PHOTOSYNTHETICA 43 (4): 559-565, 2005

Effects of grazing on photosynthetic characteristics of major steppe species in the Xilin River Basin, Inner Mongolia, China

S.P. CHEN*, Y.F. BAI, G.H. LIN, Y. LIANG, and X.G. HAN

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Haidian District, Beijing, 100093 China

Abstract

Species composition and photosynthetic characteristics of dominant species of ungrazed plot (UG), overgrazed plot (OG), and restored grazed plot (RG) were determined in the Xilin River Basin, Inner Mongolia, China. Both heavily grazing and restoration significantly affected the composition of different species and life forms. *Leymus chinensis*, *Stipa grandis*, and *Cleistogenes polyphylla*, three dominant perennial grasses in UG plot, contributed 58.9 % aboveground biomass to that of whole community, and showed higher net photosynthetic rate (P_N), transpiration rate (E), and intrinsic water-use efficiency (WUE). In OG plot, relative biomass of *L. chinensis* and *S. grandis* significantly decreased, while relative biomass of three shrubs/sub-shrubs, *Caragana microphylla*, *Artemisia frigida*, and *Kochia prostrata*, obviously increased. Heavy grazing significantly decreased P_N, E, and WUE of *L. chinensis* and *S. grandis*, while shrubs/sub-shrubs showed significantly higher photosynthetic activity and WUE than the grasses. After 18-year restoration, photosynthetic activities of *L. chinensis* and *S. grandis* were significantly higher than those in the OG plot. The proportion of *L. chinensis*, *S. grandis*, and *C. microphylla* significantly increased, and relative biomass of *C. polyphylla*, *A. frigida*, and *K. prostrata* markedly declined in RG plot. We found close relationships between physiological properties of species and their competitive advantage in different land use types. Higher photosynthetic capability means more contribution to total biomass. The variations in physiological characteristics of plants could partly explain the changes in species composition during degrading and restoring processes of Inner Mongolia typical steppes.

Additional key words: intercellular CO_2 concentration; net photosynthetic rate; overgrazing; restoration; species composition; stomatal conductance; transpiration; water use efficiency.

Introduction

China is one of the countries with the most plentiful grassland resources in the world. Natural grassland is one of the most important renewable resources in arid and semi-arid regions of North China, such as Inner Mongolia, Tibet, Gansu, *etc*. In recent decades, however, severe degradation and desertification were found in some grassland due to intense human activities, such as overgrazing, mowing, crop cultivation, *etc*. (Katoh *et al*. 1998, Zhou *et al*. 2002, Christensen *et al*. 2004). At present, about one third of the available grassland area degraded in China and overgrazing is one of the most important reasons inducing the widespread degradation and desertification (Zhou *et al*. 2002). Therefore, it is an urgent task to improve the understanding how grassland ecosystems will respond to overgrazing, since the sustainable utilization of grassland is important for the maintenance of nature ecosystems as well as farmers' life there.

Grazing by herbivores can substantially influence the dynamics of plant communities altering primary production, decomposition of organic matter, the cycling and distribution of nutrients, and competitive relationships among plant species (McNaughton 1985, Fahnestock and Detling 1999). Effects of grazing intensity on primary production, species composition, and community structure were well documented (Li 1989, 1993, Fahnestock and Detling 1999, Lavorel *et al*. 1999, Wang and Li 1999, Fernandez-Gimenez and Allen-Diaz 2001). In general, the process of grassland degradation is: first, community productivity declines, with a decrease in plant height, cover, and density, and second, changes in species composition appear, including a decline in the number of palatable grasses and an increase of unpalatable species (Wu and Loucks 1992). Although changes in water content, structure, and organic matter of soil, and selective

———

Received 22 November 23004, *accepted* 11 April 2005.
*Author for correspondence; fax: 86-10-62599059, e-mail: xghan@ibcas.ac.cn
Acknowledgements: This research was supported by the National Natural Science Foundation of China (90211012), the "100 People" project of the Chinese Academy of Sciences to G. Lin.

browsing are believed responsible for changes in vegetation, the mechanisms behind this phenomenon remain poorly understood.

In this study, we surveyed species composition of ungrazed, overgrazed, and restored plots and measured physiological properties (including photosynthesis, transpiration, intrinsic water-use efficiency, *etc*.) of six dominant species in three plots. Our objectives were to determine effects of grazing and restoration on photosynthetic characteristics of dominant species and to find physiological mechanisms of grassland degradation.

Materials and methods

Study site and plot selection: This study was conducted in the Xilin River Basin (43º26′N–44º29′N, 115º32′E–117º12′E), which is located in the typical steppe zone of Inner Mongolia Plateau. Topographically, this area, covering an area of about 10 000 km^2, declines gradually from east (the highest elevation 1 505 m) to west (the lowest elevation 902 m). Climate in the Xilin River Basin is semi-arid continental temperate steppe climate with dry spring and moist summer. Annual mean temperature increases from southeast to northwest, ranging from 0.5 to 2.1 °C. Annual precipitation decreases gradually from 400 mm in the southeast to 250 mm in the northwest (Chen 1988). More than 70 % of annual precipitation occurs during May–August. Chestnut and dark chestnut soils are the zonal soil types (Wang and Cai 1988).

Leymus chinensis community is a typical zonal vegetation type in Inner Mongolia. Three *L. chinensis* steppes with different land use types were selected as study plots: a typical *L. chinensis* steppe, fenced since 1979 as ungrazed plot (UG plot); a severe degraded steppe due to overgrazing as overgrazed plot (OG plot, it was a typical *L. chinensis* steppe before degradation); a restoring steppe, restored from a degraded *L. chinensis* steppe since 1985, as restored grazing plot (RG plot). Because the three plots were located in a relatively small area, within a distance of less than 10 km, they presumably were subjected to similar climatic conditions, such as temperature and precipitation. For more details about the three plots see Table 1.

Table 1. Characteristics of the study plots in the Xilin River Basin, Inner Mongolia, China. Means ± SE. Soil type was chestnut soil in all cases. *Different letters* indicate the significant difference in value among three plots (Duncan test, $p<0.05$).

Location	Ungrazed plot (UG) N 43º32.895' E 116º40.708'	Overgrazing plot (OG) N 43º37.967' E 116º39.397'	Restored grazing plot (RG) N 43º35.748' E 116º44.419'
Area [ha]	24	20	27
Altitude [m]	1 250	1 210	1 180
Soil nitrogen content [%]	0.17±0.03 [a]	0.14±0.03 [b]	0.13±0.03 [b]
Soil water content [%]	13.2±1.1 [a]	3.9±0.9 [c]	9.7±1.5 [b]
Land use type	Fenced plot	Heavy grazing	Fenced plot
Dominant species	*Leymus chinensis* *Stipa grandis*	*Artemisia frigida* *Cleistogenes polyphylla*	*Caragana microphylla* *Leymus chinensis* *Stipa grandis*

Methods: In each community, we randomly selected a 100 m sampling transect and sampled one quadrat (1×1 m in size) each 10 m (10 quadrates was sampled in each community) from August 10 to 12, 2002 when a maximum aboveground biomass usually appears according to our 22-year monitoring. In each quadrate, the height and number of individuals/ramets of each plant species were measured and counted, and the aboveground part of each species was collected and taken back to the laboratory for analysis. Fresh samples of each plant species were oven-dried at 70 ºC for about 48 h, and then weighed to determine their aboveground biomass. Relative biomass of each species was obtained by calculating the ratio of the total biomass of each species to the sum of biomass in all quadrates.

In each plot, plant species were grouped based on their life forms into shrubs, sub-shrubs, perennial grasses, perennial forbs, and annuals according to life form classification in Flora of Inner Mongolia (Editorial Committee of Flora of Inner Mongolia 1994). The relative biomass of each life form was determined based on the ratio of the biomass of each life form to the total biomass of the community. The relative abundance of life forms was obtained by calculating the ratio of the number of species in each life form to the total number of species in the community.

Soil water content (SWC) of surface layer (0–20 cm) was determined by the difference between moist and oven-dried (105 ºC to constant mass) samples according to the following equation: SWC [%] = [(wet – dry soil mass)/dry soil mass] ×100.

Soil samples of 0–20 cm at each spot were collected, wind-dried, and ground to pass a 100-mesh screen for total nitrogen content (TNC) analysis. About 0.5–1.0 g subsamples were used for determination of soil TNC by the Auto-Kjeldahl method (*Kjektec System 1026 Distilling Unit*, Sweden) at the Research Centre of Plant Ecology and Biodiversity Conservation, Institute of Botany, the Chinese Academy of Sciences. Soil total nitrogen content (TNC) [%] was expressed as the amount of total soil N per unit dry mass.

Six dominant species, *Leymus chinensis*, *Stipa grandis*, *Cleistogenes polyphylla*, *Artemisia frigida*, *Kochia prostrata*, and *Caragana microphylla*, were subjected to physiological measurements. Net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of the two species were measured at ambient CO_2 concentration and saturating irradiance (1 500 µmol m^{-2} s^{-1}, provided by a built-in red LED source) with a *LI-6400* Portable Photosynthetic System (*Li-Cor*, Lincoln, NE, USA). Instantaneous water use efficiency (WUE) was calculated by P_N/E. For each species, 3–4 replicate samples were measured.

Meteorological data including monthly precipitation and air temperature during growing season in 2002 were collected from weather station of IMGERS (Fig. 1).

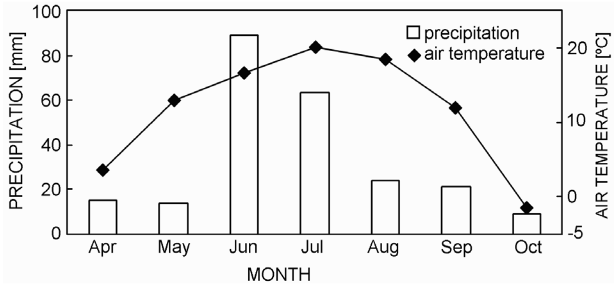

Fig. 1. Monthly precipitation and mean air temperature in the Xilin River Basin during growing season, 2002.

Statistical analyses were performed using *SPSS 10.0* procedures. Multiple comparisons were made on aboveground biomass, soil water content (SWC), and TNC among different plots. The significance of differences was tested by *t*-test or one-way ANOVA (Duncan test) at $p<0.05$ level. The same method was also used to separate the significance of the means of P_N, E, g_s, C_i, and WUE of different species in three plots.

Results

Floristic composition: Totally 37 species in 28 genera and 11 families were found in the three plots: 22, 22, and 32 species in UG, OG, and RG plots, respectively (Table 2). Species compositions were different between the three plots. In UG, three perennial grasses, *L. chinensis*, *S. grandis*, and *C. polyphylla*, were dominant species and contributed 21.7, 37.2, and 23.8 % to total aboveground biomass of community, respectively. In OG, relative biomass of *L. chinensis* and *S. grandis* significantly decreased, while *Artemisia frigida* and *Kochia prostrata* (two sub-shrubs) became dominant and the relative biomass of them was up to 61.6 % in whole community. After long-term restoring, the proportion of *L. chinensis*, *S. grandis*, and *C. microphylla* significantly increased, and relative biomasses of *C. polyphylla*, *A. frigida*, and *K. prostrata* markedly declined.

Significant variations were also found in life-form composition of three plots (Fig. 2). There was no difference in the amount of species in UG and OG plots and a similar distribution in the number of species in different life-from was found. However, the relative biomass of different life form changed sharply. About 95.4 % of aboveground biomass of community was perennial grasses in UG plot, while the percentage was reduced to 21.8 % and the proportion of sub-shrubs markedly increased up to 61.6 % in OG plot. Relative biomass of shrubs and perennial forbs in RG plot were significantly higher than that of the other two plots. Compared with OG plot, the proportions of perennial grasses obviously enhanced, while that of sub-shrubs decreased in RG plot.

$\boldsymbol{P_N}$ of *L. chinensis*, *S. grandis*, and *C. polyphylla* was significantly different among the three plots (Table 3). P_N of plants in UG and RG was higher than that of plants in OG plot and plants in OG had a much lower saturation irradiance than plants in other plots. P_N of *C. microphylla* and *A. frigida* in RG plot were significantly higher than in OG plot. There were no significant differences in P_N of *K. prostrata* between RG and OG plots.

E of *L. chinensis* in UG and RG was distinctly higher than that in OG (Table 3). *S. grandis* showed similar changes in *E*, but the differences were lessened. There were no obvious differences in *E* of *C. polyphylla* among the three plots. *E* of *C. microphylla* and *A. frigida* in RG were significantly higher than those in OG plot. There was no difference in *E* of *K. prostrata* between RG and OG plots.

WUE: Similar changes in WUE were found in three perennial grasses among the three plots, that is, WUE of grasses in UG and RG plots was obviously higher than that of plants in OG plot. However, WUE of the three shrubs/sub-shrubs was not significantly different between RG and OG plots (Table 3).

Discussion

Overgrazing by grazers alters the ecosystem process by consuming most of the aboveground plant biomass, reducing the cover of herbaceous plants and litter, disturbing and compacting soils, reducing water infiltration, and increasing the proportion of bare ground and soil erosion (Belsky and Blumenthal 1997). Water is a key-limiting factor for the growth of steppe plants in arid and semi-arid regions. Our results showed significant differences in soil water availability among the three plots, the rank of soil water content was as follows: UG>RG>OG (Table 1). Lower soil moisture content in turn reduced plant productivity and vegetative cover, creating negative feedback loops.

Heavily grazing and restoration both significantly affected species composition. The biomasses of tall perennial grasses, mainly *L. chinensis* and *S. grandis*, were markedly decreased because they are palatable and easier to be grazed. Once grazers were removed, the proportion

Table 2. Name, photosynthetic pathway, life form, and relative biomass of plant species of three plots in the Xilin River Basin, Inner Mongolia, China. **Bold words** represent the species investigated in this study. Means ± SE. *Different letters* indicate the significant difference in value among three plots (Duncan test, $p<0.05$). S, SS, PG, PF, and A represent shrubs, sub-shrubs, perennial grasses, perennial forbs, and annuals, respectively.

Species	Photosynth. pathway	Life form	Relative biomass [%] UG	OG	RG
Achnatherum sibiricum	C_3	PG	3.34±0.72	0.01±0.00	0.36±0.28
Agropyron cristatum	C_3	PG	8.07±1.78	0.92±0.51	23.70±2.70
Allium anisopodium	C_3	PF	0.01±0.01	-	-
Allium bidentatum	C_3	PF	0.02±0.02	-	0.83±0.66
Allium ramosum	C_3	PF	0.02±0.01	-	2.23±1.21
Allium tenuissimum	C_3	PF	0.06±0.03	-	0.85±0.36
Artemisia frigida	C_3	**SS**	**0.01±0.01** [c]	**54.0±6.4** [a]	**13.90±3.60** [b]
Artemisia pubescens	C_3	PF	-	-	1.11±0.92
Artemisia scoparia	C_3	A	-	0.92±0.48	0.04±0.04
Astragalus galactiters	C_3	PF	-	0.15±0.10	-
Axyris amarantoides	C_3	A	0.01	1.34±0.69	0.05±0.02
Caragana microphylla	C_3	**S**	**-**	**2.40±1.37** [b]	**15.90±4.70** [a]
Carex korshinskyi	C_3	PF	3.99±0.86	1.92±0.58	0.89±0.38
Chenopodium aristatum	C_3	A	0.07±0.04	0.01±0.01	-
Chenopodium glaucum	C_3	A	0.01±0.01	1.07±0.73	0.01±0.01
Cleistogenes squarrosa	C_4	**PG**	**23.80±2.80** [a]	**19.60±3.50** [a]	**2.63±0.40** [b]
Cymbaria dahurica	C_3	PF	0.21±0.14	-	0.18±0.18
Festuca dahurica	C_3	PG	-	0.07±0.07	-
Gueldenstaedtia verna	C_3	PF	-	-	0.03±0.03
Heteropappus altaicus	C_3	PF	-	0.04±0.04	0.08±0.07
Iris tenuifolia	C_3	PF	-	0.12±0.08	0.11±0.10
Kochia prostrata	C_4	**SS**	**0.02±0.02** [b]	**7.64±1.71** [a]	**1.05±0.48** [b]
Koeleria cristata	C_3	PG	1.28±0.62	-	1.77±0.61
Leymus chinensis	C_3	**PG**	**21.70±3.10** [a]	**1.05±0.49** [b]	**13.60±4.20** [a]
Melilotoides ruthenica	C_3	PF	-	0.19±0.13	0.09±0.06
Oxytropis myriophylla	C_3	PF	-	-	0.51±0.51
Poa pratensis	C_3	A	0.09±0.08	-	0.27±0.14
Potentilla acaulis	C_3	PF	0.01±0.01	1.88±1.14	-
Potentilla bifurca	C_3	PF	0.03±0.03	-	1.06±0.50
Potentilla tanacetifolia	C_3	PF	-	1.04±0.45	1.16±1.10
Salsola collina	C_3	A	0.01±0.00	5.43±1.74	0.51±0.22
Saposhnikovia divaricata	C_3	PF	-	-	0.71±0.52
Saussurea japonica	C_3	PF	-	-	0.01±0.01
Stipa grandis	C_3	**PG**	**37.20±2.80** [a]	**0.24±0.08** [c]	**14.90±3.70** [b]
Thalictrum petaloideum	C_3	PF	0.01±0.01	-	0.40±0.22
Thalictrum squarrosum	C_3	PF	-	-	0.95±0.59
Thermopsis lanceolata	C_3	PF	-	-	0.11±0.08
Sum of species			22	22	32

of them significantly increased again. Opposite trend was found in *A. frigida* and *K. prostrata*. Our results are in agreement with that of Li (1989) who, based on the studies in Inner Mongolia steppes, classified steppe species into five ecological groups according to their reaction to grazing pressure: invader, increaser, relative increaser, fluctuating species, and decreaser. *L. chinensis*, *S. grandis*, and *K. prostrata* are decreasers, whereas *A. frigida*, *C. squarrosa*, and *C. microphylla* are increasers.

The two most important dominant C_3 species in the typical steppe zone of Inner Mongolia, *L. chinensis* and *S. grandis*, contributed by 58.9 % aboveground biomass to that of whole community. They showed higher P_N, E, and WUE in UG plot, because higher g_s sustained higher P_N in wetter habitats (Table 3). Moreover, more efficient water use pattern made them producing more biomass to keep overwhelming competitive advantages. Heavy grazing decreased significantly P_N, E, and WUE of *L. chinensis* and *S. grandis*. Both *L. chinensis* and *S. grandis* were high and palatable grasses and more likely to be grazed by herbivores. Defoliation by grazers lowering the photosynthetic surface area might be one reason of the rapid declines in photosynthetic activities. Moreover, g_s of *L. chinensis* and *S. grandis* distinctly declined in OG plot showing that grasses might respond to lower water availability by increasing stomatal closure to limit E and then greatly reduce photosynthetic activities. Stomatal response of *L. chinensis* was more sensitive than that of *S. grandis.*

Compared with two C_3 grasses, *C. polyphylla* kept higher g_s and E (Table 3). There were negative effects of

Table 3. Photosynthetic characteristics of six dominant species of three plots in the Xilin River Basin, Inner Mongolia, China. Means ± SE. *Capital letters* indicate the difference in mean value of each species among different plots, whereas *small letters* represent the difference in mean values among species in the same plot. Significant difference among variables was determined by *t*-test or ANOVA (Duncan test, $p<0.05$). Values with any letter in common are not significantly different. Lc, Sg, Cs, Cm, Af, and Kp represent *Leymus chinensis*, *Stipa grandis*, *Cleistogenes squarrosa*, *Caragana microphylla*, *Artemisia frigida*, and *Kochia prostrata*, respectively.

	Species	Plots UG	OG	RG
P_N	Lc	10.95±1.76 ^{Aa}	1.29±0.63 ^{Bb}	11.05±0.65 ^{Aa}
	Sg	5.17±1.79 ^{Ab}	2.01±0.74 ^{Ab}	4.75±0.89 ^{Ab}
	Cs	7.40±0.91 ^{Aab}	7.21±0.83 ^{Ab}	7.01±0.99 ^{Aab}
	Cm	-	5.15±1.71 ^{Bab}	10.41±1.05 ^{Aa}
	Af	-	7.15±1.05 ^{Aa}	11.29±1.51 ^{Aa}
	Kp	-	8.11±1.78 ^{Aa}	8.18±1.92 ^{Aab}
E	Lc	3.76±0.58 ^{Aa}	0.63±0.08 ^{Bc}	3.02±0.45 ^{ABb}
	Sg	1.80±0.41 ^{Ab}	1.16±0.40 ^{Abc}	1.91±0.46 ^{Ab}
	Cs	2.57±0.56 ^{Aab}	2.51±0.44 ^{Aab}	2.45±0.27 ^{Ab}
	Cm	-	1.76±0.41 ^{Aabc}	3.99±0.87 ^{Aab}
	Af	-	2.95±0.97 ^{Aa}	5.29±1.45 ^{Aa}
	Kp	-	2.17±0.26 ^{Aab}	2.12±0.35 ^{Ab}
g_s	Lc	0.21±0.08 ^{Aa}	0.02±0.00 ^{Ac}	0.18±0.08 ^{Aab}
	Sg	0.08±0.03 ^{Aa}	0.03±0.01 ^{Abc}	0.06±0.01 ^{Ab}
	Cs	0.08±0.00 ^{Aa}	0.08±0.01 ^{Aa}	0.073±0.04 ^{Ab}
	Cm	-	0.05±0.02 ^{Babc}	0.16±0.04 ^{Aab}
	Af	-	0.09±0.02 ^{Aa}	0.27±0.15 ^{Aa}
	Kp	-	0.06±0.01 ^{Aab}	0.08±0.03 ^{Ab}
C_i	Lc	211±22 ^{Aa}	229±27 ^{Ab}	216±55 ^{Aa}
	Sg	217±9 ^{Aa}	230±16 ^{Ab}	208±12 ^{Aa}
	Cs	177±20 ^{Aa}	173±77 ^{Ab}	169±25 ^{Aa}
	Cm	-	174±12 ^{Aab}	208±22 ^{Aa}
	Af	-	208±26 ^{Ab}	235±36 ^{Aa}
	Kp	-	125±11 ^{Ab}	145±20 ^{Aa}
WUE	Lc	3.04±0.47 ^{Aa}	1.82±0.65 ^{Aab}	3.71±0.33 ^{Aab}
	Sg	2.70±0.55 ^{Aa}	1.71±0.20 ^{Ab}	2.59±0.31 ^{Ac}
	Cs	3.04±0.41 ^{Aa}	2.94±0.75 ^{Bab}	2.84±0.15 ^{ABabc}
	Cm	-	2.71±0.33 ^{Aab}	2.75±0.34 ^{Abc}
	Af	-	2.77±0.58 ^{Aab}	2.22±0.32 ^{Ac}
	Kp	-	3.87±1.08 ^{Aa}	3.77±0.26 ^{Aa}

heavy grazing on P_N and WUE of *C. polyphylla*, but the range of changes was little. Another study in the same area found that *C. polyphylla* required an average air temperature of >20 °C to initiate growth, most probably due to its C_4 photosynthetic pathway. In this region, temperatures above 20 °C also coincide with periods of most reliable rainfall, which may explain the success of *C. polyphylla* in grassland degraded by overgrazing. It does not waste scarce root reserves trying to initiate growth earlier in the season when rainfall is erratic and grazing intensity is most intense. In contrast, competing C_3 species (*e.g*. *Stipa* spp. and *L. chinensis*) initiate growth earlier in spring when rainfall is highly variable and when small plants are most exposed to severe grazing pressure by livestock emerging from winter in poor condition (Liang *et al*. 2002).

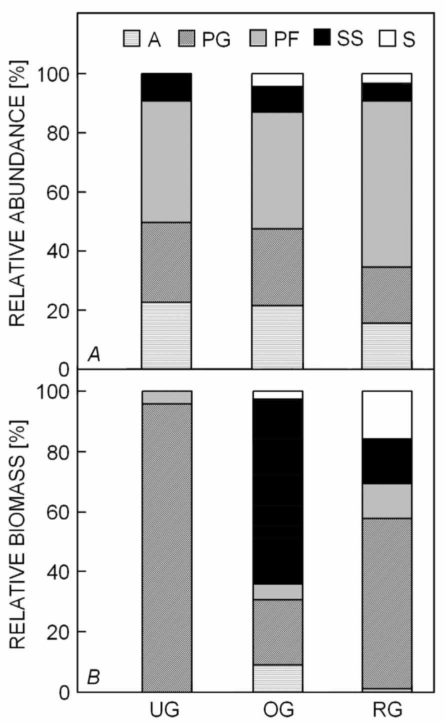

Fig. 2. Relative abundance (*A*) and relative biomass (*B*) of different life forms in three plots. A: annuals, PG: perennial grasses, PF: perennial forbs, SS: sub-shrubs, S: shrubs.

Some studies indicated that large grazers can directly influence the growth and demography of defoliated plants and plant parts (McNaughton 1983, Belsky 1986), and indirectly influence co-occurring ungrazed plants as a result of selective grazing of competitively dominant grasses and a competitive release of subordinate species (Fahnestock and Knapp 1994, Damhoureyeh and Hartnett 1997, Hickman and Hartnett 2002). In our study, relative biomass of three shrubs/sub-shrubs, *C. microphylla*, *A. frigida*, and *K. prostrata*, obviously increased due to heavy grazing. P_N, *E*, and WUE of shrubs/sub-shrubs were significantly higher than those of grasses, that is, shrubs/sub-shrubs not only could sustain higher photosynthetic activities in low water availability conditions and also enhance WUE to produce more saccharides using limiting water resource. Other studies in Inner Mongolia steppes showed that the proportion of *A. frigida* increased with increasing stocking rate and consequently the degraded grassland was dominated by *A. frigida* (Li 1993, Wang and Li 1999, Wang *et al*. 2001). In addition to high P_N and conservative water use pattern, different growth and vegetative reproduction strategies of *A. frigida* responding to grazing also strengthened competitive advantage in heavy grazing condition. *A. frigida*, a sub-shrub with vegetative reproduction by stolons, could change its life type from erect growth to reptant growth and trample of herbivores could stimulate differentiating of stem buds and adventitious roots to accelerate reproduction (Li 1993). Moreover, during florescence the special smell of *A. frigida* could avoid grazing by herbivores.

After enclosed 18-year, not only the number of species of restoring degraded steppe obviously increased, but also the relative biomass of different species in community changed markedly. Soil water availability was significantly enhanced during steppe restoring process, which led to appearance of many perennial forbs (most of them mesophytes) and increased species richness of community. Although perennial forbs were numerous, their aboveground biomass only accounted for little proportion of whole community. The relative biomass of *L. chinensis* and *S. grandis* markedly increased, which favoured the recruitment of perennial grasses. Our results showed that photosynthetic capabilities of *L. chinensis* and *S. grandis* were significantly improved and P_N, *E*, and WUE were close to the level in un-grazed steppe. For *A. frigida* and *K. prostrata*, higher P_N, *E*, and *WUE* were also found in restoring steppe, but the relative biomass of them distinctly decreased. Our results indicated perennial grasses had stronger competitive ability than sub-shrubs when grazers were removed from steppes. Other studies in the same area found similar results (Wang *et al*. 1996a,b). Unlike sub-shrubs, the proportion of *C. microphylla*, a deep-root shrub, obviously increased in RG steppe, not only because they kept high photosynthetic capability, but because they could utilize water and nutrient resources in deep soil layer and due to deeper root distribution diminishing competition with perennial grasses.

In conclusion, we found that both overgrazing and restoring of steppe significantly affected the physiological characteristics including P_N, *E*, g_s, and WUE. There are close relationships between physiological properties of the species and their competitive advantage in different land use types. Higher photosynthetic capability means more contribution to total biomass. The variations in photosynthetic characteristics of plants could partly explain the changes in species composition during degrading and restoring processes of Inner Mongolia typical steppes.

References

Belsky, A.J.: Does herbivory benefit plants? A review of the evidence. – Amer. Naturalist **127**: 870-892, 1986.

Belsky, A.J., Blumenthal, D.M.: Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. – Conserv. Biol. **11**: 315-327, 1997.

Chen, Z.Z.: [Topography and climate of Xilin River Basin.] – In: Inner Mongolia Grassland Ecosystem Research Station, the Chinese Academy of Sciences (ed.): Research on Grassland Ecosystem. No. 3. Pp. 13-22. Science Press, Beijing 1988. [In Chin.]

Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z.Z.: Vulnerability of the Asian typical steppe to grazing and climate change. – Climate Change **63**: 351-368, 2004.

Damhoureyeh, S.A., Hartnett, D.C.: Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. – Amer. J. Bot. **84**: 1719-1728, 1997.

Fahnestock, J.T., Detling, J.K.: The influence of herbivory on plant cover and species composition in the Pryor Mountain Wild Horse Range, USA. – Plant Ecol. **144**: 145-157, 1999.

Fahnestock, J.T., Knapp, A.K.: Plant responses to selective grazing by bison: interactions between light, herbivory and water stress. – Vegetatio **115**: 123-131, 1994.

Fernandez-Gimenez, M., Allen-Diaz, B.: Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. – Plant Ecol. **157**: 101-118, 2001.

Hickman, K.R., Hartnett, D.C.: Effects of grazing intensity on growth, reproduction, and abundance of three palatable forbs in Kansas tallgrass prairie. – Plant Ecol. **159**: 23-33, 2002.

Katoh, K., Takeuchi, K., Jiang, D., Nan, Y., Kou, Z.: Vegetation restoration by seasonal exclosure in the Kerqin Sandy Land, Inner Mongolia. – Plant Ecol. **139**: 133-144, 1998.

Lavorel, S., McIntyre, S., Grigulis, K.: Plant response to disturbance in a Mediterranean grassland: how many functional groups? – J. Veget. Sci. **10**: 661-672, 1999.

Li, Y.H.: Impact of grazing on *Aneurolepidium chinense* steppe and *Stipa grandis* steppe. – Acta oecol./Oecol. appl. **10**: 31-46, 1989.

Li, Y.H.: [Grazing dynamics of the species diversity in *Aneurolepidium chinense* steppe and *Stipa grandis* steppe.] – Acta bot. sin. **35**: 877-884, 1993. [In Chin.]

Liang, C., Michalk, D.L., Millar, G.D.: The ecology and growth patterns of *Cleistogenes* species degraded grasslands of eastern Inner Mongolia, China. – J. appl. Ecol. **39**: 584-594, 2002.

McNaughton, S.J.: Compensatory plant growth as a response to herbivory. – Oikos **40**: 329-336, 1983.

McNaughton, S.J.: Ecology of a grazing ecosystem: the Serengeti. – Ecol. Monogr. **55**: 259-294, 1985.

Wang, J.W., Cai, C.: [Studies on genesis, types and characteristics of the soils of the Xilin River Basin.] – In: Inner Mongolia Grassland Ecosystem Research Station, the Chinese Academy of Sciences (ed.): Research on Grassland Ecosystem. No. 3. Pp. 23-83. Science Press, Beijing 1988. [In Chin.]

Wang, S.P., Li, Y.H.: [Degradation mechanism of typical grassland in Inner Mongolia.] – Chin. J. appl. Ecol. **10**: 437-441, 1999. [In Chin.]

Wang, S.P., Li, Y.H., Wang, Y.F., Chen, Z.Z.: [Influence of different stocking rates on plant diversity of *Artemisia frigida* community in Inner Mongolia steppe.] – Acta bot. sin. **43**: 89-96, 2001. [In Chin.]

Wang, W., Liu, Z.L., Hao, D.Y., Liang, C.Z.: [Research on the restoring succession of the degenerated grassland in Inner Mongolia I. Basic characteristics and driving force for restoration of the degenerated grassland.] – Acta phytoecol. sin. **20**: 449-459, 1996a. [In Chin.]

Wang, W., Liu, Z.L., Hao, D.Y., Liang, C.Z.: [Research on the restoring succession of the degenerated grassland in Inner Mongolia II. Analysis of the restoring processes.] – Acta phytoecol. sin. **20**: 460-471, 1996b. [In Chin.]

Wu, J.G., Loucks, O.: Xilingele. – In: Committee on Scholarly Communication with the People's Republic of China, National Research Council (ed.): Grasslands and Grassland Sciences in Northern China. Pp. 67-84. National Academies Press, Washington 1992.

Zhou, G., Wang, Y., Wang, S.: Responses of grassland ecosystems to precipitation and land use along the Northeast China Transect. – J. Veget. Sci. **13**: 361-368, 2002.