM_7 and HM_7) and heavy-mowing (include NM_2 and HM_2).

CO_2 flux	Treat	2012 HW			2013 HW			2014 HW		Mean		
		Rapid (%)	Post (%)	Legacy (%)	Rapid (%)	Post (%)	Legacy (%)	Rapid (%)	Post (%)	Rapid (%)	Post (%)	Legacy (%)
NEE	Unmowed	−21.7	−29.7	−24.4	−44.4	−26.1	−24.8	−38.4	−48.5	−34.8	−34.8	−24.6
	Light-mowed	–	–	−21.0	−24.0	−26.9	−33.1	−32.4	−31.2	−28.2	−29.1	−27.1
	Heavy-mowed	–	–	−34.3	−33.2	−31.0	−39.1	−43.6	−33.7	−38.4	−32.3	−36.7
Re	Unmowed	−3.4	−14.5	+3.0	−13.1	−12.7	+4.8	−9.3	+0.6	−8.6	−8.9	+3.9
	Light-mowed	–	–	−5.4	−7.9	−5.9	+1.7	−2.9	−5.9	−5.4	−5.9	−1.9
	Heavy-mowed	–	–	−4.1	−9.6	−4.9	−16.8	−12.2	−15.9	−10.9	−10.4	−10.5
GEP	Unmowed	−12.9	−21.8	−3.9	−27.9	−18.7	−4.8	−20.2	−20.8	−20.3	−20.4	−4.4
	Light-mowed	–	–	−9.2	−15.2	−15.9	−8.9	−13.8	−15.5	−14.5	−15.7	−9.1
	Heavy-mowed	–	–	−12.3	−20.6	−17.2	−23.4	−24.3	−22.6	−22.5	−19.9	−17.9

4.2. Rapid, post and legacy effects of HWs on ecosystem CO_2 fluxes

HWs caused rapid decreases in all ecosystem CO_2 fluxes during the HW period (Fig. 2), with NEE, Re and GEP decreasing by 34.8%, 8.6% and 20.3%, respectively. These decreases indicated direct impacts of HWs on ecosystem CO_2 fluxes, likely through reductions in plant photosynthesis and growth (Wang et al., 2016). The optimal temperature for photosynthesis ranges between 20 °C and 35 °C for most plant species, suggesting that the direct HW effect might cause thermal damage to photosynthesis (Rennenberg et al., 2006). High temperature reduces stomatal conductance and down-regulates the quantum yield of photosystem II, which is an effective strategy for conserving water before additional damage caused by temperature and drought stresses, and restriction of CO_2 causes further decreases in plant photosynthesis (Bauweraerts et al., 2013).

The observed post effects were derived directly from plant carbon starvation, as the respiration rate was higher than the photosynthesis rate under high-temperature conditions (Table 3). Under several days of sustained heat treatments, starvation and increased respiration may cause ammonia poisoning, damage from biofilm development and protein denaturation (Berry and Bjorkman, 1980; Crafts-Brandner and Salvucci, 2002; Qu et al., 2016), preventing leaf expansion and increasing plant mortality (Ruehr et al., 2016). The loss of intracellular water due to drought after a HW might damage plant cell integrity and ultimately lead to cell death (Billi and Potts, 2002). The lower biomass

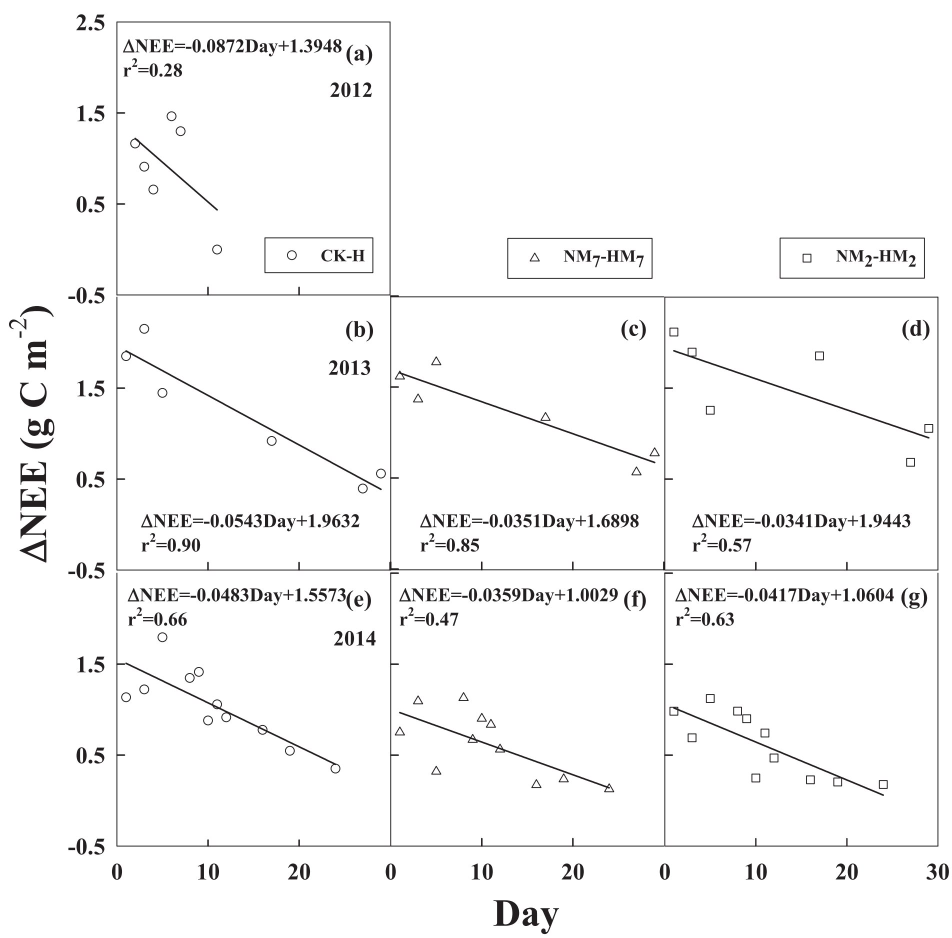

Fig. 3. NEE difference (ΔNEE) after HW treatment under different mowing intensity in 2012 (a), 2013 (b, c, d) and 2014 (e, f, g).

and high litter mass recorded in the HW plots further indicated that more plant tissues were senescent (Table 2).

The observed legacy effects were derived from the changes in grassland composition and structure. We found that community structure changed significantly under HW stress. For example, the important value index (IV, calculated based on plant height, coverage and abundance) of the dominant species *Stipa krylovii* decreased significantly by 24.8%. This decrease in IV indicated that *Stipa krylovii* lost its dominant place in the community and that the community structure was altered due to HW treatment. Some authors have indicated that productive species, such as most grass species, are expected to recover quickly after climate extremes, especially in the case of nitrogen-fixing legumes (Elst et al., 2017; Hoekstra et al., 2015; Pauline and Catherine, 2016; Wang et al., 2016). We noted that the legacy effect on the ecosystem CO_2 flux might have accumulated and been amplified. The legacy effect of the first year HW event on NEE and GEP was insignificant in the unmowed plots (Fig. 4, a, g, BE-H), but the HW event in the second year (2013) resulted in a significant legacy effect (Fig. 4, c, i, BE-H). The negatively effects on photosynthesis, chlorophyll II fluorescence, stomatal conductance and chlorophyll II content observed under HW stress in *Arabidopsis thaliana* could be hereditary (Zinta et al., 2014).

4.3. Combined HWs and mowing effects on ecosystem CO_2 fluxes

Continuous HWs over multiple years produced clear cumulative effects, with NEE decreasing by 19.8%, 33.9% and 40.2% in the first, second and third HW years, respectively (Table 4). Previous studies have shown that a single HW event can cause small, directly measureable effects on plant function (De Boeck et al., 2015; Hoover et al., 2014; Ruehr et al., 2016). Our results are in agreement with this finding, as the first HW treatment did not produce any significant legacy effect (Fig. 4b BE-H). However, multiple HWs caused significant legacy effects (Fig. 4c BE-H). From a global perspective, the atmospheric CO_2 concentration has increased by 40% since 1750 (IPCC, 2013; Lin et al., 2017). Numerous studies have suggested that increases in CO_2 concentrations can buffer plants from the effects of HWs (Ameye et al., 2012; Bauweraerts et al., 2013; Fitzgerald et al., 2016) because elevated CO_2 can reduce stomatal conductance and transpiration, while potentially increasing soil water content later in the season (Leakey et al., 2009). Additionally, global warming as a result of

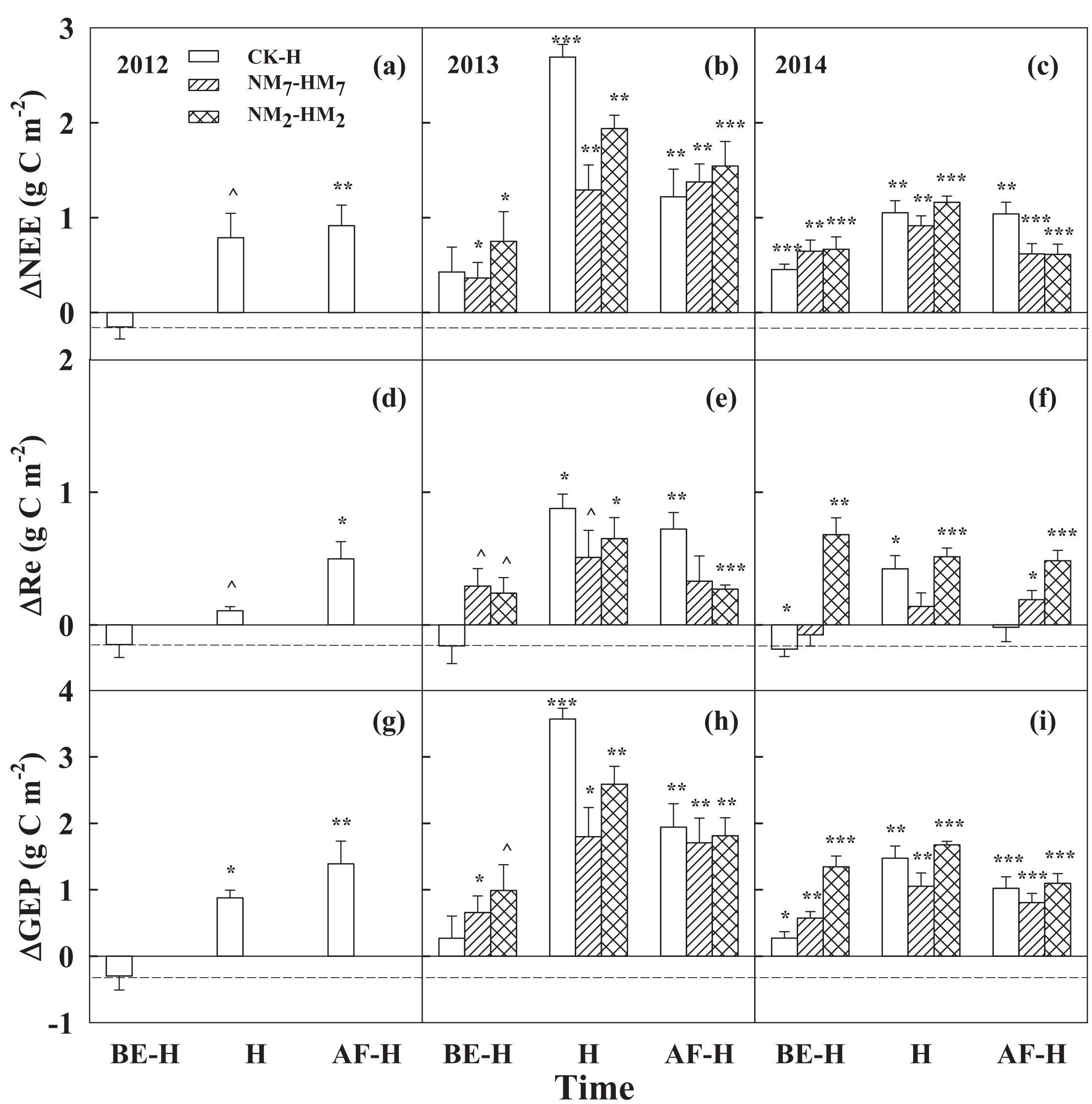

Fig. 4. Difference in NEE (a, b, c), Re (d, e, f) and GEP (g, h, i) from the reference (i.e., no heat, HW) under different mowing levels of HWs and mowing at a *Stipa krylovii* steppe on the Mongolian Plateau during 2012–2014. Statistic analysis for the paired samples *t*-test. ^$P < 0.1$, *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$. BE-H: before HW treatment in the year, H: HW treatment period in the year and AF-H: after HW treatment in the year. See Fig. 2 for abbreviations. The long dashed line shows there is an insignificant difference among the plots prior to the treatments.

increasing CO_2 concentrations is linked to intensified and more frequent HWs (IPCC, 2013). Based on this study, an increase in the HW frequency means that additional consequences should be expected for ecosystem processes and functions (i.e., additive effects).

Mowing increased the effects of HWs by extending their influence (i.e., legacy effects). A significant legacy effect from the HW in the first-year HW treatment was found only in the mowed plots (Fig. 4, b, h, BE-H shadow box) and not in the control plots (Fig. 4, b, h, BE-H white box). Mowed grasslands appeared to need more time to recover from the HW effects (Fig. 3). Therefore, we reject our hypothesis that mowing might alleviate HW effects. We reason that the removal of vegetation through mowing might have reduced ecosystem resistance to HWs (Houghton et al., 1999; Searchinger et al., 2008). Mowing can lead to more severe drought, which will in turn reduce the photosynthetic capacity more than high temperature alone (Benot et al., 2014; De Boeck et al., 2011). Although previous studies have demonstrated that moderate mowing may stimulate the ecosystem photosynthetic capacity and lengthen the daily growing time (Chen et al., 2004; Niu et al., 2013), this may only be the case under normal hydrothermal conditions without other environmental stresses, such as HW or drought (Li et al., 2005; Shao et al., 2016; Zwicke et al., 2013). In this study, we found that heavy mowing caused a similar degree of HW effects on leaf photosynthesis, plant growth and leaf expansion (De Boeck et al., 2015) and resulted in additional effects on ecosystem CO_2 fluxes. Furthermore, a small decrease in the carbon sequestration ability was found in the light-mowed plots (Table 4), likely because light mowing stimulated growth (Niu et al., 2013).

4.4. HW effect on annual ecosystem CO_2 fluxes

Two types of studies addressing HW effects on ecosystems had been reported in the literature: observational and experimental (Table 5). The observational studies are based on natural HWs and are conducted using data from eddy covariance flux towers and/or remote sensing images. While legacy effects can potentially be assessed using these data, the rapid effects of HWs on ecosystem processes are difficult to quantify. Manipulative experiments can address these pitfalls, although previous experiments have mostly been conducted on single plants or species. Here, we conducted a field simulated HW experiment and applied a sound conceptual framework, through the analysis of data on rapid, post, and legacy effects on ecosystem function. We found evidences that plant photosynthesis was directly affected by HWs, which was responsible for the significant decrease in NEE. This finding is in agreement with Wang et al. (2016), who also acknowledged the existence of legacy effects by noting that plants undergo a recovery process. More importantly, it appears that the community responses to HWs are quite different from the single-species responses.

To place our findings in a global context, we compiled data on HW effects on CO_2 fluxes in other ecosystems and compared them with our results (Table 5). Overall, HWs significantly decreased NEE, Re and GEP by 31.3%, 5.4% and 16.0%, respectively (Table 5). Compared with findings from Europe, where GEP decreased by 30.0% after the 2003 HW (Ciais et al., 2005), the reduction we recorded following HW treatments appeared small. At the leaf level, HWs have been reported to reduce the net photosynthesis of *Pinus taeda* and *Quercus rubra* seedlings by 20%–31% (Ameye et al., 2012) and that of red oak seedlings in a northern hardwood stand by 30% (Bauweraerts et al., 2013). Surprisingly, HWs caused a smaller change in Re (Fig. 4e, f) than that in NEE (Fig. 4b, c) in the present study, which agrees well with previous studies (Ameye et al., 2012; Tatarinov et al., 2016). The decrease in NEE was nearly four times greater than that in Re (34.8% and 8.6%) during the HW periods, likely because (1) Re comes from many sources (e.g., plant respiration and soil respiration) (Trumbore, 2006), and (2) the increased litter biomass in the HW plots may have promoted ecosystem soil respiration (Table 2), which would result in a smaller decrease in Re (Reichstein et al., 2007; Wan et al., 2005).

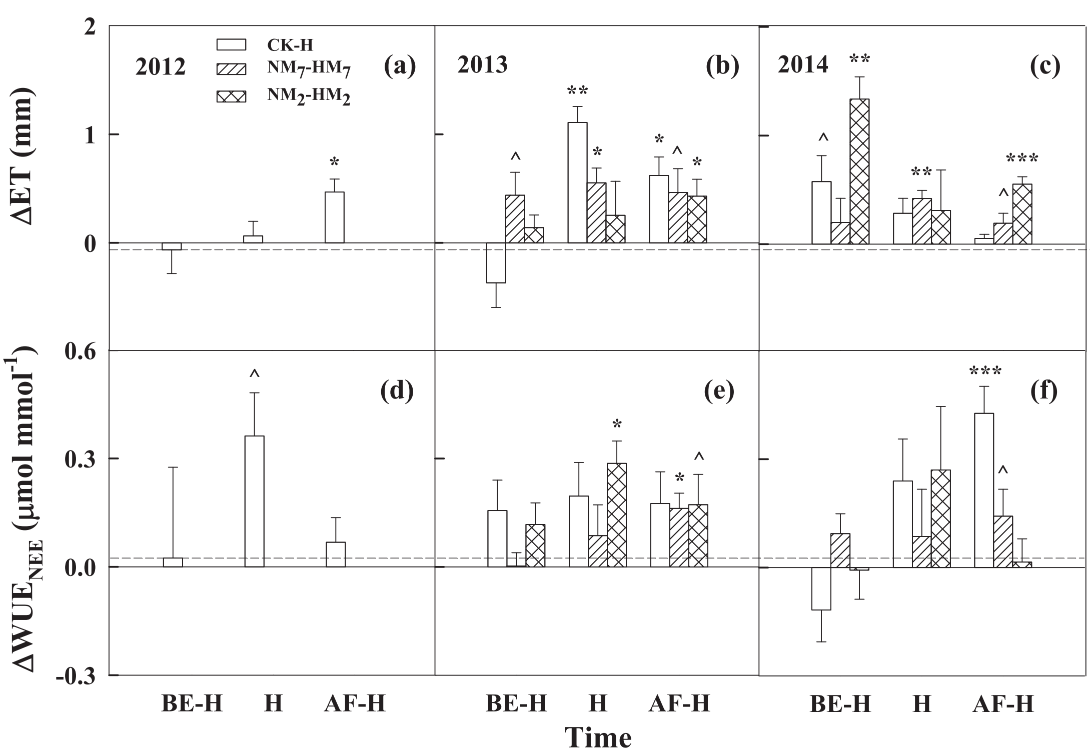

Fig. 5. The net changes in ET (a, b, c) and WUE (d, e, f) from the control plots (i.e., no heatwave and mowing) at a *Stipa krylovii* steppe on the Mongolian Plateau during 2012–2014. Statistic analysis is for the paired samples *t*-test. ^$P < 0.1$, *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$. BE-H, before HW treatment; H, HW treatment period; and AF-H, after HW treatment. See Fig. 2 for abbreviations. The long dashed line shows there is an insignificant difference among the plots prior to the treatments.

Table 5
Comparison of heat wave effects on CO_2 fluxes. Net Pho, net photosynthesis; na, data not available; T_a, air temperature. This study was calculated by the data of CK and H treatment.

HW type	Species/ecosystems	HW effects				HW strength		References
		NEE	Re	GEP	Net Pho	T_a (°C)	Days	
Natural HW	Evergreen/deciduous needle-leaf/broad-leaf forests, grassland, scrubland, 2003, Europe	na	na	−30%	na	+6		(Ciais et al., 2005)
	Mediterranean pine forest, 2010, Africa	−15%	na	−4%	na	+4–6	5	(Tatarinov et al., 2016)
	Meadow steppe, 2010, China	−50%	−30%	−38%	na	+4–7	5–8	(Qu et al., 2016)
	Mixed hardwood forest, 2010, Canada	na	na	−25%	na	+4–11	16	(Geddes et al., 2014)
	Forests, croplands and grasslands, 2013, China	−39–53%	+7%	na	na	+4		(Yuan et al., 2016)
Indoor simulated HW	*Andropogon gerardii* and *Solidago canadensis*, 2007, USA	Decrease	na	na	na	39–41	6	(Wang et al., 2016)
	Quercus rubra and *Pinus taeda* seedlings, 2009, USA	na	na	na	−23%	+12	7	(Bauweraerts et al., 2014), (Ameye et al., 2012)
	Andropogon gerardii and *Solidago canadensis*, 2010, USA	na	na	na	−80%	+8	14	(Hoover et al., 2014)
	Cherry tomato (*S. lycopersicum*) seedlings, 2016, China	na	na	na	−61%	42	7	(Duan et al., 2016)
Field simulated HW	Alpine grassland, 2009, Europe	Decrease	na	na	na	+7	10	(De Boeck et al., 2011)
	Stipa krylovii grassland, 2012–2014, China 2012	−20%	−7%	−13%	na	+6–10	3	This study
	2013	−34%	−8%	−19%	na		5	
	2014	−40%	−1%	−16%	na		5	
	Total	−31%	−5%	−16%	na			

4.5. HWs and mowing effects on ET and WUE

We also made efforts to explore the changes in WUE so that resource use could be considered as another aspect of the community response to HWs and mowing. Both HWs and mowing caused significant changes in WUE in the last year of the experiment (Table 3). Previous studies have demonstrated that different species exhibit distinct responses to HW stress in terms of WUE. For example, C3 species (*Solidago canadensis*) tend to close their stomata in response to HWs, leading to reduced transpiration and a decreased WUE, while C4 species (*Andropogon gerardii*) tend to maintain relatively open stomata and high transpiration rates, which could limit the negative effects of temperature on foliage when combined with a high WUE (Wang et al., 2016).

In the late period of our 3-year experiment, the ecosystem appeared to adapt to the multiple HW treatments in the unmowed plots, but not in the heavy-mowed plots, as demonstrated by insignificant changes in ΔET but significant changes in ΔWUE (Fig. 5, c, f, AF-H) in the unmowed plots. In contrast, significant decreases in both ΔET and ΔWUE were detected in the heavy-mowed plots. The significant decrease in WUE under both mowing treatments was coupled with a decrease of NEE, suggesting that the underlying mechanisms may be different. In the unmowed treatment, the insignificant decrease in ET indicates that the ecosystem may not have lost its ability to retain soil moisture, or that sufficient water existed to overcome the HW effects. Logically, a community with higher tolerance to heat and drought can be expected to sustain its function after repeated HWs and mowing treatments (Elst et al., 2017; Wang et al., 2016). Without mowing, plants may maintain high resistance to heat and drought (Shao et al., 2012; Zinta et al., 2014). Although both mowing and HWs caused decreases in the green parts of plants and increases in plant mortality, mowing directly removed the dead parts from the ecosystem (Table 2). In the unmowed plots, the dead parts of plants were transformed to a litter layer (Qu et al., 2016), which can serve as a very good insulator in reducing water loss and soil heat fluxes (Shao et al., 2016). The litter will decompose and increase soil nutrient levels, with high temperatures from HWs stimulating the decomposition rate (Meentemeyer, 1978). Ecosystems clearly appear to develop the necessary adaptive strategies to offset the impacts of HWs (Quesada et al., 2012).

Under the mowing treatment, significant decreases in ET suggested that the ecosystem may have lost (or reduced) its ability to maintain soil moisture, which was enhanced by the droughts caused by the HWs. To adapt to HW stress, an ecosystem must undergo passive water evaporation to maintain WUE (Hussain et al., 2011). With the limited water storage in our semi-arid grasslands, HWs may cause irreversible damage to the ecosystem when available water is already exhausted (Reichstein et al., 2007). The significantly higher ET observed in the heavy-mowed plots supported this rationale, as the ecosystem lost more water than in the unmowed plots during the entire growing season (i.e., high consumption of the ecosystem "water pool"). This greater water loss will result in less available water and an increase drought severity under HWs. As a result, the resistance of the ecosystem to the combination of stress from HWs and mowing will be reduced.

5. Conclusions

HWs were shown to significantly influence ecosystem CO_2 exchange in a *Stipa krylovii* steppe grassland, and clear legacy effects were detected. We defined three periods of HW effects; not only is there a rapid effect, but a long-term effect (post and legacy effects) also occurs, which can be referenced in other extreme climatological studies. Additionally, HWs reduced the annual CO_2 assimilation capacity. Overall, HWs caused the greatest effect on NEE, represented as 31% decrease in the average value, while was GEP was decreased less, by 16%, and Re only decreased by 5%. Continuous HWs over multiple years produced clear cumulative effects. The variation of WUE under the HW effects indicated that the ecosystem could reduce water consumption and increase the water capacity, in addition to adapting to continuous HW effects by adjusting community structure or increasing litter biomass. Furthermore, mowing (especially heavy mowing) will result in less available water and increase the drought severity under HWs. As a consequence, the resistance of the ecosystem to the combined stress from HWs and mowing will be reduced.

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