Heavy grazing led to the decrease of competitive intensity relationships among dominant populations of clustered grasses in a desert steppe

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Abstract

Aims

Desert steppe is an important ecological barrier in northern China. *Stipa breviflora* and *Cleistogenes songorica* are the dominant species in the desert steppe. Both plant populations undergo plant cluster fragmentation to varying degrees when subject to grazing interference. However, when both plant populations are present in the same plant community, changes in their inter-specific relationship under grazing is important for regulation of the plant community and its functions.

Methods

This study investigated *S. breviflora* and *C. songorica* in a desert steppe, and used variance analysis, the Jaccard index and simple linear regression model analysis methods to study differences in the density of both species under four grazing intensities (i.e., control (CK) 0 sheep·hm^{-2}·half year^{-1}, light grazing (LG) 0.93 sheep·hm^{-2}·half year^{-1}, moderate grazing (MG) 1.82 sheep·hm^{-2}·half year^{-1} and heavy grazing (HG) 2.71 sheep·hm^{-2}·half year^{-1}) at six scales (i.e., 5 cm×5 cm, 10 cm×10 cm, 20 cm×20 cm, 25 cm×25 cm, 50 cm×50 cm and 100 cm×100 cm). The study explored the competitive relationships between the plant populations.

Results

Results showed that grazing changes the relationship between dominant species. As grazing intensity increases, the competitive abilities of *S. breviflora* and *C. songorica* first increased and then decreased. Under heavy grazing conditions, the dominant populations of clustered grasses in the desert steppe resisted interference from high-intensity grazing by reducing inter-specific competition.

Conclusions

As grazing intensity increased, the densities of *S. breviflora* and *C. songorica* increased, and the increase became more obvious as the scale of analysis increased.

Introduction

Due to natural and anthropogenic interference, the global environment is undergoing rapid changes (Scales, 2005). How to accurately predict changes in plant diversity and community composition in response to future environmental changes and thus promote the stability of ecosystems is a significant research topic (Moritz and Agudo, 2013; Zhang et al., 2019). There are two common views on this topic. The first is that biodiversity promotes the stability of ecosystems (Cadotte et al., 2012; Weigelt et al., 2008), while the second view generally accepts that the stability of plant communities depends more on changes in inter-specific relationships, and this change in biodiversity depends on environmental changes (Wayne Polley et al., 2007).

Inter-specific relationships have been widely studied since the 1990s (Aiba et al., 2012; Perkins and Wilson, 2005). Inter-specific relationship refers to the interconnection of different species in spatial distribution, indicating the nature of mutual attraction or exclusion between species. Species that are interdependent, competitive and co-evolutionary, and ultimately make the community relatively more stable (Greig-Smith, 1983). Due to the influence of habitat conditions, spatial scales, plant traits, and environmental factors, plant communities show different ecological adaptations. The studies of Callaway and Armas showed that the interaction of plants affects population dynamics (Armas and Pugnaire, 2005; Callaway and Walker, 1997). Dominant species control most of the resources. When an ecosystem is disturbed, dominant species will provide short-term stability to the ecosystem (Avolio et al., 2019; Geider et al., 2001). Therefore, if the dominant species are resistant to interference, their communities would have higher resistance (Hillebrand et al., 2008).

Grazing is the most common method of grassland utilization. Usually, the competitiveness of grassland plants is affected by livestock trampling and selective feeding, and the competitiveness of plants fed on by livestock weakens, while the competitiveness of plants not fed on increases. When grazing intensity remains constant, competition between plants will eventually stabilize at a specific level (Muller-Scharer, 1991). Studies have shown that grazing leads to changes in relationships between populations, mainly due to changes in the ability of plants to intercept light (Ford and Diggle, 1981; Hay and Hunt, 1989). Many studies have shown that grazing can reduce competition between plants, and the importance of competition will decrease (McCanny et al., 1990). Plants adopt ways to improve niche and microbial symbiosis to cope with the adverse effects of herbivorous animals and achieve mutualism among species, which is an adaption of plants to the environment for survival (Brooker et al., 2008; Yin et al., 2019). Other theories argue that grazing can alter the outcome of competition but not the importance of competition (Tilman, 2020). Taylor *et al*. indicated that high-intensity grazing disturbance could change competition and coexistence among species (Taylor et al., 1997). Therefore, it is of great significance to explore the effect of grazing intensity on the inter-specific relationship of plant populations.

Due to the harsh environment, arid climate and poor soil, the structure and function of the desert steppe ecosystem are relatively fragile (Briske et al., 2015). *Stipa breviflora* and *Cleistogenes songorica* are perennial cluster grasses and dominant species in desert steppe, with strong resistance to cold, drought and trampling. It has been found that both *S. breviflora* and *C. songorica* can break up under grazing disturbance (Lv et al., 2020), but there has been little research on the inter-specific relationship of dominant grass populations in desert steppe. Therefore, this study investigated *S. breviflora* and *C. songorica* in a long-term grazing disturbance experiment to test the relationship between dominant species of perennial cluster grass under grazing disturbance. We investigated three main questions. (1) Are the changes in density of each dominant species similar or different at different levels of grazing intensity? (2) How does the inter-specific relationship of dominant species change as grazing intensity increases? (3) How do the competitive abilities of each dominant species change as grazing intensity increases?

Materials And Methods

Study site

The basic quantitative characteristics of *S. breviflora* and *C. songorica* were measured at a site in Siziwang Banner, Inner Mongolia (41°46'43.6"N, 111°53'41.7"E, elevation 1456 m). The region has a temperate continental arid and semi-arid climate, characterized by significant intra and inter-annual variability of hydrothermal conditions (Wang et al., 2011). The average annual precipitation is 223 mm, and 80% of precipitation is concentrated in May to September. The main soil type is light chestnut soil (Chinese classification) or calcic Kastanozems (FAO soil classification). The soil texture is sandy loam, and the desert steppe in this region is dominated by *S. breviflora*, *Artemisia frigida* and *C. songorica*. The composition of plant species is relatively simple, with average vegetation height of 8 cm and a canopy cover ranging from 17–20%.

Experimental design

To quantitatively test the effects of grazing intensity on the desert steppe ecosystem, twelve adjacent plots were established at a grazing experiment site in 2004. These treatments were arranged in a randomized complete block design, which included four grazing intensity treatments with three replicates (n = 3) of each treatment (see Fig. 1). Four different grazing intensities were set, namely CK (0 sheep·hm^{-2}·half year^{-1}), light grazing LG (0.93 sheep·hm^{-2}·half year^{-1}), moderate grazing MG (1.82 sheep·hm^{-2}·half year^{-1}) and heavy grazing HG (2.71 sheep·hm^{-2}·half year^{-1}). Since 2004, the annual seasonal grazing period has been from the beginning of June to the end of November, with grazing by 2-year-old Mongolian sheep. During the experiment, the management measures in each grazing treatment were basically the same. The daily grazing schedule was from 6:00 am to 6:00 pm. Water and salt were provided freely.

Vegetation sampling

In order to measure the plant population density of *S. breviflora* and *C. songorica* in the desert steppe and avoid the marginal effect of the CK treatment in block I, the CK treatment in block II was selected (see Fig. 1). In each sample plot at different grazing intensities, a representative sample plot with homogeneous terrain (5m×5m) was selected. The origin of the coordinate in each sample was defined as the upper left corner of the sample plot. A 1 m×1 m sample frame was placed 25 times in turn, and the precise spatial position of *S. breviflora* and *C. songorica* in the sample frame was determined using a tape measure. The population density of *S. breviflora* and *C. songorica* was measured on 15 August 2019.

Data analysis

At different grazing intensities, the densities (clusters) of *S. breviflora* and *C. songorica* were tested for homogeneity of variance ($P < 0.05$), and were found to follow a normal distribution. The generalized linear

model (GLM) was used to test the effect of grazing intensity on the density of *S. breviflora* and *C. songorica*. Duncan's test (Levene homogeneity test) was used to compare the mean and standard deviation between grazing treatments. The sample size of 5 m×5 m was divided into 5 cm×5 cm, 10 cm×10 cm, 20 cm×20 cm, 25 cm×25 cm, 50 cm×50 cm and 100 cm×100 cm scales. After square root transformation, the data was normally distributed, and variance analysis was used to compare the differences in density of *S. breviflora* and *C. songorica* under different grazing intensities and spatial scales. The bidirectional GLM method was used to test the effects of grazing intensity and spatial scale on the density of *S. breviflora* and *C. songorica*, and the generalized linear model was used to test the effect of spatial scale on the density of each species. In order to analyze the synergistic change of density with scale at different grazing intensities, a scatter diagram of the densities of *S. breviflora* and *C. songorica* at different grazing intensities was drawn, and linear fitting (using MS data) was carried out. The analysis of variance was performed using SAS 9.4 (SAS Institute Inc.) software and significance was set at $P < 0.05$ level. Assembly process and graphics rendering were completed in Sigmaplot 14.0 (Systat Software, 2011).

In order to study the inter-specific association of *S. breviflora* and *C. songorica* in desert steppe, the 5 m×5 m plot was regarded as the plant community in this study. Inter-specific associations of plant populations were measured using the Jaccard index applied to plots of 5 cm×5 cm, 10 cm×10 cm, 20 cm×20 cm, 25 cm×25 cm, 50 cm×50 cm and 100 cm×100 cm (Guo et al., 2014). The Jaccard index is a method applied to binary data to describe the affinity between two plant populations. The Jaccard index is negatively correlated with competitiveness, and positively correlated with affinity. The Jaccard index calculation formula is:

$$CJ = j/(a + b + j)$$

where, CJ is the Jaccard index; j is the number of small quadrats with *S. breviflora* and *C. songorica*; a is the number of small quadrats with only *S. breviflora* and without *C. songorica*; and b is the number of small quadrats with only *C. songorica* and without *S. breviflora*.

Results

Effects of grazing intensity and scale on population density of *Stipa breviflora*

Grazing intensity, spatial scale and their interaction significantly affected density of the *S. breviflora* population (Table 1, $P < 0.05$). The F value of spatial scale factors on *S. breviflora* density was large (F = 306.81), indicating that *S. breviflora* density responded to spatial scale factors.

S. breviflora population densities under different grazing intensities and at different spatial scales are shown in Fig. 2. The density of *S. breviflora* increased with increasing grazing intensity (Fig. 2A), and there were significant differences between the CK and LG, CK and MG and CK and HG treatments ($P < 0.05$). Significant differences in density of *S. breviflora* between the CK and LG treatments indicates plant cluster fragmentation. Although there were no significant differences among LG, MG and HG treatments,

there was a non-significant trend of increasing density along the grazing intensity gradient. The error bars associated with each treatment were long, indicating that *S. breviflora* was dispersed in each treatment. The density of *S. breviflora* increased exponentially with increasing spatial scale (Fig. 2B). Except for at 5 cm×5 cm and 10 cm×10 cm, and 20 cm×20 cm and 50 cm×50 cm scales, there were significant differences between the different spatial scales ($P < 0.05$). The functional relationship between density (y) and spatial scale (x) of *S. breviflora* was y = 0.5314 + 0.0112exp(1.4160x) and the goodness of fit was high ($r^2 = 0.9995$).

Table 1
Variance analysis results for the *Stipa breviflora* population

Source	*df*	SS	MS	*F* Value	*P* Value
Model	8	139.63	17.45	193.94	< .0001
Grazing intensity	3	1.58	0.53	5.83	0.0076
Scale	5	138.06	27.61	306.81	< .0001
Error	15	1.35	0.09		
Corrected Total	23	140.98			

Effects of grazing intensity and scale on population density of *Cleistogenes songorica*

Grazing intensity, spatial scale and their interaction had significant effects on density of the *C. songorica* population (Table 2, $P < 0.05$). The F value of the spatial scale factor was large (F = 374.19), indicating that density was sensitive to spatial scale factors.

Population densities under different grazing intensities and at different spatial scales are shown in Fig. 3. The density of *C. songorica* increased with increasing grazing intensity (Fig. 3A), and there were significant differences between the CK and HG, LG and HG, and MG and HG treatments ($P < 0.05$). This indicated that difference in the density of *C. songorica* (i.e., plant cluster fragmentation) only appeared in the HG treatment and that heavy grazing led to a significant increase in the density of *C. songorica*. Although there were no significant differences in density among CK, LG and MG treatments, there was a non-significant trend of increasing density with increasing grazing intensity. The error bars associated with each treatment were long, indicating that *C. songorica* was unevenly distributed in each treatment. The density of *C. songorica* increased exponentially with increasing spatial scale (Fig. 3B). Except for between the 5 cm×5 cm and 10 cm×10 cm, and 20 cm× 20cm and 50 cm×50 cm scales, there were significant differences in density between different spatial scales ($P < 0.05$). The functional relationship between density (y) and spatial scale (x) of *C. songorica* was y = 0.1412 + 0.0026exp (1.4189x), and the goodness of fit was high ($r^2 = 0.9994$).

Table 2
Variance analysis results of the *Cleistogenes songorica* population

Source	*df*	SS	MS	*F* Value	*P* Value
Model	8	33.42	4.18	236.2	< .0001
Grazing intensity	3	0.33	0.11	6.21	0.0059
Scale	5	33.09	6.62	374.19	< .0001
Error	15	0.27	0.02		
Corrected Total	23	33.69			

Inter-specific association between *Stipa breviflora* and *Cleistogenes songorica* populations

From the Jaccard index of *S. breviflora* and *C. songorica* populations (Table 3) one can see that the values of the Jaccard index under grazing treatments were greater than that under the non-grazing treatment at different scales, indicating that grazing increased the inter-specific affinity of *S. breviflora* and *C. songorica*. At the same grazing intensity, as spatial scale increased, the value of Jaccard index gradually increased, i.e., inter-specific affinity of these dominant species increased. At the spatial scale of 5 cm×5 cm, the Jaccard index showed strong inter-specific competition between *S. breviflora* and *C. songorica*. At the spatial scale of 100 cm×100 cm, the inter-specific compatibility between *S. breviflora* and *C. songorica* reached its maximum in the grazing treatments. The data show differences in inter-specific compatibility between grazing and non-grazing treatments at this scale, but grazing intensity has little effect on the degree of affinity. As grazing intensity increased, inter-specific affinity between the two species increased greatly at small scales, while the increase was small at large scale. In summary, grazing increased the inter-specific relationship affinity (i.e., competitive ability decreased) between *S. breviflora* and *C. songorica* in order to resist grazing disturbance, and this affinity was particularly obvious at large scale.

Table 3
Jaccard index of *Stipa breviflora* and *Cleistogenes songorica* populations

Grazing intensity	Scale					
	1	2	3	4	5	6
CK	0.0111	0.0545	0.2588	0.3194	0.7653	0.9200
LG	0.0190	0.0803	0.3108	0.4692	0.9100	1.0000
MG	0.0243	0.0797	0.3440	0.4722	0.8600	1.0000
HG	0.0297	0.1151	0.4027	0.5342	0.8900	1.0000
Abbreviations: (1) 5 cm×5 cm; (2) 10 cm×10 cm; (3) 20 cm×20 cm; (4) 25 cm×25 cm; (5) 50 cm×50 cm; (6) 100 cm×100 cm.						

Synergistic changes in the density of *Stipa breviflora* and *Cleistogenes songorica* with scale at different grazing intensities

Fig. 4 shows the co-variation of the densities of *S. breviflora* and *C. songorica* with scale at different grazing intensities. No matter how grazing intensity changed, there was a significant positive correlation between the densities of the two plant populations ($P<0.05$). The determination coefficients were all close to 1, indicating that at different grazing intensities, there was a good fit between the densities of *S. breviflora* and *C. songorica*a. As grazing intensity increased, the regression slope first decreased and then increased, showing that along the grazing intensity gradient from the CK to the MG treatment, the density of *C. songorica* decreased as the density of *S. breviflora* increased. Thus, in these three treatments, the competitiveness of *S. breviflora* was higher than that of *C. songorica*, but under the HG treatment, the competitiveness of *C. songorica* increased and the competitiveness of *S. breviflora* decreased. Fig. 3 also shows that compared with other three treatments, the increase of *C. songorica* density in the HG treatment was the largest. The intercept of this linear relationship in the LG treatment was 0.0223, while the value for the HG treatment was 0.0201, indicating that the linear relationship between *S. breviflora* and *C. songorica* is affected by the initial density of *S. breviflora* in the LG and HG treatments. However, in the HG treatment, because the competitiveness of *C. songorica* improved, the impact of the initial density of *S. breviflora* was somewhat reduced.

Discussion

When the external environment changes, dominant species can adopt different strategies to maintain growth, survival and fecundity (Liu et al., 2016). New biomass, for example, is allocated to leaves and roots, or to organs such as stolons, rhizomes and seeds, to improve plants' access to resources (Drenovsky et al., 2008; Hermans et al., 2006). *S. breviflora* and *C. songorica* are the dominant species in the desert steppe, and have obvious control effects on the formation of community structure and the community environment in the desert steppe. Due to the strong grazing resistance of these two species,

density increased with increasing grazing intensity and spatial scale, and the response of density to spatial scale was more sensitive (Fig. 2-3). This may be related to the random walking, trampling and foraging behaviors of grazing livestock (Limb et al., 2010; Lin et al., 2010). *S. breviflora* and *C. songorica* are gramineous plants that can quickly absorb nitrogen and regenerate from the basic meristem, which may also be one of the reasons for changes in plant population density (Stampfli et al., 2018).

Both *S. breviflora* and *C. songorica* are perennial clumpy grasses, but *S. breviflora* is a dense clumpy grass, and its tillering node is located on the ground, which is easily affected by grazing behavior, resulting in the fragmentation of plant clusters. In contrast, *C. songorica* is a sparse clumpy grass, and the tillering node is located underground. Simple grazing behavior does not change the number of plant clusters, which explains the increase in density of *S. breviflora* in the LG treatment and of *C. songorica* in HG treatment density as clusters fragmented due to division of large clusters into several small clusters as plants adapted to the environment (An and Li, 2015; Lv et al., 2019; Salt and Mayes, 1991) . In this experiment, the competitive ability of *C. songorica* in the HG treatment was improved (the slope of linear regression increased, Fig. 4), which also supported the above observations. As grazing intensity increased, the linear relationship between *S. breviflora* and *C. songorica* was also affected by the initial density of *S. breviflora* (as indicated by the intercept of the regression line in Fig. 4). The shift of the regression line on the longitudinal axis and the increase of the regression slope indicates a complex relationship between the two species under grazing conditions.

The formation of plant population relationships is closely related to the environmental conditions of the community (Wang et al., 2015). Grazing may alter the availability of environmental resources in communities and ultimately alter interactions between species (Liu et al., 2000). The change in relationship caused by grazing is attributed to differences in population ecological adaptability and the response of niche overlap to the change in community conditions. In this study, as grazing intensity and spatial scale increased, the inter-specific relationship affinity between *S. breviflora* and *C. songorica* increased, and the inter-specific competition decreased. This is consistent with the results of Soltani *et al*., who reported that long-term grazing changed the adaptability of the community to the environment, resulting in a decrease in the competitiveness of dominant species (Soltani et al., 2020). Only increasing the affinity of the two species can enable them to resist grazing disturbance (Levine and HilleRisLambers, 2009). It should also be noted that at the scales of 10 cm×10 cm and 50 cm×50 cm, the inter-specific affinity of *S. breviflora* and *C. songorica* in the LG treatment was higher than that under CK and MG treatments, which may be due to the existence of special inter-specific or scale-critical points of inter-specific relationship transformation.

The change in inter-specific association can also be explained by the ecological compensation effect caused by grazing. In the *S. breviflora* desert steppe, grazing could lead to niche differentiation in the ecosystem, which could be directly reflected by the ecological compensation effect between species. This ecological compensation effect changed the resource utilization mode of species (Fock and Kraus, 2016; Liu, 2019). Without grazing, the limiting factor on population growth is natural resources, and the difference between populations' abilities to occupy resources produces the competitive relationship

between species, while the community generally shows no obvious negative correlation. Under grazing, the main limiting factor on population growth becomes livestock feeding and trampling, and only reducing inter-specific competition can enable plants to deal with the grazing disturbance (Levine and HilleRisLambers, 2009). The pressure gradient hypothesis also points out that competition plays a major role in this low pressure environment. When interference exceeds a certain limit, inter-specific interaction between plants will decrease (Bertness and Callaway, 1994; Wan et al., 2011). Therefore, in this experiment, heavy grazing led to the decrease in inter-specific competitive abilities of dominant grass populations in the desert steppe.

The stability of plant communities is the manifestation of the interaction between populations in competition or symbiosis, so as to achieve dynamic equilibrium (Levine and HilleRisLambers, 2009). Some studies have suggested that the temporal stability of the community increases with increasing inter-specific competition (Tilman, 1999). However, grazing may lead to extremely unbalanced population development, enhancing the dominant position of major species, reducing species diversity, and simplifying community structure and function (Armas et al., 2011). Thus, studies have also shown that inter-specific competition makes communities more unstable (Loreau and De Mazancourt, 2013). In order to better understand changes in inter-specific relationships of plant populations under grazing disturbance, specific analysis should be carried out in combination with habitat conditions, plant physiological and biochemical characteristics, in order to elucidate the internal mechanisms of change in plant populations.

Conclusions

The conclusion of this study is that the inter-specific relationship of dominant grass species is not only affected by grazing intensity, but also by initial population density and research scale. Our study produced three main results. First, increasing grazing intensity and spatial scale will increase the density of *S. breviflora* and *C. songorica* populations in the Inner Mongolian desert steppe, with a more obvious response of density to spatial scale. Second, as grazing intensity increases, the affinity of *S. breviflora* and *C. songorica* increased greatly at small scale, but as scale increased, the increase in affinity gradually became smaller. Finally, as grazing intensity increased, competition between *S. breviflora* and *C. songorica* first increased and then decreased, as heavy grazing led to decrease in inter-specific competition between the two species. Understanding inter-specific relationships is the basis for exploring the stability and evolution of plant communities. Change in the inter-specific relationship of dominant grass species in the desert steppe may further affect the stability and sustainability of the grassland ecosystem, so further understanding of the mechanisms of these changes can provide a theoretical basis for formulating reasonable and scientific grazing systems in the *S. breviflora* desert steppe.

Declarations

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Author's contributions

Study design: Guodong Han, Zhongwu Wang. Sampling: Zihan Wang, Chen Chen, Xinyang Men. Analyses: Shijie Lv, Hongmei Liu. Data interpretation & discussion: Shijie Lv, Zihan Wang, Zhongwu Wang, Zhiguo Li. All authors contributed to the writing and critical evaluation of the manuscript.

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Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Code availability

Not applicable.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Conflicts of interest

There are no conflicts of interest or competing interest.

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Figures

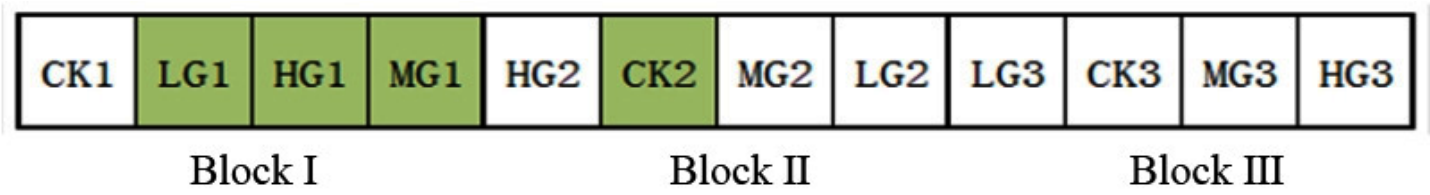

Figure 1

Schematic diagram of the grazing experiment treatments. Dark color treatments indicate sampled treatments. The grazing experiment treatments (each ca. 4.4 ha) were arranged in a randomized complete block design, which included four grazing intensity treatments with three repeats at each grazing intensity.

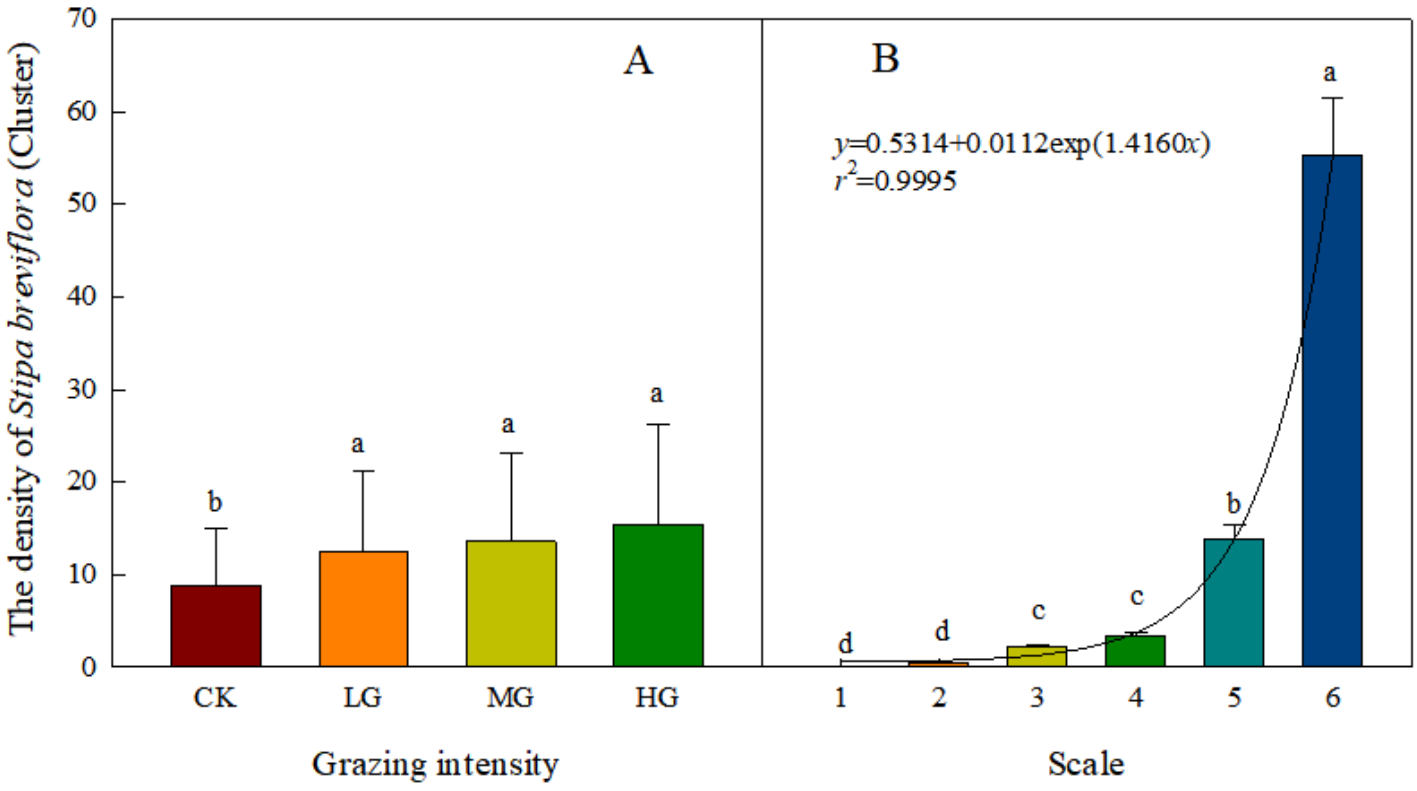

Figure 2

Population density difference diagrams of *Stipa breviflora* at different grazing intensities and scales. Mean values (±SD; n = 24) of density. Different lowercase letters indicate that grand means differ significantly between the grazing treatments ($P < 0.05$). y represents the density of *S. breviflora*, and x represents the scale of *S. breviflora*; r^2 represents the determination coefficient. (1) 5 cm×5 cm; (2) 10 cm×10 cm; (3) 20 cm×20 cm; (4) 25 cm×25 cm; (5) 50 cm×50 cm; (6) 100 cm×100 cm.

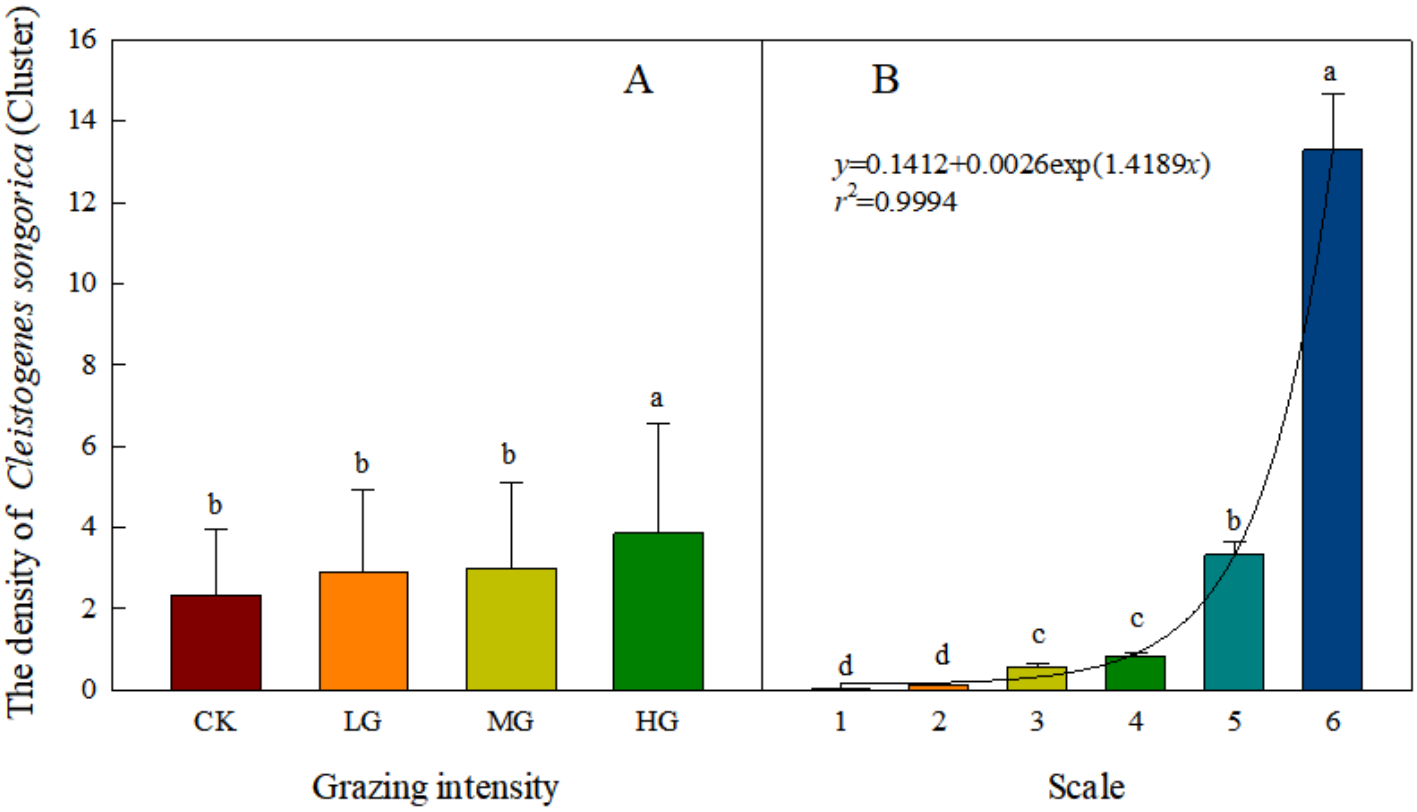

Figure 3

Population density difference diagrams of *Cleistogenes songorica* at different grazing intensities and spatial scales. Mean values (±SD; n = 24) of density. Different lowercase letters indicate that grand means differ significantly between the grazing treatments ($P < 0.05$). y represents the density of *C. songorica*, and x represents the scale of *C. songorica*; r^2 represents the determination coefficient. (1) 5 cm×5 cm; (2) 10 cm×10 cm; (3) 20 cm×20 cm; (4) 25 cm×25 cm; (5) 50 cm×50 cm; (6) 100 cm×100 cm.

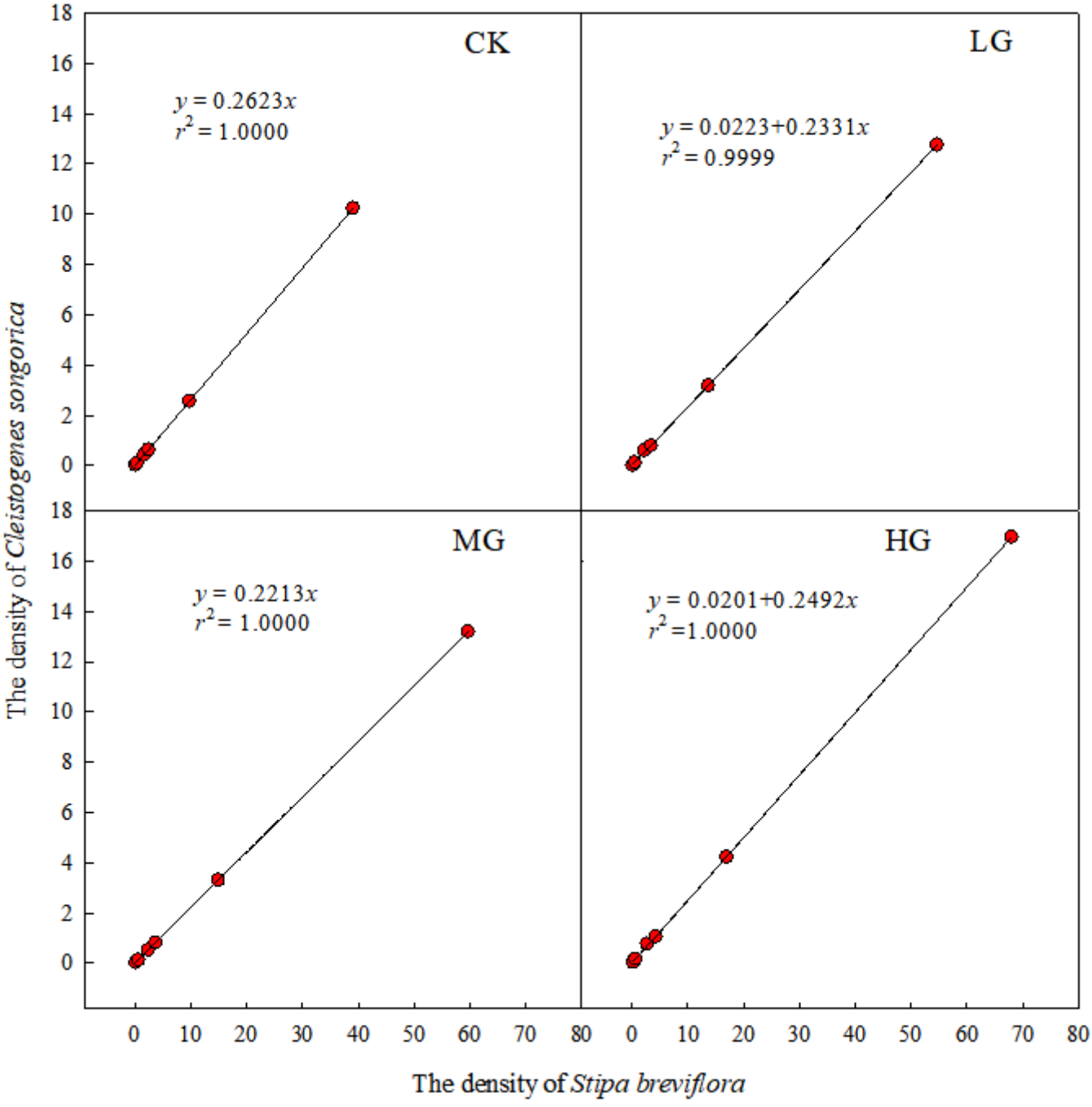

Figure 4

The relationship between the density of *Stipa breviflora* and the density of *Cleistogenes songorica* under different grazing intensities. CK, no grazing; LG, light grazing; MG, moderate grazing; and HG, heavy grazing. y represents the density of *C. songorica*, and x represents the density of *S. breviflora*; r^2 represents the determination coefficient.