Plant Soil (2011) 340:141–155
DOI 10.1007/s11104-010-0369-3

REGULAR ARTICLE

Differential responses of plant functional trait to grazing between two contrasting dominant C3 and C4 species in a typical steppe of Inner Mongolia, China

**Shuxia Zheng · Zhichun Lan · Wenhuai Li ·
Ruixin Shao · Yumei Shan · Hongwei Wan ·
Friedhelm Taube · Yongfei Bai**

Received: 30 December 2009 / Accepted: 25 March 2010 / Published online: 7 April 2010

Abstract Plant functional traits have been widely used to study the linkage between environmental drivers, trade-offs among different functions within a plant, and ecosystem structure and functioning. Here, the whole-plant traits, leaf morphological and physiological traits of two dominant species, *Leymus chinensis* (C_3 perennial rhizome grass) and *Cleistogenes squarrosa* (C_4 perennial bunchgrass), were studied in the Inner Mongolia grassland of China, with a grazing experiment including five stocking rates (0, 3.0, 4.5, 7.5, and 9.0 sheep/ha) in 2008 (wet year) and 2009 (dry year). Our results demonstrated that, for both species, the effects of stocking rate, year, and stocking rate × year on whole-plant traits and leaf morphological and physiological traits were highly significant in most cases. The differential responses of plant trait to variation in precipitation were caused by trait trade-offs between the wet and dry years. *L. chinensis* adopted the high N content and net photosynthetic rate (P_n) in the wet year but both the low N content and P_n in the dry year under grazed conditions. The trait trade-offs of *C. squarrosa* were characterized by high specific leaf area (SLA) and P_n in the dry year vs. low SLA and P_n in the wet year. Our findings also indicate that *C. squarrosa* is more resistant to grazing than *L. chinensis* in terms of avoidance and tolerance traits, particularly under heavy grazing pressure and in the dry year.

Responsible Editor: Klaus Butterbach-Bahl.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-010-0369-3) contains supplementary material, which is available to authorized users.

S. Zheng · Z. Lan · W. Li · Y. Bai (✉)
State Key Laboratory of Vegetation and Environmental
Change, Institute of Botany, Chinese Academy of Sciences,
20 Nanxincun, Xiangshan,
Beijing 100093, China
e-mail: yfbai@ibcas.ac.cn

R. Shao
State Key Laboratory of Soil Erosion and Dryland Farming
on the Loess Plateau, Institute of Soil and Water
Conservation, Chinese Academy of Sciences,
Yangling, Shaanxi 712100, China

Y. Shan
College of Ecology and Environmental Science,
Inner Mongolia Agricultural University,
Hohhot, Inner Mongolia 010018, China

H. Wan · F. Taube
Institute of Crop Science and Plant Breeding—Grass
and Forage Science/Organic Agriculture,
Christian-Albrechts-University,
Hermann-Rodewald-Str. 9,
24118 Kiel, Germany

Keywords Grazing · Whole-plant trait · Leaf morphological trait · Leaf physiological trait · Stocking rate · *Leymus chinensis* · *Cleistogenes squarrosa*

Introduction

Plant functional traits are considered as reflecting the adaptations to environmental change and trade-offs among different functions within a plant, thus they can better link environmental drivers and plant responses to ecosystem structure and functioning (Díaz et al. 1998; Díaz et al. 2007; Lavorel et al. 2007; Wright et al. 2004). In recent years, more attempts to predict plant responses to grazing have focused on using plant functional traits, especially for some 'soft' traits, which can be easily and quickly measured, such as plant height, leaf size, leaf toughness, leaf dry matter content, and specific leaf area (SLA) (Adler et al. 2005; Díaz et al. 2007; Díaz et al. 2001; De Bello et al. 2005; Golodets et al. 2009; Vesk et al. 2004). Generally, these 'soft' traits are closely correlated with the 'harder' traits, such as photosynthetic capacity, relative growth rate, leaf nutrient concentrations, and leaf turnover rate, which further reflect the fundamental trade-offs between fast growth and anti-herbivore defence (or nutrient storage) in plant functioning (Grime 2001; Reich et al. 1997; Reich et al. 2007; Westoby et al. 2002).

Many studies showed that plant height and leaf size decreased under grazing pressure (Díaz et al. 2001; Klimesova et al. 2008; Landsberg et al. 1999; Rusch et al. 2009). Because tall species receive most grazing pressure and short species are protected from grazing by tall species. Also, larger leaves provide better bites for grazer, and smaller leaves require more bites at a given leaf area (and mass) if taken in the same number of bites (Vesk et al. 2004). SLA, the ratio of leaf area to leaf mass, as an important leaf trait that integrates plant investment into growth and storage, has been widely used to predict plant strategy. Westoby (1999) reported that SLA might be related to grazing responses in a different manner at low and high grazing intensities. The high SLA species decreased faster than low SLA species at low grazing intensity. However, under high and non-selective grazing intensity, all species are grazed and high SLA species may be advantaged by faster regrowth. Therefore, plant resistance to grazing is associated with both avoidance traits (e.g., small height and leaf size), and tolerance traits (e.g., high SLA and leaf N content) (Cingolani et al. 2005; Díaz et al. 2001). Díaz et al. (2001) proposed plant species responses to grazing could be predicted from simple traits, such as plant height, leaf size, life history, and SLA in subhumid grasslands. Yet, Vesk et al. (2004) found little evidence for predictability of grazing effect on plant growth with simple traits in the semi-arid and arid shrublands and woodlands. Recently, several studies demonstrated plant traits response to grazing are largely mediated by resource availability (e.g., precipitation and soil nutrients) (Adler et al. 2004; Osem et al. 2004; Pakeman 2004; Vesk et al. 2004) and grazing intensity or evolutionary history of grazing (Adler et al. 2004; Díaz et al. 2007; Graff et al. 2007). For example, Adler (2004) found that aridity favored grazing resistance traits, while grazing impact was intermediated in wetter sites. Thus, there are still large uncertainties associated with the effects of grazing on plant functional traits and the causal linkage between shifts in species traits and change in ecosystem functioning under different environmental conditions.

As typical semi-arid grasslands, the Xilin River Basin is characterized by sparse and irregular rainfall and soil nutrient deficiency (Chen 1988; Wang and Cai 1988). The traditional land use type in this area is grazing, which changed from semi-nomadic farming systems to intensified settled livestock farming in the last 20 years. Consequently, species diversity and aboveground net primary productivity (ANPP) decreased markedly in recent decades, and grassland degradation has become a severe problem in Xilin River Basin (Tong et al. 2004). *Leymus chinensis* (tall perennial C_3 rhizome grass) and *Cleistogenes squarrosa* (short perennial C_4 bunchgrass) are two dominant species distributed widely across a broad range of grassland ecosystems on the Mongolian plateau (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia 1985; Hilbig 1995). However, both species have distinctly different habitats: *L. chinensis* predominates in relatively wet and fertile habitats with high vegetation cover, while *C. squarrosa* dominates in dry and infertile habitats with low vegetation cover, particularly in the overgrazed communities. In the lightly and moderately grazed communities, *L. chinensis* is located at the upper canopy layer of the community while *C.*

squarrosa is at the lower canopy layer. Previous studies demonstrated that both species have distinct individual traits in terms of leaf morphology (Wan et al. 2008), photosynthetic physiology (Chen et al. 2002; Chen et al. 2005; Cui et al. 2001), root distribution (Chen et al. 2001), seed size and seed mass (Zhong et al. 2001). Yet, little is known about how functional traits of the two contrasting species respond to grazing and their differences in avoidance and tolerance strategies under different stocking rates. Several previous studies have predicted that overgrazing will lead to a shift in dominance from *L. chinensis* to *C. squarrosa* and consequently cause a decrease in biodiversity and ecosystem functioning (Auerswald et al. 2009; Bai et al. 2000; Bai et al. 2007; Wang et al. 2003), although mechanisms underpinning this shift are not very clear.

In this study, both morphological and physiological traits of *L. chinensis* and *C. squarrosa* grown in a traditional grazing system with different stocking rates were examined in 2008 (a wetter year) and 2009 (a dry year). Specifically, we address the following three research questions: First, how do functional traits of the two dominant species vary with grazing intensity and precipitation? Second, are there any fundamental trades-offs linked to trait responses to grazing and variation in precipitation? Third, what are the avoidance and tolerance strategies employed by two species to improve their grazing resistance?

Materials and methods

Study area and experimental design

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences, which is located at the middle reach of the Xilin River (Bai et al. 2004). Based on the long-term meteorological data (1970–2007), the mean annual temperature in the study area was 0.4°C with mean monthly temperature ranging from −21.4°C in January to 19.0°C in July, and annual precipitation was 336.9 mm, with 51–89% occurring in the growing season (May–August). The meteorological data collected within the experimental site showed that the patterns of monthly mean temperature were similar between 2008 and 2009, but the patterns of monthly precipitation were quite different between the 2 years (Fig. 1), with much higher total annual precipitation occurred in 2008 (297 mm) than that in 2009 (226 mm). The growing season precipitation (May–August) was 263 mm in 2008 but only 157 mm in 2009.

The topography at our experimental site is consisted of two landscape units, i.e., slope and flat ground, with elevations ranging from 1220 to 1280 m. The soil is dark chestnut soil (Calcic Chernozem according to ISSS Working Group RB, 1998), with a loamy sand texture (Bai et al. 2010). Topsoil organic carbon, total nitrogen, and total phosphorus contents (0–10 cm) are 20.0, 1.90 and 0.32 $g.kg^{-1}$, respectively. Topsoil pH ranges from 6.61 to 7.98 and the topsoil cation exchange capacity (CEC) is 15.7 $cmol.kg^{-1}$. The vegetation at the study area is dominated by *L. chinensis* and *Stipa grandis* (C_3 perennial bunchgrass), which is a widely distributed community type in the Eurasia steppe (Bai et al. 2008; Coupland 1993).

Field sampling and measurements were carried out at the Sino-German grazing experimental site, which was established in June 2005 and occupied a total area of 160 ha including 56 experimental plots (Schonbach et al. 2009). The experimental treatment was composed of two management systems (e.g., traditional versus mixed system) and 7 levels of stocking rate (SR=0, 1.5, 3.0, 4.5, 6.0, 7.5, and 9.0 sheep/ha). The standard plot size was 2 ha for SR=0, 3.0, 4.5, 6.0, 7.5, and 9.0 sheep/ha, while it was 4 ha for SR=1.5 sheep/ha in order to achieve a minimum of 6 sheep per plot. All plots have been fenced against sheep migration between plots since the beginning of the experiment. The traditional system was managed with grazing and haymaking on two different areas. In the grazing area, sheep was allowed to graze continuously during the vegetation period from June to September. The mixed system was managed with a yearly shift between grazing and haymaking (Schonbach et al. 2009). In this study, the traditional grazing system including 5 levels of stocking rates (i.e., 0, 3.0, 4.5, 7.5 and 9.0 sheep/ha), representing a gradient of increasing grazing intensity, was selected as our field sampling and measurement plots.

Vegetation and soil properties

Within each plot, three 2 m×2 m grazing exclosures were established randomly in the early June to

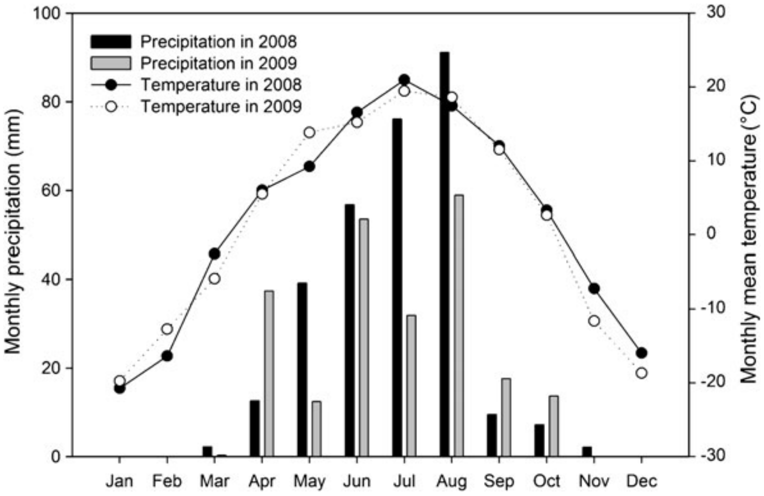


Fig. 1 Monthly precipitation (*bars*) and monthly mean air temperature (*line*) of the Xilin River Basin in 2008 and 2009. Meteorological data were collected from the eddy tower adjacent (approximately 100 m) to the experimental plots

determine the aboveground biomass before sheep grazing started, and the exclosures were monthly moved to new locations to measure the productivity of grazed plots until the end of September each year. Two sampling quadrats (1 m×1 m) were randomly located inside and outside each exclosure and paired into block each month. The difference in total biomass between each pair of quadrats was used for estimating monthly biomass increment. On the 8–10th of each month, all living biomass within each quadrat was harvested by clipping to the soil surface, separated to species, oven dried at 70°C for 24 h to constant mass, and weighed. Litter biomass within each quadrat was collected. The total aboveground biomass available for grazing sheep (B_g) and the ungrazed aboveground biomass (B_u) were collected outside and within each grazing exclosure during June, July, August, and September, thus the monthly biomass increment could be estimated. Annual biomass accumulation (B_a) was calculated by the biomass at the initial date of grazing (early June) summed to the monthly biomass growth using the following equation as per suggested by Schonbach et al. (2009).

$$B_a = B_{g1} + \left(B_{u2} - B_{g1}\right) + \left(B_{u3} - B_{g2}\right) + \left(B_{u4} - B_{g3}\right)$$

where B_{gi} and B_{ui} are the aboveground biomass collected outside and inside the exclosure at sampling time i (i=1, 2, 3, 4, i.e., beginning of June, July, August, and September, respectively).

Since the standing aboveground biomass of this area usually reaches its annual peak in August, thus aboveground net primary productivity (ANPP) for each treatment approximated B_a (Bai et al. 2004). For SR=0, the peak aboveground biomass sampled in August was equated with B_a.

Five soil samples were collected at the surface layer (0–10 cm) for each plot, oven-dried at 105°C for 48 h, and weighed to determine soil moisture (%) in mid July, 2008 and 2009.

Plant traits

On July 25–26, 2008 and 2009, we randomly collected 30 individuals (ramet) of *L. chinensis* (a clonal plant) and the same number of bunches for *C. squarrosa* at each plot. The height was determined by the distance from the basal stem to the natural crown of each plant individual. After the height measurement, the aboveground part of each individual was collected and taken back to the laboratory for separating stem and leaf biomass. All stem and leaf samples were oven-dried at 70°C for 24 h to constant mass and weighted. Thus, stem biomass, leaf biomass, stem: leaf ratio (S/L), and plant individual biomass were calculated.

For each species, 30–50 individuals with fully expanded leaves were chosen for measuring leaf morphological traits. According to leaf size, 5–20 leaves were picked as a sample and totally 30 replicates for each species. The projected area of each sample was measured with a planimeter (Li-3100, Li-

Cor, Lincoln, NE, USA), and then oven-dried at 70°C for 24 h to a constant mass. The specific leaf area (SLA, $cm^2 g^{-1}$) was calculated as the ratio of leaf area (LA) to leaf dry mass (LM). After SLA measurement, leaf sample was grounded to 80-mesh and leaf N content was analyzed using a Kjeltec analyzer (Kjeltec 2300 Analyzer Unit, Foss, Sweden). The leaf N content was expressed on both mass basis (N_{mass}, %) and area basis (N_{area}, $g \cdot m^{-2}$), which was calculated as N_{mass} divided by SLA.

Gas exchange

The photosynthetic gas exchange parameters of two species were measured with a Li-6400 Portable Photosynthetic System (Li-6400, Li-Cor, Lincoln, NE, USA) on 25–26 July, 2008 and 2009. Net photosynthetic rate (P_n), transpiration rate (T_r), stomatal conductance (G_s), and intercellular CO_2 concentration (C_i) were measured at a CO_2 concentration of 400 μmol mol^{-1} (using the built-in Li-Cor 6400 CO_2 controller) and a saturating irradiance of 1500 μmol $m^{-2}s^{-1}$ provided by a built-in red LED light source. Instantaneous water use efficiency (WUE) was determined by P_n/T_r. The value of stomatal limitation (L_s) was calculated by the following formula:

$$L_s = 1 - C_i/C_a$$

where C_a is atmosphere CO_2 concentration, which is controlled at 400 μmol mol^{-1} in this study.

For each treatment, the photosynthetic gas exchange parameters were measured on three fully expanded leaves of the plant, and a total number of 10 individuals for each species were measured.

Statistical analysis

Statistical analyses were performed with the software SAS version 9.1 (SAS Institute Inc., Cary, NC, USA) and Multi-Variate Statistical Package (MVSP, Kovach Computing Services, Anglesey, UK). The effects of stocking rate, sampling year, and their interaction on plant functional traits were tested by two-way ANOVAs. One-way ANOVAs followed by the LSD multiple range tests were used for multiple comparisons of plant traits among treatments. The differential responses of plant trait to grazing between *L. chinensis* and *C. squarrosa* were tested using Independent-Samples T test at $P<0.05$. The canonical correlation analyses were used to test the relationships between whole-plant traits (height, plant biomass, stem biomass, leaf biomass, stem: leaf ratio) and leaf traits (LA, LM, SLA, P_n, T_r, G_s, C_i, WUE, L_s, N_{mass}, and N_{area}), and between leaf morphological (LA, LM, and SLA) and physiological traits (N_{mass}, N_{area}, P_n, T_r, G_s, C_i, WUE, and L_s). For both species, trait data were pooled into three groups, i.e., no grazing (control), low grazing intensity (SR=3.0 and 4.5 sheep/ha), and high grazing intensity (SR=7.5 and 9.0 sheep/ha) in both years. For each group, canonical redundancy analysis was conducted to explore the variance explained by the canonical variates. The relationships between plant functional traits were tested by Pearson correlation analysis. The principal components analysis (PCA) was conducted to identify fundamental trade-offs between traits and associated trait syndromes between the two species at no grazing, low grazing intensity, and high grazing intensity. Data were standardized before the analysis. The differences in loading score on PCA 1 for traits between 2 years or two species were tested using Independent-Samples T test at $P<0.05$. Using regression analysis, we also analyzed the relationships between the responses of ecosystem properties (soil moisture, ANPP) and plant functional traits (P_n, and plant biomass) to grazing. Before regression analysis, the response ratios of treatment to control at different stocking rates were transformed with the natural logarithm to improve the normality.

Results

Response of whole-plant traits

The whole-plant traits including height, total individual aboveground biomass, stem biomass, and leaf biomass for both species, and stem: leaf ratio (S/L ratio) for *C. squarrosa* were all significantly affected by grazing ($P<0.001$). The effect of sampling year was only significant for *C. squarrosa* ($P<0.05$), except for S/L ratio. However, the interactive effects of stocking rate×year on whole-plant traits were all highly significant for both species ($P<0.01$).

For *L. chinensis*, height, total individual biomass, stem and leaf biomass decreased significantly at the highest stocking rate (9.0 sheep/ha) in the wet year

(2008), and at high stocking rates (7.5 and 9.0 sheep/ ha) in the dry year (2009); although no significant changes in total individual biomass, stem and leaf biomass were observed at low and moderate stocking rates (3.0 and 4.5 sheep/ha) compared to control (no grazing) in the dry year (Fig. 2). Compared with control, total individual biomass of *L. chinensis* was decreased by 72% in 2008 and by 70% in 2009 at the highest stocking rate (9.0 sheep/ha). The stem: leaf (S/L) ratio generally increased at low, moderate, and high stocking rates in the wet year, but declined in the dry year (Fig. 2).

For *C. squarrosa*, height, total individual biomass, stem and leaf biomass diminished significantly with increasing stocking rate in both years, with a greater reduction occurred in the wet year than that of the dry year (Fig. 2). At the highest stocking rate, plant biomass of *C. squarrosa* was declined by 92% in 2008 and by 81% in 2009 compared to control. Under moderate to high stocking rates, grazing also reduced the S/L ratio of *C. squarrosa* in the wet year, but enhanced it in the dry year (Fig. 2).

In the control plots, total individual biomass, stem and leaf biomass of *L. chinensis* were significantly

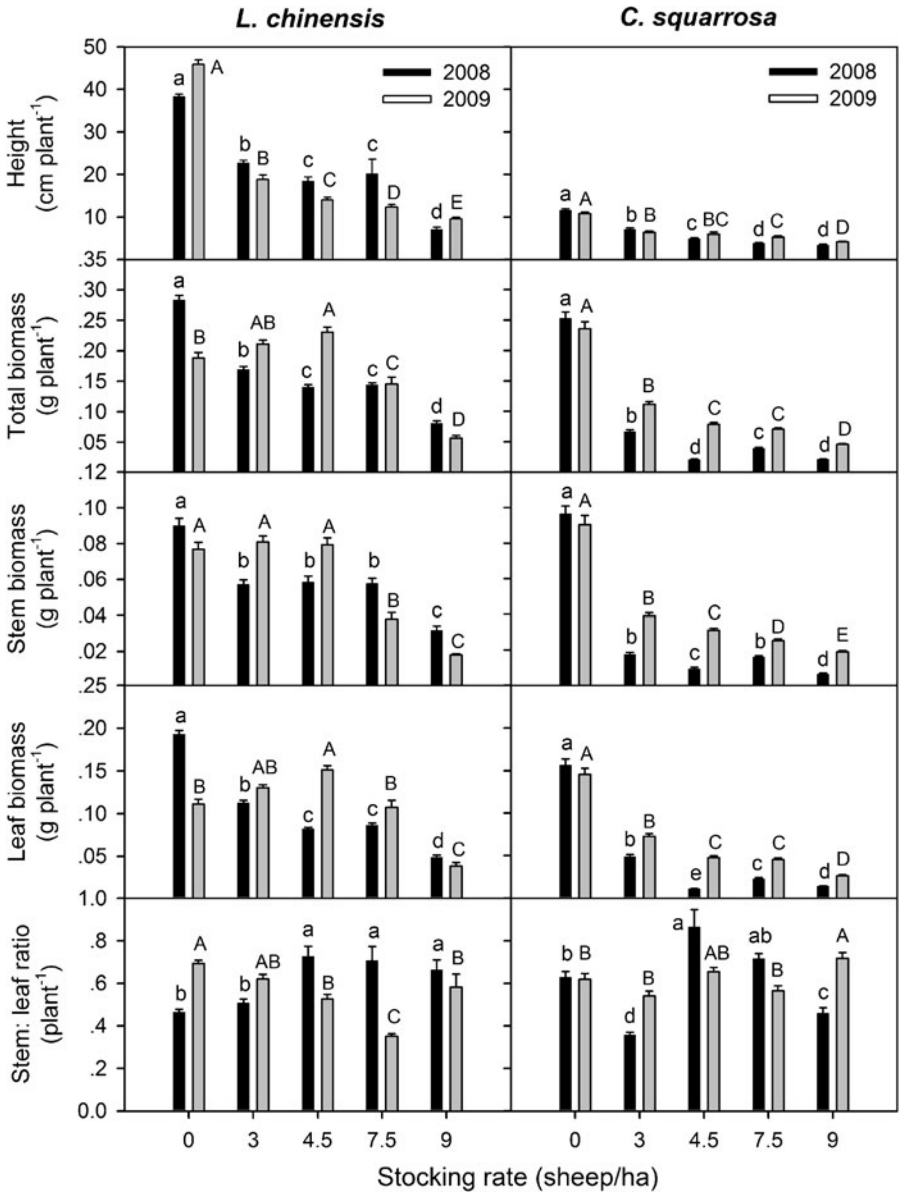


Fig. 2 Effects of grazing on whole-plant traits of *L. chinensis* and *C. squarrosa*. Vertical bars indicate standard errors of the mean (n= 30). Different letters represent significant differences among treatments (LSD test, P<0.05), with lowercases for 2008 and capital letters for 2009

higher in the wet year than in the dry year ($P<0.05$), while height and stem:leaf ratio showed a reverse pattern ($P<0.0001$). For *C. squarrosa*, however, there was no significant difference in each trait between the wet and dry years.

Response of leaf morphological traits

For both *L. chinensis* and *C. squarrosa*, the effects of stocking rate, year, stocking rate × year on leaf morphological traits, i.e., leaf area, leaf dry mass, and specific leaf area, were highly significant ($P<0.01$), except for the interactive effect of stocking rate × year on leaf dry mass of *C. squarrosa*.

The leaf area of *L. chinensis* did not show a significant change at low and moderate stocking rates but declined significantly at high stocking rates in the wet year. In the dry year, however, the leaf area of *L. chinensis* was significantly reduced by grazing at moderate and high stocking rates (Fig. 3). The leaf dry mass of *L. chinensis* also showed a slight but significant decrease at low, moderate, and high stocking rates and a marked reduction at the highest stocking rate in the wet year, whereas it was diminished sharply by grazing at moderate and high stocking rates in the dry year (Fig. 3). Grazing generally increased the specific leaf area of *L. chinensis* in the wet year. In the dry year, in contrast, the response of specific leaf area of *L. chinensis* was much complex, declined first at low and moderate stocking rates and enhanced then at high stocking rates (Fig. 3).

Leaf area and leaf dry mass of *C. squarrosa* were diminished by grazing for almost all treatment plots and in both wet and dry years (Fig. 3). In the wet year, grazing enhanced specific leaf area of *C. squarrosa* at low and moderate stocking rates. In the dry year, however, grazing increased SLA of *C. squarrosa* only at low stocking rate and had no effect on SLA at moderate and high stocking rates (Fig. 3). For all treatment and control plots, the SLA of *C. squarrosa* increased significantly in the dry year compared to the wet year ($P<0.0001$).

In the control plots, leaf area and leaf dry mass of *L. chinensis* and leaf dry mass of *C. squarrosa* were significantly higher in the wet year than in the dry year ($P<0.05$), however, the SLA of both species were significantly higher in the wet year than in the dry year ($P<0.0001$). Also, *L. chinensis* had much higher leaf area and leaf dry mass but significantly

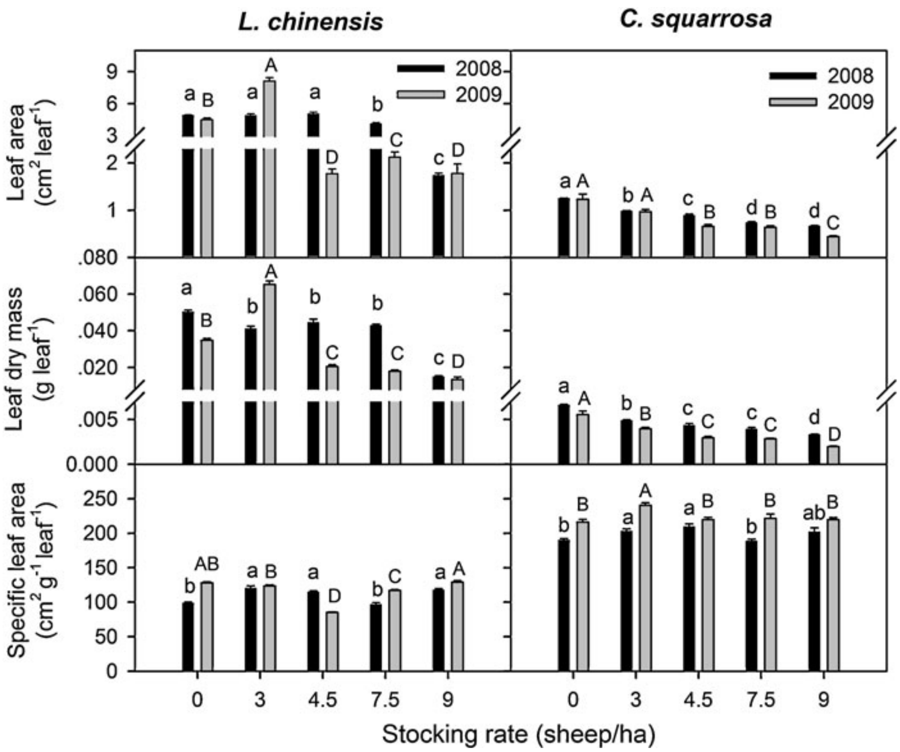


Fig. 3 Effects of grazing on leaf morphological traits of *L. chinensis* and *C. squarrosa*. Vertical bars indicate standard errors of the mean ($n=30$). Different letters represent significant differences among treatments (LSD test, $P<0.05$), with lowercases for 2008 and capital letters for 2009

lower SLA than *C. squarrosa* across all treatment and control plots ($P<0.0001$).

Response of leaf physiological traits

All leaf physiological traits of the two species were significantly affected by grazing ($P<0.001$), and the effects of year and stocking rate×year were mostly significant ($P<0.05$). In the wet year, P_n, T_r, G_s, and C_i of *L. chinensis* first decreased at low stocking rate, then increased at moderate and high stocking rates, and declined again at the highest stocking rate; whereas WUE and L_s of *L. chinensis* first increased with stocking rate and then decreased at high stocking rates but still significantly higher than those of control (Fig. 4). In the dry year, T_r, G_s, and C_i of *L. chinensis* also declined at low stocking rate, then increased at moderate and high stocking rates, and elevated to the level of control at the highest stocking rate, with P_n declining first at low stocking rate and then increasing slightly at moderate and high stocking rates (Fig. 4). A significant reduction in WUE and L_s of *L. chinensis* was observed only at the highest stocking rate, while they were relatively unchanged at low, moderate, and high stocking rates (Fig. 4). On the whole, grazing had more negative effects on photosynthetic capacity of *L. chinensis* in the dry year than that in the wet year.

In most cases, grazing significantly diminished P_n, T_r, G_s, and WUE of *C. squarrosa* in the wet year (Fig. 4). On average, P_n, T_r, G_s, and WUE of *C. squarrosa* decreased by 72%, 17%, 58%, and 62% in 2008, respectively, compared to control. In the dry year, however, grazing generally had no effect on P_n T_r, G_s, and WUE (Fig. 4). In both wet and dry years, grazing elevated C_i but reduced L_s of *C. squarrosa* in most cases. Compared to control, the average value of C_i in the grazed plots increased by 31% in 2008 and by 55% in 2009; whereas L_s decreased by 22% in 2008 and by 30% in 2009. Across all grazed plots, the values of WUE of *C. squarrosa* were much higher in 2009 than those in 2008 (Fig. 4). Moreover, compared with *L. chinensis*, *C. squarrosa* showed much lower P_n, T_r, G_s, C_i, N_{mass}, and N_{area}, but higher L_s (Figs. 4, 5).

For both *L. chinensis* and *C. squarrosa*, values of N_{mass} and N_{area} were consistently higher in the wet year than those in the dry year (Fig. 5). Grazing increased N_{mass} and N_{area} of *L. chinensis* in the dry year, whereas decreased N_{area} of *L. chinensis* and generally had no effect on N_{mass} in the wet year (Fig. 5). For *C. squarrosa*, however, grazing enhanced N_{mass} and N_{area} in both wet and dry years.

Relationships between plant functional traits

The canonical correlation analysis showed that whole-plant traits were significantly correlated with leaf morphological and physiological traits when all data of the two species were pooled together. The correlation coefficient (*r*) for the first group of canonical variates was 0.98 ($P<0.001$) at no grazing (control), 0.95 ($P<0.001$) at low grazing intensity (3.0 and 4.5 sheep/ha), and 0.93 ($P<0.001$) at high grazing intensity (7.5 and 9.0 sheep/ha). Canonical redundancy analysis further showed that the canonical variates were P_n, G_s, T_r, C_i, L_s, C_i, LA, LM, SLA, and N_{area} for leaf traits at control plots, explaining 66% of total variation; for whole-plant trait, height was the canonical variate, accounting for 24% of the total variation. For both species, the height was positively correlated with P_n, G_s, T_r, C_i, LA, LM, and N_{area}, but negatively correlated with SLA, WUE, and L_s (Appendix 1). Plant height had a predominant effect on leaf physiological traits at the control plots, explaining 63% of total variance. Canonical redundancy analysis also showed that the canonical variates for leaf trait were P_n, G_s, T_r, LM, LA, SLA, and N_{area}, which explained 32% of the total variation at the low grazing intensity and 36% at the high grazing intensity. The canonical variates for whole-plant trait were total individual biomass, stem biomass, leaf biomass, and height, which accounted for 69% and 67% of total variation at low and high grazing intensities, respectively. All whole-plant traits were positively correlated with P_n, G_s, T_r, LM, LA and N_{area}, but negatively correlated with SLA (Appendix 1). Leaf physiological traits had predominant effects on plant biomass at low grazing intensity, explaining 63% of total variance. However, leaf morphological traits had leading influence on plant biomass at high grazing intensity, accounting for 57%.

Results from canonical correlation analysis also demonstrated that leaf physiological traits were positively correlated with leaf morphological traits under no grazing disturbance ($r=0.997$), at low ($r=0.989$) and high ($r=0.987$) grazing intensities. P_n, G_s, T_r, and N_{area} were positively correlated with LA and

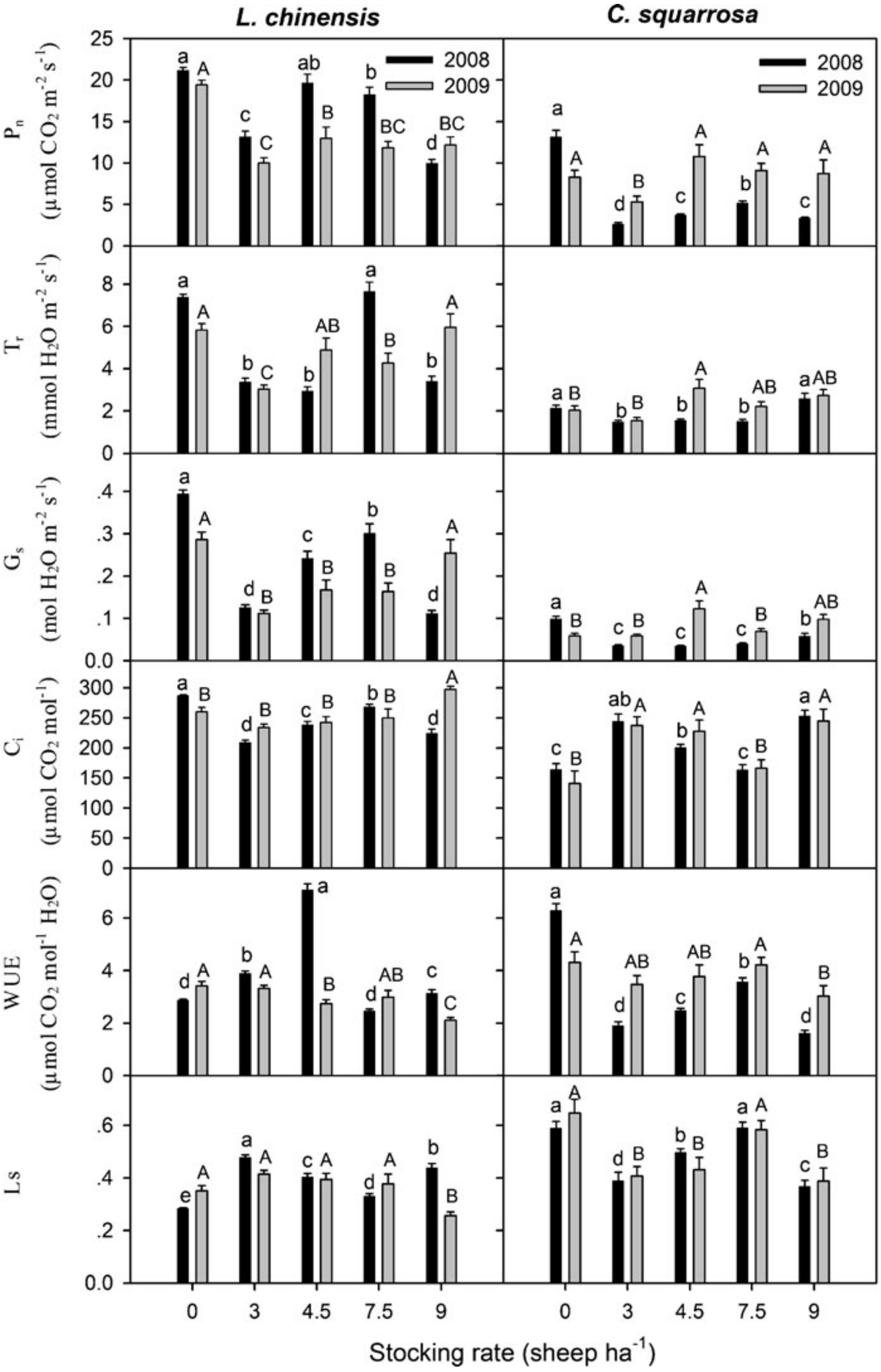
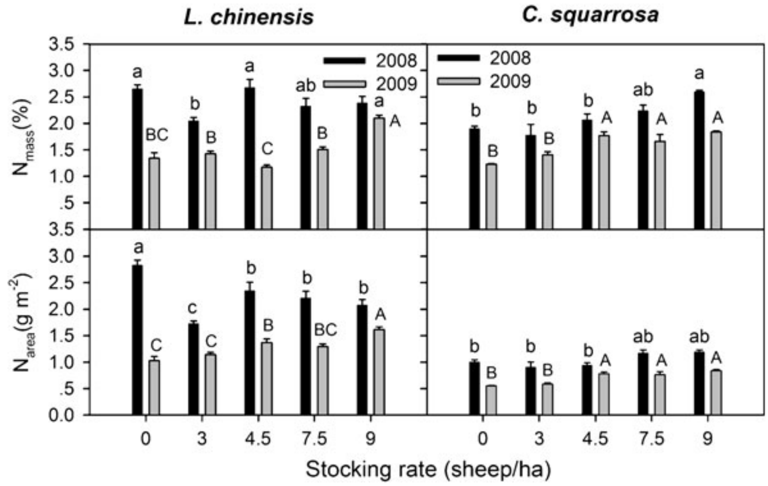


Fig. 4 Effects of grazing on leaf photosynthetic traits of *L. chinensis* and *C. squarrosa*. Vertical bars indicate standard errors of the mean ($n=10$). Different letters represent significant differences among treatments (LSD test, $P<0.05$), with lowercases for 2008 and capital letters for 2009

LM, but negatively correlated with SLA (Appendix 1). The canonical variate for leaf morphological traits was LM and LA under no grazing disturbance (accounting for 83%) and at low grazing intensity (58%), and was SLA at high grazing intensity (83%). The canonical variate for leaf physiological traits was N_{area} under no grazing disturbance (accounting for 64%), at low (23%) and high grazing intensities (32%). The canonical redundancy analysis further illustrated that N_{area} explained separately 83%, 57%,

Fig. 5 Effects of grazing on mass (N_{mass}) and area (N_{area}) based leaf nitrogen contents of *L. chinensis* and *C. squarrosa*. Vertical bars indicate standard errors of the mean (n=5). Different letters represent significant differences among treatments (LSD test, $P<0.05$), with lowercases for 2008 and capital letters for 2009



and 81% of variation in leaf morphological traits under no grazing disturbance, at low and high grazing intensities.

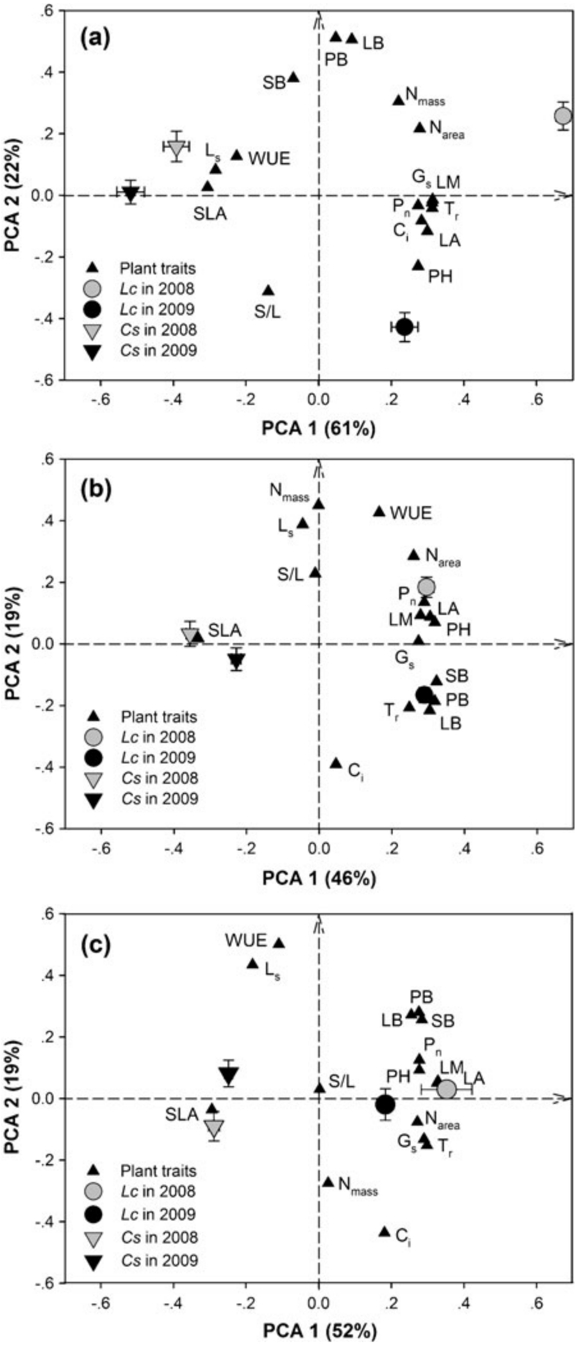
Differential response between two species

The principal components analysis (PCA) showed that the first PCA axis (PCA 1) was positively correlated with traits related to plant height, leaf size, and photosynthetic capacity under no grazing disturbance, explaining 52% of the total variance, while the second axis (PCA 2) was related to plant biomass, accounting for only 22% (Fig. 6). We identified two fundamental trade-offs linked to consumptive and conservative plant growth strategies at low and high grazing intensities. The PCA 1 was correlated with traits related to leaf size, photosynthetic capacity, and plant size, which increased, while SLA decreased along the PCA 1 (Fig. 6). The PCA 1 explained separately 46% and 52% of the total variance at low and high grazing intensities. The PCA 2 was positively correlated with WUE and L_s, but negatively correlated with C_i, reflecting the conservative water utilization for plant growth. The PCA 2 explained only 19% of total variance at both low and high grazing intensities.

The PCA 1 distinctly separated *L. chinensis* with higher height, plant size, leaf size, and photosynthetic capacity from *C. squarrosa* with higher SLA under no grazing disturbance, at both low and high grazing intensities (Fig. 6). For *C. squarrosa*, there was a significant difference in loading score on PCA 1 between the wet and dry years under no grazing disturbance (P=0.025), at low ($P<0.001$) and high (P=0.043) grazing intensities. For *L. chinensis*, however, there was no significant difference in loading score on PCA 1 between the 2 years at low grazing intensity, while the difference was significant under no grazing disturbance ($P<0.001$) and at high grazing intensity (P=0.031). Thus, high grazing intensity decreased inter-variation of two species, and grazing had more influence on *L. chinensis* than *C. squarrosa*. For a given grazing intensity or year, the loading score on PCA 1 was also significantly different between the two species ($P<0.01$). Also, the difference between the two species gradually diminished from no grazing disturbance, low grazing intensity to high grazing intensity, especially in the dry year (Fig. 6).

Relationship between responses of species and community

Under grazing treatment, the P_n response of *C. squarrosa* was negatively correlated with soil moisture response, whereas the P_n response of *L. chinensis* was little affected by change in soil moisture (Fig. 7). For both species, the response of total individual biomass to grazing was also negatively correlated with soil moisture response (Fig. 7). The plant biomass response of *C. squarrosa* was positively correlated with its P_n response, while no significant relationship was found between the plant biomass response and P_n response of *L. chinensis* (Fig. 7). The ANPP response was positively correlated with plant biomass responses of two species, especially with *L. chinensis* (Fig. 7).



◀**Fig. 6** PCA biplot diagram for first two axes showing the functional traits of *L. chinensis* and *C. squarrosa* at no grazing (**a**) and low (**b**) and high (**c**) grazing intensities. The absolute values of each point on x- and y-coordinate represent loading scores of each trait for PCA 1 and 2. Trade-off is characterized by negative correlation between two traits when they have high loading on the same axis but in an opposite direction. For each species, whiskers denote standard error of the mean of PCA weighted loading scores. Abbreviations: PH, plant height; PB, plant biomass; SB, stem biomass; LB, leaf biomass; S/L, stem: leaf ratio; LA, leaf area; LM, leaf dry mass; SLA, specific leaf area; P_n, net photosynthetic rate; T_r, transpiration rate; G_s, stomatal conductance; C_i, intercellular CO_2 concentration; WUE, instantaneous water use efficiency; L_s, stomatal limitation; N_{mass}, mass based nitrogen content; N_{area}, area based nitrogen content; *Lc*, *L. chinensis*; *Cs*, *C. squarrosa*

Discussion

Grazing impact on plant functional traits of two species

In this study, we demonstrated that the whole-plant traits of the two species, including plant height, total individual biomass, leaf biomass, and stem biomass, decreased with increasing stocking rate, which are consistent with previous studies (Díaz et al. 2001; Klimesova et al. 2008; Landsberg et al. 1999; Rusch et al. 2009). The magnitude of change for each species, however, was generally greater in the wet year than that in the dry year. The decreased total individual biomass of both species was attributed mainly by the reduction in both leaf biomass and leaf area that diminished assimilation production of the plant at high stocking rates. This is because leaf P_n is closely related to plant photosynthetic capacity and relative growth rate (Field and Mooney 1986; Shipley 2002, 2006), and plant stature and leaf size are directly associated with light interception for photosynthesis (Milla and Reich 2007; Poorter and Rozendaal 2008). For both species, the less negative impact of grazing on whole-plant traits was likely caused by the increased stomatal conductance and intercellular CO_2 concentration in the dry year, which made the net photosynthetic rate unchanged or even enhanced, particularly for *C. squarrosa*.

The canonical correlation and redundancy analyses further suggest that grazing at low intensity decreased plant stature and consequently had a negative impact on leaf photosynthetic capacity, while grazing at high intensity diminished leaf size and resulted in the decrease of plant biomass. Our findings indicate that species mainly suffers from light competition associated with plant stature at no grazing or low grazing intensity, while heavy grazing generally leads to miniaturization of plant individual (Wang et al. 2000). In addition, our results have shown that the response of community ANPP to grazing was positively correlated with the responses of plant

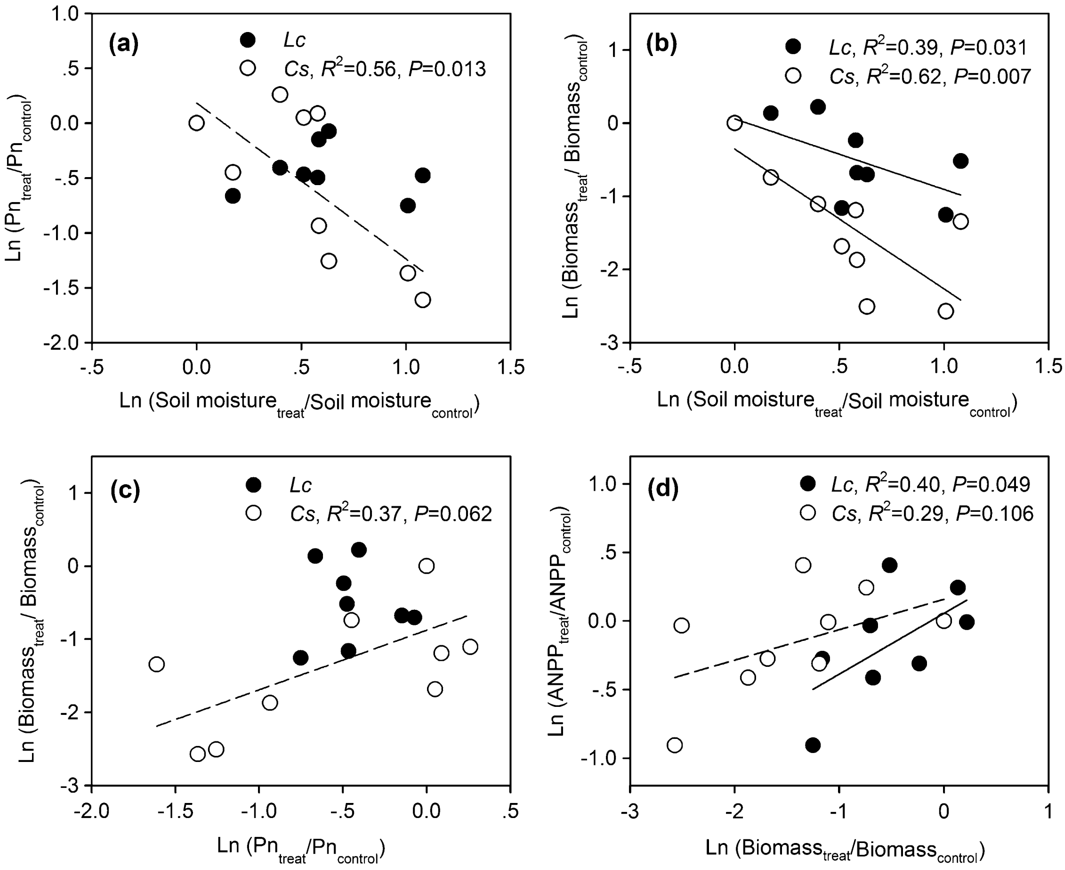


Fig. 7 Relationships between responses of net photosynthetic rate (P_n, **a**) and total individual biomass (**b**) and soil moisture, between plant biomass response and P_n (**c**) and ANPP responses (**d**). Data were log-transformed (base e) before analysis to improve normality. *Lc, L. chinensis*; *Cs, C. squarrosa*

biomass of the two species, especially with that of *L. chinensis*. This suggests that heavy grazing, which decreased plant growth of dominant species, greatly influenced the ecosystem functioning.

Compared with *C. squarrosa*, total individual biomass of *L. chinensis* was relatively less affected by grazing at low and moderate stocking rates in both wet and dry years. This is due mainly to the relatively low impact of grazing on both leaf biomass and leaf area of *L. chinensis*. At high stocking rates, however, the plant individual biomass of both species was significantly reduced by grazing. The high plasticity of *L. chinensis* at low and moderate stocking rates partly support the hypothesis that the effect of grazing on plant traits could be mediated by grazing intensity (Adler et al. 2004). For *C. squarrosa*, however, plant individual biomass, leaf biomass, and leaf area were all decreased sharply by grazing even at low and moderate stocking rates.

Trade-offs among plant functional traits in dry and wet years

Water availability is the key limiting factor controlling plant growth and biomass production in arid and semiarid grassland ecosystems (Bai et al. 2004; Bai et al. 2008). In this study, the differential responses of plant trait to variation in precipitation suggest that some fundamental trade-offs among traits may exist in wet versus dry years. For *L. chinensis*, both mass and area based leaf N contents and net photosynthetic rate were significantly higher in the wet year than those in the dry year under grazed conditions. These trade-offs indicate that *L. chinensis* may adopt the high regrowth rate to compensate for the biomass loss by frequent grazing disturbance in the wet year. In the dry year, however, it may adopt the low growth rate for more conservative resource use to survive under water stress conditions and grazing disturbance. Our findings are also corroborated by previous studies that trade-offs among plant functional traits within a species may promote its survivorship under the fluctuating environments (Grime 2001; Reich et al. 1997; Reich et al. 2007; Westoby et al. 2002).

For *C. squarrosa*, the trade-offs of high SLA and net photosynthetic rate in the dry year versus low SLA and P_n in the wet year suggest that it is likely to adopt high growth rate to deplete the available resources and improve its competitive ability when the growth of *L. chinensis* was inhibited by water stress. This was further supported by the results that plant individual biomass and stem and leaf biomass were much higher in the dry year than those in the wet year under grazed conditions. It has proposed that C_4 species generally exhibit high photosynthetic capacity due to their particular mechanisms of CO_2 fixation and high resource use efficiency in dry habitats with high irradiation (Sage et al. 1999). Our results also revealed that *C. squarrosa* was more resistant to droughts as indicated by the negative relationships between P_n and biomass responses and soil moisture response under the grazed conditions.

In the present study, the impacts of grazing on leaf area, leaf dry mass, and net photosynthetic rate of *L. chinensis* were less negative in the wet year than that in the dry year. However, grazing enhanced the net photosynthetic rate of *C. squarrosa* in the dry year but decreased it in the wet year. This implies that high annual precipitation may modulate the negative grazing effect on functional traits of *L. chinensis*, whereas low annual rainfall is likely to promote the growth of *C. squarrosa*. Thus, the effect of grazing on the functional traits was also mediated by water availability (Adler et al. 2004; Osem et al. 2004; Pakeman 2004; Vesk et al. 2004).

Plant avoidance and tolerance strategies to grazing

Plant species may adopt some avoidance (escape from grazers) and tolerance (regrowth capacity after defoliation) strategies to improve their grazing resistance (Cingolani et al. 2005; Díaz et al. 2001; Klimesova et al. 2008; Landsberg et al. 1999; Rusch et al. 2009). In this study, we found that the two species exhibited both similar and different strategies in terms of their avoidance and tolerance to grazing pressure.

First, plant height and leaf size of both species decreased with increasing stocking rate, which reduced foraging selectivity by herbivores (Vesk et al. 2004), with *C. squarrosa* being much shorter than that of *L. chinensis*. Second, the SLA, leaf N_{mass} and N_{area} (except *L. chinensis* in the dry year) of both species increased or relatively unchanged under high grazing pressure, which might be favorable for leaf turnover and shoot regrowth (Cingolani et al. 2005; Evju et al. 2009; Pérez-Harguindeguy et al. 2003; Westoby 1999). *C. squarrosa* had much higher SLA but lower area based N content compared with *L. chinensis*. Third, both *L. chinensis* and *C. squarrosa* employed more conservative water use strategy to maintain or improve their photosynthetic capacity in the dry year. This is because G_s and C_i of both species increased, L_s decreased at high grazing intensity, whereas WUE was relatively unchanged. Compared with *L. chinensis*, *C. squarrosa* had the higher WUE in the dry year. Collectively, compared with *L. chinensis*, *C. squarrosa* had shorter plant height and lower total individual biomass, stem and leaf biomass, LA, LM, P_n, and N_{area} but higher SLA. This implies that *C. squarrosa* is more resistant to grazing in terms of its avoidance and tolerance traits than that of *L. chinensis*, particularly under heavy grazing pressure and in the dry year.

Our findings have important implications for understanding species coexistence and for the management of semiarid ecosystems in the face of climate change. First, future climate change is likely to produce more frequent extreme precipitation and drought events (Easterling et al. 2000), which may have greater impacts on the functioning of *L. chinensis* and *C. squarrosa* dominated steppe ecosystems. The dominance of *L. chinensis* is likely to increase in the wet yeas because it has the competitive advantage both in light and soil moisture competition. In the dry years, however, when *L. chinensis* is suppressed, *C. squarrosa* may take advantage of available resources because of its drought-resistance traits. Second, we expect that the increased droughts together with heavy grazing may accelerate the process of shift in dominance from *L. chinensis* to *C. squarrosa* in the typical steppe, and consequently decrease the ecosystem functioning, such as primary production and carbon sequestration (Li 1989; Wittmer et al. 2010; Xiong et al. 2003). Third, it seems clear from our study that the currently high stocking rate in the Inner Mongolia grassland should be reduced in order to avoid drastic alterations of ecosystem structure and functioning in a long run.

Acknowledgements We thank S. P. Chen for providing meteorological data of the study site. This research was supported financially by the National Natural Science Foundation of China (30825008, 30900193) and the State Key Basic Research Development Program of China (2009CB421102).

Reference

Adler PB, Milchunas DG, Lauenroth WK, Sala OE, Burke IC (2004) Functional traits of graminoids in semi-arid steppes: a test of grazing histories. J Appl Ecol 41:653–663

Adler PB, Milchunas DG, Sala OE, Burke IC, Lauenroth WK (2005) Plant traits and ecosystem grazing effects: comparison of US sagebrush steppe and Patagonian steppe. Ecol Appl 15:774–792

Auerswald K, Wittmer MHOM, Männel TT, Bai YF, Schäufele R, Schnyder H (2009) Large regional-scale variation in C3/C4 distribution pattern of Inner Mongolia steppe is revealed by grazer wool carbon isotope composition. Biogeosciences 6:795–805

Bai YF, Li LH, Wang QB, Zhang LX, Zhang Y, Chen ZZ (2000) Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin River Basin, Inner Mongolia. Acta Phytoecologica Sinica 24:667–673

Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431:181–184

Bai YF, Wu JG, Pan QM, Huang JH, Wang QB, Li FS, Buyantuyev A, Han XG (2007) Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. J Appl Ecol 44:1023–1034

Bai YF, Wu JG, Xing Q, Pan QM, Huang JH, Yang DL, Han XG (2008) Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology 89:2140–2153

Bai YF, Wu JG, Clark CM, Naeem S, Pan QM, Huang JH, Zhang LX, Han XG (2010) Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from Inner Mongolia Grasslands. Glob Change Biol 16:358–372

Chen ZZ (1988) Topography and climate of Xilin River Basin. In: Inner Mongolia Grassland Ecosystem Research Station of Chinese Academy of Sciences (ed) Research on Grassland Ecosystem No.3. Science, Beijing, pp 13–22

Chen SH, Zhang H, Wang LQ, Zhanbula ZML (eds) (2001) Root systems of grassland plants in Northern China. Jilin University Press, Changchun

Chen SP, Bai YF, Han XG (2002) Variation of water-use efficiency of *Leymus chinensis* and *Cleistogenes squarrosa* in different plant communities in Xilin River Basin. Nei Mongol Acta Bot Sin 44:1484–1490

Chen SP, Bai YF, Lin GH, Liang Y, Han XG (2005) Effects of grazing on photosynthetic characteristics of major steppe species in the Xilin River Basin, Inner Mongolia, China. Photosynthetica 43:559–565

Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia (ed) (1985) The vegetation of Inner Mongolia. Science, Beijing

Cingolani AM, Posse G, Collantes MB (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. J Appl Ecol 42:50–59

Coupland RT (1993) Ecosystems of the World 8B. Natural Grasslands: Eastern Hemisphere and Résumé. Elsevier, Amsterdam

Cui XY, Chen ZZ, Du ZC (2001) Study on light- and water-use characteristics of main plants in semiarid steppe. Acta Pratacult Sin 10:14–21

Díaz S, Cabido M, Casanoves F (1998) Plant functional traits and environmental filters at a regional scale. J Veg Sci 9:113–122

Díaz S, Noy-Meir I, Cabido M (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? J Appl Ecol 38:497–508

Díaz S, Lavorel S, McIntyre S, Falczuk V, Casanoves F, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir I, Landsberg J, Zhang W, Clark H, Campbell BD (2007) Plant trait responses to grazing: a global synthesis. Glob Change Biol 13:313–341

De Bello F, Leps J, Sebastia MT (2005) Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. J Appl Ecol 42:824–833

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074

Evju M, Austrheim G, Halvorsen R, Mysterud A (2009) Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. Oecologia 161:77–85

Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of form and function. Cambridge University Press, Cambridge, pp 25–55

Golodets C, Sternberg M, Kigel J (2009) A community-level test of the leaf-height-seed ecology strategy scheme in relation to grazing conditions. J Veg Sci 20:392–402

Graff P, Aguiar MR, Chaneton EJ (2007) Shifts in positive and negative plant interactions along a grazing intensity gradient. Ecology 88:188–199

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties. John Wiley and Sons, Chichester

Hilbig W (1995) The vegetation of Mongolia. SPB, Amsterdam

Klimesova J, Latzel V, de Bello F, van Groenendael JM (2008) Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. Preslia 80:245–253

Landsberg J, Lavorel S, Stol J (1999) Grazing response groups among understorey plants in arid rangelands. J Veg Sci 10:683–696

Lavorel S, Díaz S, Cornelissen JHC, Garnier E, Harrison SP, McIntyre S, Juli GP, Perez-Harguindeguy N, Roumet C, Urcelay C (2007) Plant functional types: Are we getting any closer to the Holy Grail? In: Canadell JG, Pataki DE, Pitelka LF (eds) Terrestrial ecosystems in a changing World. Springer, Berlin, pp 149–164

Li YH (1989) Impact of grazing on *Aneurolepidium chinense* steppe and *Stipa grandis* steppe. Acta Oecol-Oecol Appl 10:31–46

Milla R, Reich PB (2007) The scaling of leaf area and mass: the cost of light interception increases with leaf size. Proc R Soc B-Biol Sci 274:2109–2114

Osem Y, Perevolotsky A, Kigel J (2004) Site productivity and plant size explain the response of annual species to grazing exclusion in a Mediterranean semi-arid rangeland. J Ecol 92:297–309

Pakeman RJ (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. J Ecol 92:893–905

Pérez-Harguindeguy N, Díaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. Austral Ecol 28:642–650

Poorter L, Rozendaal DMA (2008) Leaf size and leaf display of thirty-eight tropical tree species. Oecologia 158:35–46

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734

Reich PB, Wright IJ, Lusk CH (2007) Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. Ecol Appl 17:1982–1988

Rusch GM, Skarpe C, Halley DJ (2009) Plant traits link hypothesis about resource-use and response to herbivory. Basic Appl Ecol 10:466–474

Sage RF, Wedin DA, Li M (1999) The biogeography of C_4 photosynthesis: Patterns and controlling factors. In: Sage RF, Monson RK (eds) C_4 plant biology. Academic, San Diego, pp 313–373

Schonbach P, Wan H, Schiborra A, Gierus M, Bai Y, Muller K, Glindemann T, Wang C, Susenbeth A, Taube F (2009) Short-term management and stocking rate effects of grazing sheep on herbage quality and productivity of Inner Mongolia steppe. Crop Pasture Sci 60:963–974

Shipley B (2002) Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. Funct Ecol 16:682–689

Shipley B (2006) Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Funct Ecol 20:565–574

Tong C, Wu J, Yong S, Yang J, Yong W (2004) A landscape-scale assessment of steppe degradation in the Xilin River Basin, Inner Mongolia. China J Arid Environ 59:133–149

Vesk PA, Leishman MR, Westoby M (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. J Appl Ecol 41:22–31

Wan HW, Yang Y, Bai SQ, Xu YH, Bai YF (2008) Variations in leaf functional traits of six species along a nitrogen addition gradient in *Leymus chinensis* steppe in Inner Mongolia. J Plant Ecol 32:611–621

Wang JW, Cai C (1988) Studies on genesis, types and characteristics of the soils of the Xilin River Basin. In: Inner Mongolia Grassland Ecosystem Research Station of Chinese Academy of Sciences (ed) Research on Grassland Ecosystem No.3. Science, Beijing, pp 23–83

Wang W, Liang CZ, Liu ZL, Hao DY (2000) Analysis of the plant individual behaviour during the degradation and restoring succession in steppe community. Acta Phytoecologica Sinica 24:268–274

Wang S-P, Wang Y-F, Chen Z-Z (2003) Effect of climate change and grazing on populations of *Cleistogenes squarrosa* in Inner Mongolia steppe. Acta Phytoecologica Sinica 27:337–343

Westoby M (1999) The LHS strategy scheme in relation to grazing and fire. In: Eldridge D, Freudenberger D (eds) VIth International Rangeland Congress. International Rangeland Congress, Townsville, pp 893–896

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159

Wittmer M, Auerswald K, Bai YF, Schaufele R, Schnyder H (2010) Changes in the abundance of C3/C4 species of Inner Mongolia grassland: evidence from isotopic composition of soil and vegetation. Glob Change Biol 16:605–616

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Xiong XG, Han XG, Bai YF, Pan QM (2003) Increased distribution of *Caragana microphylla* in rangelands and its causes and con sequences in Xilin River Basin. Acta Pratac Sin 12:57–62

Zhong YK, Bao QH, Sun W, Zhang HY (2001) The influence of mowing on seed amount and composition in soil seed bank of typical steppe. Acta Scientiarum Naturalium Universitatis Neimongol 32:308–314