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Joint forcing of heat waves and mowing poses a threat to grassland ecosystems: Evidence from a manipulative experiment

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Running Head: Joint forcing of heat waves and mowing effects on grassland ecosystem
Abstract

The frequency and intensity of heat waves (HWs) have increased in recent years, but it remains unclear how grassland ecosystem respond to such extreme weather. A 3-year manipulative field experiment was conducted to simulate HWs under different mowing intensities in a *Stipa krylovii* steppe on the Mongolian Plateau to examine their effects on plant morphology, phenology and community. At the species level, the morphology and phenology of the three main herb species (*Stipa krylovii, Melilotoides ruthenica* and *Potentilla tanacetifolia*) showed species-specific responses to the HW and mowing treatments. The major dominant species *Stipa krylovii* shed ~50% of the tiller outer layer to protect the internal tiller from HW stress, thereby directly decreasing the heat load and water loss from green plant tissue and indirectly increasing the litter biomass. HWs also caused increases of community index (richness, diversity, and evenness), but associated with a 30% decrease in the importance value of *Stipa krylovii*, whereas mowing enhanced this value by 27%. When HWs were combined with mowing, the joint forcing of mechanical damage and low C accumulation aggravated negative effects of stress on plant health and growth, which further decreased community index. We constructed a framework to fully describe the effects of HWs and mowing and their interrelationship on different ecological levels and explain how short-term effects, such as extreme climate, produce long-term effects on ecosystems. In conclusion, we found that synergisms between climate extremes (HWs) and human activities (mowing) can reduce ecosystem stability, posing a threat to the grasslands.
Introduction

Heat waves (HWs) are naturally occurring hazards characterized by sudden anomalously high (absolute or relative) temperatures which last for a relative short period, that can cause negative effects on ecosystem function and stability (Chen, Hu, Yang, & Qian, 2017; Reichstein et al., 2013). Mounting evidence points to an increase in the frequency and intensity of HWs, which have affected more than 73% of the global terrestrial area since the mid-20th century (IPCC, 2013; Perkins-Kirkpatrick et al., 2016), and have caused large and widespread impacts at all ecological scales from the species level to the ecosystem level. Severe HW events not only rapidly reduce plant photosynthesis and respiration (Crous Kristine et al., 2018), decrease aboveground and belowground biomass accumulation (Qu, Chen, Dong, & Shao, 2018) and alter the (re)allocation of carbon and nitrogen within a plant (Li et al., 2017), but also result in a decrease in ecosystem gross primary productivity (GPP) and net ecosystem carbon exchange (NEE) (Ciais et al., 2005; Qu et al., 2018; Tatarinov et al., 2016). However, these studies mostly concentrate on HWs effects on plant growth (photosynthesis system) or ecosystem carbon exchange, but how plant morphology, phenology and community structure respond to such extreme events remains poorly understood.

Compared with gradual temperature increases, the sudden high temperatures associated with HWs have a greater and more rapid impact on plant health and ecosystem carbon exchange, and are associated with an increased risk of fire (Sanz-Lázaro, 2016; Xia, Niu, & Wan, 2009). Such conditions cause increases in plant mortality (Teskey et al., 2015; Wang, Heckathorn, Mainali, &
Tripathee, 2016), resulting in the elimination of individuals that are unsuited to the new environment, thus altering the community and ecosystem structure (Gutschick & BassiriRad, 2003; Li et al., 2017; Zinta et al., 2014). Legacy effects of HWs are associated with changes in plant species and trophic interactions (Kreyling et al., 2017) that lead to complex responses at the community level (Elst et al., 2017; Sentis, Hemptinne, & Brodeur, 2013). However, until now, direct evidence on the effect of HWs at the community level has been lacking because prior research on HWs usually did not focus at this level. Early observational research on naturally occurring HW events primarily focused on ecosystem responses (e.g., carbon and water cycles), and fewer studies focused on the responses at the scale of plant communities because natural HWs occur at random and control groups are lacking (Ciais et al., 2005; Yuan et al., 2016).

Meanwhile, laboratory-based studies of HWs have mainly focused on the characteristics and phenological variations among individual plant species, with plant communities being relatively ignored (Ameye et al., 2012; Bauweraerts et al., 2013). Plants may respond very differently to climate change when growing in a community because of the occurrence of interspecific interactions (De Boeck et al., 2018; Isbell et al., 2015), such as the presence of nitrogen-fixing legumes can increase the speed at which neighbouring plants recover after an extreme climate event (Hoekstra, Suter, Finn, Husse, & Lüscher, 2014; Kreyling et al., 2017). Here, we acknowledge the importance of such community-scale effects in this study and focus on the mechanisms underlying the effects of HWs on different ecological levels and how these are connected.
Beside direct HW effects on plant health, plant phenology may also be affected by such an extreme. Phenology refers to the seasonal timing of phenomena (e.g., flowering and fruiting), and it is regulated by environmental factors and sensitive to climate change (Chen, Hu, & Yu, 2005; Dunnell & Travers, 2011; Liu & Sun, 2011; Wolkovich et al., 2012). When plant phenology changes, it will eventually alter the plant community structure, inter-species interactions (Xia et al., 2015), and ecosystem CO\textsubscript{2} and water exchange (Musolin, Tougou, & Fujisaki, 2010). Cremonese et al. (2017) reported that a HW was responsible for the observed reduction of canopy greenness in a mountain grassland, but did not measure the responses of the individual species. Several manipulative field experiments observed advancements in the timing of flowering phenology under warmer conditions (Lambrecht, Loik, Inouye, & Harte, 2007; Wolkovich et al., 2012), likely caused by warming-accelerated spring biomass growth (Carbognani, Bernareggi, Perucco, Tomaselli, & Petraglia, 2016; Whittington, Tilman, Wragg, & Powers, 2015), but these phenological studies have mostly focused on responses to general warming. High absolute temperatures usually occur during summer rather than during spring, and do not last for the whole growing season, indicating that the mechanisms underlying plant phenological responses to general warming and HWs may be different. However, due to the lack of field experiments evaluating the phenological response of individual plant species to HWs, a critical unknown is whether short, hot periods (i.e. HWs) can affect plant phenology. The answer to this question is fundamental in assessing plant resistance to HW stress and in identifying future community composition and structure under elevated and frequent HW events.
In addition to the HW effect caused by global change, land use changes caused by human activities also deserve attention on the Mongolian Plateau, especially if there are interactive effects on grassland ecosystem. The Mongolian Plateau covers an area of 2.73 million km², with >60% composed of grassland, and because of this relatively simple vegetation type, nomadism represents the main land-use practice on the plateau. However, with the increasing settlement of herdmen, mowing for hay has become a widely practised pasture management method in recent decades (Chen, John, Zhang, et al., 2015). Although increases in mowing intensity have economic benefits, they significantly alter the carbon flux and energy budgets by changing the photosynthetic activity and stimulating compensatory growth (Niu et al., 2013; Shao et al. 2014). They also influence the microclimate (Shao et al., 2016) and associated plant traits, such as plant height and specific leaf area (Reisch & Poschlod, 2011), which in turn will affect plant reproductive phenology (Benot et al., 2014). More importantly, increases in mowing intensity not only have profound consequences for grassland ecosystems (Shao, Chen, & Li, 2013) but can also increase the sensitivity of grassland ecosystems to climate change (Chen, John, Shao, et al., 2015). Here, we hypothesize that mowing may interact with global warming and reduce ecosystem resilience to extreme weather (Benot et al., 2014), thereby further exacerbating the effects of HWs on ecosystem carbon and water fluxes (Gourlez de la Motte et al., 2018; Qu et al., 2018). However, significant knowledge gaps remain regarding the interactions between HWs and land use, especially their joint influences on plant morphology, phenology, community structure, and the underlying processes responsible for ecosystem
The main aim of this study was to assess the responses of a natural ecosystem to climate extremes (HWs) and human activity (mowing) and determine their interactions at the plant and community level. For this purpose, a 3-year field experiment was designed on a Mongolian Plateau grassland ecosystem to determine plant morphology, phenology, and community structure responses to imposed HWs in conjunction with different mowing practices. We hypothesized that: (1) HWs and mowing have significant effects on each species, including changes in plant morphology and phenology, and suggest that plants might prolong the flowering of fruit phenology due to decreased carbon accumulation; (2) diversity may decline because species sensitive to HWs, mowing or their combination perish, thus causing additional variation in community structure.

**Materials and Methods**

**Study site**

The manipulative experiment was conducted in a semi-arid area in Duolun County (42°02’ N, 116°17’ E), Inner Mongolia, China. The mean annual precipitation at this site is 385 mm, the mean annual air temperature is 2.1 °C, and the monthly mean temperatures range from -17.5 °C in January to 18.9 °C in July (data from 1965-2013). The soils are classified as chestnut soils in the Chinese classification or Haplic Calcisols using the FAO classification, and they are composed of 62.75±0.04% sand, 20.30±0.01% silt, and 16.95±0.01% clay. The mean soil bulk
density 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. A total of 36 species were recorded at the end of the experiment, and they fell into four functional groups (Table S1): Perennial Bunchgrass (PB, 4 species), Perennial Forb (PF, 26 species), Perennial Rhizome grass (PR, 4 species), and Shrub and Semi-shrub (SS, 2 species). Three common species were chosen for continuous observation: one PB species (*Stipa krylovii*), which is a perennial tussock-forming C3 grass and the dominant species in the community, and two PF species, *Melilotoides ruthenica*, a perennial legume species widely distributed in high-quality pasture on the Mongolian Plateau, and *Potentilla tanacetifolia*, a perennial Rosaceae species that is mainly distributed as a common auxiliary species in typical meadow steppes on the plateau.

**Experimental design**

A fully factorial experimental design with two factors, HW and mowing, was implemented. The HW treatment included two levels (HW and no HW), while the mowing treatment had three levels: no mowing, light mowing (to a plant height of 7 cm, M$_7$), and heavy mowing (to a plant height of 2 cm, M$_2$). This experimental design yielded six treatments: C (control, no HW+no mowing), HW (HW+no mowing), NM$_7$ (no HW+7 cm stubble), NM$_2$ (no HW+2 cm stubble), HM$_7$ (HW+7 cm stubble) and HM$_2$ (HW+2 cm stubble). The study site had not been mowed
since it was fenced in 2001 (Shao, Li, Dong, & Chen, 2014). The M7 and M2 treatments were used to simulate local grassland harvesting; the 7 cm treatment was the common plant height after normal mowing, whereas the 2 cm treatment simulated the plant height after over-mowing. The mowing treatments were conducted using a field mower (Yard-Man 160CC, USA) at the end of August, when local harvesting normally occurs. Each treatment had 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 a total area of 308 m², with a 2 m buffer zone between any two neighbouring plots. The same experimental design has been used to investigate the effects of HWs and mowing on ecosystem carbon sink strength and carbon and water fluxes (Qu et al., 2018).

**Heat wave treatment**

The effects of HWs were simulated using octagonal open-top chambers (OTCs; diameter, 2.0 m; height, 1.5 m) that were constructed using steel tubes. A heater (0.20 m × 0.15 m × 0.15 m) was installed within each OTC at 1.5 m above the ground and powered with a 3500 W power supply (Fig. S1). During the implementation of the HW treatments, the OTCs were covered with transparent PVC film that had a light transmittance of >90% based on measurements of the photosynthetically active radiation (PAR) inside and outside. OTCs have been reported to exacerbate temperature peaks under sunny conditions (Hans J De Boeck, De Groote, & Nijs, 2012), which made them suitable for our HW simulation. The OTCs were open for 1 h per day at 05:00-06:00 h to avoid large inconsistencies between the internal and external environment.
(apart from temperature). The non-heated plots were also covered with a similar chamber to ensure comparable conditions. Our simulated HWs were carried out to ensure similarity to naturally occurring HWs (Qu et al., 2018). According to local historical climate data (http://cdc.cma.gov.cn/), HWs predominantly occur in July, which is when we carried out our heat simulation experiments. Dry sunny days were selected for the heating periods, which is in accordance with the conditions of natural HWs. The simulated HW intensity (canopy temperature increased by ~6-10 °C during the day and by ~4 °C at night) and duration (3-5 days) were also similar to the local historical conditions. The HW treatments were carried out during three consecutive years: over 3 days in 2012 during a preliminary experiment and over 5 days in 2013 and 2014 (Fig. S2).

**Biomass & measurement**

The peak aboveground biomass was estimated by harvesting the vegetation within a 0.15 m × 0.50 m quadrat in each plot in late August one day before the mowing treatment. After the aboveground plant residue was removed, one soil core (10 cm diameter) was collected from each plot to estimate the belowground biomass in the 0-15 cm and 15-30 cm soil layers. The soil cores were transported to the laboratory on the day of collection and 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 treated as the aboveground and litter biomass for the current year.
The number of seedlings ($N_s$) of all plant species was measured in a subplot of 0.2 m × 1.0 m in each plot four times a year: twice before the HW treatment (6 and 24 July 2013, 10 and 27 July 2014) and twice after HW treatment (15 and 30 August 2013, 16 and 30 August 2014). The number of tillers ($N_t$), nutritive plant height ($H_p$), plant species cover ($C_p$) and crown width ($C_w$) were measured. The percent cover of each plant species was estimated by a 1 × 1 m frame with 100 equally distributed cells (10 cm × 10 cm) held above the canopy. Crown width was calculated as the product of the measured north-south and east-west trending lengths. The species importance value (IV) was calculated based on the relative height ($H_r$, the ratio of a single species height to all species height), relative cover ($C_r$, the ratio of a single species coverage to all species coverage) and relative abundance ($A_r$, the ratio of a single species abundance to all species abundance) according to Peet (1974), Curtis and McIntosh (1951):

\[
IV = \frac{H_r + C_r + A_r}{3}
\]

Various indices of vegetation diversity were calculated for the plant community in each treatment. The Margalef richness index ($D_{ma}$), Simpson diversity index ($D$) and Pielou’s evenness index ($J$) were calculated using Equations 2-4.

Margalef richness index:

\[
D_{ma} = \frac{(S - 1)}{\ln (N)}
\]

Simpson diversity index:
\[ D = 1 - \sum p_i^2 \]  

Pielou’s evenness index:

\[ J = \left( -\sum p_i \ln(p_i) \right) / \ln S \]

where \( S \) represents the number of species; \( p_i = n_i / N \) indicates the relative number of species \( i \); \( n_i \) represents the individual number of species \( i \); and \( N \) represents the total individual number of all species in the community.

**Phenology**

At the beginning of the growing season, we tagged five mature individuals of *Stipa* and three mature individuals of *Melilotoides* and *Potentilla* in each plot as soon as any of the species had produced obvious buds, and we then recorded the timing and duration of the flowering and fruiting of the three studied species (*Stipa, Melilotoides, and Potentilla*) from early May to early September. The changes in plant reproductive phenology over time followed a logistic growth curve (Sadras, Bange, & Milroy, 1997), and the reproductive phenology of both the graminoid (grass) and non-graminoid (forb and semi-shrub) species was divided into several stages (Dunne, Harte, & Taylor, 2003; Sherry et al., 2007). We divided the phenology of the grasses into the following stages: plants with flower stalks (stage 0), most culms in the boot visible (stage 0.5), spikelets present (stage 2), dried and broken off anthers and styles (seed development; stage 3), and disarticulated seeds (stage 4). For the forbs and semi shrubs, plant phenology was divided into 6 stages: non-flowering plant (stage 0), unopened buds (stage 1), open flowers (stage 2), old
flowers or post-anthesis (stage 3), initiated fruit (stage 4), expanding fruit (stage 5) and dehisced fruit (stage 6). In addition, we continuously monitored the current stages of all individuals every 3-4 days. If a plant had more than one flower, we recorded the current stage for each flower and then calculated an average score for each plant as the mean stage number across all flowers. Based on these values, we obtained a single ‘phenological score’ for the individuals in each plot and recorded the observation date.

Based on the phenological observations, we fitted the observed scores to the Richards growth equation (Richards, 1959), which is thought to be very flexible in describing different shapes of growth data distributions and has been successfully applied in the study of plant phenology in the Inner Mongolian steppe of North China (Xia & Wan, 2013). We applied the Richards growth equation with the contraction-expansion algorithm (Gu, Hui, & Bian, 1998) to fit the phenological scores ($Y$) of each species against the Julian day ($X$) for each plot. The equation is as follows:

$$Y = \frac{K}{(1 + a \times e^{-b \times X})^m}$$

(5)

where $Y$ is the phenological stage score (0–6 for forbs and 0–4 for grasses), $K$ is the maximum growth (here the final phenological stage, 6 for forbs and 4 for grasses), $a$ is an empirical coefficient representing the first observation date, $b$ is the growth rate (change in phenological stage per day) over time $X$ (days since the first observation date), and $m$ is a parameter reflecting the shape of the curve. The timing of each phenological event is calculated as follows:
\[ X = -\frac{1}{b} \ln \left( \frac{m}{a} \sqrt{\frac{K}{Y} - 1} \right) \]  

(6)

We calculated the timing and duration of reproduction using the following steps. First, the sequences of calculated phenological scores from a species in each plot for each season were fitted to Eq. 5. The best parameter estimates of \( K \), \( a \), \( b \), \( X \), and \( m \) were obtained for individuals by plot and by year (\( r^2 > 0.95 \), \( P < 0.05 \)). Second, based on Eq. 6, the flowering time was calculated as \( Y = 2 \) for all species and the fruiting time was calculated as \( Y = 2.5 \) and \( Y = 3.5 \) for grasses and forbs/semishrubs, respectively. The phenological duration was calculated as \( X \) between stages 0.5 (\( Y = 0.5 \)) and 3 (\( Y = 3 \)) for grasses and between stages 1 (\( Y = 1 \)) and 5 (\( Y = 5 \)) for forbs/semishrubs (Gu et al., 1998). Finally, the calculated flowering and fruiting times as well as the phenological duration were used in further statistical analyses for treatment effects. The scoring of phenology was performed following the modified method described by Dunne, Harte, and Taylor (2003), Sherry et al. (2007), and Xia and Wan (2013).

Data analysis

A repeated-measures ANOVA was applied to examine the effects of HWs, mowing and their possible interactions on \( N_s \), \( C_p \), \( N_t \), \( H_p \), \( W_c \) and IV value of Stipa, Melilotoides and Potentilla in 2013 and 2014 together. Two-way ANOVA was used to examine the effects of HWs, mowing and interactions on flowering time, fruiting time and phenology duration of 3 species in 2013. Subsequently, the two-way ANOVAs were used again to examine the treatment effects on community structure (richness, diversity and evenness index) and biomass (aboveground and...
litter) separated per year (2013 and 2014), and also used to examine differences in mean IV values across both years. Finally, one-way ANOVA was used to examine the differences of \( N_s \) and \( C_p \) among the six treatments in 2013 (15 August) and 2014 (16 August) \( (P<0.05, \text{Duncan's post hoc test}) \). Multiple one-way ANOVAs were also used for \( N_i, H_p, \) and \( W_c \) (2014), the phenology of the three species (2013) and their 2-year mean IV value, and aboveground, litter biomass, and community structure (2013 and 2014). Prior to the ANOVA, all data were tested to satisfy the assumptions of normality \( (P>0.05) \) and homogeneity of variance \( (P<0.05) \). All statistical analyses were conducted using SPSS 22.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

Results

Effects of HWs and mowing on the species level: number, coverage, morphology and phenology

The daily mean air temperature during the growing season (May-September) in 2012, 2013 and 2014 was 15.7 °C, 16.6 °C and 15.6 °C, respectively, while the total precipitation over the growing season was 307 mm, 418 mm and 286 mm, respectively. The mowing treatment was conducted at the end of August in 2012; thus, our analysis began in 2013. \textit{Stipa}, \textit{Melilotoides}, and \textit{Potentilla} responded differently to the HWs, mowing treatments, and their interaction effects (Table 1). The effects of HWs and mowing on \textit{Stipa} were most evident through changes in \( H_p, C_p \) and \( N_s \). HWs resulted in a significant increase in the \( N_s \) of \textit{Stipa} in the heavily mown plots in 2013 but not in the unmown plots, and this effect did not persist into 2014 (Fig. 1c, d). HWs
lowered the $C_p$ in both the unmown and heavily mown plots in both 2013 and 2014 (Fig. 1a, b) and restricted the growth ($H_p$) of *Stipa* (Fig. 2a). Compared with the HWs, mowing significantly decreased the $N_s$, $C_p$, and $H_p$ of *Stipa* and a significant D×HW×M interaction was observed for $H_p$ ($P=0.018$, Table 1). Based on the comparison of the C and HM$_2$ treatments, HWs and mowing significantly increased the $N_t$ of *Stipa* in 2013 ($P<0.05$) but not in 2014 ($P>0.05$, Fig. 1c, d), significantly decreased the $H_p$ and $C_w$ ($P<0.05$), and did not significantly affect the $N_t$ ($P>0.05$, Fig. 2a).

The response of *Melilotoides* to the HW and mowing treatments was characterized by significant changes in $C_w$ and $H_p$ (Fig. 2b). HWs, mowing, and their combination had significant effects on $C_w$, while $H_p$ was significantly affected by mowing and the HW×M interaction (Table 1). For the $N_s$ and $C_p$ of *Melilotoides*, the only significant difference over the two years was in terms of the $N_s$ in 2014, when it was higher in the light mowing treatment (NM$_1$) compared to the control (C) (Fig. 1e-h). While HWs had no significant effect on *Potentilla*, mowing alone had significant effects on $C_p$ ($P=0.038$, Table 1). No significant effects of the treatments on the $N_s$ and $C_p$ of *Potentilla* were observed at the end of the experiment (Fig. 1i-l). However, light mowing increased the $H_p$ of *Potentilla*, while heavy mowing had the opposite effect ($P>0.05$, Fig. 2c).

HWs significantly affected the timing of the flowering and fruiting of *Stipa*, while mowing led to significant changes in all phenological characteristics (Table 2). Specifically, HWs advanced the timing of flowering and fruiting by approximately 2 days (unmown plots), and the interactive
effect with mowing delayed these phenological stages by ~3 days (light and heavy mowing plots) (Table 3). Interestingly, HWs had no significant effect on the phenology of Melilotoides, while mowing significantly affected the timing and duration of flowering and fruiting (Table 2). In general, HWs extended the phenological durations of the different stages under all mowing levels (Table 3), with the changes ranging from no significant effect of HWs in the unmown and lightly mown plots to significant delays in the heavily mown plots (5-6 days). Unlike Stipa and Melilotoides, HWs and mowing did not independently affect the phenology of Potentilla, although their interaction significantly affected the timing of duration and fruiting (Table 2). Of the 3 species, the phenology of Potentilla appeared to be the most sensitive to the combination of HWs and mowing. In the heavily mown plots, HWs delayed fruiting by 7 days and increased the phenological duration by 14 days (Table 3). Overall, the phenological duration of Stipa and Melilotoides and the flowering time of Potentilla seemed stable under the main effect of HW or mowing. However, HWs delayed the flowering time of all species and showed an interactive effect with mowing (Table 3).

Effects of HWs and mowing on the community level: IV, diversity and functional group biomass

The time series of IV values for the three species over the 2013-2014 growing seasons provided direct evidence of both instantaneous and delayed responses to the HW treatments under the different mowing conditions (Table 1). Generally, Stipa was confirmed to be the dominant species in the grassland and had a mean IV of 47.90 across all treatments in 2013 and 2014,
whereas *Melilotoides* and *Potentilla* were co-dominants, with mean IV values of 9.26 and 4.34, respectively (Fig. 3). From a long-term perspective (2 years mean IV value), mowing significantly affected *Stipa* \( P = 0.006 \) and *Potentilla* \( P = 0.029 \), but there was no significant effect of HWs and their interactions (Table 4), and none of these effects changed the dominance ranking of the species (Fig. 3). We noticed that the IV of *Stipa* began to decrease in the unmown plots after the first HW event in 2013 and continued to decline in 2014 (Fig. 4a), this phenomenon was more obvious in the heavy mowing treatment (Fig. 4c). For the mown treatments, the IV values of *Stipa* in 2013 were nearly identical in the plots with or without HWs, whereas in 2014, the IV values were higher under the HW treatments. On average, HWs significantly decreased the mean IV of *Stipa* in the unmown plots, while mowing significantly increased the mean IV of *Stipa* (Fig. 3a). In contrast, the mean IV values for *Melilotoides* increased after the first HW events and continued to increase in 2014 (Fig. 4d). Light mowing (NM\(_7\)) resulted in a decreased IV for *Melilotoides* in both 2013 and 2014, while heavy mowing had no effect in either year (NM\(_3\), Fig. 4e, f). In conclusion, HWs caused a significant increase in the IV of *Melilotoides* in the unmown plots, but a significant decrease in the lightly mown plots (comparison of NM\(_7\) and HM\(_7\)), and had no significant effects in the heavily mown plots (Fig. 3b). For *Potentilla*, HWs had nonsignificant effects on the IV values, but mowing decline its IV since the first treatment (Fig. 4h, i), which caused a significant decrease in the mean IV (Fig. 3c).

The variation of species IV actually indicated changes in community structure, with mowing causing significant effects on the community diversity index and evenness index, and HWs
having interactive effects with mowing on evenness (Table 5). Under the combination of HWs and heavy mowing (HM<sub>2</sub> plots), the community diversity and evenness indices significantly decreased in both 2013 and 2014 while the richness index values presented nonsignificant decreases (Table 6). The community richness in the control plots in 2013 was identical to that in 2014 (2.29 vs 2.25), indicating stable conditions throughout the study period, which is inconsistent with the richness in the HM<sub>2</sub> plots, which decreased by 14% between 2013 (2.16) and 2014 (1.86).

Mowing led to a significant decrease in the aboveground and litter biomass in both 2013 and 2014 (Fig. 5). HWs accelerated the accumulation of litter biomass in 2013, although the effect did not last into 2014 (Fig. 5c, d), and HWs did not have a significant effect on aboveground biomass in either year (Table 5). Of the four plant functional groups, PB and PF were the main components of the ecosystem biomass and composed ~90% of the aboveground biomass (Fig. 5a, b). Compared to the unmown plots, heavy mowing decreased the percentage of PF in the aboveground biomass (44.5% to 31.5% in 2014). Moreover, the effects of HWs on the biomass composition were affected by the mowing level. In 2013 and 2014 combined, HWs alone increased the PF percentage in unmown plots from 44.9% (C) to 60.6% (HW) and from 47.3% to 54.1% under light mowing (NM<sub>7</sub>), but no significant change was observed in the heavy mowing treatments (38.8% in NM<sub>2</sub> and 38.0% in HM<sub>2</sub>).

**Conceptual understanding of HW and mowing effects**

Based on our results, we developed a conceptual framework to explain how HWs and mowing
affect ecosystems from the cellular to the ecosystem level (Fig. 6). We considered three periods related to HWs, namely, rapid effects (effects during the HW period), post effects (effects after the HW period in the same year) and legacy effects (effects after the HW period in the following years) (Qu et al., 2018). The rapid effects were most evident on the cellular and plant levels, including changes in photosynthesis and morphology. The impacts on these levels and processes then fed forward to the community, where responses were observed mostly as post and legacy effects of HW and mowing. Prior studies have shown that HWs will lead to a less efficient photosynthetic system, which will further result in the lower availability of nutrients and carbon starvation and the lowered accumulation of nutrients and carbon. HWs are normally accompanied by drought, which will lead to hydraulic failure. Mowing then directly removes part of the plant, causing mechanical damage; moreover, most plant reproductive organs are located in the top portion of the plant, which is the most likely part to be cut off during mowing. Moreover, the interaction between HWs and mowing makes these effects more significant; in association with the mortality of some plants, the community structure is greatly changed. This altered community structure is usually characterized by low water use efficiency (WUE), changes to carbon fluxes, etc., which are considered to be the effects of HWs and mowing on carbon and water fluxes and other processes at the ecosystem level.

Discussion

Species-specific responses of plant number, coverage and morphology to HWs and mowing
Because individual plants represent the basic units of a grassland community, we first focused on the effects of HWs on plant characteristics, such as seedling abundance, cover, and morphology. Here, the three main local species (*Stipa, Melilotoides,* and *Potentilla*) responded differently to the HW and mowing treatments, suggesting that they exhibit different species-specific adaptive strategies to address climate extremes and grazing.

In general, HWs caused a reduction in the density of *Stipa* in terms of the number of both clusters and individuals (as indicated by the decrease in IV). In contrast, mowing represented mechanical damage to the plants and lowered plant height but enhanced the dominance of *Stipa* by fragmenting the clusters while increasing its IV. The strategy used by *Stipa* to cope with HWs involves losing the outer tiller layer to protect the internal tiller. Although we did not formally quantify the litter fractions, most of the increase in litter biomass seemed to arise from the PB group, especially the withered biomass of *Stipa*. The strategy of shedding the outer tiller layer directly decreases the energy loads and moisture consumption of the inner (green) tissues, while the thicker litter layer does the same for the soil, which in turn stimulates decomposition and mineralization (Meentemeyer, 1978). These changes in *Stipa* appear to have developed as necessary adaptive strategies to offset the impacts of HWs (Quesada, Vautard, & Yiou, 2012).

Furthermore, because *Stipa* is the dominant species, these changes are also important in terms of the adaptation of the community to HW stress (Zhao et al., 2016). Compared to other species, *Stipa* was the most resistant to mowing, which was likely because mowing has historically been the major land-use activity in this grassland (Niu, Sherry, Zhou, & Luo, 2013; Shao et al., 2016).
As mowing directly removes the green parts of plants from the ecosystem, ecological spatial niches are created that *Stipa* can occupy (Belsky, Carson, Jensen, & Fox, 1993). When mowing and HWs occurred simultaneously, the *Stipa* plants decreased in size. However, more *Stipa* clusters were found and less litter biomass was observed. These effects were observed only in the first year, which hints at resource exhaustion in the following years and suggests that *Stipa* exhibits self-survival rather than ecosystem facilitation because it is the dominant species under the interactive effects of HW and mowing.

*Melilotoides* appeared to tolerate both HW and mowing stress, thus maintaining its initial importance throughout the experiment under both single-factor treatments. Previous studies on its morphology and anatomy showed that *Melilotoides* has structures that are suitable for resisting drought stress (Li et al., 2012) and important in the avoidance of the worst heat stress effects (De Boeck, Dreesen, Janssens, & Nijs, 2011). The procumbent form of *Melilotoides* in our steppe ecosystem has been shown to be more drought resistant than other forms (Li, Shi, Li, & Liu, 2010; Shi, Guo, & Li, 2005) due to its small celadon leaves, large stomatal density, small cell size, compact palisade tissue, hairy epidermal cells, and thick layer of cutin in the leaves (Shi et al., 2005), which are associated with high water retention capacity, photosynthetic rate and water use efficiency. In addition to its high drought resistance, *Melilotoides* is a nitrogen-fixing species (Hoekstra et al., 2014; Isbell et al., 2015) and can enable rapid ecosystem recovery after HW stress through its fertilization effects (Elst et al., 2017; Kreyling et al., 2017).

It has been reported that *Melilotoides* is resistant to mowing and that light mowing promotes the
development of the species (Bouton & Gates, 2003); however, the significant decrease in its IV (Fig. 3b) in the combined treatment indicates that Melilotoides is not well adapted to the interactive effects of HW and mowing. This finding most likely occurred because the stem of Melilotoides is strong and its leaves mostly occur on the upper ends of branches; thus, the stem is difficult to repair after mowing. The repair process is further hampered by the lack of leaves and decreased photosynthetic rate.

Potentilla has thick, sinuate, anticlinal walls on its leaf cells, which are coupled to nearby epidermal cells to enhance its resistance to drought, thus supporting our finding that HWs did not significantly affect Potentilla. However, Potentilla was less tolerant to mowing and appeared to adopt a strategy of rapid reproductive phenology and increased seed production to adapt to a harsh environment (Stinson, 2004). Evidence for this strategy was observed through the increased seedling abundance in the HM2 plots, which helped maintain the IV of Potentilla under the HW and mowing conditions in 2013 (Fig. 3c). However, the lower abundance of seedlings in the same plots in 2014 (Fig. 1l) indicated that this species was unable to maintain the production of more seeds, which was likely because of a nutrient shortage and decreased photosynthesis caused by continuous HWs and the physical damage resulting from mowing.

HWs and mowing prolong plant phenology

Plant phenology is one of the most effective biological indicators of climate change (Scheffers et al., 2016) because plants often adjust their phenology according to the weather, including
In our study, HWs advanced both flowering and fruiting of the three focal species. We attribute this result to the increased litter biomass in the HW plots, where the thicker litter layer may have helped accelerate the rate of heat accumulation at the beginning of the following growing season (Facelli & Pickett, 1991). This litter layer-induced warming will advance plant phenology in a manner similar to the effects of global warming (Körner & Basler, 2010; Menzel et al., 2006) while also providing a moister environment for plant growth (Kelemen, Török, Valkó, Miglécz, & Tóthmérész, 2013). This positive effect of HWs may have benefited the plants emerging in early spring the most by helping them complete their phenological cycles faster. Indeed, the fruiting time of Potentilla advanced by 3 days, and its phenological duration shortened by 8 days (Table 3). Here, mowing mostly had a negative effect on plant phenology because mowing removes the top parts of plants, which is where the reproductive parts of most plant species are abundant (Liu et al., 2017; Yang et al., 2012). When HWs and mowing occurred together, the litter layer that buffered HWs disappeared due to hay removal. Furthermore, high temperatures and drought caused by HWs can reduce plant stomatal conductance and downregulate the quantum yield of photosystem II (Wang et al., 2016). These changes will affect tissue viability by slowing the transfer of photosynthates to the ear during ovule fertilization (Suwa et al., 2010), thereby leading to lower kernel sugar content and greater kernel abortion rates and also decreasing pollen viability (Siebers et al., 2017) because plants need more time to accumulate the energy and materials necessary to regenerate their reproductive organs. Taking Potentilla as an example, the phenological duration was prolonged by nearly 14 days in
the HM2 treatment relative to NM2. Although this strategy might effectively increase plant survival under severe environmental conditions, it can also increase plant mortality (e.g., if frost occurs before *Potentilla* completes its fruiting process).

Opposite effects of HW and mowing on dominant species and significant negative effects of their interactions on community structure

HWs increased the community diversity and evenness indices, whereas mowing had the opposite effect. These changes align well with the variation in IV in the dominant plant species, *Stipa*. Specifically, HWs decreased the IV of *Stipa*, thereby creating open niches for other species and increasing the community richness, diversity and evenness. The higher species richness and diversity that resulted from the HWs in our study may protect the community from the negative impacts of other extreme events (Bartelheimer, Poschlod, & Stevens, 2016; Hoekstra et al., 2014; Isbell et al., 2015), although a reversed effect is also possible (Van Peer, Nijs, Reheul, & De Cauwer, 2004) because several factors can modulate or confound diversity-stability relationships in response to extreme events (De Boeck et al., 2018). Compared with the HWs, light mowing enhanced the dominant species (*Stipa*), which was found to be well tolerant to mowing. Moreover, a comparison of the different mowing intensities indicated that light mowing retained some of the aboveground green part of the plant, which gave the plant a chance to regenerate; thus, this treatment had an insignificant effect on community structure over the 3 years of our experiment (Table 4). Long-term studies have indicated that light mowing offers a better
opportunity for some late-growing plants to due to the empty niche caused by mowing, resulting in an increase of community diversity (Yang et al., 2012). However, heavy mowing nearly cut off all the aboveground green parts of the plant, and if this mowing occurred before certain plant species had finished their reproductive phenological development, the plant would experience a lack of nutritional reproductive capacity, meaning that the species would likely disappear in this ecosystem (Hart, 2001; Socher et al., 2012). Thus, in a short time, heavy mowing decreased the community richness, diversity and evenness (Table 4). The same trend was also detected when HWs and heavy mowing occurred at the same time. The positive effect of HWs on community structure was no longer apparent in the ecosystems most affected by mowing. Under such conditions, species with a high carbon sink strength and low tolerance (e.g., leguminous plants) may disappear, while some low-efficiency forbs will survive, thus causing a further decrease in nutrient accumulation and productivity. In sum, a spiral of reinforcing negative feedback may occur if combined disturbances continue, which will ultimately result in profound changes to the ecosystem.

Conceptual framework explains the rapid effects, post effects and legacy effects of HWs and mowing

The results of this study showed that the HWs and mowing effects on plant individual growth are just the beginning of a series of effects on the ecosystem (Fig. 6). The short-term (rapid) effects of HWs and mowing will further lead to changes in population size and community structure,
thereby leading to long-term (post and legacy) effects (Qu et al., 2018). As several prior laboratory-based studies showed, the HW effect was first noticed at the cellular level, which resulted in a decrease in photosynthetic enzyme activity and low stomatal conductance and had effects on other eco-physiological characteristics (Wang et al., 2016; Zinta et al., 2014). Recent findings have confirmed that HWs significantly alter plant photosynthesis and respiration (Qu, Chen, Bunce, Zhu, & Sicher, 2018; Rashid et al., 2018), reduce CO₂ uptake (Tatarinov et al., 2016), and lead to the redistribution of carbon and nitrogen in a plant or community (Birami et al., 2018; Giri, Heckathorn, Mishra, & Krause, 2017). Here, mowing had a similar effect on the community but directly removed plant parts (photosynthetic product) rather than reducing the accumulation rate. These were considered as rapid effects, which mainly occurred during the HW or mowing treatment and over a short period after treatment. The rapid effects, such as a decrease in plant net photosynthesis, will cause variations in plant morphology due to the lowered C accumulation (Crafts-Brandner & Salvucci, 2002; Siebers et al., 2017), whereas mowing also affects plant morphology through physical damage (Benot et al., 2014; Liu et al., 2017). Most of the variation in plant morphology due to the effects of HWs and mowing, including mechanical damage, carbon starvation and hydraulic failure, ultimately have a negative effect on plant health and growth (Li et al., 2017; Zinta et al., 2014), lead to the mortality of plants with low tolerance and have similar negative effects on plant phenology, and they eventually cause variation in the community structure (Drake et al., 2018; Elst et al., 2017). Changes of the species number were indicated that HWs and mowing will cause long-term
effects on ecosystem, which was considered as post effects and legacy effects (Fig. 6). Then, the effects of HWs and mowing on the population extend to the community level as demonstrated by variations in the community richness, diversity and evenness (Table 4), and they eventually lead to variations at the ecosystem level, which include changes in the carbon and water flux, LAI (leaf area index) and biomass (Qu et al., 2016). These alterations ultimately cause changes in the plant growth environment, especially the soil environment and soil microbes (Bérard, Ben Sassi, Kaisermann, & Renault, 2015). We further assume that the post and the legacy effects will become more significant if these disturbances occur repeatedly.

In conclusion, our final hypothesis that the ecosystem presents a stress threshold for negative effects (such as those caused by HWs or mowing) seems to be valid (De Boeck et al., 2018). When a stressor does not exceed this threshold, the ecosystem can be trained to increase its tolerance to this particular stress (Gutschick & BassiriRad, 2003). This ‘training’ process can involve a gradual change in plant community structure (Elst et al., 2017). For example, the species-specific responses of Stipa, Melilotoides, and Potentilla to HWs and mowing in this study made the ecosystem less vulnerable when facing future HWs or mowing threats. However, when the stress exceeded the threshold, such as the stress caused by the interactive effect of HWs and heavy mowing, the response of the ecosystem became negative, which led to changes that included a sharp decline in plant or community characteristics. Although some urgent response strategies were observed (such as the significant increase in cluster number in Stipa or the prolonged phenological duration in Potentilla), the studied species were unable to respond
consistently when the stress continued to occur, and some strategies will increase the risk of species inheritance (Teskey et al., 2015). Furthermore, the loss of species actually indicated reduce the stability of the ecosystem due to the decrease of diversity and evenness, which will weaken the resilience of the ecosystem to future climate change or human disturbance. Therefore, we suggest that the conventional means of grassland utilization (heavy mowing) may need to be revisited, especially in the face of more extreme events, because intensive human activities will reduce the tolerance of ecosystems to climate change and ultimately cause irreparable damage to these ecosystems.

Acknowledgments

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Table 1 Outcome of the repeated-measurement ANOVA (P-values indicated) for the responses of *Stipa krylovii*, *Melilotoides ruthenica* and *Potentilla tanacetifolia* cluster or seedling number (Nₙ), cover (Cₚ), tiller number (Nₜ), nutritive plant height (Hᵢ), crown width (Cₚ) and importance value (IV) to heat waves (HWs), mowing (M), day (D, including 2 years, 4 days for each year) and their interactions. P-values of <0.05 are in bold.

<table>
<thead>
<tr>
<th>Treatment</th>
<th><em>Stipa krylovii</em></th>
<th><em>Melilotoides ruthenica</em></th>
<th><em>Potentilla tanacetifolia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nₙ</td>
<td>Cₚ</td>
<td>Nₜ</td>
</tr>
<tr>
<td>HW</td>
<td>0.989</td>
<td>0.935</td>
<td>0.176</td>
</tr>
<tr>
<td>M</td>
<td><strong>0.003</strong></td>
<td><strong>0.027</strong></td>
<td>0.496</td>
</tr>
<tr>
<td>HW×M</td>
<td>0.225</td>
<td>0.468</td>
<td>0.121</td>
</tr>
<tr>
<td>D</td>
<td>0.000</td>
<td>0.006</td>
<td><strong>0.000</strong></td>
</tr>
<tr>
<td>D×HW</td>
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<td>D×HW×M</td>
<td>0.571</td>
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Table 2: Outcome of the multivariate ANOVA analysis (P-values indicated) on the effects of heat waves (HWs), mowing (M) and their interactions on flowering time, fruiting time and phenology duration of *Stipa krylovii*, *Melilotoides ruthenica* and *Potentilla tanacetifolia* in 2013. P-values of <0.05 are in bold, and *, **, *** indicate significance at the level of P<0.05, 0.01, and 0.001, respectively.

<table>
<thead>
<tr>
<th>Treatment</th>
<th><em>Stipa krylovii</em></th>
<th><em>Melilotoides ruthenica</em></th>
<th><em>Potentilla tanacetifolia</em></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Flowering Time</td>
<td>Fruiting Time</td>
<td>Phenology duration</td>
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<tr>
<td>HW</td>
<td>0.027*</td>
<td>0.025*</td>
<td>0.725</td>
</tr>
<tr>
<td>M</td>
<td>0.007**</td>
<td>0.011*</td>
<td>0.043*</td>
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<td>HW × M</td>
<td>0.796</td>
<td>0.842</td>
<td>0.438</td>
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Table 3 Flowering time, fruiting time and phenology duration (mean±SE) of *Stipa krylovii*, *Melilotoides ruthenica* and *Potentilla tanacetifolia* for different treatments in 2013: C (control, no heat+no mowing), HW (heat+no mowing), NM7 (no heat+7 cm stubble), NM2 (no heat+2 cm stubble), HM7 (heat+7 cm stubble) and HM2 (heat+2 cm stubble). D-values indicate the difference between the heat and no-heat treatments under the background of no mowing, light mowing, and heavy mowing. Positive D-values indicate that HWs delay the phenological phase, and negative values indicate that HWs advance the phenophases. Different letters indicate significant differences among treatments (*P*<0.05, one-way ANOVA, Duncan’s post hoc test).

<table>
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<tr>
<th>Treatment</th>
<th>Flowering time (day of year)</th>
<th>D-value</th>
<th>Fruiting time (day of year)</th>
<th>D-value</th>
<th>Duration (days)</th>
<th>D-value</th>
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<td>C</td>
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<td>233.09±0.78&lt;sup&gt;bc&lt;/sup&gt;</td>
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Table 4 Outcome of the multivariate ANOVA analysis (P-values indicated) on the effects of heat waves (HWs), mowing (M) and their interactions on mean important value (IV). P-values of <0.05 are indicated in bold, and *, **, *** indicate significance at the level of P<0.05, 0.01, and 0.001, respectively.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean important value (IV)</th>
</tr>
</thead>
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<td><em>Stipa krylovii</em></td>
</tr>
<tr>
<td>HW</td>
<td>0.663</td>
</tr>
<tr>
<td>M</td>
<td><strong>0.006</strong></td>
</tr>
<tr>
<td>HW×M</td>
<td>0.264</td>
</tr>
</tbody>
</table>
Table 5 Outcome of the multivariate ANOVA analysis ($P$-values indicated) on the effects of heat waves (HWs), mowing (M) and their interactions on community structure (richness, diversity and evenness index) and biomass (aboveground and litter biomass) in 2013 and 2014. $P$-values of $<0.05$ are indicated in bold, and *, **, *** indicate significance at the level of $P<0.05$, 0.01, and 0.001, respectively.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Community structure</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Richness Index (Margalef index)</td>
<td>Diversity Index (Simpson index)</td>
</tr>
<tr>
<td>2013</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HW</td>
<td>0.713</td>
<td>0.719</td>
</tr>
<tr>
<td>M</td>
<td>0.845</td>
<td><strong>0.003</strong></td>
</tr>
<tr>
<td>HW × M</td>
<td>0.752</td>
<td>0.168</td>
</tr>
<tr>
<td>2014</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HW</td>
<td>0.871</td>
<td>0.408</td>
</tr>
<tr>
<td>M</td>
<td>0.345</td>
<td><strong>0.016</strong></td>
</tr>
<tr>
<td>HW × M</td>
<td>0.850</td>
<td>0.407</td>
</tr>
</tbody>
</table>
Table 6 Richness, diversity and evenness index values (mean ± SE) under the six experimental treatments in 2013 and 2014. Different letters indicate significant differences (*P*<0.05, one-way ANOVA, Duncan’s post hoc test) among the treatments. See Table 3 for the abbreviations.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>2013</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Richness Index (Margalef index)</td>
<td>Diversity Index (Simpson index)</td>
</tr>
<tr>
<td>C</td>
<td>2.293±0.30&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.747±0.04&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>HW</td>
<td>2.336±0.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.799±0.03&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>NM&lt;sub&gt;7&lt;/sub&gt;</td>
<td>2.198±0.34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.729±0.01&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>HM&lt;sub&gt;7&lt;/sub&gt;</td>
<td>2.471±0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.720±0.05&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
<tr>
<td>NM&lt;sub&gt;2&lt;/sub&gt;</td>
<td>2.250±0.29&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.686±0.02&lt;sup&gt;bc&lt;/sup&gt;</td>
</tr>
<tr>
<td>HM&lt;sub&gt;2&lt;/sub&gt;</td>
<td>2.157±0.07&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.615±0.02&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Figure Captions:

**Fig. 1** Heat wave and mowing effects on the number of clusters or seedlings ($N_s$) and cover ($C_p$) (mean±SE) of *Stipa krylovii* (a, b, c, d), *Melilotoides ruthenica* (e, f, g, h) and *Potentilla tanacetifolia* (i, j, k, l) in 2013 and 2014. C (control, no heat+no mowing), HW (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). The grey columns indicate the heat wave treatment, and the hatched columns indicate the mowing treatment. Different letters indicate significant differences among treatments ($P<0.05$, one-way ANOVA, Duncan’s post hoc test). Based on data of 15 August (2013) and 16 August (2014).

**Fig. 2** Morphological characteristics of *Stipa krylovii* (a), *Melilotoides ruthenica* (b) and *Potentilla tanacetifolia* (c) under different treatments based on data from 16 August 2014. Number of plant tillers ($N_t$) is plotted on the x-axis, nutritive plant height ($H_p$) is plotted on the y-axis, and the circular area indicates the plant crown width ($C_w$); the grey circles denote the heat wave treatment; the hatched circles denote the mowing treatment. See Fig. 1 for the treatment abbreviations. Different letters indicate significant differences among treatments ($P<0.05$, one-way ANOVA, Duncan’s post hoc test), with ‘abc’ representing differences in nutritive plant height, ‘ABC’ representing differences in number of tillers and ‘xyz’ representing differences in crown width.

**Fig. 3** Mean importance values (IV, mean±SE) of *Stipa krylovii* (a), *Melilotoides ruthenica* (b) and *Potentilla tanacetifolia* (c) under different treatments in 2013 and 2014. The grey columns indicate the heat wave treatment and the hatched columns indicate the mowing treatment. See Fig. 1 for the treatment abbreviations. Different letters indicate significant differences among treatments ($P<0.05$, one-way ANOVA, Duncan’s post hoc test).

**Fig. 4** Time series comparing the importance values (IV, mean±SE) of *Stipa krylovii* (a, b, c), *Melilotoides ruthenica* (d, e, f) and *Potentilla tanacetifolia* (g, h, i) in 2013 and 2014 under
different treatments. The grey arrow and HW denote the timing of the heat wave treatment; the black arrow and M indicate the timing of mowing treatment. See Fig. 1 for the abbreviations.

**Fig. 5** Aboveground biomass and litter biomass (mean±SE) of different functional groups (see appendix) under the different treatments in 2013 (a, c) and 2014 (b, d). See Fig. 1 for the treatment abbreviations. Different letters indicate significant differences in the total aboveground biomass among treatments ($P<0.05$, one-way ANOVA, Duncan’s post hoc test). Aboveground biomass was separately collected by plant functional groups, the litter biomass was not separated.

**Fig. 6** Conceptual framework of the cell-plant-community-ecosystem feedback to heat waves (HWs) and mowing (M) on the grassland ecosystem (see text). H and red letters indicate the effect of heat waves, M and blue letters indicate the effect of mowing. ‘+’ and ‘−’ indicate the respective positive or negative impacts, ‘±’ indicates the impacts were different for different plant species, and ‘?’ indicates uncertain impacts. The solid box shows the reported results with data support, the dashed box shows the results that are mentioned in prior studies but lack data support and the effect was uncertain. Solid arrows show the connection between different indications.