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Leaf gas exchange and photosynthesis curves of *Elymus nutans* and *Potentilla anserina* under fencing and grazing conditions in the Qilian Mountains, Northwest China

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Abstract: *Potentilla anserina* L. and *Elymus nutans* Griseb. are dominant species in the subalpine meadows of China. Grazing is one of the most important factors that influence community structure and productivity of subalpine meadows. Understanding how grazing changes photosynthetic capability is essential for preservation and restoration of grasslands. However, information about the effects of grazing on photosynthetic capability remains inadequate. Experiments were conducted in fencing and grazing areas in the Qilian Mountains, Northwest China. The leaf gas exchange and photosynthetic curves of *P. anserina* and *E. nutans* were measured at different growth stages. Results showed that grazing decreased the values of leaf gas exchange parameters, such as net photosynthetic rate, stomatal conductance, transpiration rate, and intercellular CO_2 concentration of *P. anserina* and *E. nutans*. In addition, grazing decreased the values of net photosynthetic rate-photosynthetically active radiation (P_N-PAR) curve parameters, such as light-saturated net photosynthetic rate, apparent quantum efficiency, light compensation point, light saturation point, and dark respiration rate. Our results demonstrated that grazing was the primary limiting factor for photosynthesis of dominant grassland species in the study area.

Keywords: grazing; diurnal variation; gas exchange; *Potentilla anserina*; *Elymus nutans*; photosynthetic capacity

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1 Introduction

Plant growing in natural conditions is limited by multiple environmental factors (i.e., light, water, temperature, and nutrition) and human disturbances (i.e., grazing, land use transformation, mining, deforestation, and environmental pollution) (Guo et al., 2007; Andrew et al., 2016; Busso et al., 2016; Casazza et al., 2016). The effects of environmental factors on plant growth are mainly slow and gradual, whereas those of human activities are mainly rapid and abrupt (Chesson, 2000; Wertin et al., 2015; Humphrey et al., 2016). Grazing, an anthropogenic activity has played an important role in controlling grass growth in natural grasslands. Some researchers have reported

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that heavy grazing restricts plant growth and production in grasslands (Bai et al., 2015; Strahan et al., 2015; Pulido et al., 2016), while fencing and light grazing promote the normal growth of herbage (MãLler et al., 2014; Ruizalbarran et al., 2016). On the one hand, grazing directly affects photosynthesis by eating the ground part of grass. On the other hand, grazing affects the soil physical and chemical properties (i.e., bulk density, water infiltration, soil organic matter, total nitrogen, and total phosphorus) that subsequently influence the ability of plants to assimilate photosynthate; thus, it is the major determinant of the potential productivity of grasslands (Wang et al., 2015; Ren et al., 2016).

Livestock population has increased with increasing human population growth. Thus, grazing areas have expanded worldwide and seriously degraded grasslands (Wang and Wesche, 2016; Qian et al., 2017). Grazing not only controls grassland species diversity and composition, but also affects photosynthetic characteristics of major steppe species (Chen et al., 2005; Herrero-Jáuregui and Oesterheld, 2017). Grazing restriction is a common approach for protection of grasslands, including rotational grazing and controlled grazing (Pei et al., 2008; Hu et al., 2009; Wu et al., 2010; Mekuria, 2013; Zhang et al., 2013). It is common knowledge that degraded grasslands resulting from overgrazing have been restored under five years after fencing conditions (i.e., five years of no grazing). However, studies on the difference in photosynthetic parameters of plants between under grazing and five years of fencing conditions are scarce. *Potentilla anserina* L. and *Elymus nutans* Griseb. are C_3 perennial plants and the dominant species of subalpine meadows in China. They have high photosynthetic capacity and good forage quality (Xu et al., 2006, 2011; Liu et al., 2016). In addition, they have an elaborate root system and high coverage, making them be important species in reducing water and soil losses (Jiao et al., 2009; Zhao et al., 2017). Heavy grazing has significantly decreased the photosynthetic capacity of these species. However, information on the interaction between grazing and photosynthetic characteristics of these species remains limited. Therefore, this study is conducted to obtain such information by investigating the leaf gas exchange and photosynthetic curves of *P. anserina* and *E. nutans* in the subalpine meadows of China. Our objectives are (1) to compare the diurnal patterns of leaf gas exchange parameters of plants under fenzing and grazing conditions for five years; (2) to clarify the response curves of net photosynthetic rate-photosynthetically active radiation (P_N-PAR) of plants under two regimes; and (3) to identify the difference in the photosynthetic capacity of plants under two regimes.

2 Materials and methods

2.1 Study area and experimental design

Our study area is located in the Tianlaochi Catchment (38°23′56″–38°26′47″N, 99°53′57″–99°57′10″E) in the central region of the Qilian Mountains, China. Tianlaochi Catchment is part of the upper reaches of the Heihe River, Northwest China, and covers an area of approximately 12.8 km^2 with an elevation range between 2660 and 4419 m a.s.l. (Fig. 1). The climate is characterized by short and warm summers and long and cold winters. Annual mean temperature ranges from –0.6°C to 2.0°C with a maximum monthly temperature of 11.6°C in July and a minimum monthly temperature of –14.5°C in December. The mean annual precipitation is 435.5 mm. Precipitation mainly occurs from May to September and accounts for 89.2% of the annual precipitation. Temperature decreases and precipitation increases with increasing elevation. The combination of temperature and precipitation causes a distinct vertical distribution of plant communities. The sequence of plant communities from lower to upper is as follows: desert steppe, forest steppe, subalpine shrub, and subalpine meadow. Subalpine meadow is rich in species and dominated by *P. anserina* and *E. nutans* (Table 1). The soil is alpine gray brown soil (approximately 50 cm in depth) and root systems are mainly distributed at the depth of 20 cm. The physical and chemical properties of the soil in the experimental site are shown in Table 2. Generally, the growth period of *P. anserina* and *E. nutans* is from late April to early September (Shi et al., 2010).

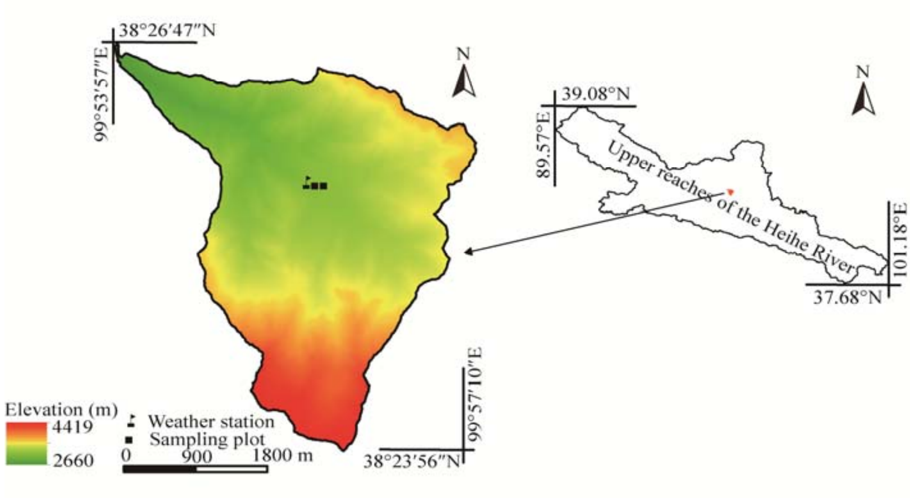

Fig. 1 Location of study area and sampling plots

Table 1 Summary of characteristics for the species selected in the experimental site

Species	Family	Life cycle	Plant type	Morphological characteristics	Ecology habit	Palatability
P. anserina	Rosaeeae	Perennial	C_3	Typical stoloniferous herb	Cold and drought resistant; sciophiles	Medium
E. nutans	Poaceae	Perennial	C_3	Hydrophobic cluster herb	Cold resistant; heliophile	High

The experimental area was fenced to prevent grazing in 2012. Other areas in the subalpine meadow have been overgrazing by livestock (approximately 691×10^3 sheep units) for more than 30 years (Wang et al., 2014). In 2016, we selected one plot with an area of 8 m×12 m in fencing and grazing regions with a buffer zone of 10 m in width between two plots for protection against disturbance and the edge effect. Both plots have similar slopes and slope positions.

Table 2 Physical and chemical properties of the soil in the experimental site

Soil property	Component		Mean	Coefficient of variation
Chemical property	Soil organic matter (g/kg)		94.67	0.24
	Soil organic carbon (g/kg)		68.43	0.26
	pH		7.95	0.11
	C/N		12.71	0.16
Physical property	Soil bulk density (g/cm)		1.00	0.20
	Slope (°)		11.35	0.14
	Soil thickness (m)		0.44	0.12
	Soil total porosity (%)		62.28	0.12
	Soil texture (%)	Sand	24.31	0.21
		Silt	52.65	0.12
		Clay	23.04	0.11

2.2 Data collection

Each plot was divided into six subplots (4 m×4 m). Photosynthetic parameters, including gas exchange parameters and P_N-PAR response curves were measured for each subplot with six duplicates.

Gas exchange parameters were measured during one completely sunny day in each month of the growing season (i.e., June, July, and August in 2016). Three plants of each species with similar growth status were selected from the center of each subplot. One leaf was selected per plant. Selection criteria are leaves being newly expanded, healthy, and at the similar growing positions. The middle section of the selected leaf was measured at 1-hour intervals from 08:00 (LST) to 20:00 using a portable photosynthesis system (LI-6400, LI-COR Inc., Lincoln, NE, USA). We obtained the following gas exchange parameters, i.e., net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i). Environmental parameters, such as photosynthetically active radiation (PAR), ambient CO_2 concentration (C_a), air temperature (T_{AIR}), leaf temperature (T_{LEAF}), vapor pressure deficiency (VPD), and relative humidity (RH), were simultaneously obtained. Diurnal mean values of P_N, E, g_s, and C_i were obtained by averaging the hourly values over the period from 08:00 to 20:00.

The P_N-PAR response curves of the leaves were determined by gas exchange parameters using the LI-6400 portable photosynthesis system with a red-blue LED light source (6400-02B). P_N was obtained from the selected leaf after 20 min of illumination at a photosynthetic photon flux density (PPFD) of 2000 μmol/(m^2•s). P_N-PAR response curves were obtained at 14 levels of PPFD (i.e., 2000, 1800, 1500, 1200, 1000, 800, 600, 400, 200, 150, 100, 50, 20, 0 μmol/(m^2•s)) under natural conditions from 09:30 to 11:30. P_N-PAR response curves were fitted by the highly popular nonrectangular hyperbola (NRH) equation (Marshall and Biscoe, 1980; Thornley, 1998; Prieto et al., 2010; Calama et al., 2013), which is expressed as follows:

$$P_N(I) = \frac{\alpha I + P_{Nmaxcal} - \sqrt{(\alpha I + P_{Nmaxcal})^2 - 4\theta\alpha I P_{Nmaxcal}}}{2\theta} - R_D, \tag{1}$$

where α is the initial slope of the photosynthetic light-response (PLR) curves (i.e., apparent quantum efficiency, AQE); I is the PPED (μmol/(m^2•s)); θ is the convexity; $P_{Nmaxcal}$ is the calculated maximum net photosynthetic rate (μmol CO_2/(m^2•s)); and R_D is the dark respiration inferred from response curves (μmol/(m^2•s)). Parameters α, θ, $P_{Nmaxcal}$, and R_D were estimated using the nonlinear regression module in the SPSS statistical package (Version 16.0 for Windows, SPSS, Chicago, IL, USA).

After photosynthetic parameters were acquired, the following indices for the photosynthetic capacity of plants were obtained, i.e., water-use efficiency (WUE), stomatal limitation value (L_s), light compensation point (LCP), light saturation point (LSP$_{obs}$), and variation ratio (VR). WUE was calculated as follows (Nijs et al., 1997):

$$\text{WUE} = P_N/E. \tag{2}$$

L_s is expressed as follows (Berry and Downton, 1982):

$$L_s = 1 - C_i/C_a. \tag{3}$$

LCP, which occurred in the PPFD range of 0–200 μmol/(m^2•s), was estimated from the linear section of the P_N-PAR response curves (Singsaas et al., 2001). The linear section was fitted with a linear function, and LCP was the intercept between the linear function and x-axis of PPFD. The observed maximum net photosynthetic rate, which was designated as $P_{Nmaxobs}$, was observed at 14 levels of PPFD. The point of PPFD that corresponded with $P_{Nmaxobs}$ was LSP$_{obs}$. VR was the ratio between the deviations in two regions to the values in grazing plot.

2.3 Statistical analysis

We used SPSS (Version 19.0, SPSS Inc., Chicago, IL, USA) and Sigmaplot (Version 12.5, Systat Software Inc., San Jose, CA, USA) statistical packages to analyze measurements. The effects of fencing after years on the photosynthetic capacity of the selected species were analyzed using one-way ANOVA (P<0.05). Differences in photosynthetic parameters between grazing and fencing plots were compared using least significant difference (LSD) multiple range tests at the 0.05 probability level.

3 Results

3.1 Diurnal variations in environmental parameters

PAR ranged from 62.03 to 2130.65 μmol/(m^2•s) during the measurement period. The highest daily values for the measurement in three days occurred at 13:00 (Fig. 2a1) and 14:00 (Figs. 2b1 and c1). The variation trend in C_a during the observation period was expressed as a "W" shape (Figs.

2a1, b1, and c1). The maximum C_a value was observed at 08:00, then decreased and reached a lower value at 11:00, then increased and reached a higher value at 14:00, and then decreased to the lowest value at approximately 18:00, from then increased again until 20:00. The diurnal patterns of T_{AIR} and T_{LEAF} were similar, and their maximum values appeared at approximately 13:00 (Figs. 2a2, b2, and c2). The maximum and minimum values of RH were observed at 08:00 and at approximately 14:00, respectively. The diurnal pattern of VPD was opposite to that of RH (Figs. 2a3, b3, and c3).

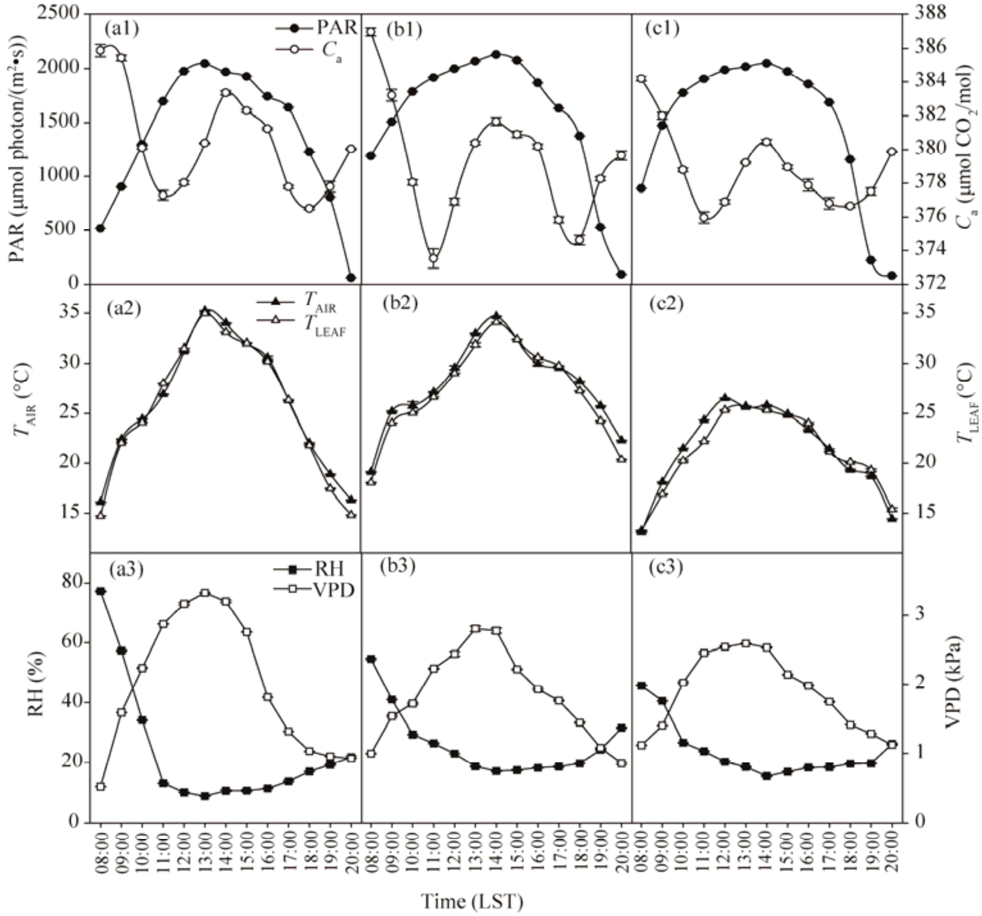

Fig. 2 Diurnal variations of photosynthetically active radiation (PAR) (a1, b1, and c1), ambient CO_2 concentration (C_a) (a1, b1, and c1), air temperature (T_{AIR}) (a2, b2, and c2), leaf temperature (T_{LEAF}) (a2, b2, and c2), relative humidity (RH) (a3, b3, and c3), and vapor pressure deficient (VPD) (a3, b3, and c3). a, b, and c are the dates of 25 June, 23 July, and 26 August in 2016, respectively. Bars mean standard errors; *n*=6.

3.2 Diurnal variations in photosynthetic parameters

According to plant growth period, we chose the early (25 June), medium (23 July) and late (26 August) stages of plant growth for the measurement of the photosynthetic parameters. Diurnal variations in P_N, E, and g_s exhibited double-peaked curves under grazing and fencing conditions (Figs. 3 and 4). There existed lower values between two peaks. This phenomenon, which is called midday photosynthetic depression, occurred from 12:00 to 16:00 (Figs. 3a1, b1, and c1 and Figs. 4a1, b1, and c1).

3.2.1 Diurnal patterns of photosynthetic parameters for *E. nutans*

Under fencing conditions, the maximum values of P_N on 25 June, 23 July, and 26 August were 13.20, 16.40, and 14.92 μmol CO_2/(m^2•s), respectively. The maximum values in grazing plot

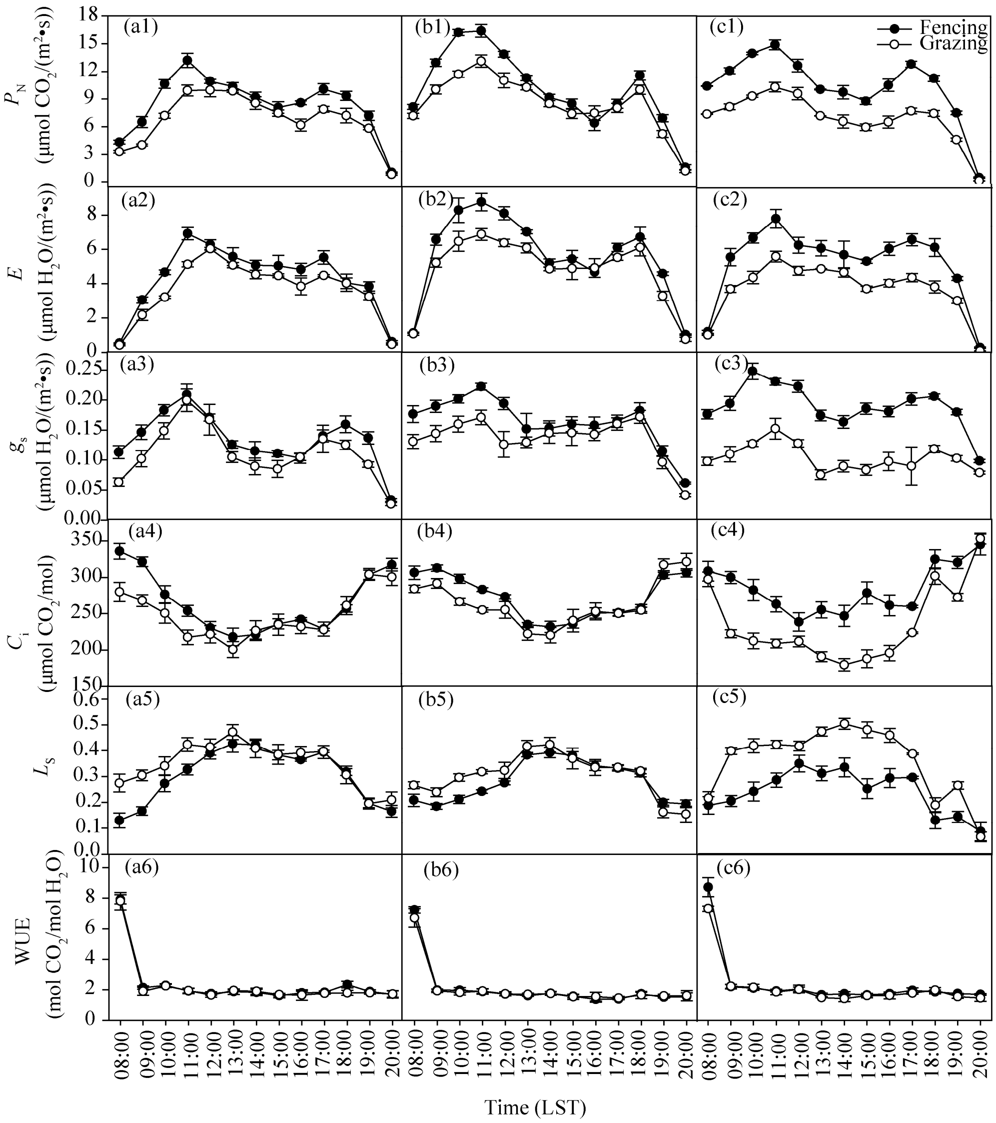

Fig. 3 Diurnal patterns of net photosynthetic rate (P_N) (a1, b1, and c1), transpiration rate (E) (a2, b2, and c2), stomatal conductance (g_s) (a3, b3, and c3), intercellular CO_2 concentration (C_i) (a4, b4, and c4), stomatal limitation value (L_S) (a5, b5, and c5), and water-use efficiency (WUE) (a6, b6, and c6) for *E. nutans* grown in fencing and grazing plots. a, b and c are the dates of 25 June, 23 July, and 26 August in 2016, respectively. Bars mean standard errors; n=6.

were lower than those in fencing plot. The first peak occurred at 11:00 under fencing and grazing conditions. The second peak occurred at approximately 17:30 for both regimes (Figs. 3a1, b1, and c1).

The diurnal patterns of E and g_s were similar to that of P_N and formed an "M" shape. E and g_s increased with time and the first peak occurred at 11:00 and then decreased and reached the lower values at approximately 15:00, after that, E and g_s increased again to the second peak at approximately 17:30, and then, declined until 20:00 (Figs. 3a2, b2, and c2). However, the maximum g_s values occurred 1 h earlier in fencing plot than in grazing plot on 26 August (Figs. 3a3, b3, and c3).

The diurnal pattern of C_i differed from those of P_N, E, and g_s. In our study area, C_i firstly reached the maximum values at 08:00 except on 26 August, then decreased and reached the daily minimum values at approximately 12:00, and remained at the low levels for approximately 5 h until 17:00 (Figs. 3a4, b4, and c4). The trends of the diurnal variations in L_s were opposed to those of C_i (Figs. 3a5, b5, and c5).

Diurnal variations in WUE followed an "L" shape under fencing and grazing conditions. The maximum WUE appeared at 08:00, then sharply declined to a lower value approximately at 09:00, and remained the low level for approximately 11 h (Figs. 3a6, b6, and c6).

Through statistical analysis, we found that there were significantly different photosynthetic parameters in fencing and grazing plots (Table 3). The daily mean values of photosynthetic parameters (P_N, E, g_s, and C_i) in fencing plot were significantly higher than those in grazing plot. On the contrary, the daily mean values of L_s in fencing plot were significantly lower than those in grazing plot. There were no significantly differences of WUE on 23 July between fencing and grazing plots. In addition, the daily mean values of parameters (E, g_s, C_i, and L_s) significantly differed on different observation dates in fencing plot, while daily mean values of WUE significantly differed on different observation dates in grazing plot (Table 4). Under fencing condition, the percentages of variation of the P_N, E, g_s, C_i, L_s, and WUE for the *E. nutans* were 30.3%, 26.1%, 41.3%, 9.7%, –17.8%, and 4.5%, respectively (Table 3).

Table 3 Analysis of differences of P_N, E, g_s, C_i, L_s, and WUE for *E. nutans* and *P. anserina* in fencing plots

Species	Regime	Date	P_N/(VR)	E/(VR)	g_s/(VR)	C_i/(VR)	L_s/(VR)	WUE/(VR)
E. nutans	Fencing	25 June	**/(24.0%)	**/(18.8%)	**/(20.9%)	**/(6.7%)	**/(–12.5%)	*/(3.6%)
		23 July	**/(18.3%)	**/(17.9%)	**/(20.7%)	**/(3.3%)	**/(–7.5%)	*/(1.1%)
		26 August	**/(48.5%)	**/(41.6%)	**/(82.3%)	**/(19.0%)	**/(–33.4%)	**/(9.0%)
		Total	**/(30.3%)	**/(26.1%)	**/(41.3%)	**/(9.7%)	**/(–17.8%)	*/(4.5%)
P. anserina	Fencing	25 June	**/(19.9%)	**/(17.0%)	**/(10.6%)	**/(6.7%)	**/(–17.1%)	*/(4.0%)
		23 July	**/(14.7%)	**/(18.3%)	**/(7.8%)	**/(5.8%)	**/(–18.2%)	*/(0.3%)
		26 August	**/(11.6%)	NS/(4.0%)	NS/(8.9%)	NS/(0.7%)	NS/(–2.0%)	NS/(5.2%)
		Total	**/(15.4%)	*/(13.1%)	*/(9.1%)	*/(4.4%)	*/(–12.5%)	NS/(3.1%)

Note: P_N, net photosynthetic rate; E, transpiration rate; g_s, stomatal conductance; C_i, intercellular CO_2 concentration; L_s, stomatal limitation value; WUE, water-use efficiency. * and ** indicate the significances at $P<0.05$ and $P<0.01$ levels, respectively; NS, not significant. VR, variation ratio.

3.2.2 Diurnal patterns of photosynthetic parameters for *P. anserina*

Under fencing conditions, the maximum values of P_N on 25 June, 23 July, and 26 August were 19.84, 22.91 and 18.99 μmol CO_2/(m^2•s), respectively (Fig. 4). The maximum values in fencing plot were significantly higher than those in grazing plot. The peak values occurred at the same time as *E. nutans* (Figs. 4a1, b1, and c1).

The diurnal patterns of E and g_s were similar to that of P_N. However, the second peak values of E and g_s occurred 1 h later on 23 July and 26 August than those of P_N in fencing and grazing plots (Figs. 4b2, c2 and Figs. 4b3, c3).

Diurnal pattern of C_i differed from that of P_N. The maximum C_i values occurred at 08:00, decreased to the daily minimum values at approximately 15:00, and remained at low levels for approximately 4 h until 19:00 (Figs. 4a4, b4, and c4). The trends of the diurnal variations in L_s were opposed to those of C_i (Figs. 4a5, b5, and c5).

The diurnal pattern of WUE followed an "L" shape under two regimes. The maximum values of WUE appeared at 08:00, declined sharply to lower value at approximately 09:00 except on 25 June, and remained low for approximately 10 h (Figs. 4a6, b6, and c6).

Through statistical analysis, there were significantly different photosynthetic parameters on 25 June and 23 July in fencing and grazing plots. There were no significantly differences of these parameters (E, g_s, C_i, L_s, and WUE) on 26 August under two regimes (Table 3). The daily mean values of photosynthetic parameters (P_N, E, g_s, and C_i) were significantly higher in fencing plot than in grazing plot on 25 June and 23 July. On the contrary, the daily mean values of L_s were significantly lower in fencing plot than in grazing plot on 25 June and 23 July. Furthermore, the daily mean values of g_s, C_i, and L_s significantly differed on different observation dates both in grazing and fencing plots. Daily mean values of P_N and E significantly differed on different observation dates in fencing plot (Table 4). Compared with grazing plot, the percentages of variation of the P_N, E, g_s, C_i, L_s, and WUE in fencing plot for the *P. anserina* were 15.4%, 13.1%, 9.1%, 4.4%, –12.5%, and 3.1%, respectively (Table 3).

Table 4 Daily photosynthetic parameters (P_N, E, g_s, C_i, L_s, and WUE) in *E. nutans* and *P. anserina* on different measuring dates in fencing and grazing plots

Species	Parameter	Treatment	25 June	23 July	26 August
E. nutans	P_N (μmol CO_2/(m^2•s))	Grazing	6.80±0.36^{bB}	8.56±0.40^{aB}	7.01±0.31^{bB}
		Fencing	8.43±0.32^{bA}	10.12±0.35^{aA}	10.40±0.33^{aA}
	E (mmol H_2O)/(m^2•s))	Grazing	3.63±0.05^{bB}	4.80±0.08^{aB}	3.68±0.08^{bB}
		Fencing	4.31±0.21^{cA}	5.67±0.22^{aA}	5.22±0.24^{bA}
	g_s (mol H_2O/(m^2•s))	Grazing	0.111±0.007^{bB}	0.136±0.010^{aB}	0.104±0.008^{bB}
		Fencing	0.134±0.005^{cA}	0.164±0.011^{bA}	0.190±0.004^{aA}
	C_i (μmol CO_2/mol)	Grazing	248.20±10.5^{bB}	263.80±6.30^{aB}	241.40±7.40^{bB}
		Fencing	264.80±6.80^{cA}	272.50±2.40^{bA}	287.40±10.80^{aA}
	L_s	Grazing	0.348±0.028^{aA}	0.304±0.017^{bA}	0.363±0.020^{aA}
		Fencing	0.304±0.018^{aB}	0.281±0.006^{bB}	0.241±0.029^{cB}
	WUE (mol CO_2/mol H_2O)	Grazing	2.29±0.06^{aB}	2.07±0.07^{cA}	2.19±0.08^{bB}
		Fencing	2.37±0.07^{aA}	2.10±0.05^{bA}	2.39±0.07^{aA}
P. anserina	P_N (μmol CO_2/(m^2•s))	Grazing	11.95±0.59^{bB}	14.52±0.59^{aB}	11.38±0.65^{bB}
		Fencing	14.33±0.62^{bA}	16.67±0.45^{aA}	12.70±0.67^{cA}
	E (mmol H_2O/(m^2•s))	Grazing	4.83±0.09^{bB}	6.11±0.13^{aB}	4.80±0.25^{bA}
		Fencing	5.65±0.20^{bA}	7.23±0.16^{aA}	5.00±0.26^{cA}
	g_s (mol H_2O/(m^2•s))	Grazing	0.303±0.019^{bB}	0.464±0.011^{aB}	0.267±0.003^{cA}
		Fencing	0.335±0.029^{bA}	0.500±0.008^{aA}	0.291±0.006^{cA}
	C_i (μmol CO_2/mol)	Grazing	273.80±0.90^{cB}	287.40±1.50^{aB}	280.40±0.20^{bA}
		Fencing	292.20±1.10^{bA}	304.10±0.10^{aA}	282.40±0.60^{cA}
	L_s	Grazing	0.280±0.002^{aA}	0.242±0.004^{bA}	0.260±0.001^{cA}
		Fencing	0.232±0.003^{cB}	0.198±0.001^{bB}	0.255±0.002^{aA}
	WUE (mol CO_2/mol H_2O)	Grazing	3.06±0.14^{bB}	3.03±0.14^{bA}	3.22±0.45^{aA}
		Fencing	3.19±0.14^{abA}	3.04±0.09^{bA}	3.39±0.29^{aA}

Note: P_N, net photosynthetic rate; E, transpiration rate; g_s, stomatal conductance; C_i, intercellular CO_2 concentration; L_s, stomatal limitation value; WUE, water-use efficiency. Different lowercase letters mean significant differences in the same treatment at P<0.05 level under different observation dates. Different uppercase letters indicate significant differences on the same measuring date at P<0.05 level under two treatments. Mean±SE, n=6.

3.3 P_N-PAR curves

The P_N-PAR response curves were well fitted by NRH (R^2>0.997; Fig. 5; Table 5), suggesting that these two species exhibited distinct light saturation phenomenon. Differences of $P_{Nmaxobs}$, $P_{Nmaxcal}$, AQE (i.e., α in Equation 1), R_D, LCP, and LSP_{obs} in two included species between fencing and grazing plots were statistically significant (Table 6).

The values of $P_{Nmaxobs}$, $P_{Nmaxcal}$, AQE, R_D, LCP, and LSP_{obs} from *E. nutans* and *P. anserina* on different measuring dates in fencing plot were significantly higher than their corresponding values in grazing plot (Table 5). Significant differences were found in parameters ($P_{Nmaxobs}$, $P_{Nmaxcal}$, R_D, and LSP_{obs}) for both species among three measurement dates within a given regime. Under grazing conditions, the AQE of *E. nutans* was not significantly different between 23 July and 26 August, and *P. anserina* exhibited the same results between 25 June and 26 August. The LCP values of *E. nutans* between 25 June and 26 August were not significantly different under grazing conditions but were significantly different under fencing conditions. LCP values of *E. nutans* between 23 July and 26 August were not significantly different under fencing conditions but were significantly different under grazing conditions. The LCP values of *P. anserina* were significantly different between two regimes, and across different observation dates. The maximum parameter values ($P_{Nmaxobs}$, $P_{Nmaxcal}$, AQE, R_D, LCP, and LSP_{obs}) of *E. nutans* occurred on 23 July

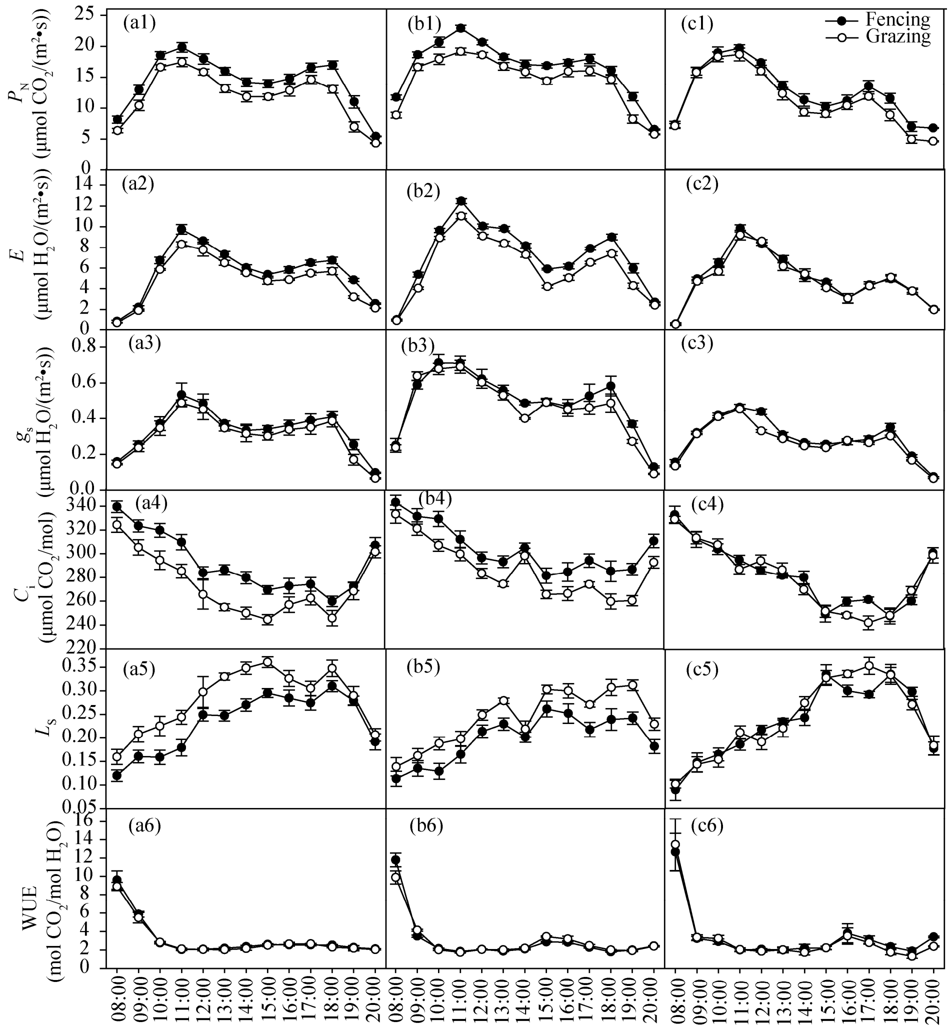

Fig. 4 Diurnal patterns of net photosynthetic rate (P_N) (a1, b1, and c1), transpiration rate (E) (a2, b2, and c2), stomatal conductance (g_s) (a3, b3, and c3), intercellular CO_2 concentration (C_i) (a4, b4, and c4), stomatal limitation value (L_S) (a5, b5, and c5), and water-use efficiency (WUE) (a6, b6, and c6) for *P. anserina* grown in fencing and grazing plots. a, b and c are the dates of 25 June, 23 July, and 26 August in 2016, respectively. Bars mean standard errors; *n*=6.

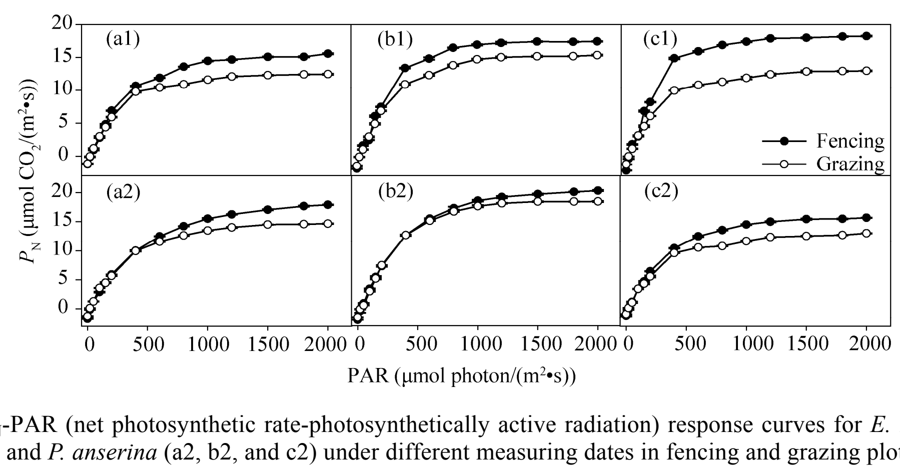

Fig. 5 P_N-PAR (net photosynthetic rate-photosynthetically active radiation) response curves for *E. nutans* (a1, b1, and c1) and *P. anserina* (a2, b2, and c2) under different measuring dates in fencing and grazing plots. a, b, and c are the dates of 25 June, 23 July, and 26 August in 2016, respectively. Bars mean standard errors; *n*=6.

in grazing plot, and on 26 August in fencing plot. Whereas the minimum parameter values of *E. nutans* occurred on 25 June in both grazing and fencing plots. For each plot of *P. anserina*, the maximum and minimum parameter values ($P_{Nmaxobs}$, $P_{Nmaxcal}$, AQE, R_D, LCP, and LSP_{obs}) occurred on 23 July and 25 June, respectively. $P_{Nmaxobs}$ and $P_{Nmaxcal}$ exhibited similar variation trends across different observation dates and under both regimes (Table 5). However, $P_{Nmaxcal}$ was higher than $P_{Nmaxobs}$ for both species under both regimes.

Table 5 Values of parameters ($P_{Nmaxobs}$, $P_{Nmaxcal}$, AQE, R_D, LCP, and LSP_{obs}) for *E. nutans* and *P. anserina* on different measuring dates in fencing and grazing plots

Species	Parameter	Treatment	25 June	23 July	26 August
E. nutans	$P_{Nmaxobs}$ (μmol CO_2/(m^2•s))	Grazing	12.46±0.08^{cB}	15.38±0.08^{aB}	12.96±0.08^{bB}
		Fencing	15.58±0.10^{cA}	17.46±0.05^{bA}	18.26±0.06^{aA}
	$P_{Nmaxcal}$ (μmol CO_2/(m^2•s))	Grazing	14.11±0.09^{cB}	17.84±0.08^{aB}	14.86±0.21^{bB}
		Fencing	17.99±0.12^{cA}	19.69±0.07^{bA}	20.45±0.14^{aA}
	AQE (μmol CO_2/μmol photon)	Grazing	0.044±0.001^{bB}	0.049±0.001^{aB}	0.047±0.001^{aB}
		Fencing	0.049±0.001^{cA}	0.051±0.001^{bA}	0.059±0.001^{aA}
	R_D (μmol CO_2/(m^2•s))	Grazing	1.052±0.042^{cB}	1.323±0.017^{aB}	1.141±0.013^{bB}
		Fencing	1.284±0.018^{cA}	1.490±0.042^{bA}	1.792±0.036^{aA}
	LCP (μmol photon/(m^2•s))	Grazing	23.72±0.90^{bB}	28.47±0.54^{aB}	24.34±0.77^{bB}
		Fencing	27.91±0.48^{bA}	31.53±0.92^{aA}	32.08±0.29^{aA}
	LSP_{obs} (μmol photon/(m^2•s))	Grazing	1109.40±7.10^{cB}	1193.80±3.30^{aB}	1141.80±6.40^{bB}
		Fencing	1199.40±6.30^{cA}	1256.60±7.10^{bA}	1291.20±8.70^{aA}
	R^2	Grazing	0.997	0.999	0.998
		Fencing	0.998	0.997	0.997
P. anserina	$P_{Nmaxobs}$ (μmol CO_2/(m^2•s))	Grazing	14.65±0.03^{bB}	18.39±0.06^{aB}	12.99±0.03^{cb}
		Fencing	17.90±0.04^{bA}	20.25±0.11^{aA}	15.67±0.04^{cA}
	$P_{Nmaxcal}$ (μmol CO_2/(m^2•s))	Grazing	17.24±0.05^{bB}	21.07±0.09^{aB}	14.66±0.06^{cB}
		Fencing	22.86±0.15^{bA}	24.07±0.10^{aA}	18.31±0.06^{cA}
	AQE (μmol CO_2/μmol photon)	Grazing	0.046±0.001^{bB}	0.048±0.001^{aB}	0.045±0.001^{bB}
		Fencing	0.050±0.001^{bA}	0.055±0.001^{aA}	0.048±0.001^{cA}
	R_D (μmol CO_2/(m^2•s))	Grazing	0.982±0.019^{bB}	1.511±0.018^{aB}	0.886±0.043^{cB}
		Fencing	1.343±0.023^{bA}	1.791±0.087^{aA}	1.136±0.016^{cA}
	LCP (μmol photon/(m^2•s))	Grazing	21.79±0.41^{bB}	32.99±0.47^{aB}	18.94±0.95^{cB}
		Fencing	29.83±0.87^{bA}	35.18±1.64^{aA}	24.33±0.57^{cA}
	LSP_{obs} (μmol photon/(m^2•s))	Grazing	1405.40±7.10^{bB}	1498.50±4.40^{aB}	1388.30±5.40^{cB}
		Fencing	1500.40±0.64^{bA}	1542.90±5.70^{aA}	1441.00±6.40^{cA}
	R^2	Grazing	0.998	0.999	0.997
		Fencing	0.999	0.999	0.999

Note: $P_{Nmaxobs}$, observed maximum net photosynthetic rate; $P_{Nmaxcal}$, calculated maximum net photosynthetic rate; AQE, apparent quantum efficiency; R_D, dark respiration; LCP, light compensation point; $LSP_{obs,}$ light saturation point; The abbreviations are the same as in Table 6. Mean±SD; n=6. R^2, coefficient of determination. Different uppercase letters mean significant differences for each parameter between two treatments on the same measuring date (P<0.05). Different lowercase letters mean significant differences among different observation dates for the same treatment (P<0.05).

4 Discussion

Grazing significantly decreased leaf gas exchange parameters (i.e., P_N, E, and g_s) and negatively affected the photosynthetic capacity in both *E. nutans* and *P. anserina*. Five years fencing significantly improved the photosynthetic capacity in both species. In addition, fencing increased the daily mean P_N values in both species, which is consistent with the previous research

Table 6 Analysis of differences of parameters ($P_{Nmaxobs}$, $P_{Nmaxcal}$, AQE, R_D, LCP, and LSP_{obs}) in fencing plots

Species	Treatment	Date	$P_{Nmaxobs}$/(VR)	$P_{Nmaxcal}$/(VR)	AQE/(VR)	R_D/(VR)	LCP/(VR)	LSP_{obs}/(VR)
E. nutans	Fencing	25 June	**/(25.0%)	**/(27.5%)	**/(9.7%)	**/(22.0%)	**/(17.6%)	**/(8.1%)
		23 July	**/(13.6%)	**/(10.4%)	**/(3.7%)	**/(12.7%)	**/(10.7%)	**/(5.3%)
		26 August	**/(40.8%)	**/(37.6%)	**/(23.6%)	**/(57.1%)	**/(31.8%)	**/(13.1%)
		Total	**/(26.5%)	**/(25.2%)	**/(12.4%)	**/(30.6%)	**/(20.1%)	**/(8.8%)
P. anserina	Fencing	25 June	**/(22.2%)	**/(32.5%)	**/(8.3%)	**/(36.8%)	**/(36.8%)	**/(6.7%)
		23 July	**/(10.1%)	**/(14.2%)	**/(12.7%)	**/(18.5%)	*/(6.6%)	**/(2.9%)
		26 August	**/(20.6%)	**/(24.8%)	**/(6.3%)	**/(28.3%)	**/(28.4%)	**/(3.8%)
		Total	**/(17.6%)	**/(23.9%)	**/(9.1%)	**/(27.8%)	**/(23.9%)	**/(4.5%)

Note: * means significant difference at P<0.05 level; ** means significant difference at P<0.01 level. VR, variation ratio.

results (Zhang et al., 2009; Zlatev and Fernando, 2012; Tao et al., 2015; Ren et al., 2017). However, the patterns of P_N under both regimes varying across the three observation dates were different in *E. nutans* and *P. anserina*, which was likely attributed to the different adaptions of the two species. The higher P_N values of plants in fencing plots indicated that the appropriate protective measurement could improve the photosynthetic performance and alleviate the detrimental effects of grazing pressure (Zhao et al., 2008; Zhang et al., 2013; Liu et al., 2017). The second peak of P_N, firstly discovered in our study area, appeared at approximately 17:30, which is inconsistent with previous results (Xiao et al., 2006; Liu et al., 2017), who reported that it occurred at approximately 14:00. Previous results indicated that "noon break" was related to the environmental factors (Jiang et al., 2010; Yang et al., 2016). Our result was different from those of other studies, and the difference may be attributed to the mountain environment with high temperature and high PAR during the period from 12:00 to 16:00. Our results showed that grazing significantly decreased P_N. This result was consistent with the conclusion of Ghorbani et al. (2012), who reported that grazing decreased the carbon accumulation in mountainous arid and semi-arid rangelands. Fencing increased the daily mean values of P_N, $P_{Nmaxcal}$, and $P_{Nmaxobs}$, showing that five years of fencing could enhance the potential photosynthetic capacity of *E. nutans* and *P. anserina* under natural conditions.

External stress could decrease the photosynthetic activity of plants by reducing carboxylation efficiency (e.g., stomatal closure and inhibiting light reaction) (Mudrik et al., 2003; Gu et al., 2017; Liu et al., 2017; Wang et al., 2017). The control of stomatal activity (i.e., transpiration, opening, and closure) is an active adaptive pattern of pasture species in response to environmental stress in semi-arid regions (Xoconostle-Cazares et al., 2010; Wu et al., 2015). Stomatal closure is the first response of grass species to external stress, such as mild to moderate drought stress. However, nonstomatal limitation factors dominate under severe drought stress (Flexas and Medrano, 2002; Jia et al., 2012; Wang et al., 2015; Abdi et al., 2016). Farquhar and Sharkey (1982) demonstrated that the stomatal factor is the dominant limiting factor of photosynthetic capacity only if L_s increases and P_N and C_i simultaneously decrease. Otherwise, nonstomatal factors are the limiting and dominant factors of photosynthetic capacity. In our study, the reduction in the P_N values of *P. anserina* under fencing and grazing conditions was caused by stomatal limitation. However, the decreases in the P_N and L_s of *E. nutans* were accompanied by an increase in C_i from 13:00 to 16:00, indicating that nonstomatal factors are the limiting factors for the photosynthetic capacity. The difference in the photosynthetic capacities of the two species might be caused by g_s and environmental factors. *P. anserina* has conspicuously higher g_s values than *E. nutans*, hence, *P. anserina* is less sensitive to external stress than *E. nutans*. Nonstomatal limitation for *E. nutans* during the period of 13:00 to 16:00 might be also caused by high air temperature and radiation. Some studies have shown that the change in P_N induced by stomatal limitation is often caused by environmental factors (Xia et al., 2015; Urban et al., 2017), and some studies pointed that extreme environmental factors might act as nonstomatal limitation factors for photosynthetic capacity (Borchard et al., 2015; Erel et al., 2015; Fu et al., 2015; Ramalhosa et al., 2017).

WUE is an index of plant growth performance in the presence of any environmental constraint (Guo et al., 2011; Acuña et al., 2015; Elazab et al., 2016). In the study, the daily mean WUE of the two species was higher in fencing plot than in grazing plot. However, the variation in daily mean WUE for both plant species under fencing and grazing conditions was greater on 25 June and 26 August than on 23 July. This finding may be attributed to higher rainfall during July than other months. By comparing the WUE of the two species under both regimes, we inferred that grazing might affect photosynthetic capacity and subsequently affect the normal growth of grass.

The P_N-PAR response curves of the plants were accurately fitted by the NRH with high R^2 values. Parameters were obtained from the fitted equations. AQE, an estimate of the maximum efficiency of light harvesting during CO_2 assimilation (Linkosalo et al., 2016; Liu et al., 2017), was significantly higher in fencing plot than in grazing plot. And other parameters were also significantly increased under fencing treatment, which in turn improve the photosynthetic capability of the two species. Whereas, grazing significantly decreased the photosynthetic capability of herbages in study area.

R_D and LCP play critical roles in decreasing plant biomass accumulation in the individual, community, and ecosystem levels (Qiao et al., 2007; Zhang et al., 2015; Zhu et al., 2016). In our study, plants have higher R_D, LCP, and LSP_{obs} in fencing plot than in grazing plot. The relative increases in R_D and LCP were smaller than that in LSP_{obs} in plants in fencing plot, indicating that fencing enhanced CO_2 and H_2O assimilations (Table 5). Thus, the increased assimilations could promote plant productivity and growth (Yin et al., 2006; Wu et al., 2008; Augé et al., 2015; Reef et al., 2015). This is consistent with our results that P_N was significantly higher in fencing plot than in grazing plot.

5 Conclusions

The diurnal patterns of leaf gas exchange parameters showed that five years of fencing significantly increased the photosynthetic parameters values of *E. nutans* and *P. anserina*, which increased the photosynthetic capacity. The enhanced effects were more sensitivity in *E. nutans* than *P. anserina* with five years of fencing, particularly at the end of the growing season. Hence, five years of fencing improved the potential photosynthetic capacity of both *E. nutans* and *P. anserina*. Our result provides a new insight in the grassland protection and gives grassland managers theory supporting for decision-making. However, our result should be further validated by data collected from different plant species that grow under different environments, particularly under environments that had been subjected to different periods of restricted grazing.

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