

# Grazing Gradient versus Restoration Succession of *Leymus chinensis* (Trin.) Tzvel. Grassland in Inner Mongolia

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## Abstract

Grazing-induced degradation of grasslands is the primary impediment to the socioeconomic development of Inner Mongolia. It affects the entire environment of northern China. Understanding grassland dynamics is necessary for restoration and sustainable management of these degraded ecosystems. The recovery dynamics of a degraded *Leymus chinensis* (Trin.) Tzvel. grassland after removal of grazing was studied in comparison with its spatial variation along a grazing gradient, using its climax community as a benchmark. The species composition, diversity, and biomass of the grassland vegetation, as well as the attributes (height, density, and individual mass) of major species, were examined on the eight sites along the grazing gradient and in the recovering grassland over 11 years. The spatial pattern of grassland vegetation along the grazing gradient closely reflected its recovery trajectory over time. Both the spatial and the temporal processes exhibited the same shift in species dominance in association with grazing removal or less grazing intensity. Grassland degradation was accompanied by an increase in species

density and a decrease in species size; this trend was reversed during recovery. This result suggested that the degraded grassland is highly resilient and that restoration could occur naturally by reducing or excluding grazing animals. However, some differences existed between the spatial and the temporal processes. Species richness was high on the light- or no-grazing sites along the gradient, but varied little during the recovery of the degraded grassland. Species evenness was high under moderate to light grazing along the gradient and was high at the beginning of the recovery period but not at the end. Although standing biomass improved significantly during the recovery period, it did not change significantly along the grazing gradient. These observed discrepancies were related to the intrinsic difference in the spatial versus temporal processes and are discussed together with the advantage/disadvantage of the grazing gradient versus dynamic monitoring methods in grassland dynamics studies.

**Key words:** biomass, degradation, size/density compensation, space-for-time substitution, species diversity.

## Introduction

The grazing gradient method has been widely used to study the effects of animal grazing on grasslands (Austin 1977; Andrew 1988; Bosch & Kellner 1991; Fusco et al. 1995; Pickup et al. 1998; Turner 1998; Fernandez-Gimenez & Allen-Diaz 2001; Adler & Hall 2005). In this method, grassland sites with different grazing intensities are compared and the spatial changes drawn from the comparison are used to infer grazing-associated grassland dynamics. The assumption in this space-for-time substitution approach is that the compared sites are subject to the same conditions and have the same species available to them (Pickett 1989; Hooper 2004). But this assumption is not realistic. The sites along grazing gradients are not of

different ages but have experienced and are experiencing different grazing impacts. They may, at the time of observation, be in the process of retrogressive or recovery succession under the influence of current grazing practices or be in equilibrium with them (Pickup et al. 1998).

Although recognizing the necessity and convenience of the grazing gradient method, data collection under controlled conditions is needed to confirm the results of grazing gradient studies (Fernandez-Gimenez & Allen-Diaz 2001) and to expose dynamic mechanisms (Pickett 1989). Though many grazing gradient studies, as cited above, and some monitoring studies under controlled conditions exist (e.g., Zhang & Skarpe 1995; Hart 2001), few studies have been devoted to comparing these two processes over space and time.

Grassland degradation is the principal challenge to the socioeconomic development of Inner Mongolia. It affects the entire environment of northern China. Understanding grassland dynamics in relation to animal grazing is urgently needed to guide decision-making for sustainable management of the grasslands. Both monitoring studies of grassland dynamics (Zhang & Skarpe 1995; Wang et al. 1996a, 1996b; Katoh et al. 1998) and studies investigating

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variations along grazing gradients (Wang et al. 1985; Li 1989) have been conducted in the region. Li (1992) also suggested that a relationship might exist between the spatial variation along the grazing gradient and the temporal variation during recovery of the degraded grassland. However, this conclusion was based on only two observations on the recovering grassland.

Here, we report a study of the spatial variations of the typical steppe grassland along a grazing gradient, along with temporal changes during recovery after removal of animals on a previously heavily grazed site. We had two aims: (1) to understand the processes of grazing-associated grassland dynamics in terms of species diversity and biomass, as well as the attributes of the major species, by integrating the results from both dynamics monitoring and spatial gradient studies and (2) to investigate the similarities and differences between grazing-associated grassland changes in space and in time and assess the appropriateness of the grazing gradient versus dynamics monitoring methods in grassland dynamics studies.

## Methods

### *Leymus chinensis* Grassland

*Leymus chinensis* (Trin.) Tzvel. [syn. *Aneurolepidium chinense* (Trin.) Kitag.] is a xeric rhizomatous grass with broad ecological amplitude to environmental aridity (Wu 1980). *Leymus chinensis* grassland (Photos 1 & 2) is widely distributed in the steppe zone of the Inner Mongolian Plateau and in the northeast China plain, covering an area of about 420,000 km<sup>2</sup> (Wu 1980; Wang et al. 1985). These regions have been used as grazing land for thousands of years, but the increase in livestock numbers and the shift from a nomadic to a sedentary grazing regime have led to serious degradation during the past several decades (Thwaites et al. 1997). Preventing grassland degradation and restoring the degraded areas are the major issues in current grassland management in the region.



Photo 1. Landscape of the *Leymus chinensis* grassland.

### Site Description

The field work was done at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) of the Chinese Academy of Sciences, located in the Xilingol region of Inner Mongolia, 60 km southeast of Xilinhot city (lat 43°26'N–44°08'N and long 116°04'E–117°05'E). The region experiences a temperate–semiarid climate, with an annual mean temperature around 0°C and annual precipitation around 350 mm. The precipitation has a wide inter-annual fluctuation ranging from 180 to 550 mm, 60–80% of which falls during the summer season of June to August. *Leymus chinensis* steppe on a sandy loam dark chestnut soil is the “zonal vegetation” (Jiang 1988; Wang & Cai 1988), that is, the major vegetation occurring as natural landscapes in the climatic zone (Box & Fujiwara 2005). Grazing livestock are mainly sheep and cattle, and, less importantly, goats and horses. Nomadic grazing in the region ended in the early 1950s when villages were set up and livestock were managed collectively.

### Data Collection

The vegetation in two permanent plots and along a grazing gradient (defined below) was monitored or surveyed during the plant-growing season. The plots and the gradient were located within an area of 15 × 5 km in the same topographical unit with an altitude of 1,230 m (above sea level) (Fig. 1). The vegetation at all sites was sampled using the 10 quadrats of 1 m<sup>2</sup>. The height and density (shoots of rhizomatous species *L. chinensis*, tufts of bunchgrasses, or individuals of forbs) of each species were measured or counted. The aboveground standing biomass was clipped species by species to ground level, oven dried at 60°C, and weighed. Details of the plots and the sampling time and method are as follows:

- (1) Recovery plot: A 26-ha permanent plot was set up in 1983 by IMGERS to monitor the recovery of the degraded *L. chinensis* steppe. The plot was close to



Photo 2. Community structure of the *Leymus chinensis* grassland (animal grazing was excluded during the season).

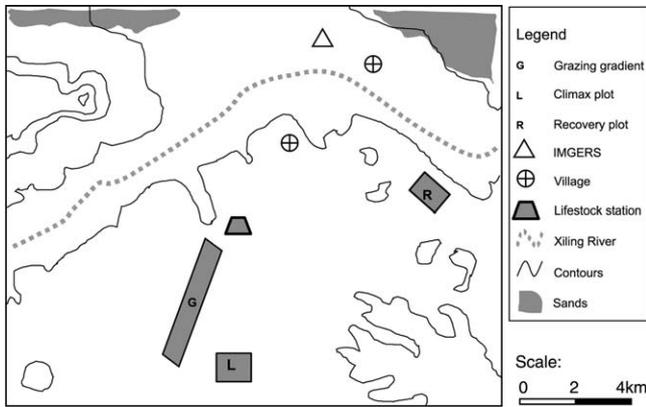


Figure 1. Layout of the sample plots and the surrounding environments (IMGERS of the Chinese Academy of Sciences).

a water source (Xilin River) and two villages. The grassland had been heavily grazed and therefore was degraded at the time of fencing, with *Artemisia frigida* Willd., *Cleistogenes squarrosa* (Trin.) Keng, and *Agropyron michnoi* Roshev. as the dominant species (Photos 3 & 4). The plot has a very slight slope, so that the 10 quadrats were randomly arranged as a line transect along the slope within a permanent area of 100 × 100 m, and sampled at seasonal peak herbage mass (on 1 August) during 1983–1993. The 11 annual samples were coded R83–R93.

- (2) Grazing gradient: This was a series of seven sites along a grazing intensity gradient within a range of 4.6 km (coded as G1–G7) plus one site in the climax plot (G8, no grazing, see below). The first site (G1) was a heavily grazed area close to a permanent livestock station for managing collective livestock (including livestock pens, hay storage, and watering facilities, etc.), with sites G2–G7 progressively further outward toward the climax plot of *L. chinensis* steppe. The distances of the sites G1–G7 to the livestock station are

0.6, 0.9, 1.6, 2.5, 3.1, 3.8, and 4.6 km, respectively. The area is flat with an average grazing intensity of about 1 sheep unit per hectare at the time of investigation (late July and early August, 1985). The 10 quadrats of 1 m<sup>2</sup> were randomly sampled within a small area (50 × 30 m) on each selected site.

- (3) Climax plot: A 25-ha permanent plot was set up by IMGERS to study the climax community of *L. chinensis* grassland. It is about 5 km distant from water sources and had been very lightly used before being fenced in 1980. The 10 quadrats were randomly sampled within a 100 × 100-m permanent area at seasonal peak herbage mass (five on 1 August and another five on 15 August) during 1983–1993. We used one observation (5 quadrats) on 1 August to analyze grassland biomass and two observations (10 quadrats) to compare species richness and diversity with the samples from the recovery plots and along grazing gradients sampled using the 10 quadrats. The 11 annual samples were coded L83–L93.

Although some of the data from these two plots and the gradient have been presented separately in other studies (Li 1989; Wang et al. 1996a, 1996b; Xiao et al. 1996), our focus here is on the dynamics of the grassland in the recovery plot compared with the spatial patterns along the grazing gradient.

The nomenclature for species names was according to Liu & Liu (1988) and Ma (1978–1985).

**Data Analysis**

Because no replications of the recovery plot were available, the vegetation in the climax plot was used as a control for analyzing the dynamics of the recovering community. This analysis was similar to the “before-after-control impact” analysis (Stewart-Oaten et al. 1986; Michener 1997), but we used the climax community instead of the degraded community as the control. The grazing intensity on the degraded community was



Photo 3. Landscape of the *Artemisia frigida* grassland.



Photo 4. Community structure of the *Artemisia frigida* grassland (animal grazing was excluded during the season).

uncontrollable because it was under public grazing, whereas the climax community was theoretically in a stable state (Li et al. 1988; Cingolani et al. 2005) and experienced no grazing-associated changes while under protection. The climax plot, situated at one end of the grazing gradient, was also a reference for spatial vegetation changes on the gradient.

Each observation, either on different sites of the grazing gradient or in different years on the same site of recovering community or climax community, was treated as a different sample. The average species attributes in the 10 quadrats of each sample, including height, density, and aboveground biomass, were used in the comparative analysis. All calculations and statistical analyses were done using MINITAB14.

- (1) The species richness of plant community was measured as the total number of species recorded in the 10 quadrats. Species diversity ( $H$ ) and evenness ( $E$ ) were calculated using Shannon-Wiener indices,  $H = \sum_{i=1}^S [P_i \times \ln(P_i)]$  and  $E = \frac{H}{\ln(S)}$ , where  $S$  is the species richness and  $P_i$  is the biomass percentage of each species in community biomass. Their variation patterns along the grazing gradient and during the recovery were compared with the diversity features of the climax plot vegetation.
- (2) Vegetation variation along the grazing gradient, and between the grazing gradient and the recovery and climax plots, was analyzed using principal component analysis (PCA). The vegetation variations, in relation with the relative grazing intensity (RGI, defined as the inverse of the distance of a site to the livestock station, and zero for G8 in the climax plot) on the grazing gradient or between recovery years (Y), were interpreted by regressing the coordinates of vegetation samples on the first two PCA axes against RGI or Y. The vegetation samples were also clustered into three community types based on their similarities (measured by Euclidean distance) to reveal species dominance and general community features on the heavy-, moderate-, or no-grazing sites compared with those in the earlier, medium, and late recovery stages.
- (3) The change tendency of species height, density, and biomass during the recovery period was examined by calculating Pearson correlations between these attributes and recovery years. For comparison purpose, their correlations with the distance of the sites to the livestock station (5 km was assigned to site G8) along the grazing gradient were also calculated. We also explored the possibility of other change patterns in these species attributes by plotting "attributes-RGI" or "attributes-recovery years" graphs.

## Results

### Species Composition

Fifty-five species were recorded in the recovery plot (110 quadrats), 56 on the grazing gradient (80 quadrats), and

64 in the climax plot (110 quadrats). Species compositions of the grassland in the two fenced plots and along the grazing gradient were very similar, with 39 species in common, which were also dominant species, including perennial grasses *Leymus chinensis*, *Stipa grandis* P. Smirn., *Agropyron michnoi*, *Cleistogenes squarrosa* and forbs *Artemisia frigida*, *A. commutate* Bess., *Potentilla tanacetifolia* Willd ex Schlecht., and *Kochia prostrata* (L.) Schrad. In addition, based on the repeated sampling each year in plant-growing season (unpublished data), all the species recorded in the recovery plot were in the species pool of the climax plot and all species, except *S. krylovii* Rosh., along the grazing gradient were also in the species pool of the climax plot.

### Species Richness and Evenness

Variations in species richness were small in the recovering community ( $33 \pm 3$  as  $\bar{X} \pm \text{SD}$ , range from 27 to 37) and in the climax community ( $39 \pm 2$ , range 37–44) during the 11-year observation period; they were larger in the communities along the grazing gradient ( $36 \pm 6$ , range 28–46). Species richness was significantly lower ( $p = 0.001$ ) on the heavy- to moderate-grazing sites (32.2 average on G1–G5) than on the light- or no-grazing sites along the gradient (42.7 average on G6–G8), but no significant change was found in the recovering community and climax community during the observation period (Fig. 2a).

The average species evenness was significantly higher ( $p < 0.001$ ) in the recovering community ( $E_r = 0.70$ ) than in the climax community ( $E_c = 0.57$ ) during the observation period, and the  $E_r$  decreased with the recovery years (Y) ( $E_r = 0.789 - 0.01495Y$ ;  $p = 0.004$ ), converging with that in the climax community, whereas  $E_c$  had no significant change ( $p = 0.139$ ) during the same period. This change differed from that along the grazing gradient, where the evenness appeared high under light to moderate grazing (Fig. 2b). The species diversity showed similar change patterns to those of species evenness in all three cases due to the relatively small variation in species richness (Fig. 2c).

### Standing Biomass

The aboveground standing biomass of both the climax community and the recovery community showed a large interannual fluctuation. It averaged  $150 \pm 50$  g DM/m<sup>2</sup> in the recovering community and increased significantly during the 11-year observation period. The biomass and recovery years were linearly correlated ( $r^2 = 0.575$ ,  $p = 0.007$ ). The biomass change could be described more reasonably as a logarithmical increase toward a biomass plateau ( $r^2 = 0.592$ ,  $p = 0.006$ ; Fig. 3). The average biomass of the climax community over the same period ( $159 \pm 48$  g DM/m<sup>2</sup>) was slightly higher than that of the recovering community but was not correlated with the years ( $p = 0.828$ ), that is, it had no directional change during the same period.

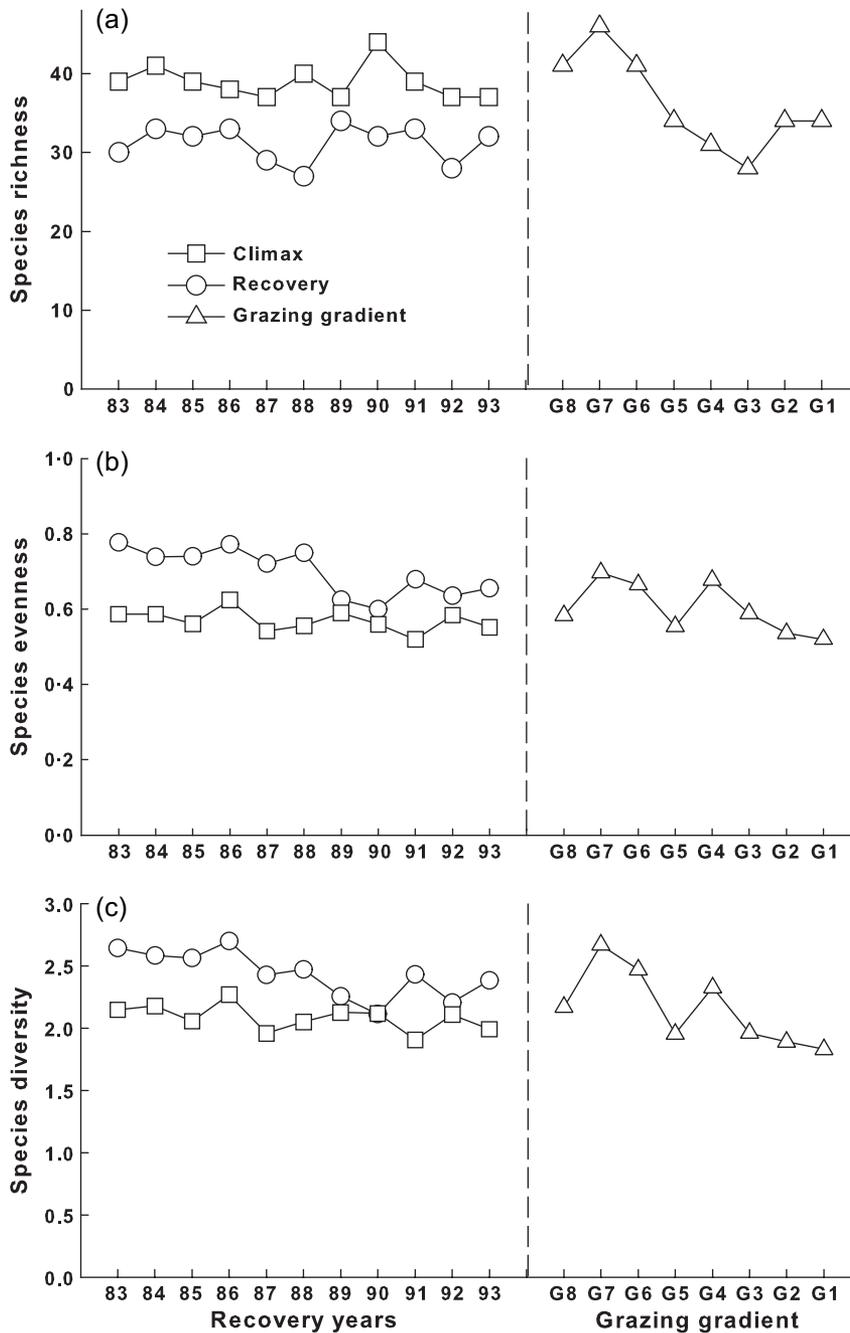


Figure 2. Changes in (a) species richness, (b) evenness, and (c) diversity of *Leymus chinensis* grassland during the recovery of a degraded community (○: 1983–1993) and along a grazing gradient (△: G1–G8), in comparison with the climax community (□: 1983–1993).

Variation in the standing biomass in the seven grazing sites along the grazing gradient was very small ( $117 \pm 4$  g DM/m<sup>2</sup>) with no directional changes. The correlation between biomass and RGI was insignificant ( $p = 0.546$ ).

**Community Relations—Correspondence Between Spatial and Temporal Changes**

The PCA of all 30 vegetation samples was conducted on the basis of species biomass percentage (Fig. 4). The loca-

tion of the vegetation samples on Figure 4a mainly reflected their relations with RGI or recovery time. The RGI of the vegetation sites along the grazing gradient was significantly correlated with their coordinates on the first ( $X_1$ ) and second ( $X_2$ ) PCA axes ( $RGI = 2.76 + 13.4X_1$ ;  $r^2 = 0.787$ ,  $p = 0.003$  and  $RGI = 0.179 - 2.39X_2$ ;  $r^2 = 0.529$ ,  $p = 0.041$ ). That is, the vegetation samples along the gradient of increasing grazing intensity moved from the top left corner to right bottom corner on the Figure 4a, whereas

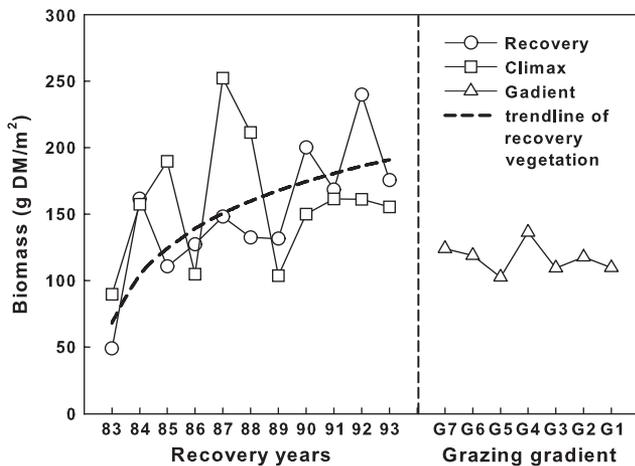


Figure 3. Changes in the standing biomass in *Leymus chinensis* grassland during the recovery of a degraded community (○: 1983–1993) and in the grazing sites of a grazing gradient (△: G1–G7), in comparison with the climax community (□: 1983–1993). The biomass (B) of the degraded community improved significantly with the recovery years (Y):  $B = 51.2 \times \ln(Y) + 168.1$ ;  $r^2 = 0.592$ ,  $p = 0.006$ .

the recovery trajectory of the degraded grassland moved in the opposite direction toward the top left corner. The recovery years (Y) of the recovering vegetation samples also had significant correlations with their coordinates on the first ( $X_1$ ) and second ( $X_2$ ) axes ( $Y = -12.2 - 100X_1$ ;  $r^2 = 0.398$ ,  $p = 0.038$  and  $Y = 8.16 + 21.5X_2$ ;  $r^2 = 0.621$ ,  $p = 0.004$ ).

Figure 4a shows an obvious similarity between the spatial changes in the grassland along the grazing gradient and the temporal changes during the recovery succession. It also shows that vegetation in the recovering community had a smaller variation during the recovery period (shorter gradient in Fig. 4a) than that along the grazing gradient, and that climax vegetation had little interannual variation in terms of species biomass composition.

#### Biomass Composition

The similarity of grassland communities shown in Figure 4a reflected mainly the biomass composition of grassland vegetation, especially the biomass changes in dominant species, as indicated by Figure 4b. All the vegetation samples were clustered into three groups (community types) based on their similarities in biomass composition (Table 1), although the vegetation change was gradual. These three relative groups were mostly related to the grazing impact on the vegetation, as shown by their location in Figure 4a.

The 21 species in Table 1 included 19 major species with biomass percentages bigger than 1% in all vegetation samples along the grazing gradient and during the 11-year recovery (R83–R93 and G1–G7). The remaining two species, *Achnatherum sibiricum* (L.) Keng and *Serratula centauroides* L., ranked 4<sup>th</sup> and 7<sup>th</sup> in biomass in the climax community but were not important components of biomass in the recovering community or along the grazing

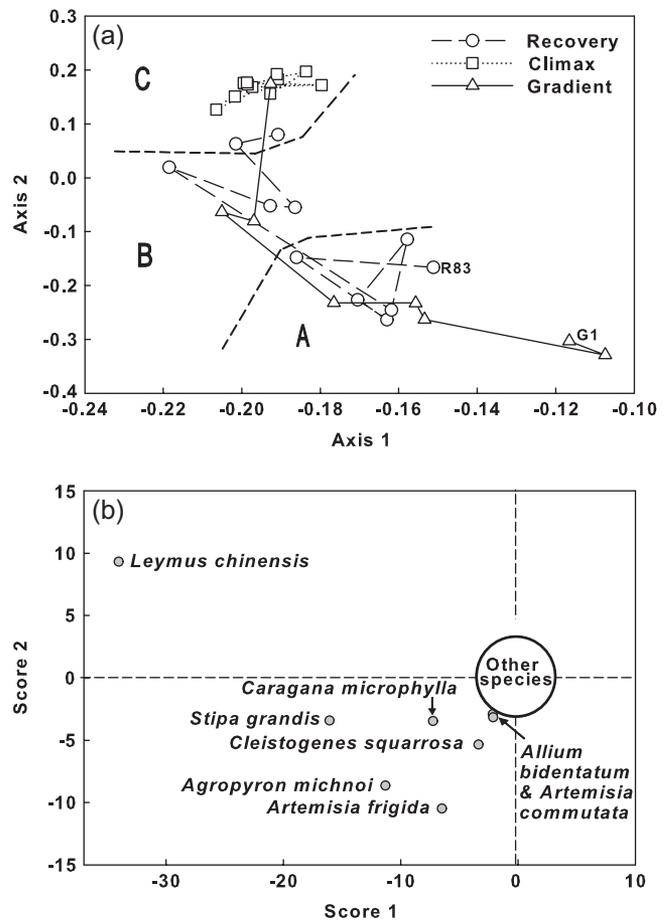


Figure 4. (a) PCA ordination of vegetation sites of the grazing gradient (△, linked sequentially according to grazing intensity, with the heaviest grazing site G1 marked) and of the recovering vegetation (○, linked according to recovery years with the first year R83 marked), together with that of climax vegetation (□). The first and the second axes represent 67.6 and 17.8% of the vegetation variation. A, B, and C are the three clusters representing community types associated with heavy, moderate, and light grazing or in early, medium, or late recovery stages. The grouping of three samples was adjusted to keep the adjacent years together (R89 from group C to B) or reduce number of groups (R83 and R87 was a separate group at the similarity level of this division, but merged in group A). (b) Plot of the species scores on the first and second principal components, indicating the roles of dominant species in PCA. The changes in biomass percentage of major species were shown in Table 1.

gradient. These 21 species comprised about 95% of plant standing biomass in the grassland under study.

Type A included the vegetation samples either surveyed on the heavy- to moderate-grazing sites of the grazing gradient (G1–G5) or observed in the first 6 years of recovery of the degraded community (R83–R88). It constituted the grazing-derived community type of the *L. chinensis* steppe, with *A. frigida* as the most dominant species.

Type B included the vegetation samples on the light-grazing sites (G6 and G7) and the recovering community during its recovery from 7 to 9 years (R89–R91). *Leymus*

**Table 1.** Percent biomass of major species (>1%) in three grazing-related community types of *Leymus chinensis* grassland.

| Community Types<br>Composition of Samples | Type A<br>(R83–R88, G1–G5)* | Type B<br>(R89–R91, G6 and G7) | Type C<br>(R92 and R93, Climax and G8) |
|---|-----------------------------|--------------------------------|--|
| <b>Grasses and sedges</b>                 |                             |                                |  |
| <i>L. chinensis</i>                       | 12.0 (9.8, 14.7)            | 20.8 (22.1, 18.8)              | 42.0 (30.8, 43.9)                      |
| <i>Agropyron michnoi</i>                  | 12.2 (14.3, 9.6)            | 14.5 (15.9, 12.4)              | 5.9 (15.7, 4.3)                        |
| <i>Stipa grandis</i>                      | 8.8 (10.5, 6.7)             | 20.5 (20.1, 20.0)              | 14.4 (7.3, 15.6)                       |
| <i>Cleistogenes squarrosa</i>             | 5.3 (4.5, 6.4)              | 3.0 (2.7, 3.6)                 | 1.2 (1.9, 1.1)                         |
| <i>Koeleria cristata</i>                  | 2.3 (2.1, 2.4)              | 3.4 (3.8, 2.8)                 | 1.7 (3.5, 1.5)                         |
| <i>Carex korshinskyi</i>                  | 0.9 (0.1, 1.9)              | 1.0 (0.1, 2.4)                 | 2.7 (0.1, 3.1)                         |
| <i>Achnatherum sibiricum</i>              | —                           | 0.1 (0.1, 0.1)                 | 3.7 (—, 4.4)                           |
| <b>Forbs</b>                              |                             |                                |  |
| <i>Artemisia frigida</i>                  | 27.0 (14.8, 41.7)           | 10.0 (8.7, 11.8)               | 1.1 (3.1, 0.7)                         |
| <i>A. commutata</i>                       | 5.3 (12.4, 1.7)             | 1.8 (2.2, 2.2)                 | 2.2 (0.9, 5.9)                         |
| <i>Potentilla tanacetifolia</i>           | 3.0 (4.1, 1.7)              | 2.2 (0.7, 4.6)                 | 0.8 (3.1, 0.5)                         |
| <i>Kochia prostrata</i>                   | 2.8 (4.9, 0.3)              | 2.3 (3.4, 0.5)                 | 1.3 (2.0, 1.2)                         |
| <i>Allium bidentatum</i>                  | 2.8 (4.3, 1.0)              | 2.6 (4.1, 0.3)                 | 1.1 (7.1, 0.1)                         |
| <i>Heteropappus altaicus</i>              | 1.4 (1.3, 1.4)              | 1.1 (1.2, 1.0)                 | 0.6 (0.1, 0.7)                         |
| <i>P. acaulis</i>                         | 1.3 (0.4, 2.4)              | 0.7 (0.6, 0.9)                 | 1.1 (5.0, 0.4)                         |
| <i>Melissitus ruthenica</i>               | 1.2 (1.7, 0.6)              | 0.8 (0.9, 0.6)                 | 0.7 (3.2, 0.3)                         |
| <i>A. ramosum</i>                         | 1.0 (1.8, 0.1)              | 1.3 (0.7, 2.3)                 | 0.2 (1.2, 0.1)                         |
| <i>Serratula centauroides</i>             | —                           | 0.4 (—, 1.1)                   | 2.8 (—, 3.3)                           |
| <b>Annuals</b>                            |                             |                                |  |
| <i>Artemisia scoparia</i>                 | 2.2 (4.0, —)                | 0.4 (0.6, 0.0)                 | 3.0 (0.1, 3.5)                         |
| <i>Salsola collina</i>                    | 1.4 (2.2, 0.5)              | 1.7 (0.1, 3.9)                 | 1.4 (0.1, 1.7)                         |
| <i>Chenopodium album</i>                  | 1.1 (0.1, 2.4)              | 1.1 (0.1, 2.5)                 | 0.2 (0.2, 0.2)                         |
| <b>Shrubs</b>                             |                             |                                |  |
| <i>Caragana microphylla</i>               | 3.8 (7.0, 0.1)              | 5.1 (8.5, 0.1)                 | 5.7 (11.1, 4.8)                        |
| Total percentage (%)                      | 95.8                        | 94.7                           | 93.8                                   |
| Biomass ± SD (g DM/m <sup>2</sup> )       | 119 ± 29                    | 149 ± 30                       | 173 ± 56                               |

The less important species not listed with biomass >1% in any one vegetation sample include *Astragalus galactites* Pall., *Axyris amaranthoides* L., *Cymbaria dahurica* L., *Dontostemon glandulosus* Karelín & Kirilov, *Iris tenuifolia* Pall., *Melandrium apricum* (Turcz.) Rohrb., *Poa attenuata* Trin., *Potentilla bifurca* L., *Saposhnikovia divaricata* (Turcz.) Schischkin, *Silene jennisensis* Willd., *Vicia unijuga* A. Braun, and *Corispermum chinganicum* Iljin.

\*Data in brackets are the percentage of average of the corresponding vegetation samples in the recovering community or on the grazing gradient.

*chinensis* and *S. grandis* were the most dominant species, and *A. michnoi* was abundant.

Type C was representative of the *L. chinensis* climax community, including all the samples in the climax plot (L83–L93 and G8) and the recovering community after 10 years of recovery (R92 and R93). *Leymus chinensis* was the predominant species, comprising 44% of the community biomass.

The similar species composition in these community types suggested that species dominance instead of species presence/absence was the main reason for vegetation change during grassland degradation and recovery. The clustering of samples along the grazing gradient and in the recovering community into the same three groups signified that the shifts in species dominance between the degraded community and the climax community were similar along the grazing gradient and during recovery.

#### Species Attributes

In addition to the changes in species biomass percentage during recovery or along the gradient shown in Table 1, the changes in biomass, density, and size (height and individual

mass calculated as species biomass divided by density) of major species were analyzed and summarized (Table 2).

**Species Biomass.** With improvements in biomass in the recovering community, the biomass of many species, especially the dominant species of the climax community, e.g., *L. chinensis*, increased significantly (positive correlation with recovery years in Table 2) during the 11-year period. In contrast, the dominant species in the degraded community, e.g., *A. frigida*, mainly showed a decrease in biomass percentage during recovery (negative correlation in Table 2). Similar biomass change patterns were found along the grazing gradient, e.g., *L. chinensis* and *S. grandis* increased, whereas *A. frigida* and *C. squarrosa* decreased, in their biomass or biomass percentage, with a decrease in grazing intensity.

**Species Density.** *Leymus chinensis* was the only species showing a significant increase in density during the 11-year recovery but not along the grazing gradient. Decreases in species density were very common during recovery and with decreasing grazing intensity along the gradient. These species included both the dominant species of the

**Table 2.** Significant correlations of the major species attributes with recovery years or with the distance along the grazing gradient (distance as the inverse of RGI).

| Species Names <sup>a</sup>            | With Recovery Years in the Recovering Grassland (n = 11) |            |          |         |                              | With Distance Along the Grazing Gradient (n = 8) |            |          |         |                 |
|---------------------------------------|--|------------|----------|---------|------------------------------|--|------------|----------|---------|-----------------|
|                                       | Biomass  | Proportion | Density  | Height  | Individual Mass <sup>b</sup> | Biomass  | Proportion | Density  | Height  | Individual Mass |
| <i>Artemisia commutata</i>            | -0.75**  | -0.94***   |          |         |                              |  |            |          | 0.73*   |                 |
| <i>Salsola collina</i>                | -0.54~   | -0.63*     | -0.53~   | 0.57~   | 0.83**                       |  |            |          | 0.75*   |                 |
| <i>A. frigida</i>                     |  | -0.67*     | -0.79**  |         | 0.90***                      | -0.98***   |            | -0.98*** | -0.89** | 0.86**          |
| <i>Cleistogenes squarrosa</i>         |  | -0.70*     | -0.86*** | 0.63*   | 0.86***                      | -0.64*   |            | -0.73*   | 0.70*   | 0.81~           |
| <i>Chenopodium album</i>              |  | -0.55~     | -0.66~   | 0.70*   |                              |  | -0.72*     |          | 0.79*   |                 |
| <i>Kochia prostrata</i>               |  | -0.68*     |          |         |                              |  |            |          |         |                 |
| <i>Heteropappus altaicus</i>          |  | -0.45*     |          |         |                              |  |            |          | 0.65~   |                 |
| <i>Potentilla tanacetifolia</i>       |  |            | -0.74**  | 0.87*** | 0.75**                       |  |            |          | 0.90*   |                 |
| <i>Carex korshinskyi</i> <sup>d</sup> |  |            |          | 0.96*** | 0.96***                      |  |            |          | 0.69~   | 0.76*           |
| <i>Serratula centauroides</i>         |  |            |          |         |                              |  | -0.65      | 0.71~    | 0.76*   |                 |
| <i>Achnatherum sibiricum</i>          |  |            |          |         |                              |  |            | 0.64~    | 0.86**  |                 |
| <i>Stipa grandis</i> <sup>d</sup>     |  |            | -0.63*   | 0.77**  | 0.70*                        | 0.93***  | 0.78*      |          | 0.95*** | 0.71*           |
| <i>Melissitus ruthenica</i>           | 0.55~  |            |          | 0.48~   |                              |  |            |          | 0.88*   | 0.82*           |
| <i>Agropyron michnoi</i>              | 0.53~  |            |          | 0.58~   | 0.56~                        |  |            |          | 0.89*   | 0.73*           |
| <i>Caragana microphylla</i>           | 0.81**   | 0.19~      |          |         | 0.89***                      |  |            |          | 0.75*   |                 |
| <i>Allium bidentatum</i>              | 0.72*  |            |          |         |                              |  |            |          |         |                 |
| <i>P. acaulis</i>                     | 0.65*  | 0.60~      | -0.68*   | 0.71*   | 0.77*                        | -0.66~   | -0.78*     | -0.67~   |         |                 |
| <i>Koeleria cristata</i>              | 0.80**   | 0.63*      | -0.70*   |         | 0.65*                        |  |            | -0.65~   | 0.70*   |                 |
| <i>Leymus chinensis</i>               | 0.77***  | 0.71*      | 0.61*    | 0.78**  | 0.89***                      | 0.61~  | 0.71       |          | 0.88**  | 0.76**          |

<sup>a</sup>The species are listed in ascending order of the correlation coefficients between species biomass in the recovering community and recovery years, thus the dominant species in the degraded community appear in the upper part of the table, whereas the dominant species in the climax community are in the lower part. Only species with biomass percentage >1% and significant coefficients are listed. The significant levels are \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , and ~ $p < 0.10$ .

<sup>b</sup>Average individual species mass.

<sup>c</sup>A quadratic relation found between the individual mass of *A. frigida* and the recovery years, with  $r^2 = 0.90$ .

<sup>d</sup>Also includes small quantities of *S. krylovii* and *C. duriuscula* C. A. May, respectively, on the heavy-grazing sites (identified by a few seed sets) but are not completely distinguishable because most of them had no seed sets when sampling took place.

degraded community, e.g., *A. frigida*, and that of the climax community, e.g., *S. grandis* (Table 2).

**Species Size (Individual Height and Mass).** No species had a significant decrease in height or individual mass during the recovery of the degraded community or along the gradient of grazing intensity decrease, but increases in the height or individual mass of species were common. Seventeen of the 21 species showed a significant height increase during recovery or with decreases in grazing intensity along the gradient. Accordingly, the individual masses of many common species, e.g., *L. chinensis* and *C. squarrosa*, became significantly bigger during recovery or with decreases in grazing intensity along the gradient (Table 2).

The combination of the size increase and density decrease in the most common species during recovery and with decreases in grazing intensity along the gradient suggested that the degradation of grassland production was, at a species level, mainly a consequence of a decrease in species size, accompanied mostly by an increase in density. The recovery succession reversed this process.

**Other Relations.** Besides calculating simple correlations between species attributes and RGI or recovery years, other possible relations were explored by plotting the

attributes–RGI or attribute–recovery years graph and relation fitting. Only one significant quadratic relation was found between the individual mass ( $M$ ) of *A. frigida* and recovery years ( $Y$ ):  $M = -1.09 + 1.20Y - 0.09Y^2$  ( $r^2 = 0.90$ ,  $p < 0.001$ ). That is, the individual mass of *A. frigida* increased at the beginning of recovery and then decreased. But this did not happen along the grazing gradient. In addition, *S. grandis* and *A. michnoi* showed a higher biomass percentage under the moderate (G6 and G7) than under both heavy and light grazing and a higher percentage in medium (R89–R91) than in either early or late recovery stages (Table 1), but no significant relationships were identified.

## Discussion and Conclusions

### Space-for-Time Substitution Approach

The widely accepted grazing gradient method (Andrew 1988; Pickup et al. 1998) in the research and management of grasslands has been applied to Mongolian steppe grassland (Li 1989; Fernandez-Gimenez & Allen-Diaz 2001). This study confirmed the general correspondence of the results from the grazing gradient method with those from direct dynamic observations. That is, the spatial changes in grassland vegetation along the grazing gradient were

generally in accordance with the recovery trajectory of the degraded grassland following removal of animals. In the *Leymus chinensis* grassland studied, both spatial and temporal processes exhibited the same shift in species dominance in association with grazing impact. Grassland degradation was accompanied by an increase in density, but a decrease in size of many common species, and this trend was reversed during recovery. However, some discrepancy existed between the spatial and the temporal processes.

### Species Diversity Patterns

Results showed lower species richness in the degraded community compared with the climax community, and also a lower species richness on the heavy than on the light- or no-grazing sites of the studied gradient. This result was in agreement with the generalized model of the effects of grazing on community diversity in lower productive grassland with a long grazing history (Milchunas & Lauenroth 1993; Cingolani et al. 2005). Although slightly higher species richness was observed on a light-grazing site along the gradient, our data were insufficient to confirm statistically higher species richness at the light- to moderate-grazing sites than at the no-grazing site. Furthermore, the species richness of the degraded community showed no significant increase during recovery, even when its community structure was approaching that at light- or at no-grazing sites. Some intrinsic differences existed between the spatial and the temporal pattern of species richness. For example, *Achnatherum sibiricum* and *Serratula centauroides* were constant and might never have disappeared on the light- to moderate-grazing sites of the studied gradient, but *A. sibiricum* was only occasionally recorded in the later recovery stage and *S. centauroides* was not recorded at all in the recovering community. Their recovery rate during the 11-year observation could not be reflected by their change rate along the grazing gradient, though the trends could be compared.

In contrast to species richness, species evenness (and diversity) was higher in the recovery community than in the climax community and decreased during recovery. This change agrees with the findings of Fernandez-Gimenez & Allen-Diaz (2001), who reported high species diversity on heavy-grazing areas close to water sources of the mountain steppe vegetation of Mongolia. However, species evenness along the studied gradient had different patterns and was higher at the moderate-grazing sites than at both no-grazing and heavy-grazing sites, as expected by the intermediate disturbance theory (Harper 1969). Because grazing intensity of the sites along the grazing gradient was relative, sites cannot be quantitatively compared along different gradients. We speculate that, based on the species evenness pattern, grazing intensities in the recovery plot before being fenced and possibly in the heavy-grazing areas of Fernandez-Gimenez & Allen-Diaz's study (2001) were lighter than those in the heavy-

grazing sites of the studied gradient. That is, the studied gradient included severely degraded sites containing the predominance of grazing-tolerant or grazing-facilitated species (e.g., *Artemisia frigida*) that led to a lower species evenness, whereas the grassland in other two cases did not include severe degradation.

### Grassland Biomass

The standing biomass of the recovering community improved during the 11-year period, as predicted by the range condition model (Dyksterhuis 1949), but the standing biomass along the grazing gradient did not change significantly. Even though the grassland was similarly productive at the different sites along the gradient, logically, the standing biomass should be lower on heavily grazed sites due to more consumption by grazing animals. The observed biomass pattern on the grazing gradient was related, to a large extent, to the sensitive biomass change of *A. frigida* in response to grazing. *Artemisia frigida* is a grazing-facilitated species. Its growth form changes from erect to prostrate under grazing, and its vegetative reproduction through stolons on prostrate stems was largely facilitated by animal trampling (Li & Wang 1997b; Li et al. 2005). It is a forage species of high protein, preferred by livestock in spring and autumn, but avoided in summer (Li & Wang 1997a). *Artemisia frigida* comprises about half of the grassland biomass at the two heavily grazed sites and this percentage decreased linearly with decreased grazing intensity. In the recovering community, the grassland was not affected by animal trampling and selective grazing. The biomass percentage of *A. frigida* was less important, although it also decreased significantly during recovery.

### Species Attributes and Size/Density Compensation

A reciprocal increase in density and decrease in size of many common species occurred along the grazing gradient and during the recovery. This phenomenon of size/density compensation (SDC) has been extensively reported in relation with self-thinning of plants in various ecosystems, including forests (Guo & Rundel 1998), pastures (Matthew et al. 1995), and arable crops (Kropff & Goudriaan 1994). The slope of log mass–log density relationship (Yoda et al. 1963) has been widely used and discussed to describe SDC relationships (Gorham 1979; Weller 1989). One consensus is that because more intensive defoliation reduces unit size and increases density, this response constitutes a mechanism whereby canopy leaf area index can remain comparatively constant over a range of defoliation intensities. However, most of the earlier reports of SDC in plant communities have been for monocultures or nearly pure stands of dominant species, whereas our study was of a complex community comprising species with a range of growth forms. The qualitative evidence of the SDC mechanism in operation was clearly seen in our case. It was also

obvious that some species were comparatively better adapted to high or low grazing intensity, and that these species adaptations to particular grazing intensities would be expected to have differing SDC slopes, though our data do not allow quantification of the SDC slopes because of the effects of interspecific competition in the mixed community (del-Val & Crawley 2004). In a mixed community, a small decrease in the size of a particular species under intensive grazing could be “over-compensated” by a large increase in its density, such as grazing-facilitated *A. frigida* and *Cleistogenes squarrosa*. The latter is a C4 plant, facilitated partly by the improved light conditions in degraded communities (Liang et al. 2002). In contrast, *Stipa grandis* had a higher density but lower per tuft mass on heavy- than on light-grazing sites or in early than later recovery stages. Its biomass increase due to increased density was outweighed by the decline in per tuft mass, resulting in a biomass decline in degraded communities.

#### Effects of Precipitation on Biomass

We did not analyze the effects of interannual variation in precipitation on the grasslands, although the effects were well recognized on grassland production in semiarid environments (Le Houerou et al. 1988). We found that whereas the biomass of the recovering community increased significantly over the observation period, the biomass of the climax community, which received the same amount and pattern of precipitation, did not increase significantly over the same period. We therefore concluded that improvements in biomass of the recovering community were the consequence of gradual recovery and not due to changes in weather conditions.

#### Effects of Spatial Heterogeneity

The effect of environmental heterogeneity in gradient studies has been well recognized (Pickett 1989). The vegetation sites along the studied grazing gradient unavoidably had a bigger variation in soil conditions than those monitored in the recovery plot, but there would have been spatial heterogeneity in all the plots. The comparability among the studied plots and gradient was based on the fact that they were on the same topographical unit and on the same soil type (Wang & Cai 1988) and based on previous long-term vegetation and land use studies in the area (Li et al. 1988). Considerable effort was put into selecting sites that minimized the effects of spatial heterogeneity and reduced the confounding effects of natural vegetation variation across the area. The grazing-induced *A. frigida* community was initially noted in the area of the recovery plot and the heavy-grazing sites of the studied gradient on a detailed vegetation map drawn in 1965 (Li et al. 1988). This was most likely associated with the establishment of villages and a livestock station in the 1950s and the 7-fold increase in livestock number during the following 15 years (Wu & Loucks 1992).

No soil factors were sampled simultaneously with the vegetation in this study, but existing studies show that soils in the two plots and along the gradient had very similar properties (Kang et al. 1992; Guan et al. 1997; Jia et al. 1997). Soil bulk density and surface hardness increased, whereas soil moisture and soil organic matter decreased as grazing intensity increased along the studied gradient. Similar differences were reported inside and outside the recovery plot. These soil changes were considered by the authors to be consequences of grazing impact instead of spatial heterogeneity among these sites. Simultaneous sampling of plant and soil would be worthwhile in future studies.

#### Gradient Investigation Versus Dynamic Observation

Dynamic observation has the advantage of determining the species or vegetation change rate, and is not influenced by environmental heterogeneity effects, making it useful for studying mechanisms of vegetation dynamics (Pickett 1989). The advantages of gradient study over dynamic observation include its cost-effectiveness. It can be done quickly over broad vegetation types (Austin 1977) and excludes the effects of interannual variations in climate. The vegetation investigated along the grazing gradient provides a “snapshot” of the vegetation in dynamics. Investigation under extreme climate conditions should be avoided for a representative sample. In the studied area, although species composition was relatively resistant to interannual climatic variation, as shown by the vegetation in the climax plot, the biomass was largely affected. The vegetation along the studied gradient was surveyed in an average year of climate, with a precipitation of 215 mm (till the end of July). The average precipitation of the 11-year observation period was 219 mm. Gradient study is more efficient and appropriate when the objective is to determine general vegetation trends in a region (Andrew 1988).

Quantification of grazing intensity on a distance from water (or from stock post) gradient provides challenges because the distance gradient represents an accumulative but not necessarily present-day gradient in grazing intensity (Adler & Hall 2005). Various methods have been used to quantify RGI on the distance gradient, including collecting animal dung accumulation, counting herd passages, or investigating the size of herds on stock posts (Turner 1998; Riginos & Hoffman 2003; Hendricks et al. 2005). Though useful for estimating current season grazing intensities, these methods are very limited in providing information on historical grazing impact. A monotonic change in grazing impact with distance is most important in a study using distance as a proxy of grazing intensities (Andrew 1988). In our case, the monotonic RGI decrease along the studied gradient was well based on the clear and short history of intensive grazing in the area, but the linear assumption between RGI and distance cannot be tested due to the lack of historical grazing intensity records; for this reason, only the vegetation or species trend was examined along the gradient, not their change rates.

### Implications for Practices

- Species richness was higher on the light- or no-grazing sites than on the heavy-grazing sites, indicating the vulnerability of some species to grazing in Inner Mongolia grasslands. Delineating protected areas in main steppe vegetation zones is needed for conservation of species diversity.
- Grazing-degraded vegetation could recover naturally after reduction or exclusion of grazing animals provided the main change was the shift in species dominance instead of in species composition, such as the *Artemisia frigida* community derived from many steppe communities in Inner Mongolia (Wang et al. 1985; Li 1991).
- Knowledge of the changes in species attributes in response to animal grazing, including SDC, is very useful when making sustainable grazing plans for various grassland types at different stages of succession and deserves further studies.
- The general correspondence of spatial and temporal vegetation variation in response to animal grazing confirms that gradient studies are a useful method in assessing and constructing general vegetation trends in a region.

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