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Effects of grazing on leaf traits and ecosystem functioning in Inner Mongolia grasslands: scaling from species to community

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Abstract

More attention has focused on using some easily measured plant functional traits to predict grazing influence on plant growth and ecosystem functioning. However, there has been much controversy on leaf traits response to grazing, thus more research should be conducted at the species level. Here we investigated the leaf area, leaf mass and specific leaf area (SLA) of 263 species in eight grassland communities along a soil moisture gradient in the Xilin River Basin, a semiarid grassland of northern China, to explore the grazing effects on ecosystem functioning. Results demonstrated that grazing decreased the leaf area and leaf mass in more than 56% of species in the Xilin River Basin, however, responses of SLA to grazing varied widely between species. Grazing increased SLA in 38.4% of species, decreased SLA in 31.3% of species and had no effect on 30.3% of species. Annuals and biennials generally developed high SLA as grazing tolerance traits, while perennial graminoids developed low SLA as grazing avoidance traits. Considering the water ecotypes, the SLA-increased and SLA-unchanged species were dominated by hygrophytes and mesophytes, while the SLA-decreased species were dominated by xerophytes. At the community level, grazing decreased the mean leaf area index (LAI) of six communities by 16.9%, leaf biomass by 35.2% and standing aboveground biomass (SAB) by 35.0% in the Xilin River Basin, indicating that overgrazing greatly decreased the ecosystem functioning in the semi-arid grassland of northern China. Soil properties, especially fielding holding capacity and soil organic carbon and total nitrogen could mediate the negative grazing impacts. The results suggest SLA is a better leaf trait to reveal plant adaptability to grazing. Our findings have practical implications for range management and productivity maintenance in the semiarid grassland, and it is feasible to take some measures such as ameliorating soil water and nutrient availabilities to prevent grassland degradation.

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1 Introduction

In the face of large-scale environmental change, predicting the response of vegetation to climate or land-use change has become a major concern in recent basic and applied ecological research (Smith et al., 1997; Thuiller et al., 2008). Grazing, which is one of the most globally widespread land use types, has dramatic effects on ecosystem structure and functioning and strongly influences plant growth and development (Pakeman, 2004; Cingolani et al., 2005; Semmartin et al., 2008). Plant functional traits are considered as reflecting the adaptations to environmental change and trade-offs among different functions within a plant (Díaz et al., 1998; Garnier et al., 2001; Wright et al., 2004). In recent years, there is much more attention focused on using functional traits to predict plant responses to grazing or the impacts of grazing on plant growth and ecosystem functioning (Díaz et al., 2001, 2007; Adler et al., 2005).

Some easily measured leaf traits ("soft" traits), such as leaf size, leaf dry matter content (LDMC) and specific leaf area (SLA), are closely related to plant functions due to correlations with "harder" traits, such as relative growth rate, photosynthetic capacity and leaf turnover rate, and further reflect fundamental growth–defence (or storage) trade-offs (Reich et al., 1999, 2007; Wilson et al., 1999). Many studies have shown that leaf size generally decreases under grazing pressure because large leaves provide better bites for grazer, and smaller leaves require either more bites for a given leaf area (Landsberg et al., 1999; Díaz et al., 2001), thus grazing avoidance traits are usually associated with low palatability, such as small leaf size and high LDMC (Wardle et al., 1998; Díaz et al., 2001). In contrast, plants that tolerate grazing should have high SLA and low leaf toughness which increase shoot regrowth ability and selectivity by herbivores (Pérez-Harguindeguy et al., 2003; Cingolani et al., 2005).

Díaz et al. (2001) suggested plant height could be the best single predictor of grazing response, followed by leaf mass, life history and SLA, and put forward it is feasible to predict plant communities response to grazing by using some easily measured plant traits. However, Vesik et al. (2004) found little evidence for predictability of grazing

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responses with simple traits in the semi-arid and arid shrublands and woodlands. Several studies also showed that plant traits responses to grazing are largely mediated by site productivity (Osem et al., 2004; Pakeman, 2004), resource availability (Bakker et al., 2003; Anderson et al., 2007) and grazing intensity or history (Adler et al., 2004; Díaz et al., 2007; Graff et al., 2007). Therefore, the effects of grazing on plant traits are complicated and may be context-specific, more research should be conducted at the species level, and then extrapolate consistent traits to community eventually biome levels, which not only helps us understand the adaptive mechanism of plants but could better predict the impacts of grazing on ecosystem functioning.

In the present study, we determined leaf traits (i.e. leaf area, leaf mass and SLA) of 263 species involving about 25 000 plant samples distributed widely in the swamp meadow, meadow steppe, typical steppe and sand dune complex along a soil moisture gradient in the Xinlin River Basin, a typical semiarid temperate grassland in northern China. It is the first attempt to systematically and precisely determine leaf traits for a large number of species with various leaf morphologies in China. We compared the leaf traits of 188 common species in the paired ungrazed and grazed sites of six grassland communities to explore the impacts of grazing on plant growth and ecosystem functioning. Specifically, we address the following three research questions: First, how do leaf traits vary across different plant functional groups (PFGs) in the Xinlin River Basin? Second, how does grazing affect leaf traits at the species, population or community levels? Third, how does grazing affect the ecosystem functioning in the semiarid grassland of northern China, and whether the effects were mediated by soil properties, such as soil water and nutrients?

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2 Methods

2.1 Study area and site selection

The Xilin River Basin (43°26′–44°29′ N, 115°32′–117°12′ E) is located in the typical steppe zone of the Inner Mongolia Plateau, northern China, which covers an area of about 10 000 km², with an elevation ranging from 900 to 1500 m. It belongs to semi-arid continental temperate steppe climate zone, with dry springs and moist summers. Annual mean temperature increases from southeast to northwest, ranging from 0.5 to 2.1°C, and annual precipitation decreases gradually from 400 mm in the southeast to 250 mm in the northwest, with 60–80% rainfall occurring in the growing season (May–August). The soil types in this area are chestnut and dark chestnut soils (Chen, 1988).

The study was conducted in the areas adjacent to the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences, which is located at the middle reach of the Xilin River. Eight grassland communities, the *Carex appendiculata* swamp meadow, *Stipa baicalensis* meadow steppe, *Leymus chinensis* typical steppe, *S. grandis* typical steppe, *Caragana microphylla* typical steppe, *Artemisia frigida* typical steppe, *Kochia prostrate* typical steppe and *Prunus sibirica* sand dune complex distributing along a soil moisture gradient in the Xilin River Basin were investigated, especially for the paired ungrazed and grazed sites in the former six communities. Eight grassland communities were subjected to similar climatic conditions, such as temperature and precipitation, but differed in floristic composition and soil properties, such as soil water and nutrients. The ungrazed sites of communities *C. appendiculata*, *S. baicalensis*, *L. chinensis*, *S. grandis*, *C. microphylla*, *A. frigida*, *K. prostrate* and *P. Sibirica* in our study were fenced by the IMGERS in 1989, 1979, 1979, 1979, 1983, 1989, 1979 and 1989, respectively, thus they have about 20–30 years grazing-forbidden history. And the corresponding grazed sites of the former six communities were free sheep-grazing since 1950s, thus they have about 60 years free-grazing history. The distances between the paired ungrazed and grazed sites of six communities are about 5–10 m. More detailed information about the eight communities is shown in

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Table 1.

2.2 Survey of vegetation composition

Vegetation composition surveys were conducted from 28 July to 14 August 2007, when the aboveground biomass approximated the net primary productivity (ANPP) in temperate grassland, China. At each site, 5–30 quadrats located randomly within an area of 100×100 m were surveyed and a total of 150 quadrats were investigated in eight communities. Generally, 10 quadrats (1×1 m each) were sampled at most sites, in particular, 5 quadrats (1×1 m) were sampled in the more homogeneous swamp meadow community and 30 quadrats including 20 herbaceous communities and 10 shrub communities (5×5 m) were sampled in the more heterogeneous sand dune community. In each quadrat, plant heights of all species were measured and the number of species was counted. The aboveground of each species was collected and transported to a laboratory for stem and leaf separation, then they were oven-dried at 70°C for 24 h to a constant mass, thus the ratio of stem to leaf and plant aboveground biomass could be calculated.

2.3 Plant sampling and leaf trait measurements

After vegetation composition surveys, plant materials for leaf trait measurements were collected near the quadrats and then taken back to the laboratory immediately. We randomly collected 30–50 individuals with fully expanded leaves for each species, and all species appeared in the community were sampled. In this study, 263 species from 51 families and 161 genera, and totally 25 000 plant samples were collected from the eight grassland communities in the Xilin River Basin, and the detailed information about sampled species in each community is shown in Appendix A.

According to the leaf size, about 150–600 mature and fully expanded leaves were picked from 30–50 individuals for each species. Generally 5–20 leaves as a sample and totally 30 replicates for each species. After leaf area measurements, leaf samples

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were oven-dried at 65°C for 24 h to the constant mass, then the specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) was calculated as the ratio of leaf area to leaf dry mass. According to the leaf morphologies, we adopted five methods for leaf area measurements (see Appendix B for detailed description).

5 2.4 Community standing aboveground biomass (SAB), leaf biomass and leaf area index (LAI) calculations

The standing aboveground biomass (SAB) of a community was the sum weights of the aboveground biomass of all species in the quadrat. The community leaf biomass was calculated by using plant aboveground biomass and shoot: leaf ratio of all species in the quadrat. Leaf area index (the area of leaves per soil surface area, $\text{m}^2 \text{m}^{-2}$) was calculated by using leaf biomass and SLA of all species in the quadrat. The formulae are as follows:

$$\text{Community SAB (g m}^{-2}\text{)} = \sum_{i=1}^n B_i$$

$$\text{Community leaf biomass (g m}^{-2}\text{)} = \sum_{i=1}^n \frac{B_i}{R_i + 1}$$

$$15 \quad \text{Community LAI (m}^2 \text{m}^{-2}\text{)} = \sum_{i=1}^n B_{Li} \times \text{SLA}_i$$

where B_i , R_i , B_{Li} and SLA_i are the aboveground biomass, stem: leaf ratio, leaf biomass and SLA of the species i in a community, respectively, and n is the number of species in a community.

In this study, 12 dominant species in the six grassland communities were selected according to their relative biomass, and their population aboveground biomass, leaf biomass and LAI were calculated by using above method. They are *C. appendiculata* and *Agrostis gigantea* in the *C. appendiculata* swamp meadow, *S. baicalensis* and 9951

L. chinensis in the *S. baicalensis* meadow steppe, *L. chinensis* and *S. grandis* in the typical steppes of *L. chinensis*, *S. grandis* and *C. microphylla*, and *A. frigida* and *K. prostrate* in the *A. frigida* typical steppe.

2.5 PFG classification

5 All species determined in this study are classified into the following PFGs on the basis of biological realm, physiology or morphology: (1) biological realm: seed plants and ferns (seed plants are divided into gymnosperm and angiosperm, and angiosperms are further grouped into dicotyledons and monocotyledons); (2) photosynthetic pathways: C_3 , C_4 and CAM species; (3) N_2 -fixing ability: legumes and non-legumes; (4) life forms: annuals and biennials (AB), perennial forbs (PF), perennial graminoids (PG), shrubs, sub-shrubs and small trees (ST); (5) water ecotypes: hygrophytes (H), hygromesophytes (HM), mesophytes (M), xeromesophytes (XM), mesoxerophytes (MX), xerophytes (X); and (6) other PFGs: vines and lianas, succulents, tuber and bulbous plants (see Appendix A for details).

15 2.6 Soil property analysis

With 100 cm^3 cylindrical soil corers, five soil samples were collected from the soil layer (0–20 cm) of the sampling quadrats in each grassland communities. All the soil samples were taken to laboratory and oven-dried at 105°C for 48 h and weighed to determine the soil bulk densities (g cm^{-3}). Soil porosity was calculated as following formula:

$$20 \quad \text{Soil porosity (\%)} = (1 - \text{soil bulk density}/2.65) \times 100\%$$

where 2.65 is the constant value of soil grain density (g cm^{-3}).

The field holding capacity (%) of soil layer (0–20 cm) was determined using the pressure chamber method (Page et al., 1982), and soil samples were collected for nutrient analyses. Soil organic carbon was determined by the method of $\text{K}_2\text{Cr}_2\text{O}_7\text{--H}_2\text{SO}_4$ solution digestion with the oil-bath heating. Soil total nitrogen was determined by Kjeldahl digestion and distillation with the Kjeltex analyzer (Kjeltex 2300 Analyzer Unit, 9952

Sweden). Soil total phosphorus was colorimetrically analyzed with blue phosphor-molybdate (6505 UV spectrophotometer, UK). The results of soil nutrients were presented in mass basis (%).

2.7 Data analysis

5 In our study, data were analyzed from three aspects: (1) leaf traits by PFG level, averaging leaf traits of different PFGs in eight grassland communities to explore variations in leaf traits across PFGs, (2) leaf traits by species level, comparing leaf traits of the 188 common species in the paired ungrazed and grazed sites of six grassland communities to explore the impacts of grazing on leaf traits at the species level, (3) leaf traits
10 by population and community levels, leaf traits of species were scaling up to calculate the LAI, leaf biomass and SAB of dominant populations and communities to explore the impacts of grazing on ecosystem functioning.

Statistical analyses were performed using a SPSS 13.0 software (2004, ver. 13.0; SPSS Inc., USA). The leaf traits of the same species in the paired ungrazed and grazed sites were compared by Independent-Samples T test ($P < 0.05$) and 188 common species were categorized as three groups according to their leaf area, leaf mass and leaf SLA values were decreased (-), increased (+) or unchanged (o) by grazing in six grassland communities. The LAI, leaf biomass and SAB of the same dominant populations and communities in the paired ungrazed and grazed sites were compared
15 by Independent-Samples T test.
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3 Results

3.1 Soil properties of four steppes in the Xilin River Basin

Soil properties of 0–20 cm soil depth differed greatly among four steppes in the Xilin River Basin (Fig. 1). The values of field holding capacity and soil porosity of four steppes followed a descending order of swamp
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meadow>meadow steppe>typical steppe>sand dune complex, but soil bulk density exhibited an opposite order. In addition, the swamp meadow had significantly higher ($P < 0.05$) soil organic carbon and soil total nitrogen and phosphorus than other three steppes. Therefore, the swamp steppe had the best soil ventilation and water and
5 nutrient availabilities, which are favorable for plant growth.

3.2 Variations in leaf traits across PFGs

Across all species from the eight grassland communities of four steppes, i.e. swamp meadow, meadow steppe, typical steppe and sand dune complex in the Xilin River Basin, three leaf traits exhibited large variations, especially for leaf area and leaf mass.
10 Leaf area varied from 0.06 to 142.97 cm² [coefficient of variation (C.V.)=2.01], with an average of 6.56 cm², leaf mass varied from 0.0003 to 0.771 g (C.V.=1.75), with an average of 0.049 g, and SLA ranged from 42.1 to 679.2 cm² g⁻¹ (C.V.=0.44), with an average of 142.8 cm² g⁻¹ (Table 2). Leaf traits varied markedly across different PFGs (Table 2, Fig. 2). Comparatively, gymnosperms had higher mean values of leaf area and leaf mass but lower SLA value than angiosperms. Dicotyledons had significantly higher SLA value (146.9 cm² g⁻¹, $P < 0.05$) than monocotyledons (131.6 cm² g⁻¹)
15 (Fig. 2), but they had similar leaf area and leaf mass (Table 2). SLA varied significantly across three PFGs with different photosynthetic pathways ($P < 0.001$), especially for C₃ species, which covered almost the entire observation range of SLA (Fig. 2). The CAM species had significantly greater mean SLA value than other two PFGs, but C₃ species had the lowest value, following a descending order of CAM species (210.1 cm² g⁻¹)>C₄ species (164.3 cm² g⁻¹)>C₃ species (138.9 cm² g⁻¹). With regard to plant N₂-fixing ability, leaf area and leaf mass of non-legumes were three times over than those of legumes, but they had similar mean SLA value.
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There was significant difference in the SLA among four life forms ($P < 0.001$, Table 2). AB had much greater mean SLA value (174.7 cm² g⁻¹) than other three life forms, and their mean SLA values followed a descending order of AB>PF>PG>ST (Fig. 2). ST
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also had the lowest values of leaf area and leaf mass. Large variations in leaf traits also exhibited across six water ecotypes ($P < 0.01$), comparatively, HM had much higher leaf area, leaf mass and SLA than other five ecotypes. The mean values of SLA for six water ecotypes were ranked in the order of $HM > H \approx M > XM > MX \approx X$ (Fig. 2).

5 3.3 Effects of grazing on leaf traits at the species level

There were totally 188 common species representing 30 families, 81 genera and 112 different species in the paired ungrazed and grazed sites of six grassland communities. It is showed that leaf area and leaf mass in more than 55.6% of species in six communities were significantly ($P < 0.05$) decreased by grazing (Fig. 3a and b), especially for the four communities of typical steppe, of which more than 72.3% of species were decreased. SLA, however, had relatively balanced proportions among three groups, that is, grazing increased SLA in 34.6% of 188 common species, decreased SLA in 37.2% and had no effect on 28.2% of 188 species (Fig. 3c). Comparatively, the SLA of most species in the *C. appendiculata* swamp meadow were increased by grazing, accounting for 51.1% of 45 species, in contrast, the SLA of most species in the four communities of typical steppe were decreased, accounting for 50.1% of 88 species. The *S. baicalensis* meadow steppe had relatively balanced proportions among three groups, 36.4% of 55 species for SLA-increased group, 36.4% for SLA-unchanged group and 27.3% for SLA-decreased group. Therefore, grazing had similar effects on leaf area and leaf mass but significantly different impacts on leaf SLA for three steppes.

SLA had relatively lower intra-species variation (Table 2), thus we pooled the 188 plants in six communities together and categorized 112 species as three groups according to their SLAs response to grazing, that is, grazing increased SLA in 38.4% of species, decreased SLA in 31.3% of species and had no effect on 30.3% of species. The correlations between leaf traits showed that whether or not grazing affected, SLA was not related to either leaf area or leaf mass for three groups (Table 3), but leaf area was significantly and positively correlated with leaf mass ($P < 0.001$). Moreover, the variations in SLA for three groups were mainly resulted from the co-decrements in leaf

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area and leaf mass, which can explain 53.1% of their total variations.

Considering the life form (Table 4), the SLA of most AB (11 of 19) were increased by grazing, while SLA of most PG (5 of 8) were decreased, such as *L. chinensis*, *S. grandis* and *Agropyron michnoi*, which are the dominant species in the typical steppe. PF distributed 28, 25 and 28 species for SLA-increased group, SLA-decreased group and SLA-unchanged group, respectively. Considering the water ecotypes, the SLA-increased and SLA-unchanged groups were dominated by M and XM and H and HM, accounting for 80.6% of 112 common species, while the SLA-decreased group was dominated by X and MX, accounting for 65.7%. Therefore, grazing had different impacts on leaf SLA of different life forms and water ecotypes, which may be related to plant life-span and soil water availability.

3.4 Effects of grazing on LAI, leaf biomass and SAB at the population level

Totally 12 dominant species populations in six grassland communities were selected, of which their relative biomass accounted for 40.9~72.6% of the community SAB. On the whole, grazing decreased the mean LAI by 25.3% ($P = 0.082$), leaf biomass by 23.9% ($P = 0.106$) and SAB by 31.1% ($P = 0.059$) when 12 populations were pooled together (Table 5). Grazing had little effects on the LAI, leaf biomass and SAB of both populations (*C. appendiculata* and *A. gigantean*) in the *C. appendiculata* swamp meadow, while it significantly ($P < 0.05$) increased the LAI, leaf biomass and SAB of both populations (*S. baicalensis* and *L. chinensis*) in the *S. baicalensis* meadow steppe. In contrast, grazing significantly ($P < 0.05$) decreased the mean LAI of eight populations in the typical steppes by 40.4%, leaf biomass by 41.6% and SAB by 50.1%, especially for *L. chinensis* population in the typical steppes of *S. grandis* and *C. microphylla*. However, grazing significantly ($P < 0.05$) increased the LAI, leaf biomass and SAB of *A. frigida* population in the typical steppe of *A. frigida*.

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3.5 Effects of grazing on LAI, leaf biomass and SAB at the community level

At the community level, the mean LAI, leaf biomass and SAB of six communities were $1.02\text{ m}^2\text{ m}^{-2}$, 113.1 g m^{-2} and 181.3 g m^{-2} in the ungrazed sites, and they were $0.85\text{ m}^2\text{ m}^{-2}$, 73.4 g m^{-2} and 117.9 g m^{-2} in the grazed sites, thus grazing decreased the LAI by 16.9% ($P>0.05$), leaf biomass by 35.2% ($P<0.05$) and SAB by 35.0% ($P<0.01$) (Fig. 4). Grazing significantly ($P<0.05$) increased the LAI but decreased the leaf biomass and SAB of the *C. appendiculata* swamp meadow. Grazing slightly increased the LAI, leaf biomass and SAB of the *S. baicalensis* meadow steppe, however, it significantly ($P<0.01$) decreased the LAI, leaf biomass and SAB of four communities of typical steppe.

3.6 Relations of LAI, leaf biomass, SAB with soil properties

Across six communities in the ungrazed sites, the LAI, leaf biomass and SAB were significantly and positively correlated with the field holding capacity, soil porosity, soil organic carbon, soil total nitrogen and phosphorus, but negatively correlated with soil bulk density. Across the same six communities in the grazed sites, the LAI, leaf biomass and SAB were significantly and positively correlated with field holding capacity and soil organic carbon and total nitrogen, but being weakly correlated with soil total phosphorus, soil porosity and soil bulk density. Therefore, soil properties, especially soil water and nutrient availabilities had important impacts on grassland productivity in the Xilin River Basin.

4 Discussion

4.1 Leaf traits of different PFGs in the Xilin River Basin

Our results demonstrated that leaf area, leaf mass and SLA varied greatly across different PFGs categorized by the biological realm, photosynthetic pathways, N_2 -fixing

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ability, life forms and water ecotypes (Table 2), indicating that leaf morphologies are closely related to plant functions, such as photosynthetic capacity, structural defence and resource allocation. SLA showed larger inter-PFG variations but lower intra-PFG variations than leaf area and leaf mass, thus SLA is a relatively stable and better leaf trait for PFG comparison analysis. Gymnosperms, PF, PG and ST had much less SLA values than corresponding angiosperms and AB (Table 2, Fig. 2), indicating that species with longer leaf life-span (LL) generally have less SLA values than shorter-lived species. It reflects a fundamental trade-off in tissue structure and function among several key eco-physiological traits, where species with low SLA/long LL tend to require greater nutrient allocation to defensive chemicals in favor of structural strength. Thus they need a longer return time on their investment in nutrients, resulting in their lower photosynthetic capacity and slow plant growth (Field and Mooney, 1986; Reich et al., 1998).

In the present study, dicotyledons had significantly greater SLA than monocotyledons ($P<0.05$), because monocotyledons generally have higher structural strength in their leaves to reach higher stature. CAM species had higher SLA but lower leaf mass than C_3 and C_4 species because of their particular anatomical traits. Most CAM species are succulent plants, such as *Orosiachys fimbriatus* and *O. malacephyllus*, which have developed cells and vacuoles for storing water and soluble matter in order to survive the xeric environment (Vendramini et al., 2002). Great variations in leaf traits among six water ecotypes (Table 2, Fig. 2) suggested that water availability plays an important role in leaf morphological plasticity. H and HM are mainly growing in the swamp meadow, while M and XM are distributed widely in four steppes of the Xilin River Basin. Surprisingly, it is HM rather than H had the greatest SLA value. Moreover, leaf SLA differed little among H, M and XM, indicating that moderate not extravagant water availability is favorable for high-SLA formation. The Xilin River Basin is a typical semi-arid grassland with an annual mean precipitation of about 350 mm, where water availability is the key limiting factor for plant growth (Chen, 1988). X is the dominant water-ecotype and had the lowest SLA value in order to survive the dry habitats. Generally, species growing

in dry habitats tend to store mineral nutrients in leaves and use a majority of them to construct protective structure, thus result in thicker and smaller leaves with more dry matters but lower SLA values.

4.2 Leaf traits response to grazing at the species level

5 Our results showed that grazing significantly decreased the leaf area and leaf mass in more than 56% of species in six grassland communities, suggesting that grazing favors small leaves and low dry mass for most species in the Xilin River Basin. However, previous studies found that leaf size generally decreased but LDMC increased under grazing pressure in order to decrease the palatability and selectivity by herbivores (Wardle
10 et al., 1998; Landsberg et al., 1999; Díaz et al., 2001), which are partially inconsistent with our results.

Many studies have shown that intense grazing would increase the abundance of annuals but decrease the abundance of perennial species (Díaz et al., 2001, 2007; McIntyre and Lavorel, 2001; Pakeman, 2004). In our study, SLA values of most AB
15 were increased while SLA values of most PG were decreased by grazing, indicating that AB generally positively response to grazing and adopt high SLA as grazing tolerance traits, while PG generally negatively response to grazing and adopt low SLA as grazing avoidance traits. In general, AB as short-lived species and opportunists have higher SLA and relative growth rates, could grow rapidly and reproduce early to increase their abundance, thus they are more tolerant to herbivory (Vesk et al., 2004).
20 In the present study, SLA values of most M and XM and H and HM were increased or unchanged by grazing, while SLA values of most X and MX were decreased, indicating that species generally developed grazing tolerance traits in wetter habitats, while they developed avoidance or resistance traits in drier habitats. It is also indirectly suggested
25 that plant response to grazing could be moderated by soil moisture. Adler et al. (2004) and Cingolani et al. (2005) also found that aridity appeared to favor grazing avoidance traits, while tolerance traits increased with water availability.

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4.3 Grazing impacts on ecosystem functioning in the Xilin River Basin

It has been widely accepted that grazing had important impacts on species composition, community structure and primary productivity (Proulx and Mazumder, 1998; Landsberg et al., 2003), nutrient cycling and litter decomposition (Semmartin et al.,
5 2008) and resource competition among species (Arsenault and Owen-Smith, 2002) in the grassland ecosystem, thus it can substantially influence the ecosystem structure, functioning and service. Plant leaves as important assimilation organs are closely related to plant growth and community productivity, which are also sensitive to environmental variables (i.e. atmospheric CO₂ concentration, precipitation, temperature, light,
10 Mott et al., 1982) and human disturbance (i.e. grazing, clipping, defoliation, Holechek et al., 2002). In the present study, the community leaf biomass accounted for 60% of SAB averagely for six grassland communities, and grazing decreased the mean LAI by 16.9% ($P > 0.05$), leaf biomass by 35.2% ($P < 0.05$) and SAB by 35.0% ($P < 0.01$) (Fig. 4), moreover, grazing also decreased the species richness of six communities
15 (Table 1), indicating that the ecosystem functioning greatly decreased due to overgrazing in the Xilin River Basin.

Grazing significantly decreased the LAI, leaf biomass and SAB for most dominant species populations in six communities, especially for *L. chinensis* population in the typical steppes. However, grazing significantly ($P < 0.05$) increased the LAI, leaf biomass
20 and SAB of *A. frigida* (a subshrub) population in the typical steppe. Moreover, the SLA of *A. frigida* changed little, but SLA of *L. chinensis* significantly decreased by grazing, implying that *A. frigida* is more tolerant to grazing disturbance. It might imply that grazing caused the ecosystem degradation might be related to dominant species replacement. Xiong et al. (2003) also showed that the distribution of *C. microphylla*,
25 a dominant shrub, increased rapidly due to overgrazing over the last 20 years in the Xilin River Basin, which led to grassland degraded more seriously in recent years. It has been widely proved that thicketization is a symbol of grassland degradation or even indesertification in the arid and semiarid areas (Archer et al., 1995; Denver et al.,

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2001).

In the present study, grazing had different impacts on leaf traits and SAB of three steppes at the species, population and community levels. It had slight even more positive effects on the swamp meadow and meadow steppe, but serious and negative impacts on the typical steppe. In addition, whether or not grazing impacts, the LAI, leaf biomass and SAB of six communities were closely correlated with soil properties, especially with field holding capacity and soil nutrients (Table 6). Moreover, field holding capacity, soil organic carbon and soil total nitrogen and phosphorus in the swamp meadow were significant higher than those in the meadow steppe and typical steppe (Fig. 1), which not only contributed to significantly higher species richness and SAB in the swamp meadow (Table 1), but also mediated the negative grazing impacts. Proulx et al. (1998) reported that the impacts of grazing on species richness were reverse under contrasting nutrient richness, it decreased the species richness in nutrient-poor ecosystems, but increased it in nutrient-rich ecosystems, indicating that resource availability could modify the negative grazing impacts. Anderson et al. (2007) also found that rainfall and soil *P* could modulate the effects of herbivores on plant diversity and composition in Serengeti National Park, which are consistent with our results.

5 Conclusions

Our results showed that grazing significantly decreased the leaf area and leaf mass for most species (>56%) in the Xilin River Basin, and the diverse variations in SLA were mainly resulted from co-decrements in leaf area and leaf mass. Grazing significantly decreased the mean LAI, leaf biomass and SAB of six grassland communities in the Xilin River Basin, suggesting that overgrazing greatly decreased the ecosystem functioning in the semi-arid grassland of northern China. Our findings also showed that soil water and nutrient availabilities could mediate the negative effects of grazing on ecosystem functioning. The results of this study have practical implications for range management and productivity maintenance in the arid and semiarid grasslands, it is

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feasible to take some management practices such as ameliorating soil water and nutrient availabilities to improve ecosystem functioning and prevent grassland degradation.

6 Supplementary material

The supplementary material for this article is available at:

<http://www.biogeosciences-discuss.net/6/9945/2009/bgd-6-9945-2009-supplement.zip>.

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Table 1. Abiotic and biotic characteristics of eight grassland communities in the Xilin River Basin, Inner Mongolia, China.

No.	Community type	Vegetation type	Location	Altitude (m)	Soil type	Land use type	Species richness (no. m ⁻²)	SAB (g m ⁻²)	No. of sampled species	Dominant species
1	<i>Carex appendiculata</i>	Swamp meadow	N 43°37.658' E 116°41.202'	1150	Swamp meadow soil	Ungrazed site (fenced since 1989)	22.6±1.9	574.9±40.2	98	<i>C. appendiculata</i> , <i>Glyceria maxima</i> , <i>Poa sphondylodes</i> , <i>Agrostis gigantea</i>
	<i>C. appendiculata</i>	Swamp meadow	N 43°37.655' E 116°41.193'	1150	Swamp meadow soil	Grazed site (free sheep-grazing since 1950s)	20.6±1.3	382.9±61.1	78	<i>C. appendiculata</i> , <i>G. maxima</i> , <i>C. rostrata</i> , <i>A. gigantea</i>
2	<i>Stipa baicalensis</i>	Meadow steppe	N 43°27.248' E 116°47.418'	1380	Dark chestnut soil	Ungrazed site (fenced since 1979)	28.3±1.0	115.8±4.4	83	<i>S. baicalensis</i> , <i>Leymus chinensis</i> , <i>Artemisia frigida</i>
	<i>S. baicalensis</i>	Meadow steppe	N 43°29.095' E 116°47.595'	1380	Dark chestnut soil	Grazed site (free sheep-grazing since 1950s)	21.5±1.8	148.3±14.8	63	<i>S. baicalensis</i> , <i>L. chinensis</i> , <i>Artemisia frigida</i>
3	<i>L. chinensis</i>	Typical steppe	N 43°32.873' E 116°40.715'	1250	Typical chestnut soil	Ungrazed site (fenced since 1979)	13.3±0.9	178.2±10.9	61	<i>L. chinensis</i> , <i>S. grandis</i> , <i>Artemisia frigida</i>
	<i>L. chinensis</i>	Typical steppe	N 43°33.107' E 116°39.981'	1250	Typical chestnut soil	Grazed site (free sheep-grazing since 1950s)	9.4±0.4	101.3±7.2	23	<i>L. chinensis</i> , <i>S. grandis</i> , <i>Agropyron michnoi</i>
4	<i>S. grandis</i>	Typical steppe	N 43°32.355' E 116°33.198'	1180	Typical chestnut soil	Ungrazed site (fenced since 1979)	11.5±0.9	178.0±6.9	60	<i>S. grandis</i> , <i>L. chinensis</i> , <i>A. michnoi</i>
	<i>S. grandis</i>	Typical steppe	N 43°32.427' E 116°33.063'	1180	Typical chestnut soil	Grazed site (free sheep-grazing since 1950s)	8.1±0.5	69.9±3.2	26	<i>S. grandis</i> , <i>L. chinensis</i> , <i>A. michnoi</i>
5	<i>Caragana microphylla</i>	Typical steppe	N 43°35.878' E 116°44.263'	1190	Typical chestnut soil	Ungrazed site (fenced since 1983)	11.0±1.6	140.5±5.8	72	<i>C. microphylla</i> , <i>L. chinensis</i> , <i>A. frigida</i> , <i>S. grandis</i>
	<i>C. microphylla</i>	Typical steppe	N 43°35.852' E 116°43.525'	1190	Typical chestnut soil	Grazed site (free sheep-grazing since 1950s)	10.0 ± 0.4	59.5±4.6	22	<i>C. microphylla</i> , <i>L. chinensis</i> , <i>A. michnoi</i> , <i>S. grandis</i>
6	<i>A. frigida</i>	Typical steppe	N 43°37.935' E 116°40.598'	1200	Typical chestnut soil	Ungrazed site (fenced since 1989)	8.9±0.9	97.1±8.1	51	<i>Kochia prostrata</i> , <i>A. frigida</i> , <i>L. chinensis</i>
	<i>A. frigida</i>	Typical steppe	N 43°37.912' E 116°40.725'	1200	Typical chestnut soil	Grazed site (free sheep-grazing since 1950s)	10.4±0.5	78.4±7.6	48	<i>K. prostrata</i> , <i>A. frigida</i> , <i>A. michnoi</i>
7	<i>K. prostrata</i>	Typical steppe	N 43°37.827' E 116°42.135'	1350	Typical chestnut soil	Ungrazed site (fenced since 1979)	8.1±1.3	134.4±8.4	56	<i>K. prostrata</i> , <i>A. frigida</i> , <i>L. chinensis</i>
8	<i>Prunus sibirica</i>	Fixed sand dune complex	N 43°38.971' E 116°39.503'	1220	Sandy soil	Ungrazed site (fenced since 1989)	9.1±0.8	229.2±76.7	112	<i>P. sibirica</i> , <i>C. microphylla</i> , <i>A. frigida</i>

Communities 1 to 6 included the paired ungrazed and grazed sites. SAB, standing aboveground biomass.

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Table 2. Statistic descriptions of leaf traits for different plant functional groups (PFGs) categorized by the biological realm, photosynthetic pathway, N₂-fixing ability, life form and water ecotype across eight grassland communities in the Xilin River Basin, Inner Mongolia, China.

Plant functional groups	Sampling size (<i>n</i>)	Leaf area (cm ²)		Leaf mass (g)		SLA (cm ² g ⁻¹)	
		Mean	C.V.	Mean	C.V.	Mean	C.V.
Biological realm							
Seed plant	587	6.56	2.01	0.048	1.75	142.69	0.44
Fern	2	12.47	0.67	0.068	0.56	175.68	0.14
Gymnosperm	3	10.58	0.50	0.242	0.57	50.46	0.20
Angiosperm	584	6.54	2.01	0.048	1.76	143.16	0.44
Dicotyledon	442	6.56 a	2.22	0.046 a	1.93	146.90 a	0.43
Monocotyledon	142	6.55 a	0.99	0.054 a	1.21	131.55 b	0.47
Photosynthetic pathway							
C ₃ species	517	6.40 a	1.73	0.050 a	1.66	138.92 c	0.45
C ₄ species	62	8.21 a	3.00	0.042 ab	2.50	164.34 b	0.37
CAM species	10	4.56 a	0.92	0.022 b	0.90	210.11 a	0.11
N ₂ -fixing ability							
Legume	51	2.20 b	1.46	0.017 b	1.67	136.93 a	0.37
Non-legume	538	6.99 a	1.95	0.052 a	1.70	143.36 a	0.445
Life form							
Annuals and biennials	125	6.73 ab	2.67	0.036 b	2.16	174.65 a	0.40
Perennial forbs	354	7.32 a	1.75	0.056 a	1.63	139.22 b	0.45
Perennial graminoids	61	4.95 b	0.86	0.046 ab	1.43	123.81 bc	0.32
Shrubs, subshrubs and small trees	49	2.57 c	1.39	0.029 b	1.93	111.10 c	0.24
Water ecotype							
Hygrophytes	8	7.80 ab	0.91	0.047 ab	0.99	172.16 b	0.36
Hygromesophytes	11	17.69 a	1.97	0.093 a	2.24	275.89 a	0.51
Mesophytes	156	10.19 ab	1.97	0.059 a	1.58	171.92 b	0.37
Xeromesophytes	83	3.15 c	2.36	0.027 b	3.17	145.54 b	0.47
Mesoxerophytes	140	7.64 b	1.09	0.065 a	1.04	120.91 c	0.32
Xerophytes	191	3.70 c	1.57	0.035 b	2.12	124.98 c	0.37
Other PFGs							
Vines and lianas	11	5.11	1.46	0.035	1.46	210.79 a	0.39
Succulents	14	3.87	0.95	0.019	0.93	210.24 a	0.09
Tuber and bulbous plants	40	5.97	0.86	0.056	0.91	115.51 b	0.54

^a ^b and ^c denote significant difference at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively, and ns denotes none significant at statistical level among different PFGs categorized by photosynthetic pathway, N₂-fixing ability, life form and water ecotype. Data within a column followed by different letters are significantly different at $P < 0.05$ according to LSD's tests if variances are homogeneous, or else Tamhane's T2 tests be used. V.C. denotes the coefficient of variation.

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Table 3. Correlation coefficients between leaf traits for three groups based on leaf SLA values increased, decreased or changed little under grazing impacts across six grassland communities in the Xilin River Basin.

SLA variation groups	Leaf traits	Leaf area		Leaf mass	
		Ungrazed	Grazed	Ungrazed	Grazed
SLA-increased <i>n</i> =43	SLA	-0.042	-0.166	-0.252	-0.294
	Leaf area			0.915 ^a	0.957 ^a
SLA-decreased <i>n</i> =35	SLA	0.067	0.014	-0.192	-0.188
	Leaf area			0.925 ^a	0.956 ^a
SLA-unchanged <i>n</i> =34	SLA	0.210	0.175	0.100	-0.008
	Leaf area			0.963 ^a	0.935 ^a

^a Correlation is significant at the 0.001 level (2-tailed). *n*=number of species

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Table 4. Grazing effects on leaf SLA of different life forms or water ecotypes across six grassland communities in the Xilin River Basin.

Plant functional groups	SLA-decreased	SLA-increased	SLA-unchanged
Life forms			
Annuals and biennials (19)	3	11	5
Perennial forbs (81)	25	28	28
Perennial graminoids (8)	5	3	0
Shrubs, subshrubs and small trees (4)	2	1	1
Water ecotypes			
Hygrophytes and hygromesophytes (8)	3	0	5
Mesophytes and xeromesophytes (54)	9	27	18
Xerophytes and mesoxerophytes (50)	23	16	11

Data in the parentheses and columns are number of species, totally 112 common species in the paired ungrazed and grazed sites were compared.

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Table 5. LAI, leaf biomass and SAB of dominant species populations in six grassland communities in the Xilin River Basin.

Community type	Dominant species population	Land use type	LAI (m ² m ⁻²)	Sig.	Leaf biomass (g m ⁻²)	Sig.	SAB (g m ⁻²)	Sig.
C.a	<i>Carex appendiculata</i>	Ungrazed	1.032±0.331	ns	58.53±18.07	ns	84.36±26.85	ns
		Grazed	0.786±0.387		50.53±18.98		65.72±25.15	
	<i>Agrostis gigantea</i>	Ungrazed	0.020±0.007	ns	1.01±0.35	ns	10.69±3.34	ns
		Grazed	0.019±0.005		0.98±0.24		13.73±3.23	
S.b	<i>Stipa baicalensis</i>	Ungrazed	0.053±0.008	a	5.57±0.82	a	7.32±1.07	a
		Grazed	0.143±0.044		12.99±3.96		20.89±6.42	
	<i>Leymus chinensis</i>	Ungrazed	0.121±0.026	a	10.05±2.12	a	14.83±3.13	a
		Grazed	0.276±0.070		25.71±6.50		37.04±9.37	
L.c	<i>L. chinensis</i>	Ungrazed	0.137±0.026	ns	12.10±2.33	ns	18.35±3.53	ns
		Grazed	0.118±0.025		12.62±2.72		17.59±3.80	
	<i>S. grandis</i>	Ungrazed	0.222±0.049	ns	21.50±4.73	ns	36.96±8.14	a
		Grazed	0.303±0.023		32.22±2.45		56.65±4.31	
S.g	<i>L. chinensis</i>	Ungrazed	0.238±0.067	b	24.33±6.82	b	36.36±10.19	b
		Grazed	0.027±0.004		3.05±0.45		3.99±0.59	
	<i>S. grandis</i>	Ungrazed	0.429±0.072	b	38.83±6.55	a	74.11±12.50	a
		Grazed	0.178±0.016		22.97±2.11		42.49±3.90	
C.m	<i>L.chinensis</i>	Ungrazed	0.506±0.031	c	45.27±2.74	c	75.32±4.55	c
		Grazed	0.028±0.006		3.11±0.71		4.52±1.03	
	<i>S. grandis</i>	Ungrazed	0.026±0.008	ns	3.11±0.92	ns	6.85±2.03	ns
		Grazed	0.049±0.010		5.50±1.11		10.78±2.17	
A.f	<i>Artemisia frigida</i>	Ungrazed	0.025±0.006	a	2.14±0.52	a	5.84±1.42	a
		Grazed	0.074±0.017		6.71±1.55		18.24±4.21	
	<i>Kochia prostrata</i>	Ungrazed	0.173±0.031	ns	17.27±3.07	ns	39.60±7.04	a
		Grazed	0.092±0.031		9.44±3.21		19.09±6.49	

C.a, *Carex appendiculata* meadow steppe; S.b, *Stipa baicalensis* meadow steppe, L.c, *Leymus chinensis* typical steppe; S.g, *Stipa grandis* typical steppe; C.m, *Caragana microphylla* typical steppe; A. f, *Artemisia frigida* typical steppe; LAI, leaf area index; SAB, standing aboveground biomass. The same as that follows. ^a, ^b and ^c denote significant difference at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively, between the ungrazed and grazed sites and ns denotes none significant at statistical level. Data in the column are means +SE.

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Table 6. Correlation coefficients between LAI, leaf biomass, SAB and soil properties across six grassland communities in the Xilin River Basin.

Community traits	Field holding capacity (%)	Soil bulk density (g cm ⁻³)	Soil porosity (%)	Soil organic carbon (%)	Soil total nitrogen (%)	Soil total phosphorus (%)
Ungrazed (<i>n</i> =6)						
LAI (m ² m ⁻²)	0.928 ^b	-0.882 ^a	0.872 ^a	0.956 ^b	0.963 ^b	0.934 ^b
Leaf biomass (g m ⁻²)	0.923 ^b	-0.875 ^a	0.876 ^a	0.996 ^c	0.986 ^c	0.934 ^b
SAB (g m ⁻²)	0.907 ^a	-0.852 ^a	0.848 ^a	0.985 ^c	0.976 ^c	0.919 ^b
Grazed (<i>n</i> =6)						
LAI (m ² m ⁻²)	0.864 ^a	-0.736	0.733	0.902 ^a	0.830 ^a	0.304
Leaf biomass (g m ⁻²)	0.898 ^a	-0.790	0.787	0.925 ^a	0.862 ^a	0.355
SAB (g m ⁻²)	0.890 ^a	-0.790	0.787	0.917 ^a	0.851 ^a	0.341

^a, ^b and ^c denote the correlations are significant at the 0.05, 0.01 and 0.001 levels (2-tailed), respectively. *n* = number of communities.

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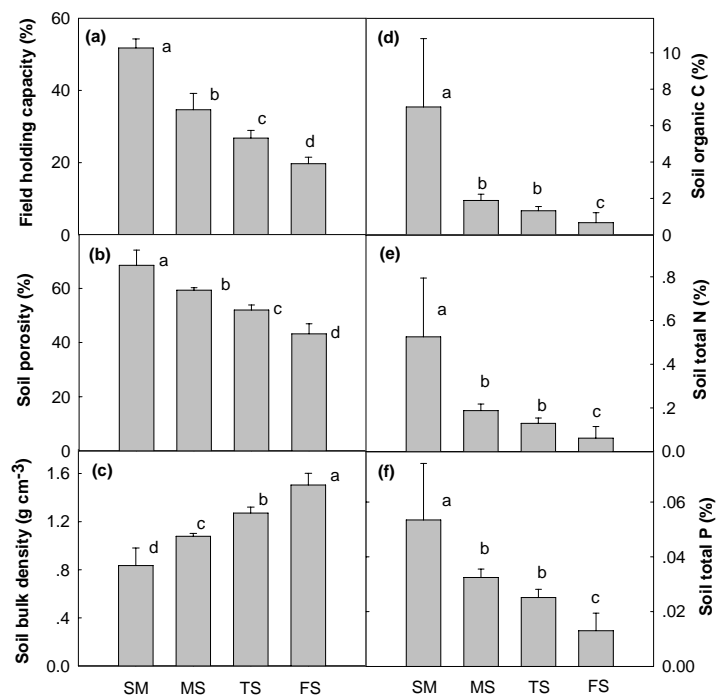


Fig. 1. Fielding holding capacity (a), soil porosity (b), soil bulk density (c), soil organic carbon (d), soil total nitrogen (e) and soil total phosphorus (f) of the soil layer (0–20 cm) in four steppes, the swamp meadow (SM), meadow steppe (MS), typical steppe (TS) and fixed sand dune complex (FS) in the Xilin River Basin, Inner Mongolia, China. Different letters followed by the columns indicate significant differences at *P* < 0.05.

9972

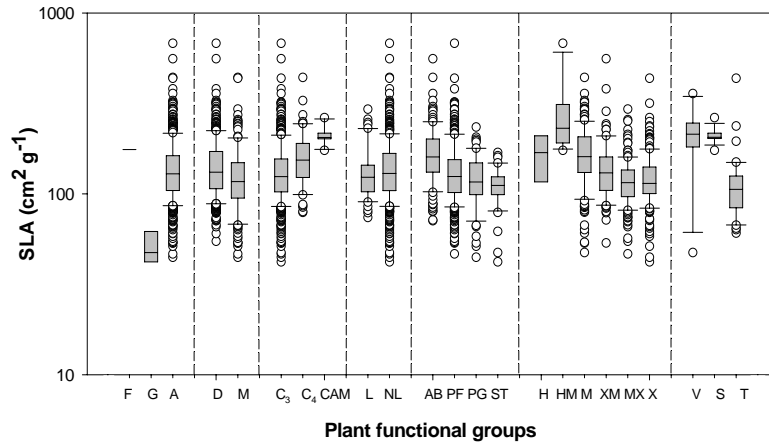


Fig. 2. Box plots of specific leaf area (SLA), with species grouped by the biological realm (F, Fern; G, Gymnosperm; A, Angiosperm; D, Dicotyledon; M, Monocotyledon), photosynthetic pathways (C_3 , C_3 species; C_4 , C_4 species; CAM, CAM species), N_2 -fixing ability (L, Legume; NL, Non-legume), life forms (AB, Annuals and biennials; PF, Perennial forbs; PG, Perennial graminoids; ST, Shrubs, sub-shrubs and small trees), water ecotypes (H, Hygrophytes; HM, Hygro-mesophytes; M, Mesophytes; XM, Xeromesophytes; MX, Mesoxerophytes; X, Xerophytes), and other PFGs (V, Vines and lianas; S, Succulents; T, Tuber and bulbous plants) in the Xilin River Basin, Inner Mongolia, China. Leaf SLA values were \log_{10} -transformed before analysis. Box plots show the interquartile range and median (central line); whiskers indicate the 10th and 90th percentiles. No whiskers are shown for groups with <10 species.

9973

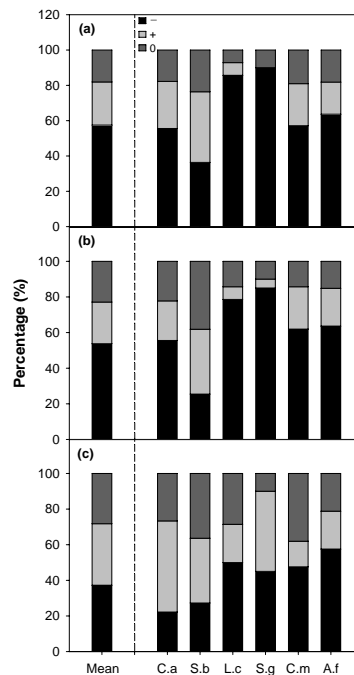


Fig. 3. Percentages of species categorized as three groups according to their leaf area (a), leaf mass (b) and leaf SLA values (c) decreased (-), increased (+) or changed little (o) by grazing in six grassland communities, C.a, *Carex appendiculata* meadow steppe, $n=45$; S.b, *Stipa baicalensis* meadow steppe, $n=55$; L.c, *Leymus chinensis* typical steppe, $n=14$; S.g, *Stipa grandis* typical steppe, $n=20$; C.m, *Caragana microphylla* typical steppe, $n=21$; and A.f, *Artemisia frigida* typical steppe, $n=33$. Means denote the mean values of six grassland communities. The same as that follows.

9974

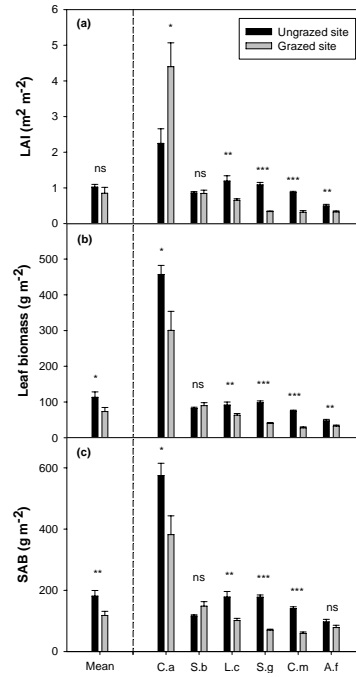


Fig. 4. Comparisons of the leaf area index (LAI), leaf biomass and standing aboveground biomass (SAB) between the ungrazed and grazed sites of six grassland communities in the Xinlin River Basin. *, ** and *** denote significant difference at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively, and ns denotes none significant at statistical level. The error bars are +SE.