



Grazing intensity affected spatial patterns of vegetation and soil fertility in a desert steppe

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ABSTRACT

Spatial heterogeneities of vegetation and soil can strongly affect ecological functions of ecosystems, particularly for arid and semi-arid ecosystems where vegetation has a patchy distribution and livestock grazing is one of the major land use types. However, little is known about the impact of grazing on spatial patterns of vegetation and soil, even though grazing has variously been shown to create, maintain or destroy those patterns. We studied how grazing intensity affected the spatial patterns of vegetation and soil fertility at scales ranging from 0.1 to 18.7 m in a desert steppe in Inner Mongolia, China. Increasing grazing intensity decreased the range of spatial autocorrelation of plant aboveground biomass at the fine scale (<2 m), indicating that vegetation patches were more fragmented under higher grazing pressure. Spatial heterogeneity of soil water content and organic C concentration decreased along the gradient of increasing grazing intensity at the fine scale. Light grazing increased soil NH_4^+ availability and its overall variability. Soil NO_3^- only had significant cross-correlation with aboveground biomass in un-grazed plots at the fine scale, suggesting that the spatial correlation between plant and soil fertility was affected by grazing. Spatial patterns of studied variables did not respond to grazing intensities at a coarse scale (1–18 m). Our results demonstrated that the grazing intensity altered fine scale processes in this desert steppe and caused divergent responses of spatial distribution of vegetation and soil fertility.

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1. Introduction

The distribution of plants, soil nutrients and animals commonly forms spatial patterns in natural ecosystems. Since ecological processes are tightly related to the spatial patterns of biotic and abiotic factors at different scales, the functions of spatial patterns are recently emphasized in ecological research. Spatially structured vegetation patterns can influence the coexistence of plant species (Lopez et al., 2009), community stability (Dayton et al., 1992; Frelich and Reich, 1995) and ecosystem function (Lovett et al., 2005; Maestre et al., 2005). Soil spatial heterogeneity can also affect the distribution and coexistence of plant species (Fransen et al., 2001; John et al., 2007) and interact with global change drivers (such as elevated atmospheric concentration of carbon dioxide) to further influence ecosystem properties and processes (Maestre and Reynolds, 2006).

Due to the important ecological function of spatial patterns, there is an increasing interest on the processes that can alter spatial patterns of biotic and abiotic factors. As a major land use type,

grazing strongly modifies ecosystem processes and presents two contrasting effects on the vegetation and soil in arid and semi-arid environments (Milchunas and Lauenroth, 1993; Augustine and McNaughton, 1998; Frank and Groffman, 1998). On one hand, grazing offers a management tool to maintain primary production, biodiversity and habitat structure (McNaughton, 1979; Hobbs, 1996; Collins et al., 1998). On the other hand, improper use of grazing, such as overgrazing, can dampen productivity, cause severe loss of soil fertility and further induce deterioration of ecosystems, including desertification (Rietkerk and van de Koppel, 1997; Su et al., 2005; Han et al., 2008). Therefore, different grazing regimes (e.g., different grazing intensities) should reveal divergent impacts on spatial patterns of vegetation and soil. However, there have been few studies to examine the impacts of grazing intensity on spatial patterns of vegetation and soil in arid and semi-arid ecosystems (except Rietkerk et al., 2000; Bisigato et al., 2005).

In arid and semi-arid ecosystems, the spatial distribution of plant communities can often be considered as a mosaic consisting of vegetation patches and bare land (Aguar and Sala, 1999). Soil nutrients could accumulate under vegetation patches, forming the so-called “islands of fertility” (Schlesinger et al., 1996; Reynolds et al., 1999). Geostatistics is one of the most widely applied ways to study the above spatial pattern of vegetation and

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soil. Spatial patchiness of the interested variable (e.g., plant above-ground biomass and soil organic carbon concentration) could be studied by semivariance analysis, which examines the variance between measurements taken at increasing distance from each other and provides useful information with regard to the average size of patches and the degree of heterogeneity (Augustine and Frank, 2001; Lane and BassiriRad, 2005; Olofsson et al., 2008). Cross-correlogram that study the spatial correlation between two dependent variables provides an useful tool to examine how vegetation patches affect the spatial distribution of soil variables (Rietkerk et al., 2000).

In arid and semi-arid grasslands, grazing can either increase or decrease the spatial heterogeneity of vegetation by modifying the structure and spatial arrangements of the vegetation patterns (Glenn et al., 1992; Rietkerk et al., 2000; van de Koppel et al., 2002; Olofsson et al., 2008). Studying the effects of grazing intensity on vegetation spatial heterogeneity can help to understand the above results and improve rangeland management due to the important functions of vegetation spatial pattern.

Grazing can also affect the spatial patterns of soil properties through trampling and wallowing that can increase soil compaction (Knapp et al., 1999), and change nutrient distribution via excreta input (Augustine and Frank, 2001). In addition to the above direct impacts, grazers can indirectly influence spatial distribution of soil properties through changing vegetation patterns. For example, Olofsson et al. (2008) found that the grazers' impact on soil nutrient heterogeneity can be consistent with their influence on vegetation patterns. However, in other studies the response of vegetation patterns to grazing did not correlate with changes in soil nutrient pattern (Rietkerk et al., 2000; Augustine and Frank, 2001). Little is known about how grazing intensity affect the relationship between spatial patterns of vegetation and soil nutrients.

In this study we examined the impact of sheep grazing intensity on the vegetation, soil fertility and their spatial heterogeneity in a desert steppe by combining a spatial sampling design with geo-statistical analyses. We also examined the relationship between spatial patterns of vegetation parameters and soil nutrients and the response of this relationship to the grazing gradient. Desert steppe accounts for 39% of total native Inner Mongolian grassland (Li et al., 2000) and is thus one of the most important ecosystem types in Inner Mongolia. However, the spatial patterns of vegetation and soil and their responses to grazing are poorly understood. We report here the spatial patterns of vegetation and soil and their responses to grazing in a dessert step studied at both a coarse scale (1–18.7 m) and a fine scale (0.1–2 m). This study provides more detailed information about the local interaction between plant and soil than most previous research in Inner Mongolia steppe, where a minimum of 1 m sample distances were used (Bai et al., 2002; Chen and Zeng, 2004; Su et al., 2006; except Wiesmeier et al., 2009).

Specifically, our questions were (1) How would grazing intensities affect the studied vegetation and soil variables and their spatial patterns? (2) Would the responses of those spatial patterns to grazing intensities differ between two studied scales? (3) How would grazing intensities alter the correlation between the spatial distributions of soil and vegetation variables?

2. Materials and methods

2.1. Study site

The study site (41°47'17"N, 111°53'46"E) is located in Siziwang Banner, Inner Mongolia Autonomous Region (IMAR), China. This site is around 140 km north of Huhhot, the capital city of IMAR. The study area has a mean annual temperature of 3.4°C with the highest monthly mean temperature in July (24.0°C). Long-term

mean annual precipitation is 280 mm. In recent years, the annual precipitation (2006, 161 mm; 2007, 162 mm; 2008, 230 mm) was relatively low at this site. The climate is arid, with windy and dry springs (March–June, with 49 mm average rainfall), and warm and comparatively rain-rich summers (July–September, with 220 mm average rainfall). The vegetation is a typical desert short-grass steppe, dominated by *Stipa breviflora* Griseb., *Artemisia frigida* Willd. and *Cleistogenes songorica* Roshev. Other species that are common include *Convolvulus ammannii* Desr., *Artemisia pectinata* Pall., *Kochia prostrata* (L.) Schrad., *Caragana stenophylla* Pojark., *Leymus chinensis* (Trin.) Tzvel. and *Salsola collina* Pall. Vegetation cover averages 20%. The soil is a light-colored Chenozemic soil (the Chinese System of Soil Classification, 2001) and equivalent to Cryolls (USDA Soil Classification System) (Li et al., 2008). Average concentrations of soil organic C (SOC), total N (TN) and mineral N were 12.95, 1.49 and 15.93 mg kg⁻¹, respectively.

2.2. Experiment design

In July 2002, ~35 ha steppe, which were used for grazing (stocking rate: 6–10 sheep-unit-month ha⁻¹) year round under collective sheep grazing for over 30 years, was fenced for this experiment. From 2002 to 2004, the site was either grazed at 6 sheep-unit-month ha⁻¹ or excluded from grazers. In 2004, this site was divided into two blocks and an experiment with a randomized complete block design was established so that each block contained four plots (Fig. 1). In total, there were eight plots, each with an average area of 4.4 ha. Four treatments (CK: control; LG: lightly grazed; MG: moderately grazed; HG: heavily grazed) were randomly applied within each block. The stocking rates were 0 sheep-unit-month ha⁻¹ (CK), 5.5 sheep-unit-month ha⁻¹ (LG), 10.9 sheep-unit-month ha⁻¹ (MG), 16.3 sheep-unit-month ha⁻¹ (HG). Grazing period was around 6 months per year, from early April to early October. The grazing gradient covered from grazer exclusion to heavy grazing and represented the most common grazing pressures in this region (Wei et al., 2000; Jiao et al., 2006).

To capture the spatial structures of soil and vegetation parameters, we applied a sampling matrix consisting of 177 points in each plot in 2008 (Fig. 1). All of the sampling matrices were located on a relatively level ground. The matrix contained two parts. The first part was a 4 m × 4 m grid where sampling points were established every 1 m (resulting in 25 points). Then, three 1 m × 1 m grids within the 4 m × 4 m grid were randomly chosen and five additional sampling points were located with a 0.5 m interval in each chosen 1 m × 1 m grid. Then one 0.5 m × 0.5 m grid was randomly chosen in the each selected 1 m × 1 m grids and another 24 points were established by every 10 cm interval within each 0.5 m × 0.5 m grid (Fig. 1). This defines the fine scale sampling. At the coarser scale, 65 points were evenly distributed within a 30 m × 10 m grid by a 2.5 m interval (Fig. 1). The 30 m × 10 m grid was established 2 m south of the 4 m × 4 m grid with the 30 m border paralleling the long edge of the plot. The coarse scale samples consisted of the 65 samples in the 30 m × 10 m grid and the 25 samples in the 4 m × 4 m grid with 1 m sampling interval as described above.

2.3. Sampling and sample analysis

Sampling was done in mid-August 2008 that corresponded to peak biomass in the growing season. Timing of sampling allowed us to compare results with some previous research in Inner Mongolia (Bai et al., 2002; Su et al., 2005). There were several precipitation events (for a total precipitation of 24.4 mm in 3 days) 2 days before the sampling. During the sampling period, soil water content was higher than usual and its availability was believed to be affected by plant uptake and microrelief (Rietkerk et al., 2000). Within a 5 cm radius of each sampling point, canopy height and species richness

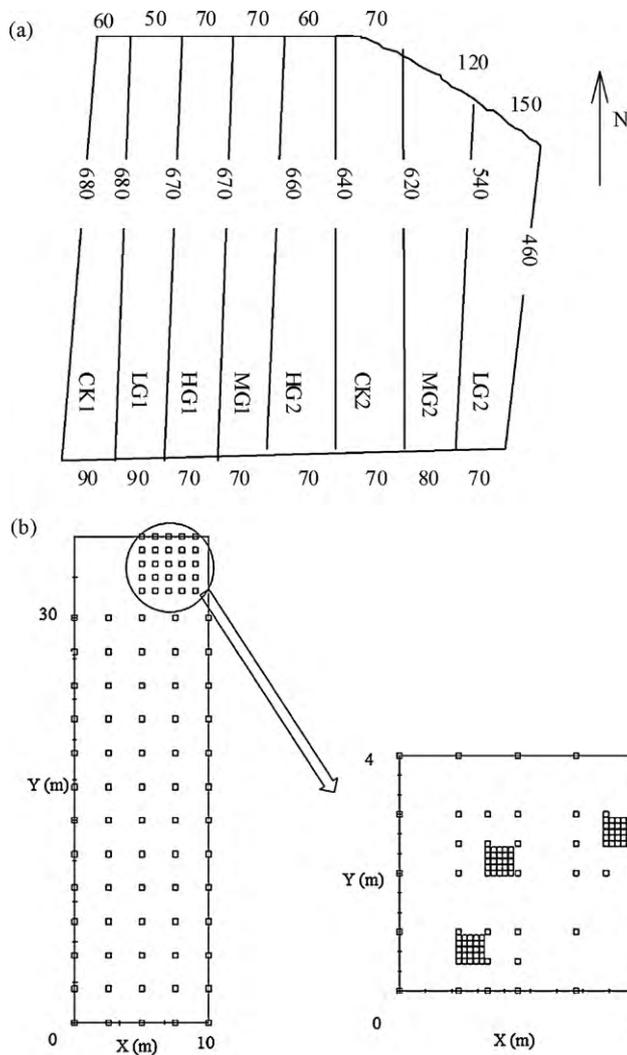


Fig. 1. (a) A schematic diagram of the experiment design. CK: control; LG: lightly grazed; MG: moderately grazed; HG: heavily grazed. Numbers indicate the length (m) of each edge. (b) A schematic diagram of the 30 m × 10 m and 4 m × 4 m sampling matrix. Each square represents a sampling point.

were measured. Then aboveground biomass (AGB) was harvested and later oven-dried at 65 °C for 2 days. In situ volumetric soil water content (SWC) in the top 6 cm was measured with a ThetaProbe ML2X (Delta-T Devices Ltd., Cambridge, UK; ±1% accuracy) at each sampling point. After the SWC measurement, the 0–6 cm soil was sampled by a 4 cm (internal diameter) auger. Each sample was temporarily stored in coolers and passed through a 2 mm sieve in the same day of sampling. A set of sub-samples was kept frozen after sieving for measuring soil mineral N availability.

The NH_4^+ and NO_3^- concentrations in the frozen soil sub-samples were extracted by 2 mol L⁻¹ KCl at a 1:3 ratio (w:v) and analyzed by a flow injection analyzer (FIAStar 5000, FOSS Analytical, Höganäs, Sweden). Another set of sub-samples were air-dried, ground to powder for total C and N analyses. Soil organic C was measured by the dichromate oxidation method (Nelson and Sommers, 1982). Soil total N was determined using micro-Kjeldahl digestion (Nelson and Sommers, 1980). Soil C/N ratio was calculated by the ratio between SOC and TN.

2.4. Data analyses

Mean values of AGB, height and soil properties were compared among grazing treatments by one-way ANOVA. Coefficients of vari-

ance (CV) of the above variables were compared by ANOVA to evaluate their degree of overall variability. The CV was also calculated separately for the fine scale and coarse scale samplings. Before the ANOVA, data were checked for the normality and equality of variances; however, no transformation was needed. If the grazing effect was significant, a post hoc comparison of means was done with a Tukey's HSD test. The Kruskal–Wallis test was used to examine the grazing effects on species richness. Due to the small sample size of this study ($n = 8$), a significance level of $\alpha = 0.10$ was used for the above analyses to control the possibility of making a Type-II error. Pearson's correlations were also performed between AGB and other variables ($n = 177$) at each of the plots. Before correlation analysis, each data set was tested for normality and logarithmic transformation was applied if necessary. When this transformation did not improve normality, a Box–Cox transformation was carried out and could improve normality in all those cases (Box and Cox, 1964). All the above analyses were carried out in SPSS software version 11.5.

The spatial pattern of soil and vegetation distribution was evaluated by semivariance analysis, which assesses the variance between measurements taken at increasing distance from each other (known as lag distance) (Schlesinger et al., 1996). In each plot, transformed data were used for this analysis. Semivariance γ for a certain lag distance h is calculated as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [y(x_i) - y(x_i + h)]^2$$

where $N(h)$ is the total number of data pairs that are separated by h , $y(x_i)$ is the value of studied variable at position x_i , and $y(x_i + h)$ is the value of variable at a distance h from x_i .

In each plot, random, linear, spherical, exponential or Gaussian models were fitted to the semivariance-lag distance distribution by using an un-weighted least-squares analysis in GS+ version 7.0 software and also by optical control (Robertson, 2000; Augustine and Frank, 2001). Random model is the best-fit if the semivariogram is flat. Both random and linear models indicate that there was no patchy spatial distribution for the variable at the studied scale. The model that minimized the reduced sum of squares was determined as the best-fit model. Data exhibiting no spatial patterns (where the semivariance forms a flat line) were fitted into a random model. For data with patterned distribution, the semivariance is relatively small at short lag distances, suggesting neighboring samples are more similar and autocorrelated, and increased when paired samples become less similar. Semivariance then reaches an asymptote at range (A), the distance over which data are spatially autocorrelated. Nugget variance (C_0), which is defined as the variance at zero lag distance, reflects either the error associated with measurement and/or analysis or the variances that can be spatially explained at a scale smaller than the minimal lag distance. The difference between total variance (also known as sill variance, $C + C_0$) and nugget variance is the spatial variance (C). Magnitude of spatial heterogeneity (MSH) can be measured by the proportion of total variance that could be spatially explained ($C/[C + C_0]$) (Lane and BassiriRad, 2005). A fitted model with a range larger than the maximum lag distance (or active lag distance) suggests that there is a large scale trend in the sampled space. To remove the trend, trend surface analysis was used by treating x and y coordinates, their interaction and higher order terms (up to 4th order) in a multiple regression analysis with the studied parameter as the dependent variable (Gallardo et al., 2006). Residuals from the significant multiple regression analysis were used for semivariance analyses and the isotropic semivariogram was chosen.

For the fine scale sampling design, the active lag distance was 2.7 m and the lag interval was 0.1 m, which was the minimum

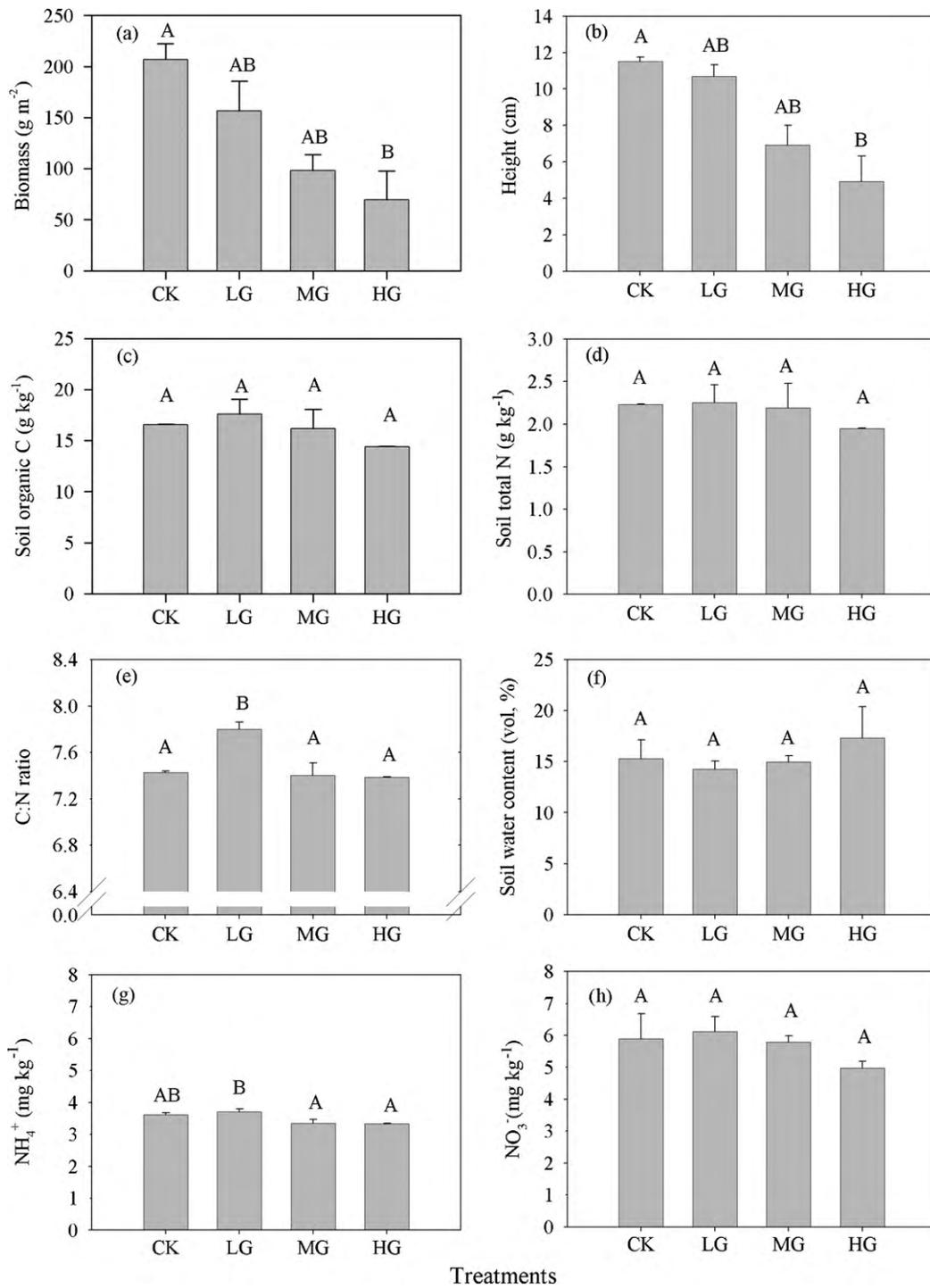


Fig. 2. Grazing effects on (a) AGB, (b) vegetation height, (c) soil organic C, (d) soil total N, (e) soil C/N ratio, (f) SWC, (g) NH₄⁺ and (h) NO₃⁻. Error bars denote S.E. Bars with different letters are significantly different at $P \leq 0.100$.

distance between sample points. The minimum and maximum number of pairs in a lag interval was 51 and 296, respectively, with a mean of 166 pairs. For the coarse scale sampling design, the active lag distance was 18.7 m and the lag interval was 1.0 m. The number of pairs per lag interval ranged from 40 to 319 (mean = 182). Range and MSH were compared among grazing intensities by one-way ANOVA (SPSS, version 11.5). Linear regression analysis (SPSS, version 11.5) was also used to determine whether grazing intensity was a significant predictor for the geostatistical metrics. ANOVA and regression analysis were done separately for the fine and coarse scale data.

Cross-correlogram (GS+ software, version 7.0) plotted the cross-correlation $r_{ab}(h)$ between two dependant variables (a and b) as a function of increasing lag distance h and was used to compare the spatial patterns of a and b . Value of $r_{ab}(h)$ was calculated as:

$$r_{ab}(h) = \frac{\sum_{i=1}^{N(h)} a(x_i)b(x_i + h) - m_a m_b}{S_a S_b}$$

where $a(x_i)$ represents the value of studied variable a at position x_i , $b(x_i + h)$ is the value of variable b at position $x_i + h$, and m_a and S_a denote the sample mean and standard deviation of a , respectively.

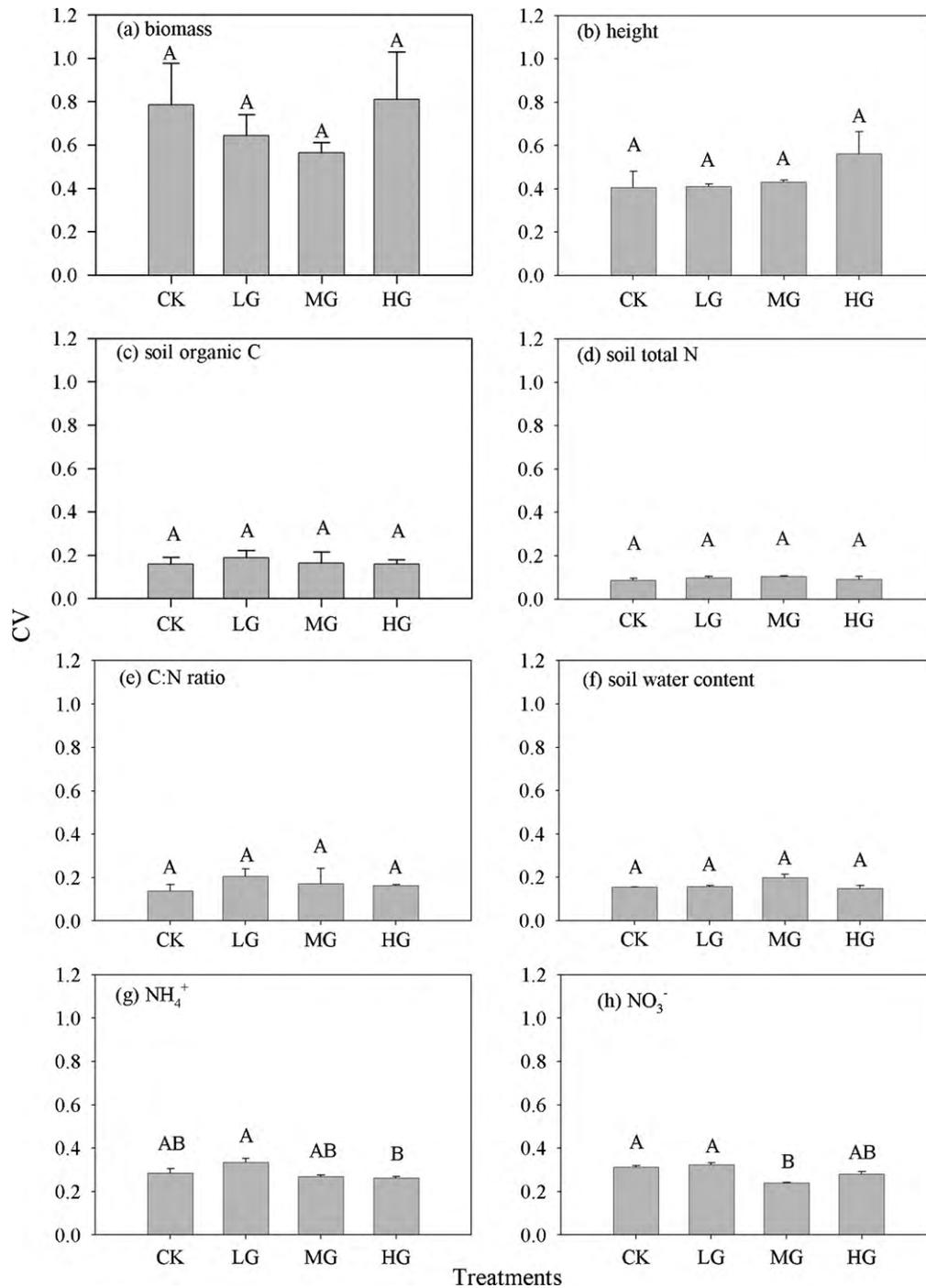


Fig. 3. Grazing effects on the coefficient of variances (CV) for (a) AGB, (b) vegetation height, (c) soil organic C, (d) soil total N, (e) soil C/N ratio, (f) SWC, (g) NH₄⁺ and (h) NO₃⁻. Error bars denote S.E. Bars with different letters are significantly different at $P \leq 0.100$.

Identical spatial patterns of a and b equate $r_{ab}(h)$ with 1, opposite patterns equate $r_{ab}(h)$ with -1 and total unrelated patterns make $r_{ab}(h) = 0$. Critical values ($\alpha = 0.05$) for Pearson's correlation coefficient r were used to evaluate the significance of $r_{ab}(h)$ at each lag interval. If $r_{ab}(h_1)$ was above the critical value at the lag distance of h_1 , then a and b would spatially depend on each other at this distance. Cross-correlation likely changes to non-significant with increasing lag distance, suggesting the range of spatial dependence between the two studied variables (Rietkerk et al., 2000).

3. Results

3.1. Mean values and CV

Mean AGB was affected by grazing intensity; biomass decreased from $207 \pm 32 \text{ g m}^{-2}$ (mean \pm SE) in CK to $70 \pm 32 \text{ g m}^{-2}$ in HG (Fig. 2a). Grazing intensity also affected vegetation height, which was 57 and 54% lower in HG than in CK and LG, respectively (Fig. 2b). The LG treatment had the highest C/N ratio in the soil among all

Table 1

Summary of semivariogram model parameters for aboveground biomass (AGB), vegetation height, soil water content (SWC), soil NH_4^+ , NO_3^- , soil organic C (SOC), total N (TN) and C/N ratio at the fine scale.

	Block 1	Model	A (m)	MSH	Block 2	Model	A (m)	MSH
AGB (g m^{-2})	CK1	S	0.88	0.631	CK2	S	1.15	0.786
	LG1	S	0.55	0.750	LG2	S	0.33	0.877
	MG1	E	0.83	0.502	MG2	S	0.14	0.425
	HG1	E	0.18	0.421	HG2	R	<0.01	<0.001
Vegetation height (cm)	CK1	R	<0.01	<0.001	CK2	S	0.73	0.739
	LG1	R	<0.01	<0.001	LG2	R	<0.01	<0.001
	MG1	S ^a	0.69	0.500	MG2	S	0.11	0.998
	HG1	R	<0.01	<0.001	HG2	E	0.78	0.500
SWC (vol%)	CK1	L	>2.85	0.116	CK2	R	<0.01	<0.001
	LG1	L	>2.85	0.168	LG2	S	0.48	0.553
	MG1	S	0.83	0.676	MG2	S	1.16	0.808
	HG1	E	0.32	0.545	HG2	S	0.55	0.547
NH_4^+ (mg kg^{-1})	CK1	R	<0.01	<0.001	CK2	R	<0.01	<0.001
	LG1	S	0.79	0.763	LG2	E	0.16	0.875
	MG1	R	<0.01	<0.001	MG2	E	0.21	0.797
	HG1	R	<0.01	<0.001	HG2	R	<0.01	<0.001
NO_3^- (mg kg^{-1})	CK1	R ^a	<0.01	<0.001	CK2	R	<0.01	<0.001
	LG1	R	<0.01	<0.001	LG2	R ^a	<0.01	<0.001
	MG1	R ^a	<0.01	<0.001	MG2	R	<0.01	<0.001
	HG1	R	<0.01	<0.001	HG2	R	<0.01	<0.001
SOC (g kg^{-1})	CK1	S	0.15	0.998	CK2	G	0.82	0.900
	LG1	S	0.23	0.892	LG2	S	0.98	0.587
	MG1	S	1.07	0.615	MG2	S	1.09	0.629
	HG1	S	0.56	0.500	HG2	S	0.57	0.661
TN (g kg^{-1})	CK1	E	0.27	0.730	CK2	S	1.40	0.500
	LG1	S	0.81	0.520	LG2	L ^a	>2.85	0.302
	MG1	S	0.17	0.690	MG2	E	0.13	0.368
	HG1	S	0.72	0.860	HG2	E	0.33	0.780
C/N ratio	CK1	R	<0.01	<0.001	CK2	E	1.14	0.501
	LG1	S	1.53	0.502	LG2	R	<0.01	<0.001
	MG1	R	<0.01	<0.001	MG2	S	1.08	0.693
	HG1	S	0.62	0.698	HG2	R	<0.01	<0.001

A, range; MSH, magnitude of spatial heterogeneity; R, random; L, linear; S, spherical; E, exponential; G, Gaussian.

^a Data were detrended.

grazing intensities (Fig. 2e). Average soil NH_4^+ concentration in LG (3.71 ± 0.11) was higher than those in MG (3.35 ± 0.11) and HG (3.33 ± 0.11) (Fig. 2g). Grazing intensity did not affect SOC, TN, SWC, soil NO_3^- (Fig. 2c, d, f and h) or species richness (data not shown).

When CV was calculated with the whole data set (including both fine and coarse scale samples) in each experimental plot, AGB and height presented higher variances than any other variables and their CV values were not affected by grazing intensity (Fig. 3). In MG plots, CV of soil NO_3^- (0.241 ± 0.011) was lower than that in CK (0.311 ± 0.011) and LG (0.323 ± 0.011) (Fig. 3h). Grazing effect was also significant for soil NH_4^+ ($P=0.074$) so that CV in HG was lower than that in LG ($P=0.076$ and Fig. 3g). The CV of any other soil variables did not respond to grazing intensities (Fig. 3). For most variables, CVs at the fine and coarse scale were similar in magnitude except that TN had a larger CV at the coarse scale ($P=0.075$, data not shown).

3.2. Geostatistics

At the fine scale. The range for plant AGB decreased with increasing grazing intensity (exponential decay model: $P=0.016$, $R^2=0.648$, Fig. 4a). There was a quadratic relationship ($P=0.034$, $R^2=0.742$, Fig. 4b) between MSH for plant AGB and grazing intensity; MSH tended to decrease around 8 sheep-unit-month ha^{-1} (between LG and MG). Spherical models were the best-fit for AGB semivariograms in two CK plots with a mean range of 1.02 m (Table 1 and Fig. 5). In contrast, AGB in HG either fitted a random model, indicating no spatial pattern in the studied scale, or an exponential

model with a 0.18 m range, suggesting spatial patterns happened in a small area (Table 1 and Fig. 5).

Grazing significantly affected MSH for SWC: MSH for MG ($P=0.034$) and HG ($P=0.098$, Table 1) were both higher than MSH for CK. The MSH for SOC declined with increasing grazing intensity from 94.9% (mean) in CK to 58.1% in HG (Fig. 4b), while the range for SOC did not show directional response to grazing (Table 1). For soil NH_4^+ and NO_3^- , spatial pattern were only found in low or intermediate grazing intensities (Table 1).

At the coarse scale. AGB did not present patchy spatial pattern at coarse scale in some - plots, while its range did not have relationship with grazing intensity, neither did vegetation height (Table 2). For plots without patchy spatial pattern of SWC at the fine scale, there were patchy spatial patterns at the coarse scale (fitted by exponential models, Table 2). To these plots, we used the ranges and MSHs at coarse scale to replace those at fine scale, and found that both range (Fig. 4a) and MSH of SWC declined (Fig. 4b) with increasing stocking rates by using the new data. For NH_4^+ , NO_3^- , TN or C/N ratio, neither range nor MSH had a relationship with increasing grazing intensities (Table 2).

3.3. Correlations and cross-correlograms

In each sampling plot, AGB had a positive relationship with vegetation height (Table 3). There was a positive relationship between AGB and soil NO_3^- in CK and LG; however, this relationship was non-significant in one of the MG plots and both HG plots (Table 3). The cross-correlograms revealed that there was significant cross-

Table 2Summary of semivariogram model parameters for AGB, vegetation height, SWC, soil NH_4^+ , NO_3^- , SOC, TN and C/N ratio at the coarse scale.

	Block 1	Model	A (m)	MSH	Block 2	Model	A (m)	MSH
AGB (g m^{-2})	CK1	S	3.4	0.820	CK2	R	<0.01	<0.001
	LG1	R	<0.01	<0.001	LG2	S	4.6	0.800
	MG1	E	8.3	0.850	MG2	G	9.3	0.841
	HG1	G	4.2	0.790	HG2	R	<0.01	<0.001
Vegetation height (cm)	CK1	S	12.7	0.902	CK2	R	<0.01	<0.001
	LG1	S	15.8	0.500	LG2	G	2.0	0.883
	MG1	L	> 18.7	0.082	MG2	G	2.6	0.998
	HG1	E	8.0	0.906	HG2	R	<0.01	<0.001
SWC (vol%)	CK1	E	2.1	0.889	CK2	E	2.0	0.873
	LG1	E	3.1	0.840	LG2	R	<0.01	<0.001
	MG1	S ^a	5.0	0.552	MG2	R ^a	<0.01	<0.001
	HG1	R	<0.01	<0.001	HG2	R	<0.01	<0.001
NH_4^+ (mg kg^{-1})	CK1	S	15.6	0.953	CK2	R	<0.01	<0.001
	LG1	G	3.2	0.842	LG2	G	2.4	0.999
	MG1	E	9.1	0.921	MG2	G	3.1	0.934
	HG1	S	3.9	0.874	HG2	S	1.8	0.999
NO_3^- (mg kg^{-1})	CK1	G	2.2	0.876	CK2	R	<0.01	<0.001
	LG1	R	<0.01	<0.001	LG2	R ^a	<0.01	<0.001
	MG1	E	11.5	0.819	MG2	S	6.7	0.695
	HG1	G	2.5	0.952	HG2	E	3.1	0.802
SOC (g kg^{-1})	CK1	E	3.1	0.600	CK2	R	<0.01	<0.001
	LG1	G	36.2	0.702	LG2	R	<0.01	<0.001
	MG1	E ^a	2.2	0.788	MG2	R	<0.01	<0.001
	HG1	G	10.0	0.821	HG2	L	>18.7	0.265
TN (g kg^{-1})	CK1	E	5.9	0.844	CK2	R	<0.01	<0.001
	LG1	E	3.8	0.831	LG2	E	1.8	0.879
	MG1	S ^a	4.8	0.587	MG2	R ^a	<0.01	<0.001
	HG1	R	<0.01	<0.001	HG2	E	2.9	0.802
C/N ratio	CK1	R	<0.01	<0.001	CK2	S	10.0	0.546
	LG1	G	29.1	0.629	LG2	R	<0.01	<0.001
	MG1	R	<0.01	<0.001	MG2	R	<0.01	<0.001
	HG1	S	14.6	0.553	HG2	E	3.0	0.857

correlation between AGB and soil NO_3^- at lag intervals of 0.1–0.14 and 0–0.14 m in CK1 and CK2, respectively (Fig. 6). At a similar interval, the cross-correlation was not significant in other plots (Fig. 6).

4. Discussion

4.1. Effects of grazing intensity

At fine scale, the decrease in AGB and vegetation height along the grazing gradient (Fig. 2) is consistent with a previous study that was conducted in a similar desert steppe in China (Wei et al., 2000). The reduction of AGB by intensive grazing led to the dramatic decline of range for AGB and disappearance of its spatial dependence in one HG plot (Table 1 and Fig. 5a), suggesting that vegetation patch size

Table 3Pearson's correlation coefficients between AGB (g m^{-2}) and vegetation height (cm), SWC (vol%), soil NH_4^+ (mg kg^{-1}), NO_3^- (mg kg^{-1}), SOC (g kg^{-1}), TN (g kg^{-1}) and C/N ratio.

	Height	SWC	NH_4^+	NO_3^-	SOC	TN	C/N
CK1	0.290	–	0.205	0.310	0.205	–	0.211
CK2	0.539	–	–	0.173	–	–	–
LG1	0.299	–	–	0.212	–	–	–
LG2	0.302	–	–	0.277	–	0.234	–
MG1	0.425	0.170	–	–	–	–	–
MG2	0.359	–	–	0.163	–	–	–
HG1	0.455	–	–	–	–0.203	–	–
HG2	0.617	–	–	–	–	–	–

The correlation analyses were performed independently for each plot and only significant correlations ($\alpha = 0.05$, $n = 177$) are shown.

decreased with increasing grazing pressures. We also found that vegetation patches (roughly circular) became more homogenous under intensive grazing (Fig. 5b). Consistent with our near-surface photographic data, which showed that relatively larger vegetation patches were broken up to many smaller ones along the grazing gradient (Lin et al., in revision), our results suggested that vegetation fragmentation increased with increasing grazing intensity in this desert steppe. In arid and semi-arid environments, vegetation patches (especially the large ones) provide favorable habitats for maintaining species richness and improving seedling establishment (Callaway, 1997; Maestre et al., 2001, 2003). With the loss of large vegetation patches under grazing, fragmented vegetation could negatively affect pollination and reproduction (Aguilar et al., 2006), and increase the risk of plant species loss (Joshi et al., 2006). Previous studies have also found that fragmented vegetation induced loss of rare animal species and altered animal community composition (Golden and Crist, 1999). Therefore, range managers should avoid the use of high intensity grazing to maintain vegetation spatial pattern.

Even though plant height was significantly correlated with AGB (Table 3), its spatial heterogeneity was not decreased by heavy grazing (Tables 1 and 2), suggesting that spatial pattern of height distribution was different from that of AGB. This might have resulted from the changed plant community by grazing. Palatability of individual plant species affects the behavior of sheep so that more palatable species would likely to be consumed first. Therefore, a less palatable species with a relatively large size, such as *A. frigid*, could increase its abundance under high grazing pressure in desert steppes (Li et al., 2008), causing the disparity of grazing effects on the spatial heterogeneity between AGB and height. Though plant height has been successfully used to study the spatial

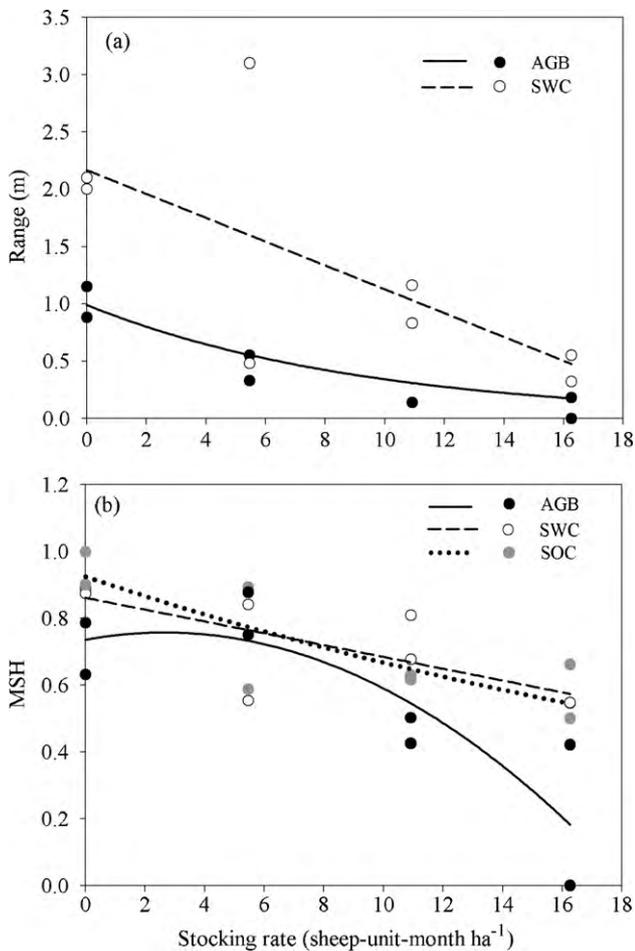


Fig. 4. (a) Relationships between the range for AGB (filled circle, solid line, exponential decay model: $P=0.016$, $R^2=0.648$) and SWC (empty circle, dash line, linear regression: $P=0.063$, $R^2=0.362$) and stocking rates at the fine scale. (b) Relationships between the MSH for AGB (filled circle, solid line, quadratic model: $P=0.034$, $R^2=0.742$), SWC (empty circle, dash line, linear regression: $P=0.033$, $R^2=0.487$) and SOC (grey circle, dotted line, exponential decay model: $P=0.012$, $R^2=0.685$) and stocking rates at the fine scale. For plots in which random or linear model were the best-fit for SWC semivariances, the range at the coarse scale was used instead.

pattern of vegetation (Olofsson et al., 2008), these results suggest that plant height only represents one aspect of spatial vegetation structure and it should be used with other parameters (e.g., AGB) for interpretation of data.

Much higher litter accumulation in LG than in MG and HG were previously found in an adjacent desert steppe (Li et al., 2008) and there was barely any litter cover observed in this site (Wang et al., unpublished data). In LG, the accumulated litter had a higher C/N ratio (~ 13 , Wang et al., unpublished data) than soil (~ 8) and was incorporated into soil to increase soil C/N ratio. It is well documented that grazing could promote plant belowground allocation and further increase resources availability through root turnover and root exudation (Holland et al., 1996; Pineiro et al., 2009). Those responses would likely happen in LG that maintained a similar plant biomass and vegetation height as CK and contribute to its higher C/N ratio, as moderate and heavy grazing strongly decreased biomass and modified spatial patterns of vegetation (Figs. 2 and 5).

Loss of soil C and N by overgrazing has been found in different types of steppes in Inner Mongolia (Su et al., 2005; Han et al., 2008; Steffens et al., 2008). These studies suggested that depletion of plant litter input and wind and water erosion were the major mechanisms for the soil total C and N loss under heavy grazing. However, neither SOC nor TN responded to grazing intensities in

this study (Fig. 2). We did observe the decreased heterogeneity of SOC patches with the increasing grazing pressure (Fig. 5b), which is consistent with the long-term (over 25 years) responses of SOC spatial patterns to grazing in a semi-arid steppe in Inner Mongolia (Wiesmeier et al., 2009). Our results suggest that grazing-induced changes in litter input and erosion could influence soil organic matter content; however, the length of treatment time (4 years) and small sample size might have limited our ability to detect responses of soil total C and N to grazing intensities. We will not be surprised to see significant degradation of soil organic matter after longer period of treatments.

Compared to SOC and TN, soil NH_4^+ and NO_3^- only had patchy spatial distribution in a few plots at fine scale and did not respond to the grazing intensity (Table 1), which is consistent with some previous research (Rietkerk et al., 2000; Augustine and Frank, 2001). This spatial pattern of soil mineral N suggests that their microbial-driven dynamics were randomly distributed in this desert steppe. Interestingly, soil NH_4^+ showed fine scale spatial patterns in LG plots, where the availability and overall variations of NH_4^+ were higher than heavy grazing (Figs. 2 and 3). Low grazing pressure likely positively influenced soil NH_4^+ availability by increasing N mineralization, litter input and plant root exudation, especially within vegetation patches (Holland et al., 1996; Frank and Groffman, 1998; Tracy and Frank, 1998). In this desert steppe, those indirect effect of sheep grazing on mineral N availability were more important than the direct effect of excreta addition (Hobbs, 1996), as HG was supposed to have higher N input from grazer excreta than LG. Our results suggest that grazing could change the small-scale spatial patterns of soil NH_4^+ and could consequently preserve soil fertility and forage production, if those influences are consistent over time.

4.2. Effects of sampling scale

Most of the studied variables had patchy spatial distributions at both fine and coarse scales; however, the patchy spatial patterns of soil NO_3^- were only present at the coarse scale and, similarly, those of soil NH_4^+ were only observed in a few plots at the fine scale (Tables 1 and 2). Those differences suggest that different mechanisms controlled the spatial distribution of soil mineral N at the two scales. At the fine scale, the availability and spatial pattern of soil mineral N are affected by plant root turnover, organic matter concentration, litter input, water availability, pH and others (Rietkerk et al., 2000; Gallardo et al., 2006; Housman et al., 2007). Those factors have complex interactions among each other and, consequently, generate a random spatial pattern of mineral N. While, topography is well known to modify the spatial variability of soil mineralization and N availability at a larger scale (Frank and Groffman, 1998; Tracy and Frank, 1998), and could be more influential in generating patchy spatial structure than the above factors.

All the responses of spatial patterns to grazing were observed at the fine scale, suggesting that grazing had limited influence on the spatial distribution of the studied variables at the coarse scale. Influenced by resources (food, water and minerals) availability, the interaction with plant community and management practices, grazing could demonstrate patchy spatial patterns at field or landscape level (reviewed by Adler et al., 2001). In this desert steppe, forage productivity was generally low compared to the need of grazers, especially in MG and HG plots, and fences around experimental plots could also make a larger proportion of land surface available for grazing (Adler et al., 2001 and references cited within). Therefore, those factors induced a more homogenous distribution of grazing that was not strong enough to alter the pre-existing spatial patterns of vegetation and soil fertility. On the contrary, grazing intensities significantly changed the vegetation patches and likely

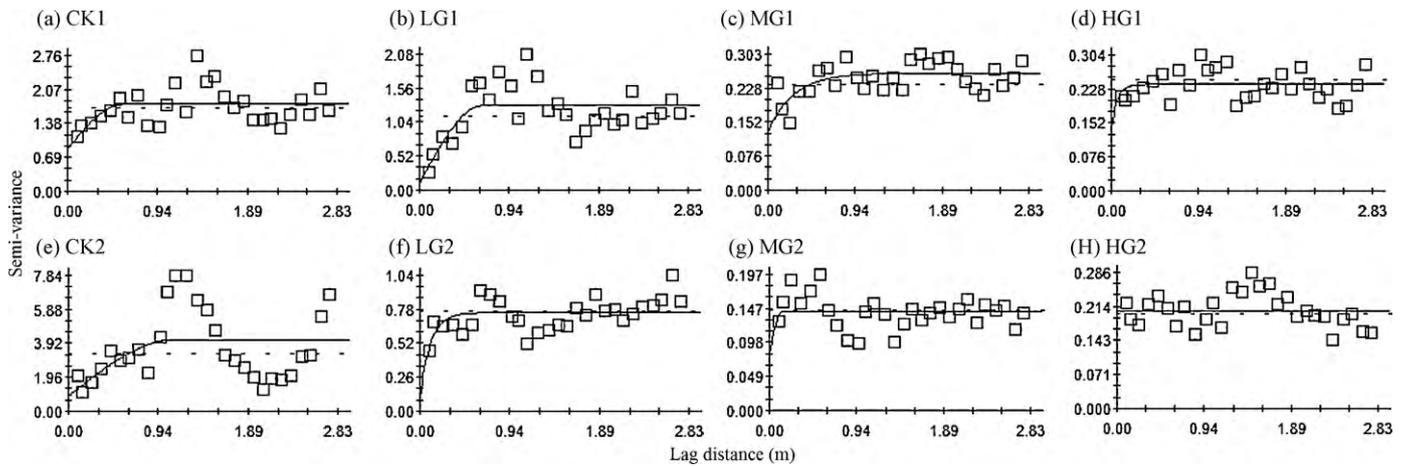


Fig. 5. Semivariogram for AGB in each plot. Refer to Table 1 for best-fit models.

affected the input of litter and plant belowground resources at the fine scale, consequently changing spatial distributions. With a recent study in a semi-arid steppe (Wiesmeier et al., 2009), our results suggest that small-scale responses of spatial patterns to grazing should be emphasized in the future to understand the influence of grazing on ecosystem processes and services in arid and semi-arid Eurasian steppes.

4.3. Relationships between vegetation and soil spatial patterns

Our results showed that only a few significant correlations (with only two have r larger than $|0.5|$) were found between AGB and soil variables (Table 3). As a large proportion of data in this study was collected at a fairly small scale (0.1–2 m), the strong variations among those samples would contribute to the weak correlations among variables. However, we did observe similar spatial responses between plant and soil to grazing intensities. For example, AGB and SWC all had the similar decreasing responses in their

ranges and MSHs to the increasing grazing pressures (Fig. 4). Even though the trends of the two variables were different in shape (Fig. 4), there was likely a relationship between the spatial distributions of AGB and SWC. Since we measured SWC after a series of rainfall events, plant water uptake would affect the spatial distribution of SWC (Rietkerk et al., 2000). As the size of vegetation patches was strongly reduced with increasing intensity (Fig. 4), the water uptake by plants could be limited to small patches under heavy grazing and caused the reduced size of SWC patches. Similarly, the SWC spatial pattern became more random when the vegetation patches were more homogenous under higher grazing pressure.

Another example of the relationship between plant and soil spatial distribution was found in the spatial cross-correlograms where the cross-correlation between AGB and soil NO_3^- at a small distance was only significant in CK (Fig. 6). Plants in CK formed larger patches and had higher aboveground biomass than those under grazing, which could create favorable microhabitats for the nitrifiers (Gallardo et al., 2006). However, those favorable conditions

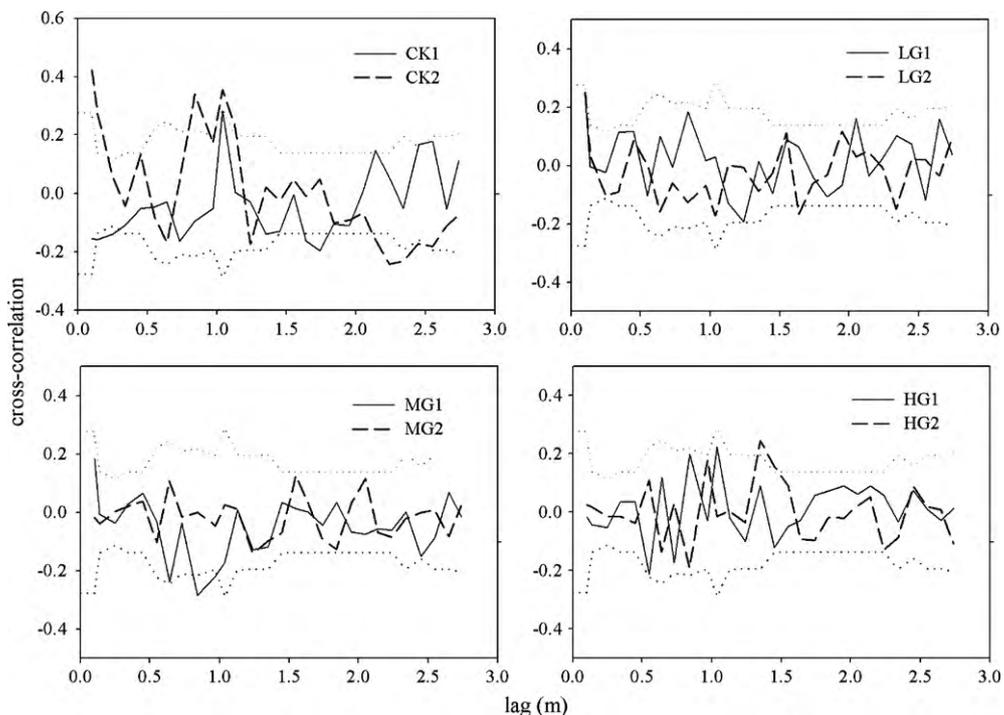


Fig. 6. Cross-correlogram between AGB and soil NO_3^- at fine scale under different grazing treatments. Dotted lines indicate critical values of the Pearson's correlation coefficient r ($\alpha=0.05$, $n=51$ –296) with the number of pairs at each lag class.

could be lost when grazing strongly modified vegetation patchiness. This result is consistent with our finding that the correlation between AGB and soil NO_3^- was not significant under heavy grazing (Table 3).

Unlike soil NO_3^- , correlation with AGB was not found in other soil variables. Schlesinger et al. (1996) found that islands of fertility were similar in size as the individual shrub and suggested this phenomenon would be more prominent in arid shrubland than in grassland ecosystems. In this perennial grass and forb species dominated steppe, it is possible that these species were less effective in forming islands of fertility than shrubs, causing the lack of overlap between the spatial patterns of soil nutrients and AGB. However, there were still connections between vegetation and soil nutrients that allow grazing to indirectly impact the spatial structure of soil nutrients through changing biotic processes such as plant community composition, litter input and plant root exudation, as discussed above. Our results revealed the importance of considering vegetation–soil feedback in the study of the spatial heterogeneity of soil nutrients even in grassland ecosystems.

5. Conclusions

Results from this study showed that grazing intensities altered the spatial patterns of vegetation and soil fertility at the fine scale in the studied desert steppe. In general, heavy grazing reduced the size of vegetation patches and increased the homogeneity of the spatial distribution of AGB, SOC and SWC. In contrast, light grazing intensity increased soil NH_4^+ availability and created the patchy spatial pattern of NH_4^+ . These results suggest that in range management light grazing is essential for preserving forage production and soil fertility. At the coarse scale, spatial patterns did not respond to grazing intensities, suggesting that grazing was spatially homogeneous in the plot. Loss of cross-correlation between AGB and soil NO_3^- in grazed plots indicates that grazing can alter the relationship between spatial patterns of vegetation and soil fertility. This study demonstrates that sheep grazing can generate, maintain and change the spatial patterns of vegetation and soil fertility in the studied desert steppe ecosystem. Future study should explore how grazing affects the ecosystem services in arid and semi-arid grasslands through changing the fine scale spatial patterns.

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