VARIATION PATTERN AND INTERACTION OF LEAF STOICHIOMETRY WITH SLOPE ASPECT IN THE CENTRAL QILIAN MOUNTAINS, NORTHWEST CHINA

LI, S. J.[1,2] – QIN, Y. Y.[2*]

[1]School of Life Science and Engineering, Lanzhou University of Technology, Lanzhou 730050, China
(e-mail: lishanjia@lut.edu.cn)

[2]Key Laboratory of Land Surface Process and Climate Change in Cold and Arid Regions, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

*Corresponding author
e-mail: qinyy06@163.com; phone: +86-931-496-7230

Abstract. Arising from differences in water, nutrient and energy balances, variations in leaf stoichiometry are complex interactions with slope aspect. The leaf stoichiometry of the dominant plant species growing on south-facing (SFS), south-west-facing (SWS), north-west-facing (NWS), and north-facing (NFS) slopes situated in the central Qilian Mountains of northwest China, was documented at the individual species, taxonomic family, and community levels. Leaf stoichiometry was species-specific, and each varied significantly. However, leaf stoichiometry for species shared by all slope aspects, the variation in stoichiometry of some species was homeostatic. Both at the family and community levels, slope aspect had a complex effect on leaf stoichiometry. Some stoichiometric variables were stable within the same slope aspect, whereas others varied under different slope aspects, suggesting that leaf stoichiometry was determined by both local-scale differences between sites and species identity. The range of variation in leaf stoichiometry showed a decreasing trend from individual species, to family, to community, indicating that a community's leaf stoichiometry cannot be derived from that of individual species or families. This suggests that research on plant response to environmental changes should focus on both the community level and the exclusive stoichiometry patterns of plants in this region.
Keywords: *leaf C:N:P, geographic factors, individual species, family, community*

Introduction

As the primary unit of photosynthesis, leaves are of fundamental functional importance to green plants (Givnish, 1987; Traiser et al., 2005), and accordingly key in describing and predicting fluxes of matter across several scales, from the plant organ to the ecosystem (Garnier et al., 2004). Leaf stoichiometry plays a vital role in providing an integrative nutrient framework linking biogeochemical cycles at a global scale to the cellular or organismal level. It further reflects a plant's adaptive strategies with respect to water use efficiency and the specific growth conditions it faces (Sterner and Elser, 2002; Watanabe et al., 2007; He et al., 2008; Elser et al., 2010; Sitters et al., 2014; Yan et al., 2016). Moreover, it can yield new insights into intra-specific, inter-specific, population, community and ecosystem biodiversity (Wang et al., 2015), as well as into the relative growth rates of plants (Niklas et al., 2005). Ratios of C:N and C:P allow the study of a plant's ability, to assimilate C while simultaneously absorbing N and P in response to the different abiotic characteristics of its surroundings. In contrast, the N:P ratio reflects potential nutrient limitations (He et al., 2006; Rong et al., 2015; Yan et al., 2016). Many

studies have shown stoichiometric ratios of critical nutrients in plant tissues to be reliable indicators of which nutrients (co-)limit plant growth and system-wide production (Gotelli et al., 2008). The variation in leaves' nutrient content under different environmental conditions (Jaenike and Markow, 2003) has implications for food quality, nutrient cycling and nutrient transfer through the trophic web, and can lead to a shift in ecosystem composition, increasing the extinction risk of some species (Sardans et al., 2012). Therefore, it is very important to identify the underlying environmental factors that influence C:N:P stoichiometry in the ecosystem (Ai et al., 2017).

In recent decades, a number of studies have focused on the response of leaf stoichiometry to variations in biomass partitioning patterns (Niklas and Cobb, 2006), elevated CO_2 and increased N availability (Esmeijer-Liu et al., 2009), livestock grazing (Zheng et al., 2012; Bai et al., 2012), P enrichment (Scott et al., 2013), soil chemical properties (Goloran et al., 2015; Pan et al., 2015), and vegetation organization levels (Fan et al., 2016), as well as variation in broad-scale environments, such as temperature, precipitation, and latitude, both in terrestrial and aquatic ecosystems (Reich and Oleksyn, 2004; He et al., 2006, 2008; Sardans et al., 2012; Sun et al., 2017; Wu et al., 2012; Wang et al., 2015; Li et al., 2014; Erickson et al., 2016). To date few studies have addressed the effect of slope aspect on leaf stoichiometry.

Slope aspect represents the cardinal direction in which a slope faces: 0° for North, 90° for East, 180° for South, and 270° for West. In montane environments slope aspect influences both abiotic and biotic factors (e.g., generating differences among localized ecosystems), thereby playing a key role in regulating water and energy balances (Sharma et al., 2010; Bale et al., 1998). Slope aspect also affects a number of floral characteristics including: species composition and distribution, cover and productivity, plant performance and association patterns, functional diversity, plant invasion, leaf $\delta^{13}C$, distribution of C3 and C4 plants, seedling establishment, and nutrient dynamics (Badano et al., 2005; Sharma et al., 2010; Sternberg and Shoshany, 2001; Kakembo et al., 2007; Wang et al., 2013; Gong et al., 2008; Bello et al., 2006; Li et al., 2011; Okubo et al., 2012).

While Ai et al. (2017) showed slope aspect to be the main environmental factor affecting a plant's C:N:P stoichiometry on China's Loess Plateau, whether this holds true for high mountain meadows in Qilian Mountains remains undetermined. Accordingly, to improve our understanding and ability to predict the responses of leaf nutrients to environmental changes in montane environments, the present study was designed to explore the effect of slope aspect on the leaf stoichiometry of a number of plant species in the Qilian Mountains. Based on previous studies (Qin et al., 2016; Hu et al., 2017; Zhu et al., 2017), the Qilian Mountains exhibited two main slope aspects (north- and south-facing; 0° and 180°), though some portions present up to four aspects: south-facing (SFS), semi-sunny (south-west) (SWS, 225°), semi-shady (north-west) (NWS, 315°), and north-facing (NFS) slope aspect. This provides a unique opportunity to investigate the influences of slope aspect on leaf C, N, and P concentrations and their stoichiometry, which we hypothesize to be significant at the species, taxonomic and community level, given the differences in water and energy (heat) balances under each slope aspect.

Materials and methods

Study area

Ranging in elevation from 2000 m to 5500 m and receiving 250-500 mm y^{-1} in precipitation, the Qilian Mountains, situated in China's arid northwest, are the source

of the Heihe River Basin, whose middle and lowers reaches supply water for agricultural production and ecosystem stabilization. Below the snow line (about 4200 m) the Qilian Mountains' vegetation types can be divided into: high mountain meadow, brush and meadow, mountain grass and forest (mainly *Picea crassifolia* Kom, Qinghai spruce).

Study sites were situated in the Heihe River source waters eco-region of the central Qilian Mountains (elev. 2200-3000 m; annual mean temperature, 0.5 °C; precipitation, 435 mm y^{-1}) (*Fig. 1*). Soil types can be classified into chestnut soil (predominantly sandy textured) on south-facing and semi-sunny slope aspects, subalpine meadow soil (predominantly silty-sand textured) on sites with semi-shady slope aspects, and grey cinnamon soil (predominantly silty-sand textured) on sites with north-facing slope aspects (more detail in Qin et al., 2016). The mean abiotic soil characteristics of the four sites under different slope aspects are presented in *Table 1*. Soil was monitored from 06:00 to 18:00 at 1-h intervals using an EM50 soil temperature datalogger (Decagon Devices Inc., USA). Three replicates for each soil core were analyzed in the laboratory (four slope aspects × 3 soil cores in each plot × 3 replicates for each soil core) with the minimum required processing for each of the analytical methods. (more details in Qin et al., 2016). While the highest soil nutrient levels found in the study region were documented at NFS sites, these levels were below the mean soil N (3.63 mg g^{-1}) and P (0.56 mg g^{-1}) across China (Zhao et al., 2014).

Table 1. Abiotic soil parameters measured at four sites differing in their slope aspect, located in the Heihe River source waters eco-region of the central Qilian Mountains (adapted from Qin et al., 2016)

Slope aspect		Mean (standard deviation) of soil parameter				
Name	**Deg**	**T° (°C)**	**Ө (g hg^{-1})**	**Org. C (mg g^{-1})**	**Tot. N (mg g^{-1})**	**Tot. P (mg g^{-1})**
SFS	180°	16.63 ± 4.71 A	21.03 ± 3.47 C	16.16 ± 7.9 D	1.24 ± 0.59 C	0.40 ± 0.06 B
SWS	225°	16.02 ± 4.46 AB	22.34 ± 3.47 C	20.63 ± 4.9 C	1.56 ± 0.51 BC	0.41 ± 0.12 B
NWS	315°	14.40 ± 2.80 B	26.68 ± 3.90 B	33.46 ± 13.00 B	2.75 ± 0.69 A	0.45 ± 0.09 B
NFS	0°	7.43 ± 0.46 C	37.52 ± 13.41A	72.50 ± 19.50 A	3.23 ± 0.90 A	0.53 ± 0.06 A

T°: daily soil temperature; θ: gravimetric soil moisture content; Org. C: soil organic carbon content; Tot. N: soil total nitrogen; Tot. P: soil total phosphorus. Different letters show a significant difference ($P \leq 0.05$, LSD, Duncan's) across slope aspects for a single soil parameter (column-wise)

Field sampling and chemical analysis

In August and September of both 2013 and 2014, three mountains, each harboring sites with the four slope aspects described above, were selected (*Fig. 1*). Apart from the NFS sites, which were dominated by trees (*Picea crassifolia*), the other sites were all dominated by herbaceous plants. At the herbaceous-plant-dominated slope aspect sites, a sample consisted of three 10 m × 10 m plots, 10 m apart along the horizontal contour, while at the NFS sites, a sample consisted of nine 10 m × 10 m plots, 10 m apart along both horizontal and vertical (up-down and contour) axes. In each sampling plot, about 10 g sun-facing fresh leaves of healthy plants of each dominant species were picked (see Qin et al., 2016) and packed individually in three sealer-bags. In all, leaves of 11, 11, 10, and 9 species were sampled on the SFS, SWS, NWS, and NFS sites, respectively (*Table 2*).

Upon their return to the laboratory, leaves were washed with distilled water, then oven dried at 80 °C to a constant weight (48 h). After grinding with a pulverizer (NM200, Retsch, Haan, Germany), samples were again oven dried to a constant weight, and ground to pass a 0.15 mm sieve. Total Carbon was determined by wet dichromate oxidation using a homogenized subsample of 0.2 g plant leaf and titrated by $FeSO_4$ (Nelson and Sommers, 1982). Total nitrogen (TN) were analyzed using a SmartChem 200 discrete chemistry analyzer (WestCo Scientific Instruments, Brookfield, CT, USA), while total phosphorus was measured using a molybdate/stannous chloride method after pretreatment by H_2SO_4-H_2O_2 digestion. Leaf C, N and P contents were expressed on a dry mass basis (Rong et al., 2015).

Table 2. *Species and taxonomic characteristics of plants from which leaves were sampled at sites differing in slope aspect, located in the Heihe River source waters eco-region of the central Qilian Mountains*

Species	Family	Genus	Lifecycle	Slope aspect			
				SFS	SWS	NWS	NFS
Agropyron cristatum (L.) Gaertn.	Gramineae	*Agropyron* Gaertn.	P	✓	✓	✓	✓
Artemisia argyi H. Lév. & Vaniot	Compositae	*Artemisia* L.	P	✓			
Artemisia mongolica (Fisch. ex Besser) Fisch. ex Nakai	Compositae	*Artemisia* L.	P	✓	✓		
Aster ageratoides Turcz.	Compositae	*Aster* L.	P				✓
Carex spp.	Cyperaceae	*Carex* L.	P				✓
Carex aridula V.I. Krecz	Cyperaceae	*Carex* L.	P	✓	✓		
Carex crebra V.I. Krecz	Cyperaceae	*Carex* L.	P	✓	✓	✓	
Fragaria orientalis Losinsk.	Rosaceae	*Fragaria*	P				✓
Heteropappus hispidus (Thunb.) Less.	Compositae	*Heteropappus* Less.	AB		✓	✓	
Leontopodium japonicum (Thunb.) Miq.	Compositae	*Leontopodium* (Pers.) R.Br. ex Cass.	P		✓	✓	
Ligularia virgaurea (Maxim.) Mattf. ex Rehder & Kobuski	Compositae	*Ligularia* Cass.	P			✓	✓
Medicago lupulina L.	Leguminosae	*Medicago* L.	P			✓	
Oxytropis spp.	Leguminosae	*Oxytropis* L.	P	✓			
Pedicularis resupinata L.	Scrophulariaceae	*Pedicularis* L.	P				✓
Polygonum macrophyllum	Polygonaceae	*Polygonum* L.	P				✓
Potentilla anserine L.	Rosaceae	*Potentilla* L.	P	✓	✓		
*Potentilla bifurca*L.	Rosaceae	*Potentilla* L.	P	✓	✓	✓	
*Potentilla multifida*L.	Rosaceae	*Potentilla* L.	P		✓	✓	
Roegneria kamoji (Ohwi) Keng & S.L. Chen	Gramineae	*Roegneria* C. Koch	P	✓			
*Stellera chamaejasme*L.	Thymelaeaceae	*Stellera*	P	✓	✓	✓	✓
Stipa capillata L.	Gramineae	*Stipa* L.	P	✓	✓	✓	
Thalictrum aquilegiifolium L.	Ranunculaceae	*Thalictrum* L.	P				✓

P: perennial; AB: annual or biennial. SFS, SWS, NWS, and NFS represent south-facing (SFS), semi-sunny (south-west) (SWS), semi-shady (north-west) (NWS), and north-facing (NFS) slope aspects, respectively

Data analysis

Data processing and statistical analysis employed Microsoft Excel and SPSS18.0 (SPSS Inc. USA), respectively. Variations in leaf C, N and P stoichiometry were analyzed by the adoption of one-way analysis of variance (ANOVA). The Fisher Least-Significant Difference (LSD) was used for multiple comparisons of variables among

slope aspects. Pearson correlation analysis was used to analyze correlations between leaf C, N and P stoichiometry. A value of P = 0.05 was used as the critical threshold for significance to determine differences in variables. In this paper, data for the leaves of *Piceacrassifolia* were excluded so as to only compare herbaceous life forms among the four slope aspects.
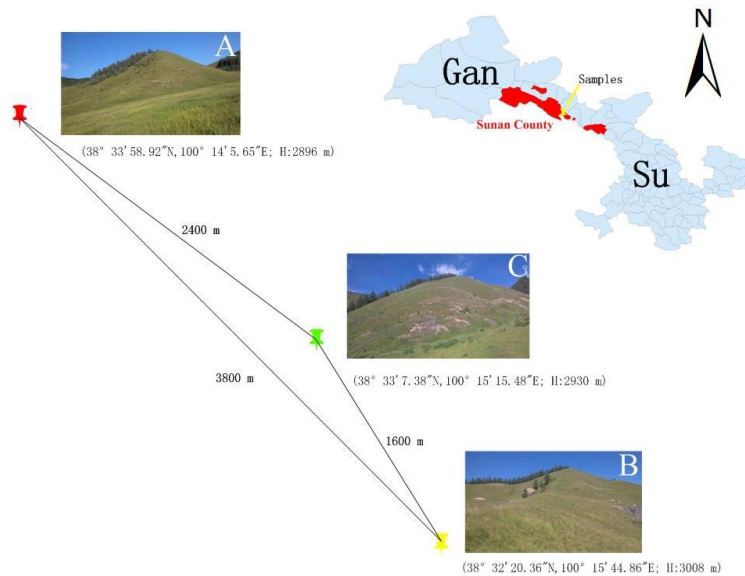

Figure 1. *Location of the three sampled mountains*

Results

Leaf stoichiometry at individual level on each slope aspect

Leaf C, N and P concentrations, and leaf C:N, C:P, and N:P ratios of each species showed a wide range of variation under all four slope aspects (*Table 3*). At the SFS site, variation in leaf C, N, and P concentrations among species were about 130%, 276%, and 281%, respectively, while variation in leaf C:N, C:P, and N:P rations were 258%, 316%, and 259%, respectively; at the SWS site, these values were 129%, 232%, and 248%, respectively, and 260%, 226%, and 197%, respectively; at the NWS site, these values were 126%, 200%, and 240%, respectively, and 213%, 282%, and 156%, respectively; while at the NFS site, these values reached 117%, 168%, and 339%, respectively, and 167%, 354%, and 304%, respectively.

At the SFS and NFS sites, leaf C, N and P concentrations, and leaf C:N, C:P, and N:P ratios differed among species. At the SWS site, measured indicators of leaf nutrients and leaf stoichiometries were all significantly different among species, except leaf N:P ratio; at the NWS site, leaf C concentration and leaf N:P showed no difference among species, while other indicators did (*Table 3*).

Leaf stoichiometry at individual level across slope aspects

Across all slope aspect sites, individual species' leaf C, N, and P concentrations ranged from 432.78 (*Roegneria kamoji*) to 549.06 mg g^{-1} (*Potentilla multifida*), 16.98 (*Carex crebra*) to 41.76 mg g^{-1} (*Oxytropis* spp.), and 1.09 (*Aster ageratoides*) to 2.58 mg g^{-1} (*Pedicularis reaupinanta*), while leaf C:N, C:P, and N:P ranged from 12.38

(*Oxytropis* spp.) to 30.10 (*Carex crebra*), 200.54 (*Pedicularis reaupinanta*) to 526.62 (*Stipa capillata* Linn.), and 7.51 (*Fragaria arientalis*) to 23.05 (*Oxytropis* spp.), respectively (*Table 4*). Variation in leaf C, N, and P concentrations among species reached a 127%, 250%, and 237%, respectively, and variation in leaf C:N, C:P, and N:P rations reached 242%, 262%, and 307%, respectively.

Table 3. *Leaf stoichiometry of herbaceous plant species living at four sites differing in slope aspect, located in the Heihe River source waters eco-region of the central Qilian Mountains*

Aspect*	Species	Leaf stoichiometry					
		C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C:N	C:P	N:P
SFS	*Artemisia argyi*	455.69 (27.32) [†]	28.50 (2.41)	2.07 (0.15)	16.12 (2.38)	221.42 (26.27)	13.78 (0.77)
	Agropyron cristatum●	500.98 (42.26)ac	20.74 (4.15)a	1.56 (0.39)a	25.00 (5.10)a	340.68 (90.81)ac	13.56 (1.77)a
	Artemisia mongolica	480.79 (61.85)	25.43 (1.91)	1.70 (0.20)	19.03 (3.09)	289.09 (59.72)	15.19 (1.86)
	Carex aridula	446.62 (11.05)	23.28 (3.68)	1.57 (0.19)	19.46 (2.64)	287.21 (28.41)	14.50 (2.78)
	Carex crebra♦	515.21 (3.80)a	16.74 (1.62)ab	1.69 (0.12)a	30.98 (3.02)a	306.82 (21.54)a	9.93 (0.42)a
	Oxytropis spp.	512.72 (36.76)	41.76 (3.54)	1.83 (0.13)	12.38 (1.92)	281.37 (19.76)	23.03 (3.53)
	Potentilla anserine	561.06 (58.46)	25.57 (4.83)	1.90 (0.52)	22.88 (6.35)	321.65 (127.67)	13.80 (1.70)
	Potentilla bifurcaΔ	542.04 (46.85)a	21.73 (3.23)a	1.32 (0.27)a	25.56 (5.36)a	422.60 (71.95)a	16.93 (3.87)a
	Roegneria kamoji	432.78 (7.66)	20.69 (0.87)	1.13 (0.25)	20.94 (0.61)	394.06 (73.41)	18.76 (3.05)
	*Stellera chamaejasme*O	467.64 (3.71)a	35.90 (5.40)a	3.18 (0.22)a	13.29 (2.61)a	147.42 (15.46)a	11.27 (1.39)a
	Stipa capillata☆	494.71 (9.30)	27.31(2.10)	1.24 (0.54)	18.21 (1.60)	465.23 (191.21)	25.67 (11.10)
	F[‡]	4.28	13.90	8.00	6.16	3.28	5.42
	P[§]	0.000	0.000	0.000	0.000	0.003	0.000
SWS	*Agropyron cristatum●*	555.91 (42.55)b	16.98 (2.65)bc	1.35 (0.19)a	33.32 (5.22)bc	415.50 (41.58)ab	12.70 (2.13)a
	Artemisia mongolica	499.57 (76.14)	24.05 (3.33)	1.61 (0.35)	21.25 (5.02)	327.32 (104.10)	15.21 (2.17)
	Carex aridula	468.71 (75.65)	17.03 (4.43)	1.41 (0.78)	28.53 (5.59)	422.73 (206.50)	14.48 (5.94)
	Carex crebra♦	481.92 (36.83)a	14.56 (2.30)a	1.54 (0.21)ab	33.09 (2.53)a	313.95 (23.99)ab	9.49 (1.34)ab
	Heteropappus hispidus	486.57 (57.58)	28.23 (1.12)	1.92 (0.04)	17.23 (1.90)	253.05 (28.25)	14.70 (0.78)
	Leontopodium japonicum	492.02 (54.06)	20.99 (3.67)	1.47 (0.01)	24.16 (6.68)	335.53 (39.67)	14.29 (2.36)
	Potentilla anserine	517.32 (32.64)	22.32 (3.45)	1.73 (0.10)	23.64 (4.09)	299.84 (25.22)	12.90 (1.89)
	Potentilla bifurcaΔ	558.70 (22.79)ab	24.21 (2.37)ab	1.90 (0.25)b	23.23 (2.05)ab	298.66 (48.17)b	13.03 (2.96)a
	Potentilla multifida	552.23 (37.90)	21.15 (2.69)	1.87 (0.17)	26.42 (3.34)	297.79 (37.31)	11.43 (2.12)
	Stipa capillata☆	562.36 (29.66)	17.79 (2.23)	1.13 (0.47)	31.93 (3.51)	572.76 (221.19)	18.68 (8.87)
	*Stellera chamaejasme*O	433.39 (58.26)a	33.81 (3.55)a	2.80 (0.71)ab	12.80 (0.61)a	380.56 (216.85)ab	12.36 (1.82)a
	F	3.36	12.61	5.09	9.73	4.30	1.63
	P	0.003	0.000	0.000	0.000	0.000	0.130
NWS	*Agropyron cristatum●*	526.95 (60.77)ab	17.08 (2.85)bc	1.24 (0.41)a	31.98 (8.29)bc	489.26 (232.21)b	14.77 (3.44)a
	Carex crebra♦	510.07 (41.99)a	19.63 (3.18)b	1.38 (0.07)b	26.23 (2.35)b	368.64 (23.04)c	14.17 (2.00)c
	Heteropappus hispidus	429.53 (14.76)	32.01 (4.40)	2.09 (0.38)	13.58 (1.87)	209.49 (34.80)	15.39 (0.72)
	Leontopodium japonicum	536.12 (41.16)	19.29 (4.33)	0.96 (0.26)	28.90 (7.62)	589.26 (168.60)	20.55 (3.92)
	Ligularia virgaurea	521.35 (32.41)	20.42 (1.17)	1.20 (0.06)	25.63 (2.79)	437.15 (47.33)	17.09 (1.25)
	Medicago lupulina	521.92 (38.65)	34.15 (2.10)	1.92 (0.11)	15.34 (1.70)	272.19 (13.53)	17.88 (2.00)
	Potentilla bifurcaΔ	435.73 (18.53)c	32.29 (7.81)c	1.91 (0.32)b	14.02 (3.27)c	231.70 (36.73)b	16.79 (2.37)a
	Potentilla multifida	542.72 (37.47)	23.65 (1.13)	1.69 (0.13)	22.94 (0.72)	324.09 (46.78)	14.11 (1.77)
	*Stellera chamaejasme*O	495.05 (22.31)a	26.97 (7.46)a	1.87 (0.75)b	19.33 (5.53)a	305.70 (158.59)b	15.56 (5.00)
	Stipa capillata☆	466.42 (91.92)	18.21 (1.94)	0.87 (0.27)	25.97 (6.47)	557.10 (148.47)	22.01 (5.60)b
	F	2.25	9.74	4.86	5.30	2.64	2.24
	P	0.051	0.000	0.001	0.000	0.026	0.052
NFS	*Agropyron cristatum●*	459.35 (12.66)c	19.14 (2.13)ac	3.16 (0.37)b	24.15 (2.12)ac	146.89 (18.05)c	6.15 (1.24)b
	Aster ageratoides	517.55 (4.00)	20.17 (0.82)	1.09 (0.15)	25.69 (1.14)	480.56 (66.27)	18.70 (2.36)
	Carex spp.	491.66 (28.23)	20.37 (3.34)	1.88 (0.89)	24.87 (5.40)	310.22 (119.48)	12.53 (4.75)
	Fragaria orientalis	501.29 (13.99)	18.56 (2.79)	2.47 (0.07)	27.43 (4.42)	202.74 (10.41)	7.51 (1.24)
	Ligularia virgaurea	446.46 (7.30)	21.12 (2.09)	2.07 (0.16)	21.26 (1.76)	216.39 (20.00)	10.28 (1.79)
	Pedicularis reaupinanta	502.36 (13.80)	29.59 (5.78)	2.58 (0.04)	17.69 (4.34)	200.54 (40.00)	11.49 (1.52)
	Polygonum macrophyllum	493.38 (26.28)	26.42 (3.58)	2.45 (0.72)	19.13 (3.95)	217.41 (63.10)	11.56 (3.40)
	Stellera chamaejasme	488.17 (12.89)a	31.13 (8.59)a	3.70 (0.77)ac	16.46 (4.37)a	136.24 (31.74)ac	8.38 (1.13)ac
	Thalictrum aquilegifolium	520.28 (9.46)	26.79 (1.92)	1.57 (0.15)	19.50 (1.65)	333.87 (29.12)	17.28 (2.88)
	F	4.57	5.89	5.47	4.06	8.46	5.80
	P	0.001	0.000	0.000	0.002	0.000	0.000

*SFS, SWS, NWS, and NFS represent south-facing (SFS), semi-sunny (south-west) (SWS), semi-shady (north-west) (NWS), and north-facing (NFS) slope aspects, respectively

†Mean (standard deviation)

‡*F* value of ANOVA discriminating between species at a given slope aspect site

§*P* value of ANOVA discriminating between species at a given slope aspect site, where $P \leq 0.05$ indicates a significant difference exists between species for a given slope aspect × leaf stoichiometry parameter combination

●, ♦, Δ, O and ☆ represent species shared across slope aspects. Different letters represent significant difference in leaf C, N, and P concentrations and leaf C:N, C:P and N:P ratios of shared species among slope aspects at a $P \leq 0.05$

Table 4. *Leaf stoichiometry of individual herbaceous plant species averaged across all four sites differing in slope aspect, located in the Heihe River source waters eco-region of the central Qilian Mountains*

Species	C (mg g⁻¹)	N (mg g⁻¹)	P (mg g⁻¹)	C:N	C:P	N:P
Agropyron cristatum	517.22 (53.87)*	18.51 (3.54)	1.58 (0.67)	29.09 (7.10)	385.30 (175.17)	12.95 (3.50)
Artemisia argvi	455.69 (27.32)	28.50 (2.41)	2.07 (0.15)	16.12 (2.38)	221.42 (26.28)	13.78 (0.77)
Artemisia mongolica	490.18 (66.86)	24.74 (2.69)	1.65 (0.27)	20.14 (4.14)	308.20 (83.85)	15.20 (1.93)
Aster ageratoides	517.55 (4.00)	20.17 (0.82)	1.09 (0.15)	25.69 (1.14)	480.56 (66.27)	18.70 (2.36)
Carex aridula	461.35 (61.07)	19.11 (5.04)	1.46 (0.63)	25.51 (6.47)	377.56 (177.33)	14.65 (4.90)
Carex crebra	502.40 (32.00)	16.98 (2.84)	1.53 (0.15)	30.10 (3.81)	329.80 (35.36)	11.19 (2.46)
Carex spp.	491.66 (28.23)	20.37 (3.34)	1.88 (0.89)	24.87 (5.40)	310.22 (119.48)	12.53 (4.75)
Fragaria orientalis	501.29 (13.99)	18.56 (2.79)	2.47 (0.07)	27.44 (4.42)	202.74 (10.41)	7.51 (1.24)
Heteropapus hispidus	458.05 (48.88)	30.12 (3.54)	2.01 (0.26)	15.41 (2.62)	231.27 (37.05)	15.04 (0.77)
Leontopodium japonicum	514.07 (49.30)	20.14 (3.71)	1.21 (0.32)	25.53 (6.91)	462.40 (176.95)	17.42 (4.49)
Ligularia virgaurea	483.90 (46.09)	20.77 (1.56)	1.63 (0.49)	23.45 (3.18)	326.77 (125.20)	13.68 (3.98)
Medicago lupulina	521.92 (38.65)	34.15 (2.10)	1.92 (0.11)	15.34 (1.70)	272.19 (13.53)	17.88 (2.00)
Oxytropis (Leguminosae)	512.72 (36.76)	41.76 (3.54)	1.82 (0.13)	12.38 (1.92)	281.37 (19.76)	23.03 (3.53)
Pedicularis reaupinanta	502.36 (13.80)	29.59 (5.78)	2.58 (0.46)	17.69 (4.34)	200.54 (40.00)	11.49 (1.52)
Polygonum macrophyllum	493.38 (26.28)	26.42 (3.58)	2.45 (0.72)	19.13 (3.95)	217.41 (63.10)	11.56 (3.40)
Potentilla anserine	543.56 (53.15)	24.27 (4.50)	1.83 (0.40)	23.18 (5.40)	312.93 (98.31)	13.44 (1.77)
Potentilla bifurca	527.45 (57.71)	24.83 (5.53)	1.67 (0.39)	22.32 (5.74)	334.84 (94.93)	15.34 (3.62)
Potentilla multifida	549.06 (35.65)	21.98 (2.53)	1.81 (0.17)	25.26 (3.18)	306.56 (39.88)	12.32 (2.32)
Roegneria kamoji	432.78 (7.66)	20.69 (0.87)	1.13 (0.25)	20.94 (0.61)	394.06 (73.41)	18.77 (3.05)
Stellera chamaejasme	483.17 (45.71)	26.48 (7.87)	2.09 (0.81)	20.07 (6.87)	272.13 (121.05)	13.31 (2.62)
Stipa capillata	516.11 (56.51)	21.68 (5.15)	1.12 (0.46)	25.25 (7.19)	526.62 (190.80)	22.15 (9.32)
Thalictrum aquilegifolium	520.28 (9.46)	26.79 (1.92)	1.57 (0.15)	19.50 (1.65)	333.87 (29.12)	17.27 (2.88)
ALL SPECIES MEAN	505.00 (51.84)	23.30 (6.22)	1.75 (0.63)	23.27 (6.75)	333.21 (142.95)	14.50 (4.91)
$F^\dagger$	2.63	9.21	4.62	5.42	4.35	5.74
$P^\ddagger$	0.000	0.000	0.000	0.000	0.000	0.000

*Mean (standard deviation)

†*F* value of ANOVA discriminating between species across slope aspect sites

‡*P* value of ANOVA discriminating between species across slope aspect sites, where $P \leq 0.05$ indicates a significant difference exists between species across slope aspects

Leaf stoichiometry at family level within each slope aspect

On a family level, leaf N:P did not differ significantly among families under any of the four slope aspects. Only leaf P concentration showed no familial differences at the SFS site. At the NWS site, leaf C concentration and leaf C:P were not different among families, but at the NFS site, except leaf P concentration other measured indicators were all different among families (*Table 5*). At the SFS site, variations in leaf C, N, and P concentrations among families were 171%, 132%, and 132%, respectively, and variation in leaf C:N, C:P, and N:P rations were 140%, 146%, and 148%, respectively; at the SWS site, these values were 118%, 150%, and 148%, respectively, and 156%, 165%, and 133%; at the NWS site, these values were 109%, 165%, and 150%,, and 167%, 182%, and 120%; and at the NFS site, these values were 107%, 111%, and 200%, and 109%, 238%, and 250%, respectively.

Leaf stoichiometry at family level across slope aspects

Across all slope aspect sites, families' leaf C, N, and P concentrations ranged from 498.02 (Gramineae) to 531.08 mg g⁻¹ (Cyperaceae), 18.60 (Gramineae) to 25.33 mg g⁻¹ (Rosaceae), and 1.38 (Compositae) to 1.74 mg g⁻¹ (Cyperaceae), while leaf C:N, C:P,

and N:P ranged from 20.06 (Rosaceae) to 27.55 (Gramineae), 315.73 (Rosaceae) to 428.15 (Compositae), and 13.50 (Gramineae) to 16.32 (Compositae), respectively (*Table 6*). Variation in leaf C, N, and P concentrations among families reached a 107%, 136%, and 126%, respectively, and variation in leaf C:N, C:P, and N:P rations reached 137%, 136%, and 121%, respectively.

Table 5. *Leaf stoichiometry of herbaceous plants at the family level at four sites differing in slope aspect, located in the Heihe River source waters eco-region of the central Qilian Mountains*

Slope aspect*	Family	C (mg g⁻¹)	N (mg g⁻¹)	P (mg g⁻¹)	C:N	C:P	N:P
SFS	Compositae	472.42 (52.29) †aA	26.45 (2.47)a	1.82 (0.26)a	18.06 (3.08)a	266.53 (59.55)a	14.72 (1.68)a
	Cyperaceae	480.91 (38.28)abA	20.01 (4.40)a	1.63 (0.16)ab	25.22 (6.80)ab	297.01 (25.00)a	12.46 (3.29)a
	Gramineae	487.52 (38.93)aA	22.92 (4.44)a	1.38 (0.45)a	22.07 (4.80)a	391.10 (136.22)a	18.46 (8.35)a
	Rosaceae	553.45 (53.19)aB	24.03 (4.56)ab	1.67 (0.52)a	23.95 (5.93)a	362.03 (117.40)a	15.05 (3.09)a
	F‡	8.33	3.07	2.52	3.13	3.03	2.31
	P§	0.000	0.037	0.070	0.035	0.039	0.098
SWS	Compositae	494.43 (61.66)aA	24.33 (3.87)ab	1.65 (0.29)a	20.97 (5.18)a	310.80 (81.65)a	14.85 (1.85)a
	Cyperaceae	473.12 (62.92)aA	16.20 (3.71)b	1.45 (0.62)ab	30.05 (5.13)b	386.47 (172.50)a	12.82 (5.32)a
	Gramineae	559.14 (35.13)bB	17.38 (2.37)bc	1.24 (0.36)a	32.62 (4.30)bc	494.13 (172.54)a	15.69 (6.90)a
	Rosaceae	542.75 (35.19)aB	22.56 (3.00)a	1.83 (0.18)a	24.43 (3.40)a	298.76 (35.77)bc	12.46 (2.35)b
	F	7.95	17.11	7.18	17.41	7.55	1.73
	P	0.000	0.000	0.000	0.000	0.000	0.174
NWS	Compositae	482.82 (64.60)aA	25.65 (7.99)ab	1.52 (0.68)a	21.24 (9.75)a	399.38 (234.78)a	17.97 (3.79)b
	Cyperaceae	525.25 (48.84)bB	19.67 (1.65)ac	1.32 (0.10)a	26.83 (2.93)ab	402.28 (61.12)a	14.99 (1.37)a
	Gramineae	511.82 (70.51)aA	17.36 (2.62)c	1.15 (0.40)a	30.48 (8.06)b	506.22 (210.16)a	16.58 (5.00)a
	Rosaceae	489.23 (64.29)bA	27.97 (6.88)b	1.80 (0.25)a	18.48 (5.32)b	277.90 (63.06)c	15.45 (2.38)a
	F	0.84	9.66	4.40	5.40	2.80	1.11
	P	0.481	0.000	0.011	0.004	0.056	0.361
NFS	Compositae	482.00 (39.29)aA	20.64 (1.51)b	1.58 (0.56)a	23.47 (2.76)a	348.48 (151.17)a	14.49 (4.98)a
	Cyperaceae	491.66 (28.23)abA	20.37 (3.34)a	1.88 (0.89)b	24.87 (5.40)a	310.22 (119.48)a	12.53 (4.75)a
	P	1.23	0.32	4.74	0.19	2.78	3.46
	F	0.321	0.728	0.025	0.829	0.094	0.052

*SFS, SWS, NWS, and NFS mean south-facing (SFS), semi-sunny (south-west) (SWS), semi-shady (north-west) (NWS), and north-facing (NFS) slope aspect, respectively

†Mean (standard deviation)

‡*F* value of ANOVA discriminating between families at a given slope aspect site

§*P* value of ANOVA discriminating between families at a given slope aspect site, where $P \leq 0.05$ indicates a significant difference （with lower case letters）exists between species for a given slope aspect × leaf stoichiometry parameter combination. The capital letters indicate the difference between each genus in different aspects. Bold fonts indicate genera with differences in aspect

Table 6. *Leaf stoichiometry of families averaged across all four sites differing in slope aspect*

	Compositae	**Cyperaceae**	**Gramineae**	**Rosaceae**	*F†*	*P‡*
C (mg g⁻¹)	510.82 (53.20) †	531.08 (53.08)	498.02 (55.98)	509.86 (56.49)	4.65	0.004
N (mg g⁻¹)	19.86 (4.20)	23.52 (4.47)	18.60 (3.47)	25.33 (4.63)	17.36	0.000
P (mg g⁻¹)	1.38 (0.57)	1.74 (0.39)	1.43 (0.38)	1.68 (0.40)	6.24	0.001
C:N	27.02 (7.14)	23.35 (4.86)	27.55 (4.93)	20.06 (5.89)	10.10	0.000
C:P	428.15 (174.25)	323.70 (95.15)	373.62 (112.45)	315.73 (130.29)	6.29	0.000
N:P	16.32 (6.91)	13.99 (3.21)	13.70 (3.60)	15.50 (2.62)	2.72	0.047

†Mean (standard deviation)

‡*F* value of ANOVA discriminating among families across slope aspect sites

‡*P* value of ANOVA discriminating among families across slope aspect sites, where $P \leq 0.05$ indicates a significant difference exists among families across slope aspects

Leaf stoichiometry at the community level under each slope aspect

At the community level, leaf C concentration differed between the SWS and NFS sites, and the leaf P concentration and leaf C:P, and N:P rations at the NFS site differed

from those recorded under the other three slope aspects. Leaf N concentration at the SWS site was different than that at the SFS or NFS sites, but no different to that at the NWS site. Leaf C:N ratio at the SWS and NWS sites were different to than those at the SFS and NFS sites, but not different within either pair (*Fig. 2*). Differences in leaf C, N, and P concentrations between the SFS and NFS sites were on the order of 105%, 132%, and 132%, respectively, and the differences in leaf C:N, C:P, and N:P rations between them were 140%, 146%, and 148%, respectively.
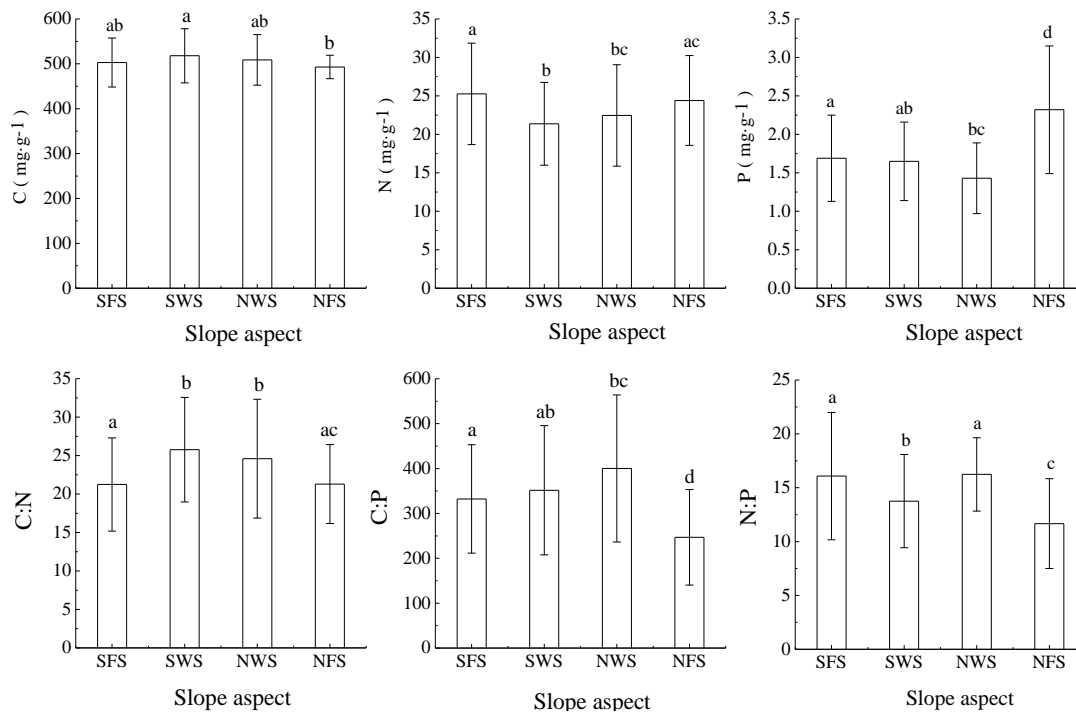
Figure 2. *Leaf stoichiometry at community level at four sites differing in slope aspect: south-facing (SFS), semi-sunny (south-west) (SWS), semi-shady (north-west) (NWS), and north-facing (NFS). Means with different letters are significantly different among slope aspects (P ≤ 0.05)*

Discussion

Variation in leaf stoichiometry at the individual species level under each slope aspect

Variation in leaf N among species reflects physiological scaling relationships linking leaf N, leaf mass and leaf respiration rates (Reich et al., 2006), and can provide a reasonable gauge of the protein "overhead" that must be synthesized to maintain balanced growth (Niklas and Cobb, 2006). Among all species, leaf N concentration of *Carexcrebra* was the lowest (*Table 4*), possibly as a result of its lower nitrogen resorption efficiency (Wu et al., 2012). Variation in leaf P among species reflects their N and P partitioning pattern (Watanabe et al., 2007) that can constrain growth rates across heterotrophs as well as photoautotrophs adapted to very different ecological conditions (Niklas et al., 2005), and offers a crude gauge of the "machinery" driving growth (Niklas and Cobb, 2006). Among all species, leaf P concentration of *Pedicularis reaupinanta* was highest (*Table 4*), possibly reflecting protein-rich leaves with higher phosphorus levels (Donovan et al., 2000). Generally, plants with higher leaf N and P concentrations grow faster than others (Güsewell and Koerselman, 2002; Wu et al.,

2012). Wright et al. (2004, 2005) found that variation in leaf N and leaf P among 2548 species was most closely correlated to dry matter per unit leaf area, leaf longevity, along with photosynthetic and respiratory rates. However, inter-specific differences in leaf stoichiometry patterns remain poorly understood (Niklas and Cobb, 2006; Wu et al., 2012).

In the present study, we found that at the individual species level, the range of variation in leaf nutrients and their stoichiometry was similar to that reported by Bai et al. (2012). While there were no differences in leaf N:P ratio between the SWS and NWS sites, and there were no species differences in leaf C concentration on the SWS site, other indicators were all significantly different between individual species (*Table 3*) in both similar and dissimilar environments (*Table 4*), which concurred with observations in other studies (Han et al., 2005; Tao et al., 2016). This suggests that shifts in leaf stoichiometry take place within a broader ecological setting and serve to utilize the available nutrients available under the specific growing conditions. In this situation, rather than there being a location-specific response, each plant competes with others for plant-specific nutrients to support plant growth, metabolism, and phenological progression (Güsewell, 2005; Gotelli et al., 2008; Jaenike and Markow, 2003; Elser et al., 2010; Li et al., 2015).

Highly divergent leaf C:N:P ratios ensure that plant species can coexist (He et al., 2008). Across species, leaf N:P varied roughly 3-fold, much less than He et al. (2008) reported across 213 species (7×), and leaf N:P of *Oxytropis* spp. was particularly high, likely the result of higher C levels in its leaves (*Table 4*). Plants with higher leaf N:P often exhibit a lower annual growth rate since leaf N:P has often been found to be negatively correlated to the relative growth rate of plants (Niklas and Cobb, 2006; Hu et al., 2017).

Variation in leaf stoichiometry at family and community levels by slope aspect

Within for uniform environment of the NFS site, except leaf P concentration, other leaf nutrient and stoichiometry variables did not differ significantly; whereas at other slope aspects sites, most of these variables did differ significantly (*Table 5*). Tao et al. (2016) similarly found that within a given habitat, family level differences existed in leaf N, P and N:P ratios. In different environments, from SFS to NFS (*Table 1*), each family presented its own leaf nutrient and stoichiometry profile (*Table 5*). Across sites, stoichiometries of all families were significantly different (*Table 6*) as confirmed by previous studies (e.g. Reich and Oleksyn, 2004; Han et al., 2005; Zhang et al., 2017). This suggests that stoichiometries of family in heterogeneous environment were more various than that in uniform environment. Accordingly, the lack of stoichiometric homeostasis may enable adaptive evolution within various environments through shifts in stoichiometric response (Jaenike and Markow, 2003).

In the present study, we selected the dominant species as being representative of the plant community because the traits of these dominant species are key elements underpinning the environment-induced changes in ecological stoichiometry. In such species-rich systems as our study area, ecosystems properties could be assessed through the measurement of relevant traits of a limited number of species (Garnier et al., 2004). At a community level, the lowest leaf C concentration were recorded at the NFS site (*Fig. 2*), likely due to the lesser photosynthetic rate, soil evaporation and plant transpiration rates occurring on the shady slope rather than on other slopes (Rong et al., 2016). However, Zhao et al. (2014) found that leaf C concentration increased as

temperature decreased, due to an increase in non-structural C, including starch, low molecular weight sugars and storage lipids, generated to balance the osmotic pressure of cells and offer resistance to freezing.

Leaf N concentration is an important indicator of the adaption of plants to abiotic environmental factors (Li et al., 2014). The highest leaf N concentrations were noted at the SFS and NFS sites, suggesting a low level of correlation between soil nutrients (STN at the SFS site being the lowest, *Table 1*) and nutrient concentration in plant tissues (Gotelli et al., 2008). This may be attributable to leaf N achieving strong stochiometric homeostasis even in an N-poor environment by the accumulation of non-protein nitrogen and synthesis of more C-compounds, in exchange for efficient water use and high temperature tolerance (Jaenike and Markow, 2003; Wang et al., 2015; Sun et al., 2017; Zhang et al., 2017). Higher leaf N at the SFS site might also be attributable to warmer temperatures that would accelerate the decomposition and mineralization of organic matter in the soil matrix and water by affecting metabolic processes and microbial activity, thereby increasing N availability (Xia et al., 2014). This also partly confirms the observation that leaf N concentrations are often positively correlated to soil total N concentration (STN at the NFS site being the highest, *Table 1*) (Han et al., 2005; Li et al., 2010; Rong et al., 2016). This is consistent with the biogeochemical hypothesis, which assumes that soil nutrient availability drives the variation in leaf nutrients (McGroddy et al., 2004; Kang et al., 2011; Wu et al., 2012). Leaf P concentration were highest at the NFS site, indicating that plants in colder areas need more P-rich ribosomes to compensate for decreases in metabolic rate and to sustain growth at lower temperatures. This is consistent with the temperature-plant physiology hypothesis (Körner, 1989; Reich and Oleksyn, 2004; Wu et al., 2012; Rong et al., 2016). Leaf P concentration at the SFS and SWS sites was greater than at the NWS site, suggesting that leaf area on the former two slope aspects may present a faster growth rate than at the latter site. This would occur since P is indispensable to the machinery of cell growth and metabolism and can thus facilitate the growth of functional tissues (leaf) (Ågren, 2008; Zhang et al., 2017).

Leaf C:N at was lowest at the SFS and NFS sites, suggesting that plants on sites with these slope aspects would have a higher growth rate (He et al., 2008). However, compared to these two slope aspects, aboveground biomass on SWS and NWS were the highest (Qin et al., 2016), with the former being 21 g, and 28 g per 0.25 m^2, respectively, and the latter being 39 g, and 7 g per 0.25 m^2, respectively. This may have been the result of insufficient water and light for plant growth on SFS and NFS sites, respectively, as suggested by Ai et al. (2017). In our study area, trees (*Picea crassifolia*) were the dominant species on NFS, and thus herbaceous plants were generally shaded. However, He et al. (2006) found leaf C:N to be stable under three different environmental conditions, irrespective of species' compositional shifts, because the elemental composition of plants in an ecosystem is simultaneously determined by the mix of species and by the physiological status of the dominant species. Compared to NFS, leaf C:P under the other three slope aspects was higher, suggesting that greater constraints exist on P content compared to C assimilation on these slope aspects (Sun et al., 2017). If we exclude the two transitional zones (SWS and NWS), leaf P concentration and N:P decreased significantly from SFS to NFS, suggesting that leaf P concentration and N:P were correlated with temperature, while leaf N concentration showed no such trend. This result differed from those of previous studies, which found that leaf N and P concentrations were each or both related to temperature (Reich and

Oleksyn, 2004; Han et al., 2005), or neither related to it (Kerkhoff et al., 2005; Yan et al., 2016), or only Leaf N:P being unrelated to it (Han et al., 2005).

Compared with other studies (*Table 7*), in the present study we found that leaf C concentration and leaf C:N and C:P were relatively high, while leaf N concentration and leaf N:P were similar to those reported in most other studies. This was tied to multiple factors (e.g., phylogeny, life form, topography, and meteorology), implying that, overall, plants in the study area exhibited a strong ability for carbon assimilation. In the present study, we found that leaf C:N:P stoichiometry varied with slope aspect (*Table 6*), in contrast to desert halophytes which showed relative stability across a salinity gradient (Wang et al., 2015). However, although there were significant differences in abiotic environments of the SFS and NWS sites (*Table 1*), no differences in leaf C concentration and N:P were found, suggesting that while variation in slope aspect or heat and water distribution contributes to explaining the variations in leaf nutrients and leaf stoichiometry, one needs to also focus on species composition to more precisely identify patterns of leaf trait variation (He et al., 2006; Wu et al., 2012).

Table 7. Leaf stoichiometry quantification in the present study and other studies

Studies	C	N	P	C:N	C:P	N:P
This study	506.08 (62.13)	23.37 (6.28)	1.76 (0.68)	23.26 (6.75)	333.53 (144.43)	14.48 (4.93)
Wang et al. (2015)	421.22 (22.00)	26.76 (9.30)	1.74 (0.37)	17.33 (5.31)	252.17 (54.9)	15.37 (3.88)
He et al. (2006, 2008)	442.4 ± 28.1	26.5 ± 8.5	1.91 ± 0.84	17.9 ± 3.2	275.2 ± 116.1	15.3 ± 5.2
Reich (2004) and Elser et al. (2000)	461.6 ± 72.2	20.1 ± 8.7	1.77 ± 1.1	22.5 ± 17.3	232.0 ± 236.8	13.8 ± 9.5
Sun et al. (2017)	397.0 (19.8)	24.0 (4.2)	1.7 (0.5)	17.1 (3.5)	256.6 (83.8)	15.1 (3.8)
Zheng and Shangguan (2007)	438.0 (43)	24.1 (8.5)	1.6 (0.55)	21.2 (10.2)	312 (135)	15.4 (3.9)
Han et al. (2005)		20.2	1.46			16.3
Tao et al. (2016)		30.81	1.77			17.72
Yan et al. (2016)		24.25	1.67			15.23
Hong et al. (2014)		23.20 (7.2)	1.38 (1.5)			17.98
Xia et al. (2014)	396 (1.9)	25.9 (0.4)	3.3 (0.06)	17.1 (0.34)	149 (3.57)	9.5 (0.23)
Zhao et al. (2014)	423.0	25.1	2.49	18.42	187.2	10.5

Variation in leaf stoichiometry of common species by slope aspect

Five species were common to the SFS, SWS, and SWS sites, and a further two were common to all slope aspect sites (*Table 3*). Leaf stoichiometry of *Agropyron cristatum* and *Stellera chamaejasme* showed little variation with slope aspect; however, that of *Potentilla bifurca* and *Carex crebra* showed a relatively larger variation with slope aspect. This concurs with the results of Gotelli et al. (2008), suggesting that some species exhibited little intraspecific variation in stoichiometry and showed a similar homeostatic response to variation in resources (Wu et al., 2012; Hu et al., 2017). Moreover, some species showed relatively greater variation in intraspecific (vs. interspecific) stoichiometry under varying environmental conditions (Jaenike and Markow, 2003; Gotelli et al., 2008). The mechanisms leading to such stoichiometric conditions reflects the physiological adaptation of plants to local environments and the dynamics of net photosynthesis of individual species. This contributes to the wide distribution of species whether in favorable or stressful environments (Li et al., 2015). Wu et al. (2012) and Hu et al. (2017) both found intraspecific variation in *Quercus* species and *Phragmites australis* leaf N and P across along wide environmental gradients, to show no clear geographic patterns across China. Ai et al. (2017) found

slope aspect to influence plant stoichiometry differently for different species. For example, they found that slope aspect had no effect on the aboveground C:N of *Artemisia sacrorum* but significantly affected the aboveground C:N of weeds. Slope aspect was also found to significantly affect the weeds' aboveground C:P, but not that of *Artemisia sacrorum*. With homeostasis, the elemental composition of individual species was constrained to a narrow range, regardless of chemical composition of the environment (Li et al., 2015). At the plant species level, leaf C, N, and P concentrations and leaf stoichiometry of some common species remain not only unchanged across environment gradients, but also across grazing gradients. For example, Zheng et al. (2012) found that leaf C, N, and P concentrations, and leaf stoichiometry remained unchanged in over half of the total common meadow steppe species (169 species) at non-grazed vs. grazed sites. This suggested that some species show less intraspecific variation, which contrasts with previous studies that found intraspecific variation to often exceed interspecific variation (Goloran et al., 2015).

Relationships among leaf stoichiometry

Leaf C was positively correlated with leaf C:N and C:P, but negatively correlated with leaf N and P; leaf N was positively correlated with leaf P, and was negatively correlated with leaf C:N and C:P; leaf P was negatively correlated with leaf C:N, C:P, and N:P; leaf C:P was both positively related to both leaf C:N and N:P (*Table 8*).

Table 8. Relationships among measured leaf stoichiometry variables

	C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C:N	C:P	N:P
C (mg g^{-1})	1	-0.16*	-0.18*	0.47**	0.33**	NS
N (mg g^{-1})		1	0.55**	-0.89**	-0.52**	NS
P (mg g^{-1})			1	-0.52**	-0.84**	-0.65**
C:N				1	0.61**	NS
C:P					1	0.69**
N:P						1

*$P \leq 0.05$, **$P \leq 0.01$, 'NS' means $P > 0.05$

Generally, leaf C concentrations have been found to be positively correlated with leaf N and P concentrations (McGroddy et al., 2004); however, in concordance with our study, Zheng and Shangguan (2007) found a negative relationship between leaf C concentration and leaf N and P concentrations. In addition, Xia et al. (2014) found leaf C concentration to be negatively correlated with the leaf P concentration but positively correlated with leaf N concentration. Most previous studies (*e.g.*, Wright et al., 2004; Han et al., 2005; Li et al., 2014; Wang et al., 2014) have shown leaf N and leaf P to be positively correlated given their similar functions, but Goloran et al. (2015) found leaf N concentration to was negatively correlated to leaf P concentration in *Hardenbergia comptoniana*. Leaf C:N and C:P ratios presented strong negative correlations with leaf N and leaf P concentrations, in concordance with Xia et al. (2014) and Sun et al. (2017). Leaf P concentration was negatively related to leaf N:P as found by Hong et al. (2014) and Xia et al. (2014), but this trend was not found by Tao et al. (2016) or Wang et al. (2015). Leaf N concentration was not related to leaf N:P, which concurs with the results of Sun et al. (2017), but contrasted with the results of Hong et al. (2014) and Wang et

al. (2015), who found leaf N:P to be highly positively correlated with leaf N concentration. These correlations suggest that leaf stoichiometry is species- or region-dependent. In the present study, we found that the correlations between C:N and leaf N concentration were much greater than those between C:N and leaf C concentration, which reflects that the variation in C:N ratio is primarily determined by leaf N, as was found by Li et al. (2015).

Nutrients limitation for plants at the community level

N and P status and N:P stoichiometry in leaves are considered to be reliable indicators of nutrient limitation at the community level, and have been studied intensively (Han et al., 2005; He et al., 2008; Yan et al., 2016). Generally, leaf N < 20 mg g^{-1} and leaf N:P < 14 are regarded as N limitations, while leaf P < 1 mg g^{-1} and leaf N:P > 16 are regarded as a P limitation. Co-limitation by N and P occurs when leaf N and P concentrations are both individually limiting and $14 \leq N:P \leq 16$ (Gotelli et al., 2008). Based on this, only *Fragaria orientalis* and *Agropyron cristatum* at the NFS site were limited by N, whilst *Stipa capillata* and *Leontopodium japonicum* at the SWS site were limited by P. No species were co-limited by N and P at the individual species level (*Table 2*). At the family level, we found that only Gramineae at the SWS site were limited by N, but no species were limited by either N or P, or both (*Table 3*). However, on the community level, individual species were not limited by any of them.

Influences of slope aspect and soil properties on leaf stoichiometry

According to *Table 1,* soil could be divided into three types, that is to say, soil on SFS and SWS represents the poorer, and soil on NWS represents the intermediate, while it on NFS represents the better. In this case, we can analyze the individual effect of slope aspect and soil and their interaction on leaf C, N, P concentrations and their stoichiometries by using two-way analysis of variance (ANOVA) with them as fixed factors. Interactions between plants, soils, and microorganisms regulate the function of terrestrial ecosystems, and biotic and abiotic interactions strongly impact ecological processes (Singh et al., 2009).

Two- way ANOVA analysis showed that leaf C, N, P concentrations and their stoichiometries both at individual and family level were only affected by slope aspect, and soil and interaction between it and the slope aspect have not effect on them. At individual level, leaf C, P concentrations and leaf C:P were not significantly affected by slope aspect, while at family level, slope aspect has no significant effects on leaf N concentration and Leaf C:P (*Table 9*), suggesting that the differences in these stoichiometries (*Tables 3* and *6*) may be caused by different life form of organisms or phylogeny of family, and unrelated to slope aspect. However, as there is lack of evidence to support this; much work should be done in future studies.

Conclusions

Leaf stoichiometry of plants from sites in the Qilian Mountains exhibiting different slope aspects were analyzed at the species, family, and community levels. At an individual plant level, each plant's leaf stoichiometry was different and a great deal of variation occurred between plants. However, at the family and community levels, leaf stoichiometries presented some homeostasis. Overall, from the species to the family to

the community, the range of variation in leaf stoichiometry decreased, suggesting that at an individual level, the plant tends to show divergent adaptation in leaf stoichiometry, whilst at a family or community level, the leaf stoichiometry tends to be convergent. Accordingly, as also shown by He et al. (2008), leaf stoichiometry derived from individual species cannot be taken to represent community-level measurements.

Table 9. Analysis on the interaction between slope aspect and soil

Leaf stoichiometry	Slope aspect	
	F	Sig
Individual species		
C	2.31	0.130
N	10.56	0.001
P	0.082	0.774
C:N	553	0.000
C:P	538	0.464
N:P	6.53	0.011
Family		
C	317	0.000
N	2.60	0.109
P	661	0.000
C:N	444	0.000
C:P	0.32	0.570
N:P	4.75	0.031

In this study, most of leaf stoichiometries were significantly affected by slope aspect, while others was not, implying that leaf stoichiometry is both species-specific and region-specific. In addition, the relationships among leaf stoichiometry parameters were complex, with no standard patterns emerging at the regional or global scale after comparison with other studies. Therefore, the site-dependence of leaf stoichiometry should be studied independently to explore the effects of global climate changes on plant adaption and evolution strategies, and to take measures to help plants in dealing with these changes.

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