

# Plant responses following grazing removal at different stocking rates in an Inner Mongolia grassland ecosystem

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**Abstract** Grazing removal is widely used in grassland management. Plant responses following grazing removal at different organizational levels, however, are not well understood. We examined plant responses at different stocking rates in an Inner Mongolia grassland ecosystem dominated by *Leymus chinensis* and *Stipa grandis*. Our results indicated that plant response patterns differed significantly among stocking rates, at different levels of organization, and between wet and dry years. Community aboveground net primary production (ANPP) recovered more quickly at low and moderate stocking rates than those

at high stocking rates. Response of aboveground net primary production ( $R_{ANPP}$ ) was significantly positively correlated with both individual biomass and density responses of *L. chinensis*. Overcompensation of *L. chinensis* after grazing removal contributed greatly to positive  $R_{ANPP}$  at the community level. Significant compensatory effects were found between the two dominant species and between dominant species and the remaining non-dominant species. Variation in precipitation significantly affected community ANPP, relationships between community and species responses, and compensatory effects between species. Our study suggests that periodic grazing removal is likely to be a useful method for grassland management and that a combination of species with compensatory effects can be advantageous for reseed-ing practices in grassland restoration.

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## Introduction

Grazing is one of the primary factors influencing vegetation structure and function by changing the abiotic and biotic components of grassland ecosystems (McNaughton 1985; Oesterheld and Sala 1990; Akiyama and Kawamura 2007; Han et al. 2008; Li et

al. 2008). It has been proposed that moderate grazing increases biodiversity and productivity of grassland ecosystems (McNaughton 1979), while heavy grazing severely decreases grassland biodiversity and productivity (Noy-Meir et al. 1989; Milchunas and Lauenroth 1993; Xie et al. 2007). Currently, overgrazing poses a dominant threat to the biodiversity and productivity of most grassland ecosystems, especially in arid and semi-arid regions (Akiyama and Kawamura 2007; Han et al. 2008). It is becoming increasingly urgent to establish a sustainable method to prevent grassland degradation. Because productivity of vegetation is likely to increase following grazing exclusion, grazing removal has recently been used as a common method for grassland management and restoration (Lunt et al. 2007; Wu et al. 2009).

Previous studies have demonstrated a variety of responses to grazing removal, from enhanced community productivity, vegetation cover of palatable perennial grasses, and species richness (Moretto and Distel 1997; Zhang et al. 2005; Firincioglu et al. 2007), to reduction of biodiversity (Pucheta et al. 1998; Wu et al. 2009) to no consistent patterns (Zhang et al. 2005; Fernandez-Lugo et al. 2009). These inconsistencies in community response patterns may be due to differences in grazing intensity and duration of grazing removal (Milchunas and Lauenroth 1993; Wu et al. 2009). Most existing study on community-level responses to grazing removal are based on comparisons between grazed sites and sites where grazing has been removed (Todd and Hoffman 1999, 2009; Spooner et al. 2002; Wu et al. 2009). To our knowledge, studies based on manipulated stocking rates and removal duration are still lacking (Li et al. 2008; Sasaki et al. 2009).

Many studies have documented that species-level responses can provide important insights into community-level changes in the face of environmental fluctuations and grazing disturbances (Milchunas and Lauenroth 1993; Bai et al. 2004; Adler and HilleRisLambers 2008). It has been suggested that the loss or decline in biomass production of some species after disturbance can be compensated for by increases of other species (Adler and Bradford 2002; Ives and Cardinale 2004; Jiang 2007). The compensatory effects among component species may markedly affect community responses and thus have a strong stabilizing effect on community-level processes (Patten 1975; McNaughton 1977; Gonzalez and

Loreau 2009). In the current ecosystem, compensatory effects are also found to be ubiquitous at different levels of organization (i.e., species, plant functional group, and community) in response to precipitation variability (Bai et al. 2004). However, it is less clear how plant community and component species respond to grazing removal and how community-level changes are affected by species-level responses during the recovery processes. Grazing intensity before grazing cessation and the duration of recovery may affect plant performance at both species and community levels after grazing removal. A previous study suggested that the aboveground net primary production (ANPP) was slightly decreased at low and moderate stocking rates (3 sheep / ha and 6 sheep / ha) and diminished heavily at high stocking rate (9 sheep / ha) (Schönbach et al. 2009). Another manipulated study also indicated that aboveground biomass of the dominant species, *L. chinensis*, exhibited a unimodal response pattern to clipping intensity due to the overcompensatory growth under low and moderate clipping intensities and undercompensatory growth under the high clipping intensity (Zhao et al. 2008). Based on theories of intermediate disturbance and niche complementarity, we hypothesized that, after grazing removal, (1) plant communities at low and moderate stocking rates would recover more quickly than those at high stocking rates; (2) changes in ANPP would be governed mainly by the strength of compensatory effects among the component species, with low and moderately grazed plots showing a greater capacity for overcompensation than that of heavily grazed plots.

In addition, because climate, especially precipitation, plays an important role in determining the ANPP of arid and semi-arid grassland ecosystems (Xiao et al. 1995; Bai et al. 2004; Loeser et al. 2007; Bai et al. 2008; Sasaki et al. 2009), response patterns of plant communities and species to grazing removal may also be strongly modified by precipitation regimes (Kraaij and Milton 2006; Sasaki et al. 2009). Many studies have shown that precipitation influences community- and species- level responses to grazing (Augustine and McNaughton 2006; Sasaki et al. 2009; Schönbach et al. 2009). However, it is not well understood how the responses of plant communities and species to grazing removal are influenced by variation in precipitation. A marked difference in precipitation

between 2008 and 2009 in the current system provides a good opportunity to address this issue.

Thus, the objectives of this study were to investigate the response patterns of community, species, and plant individuals to grazing removal at different stocking rates, to determine the dependence of community responses on species responses and the interactions between the component species, and to examine the role of precipitation variability in determining plant responses. Specifically, we wanted to address the following questions: (1) How do the plant communities and species that had been grazed at different stocking rates respond to grazing removal? (2) Do the component species exhibit compensatory effects in biomass production during the recovery of the plant community after grazing removal? (3) How are the response patterns at both community and species levels affected by variation in precipitation?

## Materials and methods

### Study site

This study was conducted in a typical steppe ecosystem located in the Xilin River Basin, Inner Mongolia Autonomous Region of China, 15 km south of the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences (116°42' E, 43°38' N, 1,100 m above sea level). The study area experiences a semi-arid continental climate, with a mean annual precipitation (1982–2008) of 346 mm and a mean annual temperature of 0.3°C. Precipitation mainly falls in June, July, and August, which is coincident with high temperatures. In 2008, annual precipitation at IMGERS was 362 mm, which was 4.7% higher than average, while in 2009, it was 279 mm, which was 19.3% lower than average. Precipitation during the growing season (from May to September) was 294 mm in 2008 and 183 mm in 2009. The mean annual air temperature was 1.6°C in 2008 and 1.9°C in 2009.

For perennial plants, the growing season lasts about 150 days from late April to mid-September, while annuals usually germinate in June or July (Bai et al. 2004). Based on a pilot study, there are about 40 plant species at the study site, with 12–18 plant species per 1 m<sup>2</sup>. The plant community is dominated by *Leymus chinensis* (Trin.) Tsvetlev (perennial rhizo-

matous grass) and *Stipa grandis* P. Smirn (perennial bunchgrass) (Bai et al. 2004). The main soil types of this region are calcic chernozems with high soil organic C and N contents (Steffens et al. 2008). Sheep are the dominant grazing livestock.

### Study design

Within the framework of the Sino-German project (Matter Fluxes in Grassland of Inner Mongolia as Influenced by Stocking Rate, MAGIM), we started a multi-factor grazing study with a total area of 160 ha in a typical steppe ecosystem in 2005. Prior to the start of the project, the study area was moderately grazed by sheep with an average stocking rate of 1.5 sheep/ha. In a relatively flat area with uniform vegetation, seven permanent plots were established and fenced for a gradient of stocking rates (0, 1.5, 3, 4.5, 6, 7.5 and 9 sheep/ha). To achieve a minimum of 6 sheep per plot, the plot size was 2 ha for all treatments except for the 1.5 sheep/ha treatment with a plot size of 4 ha. The sheep selected for grazing were 15-month-old, 35-kg live weight females. The grazing treatment began in 2005, and the grazing season continued from mid-June to mid-September (about 95d) each year.

To explore the responses of the plant community and species to grazing removal under different stocking rates, we used a split-plot design to evaluate the effects of the main plot stocking rate and the sub-plot grazing removal. Four of the initial seven plots, including stocking rates of 0, 3, 6, and 9 sheep/ha, representing control (no grazing), light, moderate, and heavy grazing intensity, respectively, were used in the current study. In May of each year from 2006 to 2009, three 2×3 m<sup>2</sup> grazing exclosures were randomly installed in each grazed plot prior to grazing in June. We also installed three exclosures in the control plot in 2006. In total, we installed 39 exclosures from 2006 to 2009. By increasing the number of exclosures each year, a gradient of time since grazing removal was established. The temporal dynamics of vegetation in response to disturbance (or disturbance removal) are usually examined based on differences between years after disturbance (or disturbance removal); however, the interannual variation in climate or precipitation, for example, may obscure vegetation responses to treatments. Our design ensures the comparison of response dynamics to grazing removal

based on plant responses in the same year, while filtering the effects of interannual climate variability.

### Vegetation monitoring and plant sampling

We divided each 6-m<sup>2</sup> enclosure into six 1×1 m<sup>2</sup> quadrats. A quadrat was randomly selected for vegetation investigation on 25–28 August 2008 and 2009, corresponding to the annual peak of community aboveground biomass. A different quadrat was harvested for aboveground biomass each year to avoid overlap. Richness and density (tillers of rhizomatous species, bunches of bunchgrasses, or individual forbs) of each species were recorded. Both standing live and dead biomass of each species was harvested by clipping all individuals of the same species within each quadrat to the ground level. After all standing materials were collected, we collected and placed the litter within the quadrat into a separate bag. The plant materials were oven dried at 60°C for 48 h and weighed. Community ANPP comprised three components: standing live, standing dead, and litter. At the species level, aboveground biomass was composed of two parts: standing live and standing dead. For the grazed areas outside the enclosures, we calculated ANPP based on the biomass measurement of monthly moved temporary cages (2×3 m<sup>2</sup>) (McNaughton et al. 1996). To facilitate our analysis and interpretations, all plant species were classified into three components, i.e., *L. chinensis*, *S. grandis* and the remaining species.

### Data analyses

At the plant community level, we calculated Simpson diversity index and evenness for each treatment (Simpson 1949). We estimated the response of community ANPP ( $R_{ANPP}$ ) as follows:  $R_{ANPP} = \ln(\text{ANPP}_T / \text{ANPP}_C)$ , where  $\text{ANPP}_T$  and  $\text{ANPP}_C$  are the ANPP in treatment and control plots, respectively. For the two dominant species and the remaining species as an assemblage, we calculated the density response ( $R_{SD}$ ) as  $R_{SD} = \ln(\text{SD}_T / \text{SD}_C)$  and individual (tiller/bunch) biomass response ( $R_{IB}$ ) as  $R_{IB} = \ln(\text{IB}_T / \text{IB}_C)$ , where  $\text{SD}_T$  and  $\text{IB}_T$  are the species density and individual biomass in treatment plots and  $\text{SD}_C$  and  $\text{IB}_C$  are species density and individual biomass in control plots, respectively. The density is defined as the total number of individuals of each species, and

the biomass is defined as the biomass of all tillers/bunches of each species within a 1×1 m<sup>2</sup> quadrat. To determine the dependence of the community level response on the species level response, we analyzed the relationships between  $R_{ANPP}$  and corresponding density and individual biomass responses of the component species. In addition, to examine compensatory responses we analyzed the relationships in biomass production between component species.

Analysis of variance (ANOVA) with linear mixed model was used to analyze the treatment effects for 2008 and 2009 separately. Stocking rate and grazing removal duration were considered as fixed factors, and grazing enclosures within each stocking rate was considered as a random factor. Duncan's multiple-range test was used to compare the effects of grazing removal duration at each stocking rate. Differences were considered to be significant if  $P < 0.05$ . For compensatory effects between species, we analyzed the correlations between biomass of different species by linear mixed-effect models because the biomass of different species were from the same plots and were not independent. All statistical analyses were performed using SAS version 9.1 (SAS Institute Inc., Cary, NC, USA).

## Results

### Community level responses

Following grazing removal, community ANPP differed significantly under different stocking rates (SR) and duration of grazing removal (fenced years, Y) (Table 1 and Fig. 1). At low and moderate stocking rates, only 1 year after grazing was removed, ANPP in the treatment plots reached or even exceeded the control levels. At the high stocking rate, however, ANPP recovered to the control level after 3 or 4 years. For treatments with no grazing removal, no significant difference in ANPP was found at the low stocking rate but a significantly lower ANPP was found at the moderate and high stocking rates, as compared with the control. For all treatments, ANPP was considerably lower in 2009 than in 2008.

The responses of community density to grazing removal differed significantly among stocking rates in 2008 (Table 1 and Fig. 1). At the low stocking rate, community density decreased with increasing time

**Table 1** F values and *P* values of analysis of variance for the effects of stocking rate (SR) and years of grazing removal (Y) on aboveground net primary production (ANPP), density, richness, Simpson diversity index and evenness index at community level in 2008 and 2009

Variable	Treatment	2008			2009		
		df	F	<i>P</i>	df	F	<i>P</i>
ANPP	SR	3	16.68	0.0003	3	8.65	0.0040
	Y	3	14.74	<.0001	4	10.34	<.0001
Density	SR	3	5.54	0.0035	3	1.26	0.3379
	Y	3	2.94	0.0482	4	2.94	0.0345
Richness	SR	3	1.02	0.4289	3	1.61	0.2466
	Y	3	1.83	0.1685	4	2.52	0.0590
Diversity	SR	3	0.06	0.9881	3	3.42	0.0635
	Y	3	3.41	0.0728	4	0.35	0.8388
Evenness	SR	3	0.23	0.8737	3	1.90	0.1458
	Y	3	2.52	0.0814	4	0.86	0.4968

since grazing removal. At the moderate and high stocking rates, a unimodal relationship between community density and duration of grazing removal was observed, with the peak density occurring in the first year (moderate stocking rate) or second year (high stocking rate) of grazing removal (Fig. 1). However, no significant difference in community density among treatments was found in 2009 due to the extreme drought during the growing season.

Stocking rate and duration of grazing removal had no significant effects on species richness, Simpson diversity index, or evenness in both 2008 and 2009 (Table 1).

Community ANPP response ( $R_{ANPP}$ ) followed a unimodal pattern, with the peak value occurring in the first year at the low stocking rate and in the second year at the moderate stocking rate. At the high stocking rate, in contrast,  $R_{ANPP}$  declined in the first year, increased in the second year, and reached the control level in the third and fourth years of grazing removal (Fig. 2).

### Species level responses

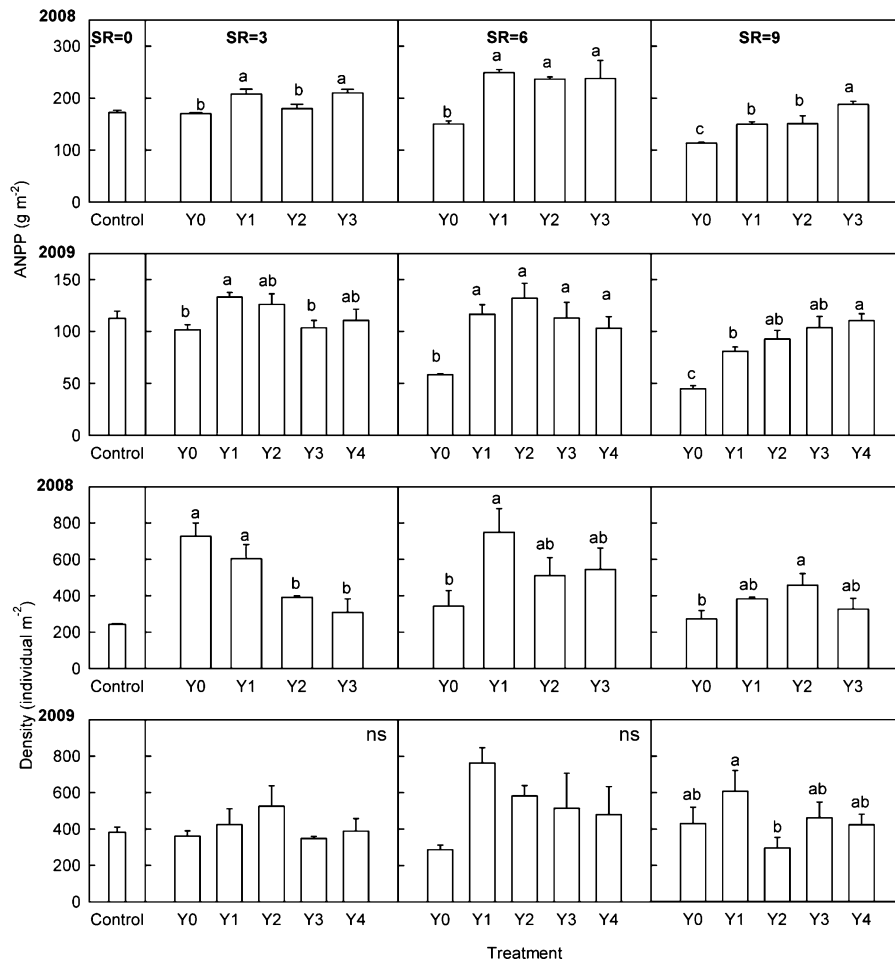
The biomass of the two dominant species and the remaining species differed significantly among grazing removal treatments and stocking rates (Fig. 3 and Table 2). In 2008, as compared with the control, the biomass of *L. chinensis* increased by 206% at the low

stocking, by 182% at the moderate stocking rate, but decreased by 7% at the high stocking rate in the first year of grazing removal. The highest aboveground biomass was observed in the first year of grazing removal at low and moderate stocking rates, but it occurred in the fourth year of grazing removal at the high stocking rate (Fig. 3). For *S. grandis*, the aboveground biomass showed a reverse pattern compared to *L. chinensis* at the low stocking rate; it decreased in the first year of grazing removal, increased in the second year, and reached the highest aboveground biomass in the third year. The recovery of *S. grandis* was slower at the moderate stocking rate, but it was much faster at the high stocking rate (Fig. 3). For the remaining species, the biomass remained largely unchanged after the removal of grazing in 2008. For all species examined, the aboveground biomass was significantly lower in 2009 than in 2008 across the grazing removal treatments.

In 2008, at the low stocking rate, the two dominant species displayed obvious compensatory effects as indicated by the opposite increases and decreases in biomass production during the recovery process after grazing removal (Fig. 3). At the moderate stocking rate, *L. chinensis* and the remaining species displayed compensatory effects, while at the high stocking rate, *S. grandis* and the remaining species showed strong compensatory effects. In 2009, compensatory effects were found between the two dominant species and between *S. grandis* and the remaining species. These compensatory interactions were further confirmed by the negative relationships between the two dominant species, and between *S. grandis* and the remaining species in biomass production in both years (Fig. 4a and b). No compensatory effects (Fig. 3) and no negatively relationship (Fig. 4c) in biomass production was found between *L. chinensis* and the remaining species in either year.

The density of the two dominant species and the remaining species differed significantly among stocking rates (Fig. 5 and Table 2). For *L. chinensis*, density decreased following grazing removal at the low stocking rate but significantly increased at the moderate and high stocking rates. For *S. grandis* and the remaining species, density differed markedly between different stocking rates and between years.

The component species also exhibited compensatory effects in density after grazing removal, espe-



**Fig. 1** Effects of years of grazing removal on community aboveground net primary production (ANPP) and density under low (SR=3), moderate (SR=6) and high (SR=9) stocking rates in 2008 and 2009. ANPP and density for each treatment were the average of three replicates (error bars indicate SE). Bars followed by the same letter are not significantly different

according to Duncan's multiple range tests, and ns indicates non-significant difference at  $P=0.05$ . Y0 = continuously grazed since 2005; Y1=the first year of grazing removal; Y2=the second year of grazing removal; Y3 = the third year of grazing removal; Y4 = the fourth year of grazing removal

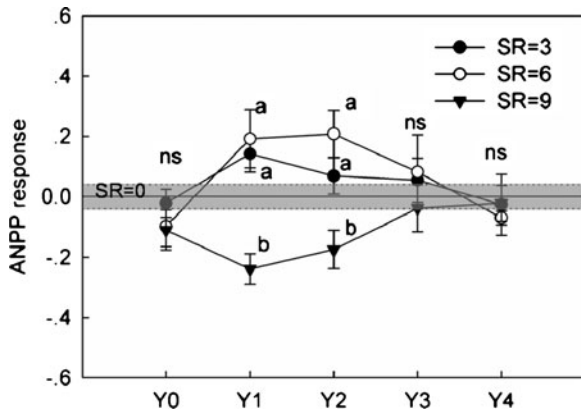
cially at the high stocking rate (Fig. 5). The compensatory effects were observed between the two dominant species and between *S. grandis* and the remaining species. However, no compensatory effect in density was found between *L. chinensis* and the remaining species.

#### Individual level responses

Compared with the control, the individual biomass of *L. chinensis* was significantly lower in grazed plots and increased after grazing removal in both years, except in the low stocking rate treatments in 2009

(Fig. 6). However, the individual biomass of *L. chinensis* following grazing removal differed among stocking rates. At low and moderate stocking rates, it reached the control level after the first year of grazing removal. At the high stocking rate, in contrast, recovery generally occurred after 2-3 years of grazing removal (Fig. 6).

In 2008, the individual biomass of *S. grandis* was significantly reduced by grazing but was significantly improved by grazing removal. In 2009, no significant difference in individual biomass of *S. grandis* was found between the grazed and grazing removal plots at low and moderate stocking rates. At the high



**Fig. 2** Response of aboveground net primary production ( $R_{ANPP}$ ) to years of grazing removal under low, moderate and high stocking rates in 2008 and 2009.  $R_{ANPP}$  for each treatment was the average of three replicates (*error bars* indicate *SE*). Bars followed by the same letter are not significantly different according to Duncan’s multiple range tests, and ns indicates non-significant difference at  $P=0.05$ . The shaded strip indicates the standard error of the control. All symbols are derived as from Fig. 1

stocking rate, the individual biomass of *S. grandis* increased significantly with increasing time of grazing removal, and the highest individual biomass occurred at the third year of grazing removal (Fig. 6).

**Table 2** F values and P values of analysis of variance for the effects of stocking rate (SR) and years of grazing removal (Y) on biomass and density of *L. chinensis*, *S. grandis*, and the remaining species, and individual biomass of *L. chinensis* and *S. grandis* in 2008 and 2009

Variable	Treatment	2008			2009		
		df	F	P	df	F	P
Biomass of <i>L.chinensis</i>	SR	3	11.61	<.0001	3	2.16	0.1549
	Y	3	6.77	0.0012	4	0.68	0.6089
Biomass of <i>S.grandis</i>	SR	3	2.88	0.0512	3	1.41	0.2994
	Y	3	1.33	0.2822	4	0.91	0.4672
Biomass of the remaining species	SR	3	4.50	0.0096	3	1.03	0.3883
	Y	3	1.70	0.1867	4	2.77	0.0399
Density of <i>L.chinensis</i>	SR	3	6.04	0.0022	3	0.13	0.9406
	Y	3	2.48	0.0789	4	3.09	0.0284
Density of <i>S.grandis</i>	SR	3	5.43	0.0039	3	1.94	0.1909
	Y	3	1.74	0.1789	4	0.31	0.8697
Density of the remaining species	SR	3	2.39	0.1277	3	1.62	0.2427
	Y	3	2.99	0.0494	4	1.87	0.1381
Individual biomass of <i>L.chinensis</i>	SR	3	9.69	0.0032	3	4.49	0.0303
	Y	3	24.00	<.0001	4	1.91	0.1321
Individual biomass of <i>S.grandis</i>	SR	3	3.06	0.0422	3	3.08	0.0933
	Y	3	7.52	0.0006	4	2.21	0.0898

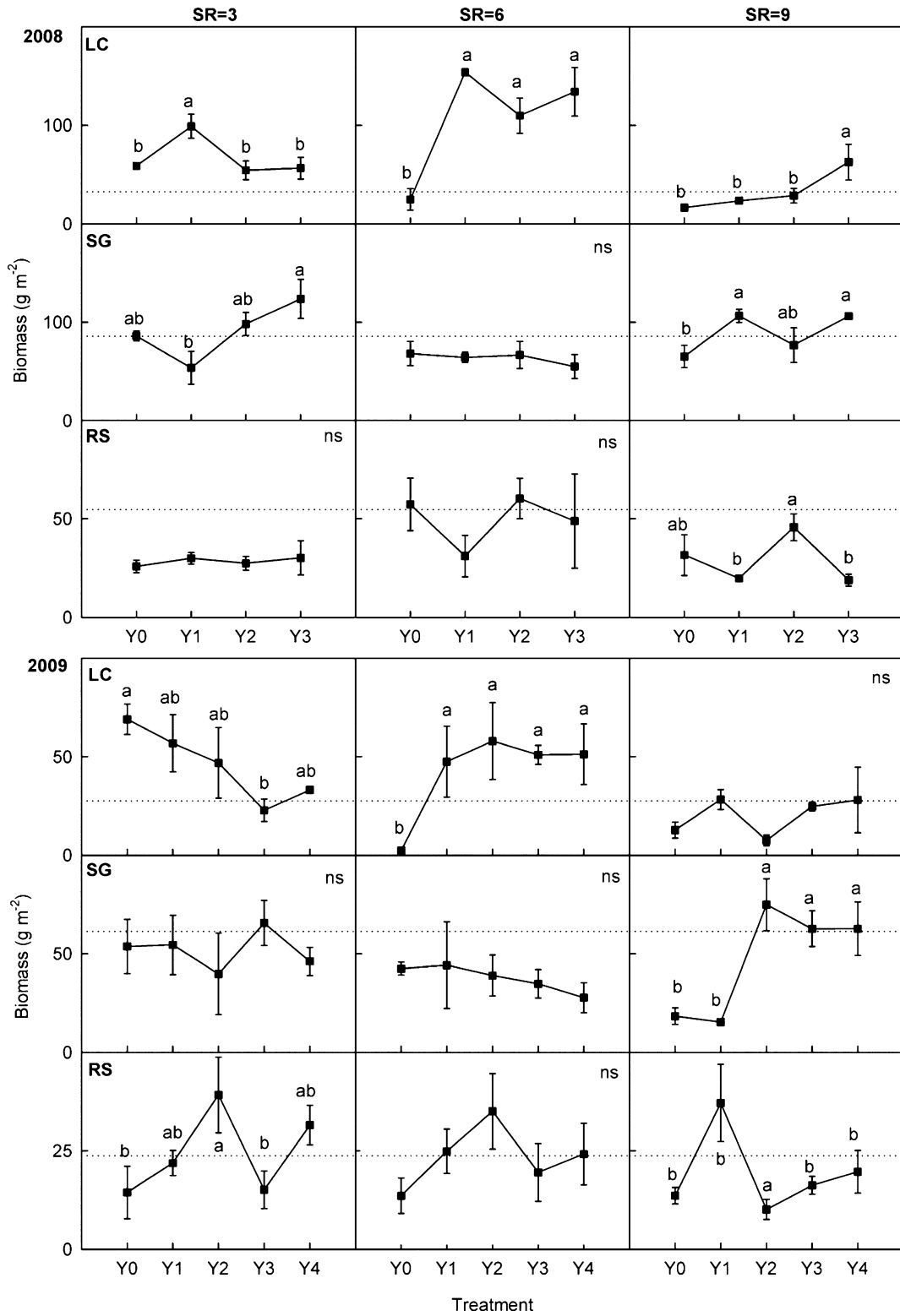
Dependence of community responses on species responses

Our results showed that  $R_{ANPP}$  was positively correlated with  $R_{SD}$  and  $R_{IB}$  of *L. chinensis* in both years (Fig. 7a and d). Our analysis also illustrated that  $R_{ANPP}$  was negatively correlated with  $R_{SD}$  but positively correlated with  $R_{IB}$  of *S. grandis* in 2008 (Fig. 7b and e). No significant relationship was found between  $R_{ANPP}$  and  $R_{SD}$  and  $R_{IB}$  for the remaining species in neither 2008 nor 2009 (Fig. 7c and f).

Discussion

Community response patterns to grazing removal at different stocking rates

Our study provides robust evidence on how processes of plant community recovery after grazing removal are affected by grazing intensity. For plots that had been grazed at low and moderate stocking rates, community ANPP recovered to the ungrazed control level only 1 year after grazing was removed. However, for plots that had been grazed at high stocking rate, the recovery of community ANPP





◀ **Fig. 3** Effects of years of grazing removal on species biomass of *L. chinensis* (LC), *S. grandis* (SG) and biomass and density of the remaining species (RS) under low, moderate and high stocking rates in 2008 and 2009. Biomass for each treatment was the average of three replicates (*error bars* indicate *SE*). Bars followed by the same letter are not significantly different according to Duncan's multiple range tests, and ns indicates non-significant difference at  $P=0.05$ . The reference line indicates the mean biomass of the control plot with three replicates. All symbols are derived as from Fig. 1

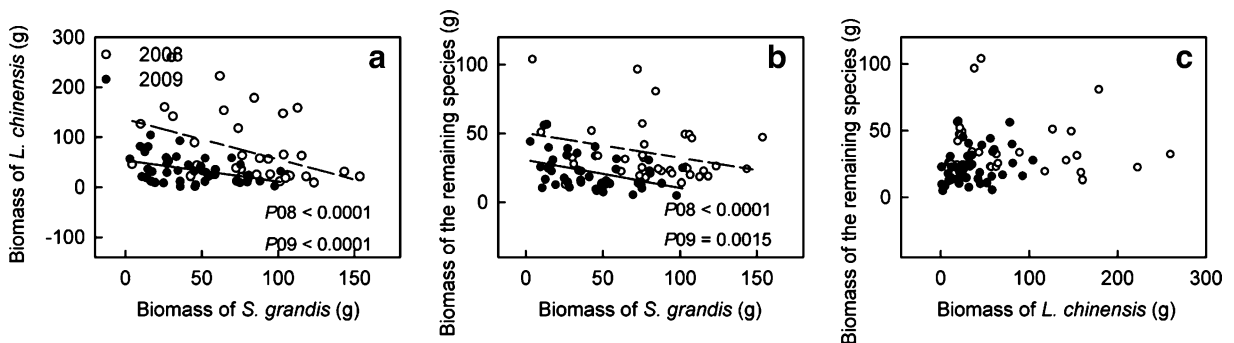
required 3 or 4 years. At low and moderate stocking rates, ANPP following grazing removal exhibited a unimodal pattern, with the largest increase in ANPP occurring in the first year and the peak value appearing in the first or second year. At the high stocking rate, ANPP declined in the first year of grazing removal and then increased to the control level in the third year. These findings support our hypothesis that plant communities at low and moderate stocking rates are more resilient and recover more quickly after grazing removal than those at high stocking rates.

Previous work has shown that heavy grazing reduces species richness, evenness, and diversity, while light and moderate grazing may increase species diversity (Noy-Meir et al. 1989; Olsvig-whittaker et al. 1993; Li et al. 2008). Our results showed that species richness, evenness, and diversity did not change markedly after 5 years of grazing though ANPP decreased significantly, especially at the high stocking rate. This is likely because the grazing gradient that was created in our study continued a relatively short term, which did not cause a shift in species richness and composition. Considering that the plants and grazing animals in the Inner Mongolia grassland have a long history of coevolution (including the plots in the current study), that the current study only lasted

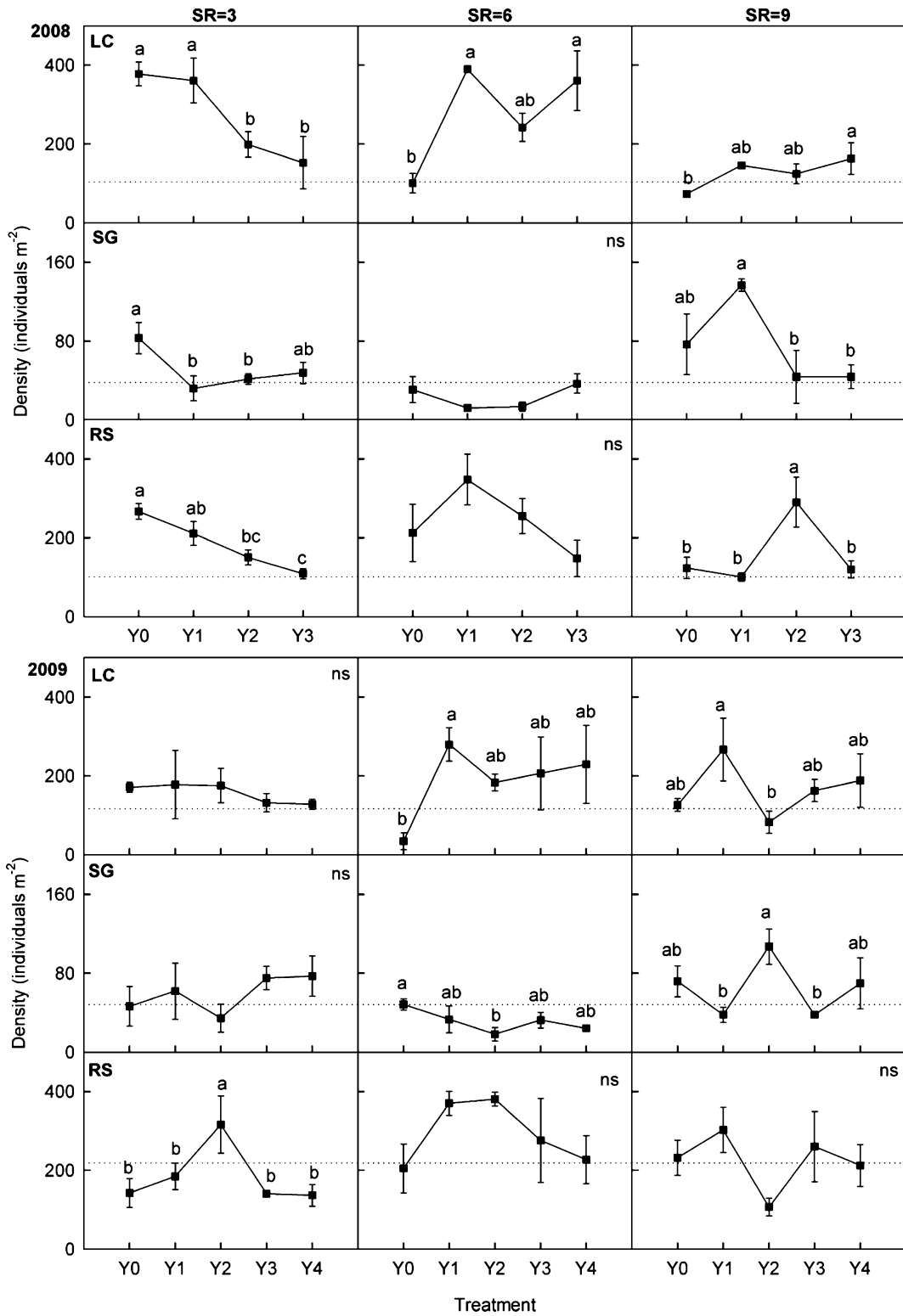
five years (starting in 2005), and that grazing only continued for about 3 months each year (from mid-June to mid-September), the grassland ecosystem of the current study may not have degraded severely. On the other hand, the relative stability of species richness, evenness, and diversity indicate the high resilience of this ecosystem to grazing disturbance. Our findings are corroborated by a recent study that showed little change had occurred in species richness during an 11-year recovery process of a degraded *L. chinensis* community (Li et al 2008). These results further suggest that the recovery of this system is very difficult when degraded, although it is relatively resistant to grazing disturbance.

#### Dependence of community-level response on species-level responses

Several studies have proposed that community response patterns to disturbance can be explained by the response patterns of component species (Milchunas and Lauenroth 1993; Ives et al. 1999; Yachi and Loreau 1999; Adler and Bradford 2002; Bai et al. 2004). In our study, the two dominant species, *L. chinensis* and *S. grandis*, together contributed 79% of the total community aboveground biomass, with the remaining species accounting for 21% of the total biomass. Our results demonstrate that differentiation of responses at the species level is the underlying cause for the different responses at the community level. At low and moderate stocking rates, the significant increases in both individual biomass and density of *L. chinensis* following grazing removal resulted in a large increase in species level biomass, which contributed to most of the increase in commu-



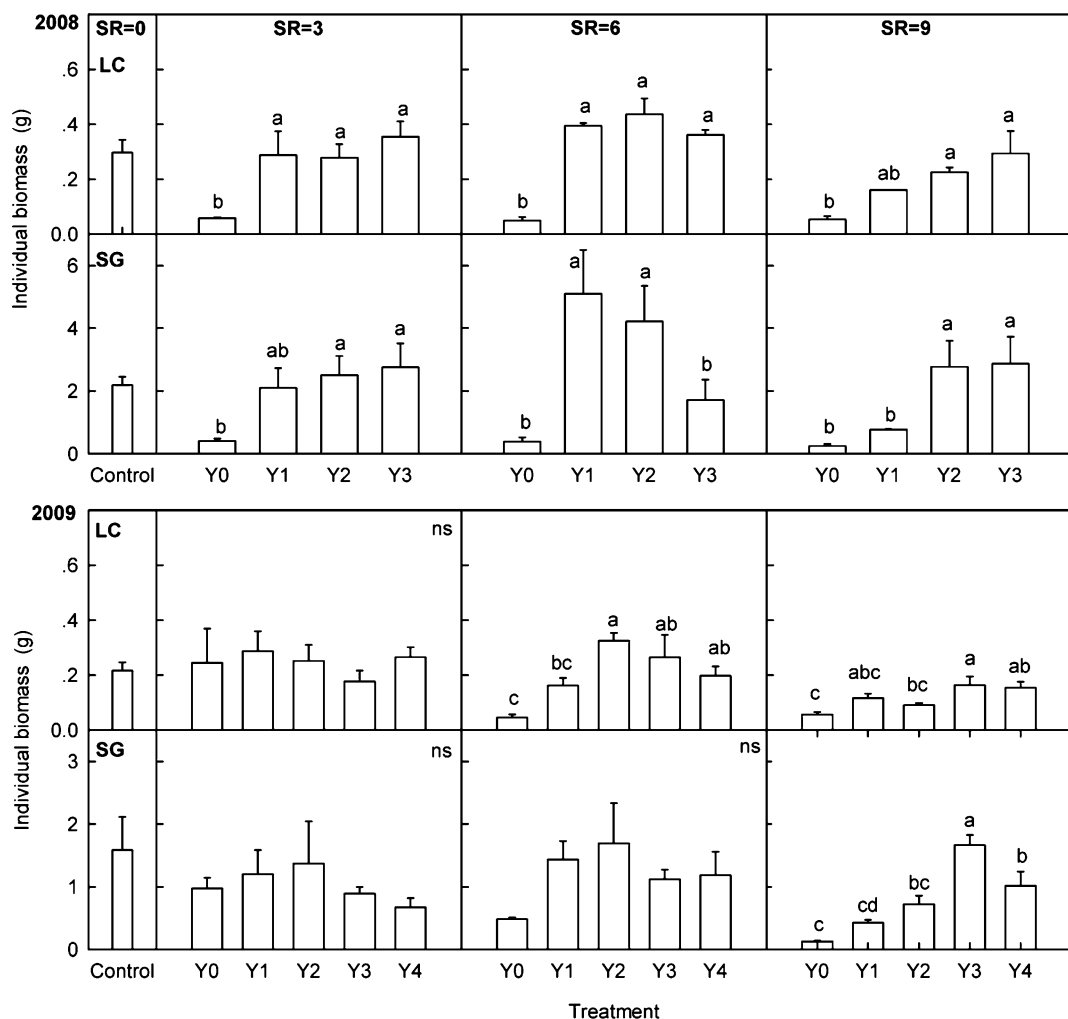
**Fig. 4** Relationships between the biomass of *S. grandis* and *L. chinensis* **a**, between *S. grandis* and the remaining species **b** and between *L. chinensis* and the remaining species **c** in 2008 (*open circle and dashed line*) and in 2009 (*filled circle and solid line*)



◀ **Fig. 5** Effects of years of grazing removal on density of *L. chinensis* (LC), *S. grandis* (SG) and biomass and density of the remaining species (RS) under low, moderate and high stocking rates in 2008 and 2009. Density for each treatment was the average of three replicates (error bars indicate SE). Bars followed by the same letter are not significantly different according to Duncan’s multiple range tests, and ns indicates non-significant difference at  $P=0.05$ . The reference line indicates the mean biomass of the control plot with three replicates. All symbols are derived as from Fig. 1

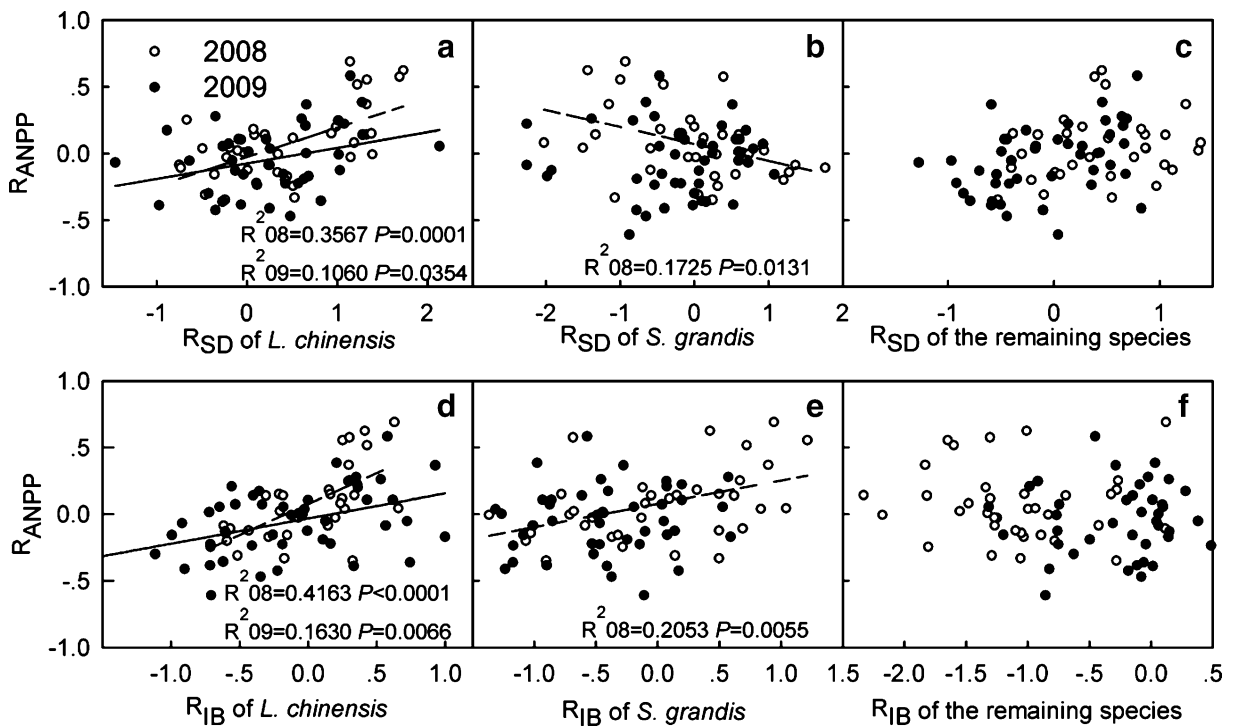
nity ANPP. A significantly positive relationship between  $R_{IB}$  and  $R_{SD}$  of *L. chinensis* suggests that overcompensatory growth of *L. chinensis* following grazing removal at low and moderate stocking rates is

an important mechanism underpinning community-level overcompensatory responses. This is further supported by a pot experiment in which *L. chinensis* exhibited overcompensatory growth at light and moderate clipping intensities (Zhao et al. 2008). The developed rhizome system of *L. chinensis* likely facilitates its quick depletion of the relative surplus of soil resources (e.g., nutrients and water) following grazing removal, which triggered its overcompensatory growth (Van Staalduinen and Anten 2005). The biomass of *S. grandis* was not significantly reduced by grazing at low or moderate stocking rates. The results of correlation analyses between  $R_{IB}$  of *S.*



**Fig. 6** Effects of years of grazing removal on individual biomass of *L. chinensis* (LC) and *S. grandis* (SG) under low, moderate and high stocking rates in 2008 and 2009. Individual biomass for each treatment was the average of three replicates

(error bars indicate SE). Bars followed by the same letter are not significantly different according to Duncan’s multiple range tests, and ns indicates non-significant difference at  $P=0.05$ . All symbols are derived as from Fig. 1



**Fig. 7** Relationships between  $R_{ANPP}$  and species density responses ( $R_{SD}$ ) of *L. chinensis* **a**, *S. grandis* **b** and the remaining species **c**, and between  $R_{ANPP}$  and individual

biomass responses ( $R_{IB}$ ) of *L. chinensis* **d**, *S. grandis* **e** and the remaining species **f** in 2008 (open circle and dashed line) and 2009 (filled circle and solid line)

*grandis* and community  $R_{ANPP}$  suggest that under these stocking rates, the response of *S. grandis* after grazing removal contributes little to community ANPP response. The insignificant relationship between the community ANPP response and biomass response of the remaining species indicates that these species also contributed little to the ANPP increase.

At the high stocking rate, the decline in  $R_{ANPP}$  in the first year of grazing removal may be explained by several mechanisms that were revealed by species responses. First, grazing at the high stocking rate significantly reduced the individual biomass of *L. chinensis* which did not exhibit overcompensatory growth at the species level. Second, the biomass of *S. grandis* remained unchanged or even declined after grazing removal. Finally, the remaining species did not compensate for the biomass decline of the two dominant species. The increase in  $R_{ANPP}$  after the second year of grazing removal was due mainly to recovery of the two dominant species.

#### Compensatory effects among component species

Numerous studies have proposed that compensatory effects among component species play an important role in stabilizing community structure and function following environmental changes (Fischer et al. 2001; Jiang 2007; Gonzalez and Loreau 2009), while others question the importance of compensatory effects in natural communities (Houlahan et al. 2007). If compensatory effects are predominant in maintaining temporal stability of an ecosystem, negative correlations in terms of biomass production or density between the major component species would be found (Bai et al. 2004). That is, the decline of some species would be compensated for by the increase in other species. The current study provides a clear picture of how component species compensate for each other in biomass production following grazing removal. Our results are also consistent with findings of a previous study that demonstrated the existence of distinct compensatory effects between two dominant

species in response to precipitation variability (Bai et al. 2004). These results together indicate that species compensatory effects play important roles in controlling responses of a grassland community to both precipitation variability and human disturbance. We further found that compensatory effects in biomass production between the remaining species and the dominant species did not appear under a low stocking rate, but it emerged at moderate and high stocking rates in 2008 and at all three stocking rates in 2009. As 2009 was a relatively dry year, results from the current study suggest that the remaining species become more important in stabilizing the ecosystem functioning under heavy grazing disturbance or severe droughts. The functional redundancy theory has proposed that the diversity of species performing the same functional role in ecosystems can stabilize ecosystem function (Walker et al. 1999). In our system, perennial bunchgrasses, such as *Agropyron cristatum*, *Cleistogenes squarrosa*, and *Achnatherum sibiricum* that contribute about 60% of the biomass of the remaining species, belong to the same functional group with *S. grandis* (Bai et al. 2004). The conspicuous compensatory effects between *S. grandis* and the remaining species also highlight the importance of compensatory effects between species within the same functional group. Thus, our results provide robust evidence that compensatory effects are important both in shaping the community responses and in buffering ANPP after grazing removal.

#### Precipitation variability and plant responses

Precipitation plays a critical role in determining community ANPP in grassland ecosystems (Knapp and Smith 2001; Bai et al. 2004; Bai et al. 2008). With one wet and one dry year, our study demonstrated that variability in precipitation significantly affected the plant responses to grazing removal at community and species levels. At the community level, the average ANPP in 2008 was 1.5 times higher than that in 2009, and there were significant differences in density among treatments at low and moderate stocking rates in 2008 but not in 2009. At the species level, the biomass and density of the same species under the same stocking rate differed significantly between the two contrasting years. In addition, precipitation variability significantly affected the relationship between community and species

responses. Finally, precipitation variability significantly affected the compensatory effects between component species. No significant compensatory effect was found between dominant species and the remaining species under the low stocking rate in 2008, but a significant effect was found in 2009. This suggests that precipitation variability is an important driver underpinning the different responses to grazing removal and plays a critical role in affecting the relationships between community and species responses and interactions among component species.

#### Implications for grassland management and restoration

As indicated by the response patterns after grazing removal, at low and moderate stocking rates,  $R_{ANPP}$  followed a unimodal pattern and gradually reverted back to control levels after 3 or 4 years, with no significant change in biodiversity. An appropriate management strategy for grassland under a moderate stocking rate would be to periodically remove grazing every 3–4 years. Recently, Wu et al. (2009) also recommend periodic grazing and resting from grazing as part of grassland management. For grasslands under high stocking rates, grazing removal should be the first step to grassland restoration. After community ANPP recovers, a more sustainable grazing system with periodic grazing removal and moderate stocking rate can be established. Certainly, the establishment of this system needs more research including grazing intensity, grazing time, duration of grazing removal, and the interactions of these factors with climate. Our results also have implications for the restoration of degraded grasslands. Given that interseeding and reseeding plant seeds into degraded grasslands have become common methods in grassland restoration (Sun 2000; Foster and Tilman 2003), the selection of appropriate species is necessary for the restoration of a particular grassland ecosystem. According to results of this study, interseeding or reseeding species with compensatory effects will promote recovery of degraded grasslands. Further research is needed to better understand the causal mechanisms behind the compensatory effects among coexisting species under different environments and disturbance regimes.

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