

Leaf nitrogen:phosphorus stoichiometry across Chinese grassland biomes

Jin-Sheng He · Liang Wang · Dan F. B. Flynn ·
Xiangping Wang · Wenhong Ma · Jingyun Fang

Received: 9 December 2006 / Accepted: 22 October 2007 / Published online: 16 November 2007
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Abstract Leaf N and P stoichiometry covaries with many aspects of plant biology, yet the drivers of this trait at biogeographic scales remain uncertain. Recently we reported the patterns of leaf C and N based on systematic census of 213 species over 199 research sites in the grassland biomes of China. With the expanded analysis of leaf P, here we report patterns of leaf P and N:P ratios, and analyze the relative contribution of climatic variables and phylogeny in structuring patterns of leaf N:P stoichiometry. Average values of leaf P and N:P ratio were 1.9 mg g^{-1} and 15.3 (mass ratio), respectively, consistent with the previous observation of a higher N:P ratio in China's flora than the global averages (ca. 13.8), resulting from a lower leaf P. Climatic variables had very little direct correlation with leaf P and N:P ratios, with growing season precipitation and temperature together explaining less than 2% of the variation, while inter-site differences and within-site phylogenetic variation explained 55 and 26% of the total variation in leaf P and N:P ratios. Across all sites and species, leaf N and P were highly positively correlated at all levels. However, the

within-site, within-species covariations of leaf N and P were weaker than those across sites and across species. Leaf N and P relationships are driven by both variation between sites at the landscape scale (explaining 58% of the variance) and within sites at the local scale (explaining 24%), while the climatic factors exerted limited influence (explaining less than 3%). In addition, leaf N:P ratios in two dominant genera *Kobresia* and *Stipa* had different responses to precipitation. This study suggests that geographic variation and between-species variation, rather than climatic variation, are the major determinants of grassland foliar stoichiometry at the biome level.

Keywords Leaf traits · Biogeographic patterns · Inner Mongolia · The Tibetan Plateau · Xinjiang

Introduction

C, N and P cycling constrain most ecosystem processes (Aerts and Chapin 2000; Chapin 1980; Tilman 1982). However, dynamics of individual elemental cycles cannot be studied in isolation, because C, N and P interact closely in terrestrial ecosystems (Chapin et al. 2002; Chapin and Shaver 1989; Vitousek 1982). Ecological stoichiometry, which approaches ecological questions by asking how the balance of the multiple elements required by organisms affects processes and interactions, provides new perspectives for studying ecosystem processes at different levels, from leaf physiology to ecosystem productivity (Dodds et al. 2004; Hessen et al. 2004; Sterner and Elser 2002). Recently, a particular focus of ecological stoichiometry has been to document large-scale patterns of, and the driving factors for, plant C:N:P stoichiometry (Güsewell 2004; Kerkhoff et al. 2006; Moe et al. 2005; Reich and Oleksyn 2004).

Communicated by Guy Midgley.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0912-y) contains supplementary material, which is available to authorized users.

J.-S. He (✉) · L. Wang · D. F. B. Flynn · X. Wang · W. Ma ·
J. Fang
Department of Ecology, Peking University,
5 Yiheyuan Road, 100871 Beijing, China
e-mail: jshe@pku.edu.cn

D. F. B. Flynn
Department of Ecology, Evolution,
and Environmental Biology, Columbia University,
New York, NY 10027, USA

N and P status and N:P stoichiometry in plant tissues, especially in leaves, have been studied intensively to determine how these factors limit plant growth (e.g., Ackerly 2004; Cornelissen et al. 1997; Cunningham et al. 1999; Elser et al. 2000; Güsewell and Koerselman 2002; Kerkhoff et al. 2005; Kerkhoff et al. 2006; Reich et al. 1999; Thompson et al. 1997; Wright et al. 2004). A number of studies have documented the influence of phylogeny and climate on leaf N, P and N:P ratios via compilations of many small-scale studies (Hou 1982a; Koerselman and Meuleman 1996; Körner 1989; Wright et al. 2005). These efforts have revealed a decline in leaf N and P and increase in the N:P ratio toward the equator as mean annual temperature (MAT) increases (McGroddy et al. 2004; Reich and Oleksyn 2004). However, studies from Chinese terrestrial plants found that leaf P was considerably lower than the global averages that excluded Chinese species, resulting in a markedly higher N:P ratios than the global average (Han et al. 2005). These unique patterns highlight the need for comprehensive, large-scale data sets, collected with uniform methods, in understudied regions (Reich 2005).

Recently, we reported the large-scale patterns of leaf C and N in the grassland biomes of China (He et al. 2006a). That paper focused on the comparison of leaf C and N between Chinese grassland species and the global data set of Reich and Oleksyn (2004), revealing that when the Tibetan data were pooled with the global dataset, the previously observed positive correlation between leaf N and MAT at very cold environments disappeared. Here we report expanded results for grassland plants based on systematic investigation on a wide range of grassland types across China, now encompassing leaf P. Our objectives were to: (1) document the patterns of P concentration and N:P stoichiometry in different functional groups, ecosystems and biogeographic regions; and (2) determine the effect of phylogeny and climatic factors in structuring leaf N:P stoichiometry of Chinese grassland species.

Materials and methods

Leaf samples of 213 species from 41 families over 199 research sites were collected in three biogeographic regions: temperate grassland on the Inner Mongolia Plateau in northern China, alpine grassland on the Tibetan Plateau, and mountain grassland in the Xinjiang mountain areas of northwestern China. Following a vegetation map of China (Hou 1982b), each site was assigned to one of nine main vegetation types: alpine meadow, alpine scrub, alpine steppe, meadow steppe, typical steppe, desert steppe, temperate meadow, temperate scrub, and desert. Descriptions of the study region, sampling protocol, leaf C and N measurements, and the climate data used are detailed elsewhere

(He et al. 2006a, 2006b). In brief, newly mature leaves of five to ten plants of each species were collected, sun-dried in the field, and oven-dried at 60°C upon returning to the laboratory. Since these data were collected by a single team of researchers using standardized collection protocols, this analysis avoids the difficulty of heterogeneous data which previous large-scale analyses of leaf traits have encountered.

We measured total P concentrations by a molybdate/stannous chloride method (Kuo 1996) after H₂SO₄–H₂O₂–HF digestion (Bowman 1988) quantified by reference to a national standard material with known P concentration (reference code GBW08513; General Administration of Quality Supervision, People's Republic of China). N was assayed for each sample using an elemental analyzer (2400 II CHN elemental analyzer; Perkin-Elmer, USA).

Mass ratios of N:P are used here to facilitate the comparison with the terrestrial ecology literature (Güsewell 2004; Sterner and Elser 2002). Of the 213 species investigated, 92 species were sampled at more than one site. We classified species into the following functional groups on the basis of morphology and physiology: grasses (71 species), herbs (104 species) and woody (38 species), and legumes (32 species) or non-legumes (181 species). If we define the occurrence of a particular species at a particular site as a population (species/site combinations), the dataset (Electronic Supplementary Material, S1) contained 525 populations.

General linear models (GLM) and *F*-tests were used for ANOVA. Explanatory terms were related to environmental variation between sites (climatic variables, vegetation type, site), functional group and to phylogenetic variation among species (family, genus, and species). We entered functional group and phylogenetic terms after the environmental terms to analyze the influence of climatic and other environmental terms on variation among and within species (Schmid et al. 2002). The sequence among the phylogenetic terms was families, genus, and then species. Climatic variables are growing season precipitation (GSP), and mean growing season temperature (GST), which were selected as the most influential climate factors in multivariate analysis. Here, “growing season” refers to May through August. Results from climate data on an annual basis [MAT, and mean annual precipitation (MAP)] did not differ substantially from those on a growing season basis, but we use growing season data to more accurately capture the environmental variation important to plant growth. We did not include interactions between climatic and phylogenetic terms in our final analysis because they only explained a very small amount of variation.

We analyzed leaf N–P correlation by partitioning the covariance between the dependent variables into components due to the explanatory terms used in the GLM ANOVAs

(Falconer and Mackay 1996). We used scatter plots to visualize the N–P relationship at different levels of analysis: (1) overall relationship at population level; (2) inter-site relationship (visualized with site means), i.e., the correlation between N and P when the effect of species had been separated out; (3) between-species correlation visualized with site means, i.e., the correlation when the effect of site had been separated out; (4) within-site, within-species relationship, the residual correlation after fitting site and species.

In addition, we examined N:P values in detail for the two dominant genera in Chinese grasslands, the 12 species of *Stipa* and the eight species of *Kobresia*. *Stipa* species are present throughout the study area ($n = 97$ measurements), including one species, *Stipa purpurea*, which was a dominant plant in 17 of the study plots. *Stipa grandis* is one of the two dominant species in Inner Mongolia, and is physiologically limited to drier sites (Chen et al. 2005). Nearly even numbers of measurements of *Stipa* were made in Inner Mongolia, Xinjiang, and Tibet. *Kobresia* species ($n = 46$ measurements) were present only in Tibet and Xinjiang, principally in the former, and tend to be limited to more moist soils (J.-S. He, personal observation). Species from both genera were measured in 14 sites, principally in the high-altitude A Li region of the Tibetan Plateau (data not shown). All statistical analyses were calculated using the statistical software R 2.5.0 (R Development Core Team 2007).

Results

Patterns of leaf P and N:P ratios

For all species, the average values of leaf P and N:P ratios were 1.9 mg g^{-1} and 15.3 respectively (mass ratio; Table 1), consistent with the previous observation (Han et al. 2005) of a higher N:P ratio in China's flora than the global averages of ca. 13.8 (Reich and Oleksyn 2004). Across species, leaf P and N:P ratios varied ca. sixfold and sevenfold, respectively. Overall, the variability in leaf P [coefficient of variation (CV) = 0.44] across all observations (site and species) was somewhat greater than that in N:P ratio (CV = 0.34). Across all species, leaf N and P were highly positively correlated at four levels: population (Fig. 1a), interspecific (Fig. 1b), inter-site (Fig. 1c), and within-site, within-species (Fig. 1d). However, it is evident that the correlations between leaf N and P at the population ($R^2 = 0.32$), interspecific ($R^2 = 0.30$) and inter-site ($R^2 = 0.21$) levels were stronger than that of within-site and within-species ($R^2 = 0.12$) levels. In addition, leaf N:P ratios were highly positively correlated with leaf P, but not with leaf N (Fig. 2), thus the variation in N:P ratios is primarily determined by leaf P.

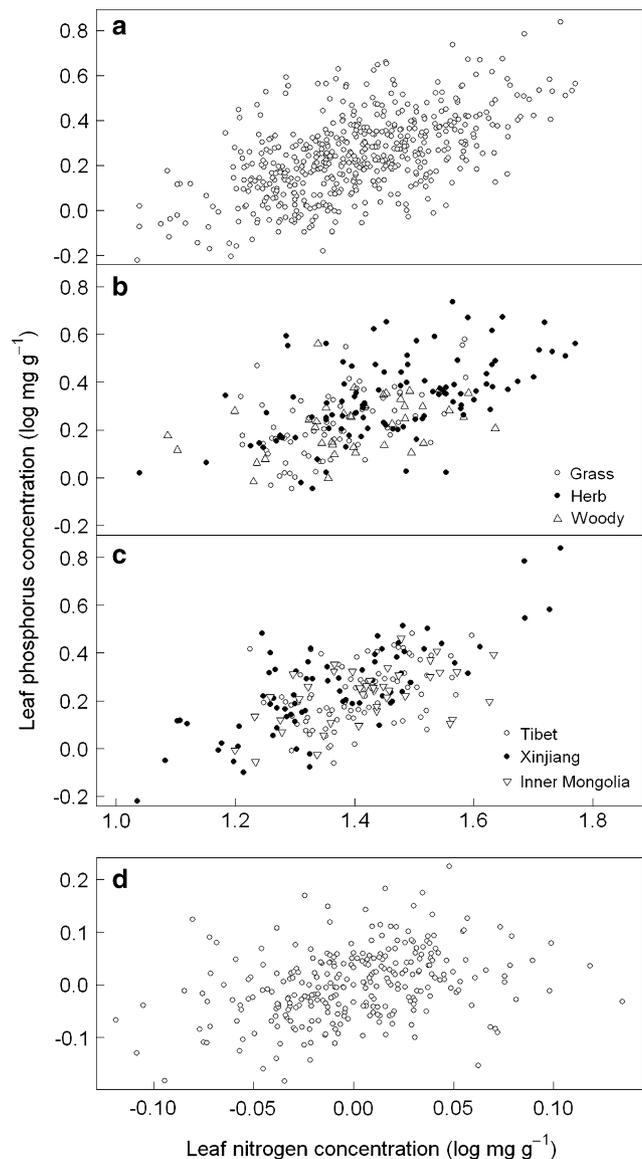


Fig. 1 Scatter plots showing the relationships between leaf N and P concentrations at different levels: **a** population level; **b** interspecific relationship, using species means; **c** regional differences, using site means; and **d** within-site, within-species relationship. Note that all axes are the same except for **(d)**, which shows residual values after accounting for species and site variation

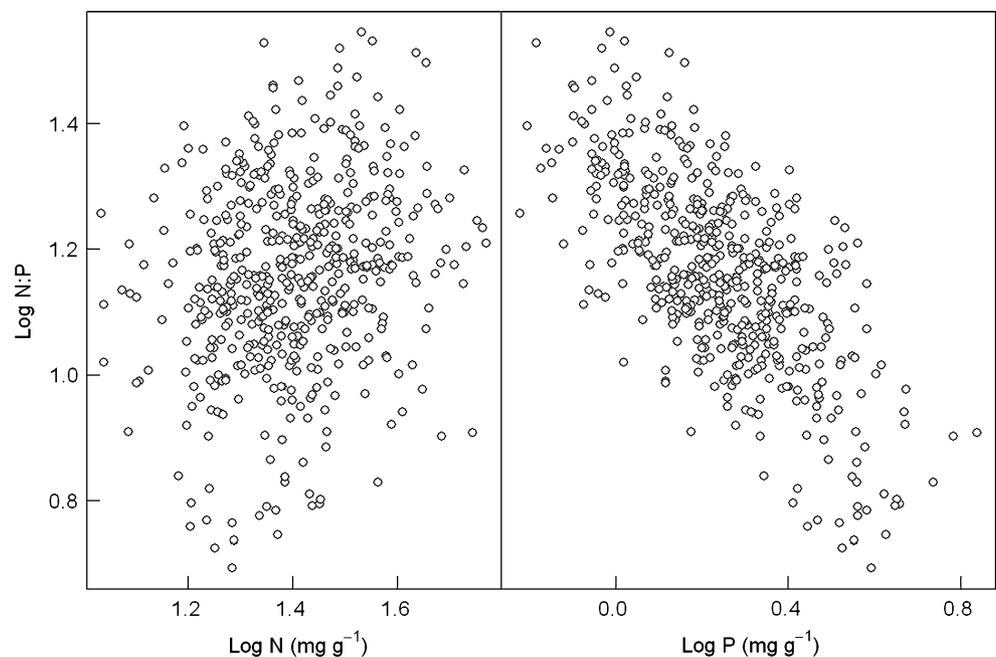
Leaf P and N:P ratios varied across functional groups, ecosystems and biogeographic regions (Table 1). For functional groups, herbs had higher leaf P than grasses and woody species, resulting in lower N:P ratios. Legumes and non-legumes showed no significant difference in leaf P, but legumes had higher N:P ratios than non-legumes. Among different ecosystems, typical steppe and alpine steppe had higher leaf N:P ratios, while the temperate scrubs had the lowest. Although average leaf P was not significantly different among the three biogeographic regions, the northwestern province of Xinjiang had the lowest N:P ratios, with the greatest variance (Fig. 1c).

Table 1 Leaf P and N:P ratios for different function groups, vegetation types and biogeographic regions^a. Number of replicates (site \times species, n), mean value, SD, coefficient of variation (CV; defined as SD/mean) are reported. Differences between each group were tested using a one-way ANOVA with a Tukey post hoc test of significance; significant differences at $P < 0.05$ are indicated by different letters

	n	P (mg g^{-1})			N:P		
		Mean	SD	CV	Mean	SD	CV
Overall	525	1.9	0.84	0.44	15.3	5.20	0.34
Function group							
Grass	261	1.7 a	0.72	0.43	15.8 b	5.37	0.34
Herb	181	2.3 b	0.96	0.42	14.2 a	4.81	0.34
Woody	83	1.8 a	0.56	0.31	15.9 b	5.19	0.33
Legume							
No	467	1.9 a	0.86	0.46	14.8 a	5.01	0.34
Yes	58	2.0 a	0.66	0.33	19.0 b	5.23	0.28
Vegetation type							
Desert	11	2.3	1.74	0.74	14.7	6.03	0.41
Alpine meadow	176	2.0	0.85	0.42	14.6	4.68	0.32
Temperate meadow	12	2.0	0.66	0.34	14.6	5.65	0.39
Alpine scrub	39	1.9	0.45	0.24	15.2	4.37	0.29
Temperate scrub	19	2.1	0.65	0.31	13.7	4.24	0.31
Alpine steppe	90	1.8	0.92	0.50	16.5	5.92	0.36
Desert steppe	59	1.8	0.95	0.53	15.4	5.00	0.33
Meadow steppe	32	1.6	0.75	0.46	15.1	5.86	0.39
Typical steppe	87	1.8	0.68	0.38	16.1	5.51	0.34
Region							
Inner Mongolia	129	1.8 a	0.71	0.39	16.4 b	5.68	0.35
Tibet	257	1.9 a	0.81	0.43	15.7 b	5.26	0.33
Xinjiang	139	2.0 a	1.00	0.49	13.4 a	4.02	0.30

^a Leaf C and N of the same dataset were reported previously in He et al. (2006a)

Fig. 2 Scatter plots showing the relationships between leaf N:P ratios versus N concentration (a) and P concentration (b) in grassland biomes of China



Influence of climate on leaf P and N:P ratios

The two climatic variables, precipitation (GSP) and temperature (GST), had little direct influence on leaf N and N:P

ratios, together explaining less than 2% of variation in leaf N and N:P ratios (Table 2, Fig. 3). Differences between sites themselves (climate, vegetation, soil conditions and other factors) explained greater than 55% of the total variation in

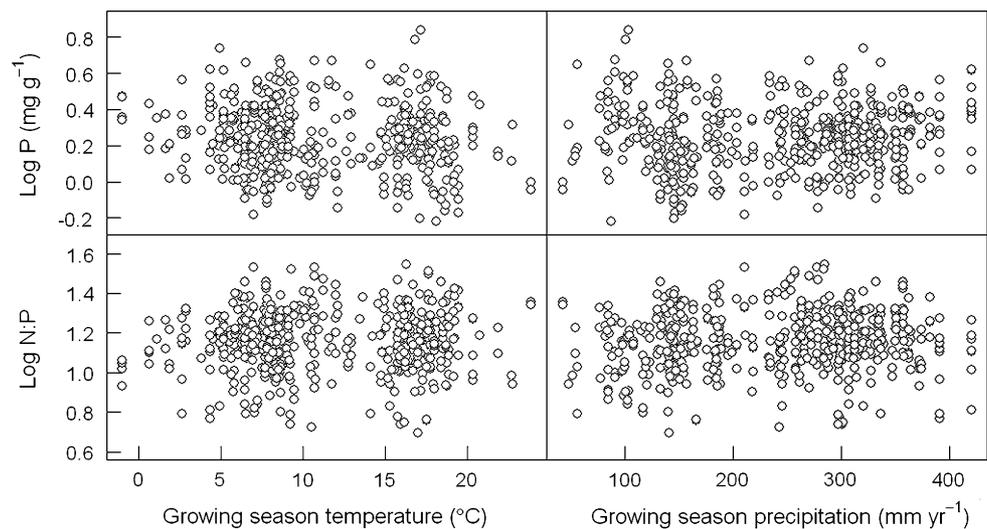
Table 2 Summary of the general linear models for the effect of environmental variation [mean growing season temperature (*GST*), growing season precipitation (*GSP*), vegetation type, site] functional

group and phylogenetic variation (family, genus, species) on leaf P and N:P ratios. Leaf traits were log-10 transformed prior to analysis. *MS* Mean sum of square, %*SS* percentage of sum of squares explained

Terms ^a	<i>df</i>	P				N:P			
		<i>MS</i>	<i>F</i>	<i>P</i>	% <i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i>	% <i>SS</i>
GSP entered first									
GSP	1	0.048	1.06	0.304	0.29	0.425	2.68	0.103	0.68
GST	1	0.111	2.45	0.119	0.66	0.646	4.07	0.045	1.03
GST entered first									
GST	1	0.157	3.47	0.064	0.94	0.179	1.13	0.290	0.28
GSP	1	0.002	0.04	0.832	0.01	0.892	5.62	0.019	1.42
Other terms									
Vegetation	8	0.068	1.52	0.154	3.28	0.424	2.67	0.008	5.39
Site	199	0.045	4.14	0.000	53.87	0.159	2.91	0.000	50.18
Functional group	2	0.661	45.10	0.000	7.92	0.554	7.19	0.001	1.76
Legume (yes/no)	1	0.014	0.97	0.328	0.08	2.623	34.04	0.000	4.17
Family	32	0.036	1.32	0.168	6.85	0.093	0.97	0.521	4.75
Genus	69	0.027	1.85	0.003	11.20	0.096	1.25	0.163	10.52
Species	91	0.015	1.34	0.065	7.99	0.077	1.41	0.039	11.14
Residuals	120	0.011			7.85	0.055			10.41

^a Explanatory terms are listed in the order of their entry into the models

Fig. 3 Relationships between leaf P, N:P ratios and growing season temperature, growing season precipitation in grassland biomes of China. *yr* Year



leaf P and N:P ratios, while within-site phylogeny (family, genus and species) explained an additional 26% of the total variation.

When the positive covariance between leaf N and P was partitioned into components due to environmental and phylogenetic variations (Table 3), the climatic variables and vegetation type together explained less than 3% of the total covariance, and remaining differences between sites explained 58% of the total covariance. Thus, to a large extent, the positive covariance between leaf N and P reflects a large-scale inter-site covariance. In addition, phylogenetic relationships explained an additional 24% of the total covariance, so the tight relationship between N and P

is both a result of edaphic conditions at sites and phylogenetic constraints.

Leaf N, P and N:P ratios of two prevalent genera, *Stipa* and *Kobresia*

Stipa and *Kobresia* are the first and second most prevalent genera in Chinese grasslands. N:P ratios for *Stipa* and *Kobresia* were similar, although leaf N was lower in *Stipa* than in *Kobresia* (Table 4). Linear regressions revealed some difference in the relationships between leaf N, P and N:P ratios and GST, GSP. For *Kobresia*, leaf N negatively correlated with GST, but positively correlated with GSP. In

Table 3 Decomposition of covariances using the sum of products for the effects of environmental variation (climate, vegetation type and site), functional group, and phylogeny (family, genus, species) on the relationship between leaf N and P concentrations. Mean SP Mean sum of products explained, %SP percentage of sum of products explained

Effect	df	Mean SP	P	%SP	Error term
Environmental variation between sites					
GSP entered first					
GSP	1	0.109	0.024	1.5	Site
GST	1	-0.007	0.575	-0.1	Site
GST entered first					
GST	1	0.0820	0.049	1.1	Site
GSP	1	0.0204	0.325	0.3	Site
Other terms					
Vegetation	8	0.014	0.701	1.6	Site
Site	199	0.021	0.000	58.4	Residuals
Taxonomic variation within sites between species					
Functional group	2	0.415	0.000	11.6	Species
Legume (yes/no)	1	-0.070	0.000	-1.0	Species
Family	32	0.020	0.021	9.2	Genus
Genus	69	0.011	0.000	11.0	Species
Species	91	0.003	0.038	4.0	Residuals
Residual covariance within sites and within species ^a					
Residuals	119	0.002	0.000	3.7	

^a The significance of the residual mean sum of products term (=residual covariance) was assessed by fitting the residuals of the two leaf traits against each other and correcting the residual df for the number of fitted parameters

Table 4 Leaf N, P and N:P ratios in *Stipa* and *Kobresia*, the two dominant genera in Chinese grassland. Number of replicates (*n*), mean value, SD, CV (defined as SD/mean) are reported. Differences between each group were tested using a one-way ANOVA with a Tukey post hoc test of significance; significant differences at $P < 0.05$ are indicated by different letters

	<i>n</i>	N (mg g ⁻¹)			P (mg g ⁻¹)			N:P		
		Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
<i>Kobresia</i>	46	23.9 ^b	4.06	0.17	1.6 ^a	0.70	0.44	16.6 ^a	4.92	0.30
<i>Stipa</i>	97	21.4 ^a	5.50	0.26	1.4 ^a	0.57	0.41	16.8 ^a	5.24	0.31

contrast, no clear trend between leaf N and GST, GSP was observed in *Stipa* (Fig. 3). It is noteworthy that leaf N:P ratios of *Stipa* increased with GSP, the limiting factor for the growth of steppe (Fig. 4).

Discussion

Patterns of N:P stoichiometry for Chinese grassland species

This work presents, to our knowledge, the largest single survey of leaf N:P stoichiometry of grassland species. Our

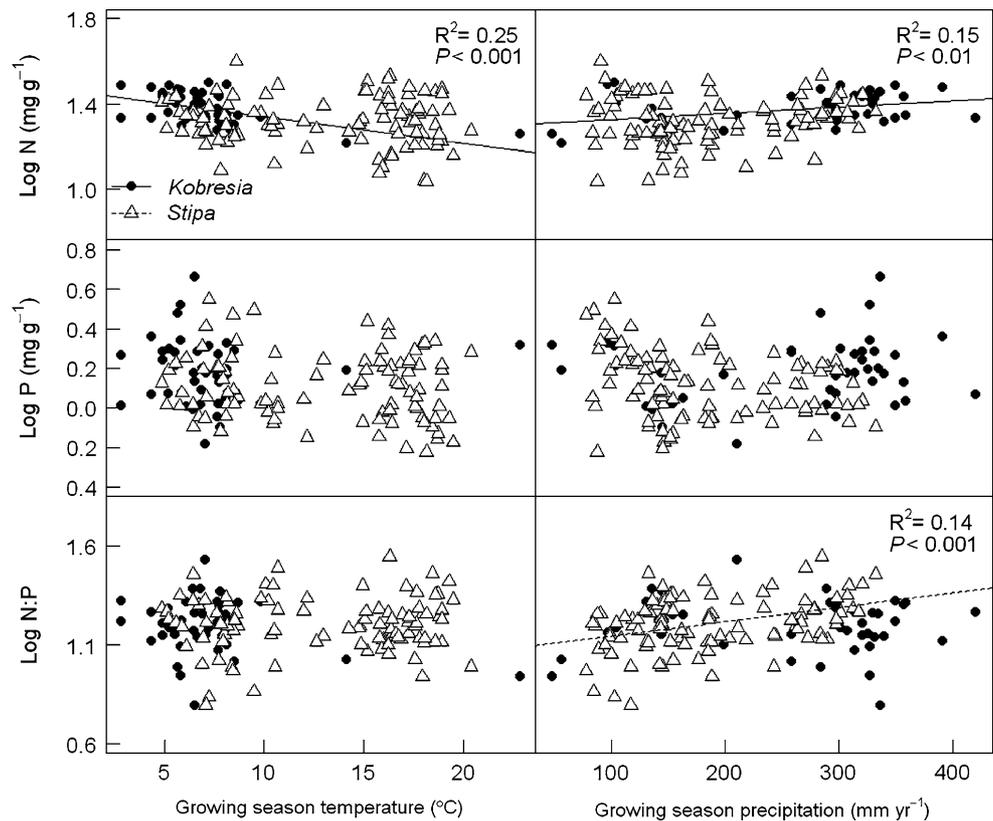
results show that leaf P (averaged 1.9 mg g⁻¹) of Chinese grassland species was significantly lower than that of the herbaceous flora of England (averaged 2.7 mg g⁻¹ for 83 species) reported by Thompson et al. (1997), resulting in N:P ratios for Chinese grassland plants 42% higher than those of England.

N:P ratios for grassland species in Xinjiang were markedly lower than for the two other regions. We previously reported stable leaf C:N ratios in Inner Mongolia, the Tibetan Plateau, and Xinjiang (He et al. 2006a), using the same set of plant samples. While leaf N varied little between the three biogeographic regions on average, leaf P varied widely, with Xinjiang exhibiting the highest level of leaf P. A nationwide soil survey of China that revealed arid soils (particularly the frigid desert soils) in Xinjiang are P rich, with a total P density of $19.1 \times 10^2 \text{ g m}^{-3}$ (Zhang et al. 2005), thus emphasizing the importance of edaphic factors in controlling foliar N:P. Across all regions, the relatively low leaf P is consistent with the findings of Han et al. (2005), who proposed that the low soil P content at the national scale probably contributes to a low leaf P and a high N:P ratio in China's flora.

The present study demonstrated that, across all grassland species in China, leaf N and P were highly positively correlated, and this correlation was stronger at the inter-site and interspecific level than the within-site, within-species level. This result is in agreement with previous studies that show, when species are sampled at different sites, leaf N and P typically correlate with each other (reviewed by Güsewell 2004). This was explained by the strong covariations of soil N and P, since within regions, habitats tend to be rich or limited in both N and P availability (Güsewell and Koerselman 2002; Sterner and Elser 2002).

Why, then, did this biogeographic variation in leaf P and N:P ratio occur, with lower N:P in Xinjiang, while generally leaf N and P were strongly correlated? Two potential explanations can be proposed, each supported to an extent by previous research. First, species differ in their optimal N:P ratios for growth and reproduction, with species-specific homeostasis achieved by nutrient-balancing mechanisms (Kay et al. 2005; Knecht and Goransson 2004; Sterner and Elser 2002). Because environmental filters determine the possible species pool within biogeographic regions, and community assembly within sites, then different species composition alone will lead to local-scale and biome-scale differences in N:P ratios. For example, environmental conditions such as growing season length, GST, and ultraviolet radiation significantly determine plant composition and chemical composition in some regions (Körner 1999). Second, regardless of species composition, soil resources can control N:P ratios. While plant N and P concentrations covary consistently, co-limitation by N and P is not universal, because sources for N and P are different

Fig. 4 Relationships between leaf N, P concentrations and N:P ratios, growing season temperature and growing season precipitation in the two dominant genera of Chinese grasslands, *Kobresia* and *Stipa*



(Schlesinger 1997). P is mainly derived from weathering and its abundance in the soil reflects the physical and chemical characteristics of the local parent material, while N is largely provided by the decomposition of organic matter (Chapin 1980; Hedin et al. 2003; Vitousek 2004). When such variation is accompanied by extreme environmental conditions, the ability of plants to store excess nutrients (Chapin et al. 1990; Lambers et al. 1998) could lead to the decoupling of leaf N and P. In Xinjiang, where relatively high soil P is accompanied by desert conditions and in some places very high elevation, this storage process appears to be a likely contributing factor to the lower N:P ratios. Some evidence suggests the N:P ratio due to storage may generally be low in plants, since fertilized plants accumulate relatively more excess P than excess N (Cordell et al. 2001; Judd et al. 1996). We are currently working to link soil N and P resources at the site level with foliar element concentrations, using soil samples collected simultaneously with these leaf samples.

Main factors shaping leaf N:P stoichiometry

In the present study, we found that climatic variables had very little direct correlation with leaf P and N:P ratios, while the inter-sites difference and within-site phylogeny explained most of the total variation in leaf N and N:P ratios. The absence of a linear relationship between

temperature and N:P is noteworthy, as this study ranged from temperate lowland (Inner Mongolia) to temperate mountainous (Xinjiang) to alpine (Tibetan Plateau) grasslands, with MATs and precipitation ranging from -9.7 to 12.0°C and 68 to 624 mm year^{-1} , respectively. So far, few synthetic studies exist to differentiate how different factors shape the C:N:P stoichiometry.

For a wide spectrum of the Earth's biota, cold-adapted organisms have greater N and P content than warm-adapted organisms (Woods et al. 2003), a pattern particularly strong in plants (Chapin and Oechel 1983). While N:P ratios remain little changed by those findings, falling foliar N and rising P has been widely observed in warmer areas with older soils at the global scale (Kay et al. 2005; Vitousek and Howarth 1991), a pattern driven in part by loss of dissolved organic N in tropical soils (Hedin et al. 2003). However, such global patterns are driven by differences between tropical and temperate regions. For example, Reich and Oleksyn (2004) analyzed 1,280 plant species across 452 locations worldwide, finding that leaf N and P declined, and N:P ratio rose toward the equator as MAT increases across biogeographic and climatic gradients. Likewise, McGroddy et al. (2004) examined global variations in leaf N, P and N:P ratio of entire forested ecosystems, finding parallel global trends. These previous studies have greatly advanced our understanding of the general patterns of leaf N, P and N:P stoichiometry in terrestrial plants. Similarly, Kerkhoff

et al. (2005) reported a pole-ward decline in foliar N:P, although they found that neither leaf N nor P individually varied systematically with latitude.

Here we only considered grasslands from temperate to alpine regions, so differences in soil age and MAT were limited compared to global ranges. Our research shows that the relationship between temperature and foliar N:P is not strong enough to be observable within regions of similar latitude, with similar vegetation composition. However, in the results of Reich and Oleksyn (2004) and McGroddy et al. (2004), each covering ca. 70° latitude from the equator, geographic distribution of evergreen vs. deciduous appeared to be a major contributor to the large-scale N and P patterns. This appears to support our current results that phylogeny was a dominant factor influencing leaf N:P stoichiometry, and the influence of climate factors was limited when only deciduous species were included.

Apart from latitude per se, temperature has been proposed as a driver of foliar N and P concentrations. For example, temperature explains increases in intraspecific leaf nutrient concentrations in terrestrial plants that occur with altitude (Körner 1989). This was further expanded to across-taxa comparisons by the temperature–plant physiological hypothesis (Reich and Oleksyn 2004), which posits that the increases in N and P concentrations at low temperature are an adaptive mechanism to offset temperature-induced reductions in metabolic reaction rates, or to enhance cold hardiness. In addition, these temperature-related trends in N and P concentrations may simply reflect changes in the relative rates of macromolecular synthesis and degradation (Woods et al. 2003). However, these temperature trends in the global analysis may not be caused by temperature itself; rather, temperature-related changes in species composition and life form may be the ultimate drivers of these patterns.

In addition, temperature-induced relative growth rates of vegetation introduce a further potential driver for shifts in leaf N:P at large scale. The growth-rate hypothesis (Elser et al. 2003; Niklas 2006; Niklas et al. 2005) predicts that selection on growth rate will tend to increase whole-body P concentration due to the role that allocation to P-rich ribosomal RNA plays in meeting the protein synthesis demands of rapid growth. For autotrophs, however, N:P ratio may show a more complex behavior with growth rate (Ågren 2004).

Since we previously observed that genus identity was the strongest single factor determining C:N ratios in Chinese grassland plants (He et al. 2006a), searching for patterns of climatic control of foliar traits within genera should maximize our ability to ascribe causation of foliar stoichiometry to climate factors. However, we found only limited and somewhat contradictory patterns. *Stipa* and *Kobresia*, the two prevalent genera in Chinese grasslands, had different

responses to GSP. These distinct patterns may be due to their contrasting habitat specializations. Species of *Stipa* dominate the relatively warm, dry temperate and alpine steppe, while species of *Kobresia* dominate relatively cool and wet alpine meadows (Chen and Wang 2000; Wang 1988). For the former, the limiting factors for plant growth is water, while for the latter, GST (Chen and Wang 2000; Wang 1988). Although further work is needed to address whether this different pattern is related to relative growth rate (Ågren 2004; Niklas 2006), these results highlight the role of species identity in determining community-wide N:P ratios.

Conclusion

Analysis of global foliar nutrient patterns is essential for fundamental ecological studies, as well as for applied studies of biogeochemical cycles (for understanding the biotic component of the C cycle, for example). This study reinforces our previous work, showing that the local-scale differences between sites and species identity, rather than direct climatic variables at the landscape scale, are the major determinants of grassland foliar stoichiometry. The divergence between these results, derived solely from direct measurement in the field, and previous meta-analyses, synthesizing the results of many small-scale studies, is notable. Further work is required to determine whether grassland plant species' coexistence depends on highly divergent C:N:P ratios, whether C:N:P ratios in Chinese grasslands are more constrained than those in other plant groups and whether these trends derived from individual species track those derived from community-level measurements.

Acknowledgements The authors are grateful to Wenyun Zuo, Hongqing Feng, Xuefei Li, Chengjun Ji and Yahan Chen for assistance with field sample collections, Cunzhi Liang, Zhongling Liu, Zongyuan Zhu, and Qing Du for plant species identification in the field, and Bernhard Schmid for statistical advice. Dali Guo and Bernhard Schmid provided constructive comments on an earlier version of the manuscript. This research was supported by the Natural Science Foundation of China (grant no. 30670322, 90411004 to J. S. H. and 90211016 to J. Y. F.). We declare that the work reported here complies with the current laws of the People's Republic of China.

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