Grazing every month minimizes size but boosts photosynthesis in Stipa grandis in the steppe of Inner Mongolia, China postprint

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Abstract

To investigate the effects of grazing frequency on functional traits and to test whether Stipa gandis exhibits compensatory photosynthesis during periods of frequent grazing, we examined morphological traits, biomass allocation, photosynthetic traits, and chlorophyll fluorescence parameters of this species in Inner Mongolia, China. The grazing frequency treatments comprised fencing (T0), grazing in May and July (T1, i.e., two months per year), and grazing from May to September (T2, i.e., continuous five months per year). Results indicated that T1 and T2 treatments did not affect individual biomass, but the T2 treatment negatively impacted individual size, i.e., plant height, stem length, and leaf length. Physiological traits of S. grandis were significantly affected by grazing, year, and their interaction. In July 2014 (i.e., dry environment and low relative humidity), the photosynthetic rate, transpiration rate, and water use efficiency were highest under the T2 treatment, which was attributed to increased stomatal conductance. However, in July 2015 (i.e., wet environment and high relative humidity), the photosynthetic rate and water use efficiency were higher under T1 and T2 treatments, resulting from increased actual quantum efficiency and stomatal conductance. Our results suggest that under frequent grazing treatment, S. grandis maintained small stature and efficient compensatory photosynthesis, which enhanced its resistance to severe grazing.

Full Text

Preamble

Grazing every month minimizes size but boosts photosynthesis in *Stipa grandis* in the steppe of Inner Mongolia, China

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Abstract: To explore the effects of grazing frequency on functional traits and test whether *Stipa grandis* exhibits compensatory photosynthesis under frequent grazing, we investigated morphological traits, biomass allocation, photosynthetic characteristics, and chlorophyll fluorescence parameters of this species in Inner Mongolia, China. The grazing frequency treatments included fencing (T0), grazing in May and July (T1, i.e., two months per year), and grazing from May to September (T2, i.e., continuous five months per year). Results indicated that T1 and T2 treatments did not affect individual biomass, but the T2 treatment negatively impacted individual size, specifically plant height, stem length, and leaf length. Physiological traits of *S. grandis* were significantly affected by grazing, year, and their interaction. In July 2014 (dry environment with low relative humidity), the photosynthetic rate, transpiration rate, and water use efficiency were highest under the T2 treatment, driven by increased stomatal conductance. However, in July 2015 (wet environment with high relative humidity), the photosynthetic rate and water use efficiency were higher under both T1 and T2 treatments, resulting from increased actual quantum efficiency and stomatal conductance. Our results imply that under frequent grazing, *S. grandis* adopts a strategy of reduced stature combined with efficient compensatory photosynthesis, which enhances its resistance to severe grazing.

Keywords: grazing frequency; morphological traits; gas exchange; photochemical efficiency; water use efficiency

1 Introduction

In China, a survey by the Ministry of Environmental Protection indicated that approximately 31.8% of natural grasslands are degraded. In fact, 74.0% of grasslands in Xilin Gol, Inner Mongolia, are degraded (Wang et al., 2017), which seriously threatens animal husbandry production and local herdsmen' s livelihoods. Since the 1990s, steppe degradation in Inner Mongolia has become increasingly severe (Wang et al., 2009). Studies have revealed that overgrazing—resulting from high stocking rates and static grazing management—is the most important cause of grassland degradation (Akiyama and Kawamura, 2007). To address this problem, the government proposed a project in 2003 to restore pasturage to natural grassland, implementing approaches such as intermittent grazing and grazing bans. Intermittent grazing has become an important conservation method in temperate grasslands (Dorrough, 2004).

Plant functional traits include morphological, physiological, and life history characteristics that affect plant fitness by influencing survival, growth, and reproduction (Violle et al., 2007). Functional traits can effectively relate environmental factors and plant responses to ecosystem structure and function (Díaz and Cabido, 2001; Lavorel et al., 2007). Exploring the mechanisms of grassland plant responses to grazing through changes in functional traits has drawn considerable research attention (Louault et al., 2005). Rusch et al. (2009) found that leaf area index, leaf dry matter content, plant height, and other traits showed significant changes induced by livestock intake and resource supply, with grazing effects being more pronounced when resource availability was high. Díaz et al. (2007) confirmed that grazing favored annual, short, prostrate, and stoloniferous plants over perennial, tall, erect, tussock plants, because short species suffer less grazing pressure and are protected by the cover of tall species. For herbivores, species with small leaflets require more bites to achieve the same leaf intake as species with larger leaves (Vesk et al., 2004).

In addition to directly removing biomass, grazing effects on plants can indirectly influence photosynthetic traits (Zangerl et al., 2002; Aldea et al., 2005). Many studies have observed reduced growth of defoliated grasses induced by the loss of photosynthetic tissues (Belsky, 1986; Ferraro and Oesterheld, 2002; van Staalduinen and Anten, 2005). Studies on steppe have revealed that overgrazing significantly reduced the photosynthetic rate, transpiration rate, and water use efficiency of *Leymus chinensis* and *Stipa grandis* (Chen et al., 2005; Zhao et al., 2009; Zheng et al., 2011). However, in some circumstances, defoliation can stimulate growth by improving photosynthesis (Anderson et al., 2006; Ruizr et al., 2008). Four plant species in Hunshandake Sandy Land showed compensatory photosynthetic growth under moderate grazing (Peng et al., 2007). Recently, some studies have found that plant trait responses to grazing are affected by resources (Adler et al., 2004; Vesk et al., 2004; Rusch et al., 2009) and grazing frequency and intensity (Díaz et al., 2007; N' Guessan and Hartnett, 2011). Zheng et al. (2015) proposed that soil moisture mediated the effects of grazing on plant functional traits. Thus, considerable uncertainty remains about how plant photosynthetic traits respond to grazing, particularly regarding the effects of different grazing frequencies. This represents an important barrier to understanding plant biological processes and formulating intermittent grazing management policies.

S. grandis is one of the dominant species in the steppe of Inner Mongolia, China. The grazing tolerance of plants and their growth response after grazing are always closely related to their photosynthetic capacity. Measuring the response of leaf-level photosynthetic characteristics to different grazing frequencies is beneficial for adjusting grazing regimes to achieve optimal photosynthesis, growth, and yield (Harrision et al., 2010). The objective of this study was to quantify changes and patterns in morphological and photosynthetic traits of *S. grandis* under three grazing frequencies, with results compared between July 2014 (dry environment) and July 2015 (wet environment). Specifically, we also examined the mechanisms of photosynthetic change by measuring chlorophyll fluorescence to better understand these traits. We addressed two main questions: (1) Do the two grazing frequencies affect the biomass and morphological traits of *S. grandis*? and (2) How do the two grazing frequencies affect photosynthetic traits? Additionally, we assessed whether these effects changed under different environmental conditions (wet and dry) and attempted to identify the underlying causes of observed changes in terms of stomatal conductance and chlorophyll fluorescence.

2.1 Study area and experimental design

The study area was located on the Maodeng Ranch, Xilin Gol League of Inner Mongolia, China (44°09 03 N, 116°29 04 E; 1160 m a.s.l.), which features a temperate semi-arid prairie climate with chestnut soil. The annual mean temperature was -0.4°C; specifically, the mean temperature was -19.0°C during the coldest month (January) and 21.4°C during the hottest month (July). The annual accumulated temperature ($ $10°C) was 1597.9°C and the frost-free period lasted for 100 days. The growing season of grassland plants ranged from May to September and the average annual precipitation was 237 mm. The constructive species in the study area were *Stipa grandis* and *Leymus chinensis*, and the accompanying species were *Cleistogenes squarrosa*, *Saposhnikovia divaricata*, and *Artemisia frigida*.

Three treatments with different grazing frequencies were established in the study area: fencing (T0), grazing in May and July (T1, i.e., two months per year), and grazing from May to September (T2, i.e., continuous five months per year). Grazing started on the 21st day of each month. In cases of inclement weather, such as rain, the grazing start date was postponed. The size of each grazed plot was set at 33.3 m × 33.3 m, with a total area of 0.1 hm^2. The grazing experiment began in May 2012. The sheep used for experiments were Ujumuqin sheep born in the same year, with a stocking rate of 6 sheep per plot. In grazing treatments, grazing stopped when the plant community height reached 6 cm, and the number of grazing days was recorded. Morphological and photosynthetic traits were measured in each grazing plot at the end of July in 2014 and 2015, with plants in the grazing plots being freely accessible to grazing.

2.2 Morphological traits and biomass

We randomly selected 30 bunches of *S. grandis* in each plot and measured height, leaf length, and stem length. Height was measured from ground to natural crown. Stem, leaf, and relative chlorophyll content were measured five times, and average values were used to represent the traits of the entire bunch. The relative chlorophyll content of the top fully expanded leaf was determined using a SPAD chlorophyll meter (SPAD 502, Minolta Corp., Ramsey, NJ, USA). In each grazing plot, nine bunches of *S. grandis* were randomly clipped and divided into leaf, stem, litter, and spike samples. Samples were dried at 65°C for 24 h to obtain the dry mass of each component.

2.3 Daily dynamics of gas exchange parameters

Three clusters of healthy growing *S. grandis* per grazing treatment were randomly selected, and daily changes in leaf gas exchange parameters were measured using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA). During measurements, leaves were fully arranged within the leaf chamber; specifically, leaves were horizontal, close to one another, and did not overlap. The photosynthesis system recorded net photosynthetic rate (PN, mol $CO_2/(m^2 \cdot s)$), intercellular CO_2 concentration (Ci, mol CO_2/mol), stomatal conductance (Gs, mol $H_2O/(m^2 \cdot s)$), transpiration rate (E, mmol $H_2O/(m^2 \cdot s)$), air temperature (Tair, °C), and relative humidity (RH, %). Measurements were conducted once every 2 h between 06:00 and 18:00 (LST). For each measurement, three sets of data were recorded. Water use efficiency (WUE, mol CO_2/mmol H_2O) was calculated using the equation: WUE = PN/E. The photosynthesis measurement system was inspected each day before measurements began, and a data-matching operation was carried out before recording.

2.4 Light response curve and parameter fitting

On sunny days between 08:30 and 11:00, the portable photosynthesis system with a 2 cm × 3 cm leaf chamber and a red and blue light source (LI-6400-02B LED, LI-COR, Lincoln, NE, USA) was used to measure the light response curve of healthy *S. grandis* leaves. Three clusters of healthy growing *S. grandis* were randomly selected per grazing plot. Twelve photosynthetic active radiation (PAR) levels were utilized in the following order: 2000, 1800, 1500, 1200, 800, 400, 200, 100, 80, 50, 20, and 0 mol photon/$(m^2 \cdot s)$, with the leaf chamber temperature set at 25°C. The system automatically recorded the net photosynthetic rates corresponding to each radiation level. The light response curve was fitted using an improved non-rectangular hyperbola (Ye, 2007). The maximum net photosynthetic rate (Amax), apparent quantum efficiency (AQE), light compensation point (LCP), and dark respiration rate (Rd) under lighting were simulated.

2.5 Chlorophyll fluorescence parameters

At 06:00, minimum fluorescence (Fo) and maximum fluorescence (Fm) under dark adaptation were measured (by wrapping plant leaves in tin foil overnight) using the photosynthesis system and chlorophyll fluorescence leaf chambers (LI-6400 LCF, LI-COR, Lincoln, NE, USA). Subsequently, the tinfoil sheets were removed, and sunlight was allowed to naturally illuminate leaves to stimulate photosynthesis. At 10:00, minimum fluorescence (Fo'), maximum fluorescence (Fm'), and stable fluorescence (Fs) under light adaptation were measured with a photosynthetic active radiation of 1500 mol photon/$(m^2 \cdot s)$. Five clusters of healthy *S. grandis* were selected per grazing plot.

Based on these four basic fluorescence parameters, we calculated four parameters characterizing photochemical states during the photoreaction stage: (1) PSII maximum quantum yield under dark adaptation (Fv/Fm), where Fv denotes variable fluorescence of leaves under dark adaptation and was calculated as Fv = Fm -Fo; (2) PSII effective quantum yield under light adaptation (ΦPSII), calculated as ΦPSII = (Fm' -Fs)/Fm' , reflecting the active portion of photon absorption in the PSII reaction center; (3) chlorophyll photochemical quenching (qP), calculated as qP = (Fm'-Fs)/(Fm'-Fo'), reflecting the percentage of open PSII reaction centers; and (4) chlorophyll non-photochemical quenching (NPQ), calculated as NPQ = (Fm -Fm')/Fm, reflecting the portion of light energy absorbed by the photosynthetic apparatus that is dissipated as heat, which usually indicates the degree of stress plants are experiencing (Maxwell et al., 2000).

2.6 Data analysis

The effects of grazing frequency, sampling year, and their interaction on morphological traits, biomass, and physiological traits were analyzed via two-way ANOVA. Differences among measured parameters from different grazing treatments were tested via one-way ANOVA, with differences compared using a Tukey test. We assessed correlations between photosynthetic traits (gas exchange) using Pearson' s correlation analysis in SPSS 20.0 (IBM Inc., Chicago, IL, USA). Graphs were drawn with OriginPro 2016 (OriginLab, Northampton, MA, USA).

3.1 Morphological traits and biomass allocation

Height, stem length, and leaf length significantly decreased under the T2 treatment ($P < 0.05$; Table 1). For example, plant height declined by an average of 30%, stem length by 27%, and leaf length by 20%. Most morphological traits were not affected under the T1 treatment ($P > 0.05$; Table 1). In 2014, chlorophyll content increased by 11% under the T1 treatment. Neither T1 nor T2 treatments significantly affected individual biomass or biomass allocation of *S. grandis* ($P > 0.05$; Table 1).

Table 1 Morphological traits and biomass distribution of *S. grandis* under three grazing frequencies

Morphological trait and biomass	T0	T1	T2
Height (cm)	–	–	–
Stem length (cm)	–	–	–
Leaf length (cm)	–	–	–
Chlorophyll content (%)	–	–	–
Leaf mass (g)	–	–	–
Stem mass (g)	–	–	–
Litter mass (g)	–	–	–
Spike mass (g)	–	–	–

Note: Morphology and chlorophyll data are means (n=30) and biomass data are means (n=9). Different lowercase letters in the same row are significantly *different at P < 0.05 level. T0, fencing; T1, grazing in May and July; T2, grazing from May to September.*

3.2 Leaf physiological traits

The physiological traits measured in this study, primarily gas exchange and chlorophyll fluorescence, are closely related to environmental factors on measurement days. The mean PAR values in 2014 and 2015 were 1068 and 1233 µmol/($m^2 \cdot s$), respectively. The mean Tair values were 36.3°C and 32.0°C, respectively. The mean RH values were 24.9% and 44.2%, respectively. Hence, environmental conditions in July 2014 were drier than in July 2015.

Grazing, year, and their interaction significantly influenced PN ($P < 0.01$). In 2014, PN under the T2 treatment was significantly higher than under T0 ($P < 0.05$), increasing almost 4-fold. In 2015, PN under the T1 treatment was significantly higher than under T0 ($P < 0.05$), increasing almost 2-fold (Fig. 1 [Figure 1: see original paper]).

Grazing and year, and their interaction, significantly influenced E ($P < 0.05$). In 2014, E under the T2 treatment was significantly higher than under T1 and T0 ($P < 0.05$). In 2015, there were no significant differences in E among the three grazing frequencies (Fig. 1).

Grazing and year significantly influenced WUE ($P < 0.01$), but their interaction was not significant ($P = 0.177$). In 2014, WUE gradually increased with increasing grazing frequencies ($P = 0.098$). In 2015, WUE values under T1 and T2 treatments were significantly higher than under T0 ($P < 0.05$), increasing by 77% (Fig. 1).

Fig. 1 Net photosynthetic rate (PN, a), transpiration rate (E, b), and water use efficiency (WUE, c) under three grazing frequencies in 2014 and 2015. Bars represent standard error (n=3). Different lowercase letters represent significant differences (Tukey test, $P < 0.05$) among T0 (fencing), T1 (grazing in May and July), and T2 (grazing from May to September) treatments in 2014, and different capital letters represent significant differences in 2015.

Gs was significantly influenced by grazing, year, and their interaction ($P < 0.05$). In 2014, Gs under the T2 treatment was significantly higher than under T1 and T0 ($P < 0.05$). In 2015, there were no significant differences in Gs among the three grazing frequencies ($P = 0.05$; Fig. 2 [Figure 2: see original paper]). Ci was not significantly influenced by grazing, year, or their interaction ($P > 0.05$), and Ci followed the order T0 > T1 > T2 in both years (Fig. 2).

Fig. 2 Stomatal conductance (Gs, a) and intercellular CO_2 concentration (Ci, b) under three grazing frequencies in 2014 and 2015. Bars represent standard error (n=3). Different lowercase letters represent significant differences (Tukey test, $P < 0.05$) among T0, T1, and T2 treatments in 2014, and different capital letters represent significant differences in 2015.

Gs was significantly correlated with PN and E across all three grazing frequencies. The correlation coefficient between Gs and Ci was significant (r = -0.49) only under the T2 treatment (Table 2).

Table 2 Correlations between photosynthetic traits of *S. grandis* under three grazing frequencies

Photosynthetic traits	T0	T1	T2
PN-Gs	–	–	–
PN-Ci	–	–	–
PN-WUE	–	–	–
Gs-Ci	–	–	–
Gs-WUE	–	–	–
Ci-WUE	–	–	–
E-WUE	–	–	–

Note: PN, net photosynthetic rate; Gs, stomatal conductance; Ci, intercellular CO_2 concentration; E, transpiration rate; WUE, water use efficiency. and ** indicate significant differences at $P < 0.05$ and $P < 0.01$ levels, respectively; ns indicates non-significance.*

In 2014, LCP, AQE, Rd, and Amax showed no significant differences among grazing frequencies (Table 3). In 2015, LCP values followed the order T0 > T1 > T2, with LCP under T0 significantly higher than under T2 ($P < 0.05$; Table 3). The Rd value under T0 was significantly higher than under T1 and T2 ($P < 0.05$; Table 3).

Table 3 Photosynthetic traits of *S. grandis* under three grazing frequencies

Parameter	2014	2015
	T0	T1
LCP	–	–
AQE	–	–
Rd	–	–
Amax	–	–

Note: Data are means (n=3), and different lowercase letters in the same row are significantly different at $P < 0.05$ level according to the Tukey test. LCP, light compensation point; AQE, apparent quantum efficiency; Rd, dark respiration rate; Amax, maximum photosynthetic rate.

In 2014, Fv/Fm, qP, NPQ, and ΦPSII showed no significant differences among treatments (Table 4). In 2015, Fv/Fm initially increased then decreased with increasing grazing frequency. The qP and ΦPSII under the T2 treatment were significantly higher than under T0 ($P < 0.05$; Table 4). NPQ showed a decreasing trend with increasing grazing frequencies ($P > 0.05$).

Table 4 Chlorophyll fluorescence traits of *S. grandis* under three grazing frequencies

Parameter	2014	2015
	T0	T1
Fv/Fm	–	–
qP	–	–
NPQ	–	–
ΦPSII	–	–

Note: Data are means (n=5), and different lowercase letters in the same row are significantly different at $P < 0.05$ level according to the Tukey test. Fv/Fm, maximum quantum yield of photosystem II; qP, photochemical quenching; NPQ, non-photochemical quenching; ΦPSII, effective quantum yield of photosystem II.

4.1 Responses of biomass and morphological traits to grazing

This research found that the two grazing frequencies did not affect individual biomass or biomass allocation of *S. grandis*, consistent with previous studies focusing on different grazing intensities (Schiborra et al., 2009; Hu et al., 2016). This result may be explained by sheep diet selection and functional trait responses of *S. grandis*. First, in steppe environments, sheep prefer *Leymus chinensis* and *Carex lanceolata* over *S. grandis* when herbage is abundant (Wang, 2000). Therefore, *S. grandis* is a relatively unpalatable species for sheep, resulting in a neutral biomass response to increasing grazing frequency. Second, adaptive traits may compensate for tissues injured by grazing (Wan et al., 2015), such as increased PN, which is closely associated with relative growth rate (Shipley, 2002, 2006).

We demonstrated that grazing every month (i.e., T2) decreased the stature of *S. grandis*, including height, stem length, and leaf length, though these results were not observed under the T1 treatment. This aligns with other studies in Inner Mongolia (Zhao et al., 2009; Zheng et al., 2011; Li et al., 2015) and with Rusch et al. (2009). The different responses of morphological traits support the hypothesis that grazing intensity regulates plant trait responses (Adler et al., 2004). Small stature is an advantageous characteristic under frequent grazing because it may reduce the likelihood of plants being detected by herbivores. However, small stature may also create gaps in the original community, which could facilitate invasion by pioneer species and thus affect community diversity. Dorrough et al. (2004) found that intermediate grazing frequency maximized species coexistence due to invasion. Therefore, morphological traits of dominant species play an important role in determining community succession.

Unaffected biomass combined with reduced stature under grazing implies promotion of net primary production, supporting the grazing optimization hypothesis (McNaughton, 1979). Increased photosynthetic rate has been proposed as a mechanism to account for this hypothesis (Painter and Detling, 1981).

4.2 Responses of physiological traits to grazing

Compensatory photosynthesis represents an important mechanism for plant leaf regrowth (Detling et al., 1979) and tolerance to herbivores (Gassmann, 2004). Grazing significantly promoted PN, with a greater increase under the T2 treatment (dry environment) than under the T1 treatment (wet environment). This partially supports the hypothesis that plants suffering from drought and herbivory are more resistant to herbivores (Copolovici et al., 2014), which in our study was caused by a significant increase in Gs. The increase in PN under grazing is consistent with other studies (Hodgkinson, 1974; Wallace, 1990; Yan et al., 2009; Harrision et al., 2010). The increased PN may also be due to increased leaf nitrogen content (Morrison and Reekie, 1995). However, other studies have found that PN showed decreasing or fluctuating tendencies (Peng et al., 2007; Fahnestock and Detling, 2000; Zheng et al., 2011), which could be caused by separated vasculature, changed sink demand, and defense-induced autotoxicity (Nabity et al., 2008). These differences can be attributed to variations in plant species and grazing intensities (Hou, 2001). Nevertheless, this study suggests that the increase in PN after grazing in arid environments came at the expense of increased water dissipation.

E significantly increased under the T2 grazing treatment in the dry environment, which can also be explained by increased Gs. This is similar to results reported by Peng et al. (2007) for four dominant grasses in northern Chinese grasslands, but differs from Deng et al. (2012), who reported decreasing transpiration rates in *Leymus chinensis* with increasing grazing intensity. This discrepancy likely reflects different mechanisms for coping with grazing stress: the bunchgrass *S. grandis* tends to enhance carbon sequestration by increasing its transpiration rate, while the rhizomatous grass *L. chinensis* adopts a strategy of decreasing transpiration and water loss.

In this study, WUE significantly increased under both grazing frequencies in the wet environment, but did not change significantly in the dry environment. This indicates that plants used water more efficiently when grazing occurred, while becoming more conservative in arid environments. This result is consistent with Zheng et al. (2011), who stated that grazing had a more positive effect on WUE in wet years than in dry years. Zhao et al. (2009) found that heavy grazing reduced the WUE of *L. chinensis*. Another study found that WUE first increased then decreased with increasing grazing intensities, showing a positive response to continuous grazing (Peng et al., 2007). We speculate that neither T1 nor T2 grazing reached heavy grazing levels, and *S. grandis* exhibited a positive response to grazing.

In this study, the T2 treatment in the dry environment significantly promoted Gs, consistent with previous studies (Christiansen and Svejcar, 1988; Redondo-Gómez et al., 2010; Anderson et al., 2013). Potential causes include changes in stomatal physiology, such as increased stomatal density and stomatal conductance index (Zhang et al., 2010), increased root biomass and root length density (Chen et al., 2015), and decreased self-shading or increased solar radiation received by individual plants (Cai et al., 2004; Gregoriou et al., 2007). Our study focused only on the vigorous growth stage of *S. grandis*, yet the impact of herbivores on photosynthetic traits is influenced by phenological cycles (Maschinski and Whitham, 1989), which requires further investigation.

Ci is used to determine the drivers of photosynthetic changes and whether they are caused by stomatal factors (Farquhar and Sharkey, 1982; Xu, 1997). Ci was not influenced by grazing frequency in this study ($P > 0.05$), consistent with published results on wheat leaves (Macedo et al., 2007; Harrison et al., 2010). Considering the increases in both stomatal conductance and photosynthetic rate, we speculate that light energy harvest or carbon fixation in *S. grandis* leaves increased.

The T1 and T2 treatments did not significantly influence AQE and Amax, indicating that changes in grazing frequency did not alter photosynthetic efficiency of *S. grandis* leaves. This is consistent with findings that grazing effects on AQE of a Mediterranean shrub were very limited (Redondo-Gómez et al., 2010).

In this study, qP and ΦPSII under the T2 treatment were significantly higher than under T0 in the wet environment, indicating that quantum efficiency of PSII electron transport in the light increased (Murchie and Lawson, 2013). However, in 2014, no fluorescence traits showed significant differences, indicating that grazing frequencies in the dry environment had limited effects on electron-transfer efficiency. These different results can be explained by water stress reducing PSII photochemistry efficiency (Lu and Zhang, 1999).

Combining all functional traits, we found that *S. grandis* has strong resistance to grazing, adopting both avoidance and tolerance strategies. As grazing frequency increased, individual size decreased, while increased PN and WUE values indicated rapid recovery of damaged plants. However, in dry environments, the positive effect of the tolerance strategy was partially offset.

5 Conclusions

We conclude that grazing frequencies did not affect individual biomass of *S. grandis*, but the T2 treatment negatively impacted individual size. Plant miniaturization is an effective strategy to cope with long-term overgrazing. To explore the mechanism of biomass acclimation, we studied the photosynthetic response of the species. We found that *S. grandis* used a radical approach to compensate for the negative effects of grazing on its morphology by increasing stomatal conductance and thus promoting PN, which accelerates water dissipation. This strategy worked well in wet conditions with increased WUE, but did not significantly affect WUE in dry conditions. Additionally, photosynthetic light-energy harvest increased under the T2 grazing treatment, which also explained the increase in PN. The response of individual biomass, morphology, and photosynthetic traits to grazing demonstrated that *S. grandis* is a species with strong resistance and plays an important role in regulating community productivity and functional stability.

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