Effects of fire and grazing on above-ground biomass and species diversity in recovering grasslands in northeast China

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Abstract

Questions: Fire and grazing can affect plant communities through different pathways in grasslands. However, little is known about how these disturbances affect plant communities in recovered semi-arid grasslands. Here we investigated effects of prescribed fire, sheep grazing and their interactions on above-ground biomass and species diversity in degraded semi-arid grasslands recovered from cropping agriculture.

Location: Keerqin grasslands, northeast China.

Methods: A short-term grazing and burning experiment with split-plot design was conducted, with burning applied at the main plot level and grazing applied at the subplot level. After 1 year of spring burning and 2 years of grazing by sheep, the above-ground biomass, species diversity, biomass proportion of plant functional groups and soil resource availability of the grasslands were measured and compared between treatments using a split-plot ANOVA model.

Results: One-year of spring fire significantly increased above-ground biomass, while 2 years of grazing by sheep significantly decreased it. Species diversity was reduced by grazing in the burned plots but enhanced by grazing in the unburned plots. Fire significantly increased the biomass percentage of grasses and reduced that of forbs. Fire also changed soil water content and inorganic N concentration, and grazing enhanced light intensity to the soil surface. Moreover, above-ground biomass was positively related to soil water content and inorganic N concentration under both disturbances. Species diversity had a positive linear relationship with biomass percentage of grasses and a negative relationship with biomass percentage of forbs under sheep grazing.

Conclusions: Both short-term fire and grazing are important in determining the above-ground biomass in degraded semi-arid grasslands, and their effects are opposite. Grazing coupled with fire has negative effects on species diversity. Thus, we advise that fire and grazing should be carefully applied when used in the same management regime to maintain above-ground biomass and species diversity in managing this grassland ecosystem.

KEYWORDS
burning, disturbance, grassland productivity, grazing, herbivore, plant community structure, species diversity
1 INTRODUCTION

Fire and grazing by large herbivores are two of the most common disturbances that have profound impacts on the structure and functions of grassland ecosystems (Archibald, Bond, Stock, & Fairbanks, 2005; Augustine, Brewer, Blumenthal, Derner, & von Fischer, 2014; Holdo, Holt, Coughenour, & Ritchie, 2007; Noy-Meir, 1995). Fire is considered to have played a central role in maintaining vegetation productivity in many types of grasslands (Briggs & Knapp, 1995). Grazing by large herbivores is a major shaper of grassland structure and species composition (Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Borer et al., 2014; Collins, Knapp, Briggs, Blair, & Steinauer, 1998). Effects of both disturbances on vegetation are variable depending greatly on the disturbance regimes, evolutionary history of grazing and burning, and the resistance and resilience of vegetation (Milchunas, Sala, & Lauenroth, 1988; Olff & Ritchie, 1998). Moreover, fire and grazing often simultaneously impact grasslands (Collins & Smith, 2006; Spasojevic et al., 2010), and the net outcomes of above-ground biomass and species diversity under both disturbances are more complex and less well known.

Fire directly consumes the biomass of plants, kills their roots or seeds and alters the competitive interactions between the species recovering from surviving roots or seeds, or by re-colonizing in the subsequent succession (Bond & Keeley, 2005). Fire also has indirect effects on above-ground biomass and species diversity by influencing soil resource availability. For example, the reduction of above-ground litter by burning can increase solar radiation to the soil surface and soil N availability but decrease soil moisture (Knapp & Seastedt, 1986; Vandvik, Heegaard, Mären, & Arrestad, 2005). These factors favour high plant productivity in tallgrass prairie where the precipitation is relatively abundant (600 mm annually; Briggs & Knapp, 1995). However, in semi-arid steppe, where soil moisture limits productivity, fire usually has neutral to negative effects on above-ground productivity (Augustine, Derner, & Milchunas, 2010; Scheintaub, Derner, Kelly, & Knapp, 2009). Fire also has the potential to change species composition and diversity of grassland communities. In tallgrass prairie, species diversity has been shown to decrease after frequent spring fire due to the increased abundance of dominant grasses and decreased abundance of forbs (Collins & Gibson, 1990). However, in shortgrass steppe in northern Colorado, responses of grasses and forbs to 1 or 2 years of spring fire frequency have opposite effects (Augustine et al., 2014; Scheintaub et al., 2009).

In addition to fire, grazing by large herbivores also imposes large impacts on vegetation dynamics in grasslands (Knapp et al., 1999; Pastor, Cohen, & Hobbs, 2006; Porensky, Wittman, Riginos, & Young, 2013). Different grazing intensity and evolutionary histories in grasslands have variable effects on the above-ground biomass (Milchunas & Lauenroth, 1993). Moderate grazing can increase vegetation biomass through grazing compensation (Hartnett, Hickman, & Walter, 1996; Pykala, 2004). Previous studies indicate that bison (Bison bison) grazing can reduce the abundance of the dominant grass species, increase light availability, create colonization opportunities for short and less competitive species and increase species diversity in North America (Martin & Wilsey, 2006; Whalley, 2005). For highly selective grazers like sheep, the foraging preference and nutrient requirement make the grazers select legumes and forbs rather than grasses, which will likely decrease species diversity in the grasslands where grasses are the dominant species (Huang, Wang, Wang, Li, & Alves, 2012; Huang, Wang, Wang, Zeng, & Liu, 2016; Zhang, Zhao, Li, & Zhou, 2004).

The independent effects of fire and grazing on many grassland systems have been relatively well studied (Fensham, Silcock, & Dwyer, 2011; Scheintaub et al., 2009). Results of their interactive effects on above-ground biomass and species diversity are not consistent and depend greatly on their regime and the site type (Belsky, 1992; Harrison, Inouye, & Safford, 2003; Milchunas & Lauenroth, 1993). Fire and grazing are together hypothesized to maximize diversity in tallgrass prairie as fire tends to increase N cycling, and grazing by bison or cattle reduces dominant grasses and creates opportunities for forbs to grow (Collins & Smith, 2006). Field research indicates that species diversity is highest when there are infrequent fires and bison grazing in tallgrass prairie (Collins & Calabrese, 2012), but frequent fire and grazing have neutral effects on diversity in both prairie and savanna grasslands (Koerner & Collins, 2014). However, effects of fire and grazing on semi-arid grassland communities are not fully understood. Patterns of above-ground biomass and species diversity under these two disturbances in semi-arid grassland need to be further studied.

Most grasslands have been degrading to different degrees due to inappropriate anthropogenic utilization (e.g., overgrazing), climate change and the invasion of exotic weeds (Boughton, Bohlen, & Steele, 2013; Boughton, Bohlen, & Maki, 2017). As the critical historical disturbances, fire and grazing by domestic animals are often considered as important management regimes to protect and restore native plant communities (Davies, Svejcar, & Bates, 2009). In rough fescue prairie and tallgrass prairie, the application of fire–grazing interaction can maintain native plant communities, improve productivity, promote heterogeneity and optimize plant diversity in restoring grasslands (Fuhlendorf & Engle, 2004; Otfinowski, Pinchebeck, & Sinkins, 2017). Targeted grazing that uses a specific kind of livestock at the appropriate season, duration and intensity to accomplish restoration goals has positive effects on controlling invasive weeds and reducing fire risk (Frost, Walker, Madsen, Holes, & Lelefldt, 2012). Besides, patch burning is also a common tool for maintaining grassland structure and desirable biomass in previously grazed or cultivated grasslands (Kerby, Engle, Fuhlendorf, Nofziger, & Bidwell, 2007).

Sandy grasslands in the Keerqin region in China, similar to shortgrass steppe in western America, are typical semi-arid grasslands and the vegetation productivity is mainly limited by soil moisture and N (Yu, Zeng, Jiang, & Zhao, 2009). The mean annual precipitation is 450 mm, with more than 60% occurring in June—August. Historically, there were productive natural grasslands that supported many wild herbivores such as Procapra przewalskii and Lasiopodomys brandtii, as well as some traditional local breeds of domestic sheep, goats, cattle and horses grazing freely before the early 1950s. Vegetation...
productivity and species diversity of the grasslands were seriously reduced after the 1950s because of the coarse texture and loose structure of soil, strong winds and intense anthropogenic disturbances (mainly overgrazing and cultivation; Li, Zhao, Zhang, & Shirato, 2004; Zhou, Li, Zhao, & Drake, 2008). In order to recover the degraded grasslands, a national grassland restoration policy (i.e., Grain-to-Green Program) was implemented by the Chinese central and local governments in 1999, which included protecting soil and water, restoring the grassland productivity, conserving species diversity and enhancing C sequestration and storage. Plant community cover and vegetation productivity have greatly recovered in recent decades (Zhang, Wang, Zhao, Xie, & Zhang, 2005). However, as many local people live on animal products, grazing of domestic livestock (primarily sheep and cattle) and fires, either natural by lightening or anthropogenic during the spring and autumn period, are now the most common disturbances in this area. Grazing by migratory ungulates has a long history in this ecosystem, and natural restoration policy restricts grazing to certain months within a year to protect areas from overgrazing. Long-term grazing has been proved to significantly decrease the leaf area, vegetative tillers and shoot internode length of the dominant grass, Leymus chinensis (Zhao, Chen, Han, & Lin, 2009). However, plant biomass and soil N availability have been shown to increase after moderate grazing (Liu, Nan, & Hou, 2011; Wang et al., 2010). Besides, fire events (wildfires or escaped prescribed fires) have become more frequent over the last two decades due to global warming and human activity in northeast China (Liu, Zhang, Cai, & Tong, 2010). Recent studies also indicate that opportune fire is an effective regulator of community composition and nutrient cycling. Vegetation total cover and species diversity can rapidly recover within 2 years following fire because the perennial species re-sprout from stem bases or rhizomes better than annual species (Wu, Zhao, Wang, & Shi, 2014). Although there have been many studies concerning the effects of fire or grazing on Keerqin sandy grasslands (Xu & Wan, 2008; Zhang et al., 2004; Zuo et al., 2008), little is known on how these disturbances affect above-ground biomass and plant species diversity in these recovering grasslands, and on how to use fire and grazing as management regimes to aid in the recovery of the degraded grasslands.

In this study, we aim to examine the responses of above-ground biomass and species diversity in the 14-year recovered grasslands to 1 year of spring fire and 2 years of sheep grazing. The experiment was set up in grasslands that had previously been used for soybean and corn production before the year 2000, and restored spontaneously following cessation of cropping and exclusion of large herbivores after 2000. The land-use history of the site was natural grassland (intensive grazing, before 1991) → cropland (1992-1999) → recovered grassland (grazing exclusion, after 2000). We tested three following hypotheses: (i) above-ground biomass and species diversity respond differently to either fire, grazing or their interaction; (ii) above-ground biomass will be mainly controlled by fire, as the recovered sandy grassland is limited by soil N availability and precipitation in this region; and (iii) species diversity will be determined by sheep grazing, and the abundance of grass species will increase while forb abundance will decrease.

2 | METHODS

2.1 | Study area

This study was conducted in semi-arid grasslands with flat topography at Daqinggou Ecological Station (42°58’ N, 122°21’ E, 260 m a.s.l.), Institute of Applied Ecology, Chinese Academy of Sciences in the southeastern Keerqin Sandy Lands, northeast China. Mean monthly temperatures range from −12.5°C in January to 23.8°C in July. Soils at this site are sandy and characterized by coarse texture and loose structure. The textural composition is 91% sand, 5% silt and 4% clay (Zeng, Hu, Chang, & Fan, 2009). Soil N concentrations are low in this region, and the total N concentration is 0.36 ± 0.02 g/kg (Zeng et al., 2010). The plant community is diverse (>30 species; Supporting information: Appendix S1), with forbs and grasses comprising more than 80% of the above-ground productivity. Native plant species are prevalent in this self-restoring grassland after cultivation, with exotic species only accounting in a small proportion. The grassland is dominated by the perennial grass Leymus chinensis (Trin.) (Gramineae), annual grass Setaria viridis (Gramineae) and perennial forbs, including Artemisia sieversiana (Compositae) and Artemisia scoparia (Compositae).

2.2 | Experimental design and sampling

We set up six experimental blocks (30 m × 50 m) in May 2013, and each block was fenced. A randomized complete block split-plot design was used, with two fire levels (burning and no burning) applied at the main plot level and two grazing levels (grazing and no grazing) applied at the sub-plot level. Each block contained one burned plot and one unburned plot with a size of 25 m × 20 m (almost half of each block was burned). Eight subplots (2 m × 2 m) were established within each main plot; four were grazed by sheep and the other four were fenced to exclude grazing. Four separate grazed subplots were established per burned or unburned plot because of the increased heterogeneity of vegetation with grazing (Knapp et al., 1999). Response values of plants and soil resource availability were averaged across the four subplots per plot for analyses. As a result, there were four treatments of subplots within each block: burned and grazed subplots (B+G+), burned and ungrazed subplots (B+G−), unburned and grazed subplots (B−G+) and unburned and ungrazed subplots (B−G−) (Figure 1). Numbers of subplots were uneven in one block due to an inadvertent fire, resulting in five subplots of B+G+, five subplots of B+G−, three subplots of B−G+, and three subplots of B−G−. We only performed the grazing treatment with 24 sheep from August to September 2013. Six groups of sheep with four sheep in each block were allowed to graze freely for 2 hr each day for 10 successive days during each grazing month. This grazing intensity for each month insured a moderate grazing regime, leaving about 50% above-ground biomass for the grasslands. Both grazing and burning treatments were performed in 2014. The prescribed fire treatment was performed at the beginning of April, as it is the common season when natural or anthropogenic fire occurs in this region, and the grazing experiment started in June and ended in August.
Pretreatment above-ground biomass data were collected before grazing in 2013 to confirm the lack of pretreatment differences in above-ground biomass and species diversity among the treatments of subplots within a block. After 2 years of grazing and 1 year of burning, above-ground biomass was harvested and compared among the four treatments across six blocks by clipping it to 2 cm above the ground in a 50 cm × 50 cm quadrat randomly placed in each subplot in late August 2014 (the peak period of plant growth). Biomass was sorted by species, dried for 48 hr at 65°C and weighed.

Soil samples were collected from the 0–15 cm layer in July 2014, because the surface layer of soil is likely to be sensitive to grazing and fire disturbances in a short period of time (Schrama et al., 2013). Soils were sampled using a soil core sampler (2.5 cm diameter) near quadrats where the above-ground biomass samples were collected. Five soil cores were randomly collected following removal of understorey plants and surface litter, and were thoroughly mixed to form a composite sample. Then the samples were sieved through a 2-mm mesh and stored at 4°C for analyses of soil inorganic N (NH₄⁺-N and NO₃⁻-N) concentrations. Soil inorganic N concentrations, as an index of plant available N, were determined by the methods described in Robertson et al. (1999). Briefly, a 20 g fresh soil sample was extracted with 50 ml 2 mol/L KCl solution for 60 min, and the filtered extract was analysed colorimetrically in an autoanalyzer (AutoAnalyzer III, Bran + Luebbe, DE). Subsamples from the same soil cores used for N measurements were oven-dried for 12 hr at 105°C to determine soil gravimetric water content at the time of sampling.

Light availability, which has been shown to be influenced by fire and grazing, is another important factor limiting above-ground biomass and species diversity (Martin & Wilsey, 2006). Light penetration to the soil surface (canopy transmittance) was measured as the photosynthetic photon flux density (PPFD) at ground level using a digital light meter. Measurements were taken in each subplot at the time of peak biomass (i.e., late August), between 10:00 hours and 14:00 hours. Each single measurement was averaged with five point measurements.

### 2.3 Data analyses

We used Simpson’s diversity index and species richness to express species diversity in this study. Simpson’s diversity index was calculated from the biomass of each species at the quadrat scale for each plot. Its value was quantified as 1/D, where $D = \sum \rho_i^2$ and $\rho_i$ is the biomass of species $i$, as a proportion of the total biomass. Species richness (S) was estimated by noting all species by separating and identifying the species in the biomass samples (Martin & Wilsey, 2006). We used Simpson’s diversity index because it (a) takes into...
account species dominance. An increase in the relative abundance of dominant species will lead to a reduction in Simpson’s diversity without any change in the number of species present. (b) Saturates with sample size more quickly than other diversity measures (Magurran & McGill, 2011; Wilsey, Daneshgara, & Polley, 2011).

Response values of plants and soil resource availability were analysed based on the average value of the four subplots within each main plot (average of the four subplots per treatment per plot). Differences among treatments for above-ground biomass, species diversity (Simpson’s diversity index and species richness), biomass proportions of plant functional groups (grass, forb, legume), soil inorganic N (NH₄⁺-N and NO₃⁻-N) concentrations, water content and light intensity were tested using a randomized block split-plot design mixed model ANOVA, with grazing within burning treatments and both as fixed effects, and block and block × fire as random effects. When the main effects or interactions were significant, mean separations were performed using least square means. Furthermore, we examined the relationships between the main response variables (above-ground biomass and species diversity) and resource availability (soil inorganic N concentrations, water content and light intensity) with Pearson’s correlation coefficient to see if resource availability could explain the effects of fire and grazing on above-ground biomass and diversity. Analyses were performed with PROC MIXED or CORR in SAS 9.12 statistical package (SAS Institute, Cary, NC, USA). Assumptions of normality, random effects and heteroscedasticity were tested prior to analyses. The significance level was set at $\alpha = 0.05$.

### 3 | RESULTS

#### 3.1 | Main effects on above-ground biomass and species diversity

There were no significant differences in above-ground biomass between the burned and unburned plots, and between the grazed and ungrazed subplots within main plots before burning and grazing treatments. The average above-ground biomass was $226 \pm 10 \, g/m^2$, $226 \pm 12 \, g/m^2$, $225 \pm 17 \, g/m^2$, $226 \pm 15 \, g/m^2$ in the burned and grazed, burned and ungrazed, unburned and grazed, and unburned and ungrazed subplots across blocks, respectively. After 2 years of grazing and 1 year of spring burning, fire significantly increased above-ground biomass by 22.6% while grazing significantly decreased it by 10.1% (Table 1, Figure 2). There were no effects of fire-by-grazing interactions on the above-ground biomass (Table 1). Simpson’s diversity index and species richness were both greatly affected by fire and fire-by-grazing interactions (Table 1, Figure 3). There were an average of $4.10 \pm 0.35$ species in a $0.5 \, m \times 0.5 \, m$ quadrat per plot across blocks in 2013 before grazing and

**TABLE 1** Tests of split-plot ANOVA $F$ statistics with $p$-values in parentheses on the responses of above-ground biomass, Simpson’s diversity index, species richness and biomass proportions of functional groups to fire and grazing

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$df$</th>
<th>Above-ground biomass</th>
<th>Simpson’s diversity index</th>
<th>Species richness</th>
<th>Percentage of grasses</th>
<th>Percentage of forbs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fire</td>
<td>1</td>
<td>34.87 (0.002)</td>
<td>5.30 (0.070)</td>
<td>11.88 (0.018)</td>
<td>32.50 (0.002)</td>
<td>25.97 (0.004)</td>
</tr>
<tr>
<td>Grazing</td>
<td>1</td>
<td>30.97 (&lt;0.001)</td>
<td>1.48 (0.25)</td>
<td>0.27 (0.62)</td>
<td>0.23 (0.64)</td>
<td>0.02 (0.89)</td>
</tr>
<tr>
<td>Fire × Grazing</td>
<td>1</td>
<td>0.24 (0.64)</td>
<td>8.03 (0.018)</td>
<td>24.12 (&lt;0.001)</td>
<td>0.00 (0.98)</td>
<td>0.09 (0.77)</td>
</tr>
</tbody>
</table>

Significant $p$ values ($p < 0.05$) are highlighted in bold.

**FIGURE 2** Above-ground biomass in treatment subplots in 2013 before burning and grazing experiment (a) and in 2014 after 1 year of burning and 2 years of grazing (b). Treatments are grazed (G+) and ungrazed (G-) interacting with burning (B+) and no burning (B−). Values are means (±SE) for above-ground biomass measured in all replicated blocks within each treatment. Values with different letters are significantly different ($p \leq 0.05$)
burning, with L. chinensis and S. viridis as the dominant grasses, accounting for about 70% of the above-ground biomass. Forbs were diverse, including A. scoparia, Acalypha australis, Oenothera biennis and Sonchus arvensis, but only accounted for about 20% of the above-ground biomass. Plots that were both grazed and burned had the lowest species richness and diversity. Plots that were not burned but grazed had the highest species richness. Grazing decreased Simpson's diversity index and species richness by 10.4% and 11.3%, respectively, when plant communities were burned by spring fire. Grazing increased them by 3.9% and 12.6%, respectively, when plant communities were not burned.

3.2 | Responses of plant functional groups to the main effects

The biomass percentages of grasses and forbs were only influenced by fire (Table 1, Figure 4). The biomass percentage of legumes was not affected by any of the factors, and only accounted for a small percentage of the total biomass (10.14 ± 0.81%). On average, grasses accounted for a large percentage of the above-ground biomass (53.4 ± 2.51%) in the unburned plots. Above-ground grass biomass significantly increased after fire (accounting for 68.56 ± 1.77% of the biomass). Furthermore, the biomass percentage of forbs was decreased by fire by 42.38%, and accounted for 35.66% and 20.55 ± 1.1% in the unburned and burned plots, respectively.

3.3 | Soil inorganic N concentration, water content and light availability

Resource variables differed among blocks. The variation in soil water content ranged from 4.14% to 6.80% among blocks. The variation in soil NH$_4^+$-N and NO$_3^-$-N concentrations ranged from 1.10 to 2.41 mg/kg and from 0.21 mg/kg to 0.71, respectively. These soil resource variables were significantly affected by fire (Figure 5; Supporting information: Appendix S2). Fire increased soil NO$_3^-$-N concentration by 35.1% (Figure 5b) and decreased soil NH$_4^+$-N concentration and water content by 37.14% and 12.48%, respectively (Figure 5a,c). In addition, grazing significantly increased the light intensity at the soil surface (Figure 5d). There were no effects of fire-by-grazing interaction on these response variables of resource availability.

3.4 | Relationships between above-ground biomass or Simpson's diversity index of plant communities and resource availability

Fire and grazing interacted to affect the relationships between above-ground biomass and resource availability (Supporting information: Appendix S3). Soil water content had a positive linear
relationship with above-ground biomass in all treatments. Above-ground biomass had a positive or marginally positive relationship with soil inorganic N concentration under burning, grazing or both disturbance conditions. However, there was no significantly linear relationship between biomass and soil inorganic N concentration when there was no burning and grazing disturbance. Above-ground biomass was negatively related to light intensity when the plant communities were not grazed by sheep. Simpson’s diversity index had significantly positive linear relationships with soil water or soil inorganic N when there was no burning and grazing. However, it was positively related to biomass percentage of grasses, and negatively related to biomass percentage of forbs when plant communities were grazed but not burned (treatment B−G+).

4 | DISCUSSION

Sandy grasslands in the Keerqin region in China have been degrading severely in recent decades due to irrational utilization (e.g., cultivation and overgrazing). The main goals for restoring these grasslands are to improve plant productivity, promote biodiversity and control soil erosion and desertification. Burning and grazing are two of the most common management regimes in achieving these goals in the Keerqin region. Results from our study provide the first experimental evidence that spring fire had positive while grazing had negative effects on above-ground biomass in the recovered semi-arid grasslands in the short term, which was consistent with our hypothesis (i). In addition, fire and grazing interacted to affect species diversity. In the burned areas, grazing reduced diversity; in the unburned areas, grazing increased diversity. These results differed from hypotheses (ii) and (iii). Thus, in order to maintain the above-ground biomass and species diversity in these recovered semi-arid grasslands, short-term fire and grazing by large herbivores should be carefully applied when they are used in the same management regime.

Both above-ground biomass and species diversity responded sensitively to fire and grazing in this short period time, indicating the important role of disturbances in determining ecosystem functions in the recovered sandy grassland ecosystem in Keerqin region.
Grazing by sheep in this study significantly decreased above-ground biomass, which was not consistent with most grazing experiments. Moderate grazing by large herbivores has been proved to suppress the growth of the dominant species, increase light intensity to the soil surface and stimulate compensatory growth of plant species (McNaughton, 1979; Olff & Ritchie, 1998). The declining biomass after grazing in this study may be due to two factors. First, sheep in northeast China always take a selective foraging strategy and prefer legumes and forbs to grasses (Huang et al., 2012; Wang et al., 2010). The observation of sheep grazing behaviour during the experiment also indicated that sheep spent much more time in grazing *A. scoparia*, *Lespedeza bicolor*, *Artemisia subulata* and *Melilotus officinalis*, only occasionally switching to select *L. chinensis* or *S. viridis*. Thus, sheep grazing did not stimulate the growth of less competitive species, but increased the abundance of grasses, which resulted in negative effects on above-ground biomass. Another possible reason that grazing decreased biomass was that the sampling time was close to the grazing experiment time, which did not provide enough time for growth responses of plant species.

The study also demonstrated that fire reduced species diversity and richness and grazing interacted with fire to affect them in the short term in the semi-arid grasslands. Fire can favour diversity in some grasslands where species are adapted to frequent fire (Boughton et al., 2013). But long-term fire has been shown to have negative effects on species diversity by favouring grasses and decreasing forbs (Collins & Calabrese, 2012), which is consistent with our results. Another reason why fire has negative effects on species diversity is that fire often decreases spatial and temporal heterogeneity in grasslands when burned annually (Collins & Smith, 2006). Heterogeneity is an important factor in maintaining species diversity (Harrison et al., 2003; Levins, 1979; Vandvik et al., 2005). We originally expected that introducing grazing would increase soil resource availability, enhance the heterogeneity and consequently increase species diversity due to the grazing behaviour of sheep. However, grazing alone had little impact on species diversity and the composition of plant functional groups in this study, but it interacted with fire to influence species diversity. Grazing by sheep significantly decreased Simpson’s diversity index and richness when the plant communities experienced spring burning. This may be due to the reduction of forb biomass under both disturbances. However, grazing by sheep increased species diversity when plants were not burned. Grazing induced a significant increase in light intensity reaching the soil surface, which was important for the growth of some short species. Therefore, grazing is important for maintaining species diversity in the unburned areas. Grazing behaviour by large herbivores proved to be a complicated process that has multiple influences on many aspects of ecosystem function (Bailey et al., 1996; McNaughton, 1979). Short-term experiments used in our study can predict long-term effects of fire and grazing on vegetation structures to some extent, but long-term experiments are needed to determine how herbivory and fire regulate plant community dynamics in semi-arid grasslands.

Above-ground biomass and species diversity in Keerqin sandy grassland in northeast China are mainly limited by nutrients (mainly N) and water. Keerqin sandy grasslands are located in an agro-pasture ecotone and this grassland ecosystem is very sensitive to disturbances. Our study demonstrated that above-ground biomass and species diversity of sandy grassland in semi-arid regions can be greatly influenced by 1 year of burning and 2 years of grazing by large herbivores. Fire and grazing were both important in controlling the above-ground biomass, but their effects were opposite in the short term. In addition, fire and grazing by sheep interacted to affect species diversity. Grazing can intensify and reduce diversity with fire and can increase diversity without fire. Therefore, we advise that fire and grazing should be carefully applied when used together in managing this grassland ecosystem. Both regimes can be confined to small patches, so that any temporary loss of diversity can be readily recovered from seeds or plants that persist nearby in surrounding undisturbed areas. Further research is needed for understanding the vegetation dynamics under disturbances over a long period of time.

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experiments; D.L. Zeng designed the experiments and revised the manuscript.

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REFERENCES


SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Table of plant species of Keerqin sandy grasslands in the study area.

Appendix S2 Table of tests of split-plot analysis on the responses of soil resource availability to fire and grazing.

Appendix S3 Figures of relationships between above-ground biomass and soil resource availability, and between Simpson's diversity index and biomass percentage of plant functional groups in fire and grazing treatments.

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