ECOSYSTEM ECOLOGY

**Jin-Sheng He · Jingyun Fang · Zhiheng Wang
Dali Guo · Dan F. B. Flynn · Zhi Geng**

Stoichiometry and large-scale patterns of leaf carbon and nitrogen in the grassland biomes of China

Abstract Nitrogen (N) and carbon–nitrogen (C:N) ratio are key foliar traits with great ecological importance, but their patterns across biomes have only recently been explored. We conducted a systematic census of foliar C, N and C:N ratio for 213 species, from 41 families over 199 research sites across the grassland biomes of China following the same protocol, to explore how different environmental conditions and species composition affect leaf N and C:N stoichiometry. Leaf C:N stoichiometry is stable in three distinct climatic regions in Inner Mongolia, the Tibetan Plateau, and Xinjiang Autonomous Region, despite considerable variations among co-existing species and among different vegetation types. Our results also show that life form and genus identity explain more than 70% of total variations of foliar N and C:N ratio, while mean growing season temperature and growing season precipitation explained only less than 3%. This suggests that, at the biome scale, temperature affects leaf N mainly through a change in plant species composition rather than via temperature itself. When our data were pooled with a global dataset, the previously observed positive correlation between leaf N and mean annual temperature (MAT) at very low MATs, disappeared. Thus, our data do not support the previously proposed biogeochemical hypothesis that low temperature limitations on mineralization of organic matter and N availability in soils lead to low leaf N in cold environments.

Keywords Biogeochemical hypothesis · C:N ratio · Inner Mongolia · The Tibetan Plateau · Xinjiang

J. S. He (✉) · J. Fang · Z. Wang · D. Guo · D. F. B. Flynn
Department of Ecology, College of Environmental Sciences and
Key Laboratory for Earth Surface Processes of the Ministry of
Education, Peking University, 5 Yiheyuan Rd.,
100871 Beijing, China
E-mail: jshe@pku.edu.cn
Tel.: +86-10-62754404
Fax: +86-10-62754404

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

Z. Geng
Department of Probability and Statistics,
School of Mathematical Sciences,
Peking University, 100871 Beijing, China

Introduction

Geographical variation in foliar traits is a challenging issue to both plant physiologists and ecologists (Chown et al. 2004; Reich et al. 2003). In particular, leaf nitrogen (N), a key foliar trait and one of the most limiting elements for terrestrial vegetation, has drawn great attention (Aerts and Chapin 2000; Chapin 1980; Körner 1999; Sterner and Elser 2002; Vitousek and Howarth 1991). Several recent studies have synthesized the results of multiple small-scale investigations to examine regional and global patterns of leaf N (Han et al. 2005; McGroddy et al. 2004; Reich and Oleksyn 2004; Wright et al. 2004). For instance, Reich and Oleksyn (2004) found that at the global scale, leaf N showed a weak negative correlation with mean annual temperature (MAT) from the 5–10°C temperature range to the warmest MAT. At very low MATs, however, there was a tendency for leaf N to increase with MAT. In contrast, Wright et al. (2004) found that modification of leaf traits, including leaf N, by climate is surprisingly modest. However, McGroddy et al. (2004) examined global variations in the plant nutrients of entire forested ecosystems, finding that global trends closely approximate those reported by Reich and Oleksyn (2004).

The strength of these syntheses comes from their use of extraordinarily rich datasets, which encompass multiple life forms (LF) at many research sites. However, such methods suffer from the difficulty in assuring standard

data collection. This challenge is particularly acute for relatively weak correlations between traits such as foliar N and climate, because regional-scale trends of leaf N are more subtle than the order-of-magnitude variation within each climatic region. In addition, some large geographic regions, such as Chinese grasslands, have been underrepresented in these previous studies (Han et al. 2005; Wright et al. 2004, 2005). In particular, the Tibetan Plateau, which represents one of the largest alpine grasslands in the world, is poorly represented in the global scale studies (Reich and Oleksyn 2004; Wright et al. 2004).

This study makes an attempt to assess the stoichiometry and patterns of leaf C and N using a large-scale sampling approach for the grassland biomes of China. The diverse habitats of these grasslands provide a unique opportunity to test the previously documented patterns and to explore new trends in foliar traits. The objectives of the present study are to determine whether there are significant differences in C:N stoichiometry under different environmental conditions, and to examine how and to what extent climate modifies leaf N across all grasslands under study. Our study is unique because we systematically sampled leaf samples following the same protocol, thus minimizing the bias in case sampling techniques. The coverage of species and sites encompasses a wide range of grassland types of China, including alpine meadow, temperate meadow, alpine steppe, meadow steppe, typical steppe, desert steppe (Wu 1980), with a few sites of alpine scrubs, temperate scrubs, and desert.

Across our sites, elevation ranges from 575 to 5,249 m, MAT from −9.7 to 12.0°C, and mean annual precipitation from 68 to 624 mm year^{-1}.

Materials and methods

The grasslands of China are distributed in three regions: temperate grassland in the Inner Mongolia Plateau (Chen and Wang 2000), alpine grassland on the Tibetan Plateau (Zhang et al. 1988), and mountain grassland in the Xinjiang mountain areas (Xu 1993) (Fig. 1). The climate of these regions is markedly seasonal, with substantial annual variation in both temperature and rainfall (Table 1).

Sample collection and measurements were conducted in late July and early August of 2002, 2003 and 2004. We selected research sites by visual inspection of the vegetation, selecting sites subject to minimal grazing and other anthropogenic disturbances. At each site, the dominant species were selected for measurement. However, at sites in species-poor grasslands, fewer species were sampled, to as few as one. Nearly all measured plants were in flower. In all, we investigated 213 species, from 41 families over the 199 research sites, with 92 species measured at more than one site. Our dataset (available on request from the lead author) contained 525 species/site combinations.
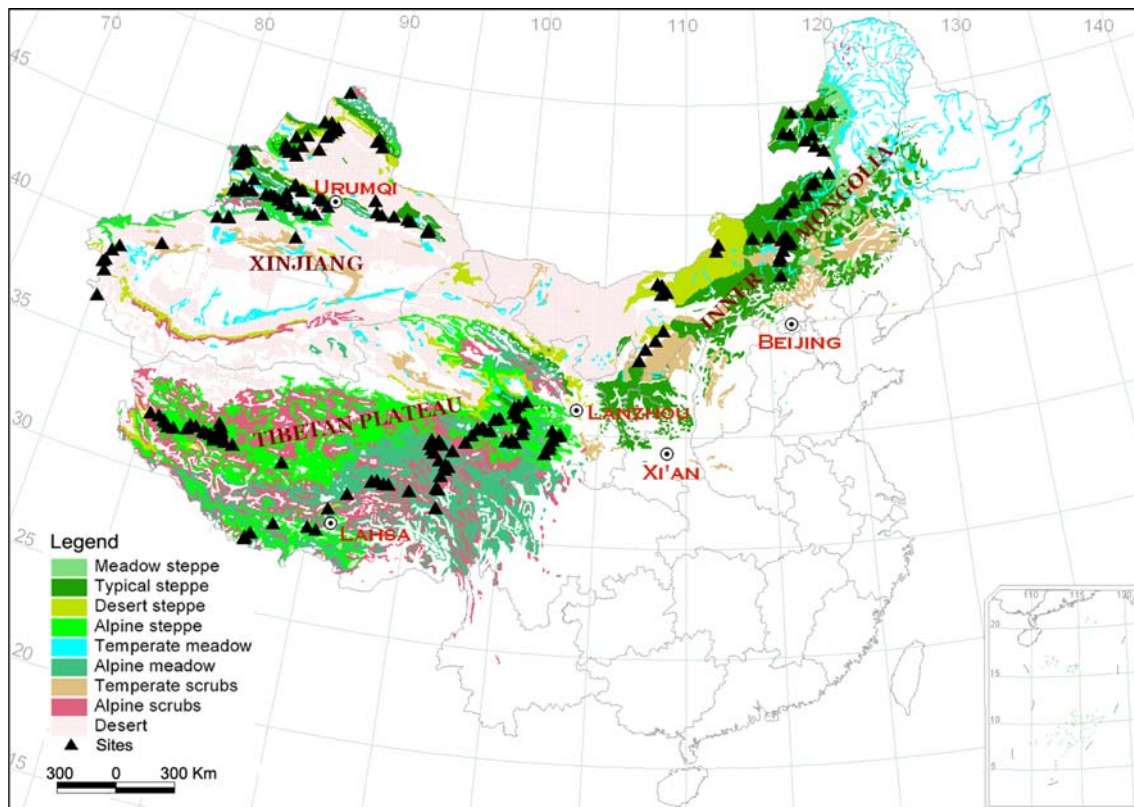
Fig. 1 A vegetation map of studied regions, selected from the Vegetation Map of China (Hou 1982), showing the sample sites

Table 1 Description of the three study regions

	Inner Mongolia	Tibetan Plateau	Xinjiang
No. of sites	42	82	75
No. of sampled species	55	110	69
Altitude (m)	1,059 (575 to 1,527)	4,162 (2,934 to 5,249)	2,083 (733 to 4,000)
Precipitation (mm year^{-1})	292.4 (183 to 427)	386.9 (110 to 624)	283.0 (68 to 534)
Growing season precipitation (mm year^{-1})	222.7 (133 to 316)	270.5 (84 to 383)	197.3 (43 to 420)
Temperature (°C)	2.0 (−2.5 to 7.9)	−1.3 (−9.7 to 7.0)	1.1 (−6.3 to 12.0)
Growing season temp. (°C)	17.4 (14.8 to 20.4)	7.5 (−1.0 to 13.6)	12.8 (1.1 to 23.9)

See Fig. 1 for site locations. Arithmetic means are shown, with the ranges of environmental variables of sampling sites in parentheses

Sun-exposed and newly matured leaves (leaf blades for grasses) of five to ten plants of each species at each site were collected, placed in paper envelopes, and dried in the sun. These samples were oven-dried at 60°C upon returning to the laboratory. Dried samples were ground to a fine powder using a ball mill (NM200, Retsch, Haan, Germany). Total C and N concentration were determined on 5–6 mg of the homogenously ground material of each sample using an elemental analyzer (2400 II CHNS/O Elemental Analyzer, Perkin-Elmer, USA) with a combustion temperature of 950°C and a reduction temperature of 640°C.

The climate data used in this study were calculated based on linear models using latitude, longitude, and altitude as variables from 50-year averaged temperature and precipitation records (1951–2000) at 680 well-distributed climate stations across China (Fang et al. 2001; Piao et al. 2003). Leaf C, N and C:N ratio were log-transformed to normalize the distributions (McGroddy et al. 2004; Reich and Oleksyn 2004; Sterner and Elser 2002; Wright et al. 2004).

Data were analyzed at three levels: (1) averaging species values for each region (Inner Mongolia, the Tibetan Plateau, and Xinjiang) to calculate C and N stoichiometry, (2) averaging by species within each vegetation type for each region, and (3) using all data (i.e., treating all observations equally). Data from (2) and (3) were analyzed to observe the overall pattern with climate, and further pooled into shrub, herb and grass LFs to examine if LFs differ in the relationship with climate. Results from (2) and (3) were generally similar, therefore only results from (2) are presented here for brevity.

We used the regression approach to the analysis of variance (ANOVA) as implemented in a general linear model (GLM), employing type I sums of squares, in the SAS statistical software package version 8.01 (SAS 1999). The full model included terms for LF, plant genus, mean growing season temperature (GST, from May to August), growing season precipitation (GSP), and the interactions GST × LF, GST × genus, GSP × LF, and GSP × genus. The significance of effects was tested with the F-ratios between mean squares of effects and residuals. We switched the order of entry into the model for GST and GSP to test for covariance. We also used MAT and mean annual precipitation (MAP) to replace GST and GSP respectively. As the results were similar, for simplicity, we here focus on the results with GST and GSP.
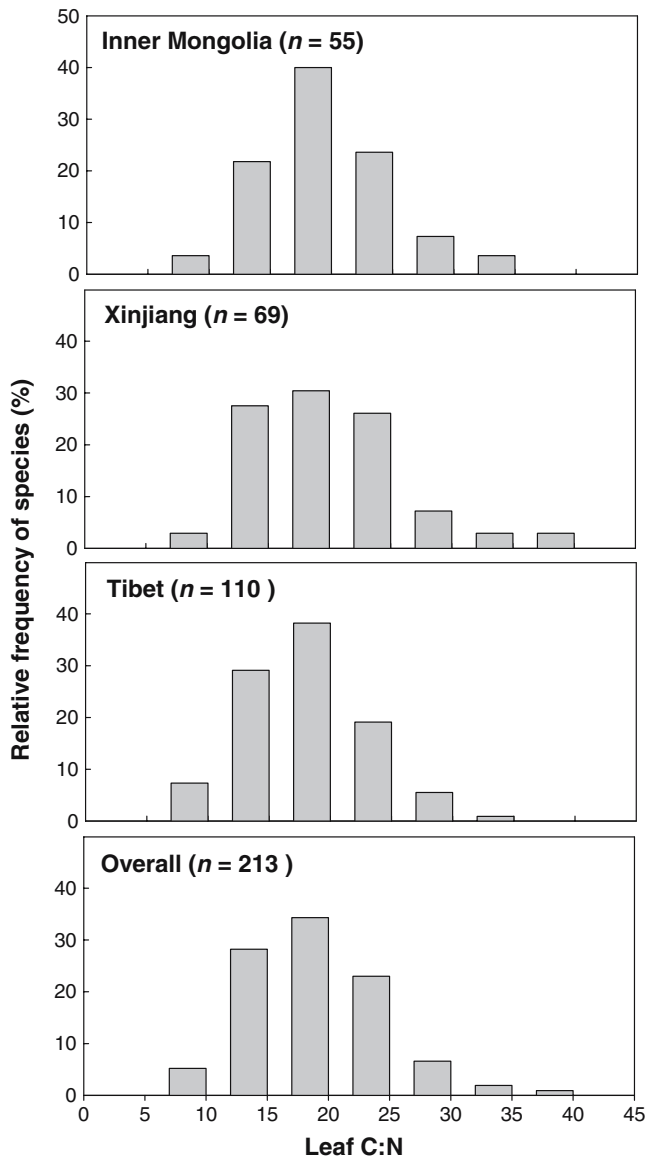
Results

The average foliar C:N mass ratio for all species across China's grasslands is 17.9 (Table 2), which falls between that of global forests (C:N mass ratio 37.1) (McGroddy

Table 2 Foliar C, N, and C:N ratios on mass basis

	n	C			N			C:N		
		Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Overall	213	43.8	3.02	6.9	2.76	0.86	31.4	17.9	5.7	32.0
Region										
Inner Mongolia	55	45.0 a	1.99	4.4	2.68 a	0.77	28.6	18.7 a	5.2	27.9
Xinjiang	69	43.4 b	2.73	6.3	2.59 a	0.89	34.2	18.8 a	6.2	33.2
Tibet	110	43.5 b	3.35	7.7	2.86 a	0.88	30.8	17.0 a	5.4	31.9
Plant life form										
Grass	72	43.6 a	2.21	5.1	2.40 a	0.54	22.5	19.6 b	4.4	22.7
Herb	103	43.5 a	3.19	7.3	3.06 b	0.99	32.2	16.0 a	5.4	34.0
Woody	38	44.9 b	3.63	8.1	2.61 a	0.72	27.4	19.2 b	7.0	36.7
Legume (Y/N)										
N	182	43.5 a	3.09	7.1	2.62 a	0.78	29.7	18.5 b	5.7	30.7
Y	31	45.2 b	2.07	4.6	3.58 b	0.90	25.2	13.9 a	4.1	29.8

Number of species (n), mean value, standard deviation (SD), coefficient of variation (CV, defined as 100 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

Fig. 2 Histograms of foliar C:N ratios in Inner Mongolia, Xinjiang, the Tibetan Plateau and all regions pooled together. All ratios were calculated on mass basis

variation for C and more than 70% for N and C:N ratio, indicating that LF and genus controlled the patterns of C, N and C:N ratio. The effects of GST and GSP depended on the order of entry into the model, as they covaried to some extent: the variation explained by both GST and GSP was less than 5% for leaf C, and less than 3% for both N and C:N ratio. As shown in Fig. 3, the effect of GST on leaf N was insignificant overall (for all groups) or for each LF.

Genus × GST and genus × GSP showed some significant interactions. For C, either genus × GST or genus × GSP was significant, with the factor entered into the model earlier resulting in a significant interaction. For N, genus × GST interaction was always significant, explaining from 4.3 to 9.7% of the variation, depending on the order of entry into the model; the genus × GSP interaction was significant only if it was entered into the model before genus × GST. For C:N ratio, genus × GSP was significant only if it was entered into the model before genus × GST. These results suggest that, although both GST and GSP interact with genus identity, genus × GST was more consistently important than genus × GSP in modulating foliar N. These patterns are generally similar when the main factors LF and genus entered the models prior to GST and GSP, or when GST and GSP are replaced with MAT and MAP, respectively (ANOVA results were not shown for brevity).

When the data of foliar N from the Tibet were pooled with the global dataset of Reich and Oleksyn (2004), a closer fit for the data was found by both linear ($R^2 = 0.11$, $P < 0.0001$) and quadratic regression ($R^2 = 0.11$, $P < 0.0001$) compared to the nonlinear regression ($R^2 = 0.050$, $P < 0.0001$) employed by Reich and Oleksyn (2004). In addition, the positive correlation between leaf N and MAT at very low MATs observed by Reich and Oleksyn (2004) disappeared when the Tibetan data were included in their dataset (Fig. 4).

Discussion

Well-constrained foliar C:N stoichiometry in China's grassland

Our findings show that C:N stoichiometry is surprisingly stable in three distinct regions under different environmental conditions: Inner Mongolia, the Tibetan Plateau, and Xinjiang. Because the overall elemental composition of plants in an ecosystem is simultaneously determined by the mix of species and by the physiological status of the dominants (Güsewell 2004; Sterner and Elser 2002), this stable C:N stoichiometry indicates a broad consonance of ecophysiological processes across the grassland systems, irrespective of species compositional shifts and climatic variations.

These three regions are geographically far-flung and climatically distinct, yet they are all dominated by grasslands, which have been shaped by congruent but distinct

et al. 2004) and marine systems (C:N mass ratio 5.7) (Redfield 1958). C:N ratios for the three regions were surprisingly constrained, at 18.7, 18.8 and 17.0 for Inner Mongolia, Xinjiang and the Tibetan Plateau, respectively (Fig. 2, Table 2). The variability in C:N mass ratio across the three regions [coefficient of variation (CV) 32%] was somewhat greater than that in freshwater zooplankton (CV 21%; Elser et al. 2000), but smaller than that in forests worldwide (CV 59%; Elser et al. 2000).

General linear model analysis showed that the overall models of LF, genus, GST, GSP, and their respective two-way interactions were all significant for leaf C, N and C:N ratio, explaining 84, 88, and 88% of their total variation, respectively (Table 3). The major factors LF and genus together explained more than 60% of the total

Table 3 Summary of analysis of variance (ANOVA) of the effects of mean growing season temperature (GST), growing season precipitation (GSP), life form (LF), genus, and the interactions, using general linear models

	df	C			N			C:N		
		SS	F		SS	F	%SS	SS	F	%SS
GST entered first										
GST	1	0.010	25.92***	4.17	0.051	9.21**	1.06	0.122	19.38***	2.32
GSP	1	0.000	0.31	0.05	0.007	1.31	0.15	0.013	2.12	0.25
LF	2	0.010	11.98***	3.85	0.539	48.42***	11.11	0.599	47.70***	11.44
Genus	106	0.148	3.45***	58.77	3.025	5.13***	62.36	3.171	4.77***	60.58
GST × LF	2	0.003	4.01*	1.29	0.005	0.49	0.11	0.002	0.14	0.03
GSP × LF	2	0.001	1.17	0.37	0.016	1.39	0.32	0.011	0.90	0.21
GST × genus	42	0.029	1.70*	11.47	0.470	2.01**	9.68	0.506	1.92	9.67
GSP × genus	22	0.009	1.03	3.64	0.170	1.39	3.50	0.171	1.24	3.27
Residuals	102	0.041		16.39	0.568		11.70	0.640		12.23
GST entered second										
GSP	1	0.004	9.62**	1.55	0.036	6.47*	0.74	0.078	12.37***	1.48
GST	1	0.007	16.62***	2.67	0.023	4.05*	0.46	0.057	9.13**	1.09
LF	2	0.010	11.98***	3.85	0.539	48.42***	11.11	0.599	47.70***	11.44
Genus	106	0.148	3.45***	58.77	3.025	5.13***	62.36	3.171	4.77***	60.58
GSP × LF	2	0.000	0.02	0.01	0.010	0.86	0.20	0.009	0.74	0.18
GST × LF	2	0.004	5.16**	1.66	0.011	1.02	0.23	0.004	0.30	0.07
GSP × genus	42	0.027	1.57*	10.57	0.432	1.85**	8.92	0.469	1.78*	8.96
GST × genus	22	0.011	1.28	4.54	0.207	1.69*	4.27	0.208	1.51	3.98
Residuals	102	0.041		16.39	0.568		11.70	0.640		12.23

Overall model for $\log(C)$, $R^2 = 0.84$, $F = 2.92$, $P < 0.0001$; $\log(N)$, $R^2 = 0.88$, $F = 4.32$, $P < 0.0001$; $\log(C:N)$, $R^2 = 0.88$, $F = 4.11$, $P < 0.0001$
df degree of freedom, *SS* sum of squares, *%SS* % of variation explained by the main factors and the interactions
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

Fig. 3 Leaf N in relation to mean growing season temperature (GST) in three major life forms (grass, herb and woody) and for all species
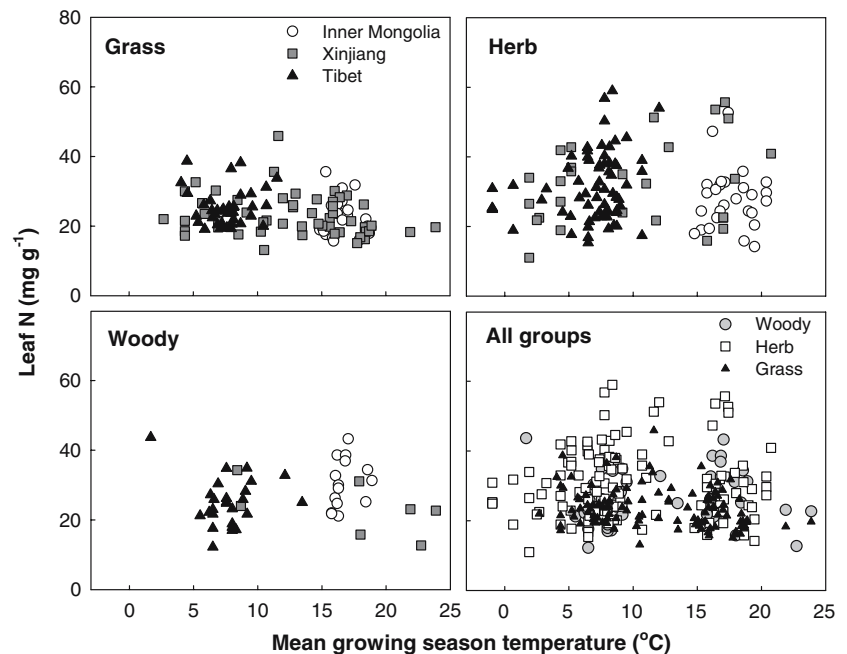
environmental conditions (Brown and Lomolino 1998; Kay et al. 2005). Plant growth is limited mainly by precipitation in the temperate grasslands of Inner Mongolia (Chen and Wang 2000), low growing season temperature in the alpine grasslands of the Tibetan Plateau (Li and Zhou 1998), and a blend of the two in the mountain grasslands of Xinjiang. While these biome-level differences have created variation in the species composition of these regions, the well-constrained foliar C:N stoichiometry suggests that evolution has set biochemical constraints on the chemical composition of grassland plants (Ågren 2004), and thus has limited the variation in the structure and LF composition of the regional vegetations.

Nutrient status of terrestrial ecosystems have strong local and regional signals due to their acquisition of mineral nutrients mainly via weathering and microbial decomposition at the local site (Chadwick et al. 1999; Chapin 1980). Therefore, C:N stoichiometry reflects traits that influence plants' performance in response to the abiotic characteristics of their immediate surroundings.
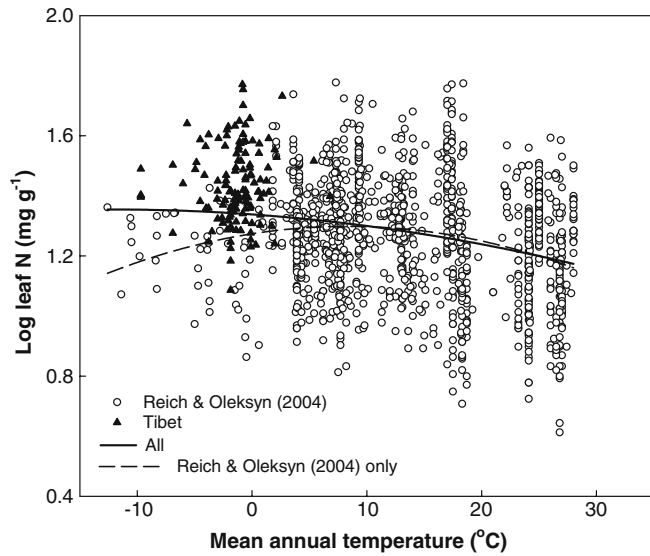
Fig. 4 Leaf N concentration in relation to mean annual temperature (MAT) for the Tibetan species (*filled triangles*) and from the global dataset of Reich and Oleksyn (2004) (*grey circles*). Quadratic fitted lines for data from Reich and Oleksyn (2004) (*dashed line*) and all data pooled together (*solid line*) are shown

For example, the frequently observed high leaf N concentrations in terrestrial plants at high altitudes have been proposed to be a result of low temperature (Körner 1989; Reich and Oleksyn 2004). Such increases in leaf N may reflect adaptive mechanisms for offsetting temperature-induced reductions in reaction rates or for enhancing cold hardiness, or they may simply reflect changes in the relative rates of cellular processes (Woods et al. 2003). In contrast, our results demonstrate a remarkably stable C:N ratio across substantial temperature, precipitation, and altitudinal variation, indicating that the responses of C:N stoichiometry to abiotic and biotic factors are possibly more evident at the organismal level than at the ecosystem level. This further suggests that each species has its own strategy in solving the challenge of nutrient acquisition; little evidence is available to support the congruence of the strategies of different species within each biome.

Data from Chinese grasslands modifies global foliar N patterns

In recent years, several studies have documented global-scale variations in leaf key functional traits and nutrient status (McGroddy et al. 2004; Reich and Oleksyn 2004; Reich et al. 1997; Sterner and Elser 2002; Wright et al. 2004). Reich and Oleksyn (2004) analyzed 1,280 plant species in 704 genera, across 452 locations worldwide, finding that leaf N rose from the warmest MAT to the 5–10°C range, across biogeographic and climatic gradients. However, when MAT fell below 5–10°C, leaf N appeared to decline or plateau with decreasing MAT, although insufficient data hindered any definitive conclusions.

Reich and Oleksyn (2004) proposed several hypotheses for the formation and maintenance of the global leaf N trend. Among them, the temperature–plant physiological hypothesis (TPPH) states that leaf N should decline with increasing temperature because cold climates may favour high leaf N to compensate for the low efficiency of physiological processes at low temperature. In contrast, the biogeochemical hypothesis (BH) argues that very low MATs not only reduce N availability through suppressing decomposition and mineralization of organic matter, but also suppresses root nutrient uptake, resulting in low leaf N in cold climates. The meta-analysis of leaf trait data conducted by Reich and Oleksyn (2004) supported both TPPH and BH: At very low MAT, the decrease in leaf N with MAT may have resulted from low soil N availability (BH); yet when MAT is above 5–10°C, high leaf N relative to C at lower MAT may arise as increasing N offsets the reduced efficiency of enzymes and physiological processes (TPPH). We are not aware of any studies that have directly tested these hypotheses. China's grasslands, particularly alpine grassland of the Tibetan Plateau, provide us a unique environment to test these hypotheses at very low MATs. Our data offer evidence against the BH, as leaf N did not increase with MAT even in very cold environments and at high elevations.

No general trend for foliar N with temperature in Chinese grasslands

The present study showed that LF and genus identity explained more than 70% of total variations for foliar N and C:N ratio, while GST and GSP explained only less than 3%, and the genus × GST interaction explained between 4.3 and 9.7% of the variations in these leaf characters. When GST and GSP were replaced with MAT and MAP, respectively, similar results were obtained. We recognized that, in the present study, a large number of the species sampled represent single genera (53/110) or even single families (17/41). Thus, the large number of degrees of freedom for genera in the analysis accounts in part for the large influence of phylogeny on leaf stoichiometry. However, when all genera represented by only a single sample were removed, similar patterns emerged, with genus identity explaining most of the variation (data not shown). These results suggest that, overall, foliar N and C:N ratio do not directly correlate with either temperature or precipitation in China's grassland biomes, and the changes in these traits were mainly due to the changes in species composition.

Recent studies by Reich and Oleksyn (2004) and McGroddy et al. (2004) identified one geographically broad trend in leaf N, namely decreasing leaf N with increasing MAT (decreasing latitude). However, it is not clear whether this trend results from a direct effect of MAT (latitude) or from an indirect effect through a change in plant species composition. From the results of Reich and Oleksyn (2004) and McGroddy et al. (2004), geographic distribution of evergreen versus deciduous species appeared to be a major contributor to the large-scale N patterns, which likely reflects two contrasting

suites of mineral nutrition strategies: low N content with a longer leaf lifespan in evergreens, and high N content with a shorter leaf lifespan in deciduous plants (Aerts and Chapin 2000; Chapin 1980; Westoby et al. 2002). As the shift from evergreens in the tropics to deciduous plants in temperate regions covaries with changes in temperature, disentangling these factors remains a formidable challenge.

It is worthy noting that, in the present study, although similar results were obtained from mean annual climate variables (MAT and MAP) and growing season climate variables (GST and GSP), the underlying mechanisms differ. Leaf traits reflect the direct effects of environment during growing season, including growing season length (Ackerly 2004; Körner 1999), thus GST and GSP are more relevant to leaf traits than MAT and MAP. As identified previously, the real driver for leaf traits is leaf lifespan (or growing season length) (see review by Westoby et al. 2002).

The present study, conducted entirely within grassland regions, tested the effect of temperature on C and N stoichiometry while maintaining nearly constant LF composition (with only two evergreen species in this study). Our results provide some evidence that the temperature effect noted in the previous studies may be negligible if no substantial LF shifts are included. Thus, our study suggests that at the biome scale, temperature affects leaf N mainly through a change in plant species composition rather than via temperature itself. These field-based results from the grasslands of China substantially modify the conclusions of previous meta-analyses, in particular refuting the dominance of the BH at very low temperatures. Standardized data collection over a broad geographical range was crucial in detecting this pattern.

The narrow range of C:N ratios across tremendous geographic and climatic variation further emphasizes the importance of plant LFs in determining mineral stoichiometry. While precipitation, temperature, and altitudinal variation contribute to explaining the variations in foliar C, N, and C:N ratios, LF and genus identity were far more important. Thus, future efforts should focus on refining LFs to more precisely identify biome-spanning patterns of foliar trait variation.

References

Ackerly DD (2004) Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. Am Nat 163:654–671

Aerts R, Chapin FS III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Ågren GI (2004) The C:N:P stoichiometry of autotrophs—theory and observations. Ecol Lett 7:185–191

Brown JH, Lomolino MV (1998) Biogeography. Sinauer, Sunderland

Chadwick O, Derry L, Vitousek P, Huebert B, Hedin L (1999) Changing sources of nutrients during four million years of ecosystem development. Nature 397:491–497

Chapin FS III (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260

Chen ZZ, Wang SP (2000) Typical steppe ecosystems of China. Science Press, Beijing

Chown SL, Gaston KJ, Robinson D (2004) Macrophysiology: large-scale patterns in physiological traits and their ecological implications. Funct Ecol 18:159–167

Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Schulz KL, Siemann EH, Sterner RW (2000) Nutritional constraints in terrestrial and freshwater food webs. Nature 408:578–580

Fang J, Piao S, Tang Z, Peng C, Ji W (2001) Interannual variability in net primary production and precipitation. Science 293:1723a

Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. New Phytol 164:243–266

Han W, Fang JY, Guo D, Zhang Y (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. New Phytol 168:377–385

Hou H-Y (1982) Vegetation map of the People's Republic of China (1:4M). Chinese Map Publisher, Beijing

Kay AD, Ashton IW, Gorokhova EC, Kerhoff AJ, Liess A, Litchman E (2005) Toward a stoichiometric framework for evolutionary biology. Oikos 109:6–17

Körner C (1989) The nutrient status of plants from high altitudes: a worldwide comparison. Oecologia 81:379–391

Körner C (1999) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin Heidelberg New York

Li WH, Zhou XM (eds) (1998) Ecosystems of Qinghai-Xizang (Tibetan) Plateau and approaches for their sustainable management. Guangdong Science and Technology Press, Guangzhou

McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. Ecology 85:2390–2401

Piao SL, Fang JY, Zhou LM, Guo QH, Henderson M, Ji W, Li Y, Tao S (2003) Interannual variations of monthly and seasonal normalized difference vegetation index (NDVI) in China from 1982 to 1999. J Geophys Res Atmos 108(D14):4401. DOI 4410.1029/2002JD002848

Redfield AC (1958) The biological control of chemical factors in the environment. Am Sci 46:205–221

Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. Proc Natl Acad Sci USA 101:11001–11006

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra, and strategies. Int J Plant Sci 164:S143–S164

SAS (1999) SAS/STAT User's guide, 8.01 edn. SAS Institute, Cary

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87–115

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159

Woods HA, Makino W, Cotner JB, Hobbie SE, Harrison JF, Acharya K, Elser JJ (2003) Temperature and the chemical composition of poikilothermic organisms. Funct Ecol 17:237–245

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M,

122

Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee WJ, Lusk C, Midgley JJ, Navas M-L, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, Lamont BB, Lee W, Oleksyn J, Osada N, Poorter H, Villar R, Warton DI, Westoby M (2005) Assessing the generality of global leaf trait relationships. New Phytol 166:485–496

Wu ZY (ed) (1980) Vegetation of China. Science Press, Beijing

Xu P (ed) (1993) Grassland resources and utilization of Xinjiang. Xinjiang Science, Technology and Public Health Publishing House, Urumqi

Zhang J, Wang JT, Chen W, Li B, Zhao K (1988) Vegetation of Xizang (Tibet). Science Press, Beijing