

Leaf N and P stoichiometry of 57 plant species in the Karamori Mountain Ungulate Nature Reserve, Xinjiang, China

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Abstract: Nitrogen (N) and phosphorus (P) are the major nutrients that constrain plant growth and development, as well as the structure and function of ecosystems. Hence, leaf N and P patterns can contribute to a deep understanding of plant nutrient status, nutrient limitation type of ecosystems, plant life-history strategy and differentiation of functional groups. However, the status and pattern of leaf N and P stoichiometry in N-deficiency desert ecosystems remain unclear. Under this context, the leaf samples from 57 plant species in the Karamori Mountain Ungulate Nature Reserve, eastern Junggar Desert, China were investigated and the patterns and interrelations of leaf N and P were comparatively analyzed. The results showed that the average leaf N concentration, P concentration, and N:P ratio were 30.81 mg/g, 1.77 mg/g and 17.72, respectively. This study found that the leaf N concentration and N:P ratio were significantly higher than those of studies conducted at global, national and regional scales; however, the leaf P concentration was at moderate level. Leaf N concentration was allometrically correlated with leaf P and N:P ratio across all species. Leaf N, P concentrations and N:P ratio differed to a certain extent among plant functional groups. C₄ plants and shrubs, particularly shrubs with assimilative branches, showed an obviously lower P concentration than those of C₃ plants, herbs and shrubs without assimilative branches. Shrubs with assimilative branches also had lower N concentration. Fabaceae plants had the highest leaf N, P concentrations (as well as Asteraceae) and N:P ratio; other families had a similar N, P-stoichiometry. The soil in this study was characterized by a lack of N (total N:P ratio was 0.605), but had high N availability compared with P (i.e. the available N:P ratio was 1.86). This might explain why plant leaves had high N concentration (leaf N:P ratio>16). In conclusion, the desert plants in the extreme environment in this study have formed their intrinsic and special stoichiometric characteristics in relation to their life-history strategy.

Keywords: leaf stoichiometry; desert plant; functional group; nutrient limitation; Junggar Desert; Karamori Mountain

Citation: TAO Ye, WU Ganlin, ZHANG Yuanming, ZHOU Xiaobing. 2016. Leaf N and P stoichiometry of 57 plant species in the Karamori Mountain Ungulate Nature Reserve, Xinjiang, China. *Journal of Arid Land*, 8(6): 935–947. doi: 10.1007/s40333-016-0019-6

Nitrogen (N) and phosphorus (P) are the basic components of all organisms. They are the major nutrients that constrain plant growth, and they play vital roles in plant functioning (Koerselman and Meuleman, 1996; Elser, 2000; Elser et al., 2000; Güsewell, 2004; Hedin, 2004). N and P also limit

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Received 2016-01-23; revised 2016-05-20; accepted 2016-05-25

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some processes in ecosystems, such as nutrient cycle, species distribution and community succession (Whittaker et al., 1979; Reich and Oleksyn, 2004; Niklas et al., 2005; Sasaki et al., 2010). Accordingly, the patterns of N and P status and their influencing factors on plant organs, especially on leaves, have become a research topic in plant functional ecology and have also formed the core of ecological stoichiometry (Hedin, 2004; Niklas, 2006; He et al., 2008; Sardans et al., 2011, 2012a; Hong et al., 2014).

Deserts are ecosystems which occupy approximately one fifth of the earth's land surface, and they are characterized as low biodiversity, stability and levels of soil nutrients (Whitford, 2002; Ward, 2009). Thereby, the patterns of plant and soil stoichiometry in desert ecosystems have been more emphasized recently. Previous studies indicated that the leaves of desert shrubs were relatively high in N concentration and N to P ratio (N:P) despite the low levels of N in most desert soils (Whittaker et al., 1979; Skujins, 1981). For example, the leaf N concentration (24.1–24.7 mg/g) and N:P ratio (15.0–15.8) in most Chinese desert ecosystems (Zheng and Shangguan, 2007; Li et al., 2013; Zhang et al., 2014) are higher than those of the global plants (Elser, 2000; Reich and Oleksyn, 2004) and Chinese flora (Han et al., 2005). Additionally, the leaf P concentrations (1.60–1.80 mg/g) in most Chinese deserts are close to the global level but higher than those of Chinese flora (He et al., 2008). However, leaf N, P concentrations and N:P ratio of plants in Alxa Desert were lower than those of the global plants, Chinese flora and most Chinese desert ecosystems. This phenomenon revealed the differences in plant nutrient limitation and soil nutrient supply ability (Sardans et al., 2011, 2012b; He et al., 2014; Wu et al., 2014). Despite that, leaf N generally scaled as the two-thirds power of leaf P, and N:P scaled allometrically with respect to N or P among major plant groups and biomes (Niklas, 2006; Reich et al., 2010), although plants in several desert ecosystems indicated a different trend, e.g. leaf N increased much more rapidly than P (i.e. the scaling exponent is 1.17) in Alex Desert, China (Zhang et al., 2014). These previous studies have greatly advanced our understanding of the variations and patterns of leaf N and P of plants across different desert ecosystems, but it remains unclear about the plant stoichiometry pattern in the Junggar Desert, a typical temperate desert in Central Asia.

The Junggar Desert is the only desert influenced by water vapor from the westerly air flow; hence, its climate, vegetation composition and richness vary as in any other deserts in China (Zhang and Chen, 2002). Meanwhile, the Junggar Desert is a typical N-deficiency desert (Zhou et al., 2011) although the soil surface is covered by biological soil crusts, which can fix N (Zhang et al., 2010). Do plants in this desert represent the same tendency of leaf stoichiometry with those in the aforementioned desert ecosystems? As such, we selected the Karamori Mountain Ungulate Nature Reserve (KMUNR) in eastern Junggar Desert, China as the study area, and then analyzed the leaf nutrients of 57 plant species. Our objectives were to (1) document the patterns of leaf N and P concentrations and N:P ratios of all species and different functional groups; and (2) clarify the relationship between leaf N and P concentrations across all species in KMUNR. The results of this study could enhance our understanding of the general pattern and difference of leaf N and P stoichiometry in different functional groups of desert plant species, reveal the limiting nutrient factors through plant growth, and further deepen our knowledge of the ecological adaptation and life-history strategy of desert plants in arid environments.

1 Materials and methods

1.1 Study area

The KMUNR (44°36'–46°00'N, 88°30'–90°03'E), located in eastern Junggar Desert, is a special nature reserve that is designed primarily to protect wild ungulate animals (e.g. *Equus przewalskii*, *Equus hemionus*, *Saiga tatarica* and *Gazella subgutturosa*), the natural environment of these wild animals' habitats and ancient biological (e.g. dinosaur fossils) and other resources. During the period of 2000–2007, the mean annual precipitation was 159.1 mm, whereas the mean annual pan evaporation reached 2,090 mm. The annual mean temperature was 2.0°C. The January mean

temperature was -24.3°C , with the minimum temperature of -45°C . The July mean temperature was 20.5°C , with the maximum temperature of 38.4°C (Xu et al., 2009). Most of the area of KMUNR consists of low-mountain and gravel desert (i.e. Gobi), and the soil type is brown desert soil. The western KMUNR is covered by aeolian sandy soil, given its proximity to the Gurbantunggut Desert (CVAEC, 2001). Plant species and community types in KMUNR are relatively less; the small tree *Haloxylon ammodendron*, genus *Ceratoides*, *Anabasis* and *Artemisia* dominate in the vegetation. In addition, most of the area of KMUNR is covered by biological soil crusts, which are commonly composed of algae.

1.2 Field survey and sampling

Five sampling sites were selected at Kamusite ($45^{\circ}38'\text{N}$, $89^{\circ}45'\text{E}$), Wucaicheng ($45^{\circ}22'\text{N}$, $89^{\circ}28'\text{E}$), Huoshaoshan ($89^{\circ}16'\text{E}$, $45^{\circ}01'\text{N}$), Wucaiwan ($44^{\circ}65'\text{N}$, $88^{\circ}86'\text{E}$) and eastern Cainan ($44^{\circ}94'\text{N}$, $88^{\circ}70'\text{E}$) in KMUNR in mid-June 2013. At each site, three sampling plots (20 m \times 20 m) were set up with an interval of 3–5 km. In each plot, three quadrats (5 m \times 5 m in size) were chosen randomly to survey the species composition and mature leaves (5–8 g). A total of 57 species were collected (Table 1). All the leaf samples were quickly placed in bubble chambers with ice blocks before they were brought to the laboratory for watering. All the samples were oven-dried at 75°C for 24 h.

Table 1 Characteristics of 57 plant species in different functional groups in the Karamori Mountain Ungulate Nature Reserve

Species	Life-form	Photosynthetic pathway	Phylogeny	Assimilative branch	Family
<i>Achnatherum splendens</i>	Herb	C ₄	Monocots		Gramineae
<i>Acroptilon repens</i>	Herb	C ₃	Dicots		Asteraceae
<i>Ajania fruticulosa</i>	Shrub	C ₃	Dicots	N	Asteraceae
<i>Allium polyrhizum</i>	Herb	C ₄	Monocots		Alliaceae
<i>Allium</i> spp.	Herb	C ₄	Monocots		Alliaceae
<i>Anabasis aphylla</i>	Shrub	C ₄	Dicots	Y	Chenopodiaceae
<i>Anabasis truncata</i>	Shrub	C ₄	Dicots	Y	Chenopodiaceae
<i>Arnebia decumbens</i>	Herb	C ₃	Dicots		Boraginaceae
<i>Arnebia guttata</i>	Herb	C ₃	Dicots		Boraginaceae
<i>Artemisia songarica</i>	Shrub	C ₄	Dicots	N	Asteraceae
<i>Astragalus lehmannianus</i>	Herb	C ₃	Dicots		Fabaceae
<i>Astragalus oxyglottis</i>	Herb	C ₃	Dicots		Fabaceae
<i>Atraphaxis frutescens</i>	Shrub	C ₄	Dicots	N	Polygonaceae
<i>Atraphaxis laetevirens</i>	Shrub	C ₄	Dicots	N	Polygonaceae
<i>Atraphaxis spinosa</i>	Shrub	C ₄	Dicots	N	Polygonaceae
<i>Atraphaxis</i> spp.	Shrub	C ₄	Dicots	N	Polygonaceae
<i>Atraphaxis virgata</i>	Shrub	C ₄	Dicots	N	Polygonaceae
<i>Calligonum junceum</i>	Shrub	C ₄	Dicots	Y	Polygonaceae
<i>Calligonum klementzii</i>	Shrub	C ₄	Dicots	Y	Polygonaceae
<i>Calligonum leucocladum</i>	Shrub	C ₄	Dicots	Y	Polygonaceae
<i>Cancrinia discoidea</i>	Herb	C ₃	Dicots		Asteraceae
<i>Caragana leucophloea</i>	Shrub	C ₃	Dicots	N	Fabaceae
<i>Ceratocarpus arenarius</i>	Herb	C ₃	Dicots		Chenopodiaceae
<i>Ceratocarpus ewersmanniana</i>	Shrub	C ₃	Dicots	N	Chenopodiaceae
<i>Chondrilla ambigua</i>	Herb	C ₃	Dicots		Asteraceae
<i>Cichorium</i> spp.	Herb	C ₃	Dicots		Asteraceae

To be continued

Continued

Species	Life-form	Photosynthetic pathway	Phylogeny	Assimilative branch	Family
<i>Cleistogenes squarrosa</i>	Herb	C ₄	Monocots		Gramineae
<i>Cynanchum auriculatum</i>	Herb	C ₃	Dicots		Asclepiadaceae
<i>Echinops gmelinii</i>	Herb	C ₃	Dicots		Asteraceae
<i>Ephedra distachya</i>	Shrub	C ₃	Gymnosperm	Y	Ephedraceae
<i>Ephedra intermedin</i>	Shrub	C ₃	Gymnosperm	Y	Ephedraceae
<i>Ephedra przewalskii</i>	Shrub	C ₃	Gymnosperm	Y	Ephedraceae
<i>Ephedra</i> spp.	Shrub	C ₃	Gymnosperm	Y	Ephedraceae
<i>Ferula meyeri</i>	Herb	C ₃	Dicots		Umbelliferae
<i>Halocnemum strobilaceum</i>	Shrub	C ₃	Dicots	N	Chenopodiaceae
<i>Haloxylon ammodendron</i>	Shrub	C ₄	Dicots	Y	Chenopodiaceae
<i>Hedysarum scoparium</i>	Shrub	C ₃	Dicots	N	Fabaceae
<i>Iris tenuifolia</i>	Herb	C ₃	Monocots		Iridaceae
<i>Karelinia caspia</i>	Herb	C ₃	Dicots		Asteraceae
<i>Kochia prostrata</i>	Shrub	C ₄	Dicots	N	Chenopodiaceae
<i>Lepidium lotifolium</i>	Herb	C ₃	Dicots		Brassicaceae
<i>Leymus racemosus</i>	Herb	C ₃	Monocots		Gramineae
<i>Nonea caspica</i>	Herb	C ₃	Monocots		Boraginaceae
<i>Peganum harmala</i>	Herb	C ₃	Dicots		Zygophyllaceae
<i>Phragmites australis</i>	Herb	C ₃	Monocots		Gramineae
<i>Reaumuria songonica</i>	Shrub	C ₃	Dicots	N	Tamaricaceae
<i>Rindera tetraspis</i>	Herb	C ₃	Monocots		Boraginaceae
<i>Sarcozygium xanthoxylum</i>	Shrub	C ₄	Dicots	N	Zygophyllaceae
<i>Scrophularia heucheriiflora</i>	Herb	C ₃	Dicots		Scrophulariaceae
<i>Senecio</i> spp.	Herb	C ₃	Dicots		Asteraceae
<i>Seriphidium transiliense</i>	Shrub	C ₃	Dicots	N	Asteraceae
<i>Seriphidium</i> spp.	Shrub	C ₃	Dicots	N	Asteraceae
<i>Seriphidium terrae-albae</i>	Shrub	C ₃	Dicots	N	Asteraceae
<i>Stipa glareosa</i>	Herb	C ₄	Monocots		Gramineae
<i>Stipagrostis pennata</i>	Herb	C ₄	Monocots		Gramineae
<i>Tamarix ramosissima</i>	Shrub	C ₃	Dicots	N	Tamaricaceae
<i>Zygophyllum fabago</i>	Herb	C ₃	Dicots		Zygophyllaceae

Note: Y in the "Assimilative branch" column indicates shrub with assimilative branch and N indicates shrub without assimilative branch.

1.3 Determination of leaf N and P concentrations

The leaf samples were powdered in a vibratory disc mill (RS200, Retsch GmbH Inc., Haan, Germany) and then stored in zip pockets. The total N (mg/g) was measured using an elemental analyzer (2400 II CHN elemental analyzer; Perkin-Elmer, USA), and the total P (mg/g) was determined using molybdenum-antimony anti-spectrophotometric method (Han et al., 2005).

1.4 Soil collection and determination

The soil samples obtained at a depth of 0–10 cm were collected from five random points of each sampling plot. The samples were air dried under shade after removal of surface organic materials and fine roots. Soil organic carbon (OC; mg/g), total N (TN; mg/g), total P (TP; mg/g), available nitrogen (AN, mg/kg), available phosphorous (AP, mg/kg), pH and electronic conductivity (EC, $\mu\text{S}/\text{cm}$) were determined in the laboratory. OC was determined using the dichromate oxidation

method; TN using the $\text{CuSO}_4\text{-Se}$ powder diffusion method; TP using the Mo-Sb and Van-Mo-yellow colorimetry methods; AN using the alkali hydrolyzation diffusion method; AP using the sodium hydrogen carbonate solution–Mo–Sb anti spectrophotometric method; pH using a PHS-3C digital pH meter in a 1:5 soil-water ratio suspension; and EC using a DDS-307A conductivity meter (Precision and Scientific Corp. Shanghai, China) in sequence alongside the pH in same suspension. All the methods were referenced from Bao (2000).

1.5 Statistical analyses

The data of the leaf N, P concentrations and N:P ratios in this study followed a normal distribution, as determined by the one-sample Kolmogorov–Smirnov test; thus, we calculated their arithmetic means (Han et al., 2005). The different function groups (e.g. photosynthetic pathways: C_3 , C_4 ; phylogeny: monocots, dicots; life-forms: herbs, shrubs; shrub with assimilative branch or not; and main families) were divided (Table 1), and the N, P concentrations and N:P ratios of the functional groups were then compared using one-way ANOVA (i.e. number of group ≥ 3) and *t*-test (i.e. number of group=2). Levene's test was used to analyze homogeneity, and post-hoc multiple comparisons among values of different groups were performed using Duncan test.

Recently, leaf N:P ratio becomes a controversial index distinguishing nutrient limitation (Ellison, 2006). We used the followings criteria to diagnose nutrient limitation (Aerts and Chapin, 2000; Ellison, 2006; Wu et al., 2012):

If N concentration >20 mg/g and P concentration >1 mg/g, growth is unlimited by N and P;

If N concentration <20 mg/g and P concentration >1 mg/g, growth is limited by N;

If N concentration >20 mg/g and P concentration <1 mg/g, growth is limited by P;

If N concentration <20 mg/g and P concentration <1 mg/g, the N:P ratio can be used. N:P ratio <14 indicates N limitation and N:P ratio >16 indicates P limitation.

The log-transformed power function (i.e. RMA linear regression) was employed to determine the allometric relationship between the leaf N and P across all species (Niklas et al., 2005; Niklas, 2006). All statistical analyses were conducted using SPSS software (ver. 19.0, SPSS Inc. Chicago, Illinois, USA).

2 Results

2.1 Species composition, soil parameters and leaf stoichiometry

The 57 species belonged to 14 families and 41 genera; among them, Asteraceae (10), Polygonaceae (8), Chenopodiaceae (8) and Gramineae (6) accounted for 56.14% (Table 1). For functional groups, these species were divided into 28 shrub species and 29 herbaceous species, or 37 C_3 species and 20 C_4 species, or 4 gymnosperm species, 11 monocots and 42 dicots. Shrubs with and without assimilative branch contained 10 and 18 species, respectively. The soil in this study presented an almost weak variation (i.e. the coefficient variations were 0.012–0.308; Table 2). The soil was to a certain extent alkaline, given its pH of 8.37. The soil OC, TN and TP concentrations were 7.28, 0.232 and 0.383 g/kg, respectively. The soil total N:P (0.605) was less than the available N:P (1.86). The coefficient variations of leaf N, P concentrations and N:P were 0.457, 0.329 and 0.387, respectively, thereby showing a moderate variability (Table 3). The values of leaf N concentration ranged from 7.26 to 65.66 mg/g, with an average of 30.81 mg/g. The values of leaf P concentration ranged from 0.75 to 3.42 mg/g, with an average of 1.77 mg/g. The leaf N:P ranged 7.94–36.11, and the mean value was 17.72.

2.2 Leaf stoichiometric characteristics among different functional groups

For groups of different photosynthetic pathways, the leaf P concentration (1.90 mg/g) of C_3 plants (most of which were herbs) was obviously higher than that (1.52 mg/g) of C_4 plants (i.e. most of which were shrubs). However, they showed no significant differences in N concentration and N:P ratio (Table 4). The leaf N, P concentrations and N:P ratio of gymnosperm, monocots and dicots showed no significant differences. The leaf P concentration (1.59 mg/g) of shrubs was obviously

Table 2 General information on the soil parameters in the Karamori Mountain Ungulate Nature Reserve

Item	OC (mg/g)	TN (mg/g)	TP (mg/g)	AN (mg/kg)	AP (mg/kg)	C:N	C:P	N:P	AN:AP	pH	EC (μ S/cm)
Mean	7.28	0.232	0.383	17.65	11.12	31.27	18.80	0.605	1.86	8.37	43.56
SE	1.00	0.015	0.011	1.74	1.35	3.90	2.21	0.036	0.23	0.044	4.954
CV	0.308	0.144	0.067	0.221	0.271	0.279	0.263	0.134	0.278	0.012	0.254

Note: SE, standard error; CV, coefficient variations; OC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; AN, available nitrogen; AP, available phosphorus; EC, electric conductivity.

Table 3 General characteristics of the leaf N and P stoichiometry of 57 plant species in the Karamori Mountain Ungulate Nature Reserve

Item	N (mg/g)	P (mg/g)	N:P
Mean	30.81	1.77	17.72
Minimum	7.26	0.75	7.94
Maximum	65.66	3.42	36.11
SE	1.882	0.078	0.916
CV	0.457	0.329	0.387

Note: SE, standard error; CV, coefficient variations.

lower than that (1.94 mg/g) of herbs. However, shrubs and herbs showed no significant differences in N concentration and N:P. Assimilative branches markedly influenced the leaf stoichiometry of shrubs. Shrubs with assimilative branches had lower N (20.68 mg/g, $P < 0.05$), P (1.27 mg/g, $P < 0.05$) concentrations, and N:P ratio (16.83, $P > 0.05$) than those of without assimilative branches (35.01 mg/g, 1.77 mg/g and 20.28, respectively). For the plant families, significant differences in N, P concentrations or N:P ratio were found among seven main families. The plant species of Fabaceae had the highest N concentration (51.03 mg/g), whereas Asteraceae presented the highest P concentration (2.32 mg/g), followed by Fabaceae (2.04 mg/g). Hence, Fabaceae showed the highest value in N:P ratio (25.64), whereas Boraginaceae and Asteraceae had the lowest values (12.70 and 14.09). Most families had similar N and P concentrations and N:P ratios.

Table 4 Comparison of the leaf N and P stoichiometry of different functional groups of 57 plant species in the Karamori Mountain Ungulate Nature Reserve

Functional group	<i>n</i>	N (mg/g)	P (mg/g)	N:P
C ₃ plant	37	32.39 \pm 3.11 ^a	1.90 \pm 0.10 ^a	17.52 \pm 1.64 ^a
C ₄ plant	20	27.88 \pm 2.32 ^a	1.52 \pm 0.10 ^b	18.08 \pm 1.10 ^a
Gymnosperm	4	21.52 \pm 3.71 ^a	1.58 \pm 0.12 ^a	15.28 \pm 1.59 ^a
Monocots	11	25.08 \pm 2.24 ^a	1.56 \pm 0.10 ^a	15.79 \pm 1.11 ^a
Dicots	42	33.20 \pm 1.58 ^a	1.84 \pm 0.26 ^a	18.45 \pm 3.61 ^a
Shrub	28	29.89 \pm 2.36 ^a	1.59 \pm 0.09 ^a	19.05 \pm 1.36 ^a
Herb	29	31.70 \pm 2.91 ^a	1.94 \pm 0.12 ^b	16.43 \pm 1.18 ^a
Shrub with assimilative branch	10	20.68 \pm 3.18 ^a	1.27 \pm 0.14 ^a	16.83 \pm 2.48 ^a
Shrub without assimilative branch	18	35.01 \pm 2.54 ^b	1.77 \pm 0.09 ^b	20.28 \pm 1.59 ^a
Asteraceae	12	32.01 \pm 2.40 ^b	2.32 \pm 0.15 ^a	14.09 \pm 0.97 ^c
Polygonaceae	8	28.00 \pm 5.68 ^b	1.54 \pm 0.17 ^b	17.77 \pm 2.82 ^{bc}
Chenopodiaceae	8	33.46 \pm 4.53 ^b	1.41 \pm 0.13 ^b	22.91 \pm 2.29 ^{ab}
Gramineae	6	26.46 \pm 4.94 ^b	1.58 \pm 0.15 ^b	16.60 \pm 2.15 ^{bc}
Boraginaceae	4	21.10 \pm 5.60 ^b	1.62 \pm 0.19 ^b	12.70 \pm 2.68 ^c
Ephedraceae	4	21.52 \pm 1.58 ^b	1.58 \pm 0.26 ^b	15.28 \pm 3.61 ^{bc}
Fabaceae	4	51.03 \pm 7.10 ^a	2.04 \pm 0.37 ^{ab}	25.64 \pm 1.74 ^a

Note: Different lowercase letters indicate significant differences ($P < 0.05$) in the leaf N, P concentrations or N:P of each functional group.

According to the standard proposed by Wu et al. (2012), all 57 plant species (Table 3) and different functional groups (Table 4) were averagely unlimited by either N or P ($N > 20$ mg/g and $P > 1$ mg/g).

2.3 Allometric relationships among leaf N, P and N:P

The leaf N and P concentrations of all 57 species showed a significantly allometric relationship (Fig. 1a), thereby indicating that leaf N increased disproportionately with leaf P, with the scaling exponent 1.47 (close to 3/2). Similarly, leaf N:P ratio also showed an allometric increasing trend (i.e. the exponent is 0.79) with an increase in leaf N (Fig. 1b). No correlation of leaf N:P ratio with leaf P was observed (Fig. 1c).

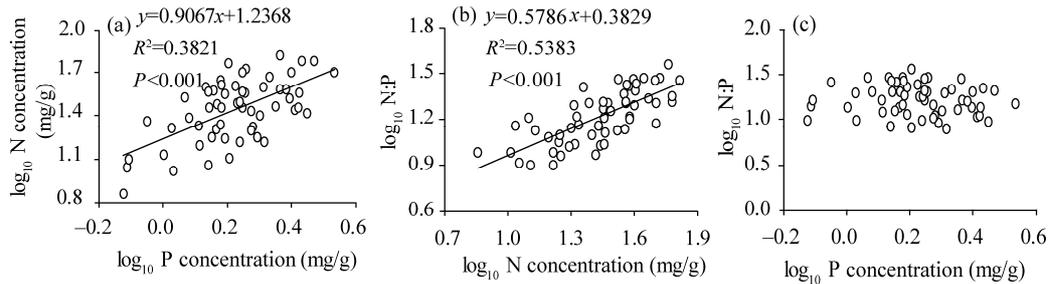


Fig. 1 Relationships between the leaf N and P concentrations and N:P ratios of 57 plant species in the Karamori Mountain Ungulate Nature Reserve

3 Discussion

3.1 Patterns of leaf N, P and N:P ratio of all species

In this study, the mean leaf N concentration (30.81 mg/g) of the 57 plant species was higher than all the results (10.65–26.46 mg/g) reported for plants in numerous terrestrial ecosystems and communities throughout the world and those reported for global plants (Table 5). However, the leaf P concentration of plants in KMUNR was at a moderate level (1.77 mg/g) relative to that of all the above-mentioned plants (1.25–2.00 mg/g, except for the lowest value of 1.04 mg/g for plants in Alxa Desert; Table 5). In detail, the leaf P concentration in the present study was significantly lower than that of forest plants in the North-South Transect of Eastern China (NSTEC) (Ren et al., 2007), Songnen Grassland (Song et al., 2012), plants in Beijing and its periphery (Han et al., 2009) and global plants (Elser, 2000; Reich and Oleksyn, 2004). By contrast, it was markedly higher than that of Chinese terrestrial plants (Han et al., 2005), Chinese grassland dominant species (Zhang et al., 2010), NSTEC (Ren et al., 2007) and plants in Alxa Desert (Zhang et al., 2014), alpine steppe in northern Tibetan Plateau (Hong et al., 2014) and Loess Plateau in China (Zheng and Shangguan, 2007). The leaf P concentration in this study was also similar to that reported by Reich and Oleksyn (2004), Han et al. (2005), He et al. (2008), Li et al. (2010), Yang et al. (2010) and Li et al. (2013) (Table 5). Given the highest leaf N, the leaf N:P ratio (17.72) of desert plants in KMUNR was obviously higher ($P < 0.05$) than that of all the above-mentioned plants (11.50–15.77), except for Chinese terrestrial plants (16.30) (Han et al., 2005), Chinese grassland dominant species (16.75) (Zhang et al., 2010) and the alpine steppe in northern Tibetan Plateau (17.87) (Hong et al., 2014).

Compared to those in arid areas and deserts, the leaf N concentration in this study was evidently higher than those in the typical desert and desertified regions of North China (25.5 mg/g) (Li et al., 2010) and in the hinterland of the Taklimakan Desert (25.5 mg/g; Li et al., 2013), and was especially higher than those of plants in the Alxa Desert (10.65 mg/g; Zhang et al., 2014). The leaf P concentration in this study was roughly equal to those of the typical desert and desertified regions of North China (1.74 mg/g) (Li et al., 2010) and Taklimakan Desert (1.82 mg/g; Li et al., 2013), but was larger than those of herbs in the Alxa Desert (1.04 mg/g; Zhang et al., 2014). For life-forms, herbs in the typical desert and desertified regions of North China (Li et al., 2010) and Taklimakan Desert (Li et al., 2013) showed lower leaf N (25 and 28.6 mg/g, respectively) but higher leaf P

concentration (2.07 and 2.5 mg/g, respectively); herbs in the Loess Plateau presented lower leaf N (25 mg/g) but similar leaf P concentration (1.77 mg/g) (Zheng and Shangguan, 2007). Consequently, plants in KMUNR had the highest leaf N concentration but moderate leaf P concentration relative to the results of previous studies.

Table 5 Comparison of the leaf N-P stoichiometry in this study and other regions

Research area/object	N (mg/g)	P (mg/g)	N:P	Data source
KMUNR	30.81 (<i>n</i> =57)	1.77 (<i>n</i> =57)	17.72 (<i>n</i> =57)	This study
Chinese terrestrial plants	20.24** (<i>n</i> =554)	1.46** (<i>n</i> =745)	16.30 (<i>n</i> =554)	Han et al. (2005)
Chinese grassland	23.31** (<i>n</i> =376)	1.83 (<i>n</i> =362)	15.35* (<i>n</i> =362)	Han et al. (2005)
Chinese grassland	26.46* (<i>n</i> =525)	1.91 (<i>n</i> =525)	15.28** (<i>n</i> =525)	He et al. (2008)
Typical desert and desertified regions, China	24.40** (<i>n</i> =214)	1.74 (<i>n</i> =214)	15.77* (<i>n</i> =214)	Li et al. (2010)
Chinese grassland dominant species	18.18** (<i>n</i> =132)	1.25** (<i>n</i> =132)	16.75 (<i>n</i> =132)	Zhang et al. (2010)
North-South Transect of Eastern China	19.09** (<i>n</i> =554)	1.46** (<i>n</i> =647)	15.40* (<i>n</i> =546)	Ren et al. (2007)
Forest plants in North-South Transect of Eastern China	18.30** (<i>n</i> =102)	2.00** (<i>n</i> =102)	11.50** (<i>n</i> =102)	Ren et al. (2012)
Alxa Desert, China	10.65** (<i>n</i> =54)	1.04** (<i>n</i> =54)	11.53** (<i>n</i> =54)	Zhang et al. (2014)
Songnen Grassland, China	24.20** (<i>n</i> =80)	2.00** (<i>n</i> =80)	13.00** (<i>n</i> =80)	Song et al. (2012)
Alpine Steppe, Northern Tibetan Plateau	23.20** (<i>n</i> =139)	1.38** (<i>n</i> =139)	17.87 (<i>n</i> =139)	Hong et al. (2014)
Grassland, Qinghai-Tibetan Plateau	23.20** (<i>n</i> =133)	1.70 (<i>n</i> =133)	13.50** (<i>n</i> =133)	Yang et al. (2010)
Loess Plateau, China	24.10** (<i>n</i> =126)	1.60* (<i>n</i> =126)	15.40* (<i>n</i> =126)	Zheng and Shangguan (2007)
Beijing and its periphery	26.10* (<i>n</i> =358)	2.00** (<i>n</i> =358)	13.90** (<i>n</i> =358)	Han et al. (2009)
Artificial plants, Taklimakan Desert	24.70** (<i>n</i> =25)	1.80 (<i>n</i> =25)	15.00** (<i>n</i> =25)	Li et al. (2013)
Global plants	20.62** (<i>n</i> =398)	1.99** (<i>n</i> =466)	12.70** (<i>n</i> =325)	Elser et al. (2000)
Global plants	20.09** (<i>n</i> =1,251)	1.77 (<i>n</i> =923)	13.80** (<i>n</i> =894)	Reich and Oleksyn (2004)

Note: KMUNR, Karamori Mountain Ungulate Nature Reserve, * and ** indicate significant difference between the leaf N and P concentrations and the N:P ratio in this study and those in other regions at $P < 0.05$ and $P < 0.01$ levels, respectively.

The N:P ratio is usually used to determine the nutrient limitation in individual plant growth and ecosystems (Koerselman and Meuleman, 1996; Güsewell, 2004). The leaf N:P ratios in most reported studies, except for few works, were significantly lower than that in the present study (Table 5). It was reported that N:P ratio < 14 indicated N limitation, N:P ratio > 16 meant P limitation, and an N:P ratio between 14 and 16 represented the co-limitation of N and P or non-limitation of N and P (Koerselman and Meuleman, 1996). Accordingly, most reported terrestrial ecosystems and communities belonged to N limitation or co-limitation of N and P (Table 5). In the present study, the plants in KMUNR indicated P limitation or N rich (Table 3). However, the determination standard of nutrient (N or P) limitation, i.e. N:P ratio, was not suitable for all terrestrial ecosystems because the criterion was based on wetland ecosystems in Europe. A new standard was proposed based on leaf N, P concentrations and N:P together (Aerts and Chapin, 2000; Ellison, 2006; Wu et al., 2012). According to this standard, all 57 plant species and functional groups in the present study were unlimited by either N or P, as well as those in most reported studies. Therefore, nutrient limitation status in the present study differed based on the different standards. Despite that, plants in this study represented relatively high N concentration and use efficiency to a certain degree.

We found that the exponent between leaf N and P was 1.47, which was higher than that (3/4) of global plants reported by Niklas (2006) and that (2/3) of major plant groups and biomes reported by Riech et al. (2010). The 2/3-power law of scaling leaf N to P was considered as a uniform rule of global plants predicted by stoichiometric theory which posited that plants with high growth rates required both high allocation of P-rich ribonucleic acid (RNA) and a high metabolic rate to support

the energy demands of macromolecular synthesis (Nielsen et al., 1996; Reich et al., 2010). However, the 3/2-power law of scaling leaf N to P in this study might reveal the particular metabolic mechanism of desert plants to cope with drought and hot stress. Desert plants also needed a high allocation of P-rich RNA to meet high growth rates (Reich et al., 2010), but these plants (especially herbs) urgently and necessarily required higher allocation of N to support the enzyme (composed of protein, an essentially important N pool) activities to enhance their resistance power to extreme arid environments (Lan and Zhang, 2008; Yuan and Tang, 2010). Therefore, desert plants had higher allocation of N compared with P. The results of plant characters in Alxa Desert supported our view (the scaling exponent is 1.171), although where leaf N, P concentrations and N:P ratio were obviously lower than those in present study (Zhang et al., 2014; Table 5).

3.2 Leaf N, P concentrations and N:P ratio in different functional groups

For plant functional groups, C₄ plants, shrubs, especially those with assimilative branches in this study, showed an obviously lower P concentration than C₃ plants, herbs, and shrubs without assimilative branches, respectively (Table 4). Shrubs with assimilative branches also had lower N concentration. Several studies supported our result. Herbaceous plants in NSTEC showed a higher leaf P than woody species (Ren et al., 2007); C₄ plants from the Chinese grassland dominant species showed a lower N:P ratio than C₃ plants (Zhang et al., 2010). Shrubs in the Alxa Desert exhibited a lower leaf P and higher N:P ratio than herbs (Zhang et al., 2014), and shrubs across the typical desert and desertified regions of North China also showed higher leaf N:P (Li et al., 2010). Meanwhile, shrubs in the Taklimakan Desert (Li et al., 2013) and Loess Plateau (Zheng and Shanguan, 2007) also showed a lower leaf P concentration than herbs.

Phosphorus is one of key elements in photosynthesis. Plants with high relative growth rate (RGH) generally have high leaf P concentration, as they must have high allocation of P-rich RNA and a high metabolic rate to support the energy demands of macromolecular synthesis (Wright et al., 2004; Reich et al., 2010). Thereby, herbaceous plants and C₃ plants showed higher leaf P concentrations (Table 4) than shrubs and C₄ plants, respectively, because the former had high RGH. Meanwhile, the corresponding leaf N presented a similar trend (but $P > 0.05$). In addition, high specific leaf area (SLA, leaf area per mass) was commonly observed with high RGH and leaf N (Gulias et al., 2003; Hoffmann et al., 2005). For example, the shrubs with cylindrical assimilative branches (formed after leaves degenerated) have relatively low SLA, thus they should have low RGH, leaf N ($P < 0.05$) and P concentrations ($P < 0.05$; Table 4). High water-use efficiency (WUE) and low leaf N concentration were generally indicated by high $\delta^{13}\text{C}$ values (Sparks and Ehleringer, 1997; Zhang et al., 2013). C₄ plants (or shrubs) showed higher $\delta^{13}\text{C}$ values than C₃ plants (or herbs), indicating the low leaf N concentration and the corresponding P concentration of C₄ plants (or shrubs) (Table 4). In the same way, the plants with axial photosynthetic organs (namely shrubs with assimilative branches) had higher $\delta^{13}\text{C}$ values, WUE and leaf thickness, than those with leafy organs (Zhang et al., 2013), also suggesting lower leaf N and P concentrations in the former (Table 4).

3.3 Influencing factors of leaf N, P concentrations and N:P ratio

A number of studies have reported plant stoichiometry varied with many biotic factors (including species identity, leaf traits, growth periods, plant functional groups and ecosystems) and abiotic factors (such as soil types, nutrient, geographical variables, climate) (Sardans et al., 2012a, b; He et al., 2014; Wu et al., 2014), and varied with study scales (Koerselman and Meuleman, 1996; Güsewell, 2004; Reich and Oleksyn, 2004; Sardans et al., 2011; Lü et al., 2012).

The leaf N or P concentration is often positively correlated to a certain degree with soil N or P (Chen et al., 2013; He et al., 2014). Thus, soil N:P ratios are generally used as an indicator to determine the saturation or lack of N and are used to determine the threshold value of nutrient limitation (Zhu et al., 2013). Leaf N and P status can usually reflect the soil N and P availability; this is beneficial to understanding the coupling relationship between plants and soils. According to the Soil-Age Hypothesis (SAH), P is the major limiting nutrient in older tropical areas, whereas N is the major limiting nutrient in younger temperate and high-latitude areas, especially in arid and desert areas (Reich and Oleksyn, 2004). Previous reports claimed that the lower leaf P

concentration (Table 5) of Chinese terrestrial vegetation was mainly due to the lower soil P (Han et al., 2005).

The soil P concentrations are distributed heterogeneously, showing an increasing trend from eastern (humid region) to northwestern China (arid region). In this study area the total soil P concentration (0.383 mg/g) was lower than the global average (2.8 mg/g) (Ren et al., 2007) and the Chinese average (0.56 mg/g) (Han et al., 2005). But in terms of soil P concentration (0.383 mg/g), the soil in this study is characterized by a significant lack of N (0.232 mg/g); hence, the soil N:P (0.605) is far less than the global average (5.9) (Cleveland and Liptzin, 2007) and Chinese average (3.9) and is also less than the average value in Chinese temperate deserts (1.2) (Tian et al., 2011), thereby indicating that the study area of the present work belongs to a typical N-lack desert (Zhou et al., 2011). This result is consistent with the SAH predicted result. The SAH also suggests that the youngest soils should have the lowest leaf N:P ratios because of the lowest N concentration (Reich and Oleksyn, 2004). If such is the case, then the plants in our study area should show N limitation, but they exhibited no limitation of N and P in leaves, even slight N rich in leaves, which was inconsistent with the soil N and P status and the SAH predicted result. Undoubtedly, the result reveals specific nutrient cycle (N transformation) and plant adaptation.

Plants absorb available nutrients that have strong motility, such as nitrate nitrogen and ammonium nitrogen; thus, the higher leaf N and N:P should be the effect of the higher soil N availability (Table 2) and N transformation rate in the study area (Lü et al., 2012; He et al., 2014). The higher AN may be associated with biological soil crusts (BSCs) composed of algae, lichen and moss (Zhang et al., 2010). BSCs can participate in the soil nutrient cycle and enhance N transformation rate (Wu et al., 2009; Zhang et al., 2010, 2015); in general, soils covered by BSCs show higher organic matter and N concentrations (Tao et al., 2013). The N-fixing microorganisms in symbiosis with BSCs are the main driving factor of the N cycle and transformation (Wu et al., 2009). Rhizobia can also enhance the soil N transformation and N absorption of roots. For example, Fabaceae plants exhibit the highest N (51.03 mg/g) and N:P ratio (25.64) among the numerous families in the study (Table 4). By contrast, the soil in KMUNR is alkaline, with a relatively high soil pH (8.4) and an abundance of CaCO_3 , which results in relatively low P bioavailability (Hong et al., 2014).

Extreme arid environments made the plants do an adaptive variation. Most herbaceous species (e.g. ephemeral and ephemeroïd plants) in the Junggar Basin can use limited water to complete their life history in a limited period (i.e. less than three months), and most shrub species have deep roots and show a strong ability to tolerate drought (Zhang and Chen, 2002). Thus, these plants must have an efficient photosynthetic mechanism (Lan and Zhang, 2008; Gong et al., 2009). Photosynthesis will not work without N and P; however the need of plant to N is much more than to P of plants (the scaling exponent is 1.47), and the patterns may vary across species and functional groups (Table 4). As we know, C_4 plants often have a special photosynthetic mechanism, showing high photosynthetic efficiency, strong ability to tolerate drought and low photorespiration (Gong et al., 2009). Similarly, the degeneration of shrub leaves and formation of assimilative branches also represent an efficient adaptation to drought and intense light. Thus, the question that is raised is: do C_4 plants, some shrubs, especially shrubs with assimilative branches, belong to P limitation? Or is this pattern of low leaf P concentration the result of a long-term adaptation related to high photosynthetic efficiency? Previous evidence generally suggest that, given their extreme environment, shrubs and herbs, or C_3 and C_4 plants in deserts may have a different leaf P utilizing pattern in relation to their lifeform (Li et al., 2010, 2013; He et al., 2014; Zhang et al., 2014). Thus, most desert plants have a convergent adaptation of N utilization (high N) in arid environments, whereas their P utilization shows a somewhat divergent adaptation (e.g. high P and low P). Accordingly, we considered the plant functional groups (life-forms, evolutionary and adaptation) and soil nutrient utilizability were the most important influencing factors on leaf stoichiometry in KMUNR.

4 Conclusions

Compared with the moderate leaf P concentration of plants in this study, they had higher leaf N concentration and N:P although the soil represented serious TN limitation rather than TP. Thus, the leaf stoichiometric characteristics of plants in KMUNR indicate their intrinsic and special features. The similarity in the leaf stoichiometry of different species or functional groups is commonly the result of convergent adaptation to the same environment; whereas their differences in leaf stoichiometry often suggest a difference in life-history strategy (e.g. shrubs and herbs and shrubs with and without assimilative branches). In conclusion, under extreme conditions of strong light and lack of water and nutrients (N), the desert plants in this study area have formed intrinsic, special physio-ecological and stoichiometric characteristics.

Acknowledgements

This work was financially supported by the National Natural Science Foundation of China (41201056), the National Basic Research Program of China (2014CB954202), the West Light Foundation of the Chinese Academy of Sciences (XBBS-2014-20) and the Program of Joint Foundation of the National Natural Science Foundation and the Government of Xinjiang Uygur Autonomous Region of China (U1503101). We thank WU Lin from Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences for his help with the field survey.

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