Сибирский экологический журнал, 3 (2014) 405–412

УДК 582.746.11:213.52

Variations in leaf and root stoichiometry of *Nitraria tangutorum* along aridity gradients in the Hexi Corridor, northwest China

N. WANG[1], J. GAO[2], S. Q. ZHANG[1], G. X. WANG[2]

[1] *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau Northwest A&F University 712100, China, Shaanxi, Yangling*

[2] *State Key Laboratory of Plant Physiology and Biochemistry Institute of Ecology College of Life Sciences Zhejiang University 310058, China, Hangzhou*
E-mail: wangn@nwsuaf.edu.cn

Статья поступила 11.09.2013

ABSTRACT

Nitrogen (N) and phosphorus (P) concentrations and N: P ratios between leafs and roots of *Nitraria tangutorum* along aridity gradients were studied. *N. tangutorum* was relatively limited by N in April (mean leaf N: P ratio = 11.13) and by P in August (mean leaf N: P ratio = 38.78). N and P in both leaves and roots were highly correlated across sampling sites. In April both leaf and root N and P concentrations increased along aridity gradients. Mean leaf N: P ratios changed slightly, but mean root N: P ratios increased with increasing aridity gradients. We suggest that leaf N: P ratios can indicate nutrient status at different plant growth stages, and root N: P ratios can signify if the amount of soil nutrients is insufficient.

Key words: *Nitraria tangutorum*, ecological stoichiometry, leaf, root, aridity gradients.

Nitrogen (N) and phosphorus (P) are generally considered as the two most limiting elements to terrestrial vegetation and play pivotal roles in plant functioning [Han et al., 2005; Reich, Oleksyn, 2004]. Leaf N and P concentrations are closely correlated with biotic and abiotic factors including plant functional group, plant development stage and habitat [Han et al., 2005; Koerselman, Meuleman, 1996; Cunningham et al., 1999; Sasaki et al., 2010; Allen, Gillooly, 2009; Foulds, 1993; Thompson et al., 1997]. Furthermore, the N: P ratios of leaves have become an indicator of nutrient limitation [Cernusak et al., 2010], showing that leaf N: P ratio < 14 generally indicates N limitation, while the ratio > 16 suggests P limitation [Koerselman, Meuleman, 1996]. In contrast, little is known about stoichiometric changes of roots and their relationships with stoichiometric changes of leaves [Liu et al., 2010]. More complete knowledge of the allocation of nutrients between plant organs is critical to interpret plant functional diversity, nutrient budget and the parameterization of global ecosystem function models [Kerkhoff et al., 2006].

A considerable body of evidence has suggested a coordinated pattern of stoichiometry between leaf and root [Liu et al., 2010; Withington et al., 2006; Freschet et al., 2010]. For example, plants with high N concentrations in their leaves have high N concentrations in their roots [Craine, Lee, 2003]. In contrast, a different trend was observed in grassland [Zhang et al., 2013]. Although nutrient patterns between leaf and root may exist for a site, there are few data on the generality of these relationships, especially across semi-arid and arid ecosystems. Drought and high soil alkalinity decrease availability of soil N and P, and the requirements for osmotic adjustment, defense and storage compounds also affect plant nutrient allocation in drought-stressed enviroment [Drenovsky, Richards, 2004]. It is important to understand how the nutrient concentrations vary between plant organs along major ecological gradients, because both leaf and root traits have ability to determine resource use and plant species composition [Craine et al., 2001]. In addition, focusing on plant optimal N: P ratios in harsh environments can be used to test the generality of our knowledge derived from benign environments.

Hexi Corridor is a region in China with severe soil erosion and degraded ecosystems [Su et al., 2007]. Aridity and overconsumption of water resource cause plant species diversity to decline in this area [Wang et al., 2003]. In contrast, *Nitraria tangutorum* Bobr. is gradually becoming the dominant species and plays a vital role in maintaining the stability and persistence of desert ecosystem. *N. tangutorum* is a typical desert halophyte that has tolerance to severe drought and salinity stresses [Yang et al., 2013]. Furthermore, *N. tangutorum* keeps sand fixation that effectively prevents desertification in the transitional zones between desert and oasis [Du et al., 2010]. However, so far, few studies have explored whether and how nutrient patterns of *N. tangutorum* vary between leaf and root along aridity gradients. This information will further our understanding regarding the effects of enhanced drought on specific plant parts, and probe whether *N. tangutorum* can be a proper solution for desertification prevention and restoration vegetation based on physiological traits.

We conducted field experiments on *N. tangutorum* in Hexi Corridor, northwest China. Our objectives were: (1) to document the patterns of N and P stoichiometry between leaf and root and (2) to determine the effects of enhanced drought in structuring leaf and root N: P ratios of *N. tangutorum*.

MATERIALS AND METHODS

Study area, sampling and element measurement. This study was conducted along a natural precipitation gradient in Hexi Corridor, Gansu Province, northwest China. Mean annual precipitation (MAP) ranges from 45.7 to 127.5 mm. Mean annual temperature (MAT) ranges from 6 to 8.8 °C. Aridity index (AI) [Deng et al., 2006] ranges from 1.21 to 1.83 (Table 1). Most precipitation falls during the growing season (April – August).

Table 1

The main geographical and climatic conditions of the six experimental sites

Sites	Parameters								
	Longitude	Latitude	Altitude, m	MAT, °C	MAP, mm	MAE, mm	AI	TN, mg g^{-1}	TP, mg g^{-1}
Zhangye	100°38′ E	38°46′ N	1617	7	127.5	2047.9	1.21	0.80	0.71
Jiayuguan	97°49′ E	39°46′ N	2120	6	80	2149	1.43	0.66	0.62
Jiuquan	98°41′ E	39°52′ N	1379	8.2	67	3000	1.65	0.74	0.25
Yumen	96°44′ E	40°02′ N	1924	6.9	67.8	3000	1.65	0.41	0.23
Shulehe	96°05′ E	40°34′ N	1386	8.8	50	3000	1.78	0.55	0.31
Guazhou	95°38′ E	40°47′ N	1250	8.8	45.7	3140.6	1.83	0.35	0.27

Note. Aridity index (AI) = log (MAE/MAP), where MAE is the mean annual evaporation and MAP is the mean annual precipitation. MAT is mean annual temperature. TN is total soil nitrogen. TP is total soil phosphorus.

T a b l e 2

Statistics of leaf and root nitrogen (N), phosphorus (P) and N: P ratios for plant species analyzed by this study

Data	N (mg g^{-1})			P (mg g^{-1})			N : P ratios		
	Leaf		Root	Leaf		Root	Leaf		Root
	April	August	April	April	August	April	April	August	April
Max	55.84	23.27	16.74	7.18	0.87	0.50	14.21	53.99	58.26
Min	27.51	12.44	6.50	2.19	0.29	0.16	6.87	25.37	19.97
Mean	40.63	18.48	11.97	3.73	0.51	0.36	11.13	38.78	34.98
SD	8.69	2.88	2.46	1.04	0.17	0.08	1.44	8.67	9.19
n	46	30	30	46	30	30	46	30	30

Leaves were sampled twice in late-April and mid-August 2009. Fully expanded and outer-canopy leaves were collected. In order to minimize disturbance of the sampling area, roots were only sampled once in late-April to analyze the stoichiometric pattern between leaves and roots along aridity gradients. At each site, a minimum of seven plant individuals were used for leaf sampling and five were used for root sampling (to minimize disturbance of the sampling area) in order to ensure the representativeness of the pool collected. The entire taproot and all coarse roots were excavated and brought back to the laboratory. The plant samples were washed with distilled water and oven-dried to a constant weight. Before chemical analysis, all samples were ground to fine powder and sieved with a 1 mm-mesh screen and then digested in the solution of H_2SO_4 + H_2O_2. We took soil samples from three soil layers (0–5 cm, 5–10 cm and 10–15 cm) and mixed them together in each sampling site. The soil samples were air-dried and ground into small particles. N and P concentrations of plant and soil were measured using SAN^{++} system elemental analyzer (SKALAR, Netherland).

Data analysis. Analysis of covariance (ANCOVA) was used to search for the differences in nutrient concentrations with respect to different parts of plant, aridity gradients and their interactions. Aridity index (AI) was included as a covariate. The homogeneity of variance among groups was assessed by Levene's test. The relationships among N, P and N: P ratios were analyzed by correlation analysis. The relationships between nutrient status and aridity gradients were analyzed using simple linear regression analysis and shown by box-and-whisker plots.

RESULTS AND DISCUSSION

Patterns of N, P and N: P ratios. Among different sites, leaf N, P and N: P ratios exhibited large variations, ranging from 27 to 56 mg g^{-1}, 2 to 7 mg g^{-1} and 6 to 14, respectively (Table 2). In late-April, means of leaf N, P and N: P ratios were 40.63 mg g^{-1}, 3.73 mg g^{-1} and 11.13, respectively (see Table 2). In mid-August, means of leaf N, P and N: P ratios were 18.48 mg g^{-1}, 0.51 mg g^{-1} and 38.78, respectively (see Table 2). Root N, P and N: P ratios appeared to vary greatly, ranging from 6 to 17 mg g^{-1}, 0.1 to 0.5 mg g^{-1} and 20 to 58, respectively (see Table 2). In late-April, means of root N, P and N: P ratios were 11.97 mg g^{-1}, 0.36 mg g^{-1} and 34.98, respectively (see Table 2). Across all sites, N and P were highly correlated in both leaf and root (Fig. 1). Both leaf and

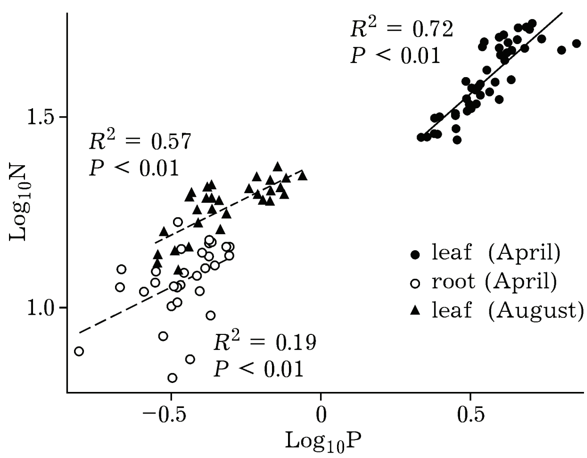

Fig. 1. Relationships between N and P of different plant parts among seasons of the whole sampling sites

Table 3

Correlation coefficients calculated between NP (total N:P including leaf and root), P (total P), N (total N), ALN (April leaf N), ALP (April leaf P), ALNP (April leaf N:P), ARN (April root N), ARP (April root P), ARNP (April root N:P), ELN (August leaf N), ELP (August leaf P) and ELNP (August leaf N:P)

	NP	P	N	ALN	ALP	ALNP	ARN	ARP	ARNP	ELN	ELP	ELNP
NP	1.000	−0.865**	−0.717**	0.000	−0.408**	−0.996**	0.104	0.029	0.022	−0.165	−0.114	0.158
P		1.000	0.943**	0.888**	0.999**	−0.391**	0.467**	0.275	0.096	0.560**	0.276	−0.011
N			1.000	0.999**	0.887**	0.026	0.631**	0.356	0.101	0.604**	0.345	−0.027
ALN				1.000	0.889**	0.019	0.618**	0.357	0.092	0.591**	0.342	−0.027
ALP					1.000	−0.390**	0.477**	0.282	0.102	0.569**	0.285	−0.023
ALNP						1.000	0.135	0.031	0.053	−0.158	−0.114	0.168
ARN							1.000	0.565**	0.282	0.698**	0.425*	−0.094
ARP								1.000	−0.560**	0.393*	0.417*	−0.391*
ARNP									1.000	0.238	−0.003	0.261
ELN										1.000	0.737**	−0.369*
ELP											1.000	−0.856**
ELNP												1.000

N o t e. Statistical significance: * – 0.05; ** – 0.01.

root N: P ratios were highly negatively correlated with P, but slightly with N (Table 3, Fig. 2).

Relationships between N, P and N: P ratios and aridity gradients. There were significantly higher N and P of leaves than those of roots along aridity gradients (Table 4, Fig. 3). N and P in leaves were positively correlated with AI, but mean leaf N: P ratios changed slightly along AI (see Fig. 3). N, P and mean N: P ratios in roots were positively correlated with AI (see Fig. 3). N and P of leaves changed faster than those of roots along aridity gradients (see Fig. 3).

Patterns of N, P and N: P ratios. The patterns of plant stoichiometry can be influenced by biotic and abiotic factors, such as tissue types, seasons and habitats [Silla, Escudero, 2003; Beale, Long, 1997; Güsewell, 2004]. Our results indicated that the means of both leaf N and P were high in April and low in August (see Table 2). Our results are consistent with previous studies and the reason is that N and P are generally high in young leaves and decline during the growing season because they either become diluted by increasing leaf biomass and structural material, or are translocated out of leaves before senescence [Zhang et al., 2013; Chapin III, Kedrowski, 1983]. Furthermore, flexible or non-homeostatic stoichiometric pattern is advantageous for plants, because the maintenance of stoichiometric homeostasis is energetically expensive for plants [Dijkstra et al., 2012].

Soil nutrient condition is one of the important factors to determine plant nutrient condition [Gьsewell, 2004]. Our study demonstrated that N and P were highly correlated in both leaf and root (see Fig. 1). This result is in agreement with previous studies, and He et al. [2008] showed that this correlation is stronger at the inter-site level than the within-site level. This phenomenon indicates that N and P availability can be increased or limited simultaneously by a habitat [He et al., 2008]. The results also suggest a coupling of the supply of N and P in our research sites.

Leaf N: P ratios can be indicators of nutrient limitation, suggesting that N: P ratio < 14 or > 16 generally correspond to N or P limitation [Koerselman, Meuleman, 1996]. Our results might imply that *N. tangutorum* was relatively limited by N in April (mean = 11.13)

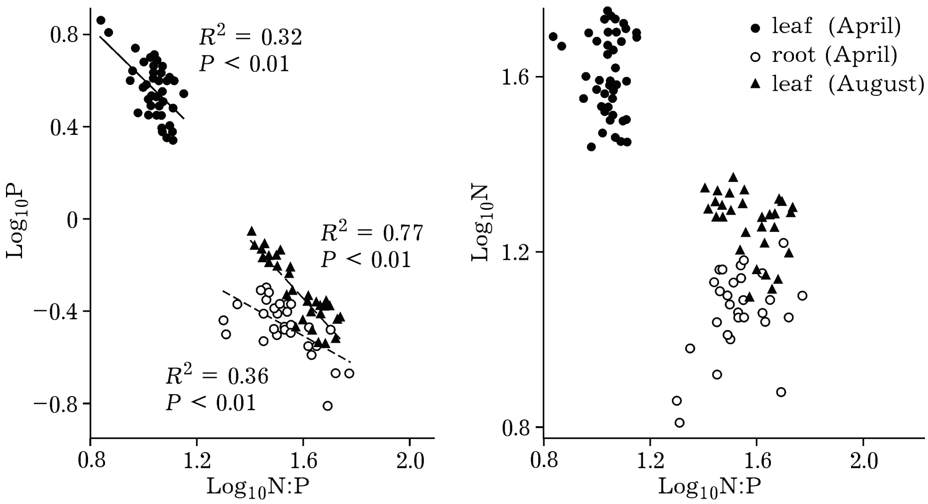

Fig. 2. Relationships between N : P ratios of different plant parts versus N and P of different plant parts among seasons of the whole sampling sites

and by P in August (mean = 38.78) (see Table 2). Two potential explanations can be proposed. The first reason is the differences in leaf ages. Previous studies indicated that leaf N: P ratios increased during the growing season [Chidumayo, 1994], and the cause of changes in N: P ratios was a drastic decline in P [Egren, 2008]. Near the end of the growing season, mature leaves no longer grow and greatly reduce the requirement of P for RNA. Therefore, nucleic-acid P can be mobilized and translocated to young leaves or other organs, leading to higher N: P ratios in mature leaves [Gьsewell, 2004]. Secondly, such a low level of leaf P may be caused by the low level of soil P. Plant and soil P are generally coupled at ecosystem scales, and soil P in most areas of China is below the global average [Han et al., 2005]. Drought could decrease the availability of soil P [Sardans, Pecuelas, 2004], and P becomes progressively less available to a plant relative to N as soil is dried gradually [Dijkstra et al., 2012]. In addition, our analysis showed that both leaf and root N: P ratios were highly correlated with P (see Table 3), suggesting that *N. tangutorum* are probably P-limited in most soils of Hexi Corridor.

Relationships between nutrient patterns and aridity gradients. A plant that has adapted to stress environment, can store more nutrients than a plant in benign environment [Chapin III et al., 1990]. At large scale, leaf N and P increase with decreasing precipitation [Wright et al., 2001; Wei et al., 2011], suggesting that higher leaf N and P are general characteristics in drier areas [Wei et al., 2011]. Our results are consistent with previous studies (see Fig. 3). Plants can use effective water-use strategies to reduce water loss. High leaf N could help achieve a given photosynthetic

Table 4

Summary of ANCOVA for the effects of plant parts (leaf and root) and aridity index (AI) on Nitrogen (N) and phosphorus (P) and N: P ratios in April. DF is degree of freedom

Variations	N		P		N : P ratios	
	DF	F	DF	F	DF	F
Plant parts	1,72	44.132**	1,72	15.819**	1,72	0.215
AI	1,72	167.752**	1,72	22.178**	1,72	8.383**
Plant parts · AI	1,72	0.691	1,72	4.167*	1,72	9.675**

Note. Data were log-transformed. * – $P \leq 0.05$; ** – $P \leq 0.01$.

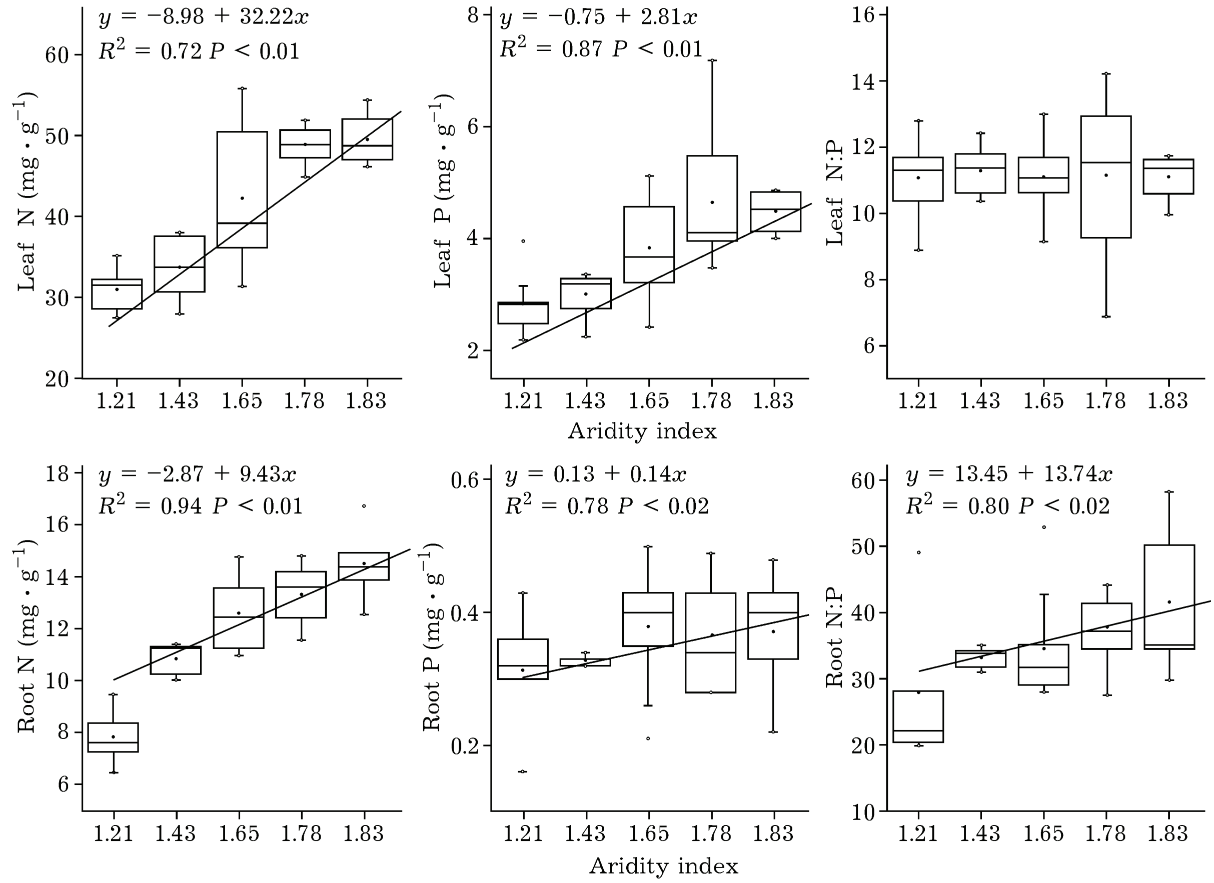

Fig. 3. Relationships between N, P and N : P ratios of different plant parts and aridity index in April. In the box-and-whisker plot, the upper and lower edges of the box indicate the 75th and 25th percentile of the distribution, respectively. The whiskers extend to the lowest and highest values. The line within the box represents the median. The point within the box represents the mean

capacity at low stomatal conductance, resulting in saving of water [Wright et al., 2001]. Leaf P shows a similar relationship with photosynthetic capacity. Photosynthetic capacity and leaf P are related because bioenergetics molecules such as ATP and NADPH are involved in metabolic processes [Wright et al., 2001].

Variation is coordinated between leaf and root traits, and significant correlations are found for N and P [Liu et al., 2010; Kerkhoff et al., 2006; Tjoelker et al., 2005]. Consistently, our results showed that increases in leaf N and P were accompanied by increases in the N and P of roots along aridity gradients (see Fig. 3). Nutrient-rich leaves generally have high metabolic and photosynthetic activity, which require relatively higher nutrient investments in stems and roots [Kerkhoff et al., 2006]. In addition, higher nutrient concentrations in stems and roots may indicate high rates of nutrient recycling in the phloem, which is associated with increased photosynthate export and phloem loading [Kerkhoff et al., 2006; Marschner et al., 1997]. Thus, leaf N and P increase with increasing root N and P.

Our study demonstrated that mean leaf N: P ratios changed slightly along aridity gradients in April, but mean root N: P ratios increased with increasing AI (see Fig. 3). Rapid spring growth is supported more by stored nutrients than by concurrent absorption [Chapin III, 1980], therefore N: P ratios of young leaves may be slightly influenced by relative availability of soil nutrient at the very beginning of growing season. Another possibility is that *N. tangutorum* might keep a critical leaf N: P ratio to maintain physiological activity and rapid spring growth, resulting in slight change of leaf N: P ratios along aridity gradients in

April. When considering only roots, variations in root N: P ratios along aridity gradients may be caused by different rates of change between root N and P. Under drought stress, the rate of P diffusion to the root is more limited than N [Dijkstra et al., 2012], causing decline in P acquisition. As mentioned above, both root N and P increased with increasing drought stress; the soils of our research sites were P-limited, therefore root N increased faster than root P along aridity gradients (see Fig. 3), resulting in increases in root N: P ratios. Thus, we suggest that leaf N: P ratios could indicate nutrient status at different plant growth stages, and root N: P ratios could show us whether there is shortage of soil nutrients.

This study was supported by Ministry of Science and Technology of China (2011AA100503) and Natural Science Fund of China (30871470).

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