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Abstract

Aims

Both extreme drought and insect herbivores can suppress plant growth in grassland communities. However, most studies have examined extreme drought and insects in isolation, and there is reason to believe that insects might alter the ability of grasslands to withstand drought. Unfortunately, few studies have tested the interactive effects of extreme drought and insect herbivores in grassland communities.

Methods

Here, we tested the drought–herbivore interactions using a manipulative experiment that factorially crossed extreme drought with the exclusion of insect herbivores in a temperate semiarid grassland in Inner Mongolia.

Important Findings

Our results demonstrated that both extreme drought and insect herbivores separately decreased total plant cover. When combined, insect herbivores reduced the impact of drought on total cover by increasing the relative abundance of drought-resistant dominant species. Our results highlight that the negative effect of extreme drought on total plant cover could be alleviated by maintaining robust insect herbivore communities.

INTRODUCTION

The frequency, intensity and duration of extreme droughts are predicted to increase globally due to the altered precipitation patterns and increased temperatures (IPCC 2013; Meehl and Teng 2007). The impacts of extreme droughts on plant community have been well documented (Hoover *et al.* 2014; Mackie *et al.* 2019; Oddershede *et al.* 2019). However, extreme droughts also have significant effects on other important ecological processes, such as herbivory. Insect herbivores play essential roles in the terrestrial ecosystems (Branson and Haferkamp 2014), whose density and abundance of insect herbivores usually increased with drought (Gely *et al.* 2019; Mattson and Haack 1987). Insect herbivores can alter plants physiological traits (Tsunoda *et al.* 2018; Visakorpi *et al.* 2018), change the nutrient supply for plants (Belovsky and Slade 2000; Lemoine and Smith 2019) and alter plant community composition (Tamburini *et al.* 2018). Thus, it is likely that insect herbivores could alter the impacts of extreme drought on plant communities. However, few studies have tested the interactive effects of extreme drought and insect herbivores on plant community. In addition, grassland ecosystems occupied 40% of the terrestrial land surface, provide valuable ecosystem services (Sala *et al.* 2017), which are sensitive to precipitation changes and insect herbivores (Bai *et al.* 2004; Cease *et* *al.* 2012; La Pierre *et al.* 2015). Thus, investigating the interactive effects of extreme drought and insect herbivores in grassland ecosystems is especially important.

Insect herbivores might either strengthen or weaken the impacts of extreme drought on plant communities through a variety of direct and indirect mechanisms. Insect herbivores might strengthen the negative effects of extreme drought on plant communities through foliar damage and reduced photosynthetic performance (Tsunoda *et al.* 2018; Visakorpi *et al.* 2018). Simultaneously, water stress increases nitrogen content and reduces secondary metabolite defenses in plant leaves, thereby improving herbivore performance and stimulating herbivory (Coupe *et al.* 2009; Franzke and Reinhold 2011; Gely *et al.* 2019). However, insects could also mitigate the effects of drought by accelerating nutrient cycling rates (Belovsky and Slade 2000; Lemoine and Smith 2019; Uselman *et al.* 2011), easing the deficiency of available nutrients for plants during the drought period. In addition, insects may weaken resource competition among plants by altering plant community composition (Kim *et al.* 2013; Tamburini *et al.* 2018), which potentially allowing the plant community to cope with the deficiency of overlapping resources resulting from extreme drought. Therefore, the interactive effects of extreme drought and insect herbivores on plant community are still not clear.

Dominant species control the majority of resources and have disproportionately large impacts on ecosystem function (Avolio *et al.* 2019; Geider *et al.* 2001; Grime 1998). The impacts of insects under extreme drought on plant dominant species might be driven by the palatability of herbivores (Tamburini *et al.* 2018). For example, grasses are less prone to herbivory than other herbaceous plants (Tamburini *et al.* 2018), because grasses are defended by silica in the foliage (Loranger *et al.* 2014). In addition, the protein contents in grasses tend to be lower than other herbaceous families, which is important for insect herbivores growth and reproduction (Roeder and Behmer 2014). Thus, insect herbivores might alleviate the negative impacts of drought on dominant species through decreasing the subordinate species and reducing the resource competition of subordinate species to dominant species in grass dominated community (Kim *et al.* 2013; Tamburini *et al.* 2018). In such cases, the community would be more dominated by grasses, which were highly resistant to drought (Hoover *et al.* 2014; Mackie *et al.* 2019; Tello-Garcia *et al.* 2020). Thus, the negative impacts of extreme drought on grass dominated community should be reduced. However, the response of dominant species to the interactive effects of extreme drought and insect herbivores and their role in regulating community responses remains unknown.

In this study, we conducted a manipulative experiment to assess whether insect herbivores exacerbate or ameliorate the impacts of drought on plant communities in a semiarid grassland of Inner Mongolia, which are dominated with grasses. We hypothesized that: (i) extreme drought and insect herbivores would separately reduce plant community cover; (ii) insect herbivores would alleviate the stress resulting from extreme drought by improving the occupation of dominant species in the grassland.

MATERIALS AND METHODS

Study system

We conducted our study in a temperate semiarid grassland near the Inner Mongolia Grassland Ecosystem Research Station (43°38′ N, 116°42′ E, 1250 m a.s.l.). The study area has been fenced since 1999 to prevent grazing by large animals. Long-term (1982–2018) mean annual temperature at the site is approximately 0 °C; mean monthly temperature ranges from −21.6 °C in January to 19.0 °C in July. Long-term (1982–2018) mean annual precipitation was 304 mm, about 70% occurring during the growing season from May to August. The dominant plant species are *Leymus chinensis*, *Stipa grandis* and *Achnatherum sibiricum*, which are all grasses. The subordinate species are forbs and sedges. The dominant species cover account for 51% of the total cover (Supplementary Fig. S1).

Experimental design and data collection

In 2014, we established the extreme drought experiment, consisting of control (ambient precipitation, without shelters) and extreme drought (a 66% reduction in ambient growing season precipitation) treatments using rainout shelters. Extreme drought was defined as a small probability climate event in a region with a frequency distribution of precipitation <10% over a long-term period (IPCC 2013). At our study site, 66% reduction of precipitation in growing season resulting 50% reduction of precipitation of the whole year. The probability of occurrence is below 10% based on 33-year precipitation records in this area (Supplementary Fig. S2). Clear rainout shelter roofs were installed on plots from May to August growing season from 2015 to 2018. The experimental design was a randomized complete block design with six replicates in a relatively flat area with representative plant communities in the region. The arched rainout shelter covered an area of 36 m^2 (6 m × 6 m), the edge of the roof was 0.6 m above the ground surface to minimize temperature and humidity effects. Four sides of the shelter were kept open, allowing for near-surface air exchange. Lateral surface water flow and hydrological exchange with the surrounding soil was avoided by using metallic flashing buried 1 m depth around each rainout shelters. Experimental plots were located 2 m away from the neighboring plots and there was a buffer zone of 1 m to minimize the edge effects along the edge of each shelters.

To examine the effects of invertebrate herbivores on plant community, we imposed herbivores removal (HR) and herbivores present (HP) treatments using cage exclosures within each plot in May 2018. The exclosures were 0.5 m × 0.5 m at the base and 1 m tall. Each exclosure consisted of aluminum frame with 18 × 16 mesh and 0.3 mm wire diameter. The screening was buried to a depth of 5 cm on all sides to prevent access by invertebrates, and all invertebrates were removed from the caged vegetation at the time of construction (HR). Cages were also erected in each HP plot to mimic the effects of the cages on light and water availability but to allow access by invertebrate herbivores. The HP cages were constructed in the same manner as the exclosures, but with several large holes cut into the sides to allow access by invertebrates (La Pierre *et al.* 2015; Lemoine and Smith 2019).

We determined plant cover in each exclosure (HR and HP) at peak plant community abundance (late August) in 2018. We placed a 0.5 m × 0.5 m square quadrat with 100 equally grids above the canopy in each plot and estimated the cover of each species via visual estimate the grids each species occupied (Griffin-Nolan *et al.* 2019). The total cover of the community, dominant species and subordinate species was the sum cover of each species, dominant species and subordinate species, respectively (the information of the species is shown in Supplementary Fig. S1).

Statistical analysis

The relative cover of dominant and subordinate species was calculated by the ratio of the summed cover of dominant and subordinate species to total plant cover, respectively. The response ratio of plant cover to extreme drought was calculated as (Drought−Control)/Control×100%

Each response ratio was calculated for paired control/drought plots within each block.

Three-way analyses of variance (ANOVAs) with a blocked nested design were performed to test the main and interactive effects of block, extreme drought, insect herbivores on the cover of the community, dominant species, subordinate species, and the relative cover of dominant species, subordinate species. A general linear model (GLM) with Tukey's *post hoc* test was conducted to assess the significance differences among treatments. Independent samples-*T* test was used to examine the significance differences of the cover response ratios of the community, dominant species, subordinate species and each species between herbivory treatments. A multiple regression was applied to examine the relationship between the response ratio of the dominant species cover, subordinate species cover and the total cover to extreme drought. The *relaimpo* package in R was used to analyze the relative contribution of the response ratio of the dominant species cover and subordinate species cover to the total cover. Three-way ANOVAs, GLM and independent samples-*T* test were performed using SPSS 20.0 and the multiple regressions were carried out by using R 3.5.1. All plotting was conducted in Origin 2018.

RESULTS AND DISCUSSION

Extreme drought and insect herbivores separately reduce the dominant and subordinate species cover (Table 1; Fig. 1a and c), which was consistent with most previous studies of extreme drought (Liu *et al.* 2018; Zhong *et al.* 2019) and insect herbivores (Myers and Sarfraz 2017; Takahashi and Huntly 2010). However, the interactive effects of extreme drought and insect herbivores were different between dominant and subordinate species. Insect herbivores alleviated the drought impact on dominant species cover, while enhanced the drought impact on subordinate species cover (Table 1; Fig. 1). This could be explained by the fact that dominant and subordinate species belonged to different functional groups. The dominant species of our field are all grasses, while subordinate species are forbs and sedges. Grasses might be less prone to herbivory than other herbaceous families under drought (Tamburini *et al.* 2018), likely because they are defended by silica (Loranger *et al.* 2014) and possess lower protein content than other plant families (Roeder and Behmer 2014). The decreasing grasses nitrogen and phosphorus content by extreme drought of our previous study (Luo *et al.* 2018) also support that extreme drought reduces the palatability of grasses. These changing of herbivores palatability under drought led to the decreasing of subordinate species occupation (Fig. 2b). The decreasing of subordinate species occupation reduced the resource competition of them to dominant species (Kim *et al.* 2013; Tamburini *et al.* 2018), and thus enhancing dominant species occupation (Fig. 2a).

Table 1: The model results for five of the plant species at the study site

Variable	**Treatment**	***L. c.***	***S. g.***	***A. s.***	***C. g.***	***P. b.***
Cover (%)	$Control_{HR}$	20.00 ± 0.68a	13.50 ± 1.26a	14.17 ± 0.87a	14.5 ± 5.38a	4.33 ± 3.16a
	$Control_{HP}$	9.83 ± 1.05c	8.50 ± 1.80b	9.67 ± 3.25ab	10.83 ± 3.02ab	3.00 ± 1.63a
	$Drought_{HR}$	7.17 ± 0.54c	3.50 ± 0.99c	2.83 ± 0.65b	4.83 ± 0.31bc	1.17 ± 0.60a

	$Drought_{HP}$	14.17 ± 1.35	6.83 ± 1.35bc	9.00 ± 2.46ab	1.00 ± 0.00c	0.67 ± 0.21a
Response ratio	HR	−0.64 ± 0.03b	−0.73 ± 0.08b	−0.80 ± 0.05b	−0.291 ± 0.05a	−0.55 ± 0.23a
	HP	0.53 ± 0.15a	0.09 ± 0.22a	0.46 ± 0.40a	−0.88 ± 0.00b	−0.86 ± 0.04a
Relative cover (%)	$Control_{HR}$	25.06 ± 1.08b	16.94 ± 1.69a	17.74 ± 1.17a	18.34 ± 6.85a	5.26 ± 3.80a
	$Control_{HP}$	19.22 ± 1.57c	16.61 ± 3.40a	19.74 ± 7.42a	20.97 ± 5.50a	6.31 ± 3.50a
	$Drought_{HR}$	29.87 ± 2.66b	13.80 ± 3.50a	11.49 ± 2.52a	19.95 ± 1.03a	5.22 ± 2.69a
	$Drought_{HP}$	41.07 ± 2.35a	20.62 ± 4.11a	24.80 ± 5.36a	2.97 ± 0.20b	2.04 ± 0.66a

Abbreviations of species name are as follows: *A. s.* = *Achnatherum sibiricum*, *C. g.* = *Chenopodium glaucum*, *L. c.* = *Leymus chinensis*, *P. b.* = *Potentilla bifurca*, *S. g.* = *Stipa grandis*. The relative cover of these 5 species was above 83%. The cover of remaining other species decreased 64% by drought ($P < 0.05$), and insect herbivores enhanced the drought impacts that their cover decreased 79% ($P < 0.05$). We did not list the covers of remaining other species separately in the table, due to their covers were too rare to analysis. Different lowercase letters indicate significant differences between treatments. Shown are means ± standard errors.

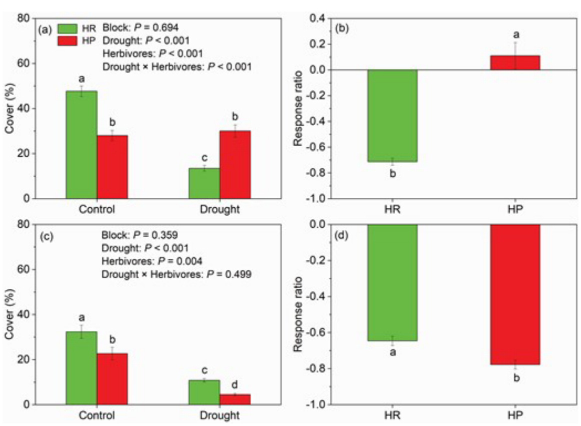

Figure 1: The response of cover of dominant and subordinate species to extreme drought and insect herbivores. Shown are the effects of drought and herbivores on dominant species cover (**a**), the response ratio of dominant species cover (**b**), and the effects of drought and herbivores on subordinate species cover (**c**), the response ratio of subordinate species cover (**d**). Different lowercase letters indicate significant differences between treatments. Error bar represents ±1 standard error.

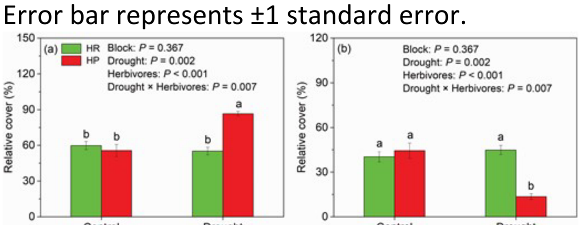

Figure 2: The effects of extreme drought and insect herbivores on dominant (**a**) and subordinate (**b**) species relative cover. Different lowercase letters indicate significant differences between treatments. Error bar represents ±1 standard error.

Extreme drought and insect herbivores separately reduce the total cover (Table 1; Fig. 3a). However, the impacts of drought on total cover depended on the presence of insect herbivores. The total cover was significantly lower in HP than that in HR with extreme drought (Fig. 3a). The response ratio of total cover to extreme drought was reduced from |−0.70| in HR to |−0.57| in HP by insect herbivores (Fig. 3b). These results indicate that insect herbivores alleviate the negative effects of extreme drought on the entire plant community. Previous studies showed that insect herbivores increased plant community photosynthetic performance by improving light penetration into partially defoliated canopies (Anten and Ackerly 2001) and increasing electron transport rates and effective quantum yields (Retuerto *et al.* 2004). In addition, insect herbivores could accelerate nutrient cycling by increasing litter decomposition rates, which might offset nutrient deficiencies during drought (Belovsky and Slade 2000; Lemoine and Smith 2019; Uselman *et al.* 2011). However, the ability of insects to alter plant community composition also mediated the drought impacts on plant community (Tamburini *et al.* 2018). In this study, insect herbivores increased occupation of dominant species (Table 1; Fig. 2a) which were highly resistant to drought (Hoover *et al.* 2014; Mackie *et al.* 2019; Tello-Garcia *et al.* 2020). Besides, we found that the response of dominant species contributed more (73.28%) to the variation of total cover than the response of subordinate species (26.69%). Thus, insect herbivores might alleviate the drought negative effects by enhancing dominant species which were highly resistant to drought.

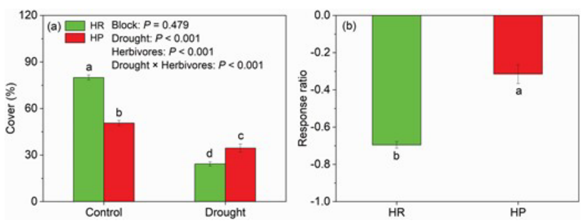

Figure 3: The response of total cover to extreme drought and insect herbivores. Shown are the effects of drought and herbivores on total plant cover (**a**), and the response ratio of total cover to drought (**b**). Different lowercase letters indicate significant differences between treatments. Error bar represents ±1 standard error.

Overall, we found that insect herbivores can alleviate negative effects of extreme drought on plant community by enhancing dominant species occupation with high drought resistance. However, our findings only established on one semiarid grassland, the effects of insect herbivores on plant community under extreme drought need more studies to test on other varied ecosystems. Despite this, our study provides new insights for the impacts of invertebrate on plant community under future climate change. These findings have important implications for the evaluation of extreme drought impacts on grasslands and their management. We propose that maintaining robust insect herbivore communities can improve the ability of plant communities to cope with extreme droughts.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Cover of all plant species in the control plots from 2015 to 2018.

Figure S2: The probability density function of long-term precipitation for the study site based on 33-year historical weather data from 1982 to 2014.

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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