

**Functional trait responses to grazing are mediated by soil moisture, plant
functional group identity and composition**

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Abstract. Abundant evidence has shown that grazing alters plant functional traits, ecological strategies, community structure, and ecosystem functioning of grasslands. Few studies, however, have tested how plant responses to grazing are mediated by resource availability and functional group identity and composition. We examined the context-dependent effects of grazing on functional traits and shifts in functional group composition across six communities along a soil moisture gradient in the Inner Mongolia grassland. A principal component analysis (PCA), based on 9 traits \times 276 species matrix, showed that the trait syndromes of plant size (e.g., individual biomass) and shoot growth (e.g., leaf N content and leaf density) distinguished plant species responses to grazing. The effects of grazing on plant functional traits were dependent on both soil moisture and functional group identity and composition. The annuals and biennials showed grazing-tolerant strategies associated with high growth rate, reflected by high leaf N content and specific leaf area. The perennial grasses exhibited grazing-tolerant strategies associated with high regrowth capacity and high palatability, whereas perennial forbs showed grazing-avoidant strategies with short stature and low palatability. Among the perennial grasses, the dominant bunchgrasses tended to exhibit mixed tolerance–resistance strategies to grazing and mixed acquisitive–conservative strategies in resource utilization. With increasing soil moisture, grazing increased the relative abundance of perennial forbs but decreased the relative abundance of perennial grasses. Our findings suggest that grazing-induced shifts in plant functional group composition and community structure are largely dependent on resource availability, particularly water availability.

1 Introduction

Functional trait-based approaches have recently emerged as a promising way to understand plant ecological strategies and plant-herbivore interactions (Westoby, 1999; Adler et al., 2004; De Bello et al., 2005; Violle et al., 2007; Laliberte et al., 2012). Many studies have proposed that plant species may exhibit some avoidance (escape from grazers) and tolerance (regrowth capacity after defoliation) strategies to improve their grazing resistance (Strauss and Agrawal, 1999; Díaz et al., 2001; Cingolani et al., 2005; Díaz et al., 2007). Plant functional traits can provide important insights into the mechanisms underpinning plant responses to grazing. For example, plant height, individual biomass, and stem-leaf biomass ratio are associated with biomass allocation and species' capacity for light competition (Poorter and Nagel, 2000; Cornelissen et al., 2003), and also linked to plant avoidance strategies to grazing (Díaz et al., 2001; Adler et al., 2004). Grazing avoidance traits are usually related to small plant size, such as low height and low individual biomass to decrease feeding selectivity of herbivores (Díaz et al., 2001; Cingolani et al., 2005). High leaf N content and specific leaf area (SLA) are tightly linked to high leaf nutrient acquisition and turnover and high potential growth rate (Reich et al., 1999; Wright et al., 2004), as well as plant tolerance strategies to grazing (Díaz et al., 2001; Zheng et al., 2011). Grazing tolerant traits are also associated with high leaf N content and SLA to increase shoot regrowth capacity (Strauss and Agrawal, 1999; Pérez-Harguindeguy et al., 2003). Plant palatability is a multidimensional trait, which depends on physical (e.g., toughness, hairiness, thorns and spines) and chemical (e.g., nutritive value, odor, taste and toxins) attributes (Milchunas and Noy-Meir, 2002; Elger and Willby, 2003), and also reflects the evolution of plant defense to grazing. Grazing as a selective disturbance generally favors unpalatable over palatable plants (Díaz et al., 2007). Several studies, however, have suggested that plant species and trait responses to grazing are largely dependent on site productivity or resource availability

(Pakeman, 2004; Díaz et al., 2007; Laliberte et al., 2012). Thus, a better understanding of the adaptive strategies of plants to grazing mediated by resource availability is fundamental to biodiversity conservation and sustainable grassland management.

The resource availability hypothesis suggests that resource availability (e.g., water and nutrients) is a major determinant of both the amount and type of plant anti-herbivore defense (Coley et al., 1985). Grazing selects species with avoidance strategies in dry and infertile (less-productive) systems and species with tolerance strategies in humid and fertile (productive) systems (Coley et al., 1985; Herms and Mattson, 1992). Moreover, plant species have developed two opposite resource use strategies (conservative vs. acquisitive) to improve their competitive abilities under environmental fluctuations (Díaz et al., 2004; Wright et al., 2004; Tecco et al., 2010). Species with resource conservative strategies usually have low SLA, low leaf N content, and long leaf life-span (Reich et al., 1999; Villar and Merino, 2001; Tecco et al., 2010). In contrast, species with resource acquisitive strategies generally have high SLA, high leaf N content, and short leaf life-span (Reich et al., 1999; Díaz et al., 2004; Tecco et al., 2010; Laliberte et al., 2012). The context-dependency hypothesis, however, proposes that plant responses to grazing are not only determined by site productivity or resource availability (Pérez-Harguindeguy et al., 2003; Daleo and Iribarne, 2009; Eldridge et al., 2013), but also by plant species or functional group identity (Wardle et al., 2008; McLaren and Turkington, 2010). Although extensive studies have shown that plant responses to grazing are mediated by resource availability (e.g., soil moisture) (Adler et al., 2004; Pakeman, 2004; Díaz et al., 2007; Laliberte et al., 2012), few studies, however, have examined the context-dependent effects of plant functional group identity and composition.

It is increasingly clear that understanding the ecological context and complexity of trait-mediated species interactions can provide new insights into the mechanisms governing

1 plant responses to grazing (Carmona and Fornoni, 2013; Turley et al., 2013). For example,
2 Carmona and Fornoni (2013) found that the complexity of herbivore communities selects for
3 mixed resistance–tolerance strategies of plants, which is contrary to a long-standing
4 prediction that resistance and tolerance are functionally redundant (Vandermeijden et al.,
5 1988). Selective pressures imposed by herbivores (Carmona and Fornoni, 2013), resource
6 availability in the environment (Coley et al., 1985), and trade-offs in allocation to growth and
7 defense (Herms and Mattson, 1992) may all constrain or promote selection on resistance or
8 tolerance, and hence cause evolution of mixed defensive strategies. Few studies, however,
9 have examined the adaptive evolution of mixed strategies of plant defense against herbivory
10 (Núñez-Farfán et al., 2007; Turley et al., 2013). Several key functional traits (e.g. SLA)
11 may provide important insights into the mixed strategies of plants to grazing and
12 environmental fluctuations. It has been widely recognized that high SLA is linked to high
13 potential growth rate (Reich et al., 1999; Wright et al., 2004), resource acquisitive strategies
14 (Díaz et al., 2004; Tecco et al., 2010), and plant tolerance to grazing (Díaz et al., 2001; Zheng
15 et al., 2011). Low SLA, in contrast, is tightly associated with physical toughness (Villar and
16 Merino, 2001; Wright et al., 2004), resource conservative strategies (Díaz et al., 2004; Tecco
17 et al., 2010), and plant resistance to grazing (Hanley et al., 2007). Thus, plant species with
18 high SLA may exhibit resource acquisitive and grazing-tolerance strategies in the wet and
19 fertile habitats, while the same species with low SLA may show resource conservative and
20 grazing-resistance strategies in the dry and infertile habitats. This suggests that plant
21 species may exhibit mixed tolerance–resistance strategies to grazing and mixed
22 acquisitive–conservative strategies to resource variation. However, the mixed strategies of
23 plant species against grazing defense and resource availability remain largely unexplored.

24 The arid and semiarid grasslands on the Mongolia plateau, which include diverse
25 community types and distribute widely across the Eurasian Steppe region, have been

historically subjected to continuous grazing by livestock with high stocking rates, leading to widespread degradation in ecosystem function and services (White et al., 2000; Bai et al., 2012). In the Inner Mongolia grassland, plant growth and primary productivity are co-limited by water and N availability (Bai et al., 2008), thus grazing impacts on functional traits and thereby ecosystem functioning are likely mediated by resource availability. In this study, we examine the effects of grazing on plant functional traits and shifts in functional group composition along a soil moisture gradient in the Xilin River Basin of Inner Mongolia grassland. Specifically, we address the following questions: first, how do plant functional traits across a broad range of species respond to grazing? Second, how do the trait responses to grazing is affected by soil moisture and plant functional group identity and composition? Third, what are the adaptive strategies of different life forms to grazing and linkage to shifts in functional group composition and community-weighted attributes? To address these questions, we hypothesize that the effects of grazing on plant functional traits are dependent on soil moisture and functional group identity and composition, and life-history strategy reflects a long evolutionary adaptation of plant species to environment. Therefore, we would expect that: (1) annuals and biennials exhibit grazing-tolerant strategies (e.g., high leaf N content and high SLA), while perennial forbs show grazing-avoidant strategies (e.g., short stature, low N content and low palatability). Perennial grasses with high regrowth rate and high palatability would also exhibit grazing-tolerant strategies although both leaf N content and SLA are low. (2) Grazing may increase the relative abundance of perennial forbs but decrease perennial grasses with increasing soil moisture, thus grazing-induced reduction in soil moisture may promote a shift in dominance from perennial forbs to perennial grasses.

2 Methods

2.1 Study area

The study was conducted in the Xilin River Basin of the Inner Mongolia grassland (43°26'–44°29'N, 115°32'–117°12'E), which covers an area of 10 786 km² with elevation ranging from 983 to 1469 meters above sea level. The climate is semi-arid continental temperate steppe, with mean annual temperature of 0.4 °C and mean annual precipitation of 336.9 mm yr⁻¹. Annual precipitation decreases gradually from 400mm in the south-east to 250mm in the north-west, and more than 80% of precipitation occurs in the growing season (May–August). Chestnut and dark chestnut soils are the zonal soil types in this region (Bai et al., 2000). In this study, six pairs of parallel grazed and ungrazed plant communities were selected along a soil moisture gradient, including *Carex appendiculata* meadow, *Stipa baicalensis* meadow steppe, *Leymus chinensis* typical steppe, *S. grandis* typical steppe, *Caragana microphylla* typical steppe, and *Artemisia frigida* typical steppe. The six plant communities are subjected to similar climatic conditions (i.e. temperature and precipitation), but they differ in soil moisture and other soil properties (e.g. soil organic carbon and nitrogen contents) (Table 1). This is mainly caused by topography-controlled wind and water erosion and deposition processes (Hoffmann et al., 2008; Kölbl et al., 2011). The *Carex appendiculata* meadow has the highest soil moisture and nutrients (e.g. soil organic matter and total nitrogen contents), followed by the *Stipa baicalensis* meadow steppe, and the four typical steppe communities have lower soil moisture and nutrients (Table 1). The ungrazed sites of communities are the permanent field sites of the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), Chinese Academy of Sciences (Bai et al., 2004), which have been fenced from grazing for about 20–30 years (Table 1). In contrast, the grazed sites, located outside the fence of ungrazed sites, were managed as free grazing pasture. Sheep grazing has been the dominant form of land use practices in this area since 1950s. Seventy-eight to ninety-one percent of the total livestock numbers was composed of

1 sheep, with numbers of cattle accounting for 5-9% and horses accounting for 2-13% of the
2 total livestock numbers (The Economics Department of Inner Mongolia University and
3 Baiyinxile Pasture, 1993).

4 5 **2.2 Vegetation and soil properties**

6 A survey on vegetation composition of the six plant communities were conducted from 28
7 July to 14 August, 2007, corresponding to annual peak aboveground biomass in this area (Bai
8 et al., 2004). At each site, 5–10 quadrats (1×1m each) were located randomly within an area
9 of 100 m ×100 m. Ten quadrats were used for meadow steppe and typical steppe, and 5
10 quadrats were for the more homogeneous meadow community. For the grazed sites, these
11 quadrats were randomly located in the areas that were not subjected to grazing during the
12 current growing season. Within each quadrat, all living biomass and current-year dead
13 materials were harvested, separated to species, and oven dried at 70 °C for 24 h to constant
14 mass and weighed. Litter biomass within each quadrat was also collected. The number of
15 individuals and aboveground biomass of each species were measured to estimate species
16 abundance and community standing biomass.

17 Soil samples within each quadrat were collected by taking three 5-cm diameter soil
18 cores from 0-20 cm depths, mixed *in situ* as one composite sample, and air-dried for soil
19 nutrient analyses. Soil organic carbon was analyzed using K₂Cr₂O₇-H₂SO₄ oxidation
20 method, and total nitrogen was determined using the Kjeldahl acid-digestion method with an
21 Alpkem autoanalyzer (Kjektec System 1026 Distilling Unit, Sweden). Subsamples of 0–20
22 cm soil layer were also collected, oven-dried at 105°C for 48 h, and weighed to determine
23 soil moisture (%).

24 25 **2.3 Plant functional traits**

After vegetation survey, plant samples were collected at each site for functional trait measurements. A total number of 276 species were sampled across six paired plant communities, with 149 species in the ungrazed sites and 127 species in the grazed sites (Appendix A). There were 113 shared species in both ungrazed and grazed sites. All species were classified into plant functional groups based on their life forms, including perennial grasses (PG), perennial forbs (PF), annuals and biennials (AB), and shrubs and semi-shrubs (SS). For each ungrazed or grazed site, 10-20 fully grown individuals of each species were randomly selected. Nine plant functional traits, including plant height (PH), plant individual biomass (PB), stem biomass (SB), leaf biomass (LB), stem-leaf biomass ratio (SLR), total leaf area (TLA) and leaf density per individual (LD), specific leaf area (SLA), and mass-based leaf N content (LNC), were determined by using standard methods (Cornelissen et al., 2003). Plant height was measured by the distance from the basal stem to the natural crown of each individual (Cornelissen et al., 2003). After the height measurement, aboveground part of each individual was collected and taken back to the laboratory for stem and leaf separation. All leaves of an individual were picked and the number of leaves was recorded for leaf density estimation. Then 3–5 fully expanded mature leaves were selected to determine the projected leaf area with a portable leaf area meter (Li-3100C, Li-Cor, Lincoln, NE, USA), and the samples were finally used for leaf N content analysis. The stem and leaf samples were oven-dried at 70 °C for 24 h to constant masses and weighted. Hence, individual leaf area, dry mass per leaf, stem biomass, leaf biomass, plant individual biomass, total leaf area and leaf density per individual could be calculated, and specific leaf area and stem-leaf biomass ratio were separately calculated as the ratio of leaf area to dry mass, and ratio of stem biomass to leaf biomass (Cornelissen et al., 2003). Leaf samples were ground to homogeneity with a ball mill (MM 2000, Retsch GmbH & Co, Haan, Germany) for analyzing N content. The palatability index was consist of five grades

(0, 0.25, 0.5, 0.75, 1) based on a forage plants handbook (Fu, 1990). For each grazed and ungrazed site, the community-weighted attributes for plant height ($height_{CWM}$), stem-leaf ratio (SLR_{CWM}), specific leaf area (SLA_{CWM}), and leaf N content (LNC_{CWM}) were calculated as trait means weighted by the relative biomass of each species within each quadrat (Violle et al., 2007).

2.4 Statistical analysis

Statistical analyses were performed with the software SAS version 9.2 (SAS Institute Inc., Cary, NC, USA) and Multi-variate Statistical Package (MVSP, Kovach Computing Services, Anglesey, UK). To detect general trends in 9 functional traits of 276 plant species, we first organized the dataset into 9 individual traits (variables) \times 276 species (cases) matrix, on which we carried out a principal component analysis (PCA) based on the correlation matrix of variables (Jongman et al., 1987; Tecco et al., 2010). The effects of grazing (G), soil moisture (M), and their interactions ($G \times M$) on five functional traits (e.g., PH, PB, SLR, SLA, and leaf N content) were tested with the generalized linear mixed model (GLMM), using species identity and communities as random factors. The relationships between the responses of four functional traits (e.g., PH, SLR, SLA, and leaf N content) to grazing and soil moisture for all species and each of life forms were analyzed by the linear regression model. The response ratios of plant height (PH), plant individual biomass (PB), stem-leaf biomass ratio (SLR), specific leaf area (SLA), and leaf N content (LNC) were separately calculated as the ratio of mean values in the grazed to ungrazed communities (e.g., $PB_{grazed}/PB_{ungrazed}$, $SLA_{grazed}/SLA_{ungrazed}$). The shrubs and semi-shrubs (SS) were excluded from analyses due to small sampling size (< 5 species). A canonical correspondence analysis (CCA) was conducted to quantify the relationships between plant community structure based on life form composition and environmental variables (e.g., soil moisture and

grazing). Using regression analysis, we examined the relationships between soil moisture and the differences in relative biomass of life forms and community-weighted attributes ($height_{CWM}$, SLR_{CWM} , SLA_{CWM} , LNC_{CWM}) in the grazed and ungrazed communities. The dissimilarity in species composition (a measure of β -diversity) between the paired ungrazed and grazed communities was calculated based on the relative biomass of each species, and the relationship between species dissimilarity and soil moisture was also analyzed. The effects of grazing on SLA of four dominant perennial grasses were examined using Independent-Samples T test at $P < 0.05$. ANOVA and LSD tests were performed to test differences in functional traits among different life forms.

3 Results

3.1 Associations among species traits

Associations among the 9 functional traits of 276 plant species were analyzed with a PCA (Fig. 1, Table A1 in the Appendix B), and the three principal components together accounted for 76% of the total variance. The first principal component (PC1) explained 43% of the total variance and represented an axis of plant size, reflected by plant individual biomass, stem biomass, leaf biomass, and total leaf area. The second principal component (PC2) was strongly associated with plant height, stem-leaf biomass ratio (SLR), and specific leaf area (SLA), accounting for 19% of the total variance. Species found at the positive end of this axis were tall plants with high SLA and more biomass allocation to supportive stem than leaf tissues (high SLR), corresponding to high capacity for aboveground/light competition. The third principal component (PC3), which explained an additional 14% of the total variance, was primarily driven by leaf N content and leaf density, representing an axis of leaf nutrient acquisition and shoot growth (Fig. 1a, Table A1 in the Appendix B). The main trend of trait variation was between fast (high leaf N content and leaf density) and slow shoot growth (low

leaf N content and leaf density).

The PC1 and PC3 axes distinctly separated species from the grazed and ungrazed communities (Fig. 1b). Grazing significantly decreased the loading score of plant size along PC1 axis ($P = 0.0163$), but greatly increased the loading score of leaf N content and leaf density along PC3 axis ($P = 0.0016$, Fig. 1c). However, the PC2 score of plant height, SLR and SLA was little affected by grazing ($P = 0.1011$).

3.2 Effects of grazing and soil moisture on plant functional traits

According to PCA analysis, five key functional traits, including plant height (PH), individual biomass (PB), stem-leaf biomass ratio (SLR), specific leaf area (SLA), and leaf N content (LNC) were further selected to examine their responses to grazing along a soil moisture gradient. The generalized linear mixed model (GLMM) analysis, using grazing (G), soil moisture (M) and their interactions ($G \times M$) as fixed effects, showed that plant height, individual biomass and SLA were significantly affected by grazing. The four functional traits, except for plant height, were significantly affected by soil moisture, while the interactions of $G \times M$ on plant height, SLA, and leaf N content were also significant (Table 2).

The response ratio of plant height ($PH_{\text{grazed}}/PH_{\text{ungrazed}}$) to grazing decreased ($P = 0.0001$), while the response ratios of leaf N content ($P < 0.0001$), SLA ($P = 0.0013$) and SLR ($P = 0.0861$) increased along the soil moisture gradient (Fig. 2). The SLR response ratio increased slightly ($P = 0.0861$) along the soil moisture gradient. For most species, grazing diminished plant height but enhanced leaf N content and SLA, while the responses of plant individual biomass and SLR to grazing were not significant along the moisture gradient. For the three life forms, plant height response ratio of annuals and biennials (AB) and perennial forbs (PF) decreased, while SLR response ratio of perennial grasses (PG) increased

1 along the soil moisture gradient (Fig. 3). Moreover, SLA of AB and PG, and leaf N content
2 of three life forms were also greatly enhanced by grazing along the moisture gradient.

3 4 **3.3 Variations in life from composition and community-weighted attributes**

5 The results of CCA showed that plant community structure in terms of life form composition
6 was significantly influenced by environmental variables (Fig. A1 in the Appendix C). The
7 first axis (CCA1) was mainly affected by soil moisture, which explained 89.8% of the total
8 variance. The second axis (CCA2) was more driven by grazing, which explained 10.2% of
9 the total variance (Fig. A1 in the Appendix C). The difference in relative biomass of
10 perennial grasses (PG) between the grazed and ungrazed communities decreased significantly,
11 while the difference of perennial forbs (PF) increased greatly with increasing soil moisture
12 (Fig. 4). Grazing decreased the relative biomass of PF in dry sites but it increased the
13 relative biomass of PF in wet sites. In contrast, grazing increased the relative biomass of PG
14 in dry sites but decreased it in wet sites. The difference in the relative biomass of annuals
15 and biennials (AB) between the grazed and ungrazed communities varied little along the
16 moisture gradient. The dissimilarity in species composition (a measure of β -diversity)
17 between the ungrazed and grazed communities showed no consistent trend along the soil
18 moisture gradient (Fig. A2 in the Appendix C).

19 The differences in the community-weighted SLA_{CWM} and LNC_{CWM} between grazed and
20 ungrazed communities increased along the soil moisture gradient, while there were no
21 consistent trends for $height_{CWM}$ and SLR_{CWM} (Fig. 5). Grazing increased the
22 community-weighted SLA_{CWM} and LNC_{CWM} in wet sites but it decreased both SLA_{CWM} and
23 LNC_{CWM} in dry sites.

24 25 **3.4 Comparisons of functional traits among different life forms**

Multi-trait comparisons showed that the five plant functional traits, including plant height, SLR, SLA, leaf N content, and palatability index, differed significantly among three life forms at the ungrazed sites (Table A2 in the Appendix B). Among the four life forms, annuals and biennials showed high plant height, high SLR, high leaf N content and high SLA, but low palatability index. The perennial grasses exhibited great plant height, high SLR and great palatability index, but low leaf N content and low SLA. The perennial forbs, however, showed low plant height, low SLR and low leaf N content, and low palatability index.

3.5 SLA responses of dominant perennial grasses to grazing

The SLA of *Leymus chinensis* (a dominant perennial rhizomatous grass) was decreased by grazing in all typical steppe communities and *Stipa baicalensis* meadow steppe (Fig. 6). For the three dominant perennial bunchgrasses, e.g. *S. baicalensis*, *Agropyron cristatum* and *Cleistogenes squarrosa*, however, grazing increased SLA in the relatively moist *S. baicalensis* meadow steppe but decreased SLA in the driest *S. grandis* and *Artemisia frigida* typical steppe communities.

4 Discussion

4.1 Plant strategy axes distinguish plant species responses to grazing

Our results demonstrated that two functional trait-based spectrums, i.e. individual biomass associated with plant size (PC1 axis), and leaf N content and leaf density related to leaf nutrient acquisition and shoot growth (PC3 axis), distinctly separated species from the grazed and ungrazed plant communities. These results suggest that plant species may have developed both tolerance strategies (e.g. increased leaf N content and leaf density) to improve shoot regrowth after defoliation (Strauss and Agrawal, 1999; Pérez-Harguindeguy et al., 2003) and avoidance strategies (e.g. decreased plant size) to reduce herbivore selectivity (Díaz et al.,

2001; Cingolani et al., 2005). These findings are corroborated by previous studies (Pakeman, 2004; Cingolani et al., 2005; Díaz et al., 2007; Evju et al., 2009) and our recent studies (Zheng et al., 2011). The variations in functional traits indicate the fundamental trade-offs between productivity and persistence in plant functioning (Warren and Adams, 2000; He et al., 2009), and further reflect the contrasting species-specific tolerance and defense strategies to grazing (Grime, 2001; Lind et al., 2013).

4.2 Context-dependency of grazing effects by plant functional group identity and composition

Our results suggest that the effects of grazing on plant functional traits are mediated by soil moisture, as indicated by the significant interactions of grazing and soil moisture on plant height, leaf N content and SLA. Generally, plant height was decreased, but leaf N content and SLA were increased by grazing for most species along the soil moisture gradient, indicating that plant species exhibit both avoidance and tolerance strategies to grazing (Díaz et al., 2001; Adler et al., 2004; Zheng et al., 2011). In addition, the among-site variations in plant height and individual biomass were mainly affected by grazing, while the among-site variations in SLR, SLA and leaf N content related to plant biomass allocation and aboveground/light competitive capacity (PC2 axis) were more driven by soil moisture. Our analysis also showed that functional trait variation between communities is mainly arisen from trait plastic responses to grazing and moisture, but not due to species replacement. This is supported by the result that the dissimilarity in species composition (a measure of β -diversity) between the ungrazed and grazed communities, which showed no consistent trend along the soil moisture gradient.

Our study demonstrated that grazing effects on plant functional traits at the community level are dependent on both plant functional group identity and composition. This is

supported by the evidence that the decrement in plant height was attributable to the negative responses of annuals and biennials (AB) and perennial forbs (PF) to grazing. The increments in leaf N content and SLA were due to the positive responses of all three life forms (except PF for SLA). Compared to the annuals and biennials (20 species), perennial forbs had greater effect on the change in plant height due to their larger sampling size (90 species). The SLR response ratio increased slightly along the soil moisture gradient, which was mainly arisen from the positive response of perennial bunchgrasses (PG) with relatively small sampling size (26 species). Our study also suggests that effects of grazing on community-weighted attributes were dependent on both plant functional group identity and composition. This is supported by the results that the increments in LNC_{CWM} and SLA_{CWM} were mainly due to the increase in the relative abundance of PF, and the positive LNC response of AB and PF, and positive SLA response of AB. These findings support our original hypothesis that the effects of grazing on plant functional traits are dependent on both the resource availability (e.g. soil moisture) (Adler et al., 2004; Pakeman, 2004) and plant functional group identity and composition (Wardle et al., 2008).

4.3 The adaptive strategies of different life forms to grazing

Our results suggest that the three life forms exhibited differential strategies as indicated by trait responses to grazing. Several factors are likely to be responsible for the observed patterns. First, the annuals and biennials with high growth rate showed more tolerant strategies to grazing as reflected by the increased leaf N content and SLA. Moreover, the annual and biennial species are mostly opportunistic or early successional species, which have short life-history, great aboveground/light competitive ability (e.g. high plant height and high SLR), high growth potential (e.g. high leaf N and high SLA), and high recruitment capacity (e.g. small seed and high reproductive output) (Westoby, 1998; Zheng et al., 2012).

1 These species with low palatability index may have the competitive advantage in rapid
2 resource capture when other life-form species were depressed by grazing (Soriano and Sala,
3 1984; Westoby, 1999). Therefore, annuals and biennials show more tolerance to herbivores,
4 especially in humid systems or wet years. Second, the perennial grasses exhibited greater
5 grazing tolerance but due to rapid regrowth capacity, indicated by the increased SLR, SLA
6 and leaf N content, and high palatability index. In this study, most perennial bunchgrasses
7 are xerophytes, which have long life-history, low growth potential (e.g. low leaf N and low
8 SLA), and great aboveground (e.g. high plant height and high SLR) and belowground
9 competitive abilities (e.g. high root: shoot ratio and high root N content) (Zheng et al., 2012).
10 Hence, these species have developed more conservative resource-use strategies and show
11 strong drought tolerance in the long-term process of evolutionary adaptation. In addition,
12 most perennial grasses are reproduced by germination of dormant buds and hence develop
13 new tillers rapidly (Redaction, 1998). Thus, these species show rapid regrowth capacity and
14 more tolerance to grazing, especially in dry and infertile systems (Strauss and Agrawal, 1999;
15 Adler et al., 2004). Third, the perennial forbs, however, have developed more avoidance
16 strategies to grazing. Generally, these species have long life-span, short stature and low
17 SLR, low growth capacity (e.g. low leaf N), and low palatability index, and some of these
18 species have evolved chemical (e.g. secondary metabolites with odor and toxins) or physical
19 defense (e.g. thorns, spines and hairiness) to decrease herbivore selectivity (Milchunas and
20 Noy-Meir, 2002). In addition, these species are dicotyledon with axial roots and seed
21 reproduction and thereby exhibit relatively slow recruitment rate (Redaction, 1998), leading
22 to a moderate response to grazing. These findings support our original hypothesis that
23 life-history strategy reflects a long evolutionary adaptation of plant species to environment,
24 and are consistent with our first prediction.

Our study demonstrated that the dominant perennial bunchgrasses, such as *Stipa baicalensis*, *S. grandis*, *Agropyron cristatum*, and *Cleistogenes squarrosa* in the Inner Mongolia grassland exhibited mixed tolerance–resistance strategies to grazing and mixed resource acquisitive–conservative strategies to variation in water availability. This is supported by the evidence that grazing increased SLA of these species in the relatively moist meadow steppe, but it decreased SLA of these species in the driest typical steppes. Although the variation in SLA could have arisen from plastic responses of these species to grazing and varying soil moisture, however, it has evolutionary advantage for these species to persist and dominate against grazing and water fluctuations in arid and semiarid grasslands. Our results suggest that the dominant perennial bunchgrasses select resource acquisitive and grazing-tolerance strategies in the wet and fertile habitats, but resource conservative and grazing-resistance strategies in the dry and infertile habitats. In contrast, the dominant perennial rhizomatous grass, *Leymus chinensis*, didn’t show mixed strategies of resource-use and herbivore-defense as indicated by decreased SLA values in all five grassland communities. These findings were partly in line with a recent study that natural selection by herbivores favors the evolution of mixed defensive strategies in plants (Carmona and Fornoni, 2013). Our results also showed that grazing increased the relative abundance of perennial bunchgrasses in dry sites, implying that the selective pressure imposed by long-term grazing and fluctuations in water availability may together promote the mixed strategies of plant anti-herbivore defense (tolerance–resistance) and resource utilization (acquisitive–conservative) in the arid and semiarid grasslands. Therefore, results from this study provide some new insights for future studies.

4.4 Grazing effects on shifts in functional group composition and community-weighted attributes

Our findings indicate that the grazing-induced shifts in functional group composition are largely dependent on site productivity, particularly water availability. Soil moisture explained 90% of total variance in plant community structure in the Xilin River Basin. Our study also demonstrated that grazing caused a shift in dominance from perennial forbs to perennial grasses in dry sites, as indicated by the increased relative abundance in perennial forbs, but decreased relative abundance in perennial grasses with increasing soil moisture gradient. This is because perennial forbs with low palatability showed more avoidance strategies to grazing, which allow them to achieve rapid growth and become more dominant in moist and fertile habitats. However, perennial grasses with high palatability exhibited more grazing-tolerance strategies and conservative resource-use strategies associated with low growth rate, which allow them to be more dominant in dry and infertile habitats. Therefore, grazing enhanced the community-weighted specific leaf area (SLA_{CWM}) and leaf N content (LNC_{CWM}) with increasing soil moisture. These findings are consistent with our second prediction. Given that plant growth is extremely limited by water availability in the Inner Mongolia grassland (Bai et al., 2008), the dominance of perennial grasses with high palatability may be attributable to their long-term evolutionary adaptation to dry environment and co-evolution with herbivores, particularly in the dry typical steppe.

4.5 Implications for ecosystem functioning under global change

Our findings have important implications for understanding the relationship between community structure and functioning and managing arid and semiarid grasslands. First, future climate change is likely to produce more frequent extreme precipitation and drought events (Easterling et al., 2000; Maestre et al., 2012), which may have profound impacts on shifts in species dominance in the Inner Mongolia grassland. The dominance of perennial forbs with low palatability is likely to increase in wet years because their grazing-avoidance

strategies. In dry years, however, perennial grasses with high palatability may become predominant because of their conservative resource-use and grazing-tolerant strategies. Second, previous studies in the same area demonstrated that heavy grazing shifted plant species and functional group composition, reduced plant species richness, primary production, soil coverage, and increased vulnerability to soil and water erosions (Kölbl et al., 2011; Schönbach et al., 2011; Wan et al., 2011). Therefore, the increase in prolonged droughts together with heavy grazing may accelerate the shifts in dominance from perennial rhizomatous grasses to perennial bunchgrasses in the typical steppe, and consequently decrease biodiversity and ecosystem functioning and services. This is because that the perennial bunchgrasses, mostly xerophytes, are more resistant to grazing than perennial rhizomatous grasses (mostly mesoxerophyte) in terms of avoidance and tolerance traits, particularly under heavy grazing pressure and in dry years (Zheng et al., 2011). In the long run, the dominance of perennial bunchgrasses in the Inner Mongolia grassland may be greatly promoted under climatic change due to their mixed strategies of defense and resource utilization, and evolutionary adaptation to dry environments and co-evolution with herbivores (de Mazancourt and Loreau, 2000; Turley et al., 2013). Third, it seems clear that destocking rate is an important management tool for restoring the vast degraded grasslands and mitigating the impacts of shifts in plant functional group composition and alterations in ecosystem functioning in the Inner Mongolia grassland and beyond.

Appendix A List of plant species classified into different life forms in six grassland communities of the Xilin River Basin, Inner Mongolia, China. “Ungrazed” and “grazed” denote plant species collected only in the ungrazed and grazed sites, respectively, and “common” means the same species shared at both the ungrazed and grazed sites. AB, annuals and biennials; PF, perennial forbs; PG, perennial grasses; SS, shrubs and

semi-shrubs.

Appendix B

Table A1. Principal components analysis (PCA) of species-trait correlation matrix. All variables were log10-transformed before analysis. Eigenvectors $>|0.40|$ are highlighted in bold. Percents reflect the percent of total variance (e.g. the sum of the diagonal elements in the correlation matrix) accounted for by each principal component.

Table A2. Comparisons of plant functional traits among three life forms. AB, annuals and biennials; PF, perennial forbs; PG, perennial grasses; SLR, stem-leaf biomass ratio; SLA, specific leaf area. *P* values following one-way ANOVAs indicate differences in functional traits among three life forms. Different lowercases represent significant differences among life forms (LSD multiple-range tests, $P<0.05$). The sample sizes are 20, 90 and 26 for AB, PF and PG, respectively.

Appendix C

Figure A1. CCA ordination diagram quantifying relationships between the distributions of plant communities (a) and life forms (b) and environmental variables. The two orthogonal axes explain respectively 89.8% (CCA 1) and 10.2 % (CCA 2) of the variance. Vectors represent two environmental variables, i.e. soil moisture and grazing. UG1 to UG6 and G1 to G6 represent six ungrazed and grazed plant communities, respectively. Error bars indicate the standard errors of biplot scores for each community along the axes 1 and 2.

Abbreviations: AB, annuals and biennials; PF, perennial forbs; PG, perennial grasses; SS, shrubs and semi-shrubs.

Figure A2. Change in species dissimilarity along the soil moisture gradient.

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Table 1 Geographical and soil properties of six grassland communities in the Xilin River Basin of Inner Mongolia, China.

No.	Community type	Vegetation type	Location	Altitude (m)	Field holding capacity (%)	Soil organic matter (g kg ⁻¹)	Soil total nitrogen (g kg ⁻¹)	Land use type
1	<i>Carex appendiculata</i>	Meadow	43°38'N 116°41'E	1150	51.75	121.20	5.25	Ungrazed site (fenced since 1989)
2	<i>Stipa baicalensis</i>	Meadow steppe	43°27'N 116°47'E	1380	34.63	32.41	1.87	Ungrazed site (fenced since 1979)
3	<i>Leymus chinensis</i>	Typical steppe	43°33'N 116°41'E	1250	31.80	28.45	1.58	Ungrazed site (fenced since 1979)
4	<i>S. grandis</i>	Typical steppe	43°33'N 116°33'E	1180	29.75	28.45	1.71	Ungrazed site (fenced since 1979)
5	<i>Caragana microphylla</i>	Typical steppe	43°36'N 116°44'E	1190	22.95	21.21	1.19	Ungrazed site (fenced since 1983)
6	<i>Artemisia frigida</i>	Typical steppe	43°38'N 116°41'E	1200	22.60	13.10	0.71	Ungrazed site (fenced since 1989)

Table 2. Results of generalized linear mixed model (GLMM) analyses on the effects of grazing (G), soil moisture (M), and their interactions on five plant functional traits. PH, plant height; PB, plant individual biomass; SLR, stem-leaf biomass ratio; SLA, specific leaf area; LNC, leaf nitrogen content.

Source	Functional traits	<i>df</i>	Mean Square	<i>F</i>	<i>P</i> -value
Grazing (G)	PH	1	174.81	83.5475	0.0000
	PB	1	171.40	9.5893	0.0023
	SLR	1	170.39	0.5082	0.4769
	SLA	1	163.17	4.9863	0.0269
	LNC	1	166.85	2.2251	0.1377
Soil moisture (M)	PH	5	209.66	0.4647	0.8023
	PB	5	210.92	3.1207	0.0097
	SLR	5	207.49	6.0931	0.0000
	SLA	5	200.42	28.0976	0.0000
	LNC	5	197.99	9.0906	0.0000
G×M	PH	5	174.81	11.9880	0.0000
	PB	5	171.40	1.5420	0.1793
	SLR	5	170.51	0.6297	0.6773
	SLA	5	163.69	3.0756	0.0111
	LNC	5	166.48	12.8496	0.0000

Figure legends

Figure 1 PCA biplot of 276 plant species based on the variance in 9 functional traits

explained by the three principal component axes. (a) Loading plot of traits. Labels display traits with the highest eigenvector scores on the three principal axes, with the brackets showing the corresponding scores. (b) PCA ordination of 149 plant species (blue circles) from the ungrazed and 127 species (red circles) from the grazed communities along PC1 and PC3 axes. (c) Box plots illustrate the score distribution of plant species from ungrazed (UG, in black, $n=149$) and grazed (G, in white, $n=127$) communities along the PC1 and PC3 axes.

Abbreviations: PH, plant height; PB, plant individual biomass; SLR, stem-leaf biomass ratio; SB, stem biomass; LB, leaf biomass; TLA, total leaf area; LD, leaf density; SLA, specific leaf area; LNC, leaf N content. Significant differences between the grazed and ungrazed communities along PC1 ($P = 0.0163$) and PC3 ($P = 0.0016$) axes are indicated by different letters. Box plots show the interquartile range, median (black thin line), and mean (red thick line).

Figure 2 Relationships between the responses of plant functional traits to grazing and soil moisture. The response ratio of each trait was calculated as the ratio of mean values in the grazed to ungrazed communities (i.e., $SLA_{\text{grazed}}/SLA_{\text{ungrazed}}$). The reference line (dashed line) in each panel indicates no change in response ratio of trait. **Abbreviations:** SLR, stem-leaf biomass ratio; SLA, specific leaf area; LNC, leaf N content.

Figure 3 Relationships between the responses of plant functional traits to grazing and soil

moisture for three life-form functional groups. The reference line (dashed line) in each panel indicates no change in response ratio of trait. **Abbreviations:** AB, annuals and biennials; PF, perennial forbs; PG, perennial grasses; SLR, stem-leaf biomass ratio; SLA, specific leaf area; LNC, leaf N content.

Figure 4 The relationships of differences in relative abundance of life forms between grazed and ungrazed communities with soil moisture. **Abbreviations:** PG, perennial grasses; PF, perennial forbs; AB, annuals and biennials; RAB, relative aboveground biomass.

Figure 5 The relationships of differences in community-weighted attributes between grazed and ungrazed communities with soil moisture. **Abbreviations:** SLR, stem-leaf ratio; SLA, specific leaf area; LNC, leaf N content; CWM, community-weighted mean.

Figure 6 Effects of grazing on specific leaf area (SLA) of four dominant bunchgrasses in *Stipa baicalensis* meadow steppe and four typical steppe communities. **Abbreviations:** Lc, *Leymus chinensis*; Sb, *Stipa baicalensis*; Sg, *S. grandis*; Ac, *Agropyron cristatum*; Cs, *Cleistogenes squarrosa*; Cm, *Caragana microphylla*; Af, *Artemisia frigida*. Significant differences between the grazed and ungrazed communities are reported from ANOVA as NS, $P > 0.1$; *, $P < 0.05$; ***, $P < 0.001$. The error bars denote SE ($n = 30$).

Figures

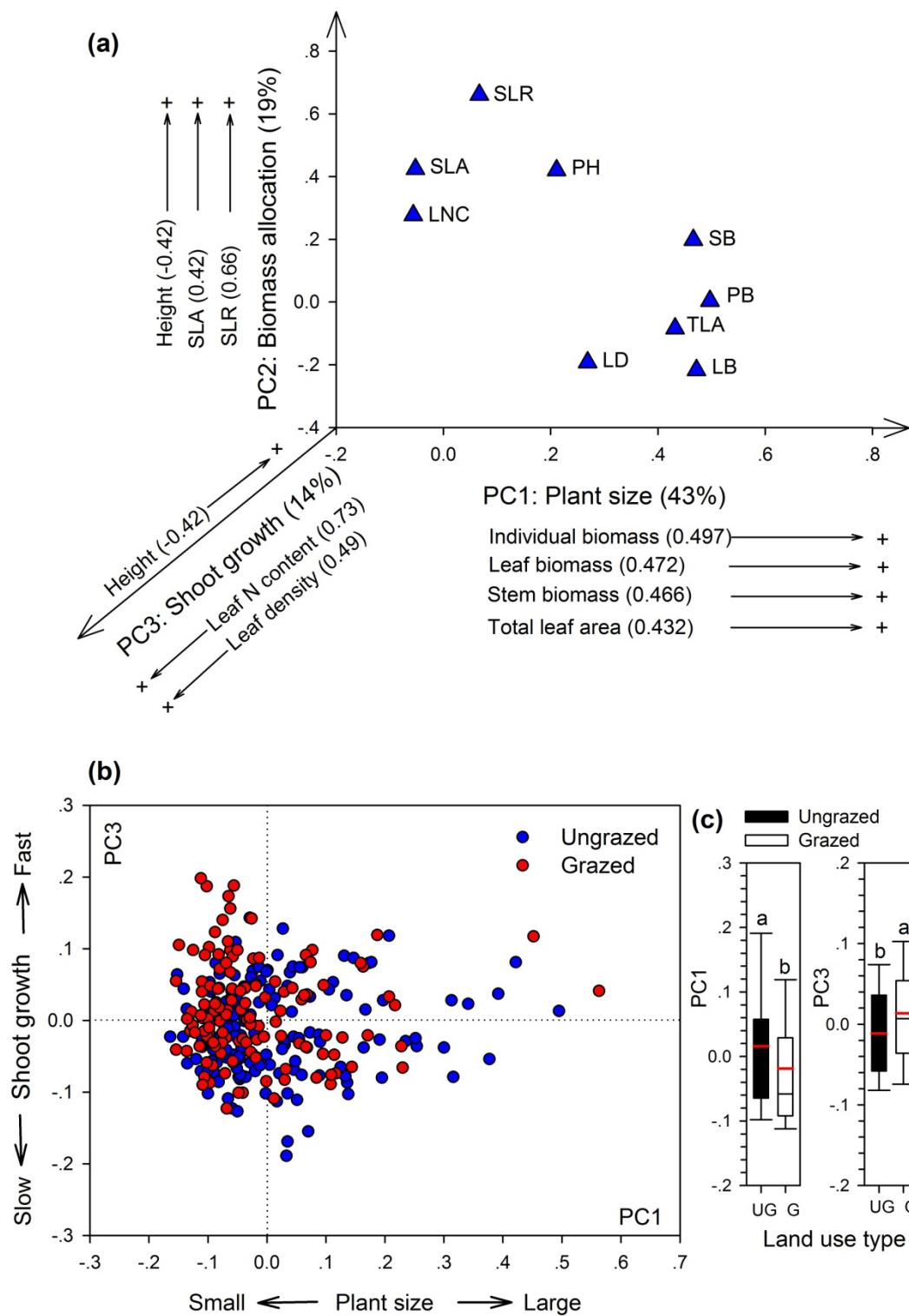


Figure 1

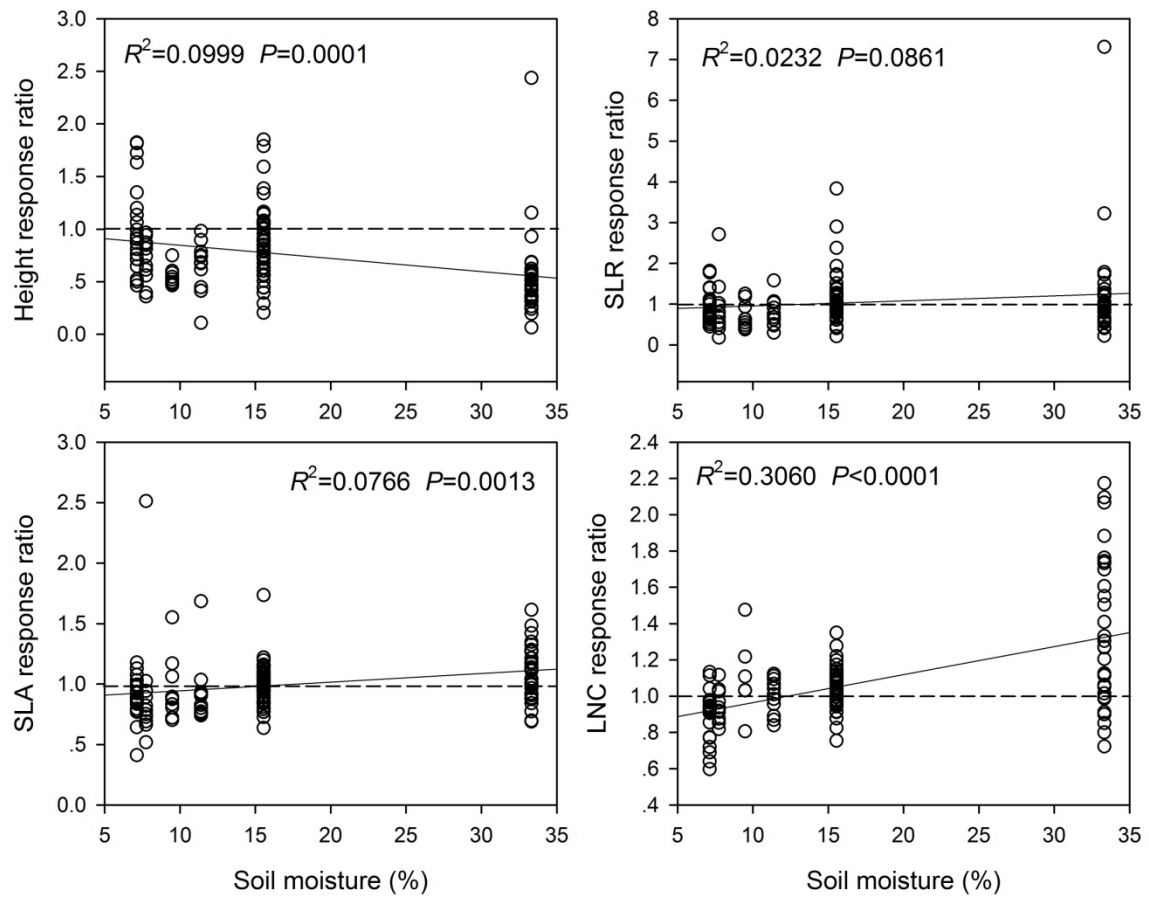


Figure 2

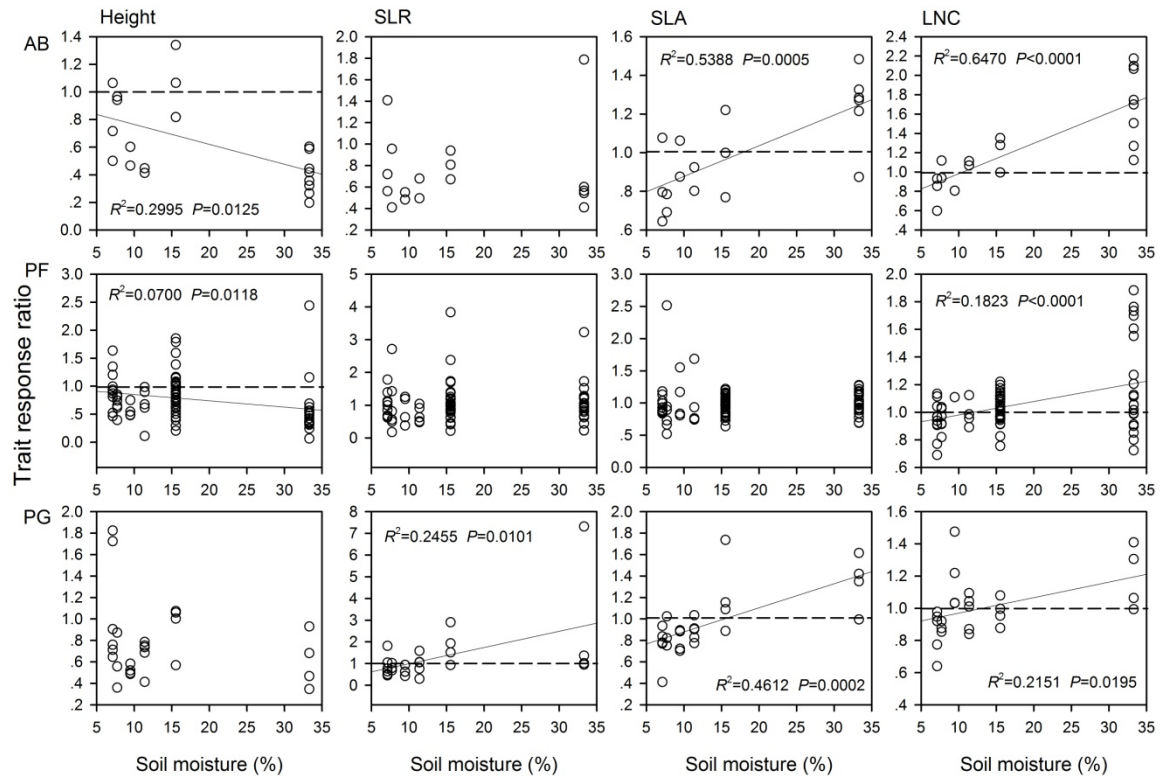


Figure 3

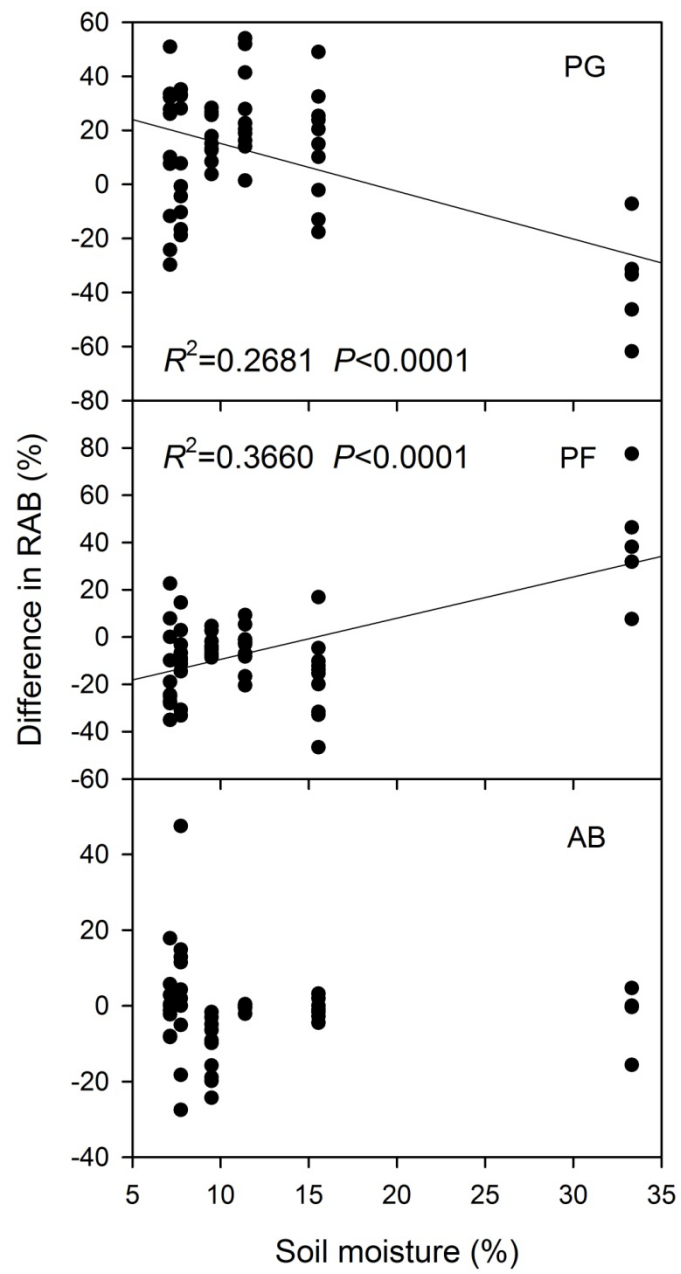


Figure 4

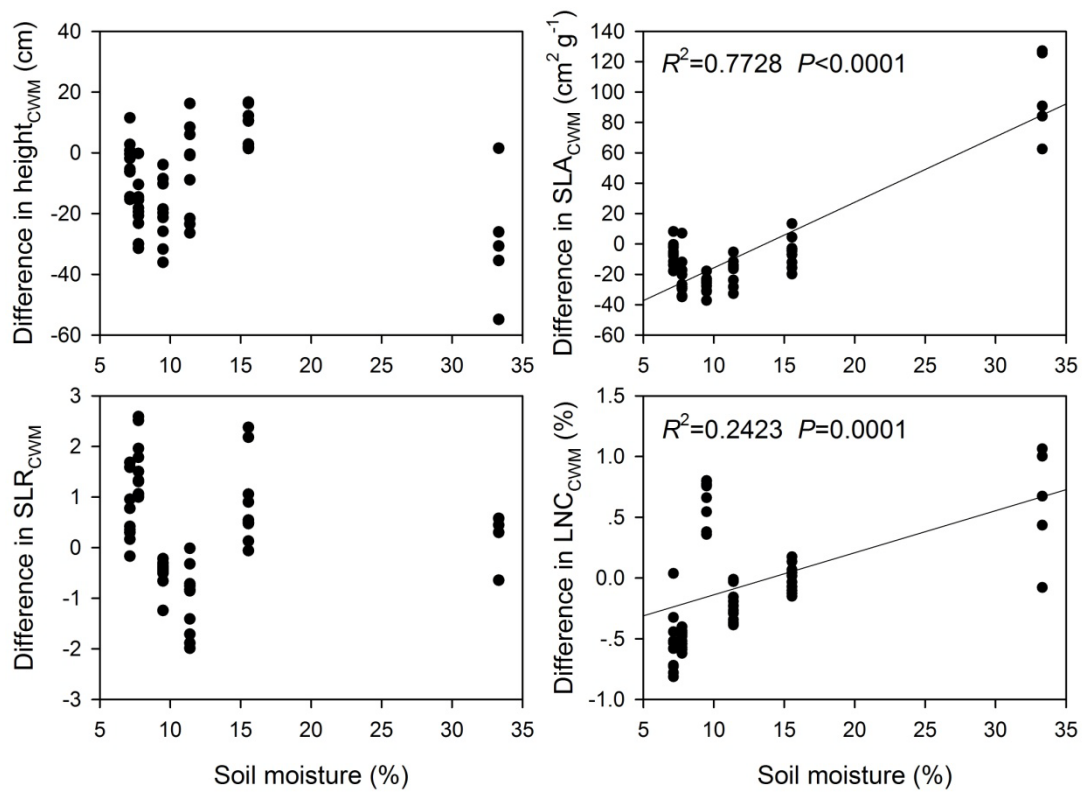


Figure 5

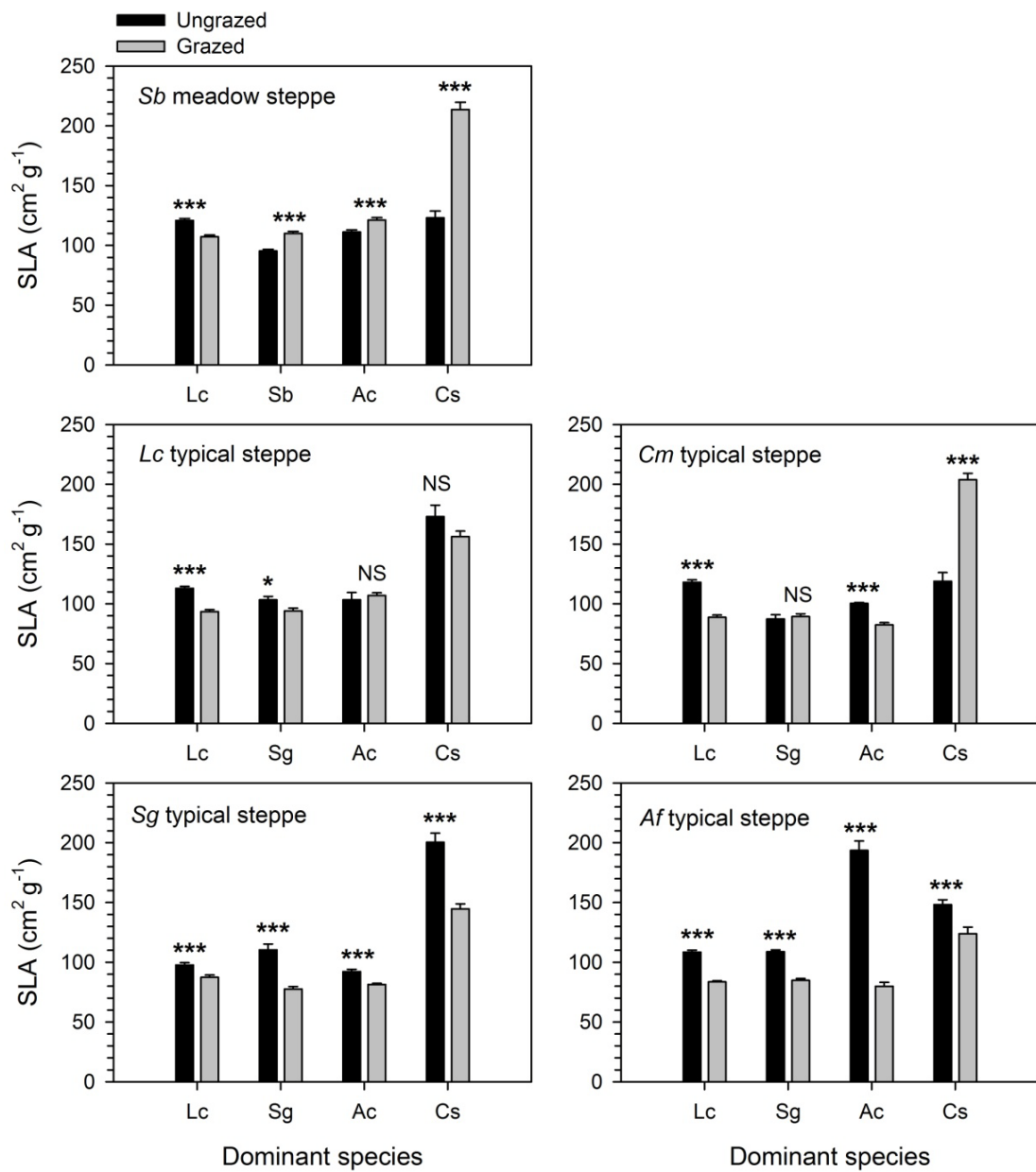


Figure 6