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Effects of temporal variation and grazing intensity on leaf C:N:P stoichiometry in Northwest desert, China

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Abstract: The *Seriphidium transiliense* desert pasture is an important spring-autumn pasture in northern Xinjiang, China, and has been subjected to grazing by livestock at different intensities, thus resulting in widespread deterioration of its biodiversity and ecosystem services. To understand the response mechanism of stoichiometric characteristics of desert vegetation to grazing, the leaf carbon (C), nitrogen (N), phosphorus (P) and C:N:P ratios of *S. transiliense* were studied under different grazing intensities. The results show that the control *S. transiliense* leaf C, N and P contents and C:N, C:P and N:P ratios were 458.79 ± 53.5 g/kg, 20.6 ± 7.18 g/kg, 2.83 ± 1.24 g/kg, 25.69 ± 11.08, 190.28 ± 75.65 and 8.21 ± 4.01, respectively. The differences in these characteristics varied with grazing intensity in accordance with sampling time, so both factors need to be considered comprehensively. General linear model (GLM) analysis indicated that grazing intensity had a strong main effect on *S. transiliense* leaf C, N, and P content, C:N ratio and N:P ratio. As grazing intensity increased, the leaf N content and N:P ratio increased ($P < 0.01$), and the C:N ratio decreased ($P < 0.01$). N content was the limiting factor for the growth of *S. transiliense*, but the grazing intensity, sampling year and growth season each affected the degree of N limitation. Our findings suggest that the remaining moderate stocking rate was essential for sustaining desert stabilisation in Xinjiang, and although *S. transiliense* could adapt its nutrient content and leaf stoichiometry to the grazing intensity, N was always the limiting element for the growth of *S. transiliense*.

Keywords: plant growth rate; cycling; nutrition; grassland; *Artemisia* deserts

Carbon (C), nitrogen (N) and phosphorus (P) are the elements necessary for plant growth and development. They are major participants in a plant's physiological mechanisms (Han et al. 2005, Niklas et al. 2005, Xiang et al. 2006, Sistla et al. 2012, Li et al. 2017). The stoichiometric ratio of C, N and P explains a plant's strategy of ecological adaptation (Agren 2004, Liu et al. 2010, Yang et al. 2012). The C:N and C:P ratios reflect the plant growth rate and the absorbance efficiency of N and P (Agren 2004), and the N:P ratio is the key factor restricting plant growth (Liu et al. 2010, Yang et al. 2012). Therefore, patterns of C, N and P concentrations and stoichiometry in plant biomass, and especially in the leaf, which is one of the organs most sensitive to external disturbance, have been studied intensively (Han et al. 2005, Niklas et al. 2005, Agren and Weih 2012, Li et al. 2017).

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Previous studies have revealed that plant C, N and P contents relate to numerous abiotic and biotic factors, including plant growth stage (Elser et al. 2000), grazing (Zheng et al. 2012, Zhang et al. 2014), and plant functional traits (Reich et al. 1999). As such, studies often investigate the changes in N, C and P in accordance with a single ecological factor at the regional scale or in one habitat (Niu et al. 2013, Hu et al. 2014). Most previous studies have focused on steppe or meadow habitats; few have considered the desert. Many studies also have ignored the effect of sampling time, which can change the stoichiometry significantly (Zhang et al. 2013). Additionally, it is accepted that grazing significantly affects aboveground productivity, community characteristics, community structure and nutrient state (Takehiro et al. 2008, Deng et al. 2014, Yang et al. 2018), but the effects of grazing on ecosystem C, N and P cycling have yet to be agreed upon. For instance, concerning N cycling, some studies have indicated that livestock grazing augments N concentration and accelerates N cycling (McNaughton et al. 1997, Gao et al. 2008). This posits that livestock grazing deposits urine and faeces to increase soil available N and that it stimulates N mineralisation and utilisation by plants, which enhances shoot nutrients (Zheng et al. 2012). On the contrary, some other studies have demonstrated that grazing reduces N cycling (Ritchie et al. 1998). These put forward that herbivores restrict the growth of N-rich and palatable species due to livestock selectivity, thus increasing the dominance of non-palatable or N-poor species. This slows N utilisation and reduces shoot nutrient content. Previous studies have indicated that the N:P ratio of leaves in plant biomass can reflect the status of community functioning and nutrient limitation (Han et al. 2005). An N:P ratio > 16 suggests P limitation, whereas a ratio < 14 indicates N limitation (Wang and Moore 2014, Hu et al. 2018). Therefore, measuring C, N and P concentrations and stoichiometry in plant leaves can not only indicate which elements limit plant growth and the state of nutrient utilisation (Cheng et al. 2016), but it can also inform our understanding of the dynamics and functioning of the grassland ecosystem (Tang et al. 2016).

The *Seriphidium transilient* desert, widely distributed in the low hills and plains (altitude 500~1 700 m a.s.l.) of the northern Tianshan Mountains, is an important composition of Xinjiang desert pasture and occupies 114.25 ×104 hectares. This desert is utilised mainly as spring-autumn pasture in northern Xinjiang, China and plays an important role in windbreak and sand fixation, biodiversity conservation and maintaining the ecological balance of the mountain-desert-oasis system (Zhu et al. 2013, Dong et al. 2017). Because of continuous overgrazing over the past few decades, the degradation of *S. transiliense* desert pasture is very serious, and it has become the frontier of grassland degradation in Xinjiang (Zhu et al. 2013). There is an urgent need to discuss the response mechanisms of plants and soil in *S. transiliense* desert pasture under grazing intensity in order to implement restoration efforts in the degraded desert pasture. Although many studies on *S. transiliense* have focused on eco-physiology, module biomass and its allocation, storage substance and regrowth ability, and seedling spatial distribution under grazing (Zhu et al. 2013), an understanding on how grazing intensity affects the stoichiometric characteristics of C, N and P has yet to be developed. In this study, we hypothesised that grazing intensity and sampling time could alter the leaf C, N and P contents and their stoichiometry. Hence, we examined the effects of grazing intensity on the leaf C, N, and P content and stoichiometry in *S. transiliense* from 2012~2014, aiming to answer the following specific scientific questions: (1) What were the leaf C, N, and P contents and their stoichiometry in *S. transiliense* in general, and which element restricted its growth? (2) How were the changes in stoichiometric characteristics of *S. transiliense* related to grazing intensity, and was grazing intensity able to change the limiting nutrient?

MATERIAL AND METHODS

Study area. The study was conducted in the Kazakh ethnic township of Ashili in Changji City (43°49'–43°56'N, 87°02'–87°05'E, 804~833 m a.s.l.), which is located in the typical desert region of Xinjiang pasture in the middle of the northern slope of Tianshan Mountain, northwest China. It has a typical temperate continental arid climate. The average annual temperatures were 2.7, 3.9, and 2.9 °C, and the average annual precipitation was 285, 294, and 295 mm, respectively, in 2012, 2013, and 2014. The mean annual sunshine duration is 2 833 hours. The annual evaporation is 1 760 mm, and the annual frost-free day count is 160–190 days. The soil type is grey desert soil, according to FAO/UNESCO taxonomy, and the depth of the soil layer is > 1 m. The organic carbon, total nitrogen, total phosphorus and total potassium

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content in the 0–30 cm soil layer are 4.85, 0.57, 1.01 and 14.17 g/kg, respectively. According to previous research, there was no significant difference in soil carbon, nitrogen, and phosphorus under different grazing intensities (Wang 2007). The experimental plot was the typical *Artemisia* deserts, where the dominant species were *S. transiliense* Poljak., *Petrosimonia sibirica* (Pall.) Bge., *Ceratocarpus arenarius* L. and *Kochia prostrate* (L.) Schrad and the accompanying species were *Nanophyton erinaceum* (Pall.) Bge., *Arnebia guttata* Bge., *Ceratocephalus orthoceras* (Crantz) Bess. and *Tetracme quadricornis* (Steph) Bge. The *Artemisia* deserts have been grazed by Xinjiang fine-wool sheep mainly in spring and autumn each year, and the habitat has been significantly degraded.

Experimental design. According to the norm of the relationship between the succession stage and grazing intensity on pasture (Ren 1998), as well as the degraded norm of *S. transiliense* desert pasture (Jin 2009), we performed the study in the field in May 2012, and four treatments (Table 1) were established based on a survey of *S. transiliense* desert pasture; ungrazed (UG), light grazing (LG), moderate grazing (MG) and heavy grazing (HG). Each grazing intensity plot was divided into three subplots to represent three replicates. The grazing intensity was calculated as the number of Xinjiang fine-wool sheep times their occupied grazing pasture area. All grazing intensities have been consistent for at least the past 10 years. Most plots of different grazing intensities had similar topography, altitude and initial condition. Continuous sheep grazing was maintained from April to June and September to October.

Field investigation, sampling and measurements. Field sampling was carried out in May and July, from 2012 to 2014. May and July, respectively, represent the peak growing and grazing times during the spring grazing period. In each subplot, 15 individuals of *S. transiliense* were selected randomly, with a distance of 1.5 m to 2.0 m maintained between adjacent individuals. Next, fully expanded and mature leaves were picked and mixed to form a single sample. The samples were brought back to the lab in a portable low-temperature refrigerator kept at 4 °C. Sampled leaves were oven-dried at 105 °C for 10 min and then at 65 °C for 48 h. Dried samples were ground into a uniformly fine powder and passed through a 0.25 mm sieve before the C, N and P contents were analysed.

The concentration of organic carbon (TOC) was determined *via* the combustion oxidation process method using an Elementary Vario TOC analyser (Elementar Analysen GmbH, Hanau, Germany). The concentration of total nitrogen (TN) was measured *via* the Kjeldahl method (Keeney and Bremner 1966) using a Kjeldahl Auto-Analyser (K9860 Jinan, China). The concentration of phosphorus (TP) was determined with $HClO_4$-H_2SO_4 (Bao 2005) using a spectrophotometer (722 types, Shanghai, China) at 660 nm. The stoichiometric ratios of C, N, and P were calculated as TOC *vs.* TN (C:N), TOC *vs.* TP (C:P), and TN *vs.*TP (N:P).

Data analysis. The differences in C, N, P and C:N:P ratios of *S. transiliense* leaves among different grazing intensities on the same sampling date were analysed using one-way repeated measures ANOVAs in SPSS 21 software (IBM, Chicago, USA) with the Duncan post hoc tests of significance (IBM, Armonk, USA),

Table 1. Grazing intensity and its community characteristics

Item	Ungrazing	Light grazing	Middle grazing	Heavy grazing
Community type	*Seriphidium transiliense, Ceratocarpus arenarius*	*S. transiliense, C. arenarius, Petrosimonia sibirica*	*S. transiliense, C. arenarius, Kochia prostrata*	*S. transiliense, C. arenarius, Ceratocephalus orthoceras*
Longitude and latitude	87°3.7', 43°54.3'	87°4.7', 43°52.7'	87°5.1', 43°53.3'	87°3.8', 43°52.1'
Elevation (m a.s.l.)	810	830	804	820
Coverage (%)*	59.8	38.1	32.3	26.3
Average height (cm)*	37.5	6.8	7.2	4.1
Aboveground biomass (g/m^2)*	382.1	108.4	107.8	78.3
Plot area (ha)	15.0	51.7	52.7	30.8
Sheep numbers (head)	0	32	50	89
Grazing intensity (sheep/ha)	0	0.56	0.95	2.89

*Data was the means of 2012, 2013, and 2014, which was measured in May

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Table 2. Descriptive statistical parameters of carbon (C), nitrogen (N) and phosphorus (P) contents and C:N, C:P and N:P of *Seriphidium transiliense*

Parameter	Range	Minimum	Maximum	Mean	Standard deviation	Coefficient of variation
P (g/kg)	6.56	1.09	7.65	2.83	1.24	0.44
N (g/kg)	26.76	7.49	34.25	20.60	7.18	0.35
C (g/kg)	235.38	328.73	564.11	458.79	53.50	0.12
C:P	366.76	55.03	421.80	190.28	75.65	0.40
C:N	49.03	13.10	62.13	25.69	11.08	0.43
N:P	21.02	2.58	23.60	8.21	4.01	0.49

and the results are expressed as "mean ± standard error of the mean".

We used the general linear model (GLM) multivariate analysis of variance to test for overall differences in group means of the compositional data between the experimental treatments in 2012, 2013 and 2014, thus analysing the effects of grazing intensity, sample month, sample year and the interaction between them. We tested whether there was any effect of grazing intensity (four-factor levels), sample month (two-factor levels), sample year (three-factor levels), or their interaction on C, N, P and C:N:P ratios of *S. transiliense* leaves using repeated measures analysis of variance (ANOVA) models (SPSS 21.0, IBM, Armonk, USA). At the same time, we analysed the relationships among C, N, P, C:N, C:P, N:P and grazing intensity with a double tail test for bi-variate Pearson correlation analysis.

The coefficient of variation (*CV*) was calculated using the formulary model *CV* = standard deviation multiplied and divided by the means.

RESULTS

C, N and P concentrations and stoichiometry of leaf. The maximum C, N, and P concentrations of *S. transiliense* leaves were 564.11, 34.25, 7.65 g/kg, and the minimums were 328.73, 7.49, and 1.09 g/kg, respectively (Table 2). The maximum C:N, C:P, and N:P ratios were 62.13, 421.80, 23.60, and the minimums were 13.10, 55.03, and 2.58, respectively. These results were likely to correlate with sampling time and grazing intensity. The average N:P ratio (8.21) was less than 14, which suggests that growth was mainly limited by N. The variation coefficients for C, N, P, C:N, C:P and N:P ranged from 0.12 to 0.49, meaning there was medium variation. In other words, the C concentration was higher than that of the N and P concentrations, and the N concentration was higher than the P concentration. The *CV* of P was higher than that of N and C, which suggests that P was relatively unstable.

Effects of grazing intensity, sample month and sample year on leaf C, N and P concentrations and stoichiometry. General linear model analysis indicated significant effects of grazing intensity on leaf C, N, and P concentrations, C:N and N:P ratios (Table 3; $P < 0.05$). Sample year and sample month also significantly impacted leaf N concentration and C:N ratio, and sample month also significantly affected P concentration and C:P ratio. Sample year significantly affected C concentration and N:P ratio

Table 3. General linear model analysis of leaves carbon (C), nitrogen (N) and phosphorus (P) contents and stoichiometry among grazing intensity, year, and month

Factor	C content		N content		P content		C:N		C:P		N:P	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Grazing intensity (G)	12.93	0.000	10.95	0.000	3.05	0.037	3.51	0.023	1.97	0.130	2.84	0.048
Month (M)	0.02	0.901	68.49	0.000	22.53	0.000	22.62	0.000	23.35	0.000	0.05	0.945
Year (Y)	15.15	0.000	82.20	0.000	2.28	0.114	84.14	0.000	1.98	0.150	8.28	0.001
G × Y × M	1.00	0.435	3.71	0.004	2.55	0.032	5.05	0.000	1.84	0.111	0.74	0.622
G × M	1.91	0.140	0.88	0.458	5.90	0.002	1.65	0.185	4.97	0.004	2.28	0.091
G × Y	2.15	0.064	1.64	0.157	3.20	0.010	1.49	0.210	3.07	0.013	1.49	0.202
Y × M	7.33	0.002	4.21	0.021	2.50	0.093	0.71	0.453	1.08	0.347	0.93	0.401

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(Table 3; $P < 0.01$). There were obvious interactions between grazing intensity, sample month and sample year for leaf N and P concentrations and C:N ratio ($P < 0.05$). Significant interactions existed between grazing intensity and sample month and grazing intensity and sample year for P content and C:P ratio ($P < 0.05$), while the interaction between sample year and sample month significantly affected C and N content ($P < 0.05$).

The effects of grazing intensity on leaf C, N and P concentrations and stoichiometry. As grazing intensity increased, the P concentration of *S. transiliense* followed a V-shaped pattern, where P concentration was significantly lower at MG than at UG and LG (Figure 1A; $P < 0.05$). Compared to UG, the N concentration decreased significantly by 21.6, 22.3, and 15.2% in LG, MG and HG, respectively (Figure 1B; $P < 0.05$), and the C concentration decreased by 9.9, 12.5, and 13.2%, respectively (Figure 1C; $P < 0.05$). The maximum values of C:N appeared in LG and MG (27.6 and 27.4) and were 23.0% and 22.1% higher than in UG (Figure 1E; $P < 0.05$). Additionally, the N:P ratio was less than 14 fluctuated in a "down-up-down" pattern as grazing intensity increased. UG and MG had a significantly higher N:P ratio than LG (Figure 1F; $P < 0.05$).

Interannual dynamics of leaf C, N and P concentrations and stoichiometry. The responses of *S. transiliense* leaf C, N and P concentrations and stoichiometry to interannual dynamics were examined in different years (2012~2014), and the results are shown in Figure 2. The P concentration did not differ obviously with year (Figure 2A; $P > 0.05$), but the N concentrations in 2013 and 2014 were 78.6% and 68.7% higher than in 2012, re-

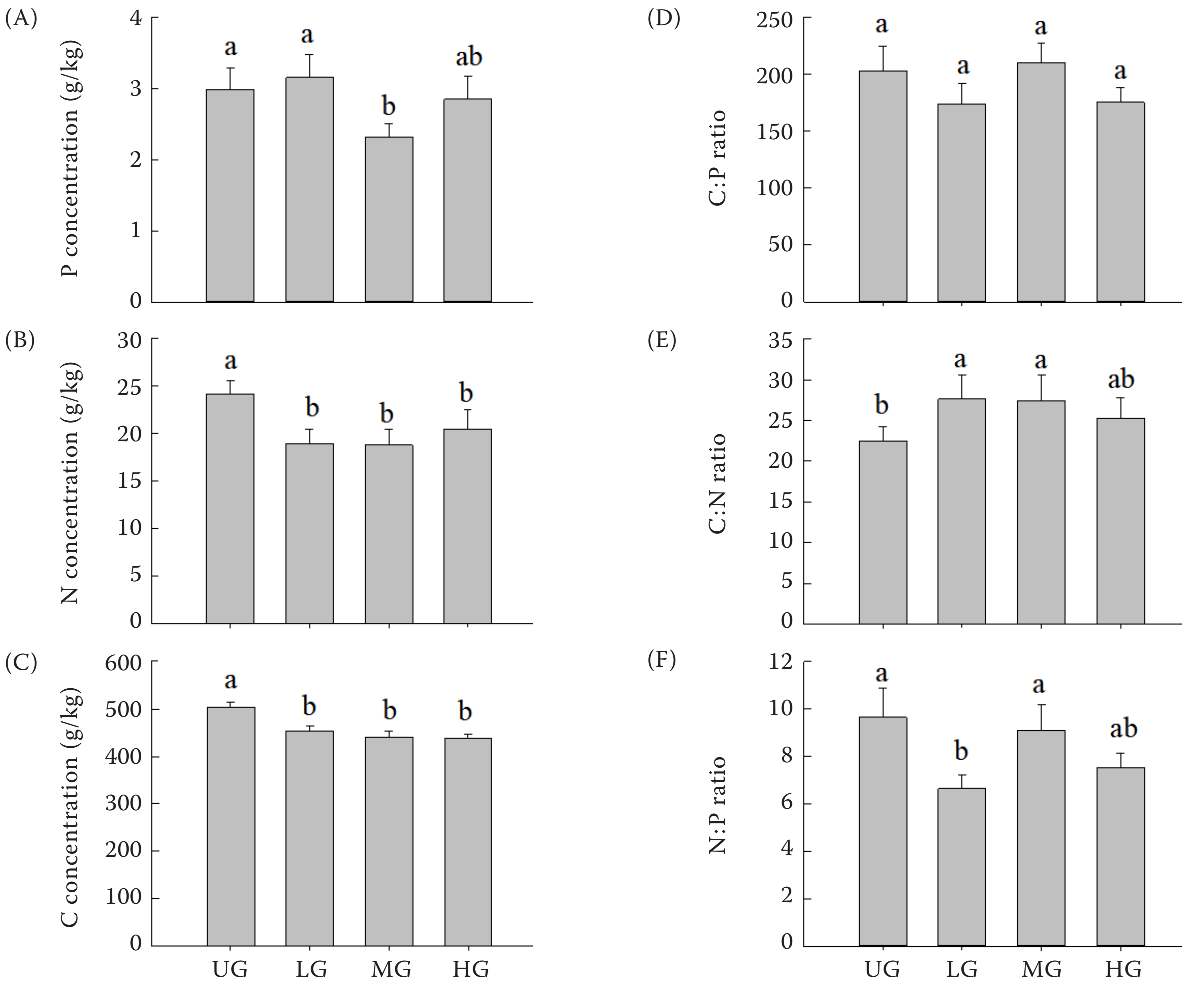

Figure 1. The response of the desert's carbon (C), nitrogen (N) and phosphorus (P) contents (A–C) and stoichiometry (D–F) to different grazing intensities. Different lowercase indicated significant differences among differences in the same years at the 0.05 level. UG – non-grazing; LG – lightly grazing; MG – moderately grazing; HG – heavily grazing

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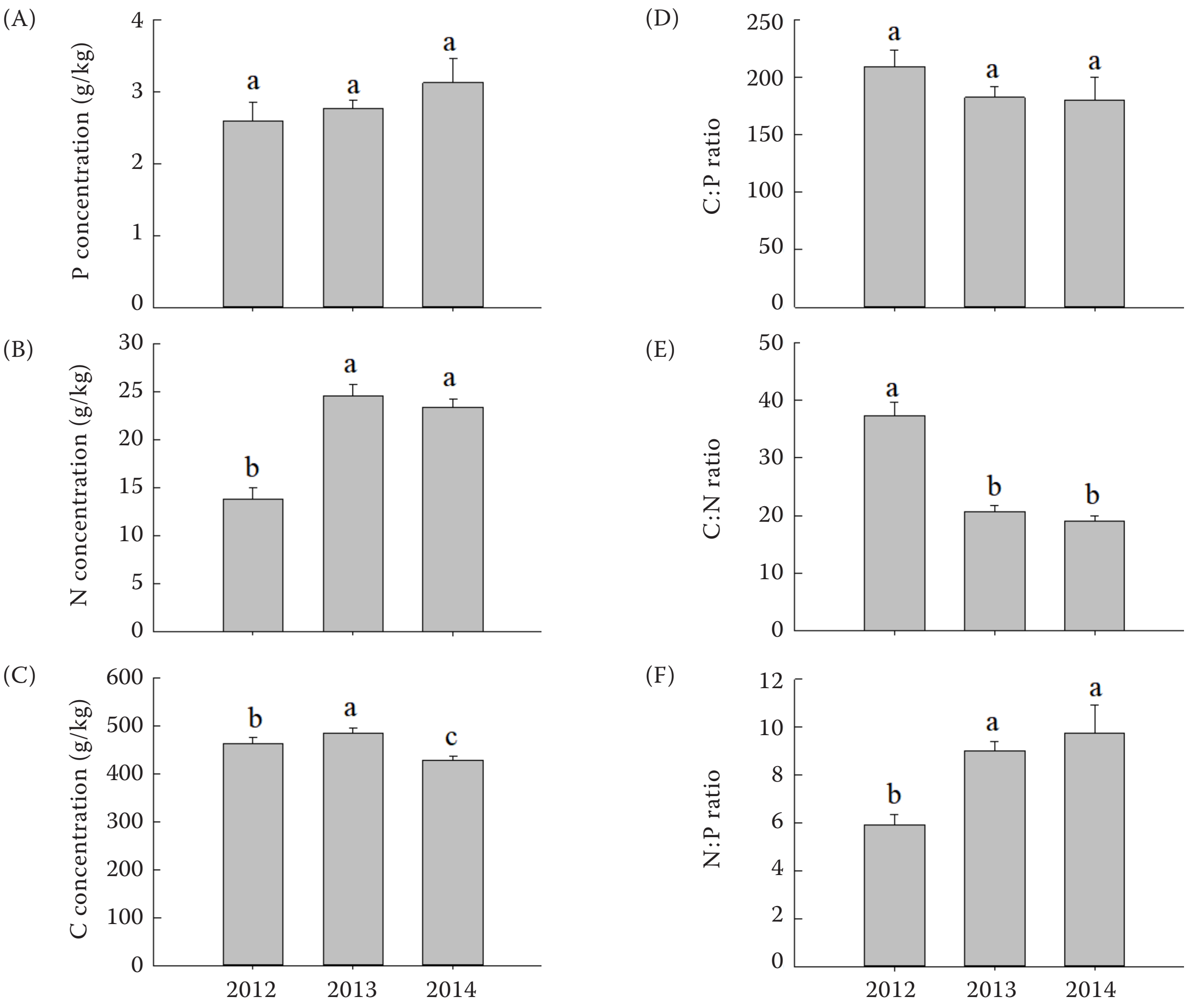

Figure 2. Interannual change of carbon (C), nitrogen (N) and phosphorus (P) contents (A–C) and stoichiometry (D–F) of the desert. Different lowercase indicated significant differences in the same years at the 0.05 level

spectively (Figure 2B; $P < 0.05$), and the C concentration was higher in 2013 than in 2012 and 2014 (Figure 2C; $P < 0.05$). The response of the C:N ratio to sample year was not significant (Figure 2D; $P > 0.05$), and the C:N ratios in 2013 and 2014 were 44.7% and 49.2% lower than in 2012 (Figure 2E; $P < 0.05$), whereas the N:P ratios in 2013 and 2014 were 52.5% and 65.1% higher than in 2012, respectively (Figure 2F; $P < 0.05$).

Seasonal dynamics of leaf C, N and P concentrations and stoichiometry. The P and N concentrations were 29.5% and 26.4% significantly higher in July than in May (Figure 3A, B; $P < 0.05$), whereas the C concentration did not differ between May and July (Figure 3C; $P > 0.05$). Additionally, the C:P and C:N ratios were 40.6% and 26.9%, significantly lower in May than in July (Figure 3D, E; $P < 0.05$), but the N:P ratio did not differ between May and July (Figure 3F; $P > 0.05$).

Correlation analysis. Correlation analysis showed that grazing intensity had a strong, positive correlation with leaf N content and the N:P ratio (Table 4; $P < 0.01$), but it had a strong negative correlation with the C:N ratio, which indicates that N content increased as grazing intensity increased, thus raising the N:P ratio and reducing the C:P ratio. In addition, there was a strong, positive correlation between N and P content, and the N:P ratio had a close positive relationship with N content and the C:P ratio ($P < 0.01$). In contrast, it negatively correlated with P content and the C:N ratio ($P < 0.01$).

DISCUSSION

The response of leaf C, N and P concentrations and stoichiometry to grazing. External interference affects the physiological and ecological processes of

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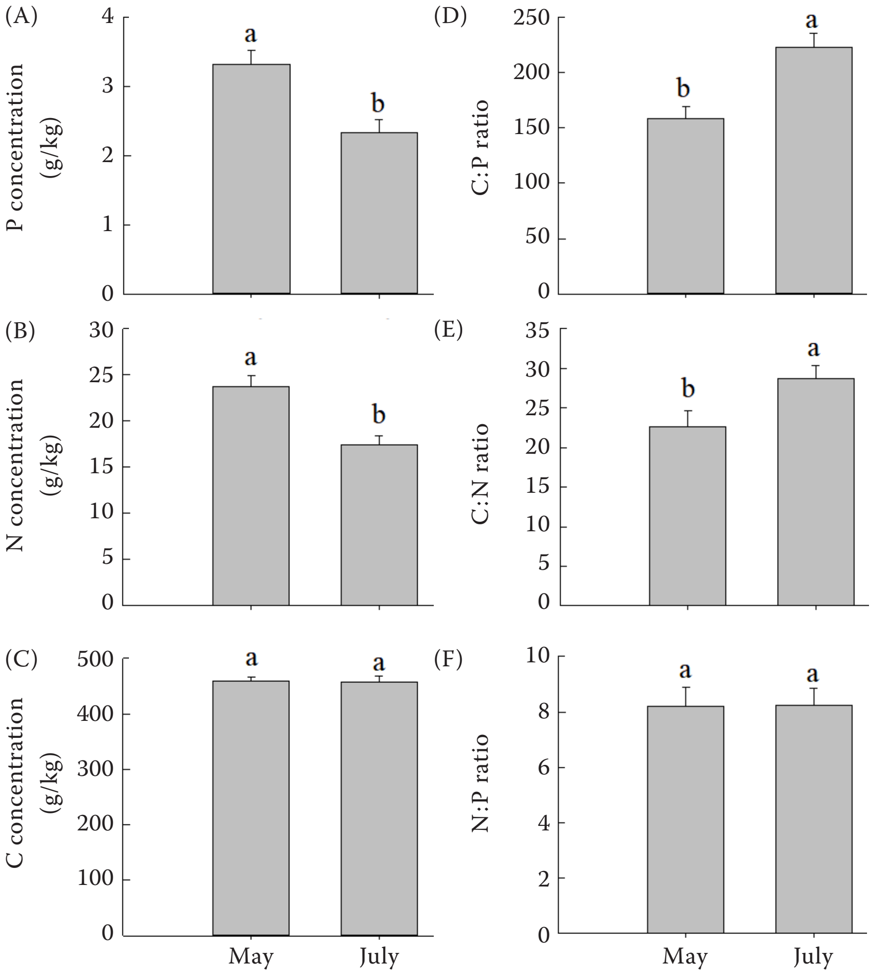

Figure 3. The seasonal variation of carbon (C), nitrogen (N) and phosphorus (P) contents (A–C) and stoichiometry (D–F) of the desert to different grazing intensities. Different lowercase indicated significant differences among differences in the same years at the 0.05 level

plant C and N elements during acquisition, transportation, distribution and storage (Rouphael et al. 2012). Similar to the results of Yang et al. (2018) and Bardgett et al. (1998), where grazing by livestock was found to enhance the plant P concentrations in natural grassland, we also observed similar P concentration results in the LG grazing treatment (Figure 1A), but there was no significant difference in P concentrations between LG and UG. This may be because grazed plants restore photosynthetic capacity to compensate for the overall reduction in photosynthesis caused by leaf loss (Zhang et al. 2015). However, the leaf P concentration was lower in MG and HG plots than in UG and LG plots (Figure 1A). Variation in the leaf P concentration was mainly attributed to the greater grazing pressure that lowered

Table 4. Correlation analysis of grazing intensity, carbon (C), nitrogen (N) and phosphorus (P) contents and stoichiometry

Index	N	C	C:P	C:N	N:P	Grazing intensity
P	0.257*	–0.010	–0.858**	–0.264*	–0.536**	–0.210
N		0.200	–0.243*	–0.896**	0.513**	0.537**
C			0.210	0.030	0.100	–0.190
C:P				0.296*	0.626**	–0.010
C:N					–0.473**	–0.510**
N:P						0.679**

* and ** showed significant differences among grazing intensity, C, N and P contents and stoichiometry at 0.05 level and 0.01 levels, respectively

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the soil moisture and restricted the adsorption and dissolution of inorganic P (Belnap 2011), thus causing plants in the MG and HG treatments to absorb less P from the soil (Wang et al. 2018).

The present study also found that grazing reduced the *S. transiliense* leaf C concentration, with the reduction rate declining as grazing intensity increased in the grazed plots (Figure 1C). In grazing grassland ecosystems, livestock directly affects vegetation leaves by feeding and trampling (Wan et al. 2011). The resulting reduction in leaf area and transpiration enhances the dilution of C concentration. In the end, the leaf C content decreases (Wang et al. 2018). Grazing by livestock removes much of the above-ground biomass (An and Li 2015), stimulates plant regrowth and reproduction, and reduces leaf C concentration, thus implying that the photosynthetic rate increases and the plant growth rate accelerates to compensate for the removed vegetation. Our findings did not accord with those of Yang et al. (2018), who found that the shoot C content increased as grazing intensity increased. The difference between leaves and shoots in how C content varied in the treatments was probably due to the increased proportion of C in the young leaves when the abundance of old leaves was reduced due to grazing, though the total area and weight of young leaves did increase with increased grazing. Additionally, in our study, the leaf N concentration was lower in grazed plots than in the UG plot (Figure 1B), and a similar pattern was found with leaf C concentration, thus implying that C and N were coupled in grazing processes.

C, N and P stoichiometry is a vital characteristic of ecosystem processes and functions (Wang et al. 2018), reflecting the dynamics of C accumulation and the pattern of N and P nutrient limitation, as well as revealing the relationship between plant growth rate and nutrient distribution (Zhang et al. 2016). C:N and C:P represent the efficiency of C sequestration by indicating the C assimilation efficiency of plants during the nutrient absorption process and reflecting their nutrient use efficiency after absorption (Wang et al. 2014). A key finding of our study is that the leaf C:N ratios were higher at lower-level grazing intensities (LG and MG) than in the UG plot (Figure 1E). This indicates that light and moderate grazing increases N utilisation efficiency, thus enhancing plant leaf C sequestration efficiency. This characteristic is favourable for resisting harsh environments (Wang et al. 2018). In the HG plot, in contrast, the leaf C:N ratio decreased (Figure 1E). This result was mainly because heavy grazing seriously increased N uptake and transportation to the young leaves in plants, thus increasing the N concentration overall. Plants maintain metabolic activity by increasing N utilisation efficiency. In addition, the leaf C:P ratios followed a twin peaks pattern ("down-up-down") in our study, although there was no significant difference between the UG and the grazed plots (Figure 1D; $P > 0.05$). This indicates that P was more sensitive to grazing than N, and the C:P ratio was consistent.

Although plants can meet their growth needs through their nutrient transfer (Chen et al. 2015), the N:P ratio is a key index for determining plant productivity when limited by nutritional elements (Yuan et al. 2011, Wang et al. 2017), mainly soil N and P. Such relationships vary according to changes in the external environment (Goddert et al. 2010). The present study shows that the N:P ratio decreased significantly more in lower-level grazing than in the UG plot (Figure 1F; $P < 0.05$). Further, the N:P ratio < 14 in all treatments implies that the effects of N restriction on leaf growth were enhanced under grazing. Additionally, the leaf N:P ratio increased significantly at first (Figure 1F; $P < 0.05$) and then decreased slightly ($P > 0.05$) along the grazing intensity gradient from LG to HG. These findings indicate that N restriction's effect on leaf growth was smaller in the MG plot and greater in the HG plot. Probably because of the lack of N fertiliser in *Seriphidium* desert soil, most plants in that habitat are restricted in their growth by the N element. Moreover, the distribution and concentration of leaf P were reduced in the MG plot, which alleviated the effects of N restriction on leaf growth.

Temporal variation of plant leaf C, N, and P contents and stoichiometry. In the arid *Seriphidium* desert, water was the most pivotal factor limiting plant growth (Li et al. 2017). Higher moisture content leads to more available soil nutrients, and the nutrient contents of plant organs are regulated by soil N and P concentration. The present study showed that leaf P concentration slightly increased from 2012 to 2014 (Figure 2A; $P > 0.05$), but the N concentrations were significantly higher in 2013 and 2014 than in 2012, and the C concentrations were significantly higher in 2012 and 2013 than in 2014 (Figure 2B, C; $P < 0.05$). The variation in leaf C, N and P concentrations was mainly due to the variation in mean annual precipitation in different years. The precipitation was higher than average in 2013, but in 2012, it was lower than average in the warm season, thus resulting in greater availability of soil nutrients and the promotion of nutrient transpor-

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tation, especially of the C and N elements, from soil to vegetative organs. In addition, we also found that the leaf C:P (Figure 2D; $P > 0.05$) and C:N ratios (Figure 2E; $P < 0.05$) were higher in 2012 than in 2013 and 2014. The increase in C:P and C:N ratios implies that the photosynthetic rate decreased and the plant growth rate slowed. P and N content accumulated in leaves 2012 enhanced the species' defence ability against harsh external environments. Another key finding in our study was that the leaf N:P ratio < 14 in all sampling years was lower in 2012 than in 2013 and 2014. This finding indicates that N limits plant growth and that the effect of N limitation increases during a drought year (2012).

For a single species, the content of structural substances unaffected by development or the environment is relatively stable. However, the content of functional and storage substances is greatly influenced by a plant's environment and growth stage (Kerkhoff et al. 2016, Li et al. 2017). The content of elements is closely related to a plant's structural characteristics and growth rhythm (Aerts and Iii 2000). The present study indicates that the leaf P and N concentrations were higher in May than in July (Figure 3A, B; $P < 0.05$) and that the C:N and C:P ratios were lower in May than in July (Figure 3D, E; $P < 0.05$). This suggests that the N and P concentrations and stoichiometry relate to grazing intensity and sampling month. In May, *S. transiliense* was in the vegetative growth stage, and the proportion of functional substances in the plant was relatively large. Hence, the leaf N and P contents were higher in May. However, the proportion of structural substances in the plants increased with the duration of the growing season (July), and the N and P contents were reduced due to dilution with the increase in aboveground biomass (Li et al. 2017). In addition, the leaf C concentration and N:P ratio did not differ significantly between May and July (Figure 3C, E; $P > 0.05$), meaning that they were not related to the sampling month (Table 3).

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