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Leaf element concentrations of terrestrial plants across China are influenced by taxonomy and the environment

Shi-Bao Zhang, Jiao-Lin Zhang, J. W. Ferry Slik and Kun-Fang Cao*

Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 650223, China

*Correspondence: Kun-Fang Cao, Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 650223, China.
E-mail: caokf@xtbg.ac.cn

ABSTRACT

Aim The productivity, functioning and biogeochemical cycles of terrestrial ecosystems are strongly affected by leaf element concentrations. Understanding the biological and ecological factors affecting leaf element concentrations is therefore important for modelling the productivity and nutrient fluxes of ecosystems and their responses to global change. The present study aimed to determine how leaf element concentrations are linked to taxonomy and the environment.

Location China.

Methods The concentrations of 10 leaf elements of 702 terrestrial plant species from different biomes were extracted from publications. The links between environmental variables, taxonomy and leaf elements were analyzed using phylogenetically comparative methods and partial Mantel tests.

Results Taxonomy had stronger effects on leaf S and SiO_2 than latitude, explaining 40.2–43.9% of total variation, whereas latitude had stronger effects on leaf N, P, K, Fe, Al, Mn, Na and Ca concentrations, explaining 19.5–52.1% of total variation. Leaf N, S, Al, Fe and Na concentrations were correlated with mean annual precipitation (MAP), while leaf N, P and Fe concentrations were correlated with mean annual temperature (MAT). Latitude, MAP and MAT were significantly correlated with the first axis of a principal components analysis (PCA). This first axis was associated with leaf elements involved in protein synthesis and photosynthesis. The other PCA axes, which were not correlated with MAT, latitude and MAP, were associated with leaf elements responsible for cell structure and enzymes.

Main conclusions Leaf element concentrations of terrestrial plants in China were correlated with climate, latitude and taxonomy. With the exception of S and SiO_2, the environmental factors were more important in explaining leaf element variation than taxonomy. Therefore, changes in temperature and precipitation will directly affect the spatial patterns of leaf elements and thus the associated nutrient fluxes and ecosystem functioning.

Keywords

Biogeography, China, climate, latitudinal gradient, leaf element, Mantel test, phylogenetically comparative method, taxonomy.

INTRODUCTION

Leaf element concentrations strongly affect the productivity, functioning, and nutrient cycling of plant communities, and thus the response of an ecosystem to global change (Kerkhoff *et al*., 2005; Amatangelo & Vitousek, 2008; Mueller *et al*., 2010). For example, calcium (Ca) constrains the ability of northern hardwood forest trees to control the availability and loss of nitrogen (Groffman & Fisk, 2011). However, leaf element concentrations are largely uncertain variables in global carbon-cycling models (Ren *et al*., 2006). Understanding their geographical gradients and the factors affecting the variation of leaf elements would help to elucidate the underlying patterns of nutrient fluxes across ecological gradients and the mechanisms

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of the response of vegetation to global change (Fyllas *et al.*, 2009; Ordoñez *et al.*, 2009).

Spatial patterns of soil nutrients are influenced by soil substrate, climate and biological factors (Xiong & Li, 1987; Ordoñez *et al.*, 2009). Acid soils have lower concentrations of potassium (K), Ca, magnesium (Mg) and phosphorus (P), but are rich in aluminium (Al) and iron (Fe). In contrast, alkaline soils are deficient in manganese (Mn), Fe and P (Xiong & Li, 1987). Leaf element concentrations depend strongly, although not always (He *et al.*, 2010; Geng *et al.*, 2011), on soil nutrient availability (Mueller *et al.*, 2010). For example, leaf N and P concentrations vary with geographical gradients in soil substrate and soil fertility (Reich & Oleksyn, 2004; Han *et al.*, 2005; Townsend *et al.*, 2007), and the leaf N/P ratio can be shifted by soil P availability in temperate rain forest in New Zealand (Richardson *et al.*, 2008).

Precipitation and temperature can also affect leaf element concentrations by influencing element allocation among plant organs, by changing concentrations of elements associated with plant metabolism or by affecting vegetation species composition (Körner, 1989; Wright *et al.*, 2001; Reich, 2005; Ordoñez *et al.*, 2009). Several studies have found that leaf N and P concentrations are affected by latitude (Reich & Oleksyn, 2004; Han *et al.*, 2005; Townsend *et al.*, 2007) and climatic factors such as temperature and precipitation (Thompson *et al.*, 1997; He *et al.*, 2008). The latitudinal variations in leaf N and P concentrations are mainly shaped by mean annual temperature (Reich & Oleksyn, 2004). However, no latitudinal pattern of leaf N/P ratio has been found across biomes in China or in tropical rain forests of Central and South America (Han *et al.*, 2005; Townsend *et al.*, 2007).

Recent studies have shown that significant variations in plant nutrient concentrations can be explained by taxonomic affiliation (Thompson *et al.*, 1997; Broadley *et al.*, 2004; Willey & Fawcett, 2006). Some plant species can heavily accumulate certain elements (White *et al.*, 2007). For example, plants in different angiosperm families and orders may accumulate significantly different concentrations of Ca, K and Mg in their shoots; eudicots generally have higher shoot Ca concentration than monocots, while commelinoid monocot species have lower shoot Ca concentration than other monocot species (Broadley *et al.*, 2003, 2004; White & Broadley, 2003). Consequently, the species composition of vegetation communities could affect the geographical variation in leaf element concentrations. However, few studies have investigated the effects of phylogeny on leaf nutrients (Thompson *et al.*, 1997; Broadley *et al.*, 2004; Kerkhoff *et al.*, 2006). Of these few studies, Kerkhoff *et al.* (2006) found significant phylogenetic signals in stem and leaf N and P concentrations of seed plants in natural vegetation, while Paoli (2006) found that within the tropical tree genus *Shorea*, the variation in N/P ratio is more strongly related to phylogeny than habitat, whereas leaf P is more related to habitat than phylogeny.

The balance of nutrients in plant tissues is of particular importance for plant growth (Ågren, 2008). Consequently, strong correlations among leaf elements have been observed from the individual plant to the global scale (Reich & Oleksyn, 2004; Ågren, 2008). Garten (1978) and Wright *et al.* (2005a) found that leaf N, P, Cu, sulphur (S) and Fe, which are related to the 'nucleic acid–protein set', are loaded on the first axis of a principal components analysis (PCA) of leaf element concentrations. Leaf Mg, Ca, K, Zn, Mn and N, which are associated with the 'structural and photosynthetic set', are loaded on the second axis, while leaf Mn, K and Mg, which are related to the 'enzymatic set', are loaded on the third axis. The strong interaction among leaf elements could possibly lead to the coordinated patterns of variation in N and P observed in leaves across plant species (Kerkhoff *et al.*, 2006).

Global change would be likely to affect the spatial patterns in temperature and precipitation, and thus species composition, leading to changes in leaf element concentrations of plant community, and subsequently affecting nutrient cycling of ecosystems. Therefore, an understanding of these processes is important for modelling the nutrient cycling of ecosystems. In this study, the concentrations of 10 leaf elements of 702 terrestrial plant species from 66 families in 30 orders across terrestrial biomes in China were analysed using phylogenetically comparative methods and partial Mantel tests to determine the factors affecting their variation, especially to address how leaf nutrients are affected by environmental factors (latitude, precipitation and temperature) across China and how much an effect phylogeny has.

MATERIALS AND METHODS

The dataset presented in Appendix S1 in the supporting information was compiled from publications containing the concentrations (g kg^{-1}) of leaf K, Fe, Mn, sodium (Na), Ca, N, P, S, silica (SiO_2) and Al of 702 wild plant species from 91 sites covering almost all terrestrial vegetation types in China (Fig. 1). Data from planted specimens and polluted samples, and from plant families that contained many species but for which we found information for fewer than three species were excluded from the analyses. Latitude, altitude, mean annual temperature (MAT) and mean annual precipitation (MAP) were obtained directly from publications if the climatic data were available for the sampling sites (Appendix S1). Otherwise, the altitude and latitude of the geographical centre of the sampling area was obtained from Google Earth and MAT and MAP were taken from the nearest weather stations and corrected by an altitudinal lapse rate of 6 °C per 1000 m for MAT. The assignments to plant order and family were based on the Angiosperm Phylogeny Group III (APG III) classification (Angiosperm Phylogeny Group, 2009).

The phylogenetic affiliation of each taxon was incorporated into the analysis using the most recent consensus tree based on the APG III classification (Angiosperm Phylogeny Group, 2009). We built an angiosperm reference phylogeny that was resolved up to family level using the freely available software PHYLOMATIC (http://www.phylodiversity.net/phylomatic/phylomatic.html). The Branch Length Adjuster (BLADJ) algorithm in

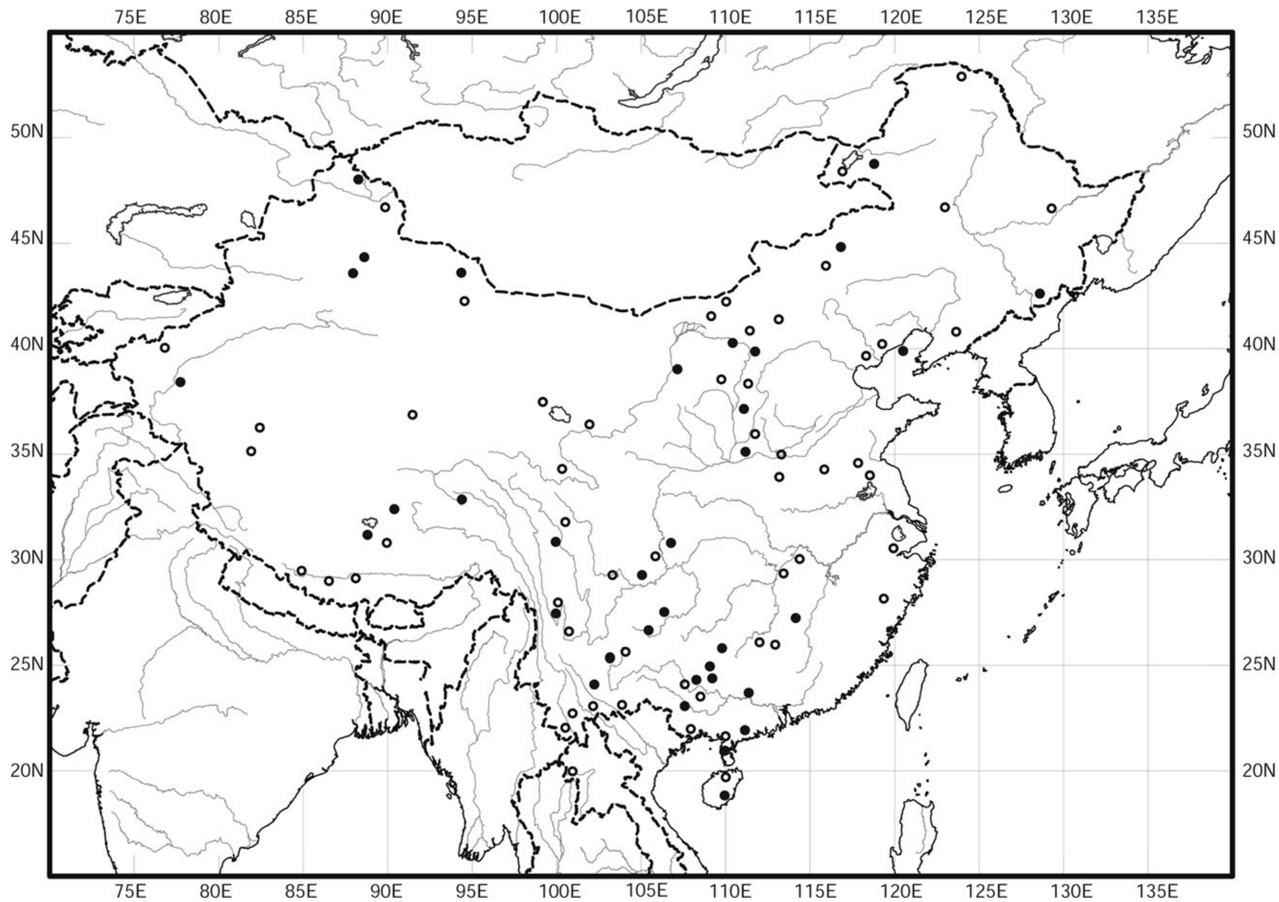

Figure 1 The geographical locations of the sampling sites of this study. ○, sites with ≤ 5 species sampled; ●, sites with > 5 species sampled.

Table 1 The concentration variations in 10 leaf elements (g kg^{-1}).

	Number	Mean	SE	Geometric mean	Minimum	Maximum	Skewness
N	370	19.96	0.43	18.33	4.50	49.90	0.79
P	578	1.41	0.05	1.12	0.05	12.60	4.60
K	608	13.05	0.42	8.69	0.10	81.82	2.14
S	500	3.26	0.23	1.55	0.10	33.60	3.11
Ca	583	15.50	0.57	9.64	0.10	98.25	1.70
Fe	604	0.57	0.06	0.05	< 0.01	14.99	5.46
Mn	606	0.23	0.02	0.01	< 0.01	4.34	3.92
SiO_2	435	14.35	0.91	6.53	0.06	99.70	2.20
Na	554	8.91	0.94	1.81	< 0.01	166.08	4.08
Al	536	0.83	0.07	0.14	< 0.01	14.07	4.42

PHYLOCOM (Webb *et al*., 2008) in combination with estimated family ages (Wikström *et al*., 2001) was used to assign branch lengths to this phylogeny.

The data distributions of leaf element concentrations were assessed by a Shapiro–Wilk test prior to analysis of variance (ANOVA). Because this test showed that none of the leaf elements were distributed normally (Table 1), the original data were transformed by natural logarithm to generate the standardized leaf element concentrations. They were then analyzed by ANOVA (aov function) to test for differences in leaf element concentrations between taxonomical levels using the R statistical platform (version 2.10; R Development Core Team, 2010). The mean concentrations of leaf N, P, K and SiO_2 were mapped on the family tree to identify their phylogenetic patterns.

A general linear mixed model was used to fit the variation components for each leaf element on the R statistical platform

(Bolker *et al.*, 2008). The variance fraction of the total variance for each leaf element was partitioned into taxonomic, environmental (latitude) and residual components by using the residual maximum likelihood (REML) method. All terms in the linear mixed model were treated as random effects. Prior to analysis, data were transformed by natural logarithm.

The possible evolutionary associations between latitude and leaf elements, and among leaf elements at family level, were assessed with the 'analysis of traits' module in PHYLOCOM (Webb *et al.*, 2008). This program calculates internal node values for continuous traits using the phylogenetic independent contrast (PIC) method (Felsenstein, 1985). Then the traditional Pearson correlation coefficients and PIC correlation coefficients were calculated by using the 'lm' function in the R package.

Partial Mantel tests were performed in the 'ecodist' package implemented in R 2.10 to evaluate the contribution of latitude, MAP and MAT to leaf nutrients. This method allows us to evaluate the pure effect of latitude on leaf nutrients by removing the MAT or MAP effect, and vice versa. The distance metrics of environmental variables and leaf nutrients were calculated by the Euclidean method in the 'distance' function of the 'ecodist' package. Then the partial Mantel correlation between the environmental matrices and leaf nutrient matrices was analysed by the 'mantel' function of the 'ecodist' package. Significant differences from zero in these coefficients were assessed by comparing reference distributions obtained after 999 iterations that randomly permuted the arrangement of the elements of one of the distance matrices.

A PCA was performed using the 'prcomp' function of the R package 'vegan' to characterize the associations of the 10 leaf elements at family level. To identify the environmental effect of the suits of the associated leaf elements, the correlations of the extracted vectors of each PCA axis with latitude, MAP and MAT were assessed by regression analysis (Wright *et al.*, 2005b).

RESULTS

Taxonomic effects on leaf element concentrations

Leaf element concentrations varied considerably across species (Table 1). The magnitudes of variation in leaf macronutrients were generally smaller than those of micronutrients and non-essential elements. The variation in leaf N concentration among species was about 20-fold, in leaf P about 250-fold, and those in leaf K, S and Ca concentrations were 336- to 8182-fold, whereas the variation among species in micronutrients and non-essential elements, except for SiO_2, were > 100,000-fold. Compared with the 'GLOPNET' dataset (Reich & Oleksyn, 2004), leaf N and P concentrations in China covered the complete range of the global data, although some phosphorus concentrations were beyond the range of the global dataset (Appendix S2).

ANOVA results showed that the concentrations of the 10 tested leaf elements varied significantly among families (Appendix S3, Fig. 2). At family level, more N was accumulated in the leaves of Brassicaceae and Zygophyllaceae, more P in Rutaceae and Daphniphyllaceae, more K in Convolvulaceae and Solanaceae, more S in Equisetaceae and Tamaricaceae, more SiO_2 in Ulmaceae and Pteridaceae, more Fe in Zygophyllaceae and Caryophyllaceae, more Al in Melastomataceae and Gleicheniaceae, more Mn in Lauraceae and Lamiaceae, more Na in Amaranthaceae and Tamaricaceae and more Ca in Celastrales and Moraceae. Angiosperms had higher leaf N, P, Fe, S, Na and Ca concentrations than gymnosperms and ferns; gymnosperms had higher Mn concentration than angiosperms and ferns; while ferns had higher SiO_2, Al and K concentrations than angiosperms and gymnosperms.

The relative importance of latitude and taxonomy on leaf element concentrations

Latitude explained 15.3–52.1% of total variation in leaf element concentration, while taxonomy explained 0.8–43.9% (Table 2). Latitude had a stronger effect on leaf N, P, K, Fe, Al, Mn, Na and Ca concentrations than taxonomy, while taxonomy had a stronger effect on leaf S and SiO_2. However, latitudinal variation in leaf S and SiO_2 concentrations still accounted for 15.3 and 20.5% of the total variation, respectively. The interaction of latitude with taxonomy had significant effects on leaf K, Al, Mn and Na concentrations, explaining more than 10% of total variation. For each leaf element, a large proportion (>17%) of total variation remained unexplained.

Both Pearson's and PIC correlation analyses indicated that leaf N, P, K, S and Fe concentrations were correlated with latitude (Fig. 3). Pearson's analysis found a significant correlation between leaf Na concentration and latitude, but this correlation disappeared after removing the phylogenetic effect. Although a weak correlation was found between leaf P and latitude when using Pearson's and PIC correlation analyses, no correlation was found when using the partial Mantel test. Leaf N/P ratio, SiO_2, Al, Mn and Ca did not show any latitudinal patterns at family level.

Climatic influences on leaf element concentrations

Mantel tests showed that latitude was correlated with leaf N, K, Fe, S and Na concentrations (Table 3). When controlled for MAP in the partial Mantel test, the significant correlation between latitude and leaf Na concentration disappeared, and the correlation between latitude and leaf Al concentration became significant. However, none of the correlations between leaf elements and latitude became insignificant when controlled for MAT.

Leaf N, S, Al, Fe and Na concentrations were correlated with MAP at family level, even when controlled for MAT (Table 4), whereas leaf P, K, SiO_2, Mn, Ca concentrations were not correlated with MAP. Leaf N, P and Fe concentrations were correlated with MAT. However, these significant correlations disappeared after controlling for MAP (Table 4). Leaf K, S, SiO_2, Al, Mn, Na and Ca were not correlated with MAT.

Correlations between leaf elements

Most leaf elements were positively correlated with each other, but leaf Mn concentration was negatively correlated with leaf N,

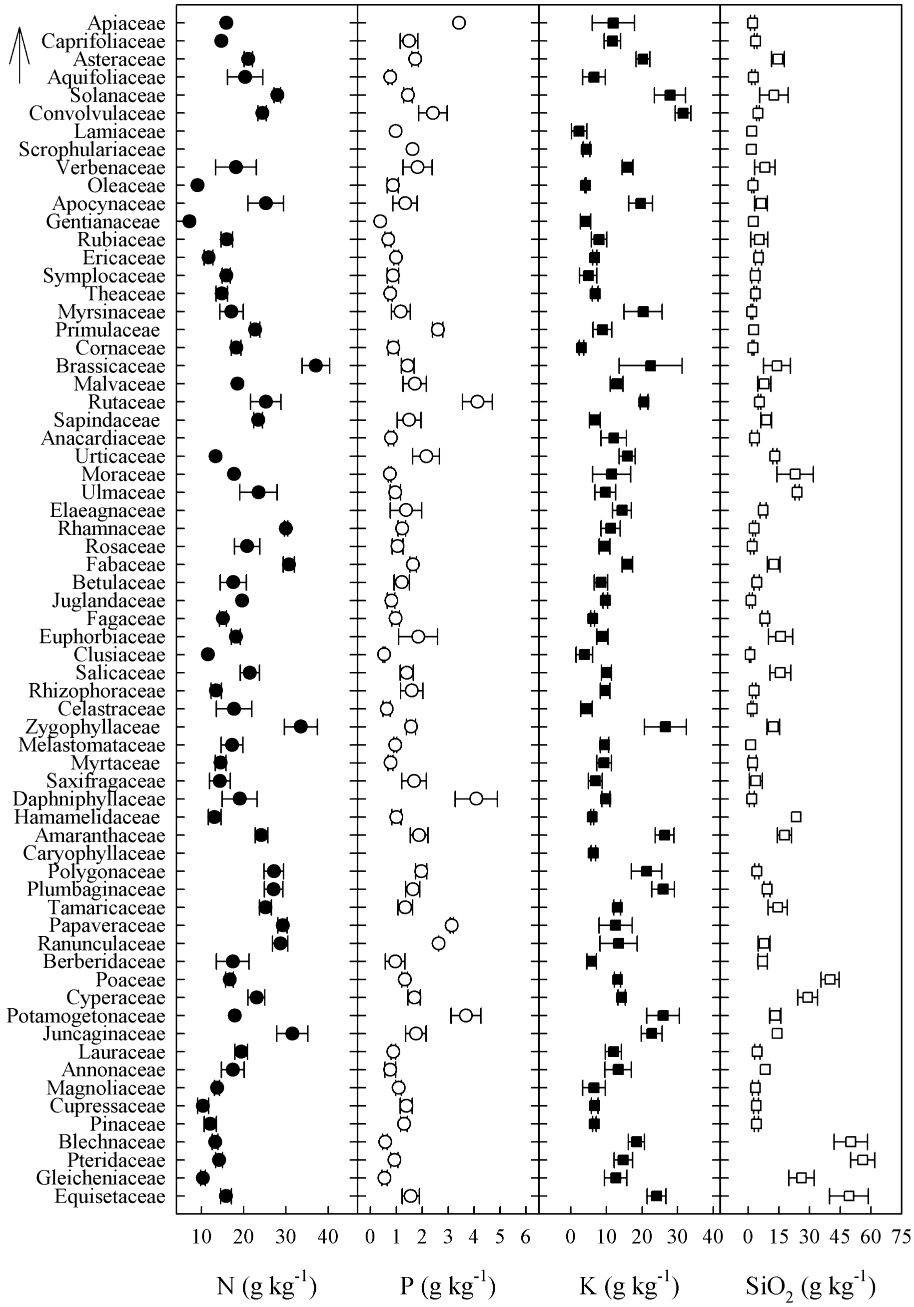

Figure 2 The phylogenetic distributions of leaf nitrogen (N), phosphorus (P), potassium (K) and silicon (SiO_2) concentrations (mean ± SE) at family level. The phylogeny is based on the Angiosperm Phylogeny Group III classification. The arrow indicates the evolutionary direction from primitive to advanced families.

Table 2 Partitioning of total variation (%) of each leaf element concentration into taxonomic and environmental (latitude) and residual components. The concentrations of all elements were transformed using natural logarithm prior to analysis.

Variation sources	N	P	K	S	SiO_2	Fe	Al	Mn	Na	Ca
Latitude	41.74	33.35	45.58	15.26	20.45	34.96	19.45	15.48	52.14	44.80
Taxonomy	4.88	5.78	10.22	43.85	40.18	0.81	12.08	13.84	14.36	21.67
Latitude × taxonomy	6.42	9.09	26.53	8.82	0.12	0.27	19.35	16.18	10.27	6.24
Residual	46.96	51.78	17.67	32.08	39.37	63.96	49.13	54.49	23.22	27.30

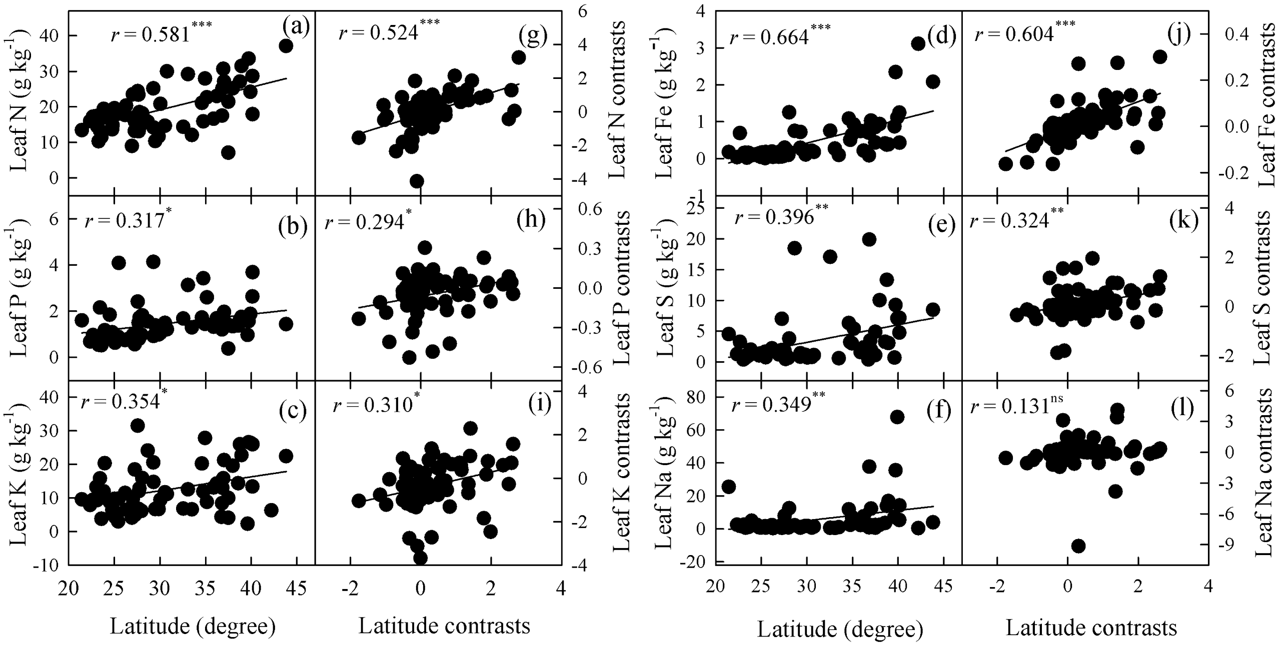

Figure 3 Correlations between the latitude and the concentration of leaf nitrogen (N), phosphorus (P), potassium (K), iron (Fe), sulphur (S) and sodium (Na) at family level by Pearson's correlation (a–f) and phylogenetically independent contrast correlation (g–l). ns, $P > 0.05$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Table 3 The correlation coefficients between the concentration of each of the 10 leaf elements and latitude assessed by partial Mantel test at family level.

	Mantel test	Partial Mantel test (controlling MAT)	Partial Mantel test (controlling MAP)
N	0.37***	0.34***	0.26***
P	0.09	0.02	0.03
NP	0.01	0.02	0.01
K	0.14**	0.21***	0.17**
Fe	0.44***	0.46***	0.33***
S	0.15**	0.19**	0.03
SiO_2	0.05	0.11	0.03
Al	0.04	0.02	0.29***
Mn	0.04	0.04	0.01
Na	0.19**	0.19**	0.07
Ca	0.06	0.05	0.01

MAP, mean annual precipitation. MAT, mean annual temperature. The significance values were obtained by randomization. $^{**}P < 0.01$; $^{***}P < 0.001$.

P, K, SiO_2 and Ca concentrations, and leaf Al concentration was negatively correlated with Ca concentration (Appendix S4). Several leaf elements, such as SiO_2, Al and Ca, were rarely correlated with other elements. When using the PIC method, leaf Ca and Al concentrations were not correlated with any other leaf elements, and the significant correlations of leaf N with Mn, Na and Fe disappeared, while the correlations between SiO_2 and Fe, and Fe and P became significant.

Leaf N, P, K, S, Na and Fe loaded mainly on the first PCA axis, explaining 29.1% of the total variation; leaf Ca and Al loaded on the second axis, explaining 17.0% of the total variation; and leaf Mn and SiO_2 loaded on the third axis, which explained 13.6% of the total variation (Table 5). The first axis of the PCA was also significantly correlated with latitude, MAT and MAP, while the second and third axes were not significantly correlated with the above three environmental variables.

DISCUSSION

Several studies have found that leaf element concentrations vary with latitudinal and environmental gradients at a global or regional scale (Reich & Oleksyn, 2004; Han *et al.*, 2005, 2011) and among taxonomic groups (Thompson *et al.*, 1997; Broadley *et al.*, 2001, 2004; Kerkhoff *et al.*, 2006). However, the relative effects of taxonomy and environmental factors on leaf element concentrations have not yet been addressed. The analyses presented here provide new insight into the relationships between leaf element concentrations and taxonomy as well as the environment of terrestrial plants over a large geographical region.

Taxonomic effect on leaf element concentrations

Our results showed that leaf element concentrations varied significantly across species and families (Table 1, Appendix S3), and that taxonomic variance accounted for up to 43.9% of this variation (Table 2). However, the proportion of the variance components attributable to taxonomy differed considerably between leaf elements. The taxonomic contribution to leaf S and

Table 4 The correlation coefficients between the concentration of each of 10 leaf elements and mean annual precipitation (MAP), and mean annual temperature (MAT) analysed by the Mantel test and partial Mantel test at family level.

	MAP		MAT	
	Mantel test	Partial Mantel test (controlling MAT)	Mantel test	Partial Mantel test (controlling MAP)
N	0.28***	0.20***	0.20***	0.03
P	0.08	0.03	0.13*	0.10
NP	0.02	0.03	0.01	0.02
K	0.07	0.09	0.02	0.06
S	0.15*	0.18*	0.05	0.11
SiO_2	0.04	0.09	0.02	0.07
Fe	0.34***	0.29***	0.21***	0.09
Al	0.19**	0.22**	0.06	0.14
Mn	0.03	0.04	0.01	0.03
Na	0.18*	0.18*	0.08	0.08
Ca	0.07	0.07	0.03	0.04

Significant values were obtained by randomization. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 5 The factor loadings of 10 leaf elements on the three principal components (PCA) axes at family level, and correlation coefficients between each PCA axis and each of three environmental factors. The significant correlations between the PCA axis and the environmental factors are marked by asterisks.

	Component 1	Component 2	Component 3
N	0.759	−0.176	0.266
P	0.507	−0.270	0.151
K	0.815	0.047	−0.015
S	0.598	0.401	0.061
SiO_2	0.220	0.244	−0.854
Fe	0.745	0.349	0.082
Al	−0.225	0.697	0.127
Mn	−0.511	0.300	0.575
Na	0.655	0.210	0.195
Ca	0.226	−0.655	0.090
Total variation explained	29.1%	17.0%	13.6%
Correlation (r) with environmental variables			
Latitude	0.701***	0.091	0.011
MAT	0.525***	0.078	0.014
MAP	0.699***	0.008	0.038

MAT, mean annual temperature; MAP, mean annual precipitation.
***$P < 0.001$.

SiO_2 variation was significantly higher than the latitudinal contribution, while the contribution of latitude to leaf N, P, K, Al, Mn, Fe, Na and Ca concentrations was significantly larger than that of taxonomy. Previous studies have confirmed that leaf heavy metal concentrations, shoot mineral concentrations, and N, P and Mg concentrations in plant organs are constrained by taxonomic affiliations (Thompson *et al*., 1997; Broadley *et al*., 2001, 2004; Kerkhoff *et al*., 2006; Fyllas *et al*., 2009).

Some plant species can heavily accumulate certain elements (White *et al*., 2007). For example, Jansen *et al*. (2002) suggested that Al hyperaccumulators are particularly common in angiosperms such as rosids and asteroids. Hodson *et al*. (2005) found that the shoot SiO_2 concentration is influenced by the higher-level phylogenetic position of a plant. Our study found that ferns accumulate more SiO_2. The accumulation of SiO_2 is largely restricted to primitive land plants and certain monocot clades (Ma & Takahashi, 2002). Unlike gymnosperms and angiosperms, ferns lack strong mechanical tissues for support. Thus they employ a network of SiO_2 fibres to enhance mechanical support of frond weight by infilling SiO_2 to the cell walls and lumen of certain cells in plant tissues. Consequently, the variation in leaf element concentrations among taxonomic groups is likely linked to differences in structural or osmotic fractions of leaf tissues and selective uptake of certain nutrients by plants (White & Broadley, 2003; Watanabe *et al*., 2007; White *et al*., 2007).

Environmental effects on leaf element concentrations

Leaf N, P, K, S, Fe and Na concentrations exhibited significant latitudinal patterns, while leaf Al, Mn, SiO_2, Ca and N/P ratio showed no latitudinal variation (Table 2, Fig. 3). Our study supports the previous finding that increasing leaf N and P concentrations are correlated with increasing latitude (Reich & Oleksyn, 2004; Han *et al.*, 2005; Townsend *et al.*, 2007), while it contradicts the report that leaf N and P concentrations are not related to latitude (Kerkhoff *et al.*, 2005). The slope of the linear relationship between leaf N concentration and latitude in China was steeper than that at global scale (Reich & Oleksyn, 2004), indicating that latitudinal effects in China are stronger than in other regions. This could be due to the large variation in MAT with latitude in China, as the slope of the negative linear relationship between leaf N concentration and MAT in China was also steeper than that at global scale (Appendix S2). The correlations between latitude and leaf S, Na and Al concentration were driven by changes in MAP, not MAT (Table 3).

Leaf N, Fe, S, Al and Na concentrations decreased with MAP, while leaf N, P and Fe concentrations increased with MAT. Previous studies have suggested that leaf N and P concentrations are negatively associated with MAT at a global or regional scale (Reich & Oleksyn, 2004; Han *et al.*, 2005; Fyllas *et al.*, 2009), and leaf S, Na and K concentrations are negatively related to temperature and precipitation (Santiago *et al.*, 2005). The correlations between MAP and leaf element concentrations did not change significantly when controlled for MAT. However, all correlations of MAT with leaf elements became insignificant when controlled for MAP (Table 4). This indicates that in China MAP has a stronger effect on leaf element concentrations than MAT.

Precipitation and temperature can either directly affect plant element concentrations by changing both the nutrient allocation among organs and the concentration of elements associated with metabolism, or indirectly by influencing the leaf N or P concentration via changing soil biogeographical processes and vegetation composition (Körner, 1989; Wright *et al.*, 2001, 2005b; Reich, 2005; Ordoñez *et al.*, 2009). For example, species with high leaf N and P concentrations usually have fast growth rates (Wright *et al.*, 2001; Fyllas *et al.*, 2009), therefore the variation in leaf elements can be linked to the physiological requirements of plants (Han *et al.*, 2011). Meanwhile, N uptake and utilization by plants are also affected by soil temperature and water status (Dong *et al.*, 2001). For example, a higher leaf concentration of macronutrients is an adaptive feature enhancing the metabolic activity of plants in cold habitats (Oleksyn *et al.*, 2002).

Climatic factors also influence the species composition of plant communities, which in turn can affect the leaf element concentrations found in a community (Ordoñez *et al.*, 2009), because root uptake ability for certain nutrients is different among species (Broadley *et al.*, 2001). For example, the plant community assembly on acid soils is largely determined by the ability of plants to tolerate excessive Al, Mn and Fe, while that on the calcareous soils is determined by the ability of plants to tolerate Fe and P deficiencies (White & Broadley, 2003). Leaf Ca and Mn concentrations are profoundly influenced by soil acidity, and this effect interacts strongly with taxonomy (Thompson *et al.*, 1997). In our study, leaf elements varied considerably across families (Fig. 2) and the interaction of taxonomy with latitude contributed considerably to this variation in leaf element concentrations (Table 2), indicating that the latitudinal variations in leaf element concentrations were related to taxonomy.

Soil nutrient availability is one of the main factors affecting the concentration of certain leaf elements (Broadley *et al.*, 2001; Ordoñez *et al.*, 2009). Tripler *et al.* (2006) suggested that tissue K concentration is affected by soil K availability around the world. However, He *et al.* (2010) found that soil total N concentration was not correlated with leaf N concentration in 171 species across Chinese grasslands. In our study, a large proportion of total variation in each leaf element remained unexplained. These unexplained variations could be related to soil nutrient availability. Unfortunately, soil nutrient data were not available for our sampling sites and we were unable to assess their correlation to leaf elements.

Correlations of suites of associated leaf elements with the environment

Many leaf elements, particularly N, P and K, were positively correlated with each other either with or without considering phylogeny (Appendix S4), indicating that they share correlated evolutionary changes. Leaf Al and Ca were not correlated with the other elements when using the PIC method, suggesting that they have evolved independently. The correlations among leaf elements can be linked to their biochemical function and chemical properties (Garten, 1976). Similar to the results of Garten (1978) and Wright *et al.* (2005a), we found that the first axis of the PCA largely represented variations in N, P, K, S, Fe and Na, the second axis represented those in Ca and Al, and the third axis represented those in Mn and SiO_2 (Table 5). The elements associated with the first PCA axis were mainly involved in protein synthesis and photosynthesis. These leaf element concentrations were significantly affected by latitude, MAP and MAT. The other two PCA axes were associated with the leaf elements involved in cell structure and enzyme activity. These leaf element concentrations were not affected by latitude, MAP and MAT.

Leaf N/P ratio remained relatively constant across latitude in China. This result is consistent with the results of Han *et al.* (2005) from China and Townsend *et al.* (2007) around the world, but contradicts other studies that showed decreasing leaf N/P ratio with increasing latitude at global or regional scales (Reich & Oleksyn, 2004; Zheng & Shangguan, 2007). However, Chinese flora had a lower P concentration at a given leaf N concentration, which explained the higher N/P ratio in China compared with that on a global scale (Reich & Oleksyn, 2004) (Appendix S2). This is probably due to the low soil P concentration in China (Han *et al.*, 2005) as the shift in leaf N/P ratio is linked to soil P (Richardson *et al.*, 2008).

CONCLUSIONS

This study comprehensively characterized the relative effects of taxonomy and environmental factors on the latitudinal patterns of leaf K, S, SiO_2, Fe, Al, Mn, Na and Ca concentrations in China. Leaf element concentrations were affected by the environment, taxonomy and their interactions. But overall, the environment had a stronger effect than taxonomy on leaf element concentrations, with the exception of S and SiO_2. Therefore, changes in temperature and precipitation will directly affect the spatial patterns in leaf element concentrations via changes in vegetation composition and subsequently affect the associated ecosystem nutrient fluxes and functioning.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Leaf element concentrations and environmental variables of 702 plant species.

Appendix S2 Comparison of bivariate relationships between leaf elements and environmental variables of Chinese terrestrial plants with a global dataset.

Appendix S3 Leaf element concentrations of 66 plant families in China.

Appendix S4 Correlations among leaf elements at family level.

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BIOSKETCHES

Shi-Bao Zhang is a senior researcher at Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (CAS). His research interests include the evolution of plant functional traits, plant functional differentiation and ecological adaptation, photosynthesis and photoprotection of tropical plants in response to low temperature.

Kun-Fang Cao is a principal research scientist at Xishuangbanna Tropical Botanical Garden, CAS. He is interested in plant physiological ecology, especially plant hydraulics, water relations, evolution of plant functional traits and ecological adaptation, photosynthesis and photoprotection of tropical and subtropical plants in response to chilling temperature.

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