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Abstract Proper grazing management practices can generate corresponding compensatory effects on plant community production, which may reduce inter-annual variability of productivity in some grassland ecosystems. However, it remains unclear how grazing influences plant community attributes and the variability of standing crop. We examined the effects of sheep grazing at four stocking rate treatments [control, 0 sheep ha^{-1} $month^{-1}$; light (LG), 0.15 sheep ha^{-1} $month^{-1}$; moderate (MG), 0.30 sheep ha^{-1} $month^{-1}$; and heavy (HG), 0.45 sheep ha^{-1} $month^{-1}$] on standing crop at the community level and partitioned by species and functional groups, in the desert steppe of Inner Mongolia, China. The treatments were arranged in a completely randomized block design over a 9-year period. Standing crop was measured every August from 2004 to 2012. Peak standing crop decreased ($P < 0.05$) with increasing stocking rate; peak standing crop in the HG treatment decreased 40 % compared to the control. May–July precipitation explained at least 76 % of the variation in peak standing crop. MG and HG treatments resulted in a decrease ($P < 0.05$) in shrubs, semi-shrubs, and perennials forbs, and an increase ($P < 0.05$) in perennial bunchgrasses compared to the control. The coefficients of variation at plant functional group and species level in the LG and MG treatments were lower ($P < 0.05$) than in the control and HG treatments. Peak standing crop variability of the control and HG community were greatest, which suggested that LG and MG have greater ecosystem stability.

Keywords Sheep grazing · Peak standing crop · Plant functional group · *Stipa breviflora* · Ecosystem stability

Introduction

Ecosystem stability is defined as the capability of a natural system to return to a steady state through self-regulating mechanisms given an outside disturbance. It plays a crucial role in maintaining healthy, productive, and sustainable

Z. Wang · G. Han (✉) · M. Zhao · H. Ding · X. Zhang · X. Wang
Department of Grassland Science, College of Ecology and Environmental Science, Inner Mongolia Agricultural University, Hohhot 010018, Inner Mongolia, People's Republic of China
e-mail: grasslandkeylab@gmail.com

Z. Wang
e-mail: zhoungwuwang1979@163.com

S. Jiao
College of Resources and Environment, Shandong Agricultural University, Tai'an 271018, Shandong, People's Republic of China

E. L. Ayers
Tristar Land Technologies, Dillon, MT, USA

W. D. Willms
Lethrridge Research Center, Agriculture and Agri-Food Canada, P.O. Box 3000, Lethbridge, AB T1J 4B1, Canada

K. Havsatad
USDA-ARS Jornada Experimental Range, P.O. Box 30003, MSC 3JER, Las Cruces, NM 88003-8003, USA

L. A · Y. Liu
Inner Mongolia Academy of Agricultural and Animal Husbandry Sciences, Hohhot 010010, Inner Mongolia, People's Republic of China

grasslands and is mainly influenced by disturbance, climatic condition, and nutrient cycling (Hooper and Vitousek 1997; Tilman et al. 1997, 2006; Tilman 1999; Wardle et al. 2000). Therefore, in order to make appropriate management decisions, it is important to understand the factors influencing grassland ecosystem stability. Among the disturbance factors, grazing is important, since it can maintain grassland health and insure a flow of ecosystem goods and services.

Productivity is one of the most important indicators to quantitatively evaluate species composition changes and variability of the plant community. In recent years, the effects of species, plant functional groups (PFGs), and community on aboveground community biomass production have been used to evaluate ecosystem stability (Tilman 1999; Pfisterer and Schmid 2002; Bai et al. 2004; Wang et al. 2005). The compensatory effect between different species and different PFGs is an important factor contributing to the relationship between community composition and stability. Bai et al. (2004) concluded that compensatory effects exist at both species and PFG levels. Reductions in biomass of one species or PFG are invariably compensated by increases from other species or PFGs (Tilman 1999; Bai et al. 2004).

Livestock grazing is one of the most prevalent grassland uses in the world. Thus, grazing management has a tremendous influence on the quantity and quality of carbon cycles into grassland ecosystems by modifying species composition and functional group diversity of plant communities (Pastor and Cohen 1997). As a kind of animal disturbance, grazing is a key, natural, evolutionarily developed, and ecological process affecting grassland ecosystems, which has crucial consequences for grassland stability and ecosystem functionality (Hickman et al. 2004). Many studies have been carried out to investigate the influence of livestock grazing on the vegetation condition and changes of PFGs (Xu et al. 2005; Derner et al. 2006; Garibaldi et al. 2007; Muller et al. 2007). PFG responses to grazing are complicated. For example, the different PFGs can be either grazing-averse or grazing-tolerant (Navarro et al. 2006); and different PFGs often respond differently to grazing intensity (Bisigato and Bertiller 1997; McIntyre and Lavorel 2001).

Much progress has been made in understanding the effects of grazing on ecosystem stability. A model of resource competition, which depends on a competitive compensation (negative covariance effect) and on over yielding (ecosystem productivity increasing with diversity), provides good prediction of population and community stability (Tilman 1999; Muller et al. 2007). Other studies on the relationship between stocking rate and soil physical and chemical properties, stocking rate and plant diversity, and stocking rate and ecosystem stability were done within the last few decades (Heitschmidt et al. 1989; Taylor et al. 1997; Weikard and Hein 2011). However, it remains unclear how stocking rate influences plant relations and the variability of plant community biomass production. Therefore, we conducted a study to determine the effect of stocking rate on biomass production stability and evaluate the compensatory responses of PFGs/species to different stocking rate treatments.

The study was conducted in the desert steppe, which accounts for 30 million hectares that represents 39 % of grassland area in Inner Mongolia, China (Angerer et al. 2008, Han et al. 2008). The desert steppe provides the largest amount of resources for livestock production in Inner Mongolia (Li et al. 2008), but is considered to be the most threatened and "at risk" grassland ecosystem due to continuous degradation. Since previous related studies have primarily focused on Inner Mongolia's typical steppe, here we studied the relationship between compensatory effect and stocking rate in the desert steppe region, which has been largely ignored so far. Our results would provide important insights into the management and conservation of this grassland.

Materials and Methods

Site Description

The study site was located in the Siziwang Banner of Inner Mongolia Autonomous Region in China (41°46′43.6″N, 111°53′41.7″E; elevation 1456 m). Climatic characteristics are described as a prototypical continental climate with an average annual precipitation of 214 mm and an average annual temperature of 3.6 °C (Table 1). Maximum average monthly air temperature occurs in July (28.3 °C), while the minimum monthly temperature occurs in January (−27.6 °C). Eighty percent or more of annual precipitation is received during the growing season (May–September). There is a frost-free period of approximately 120 days. Of the 50 species found on the study site, *Stipa breviflora* Griseb., *Artemisia frigida* Willd., and *Cleistogenes songorica* (Roshev.) Ohwi were dominant species. We classified the species into five PFGs as perennial bunch grasses, perennial rhizomatous grasses, shrubs and semi-shrubs (SS), perennial forbs (PF), and annual and biennials (Bai and Chen 2000) (Table 2). Historically, the study site was grazed by sheep on a year-long basis at a relatively high stocking rate, which was estimated as 1.0 sheep equivalent ha^{-1} (Kemp et al. 2013). The grassland condition at the initial stage of our study reflected the past heavy use with a vegetative cover of 17–20 % and an average plant height of approximately 8 cm. The soil is a Kastanozem (FAO soil classification) with a sandy loam

Table 1 Average annual air temperatures and annual total precipitation over selected periods at the experimental site in the desert steppe of the Siziwang Banner, Inner Mongolia

Year	Average air temperature (°C)	May precipitation (mm)	June precipitation (mm)	July precipitation (mm)	May–July precipitation (mm)	Total precipitation (mm)
2004	4.1	72	32	51	155	253
2005	3.0	30	<1	22	52	157
2006	4.0	24	24	42	90	161
2007	4.1	13	31	37	81	162
2008	2.9	5	45	69	119	231
2009	4.8	37	20	32	89	249
2010	4.4	35	31	41	107	264
2011	3.5	8	18	56	82	153
2012	1.6	23	49	131	203	294
Average	3.6	27	28	53	108	214

texture, a pH of 8.6 and organic C concentration of 13.7 g kg^{-1} at the soil surface.

Experimental Design

The stocking rate experiment was initiated in June 2004 as a completely randomized block design with four grazing treatments and three replicates. In total, 12 plots (4.4 ha each) were fenced and stocked with sheep at rates of 0, 0.15, 0.30, and 0.45 sheep ha^{-1} month^{-1}. These rates were defined as control, light grazing (LG), moderate grazing (MG), and heavy grazing (HG), respectively. Two-year local Mongolian weathers were used for the stocking rate experiment. For each year from 2004 to 2012, grazing plots were grazed from June 1 to November 30. Sheep were not randomly reassigned each year, but were retained in their originally assigned plots during the experimental period. The sheep were kept in the experiment for 3 years, and then replaced by 2-year old animals from the same flock. However, during this period, sheep which died would be replaced by others that were of a similar age and live weight. The sheep were given access to the plots from 06:00 to 18:00 every day, and then penned over-night. The animals were supplied with water twice every day (at early morning and evening) in their pen. Salt was offered ad libitum during the entire grazing period. In winter, all sheep were maintained in confinement on a diet of hay, stover (wheat chaff), and some grains until the end of May.

Vegetation Sampling

In each plot, ten moving cages (1.5 × 1.5 m) were randomly established prior to grazing every year. The peak standing crop was sampled by individual species in August within a 1-m^2 quadrat inside each cage. Herbaceous plants were clipped to ground level, while only the current years' growth was harvested from SS. The plant material was bagged individually by species, oven-dried at 65 °C for 48 h, and then weighed. The peak standing crop was calculated as the sum of all species.

Table 2 Species components of plant functional groups at the experimental site in the desert steppe of the Siziwang Banner, Inner Mongolia

Plant functional groups	Species
SS	*Artimisia frigida* Willd., *Caragana microphylla* Lam., *Caragana stenophylla* Pojark., *Ceratoides latens* (J.F.Gmel.) Reveal et Holmgren., *Kochia prostrata* (L.) Schrad,
PB	*Cleistogenes songorica* (Roshev.) Ohwi, *Cleistogenes squarrosa* (Trin.) Keng, *Stipa breviflora* Griseb.
PR	*Agropyron michnoi* Roshev., *Carex pediform*, *Leymus chinensis* (Trin.) Tzvel.
PF	*Allium mongolicum* Regel., *Allium tenuissinum* L., *Artemisia pubescens* L. *Astragalus galactites* Pall., *Convolvulus ammanni* Desr., *Cymbaria dahurica* L., *Euphorbia humifusa* Willd.)., *Haplophyllum dauricum* (L.) Juss., *Heteropappus altaicus* (Willd.) Novopokr., *Iris tenuifolia* Pall., *Lagochilus ilicifolius* Bunge, *Linum stelleroides* Planch., *Phlomis umbrosa* Turcz., *Potentilla acaulis* L., and *Potentilla bifurca* L. var. *major* Ledeb.
AB	*Androsace umbellate* (Lour.) Merr., *Neopallasia pectinata* (Pall.) Poljak, *Salsola collina* Pall.

SS shrubs and semi-shrubs, *PB* perennial bunch grasses, *PR* perennial rhizome grasses, *PF* perennial forbs, *AB* annuals and biennials

Meteorological data were obtained from a micro weather station (GroWeather® software version 1.2, Davis instruments corporation, USA) that was at the experimental site.

Statistical Analysis

All data on plant community productivity were analyzed as a completely randomized block design according to the MIXED procedure. Analysis of variance (ANOVA) and general linear model were performed with SAS (SAS Institute 2008). The coefficient of variation (CVs) for peak standing crop across all experimental years was calculated as: (standard deviation/mean) × 100. Pearson correlations were used to analyze potential trends among PFGs (% of standing crop) (PROC CORR, SAS Institute Inc. 2008).

The significance of peak standing crop and their CVs for each stocking rate treatment was examined to determine their ecosystem stability. The residuals of all analyses were tested for normality using the UNIVARIATE procedure of SAS (SAS Institute 2008). Where necessary, the data were transformed using the logarithmic transformation. The effects of stocking rate, year and their interactions on the standing crop of species, PFGs, and CVs were examined with analysis of variance using with the MIXED model (PROC MIXED, SAS Institute Inc. 2008). Stocking rate, year, and their interactions were fixed effects, while replication and replication × stocking rate were random effects. When treatment effects were significant ($P < 0.05$), the means were separated using the least significant difference (LSD) test of the LSMEANS procedure (SAS Institute Inc. 2008).

We sorted all species according to their proportion (%) of standing crop, which defined their species rank from 1 (highest). We then selected the seven highest-ranking species to establish the relationship between species rank and their CVs for each grazing treatment. These seven species accounted for more than 90 % of the total aboveground biomass.

Results

Relationship Between Peak Standing Crop and Precipitation

During the experimental period, the precipitation amounts varied considerably from 2004 to 2012. The May–July precipitation was 4-fold higher in 2012 with 203 mm than in 2005 when it was 52 mm (Table 1). May–July precipitation explained at least 76 % of the variation in peak standing crop across different stocking rates and all years (Fig. 1). The community biomass production was significantly greater in 2004, 2008, and 2012 than in the other years when precipitation from May to July was greater than the average precipitation over the experimental period.

Effect of Stocking Rate on Peak Standing Crop

Stocking rate, year, and their interaction affected ($P < 0.05$) the 9 year average peak standing crop. Peak standing crop in the control, LG, MG, and HG treatments were $1056 > 801 > 698 > 630$ kg ha^{-1}, respectively. These represents a 40 % reduction from the control to the HG treatment (Fig. 2).

Effect of Stocking Rate and Year on Plant Functional Groups

The proportion (% of total dry matter) of perennial bunchgrasses (PB), SS, and PF were affected ($P < 0.05$) by both the stocking rate and year. PBs had the greatest proportion (39.5 %), while SS were the second greatest (36.8 %). As stocking rate increased, the proportion of PB

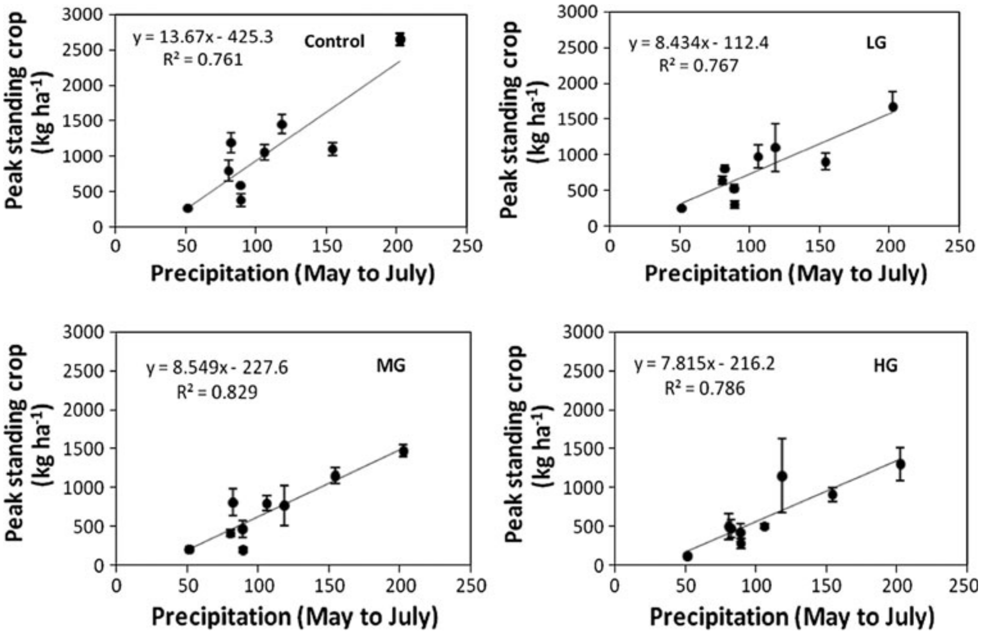

Fig. 1 Relationship between peak standing crop (kg ha^{-1}, Mean ± SE) and May–July precipitation (mm) for different stocking rate of desert steppe in Inner Mongolia

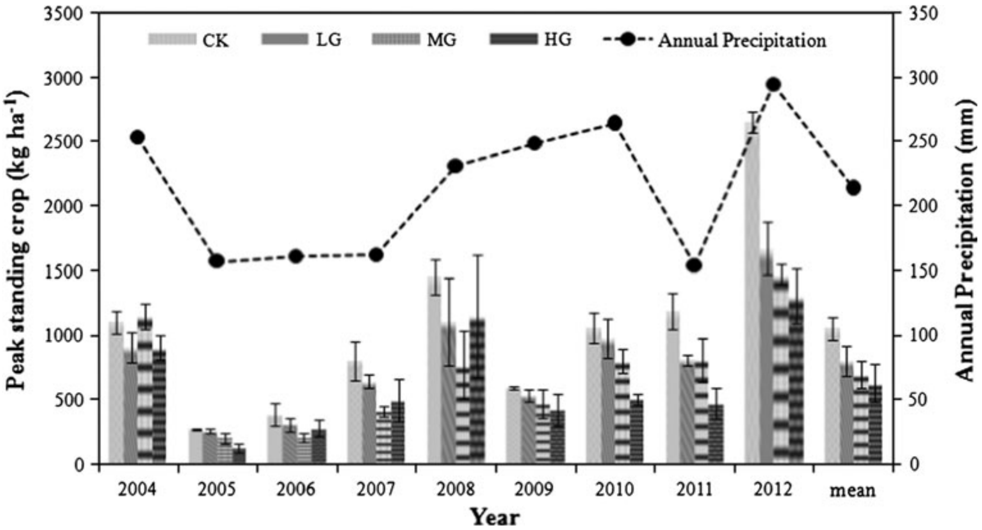

Fig. 2 The standing crop (kg ha^{-1}, mean ± SE) in different stocking rate of different year and annual precipitation (mm) of different year on the desert steppe in Inner Mongolia

Table 3 Community and the functional groups (shrubs and semi shrubs, perennial grasses, perennial rhizome grasses, perennial forbs, and annuals and biennials) standing crop and proportions in different stocking rates (SR) during the grazing period at the experimental site in the desert steppe of the Siziwang Banner, Inner Mongolia

Stocking rate	Peak standing crop						Peak standing crop proportion[b]				
	Community	SS	PB	PR	PF	AB	SS	PB	PR	PF	AB
	kg ha^{-1}						%				
Control[a]	1056.0 a[c]	440.0 a	278.1 a	3.2 a	193.2 a	141.6 a	42.3 a	29.3 c	0.3 a	17.0 a	11.1 a
LG	801.1 b	295.8 b	301.6 a	2.8 a	85.7 b	115.1 a	39.8 a	37.0 b	0.5 a	8.6 b	11.5 a
MG	698.3 bc	240.0 bc	334.1 a	3.2 a	54.2 b	66.8 a	35.2 ab	44.4 a	0.4 a	8.4 b	9.0 a
HG	630.3 c	164.5 c	282.5 a	1.4 a	55.8 b	126.0 a	30.0 b	47.4 a	0.2 a	10.3 b	10.6 a
Mean	796.4	285.1	299.1	26.6	97.2	112.4	36.8	39.5	0.3	11.1	10.6
SEm	49.2	26.7	25.1	1.1	18.2	32.3	2.6	2.6	0.1	1.1	1.8
Effects											
Stocking rate (SR)	<0.01	<0.01	0.40	0.62	<0.01	0.43	0.01	<0.01	0.52	<0.01	0.78
Year (Y)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
SR × Y	0.03	0.02	0.14	0.35	<0.01	0.10	0.32	<0.01	0.64	0.49	0.64

SS shrubs and semi-shrubs, *PB* perennial bunch grasses, *PR* perennial rhizome grasses, *PF* perennial forbs, *AB* annuals and biennials

[a] Control, LG, MG and HG represent the control, light stocking rate, moderate stocking rate and heavy stocking rate, respectively

[b] The peak standing crop proportion of the total is calculated as average of the proportions each year over study year

[c] Different letters in a column indicate significant difference in different stocking rates ($P < 0.05$)

increased ($P < 0.05$), while SS and PF decreased ($P < 0.05$) in the plant community (Table 3). Moreover, there were significant ($P < 0.05$) negative correlations between the percentage of PB and SS and PR and AB as well as a positive correlation between the percentage of PB and AB ($P < 0.05$; Table 4).

CVs at community (CVcomm), PFGs (CVPFG) and species level (CVsp)

Stocking rate had no effect ($P > 0.05$) on the community level coefficient of variation (CV_{comm}) (Table 5). An increase in the stocking rate resulted in a decrease ($P < 0.05$) the CV_{PFG} of PBs (Table 5) and no effect ($P > 0.05$) on PFs, SSs, PRs, and ABs (Table 5), although the CV_{PFG} of PFs tended ($P = 0.07$) to increase with grazing.

Stocking rate affected ($P < 0.05$) the CV_{sp} of *C. songorica* (Roshev.) Ohwi, *C. ammannii* Desr., *K. prostrata* (L.) Schrad and *Neopallasia pectinata* (Pall.) Poljak ($P < 0.05$). In general, increasing stocking rates resulted in a decrease in the CV_{sp} of *C. songorica* (Roshev.) Ohwi and, *N. pectinata* (Pall.) Poljak, and inconsistent response in *C. ammannii* Desr. and an increase in *K. prostrata* (L.) Schrad (Table 5). The CV_{sp} increased ($P < 0.05$) with

Table 4 The correlation coefficients for biomass as a proportion (%) of the total between different plant functional groups at the experimental site in the desert steppe of the Siziwang Banner, Inner Mongolia

Plant functional group[a]	SS	PB	PR	PF	AB
SS	1	−0.63632*	0.64887*	−0.1561	−0.32764
PB		1	−0.46246*	−0.24993	−0.4346*
PR				−0.27153	−0.10933
PF				1	0.1317
AB					1

SS shrubs and semi-shrubs, *PB* perennial bunch grasses, *PR* perennial rhizome grasses, *PF* perennial forbs, *AB* annuals and biennials

[a] Pearson correlation coefficient

* $P < 0.05$

Table 5 Effect of stocking rates on community, plant functional groups (PFGs) and species level coefficients of variation (CVs, %) in standing crop among years at the experimental site in the desert steppe of the Siziwang Banner, Inner Mongolia

	Control[a]	LG	MG	HG	SE	*P*
Community	77 a[b]	71 a	72 a	76 a	7	0.89
PFGs						
SS	65 a	79 a	100 a	110 a	20	0.42
PB	90 a	73 ab	63 b	61 b	7	0.03
PR	363 a	417 a	474 a	577 a	105	0.55
PF	102 a	137 a	127 a	129 a	8	0.07
AB	180 a	156 a	176 a	182 a	17	0.70
Species						
Stipa breviflora	128 a	99 a	98 a	95 a	8	0.07
Artemisia frigida	89 a	101 a	112 a	119 a	23	0.80
Cleistogenes songorica	125 a	106 ab	88 b	98 b	7	0.02
Convolvulus ammanni	776 a	507 b	786 a	768 a	50	0.03
Salsola collina	211 a	230 a	231 a	217 a	25	0.92
Neopallasia pectinata	373 a	229 b	264 b	276 b	27	0.03
Kochia prostrata	193 b	184 b	255 b	428 a	34	<0.01

SS shrubs and semi-shrubs, *PB* perennial bunch grasses, *PR* perennial rhizome grasses, *PF* perennial forbs, *AB* annuals and biennials

[a] Control, LG, MG and HG represent the control, light stocking rate, moderate stocking rate and heavy stocking rate, respectively

[b] Different letters in a row indicate significant difference in different stocking rates ($P < 0.05$)

species rank, which is based on the inverse of species biomass. The slope in LG treatment was significant lower than other treatments ($P < 0.05$) (Fig. 3).

Discussion

Standing crop and species composition on the desert steppe are influenced by stocking rate and exhibits high variability among years. This indicates that animal density is a key management variable influencing species diversity and composition (Hickman et al. 2004) and modified by annual precipitation, which is consistent with the previous findings in the Serengeti ecosystem (McNaughton 1985) and in Chihuahua Desert grasslands of New Mexico, USA (Esteban et al. 2008). While precipitation is the climatic driving force for the standing crop of Steppe communities, the greatest anthropogenic disturbance threatening the sustainability of the desert steppe is inappropriate grazing by livestock.

In general, grazing reduces perennial grasses in grasslands (McIntyre and Lavorel 2001); however, we detected opposite trends with perennial bunch grasses increasing and shrubs and semi-shrubs decreasing in response to grazing. These unexpected results may be due to the differences in plant community components and/or the grazing preference of experimental animals. The plant communities in our study plots were typical of the desert steppe of Inner Mongolia and grazed by sheep, which prefer *A. frigida* to *S. breviflora* and *C. songroca*. Similar observations were also made in subtropical pastures (McIntyre and Lavorel 2001), where perennial grasses were the more palatable and preferred species. The HG pressure on *A. frigida* resulted in a loss of vigor, competitive ability, and subsequent plant death, leading to gaps in the plant community. These gaps then provided more space and resource for other species or invaders. We found that perennial bunch grasses benefited from this compensatory effect. In addition, the compensatory effect contributed to the increased resistance to grazing and to the ecosystem stability of desert steppe.

Under our grazing treatments, the compensatory effects were consistently observed at the PFG level by the negative correlations among them. In particular, with increased stocking rate, the percentage of standing crop for perennial bunch grasses decreased and the variation in productivity increased, which is largely influenced by the presence of *C. songroca*, a C_4 plant that is highly resistant to grazing (Holechek et al. 2004). The decline of shrubs and semi-shrubs from 2004 to 2012, and the subsequent increase of the PFGs, confirm previous findings (Han 1998) and illustrate compensatory effects among functional groups.

Grazing had no effect on production stability, thus illustrating the compensatory response of the species to

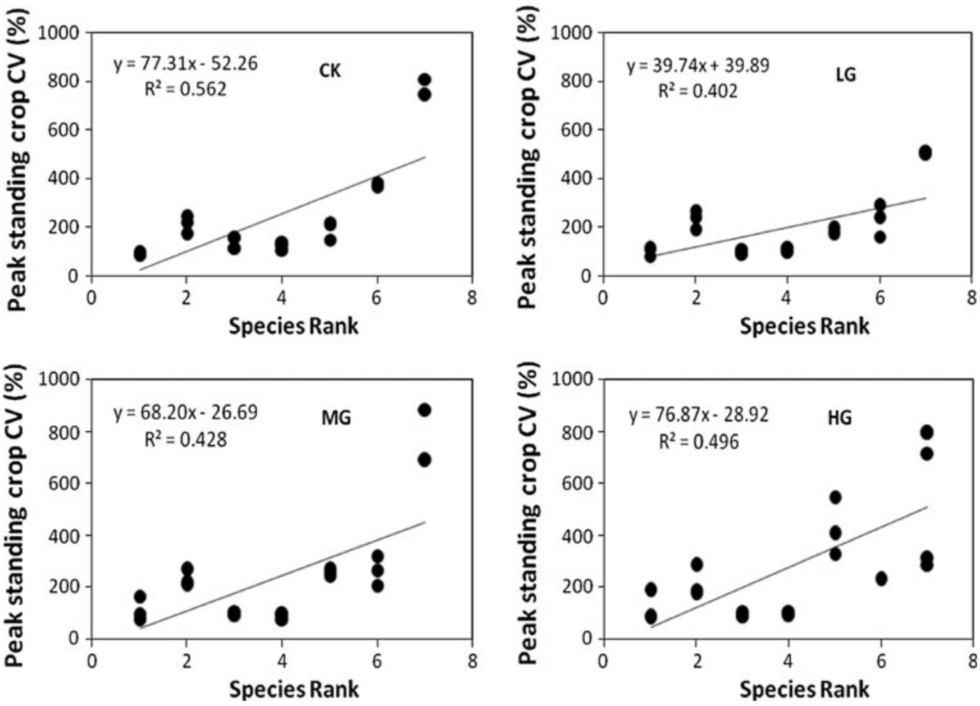

Fig. 3 The effect of species rank (1—highest; 7—lowest, according to their proportion of biomass relative to the total standing crop) on their coefficients of variation (CVs) for different stocking rates at the experimental site in the desert steppe of the Siziwang Banner, Inner Mongolia

variable stocking rates and grazing pressure on the desert steppe and its high level of resistance to grazing. However, the CVs at different PFGs and species were impacted by grazing. Most notable was the lower CV of perennial bunch grasses in the HG treatment, which supports the observation of their resistance to the grazing (Holechek et al. 2004).

The standing crop fluctuations during the nine-year study was highly responsive to fluctuations of annual precipitation so that the stocking rate in drought condition plays a secondary role (Sternberg et al. 2000). Reoccurring drought is a major challenge in the desert steppe grasslands (Wang et al. 2007) as is unpredictable precipitation timing. In our study, the precipitation for the period from May to July played a more critical role in the standing crop than total annual precipitation, which has been already reported in a previous study (Wang et al. 2011). Therefore, lower precipitation during those months would significantly decrease the standing crop as was observed in 2009 and 2010. The precipitation during the growth season was a key variable for the standing crop (Guo et al. 2006).

Ecosystem responses to spatial and temporal variations in rainfall are always greater in arid grasslands than other grasslands (Knapp et al. 2002). In our study, the proportion of annuals and biennials sharply increased in years of higher precipitation (2004, 2008 and 2012), which contributed to the greater variance in overall standing crop. Our results are thus consistent with the previous study that climatic fluctuations are related to typical steppe ecosystem stability (Bai et al. 2004).

Conclusion

The annual variation of precipitation from May to July explains most of the annual standing crop variability in desert steppe, which needs to be considered when managing grazing to achieve stability. A conservative stocking rate could achieve greater stability of livestock numbers. HG pressure can shift the composition of species and create a less stable system. However, we did not observe that because of a compensatory response among functional groups and possibly a treatment period that was too short to produce the conditions that reflect the HG pressure. From this perspective, a nine-year study is too short to elucidate the mechanisms of stocking rate, compensatory effect, and ecosystem stability. Long-term studies are required, which would not only provide more insights into plant community response and function in desert steppe, but also obtain key information for management and conservation of the grassland resource in Inner Mongolia.

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