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# Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China

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## Summary

- Leaf nitrogen and phosphorus stoichiometry of Chinese terrestrial plants was studied based on a national data set including 753 species across the country.
- Geometric means were calculated for functional groups based on life form, phylogeny and photosynthetic pathway, as well as for all 753 species. The relationships between leaf N and P stoichiometric traits and latitude (and temperature) were analysed.
- The geometric means of leaf N, P, and N : P ratio for the 753 species were 18.6 and 1.21 mg $g^{-1}$ and 14.4, respectively. With increasing latitude (decreasing mean annual temperature, MAT), leaf N and P increased, but the N : P ratio did not show significant changes.
- Although patterns of leaf N, P and N : P ratios across the functional groups were generally consistent with those reported previously, the overall N : P ratio of China's flora was considerably higher than the global averages, probably caused by a greater shortage of soil P in China than elsewhere. The relationships between leaf N, P and N : P ratio and latitude (and MAT) also suggested the existence of broad biogeographical patterns of these leaf traits in Chinese flora.

**Key words:** China, leaf nitrogen (N) and phosphorus (P) contents, N : P ratio, plant functional groups, soil P.

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## Introduction

Nitrogen and phosphorus play vital roles in plant functioning, and are among the most important limiting nutrients in terrestrial ecosystems (Chapin, 1980; Reich *et al.*, 1997). Accordingly, patterns of N and P status in plant biomass, and especially in leaves, have been studied intensely (Foulds, 1993; Koerselman & Meuleman, 1996; Nielsen *et al.*, 1996; Reich *et al.*, 1997; Thompson *et al.*, 1997; Cunningham *et al.*, 1999; Reich *et al.*, 1999, 2003; Reich & Oleksyn, 2004). A number of studies have revealed that plant N and P concentrations are associated with many biotic and abiotic factors, including habitat (Hou, 1982; Foulds, 1993; Koerselman & Meuleman, 1996; Thompson *et al.*, 1997; Cunningham *et al.*, 1999); growth stages (Nielsen *et al.*, 1996; Thompson *et al.*, 1997; Elser *et al.*, 2000a; Sterner & Elser, 2002); and plant functional groups (Reich *et al.*, 1999). Previous studies have also shown that the ratio of leaf N to leaf P content in plant biomass can be an indicator of vegetation composition, functioning and nutrient limitation at the community level (Koerselman & Meuleman, 1996; Güsewell, 2004). An N : P ratio <14 generally indicates N limitation, while a ratio >16 suggests P limitation (Koerselman & Meuleman, 1996). More recently, Reich & Oleksyn (2004) have uncovered some broad biogeographical patterns in N and P stoichiometry by analysing a global data set of leaf N and P, and found that leaf N and P increased and N : P ratios decreased with increasing latitude (or decreasing temperature), independent of taxonomic shifts.

These previous studies have greatly advanced our understanding of the variations and patterns of leaf N and P in terrestrial plants. However, no studies have yet incorporated information on leaf N and P of plant species in China, home to >10% of the global plant species and a diverse array of ecosystems from tropical rainforests to alpine tundra. Here we compiled a national data set of leaf N and P for China's terrestrial plants, based on literature previously unavailable to researchers outside China, to analyse the patterns of leaf N and P stoichiometry in Chinese plant species. Our objectives were to (1) document available information on leaf N and P for China's terrestrial plants; (2) compare patterns of leaf N and P, and N : P ratios in China, with those of global data sets such as those reported by Elser *et al.* (2000b) and Reich & Oleksyn (2004); and (3) explore the possible causes of such patterns.

## Materials and Methods

### Data set

We collected data from the published literature on leaf N and P concentrations in Chinese species, along with the geographical and climatic information associated with the leaf samples (Appendix S1, available online as supplementary material). Our database consists of 2094 observations from 127 sampling sites across China (Fig. 1), including 753 terrestrial plant species in 395 genera and 116 families. For each sampling site we recorded location (latitude and longitude), vegetation type and climate variables, and documented family/genus/species, life forms (tree/shrub/herb, evergreen/deciduous, conifer/broadleaf, gymnosperm/angiosperm) and leaf N and P content of plants, and the methods used for leaf N and P analysis (see Appendix S1 for details).

To examine biogeographical patterns of leaf N, P and N : P ratio along gradients of latitude and temperature, as described by Reich & Oleksyn (2004), we documented the information on latitude and temperature for each sampling site by the following procedure. For sampling sites where latitude and mean annual temperature (MAT) were recorded, data were obtained directly; for sampling sites lacking detailed geographical coordinates, we used the latitude of the geographical centre of the sample area (a county); and for sampling sites where MAT was not recorded, we obtained MAT estimates based on a 0.1° × 0.1° resolution climate database developed by Fang *et al.* (2001) and Piao *et al.* (2003), which was generated from 682 climatic stations in China during 1949–99.

The leaf samples for N and P analyses in this database were collected mostly during the growing season (July–September). Units from different studies were standardized (mg $g^{-1}$ d. wt for leaf N and P), and N : P ratios were expressed on a mass basis.

### Data analysis

Because frequency distributions of leaf N, P and N : P ratios were highly skewed (Fig. 2), we calculated their geometric means. We also present arithmetic means of leaf N, P and N : P mass ratios for all 753 species, for comparison with previous studies that showed only arithmetic means.

Geometric means of leaf N, P and N : P ratios were also calculated by life form (e.g. herbs, shrubs, trees; evergreen, deciduous, conifers, broadleaves); phylogeny (e.g. seed plants, ferns); and photosynthetic pathways (e.g. $C_3$ and $C_4$ herbs). Seed plants were divided into angiosperms and gymnosperms, and angiosperms were further grouped into dicotyledons and monocotyledons.

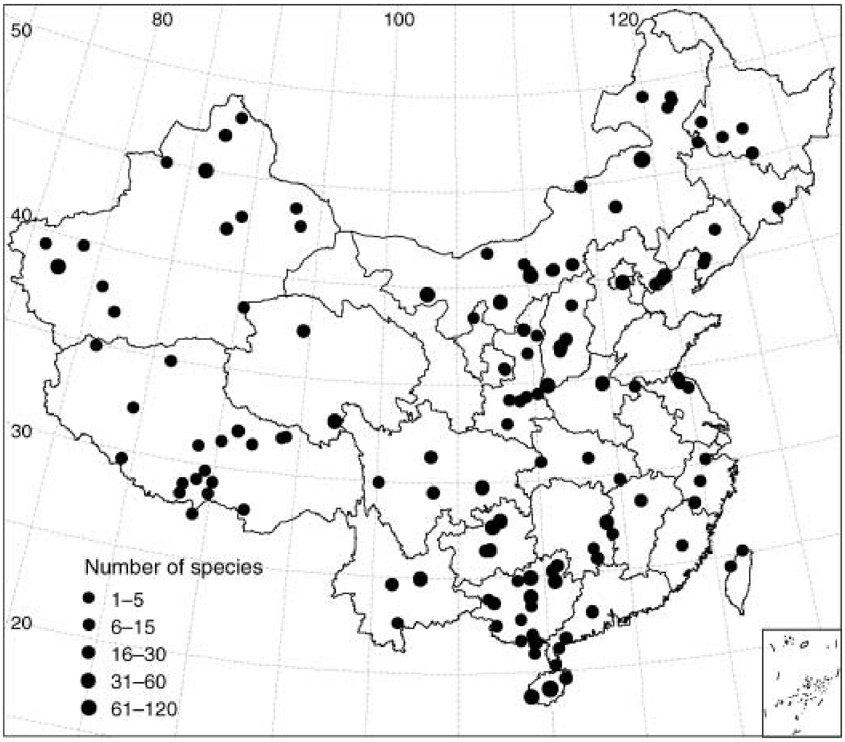

**Fig. 1** Sampling locations of leaf nitrogen and phosphorus for all species in this study. Provincial boundaries are shown.

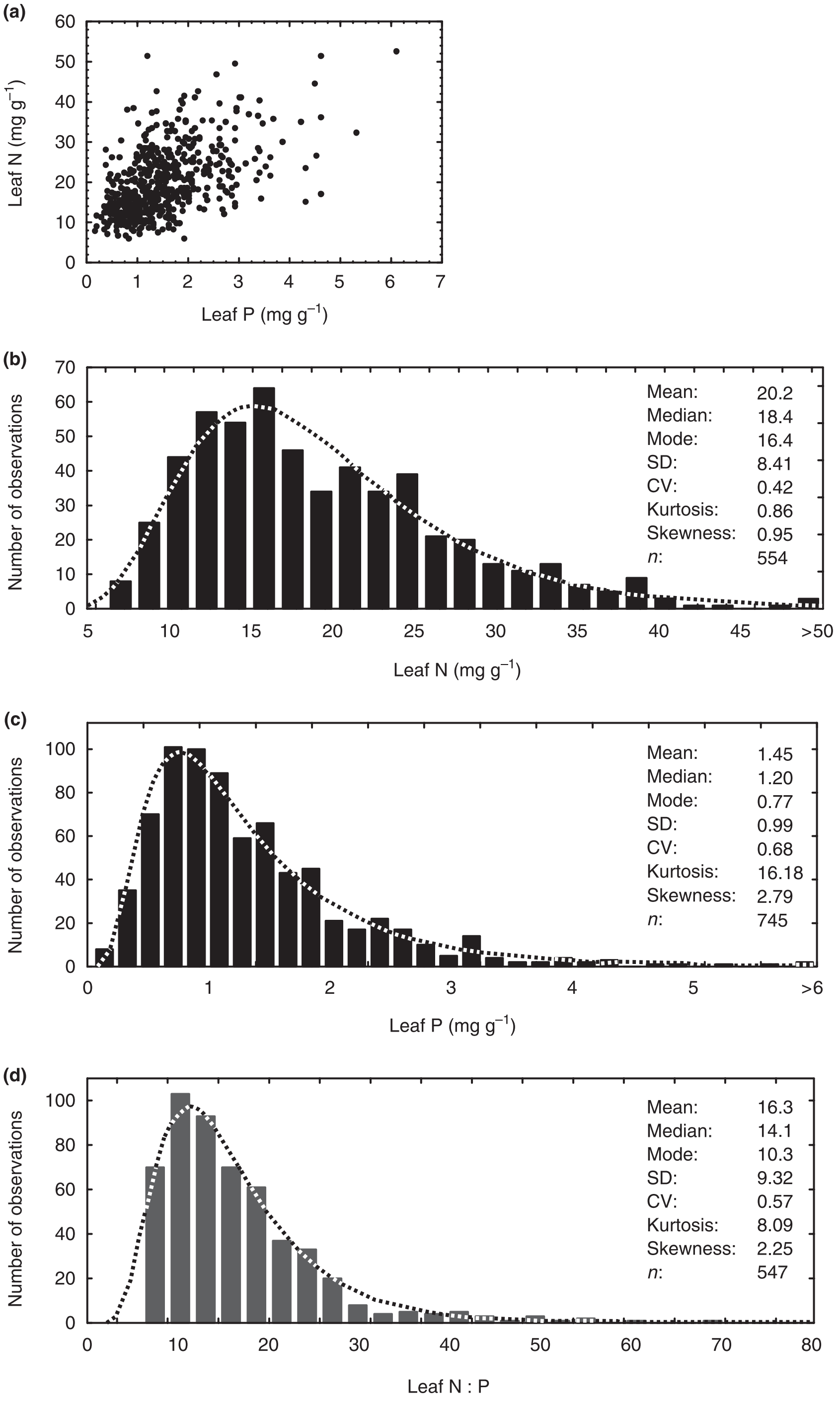

**Fig. 2** Scatter plot (a); and histograms showing the distribution of leaf nitrogen (mg g$^{-1}$) (b); phosphorus (mg g$^{-1}$) (c); N : P mass ratio (d) for all 753 species. Dashed curves in (b–d) indicate fitted log-normal curves.

We compared the statistical differences in N and P stoichiometry between different functional groups by following three steps. First, for each species the geometric means of leaf N and P were calculated, and N : P mass ratios were obtained. Second, the species-specific means of N, P and N : P ratio were log-transformed (base *e*) for all species combined and for each functional group. Finally, the log-transformed N, P and N : P ratios were compared between functional groups using one-way ANOVA. We also calculated Spearman's rank correlation coefficients between mean leaf N and P for all 753 species and for each functional group.

To characterize biogeographical patterns of leaf stoichiometry, we first computed geometric means of leaf N and P, and N : P ratios for each species for each sampling site, then log-transformed the means of leaf N, P and N : P ratios to perform linear regressions. All statistical analyses were conducted using SPSS software (2001, ver. 11.0; SPSS Inc., USA).

**Table 1** Geometric means of leaf nitrogen, phosphorus and N : P mass ratios of different plant functional groups

| | N (mg g$^{-1}$) | | P (mg g$^{-1}$) | | N : P mass ratio | | |
|---|---|---|---|---|---|---|---|
| Functional group | *n* | Geometric mean | *n* | Geometric mean | *n* | Geometric mean | $r_s$ |
| Life form | | | | | | | |
| Herb | 244 | 20.9 | 280 | 1.55 | 240 | 13.5 | 0.41* |
| Shrub | 137 | 19.1 | 209 | 1.11 | 135 | 14.7 | 0.61* |
| Tree | 148 | 15.7 | 223 | 1.00 | 147 | 15.0 | 0.39* |
| Evergreen tree | 149 | 14.1 | 229 | 0.88 | 149 | 15.2 | 0.28* |
| Deciduous tree | 129 | 22.2 | 189 | 1.30 | 126 | 14.8 | 0.41* |
| Conifer | 27 | 11.7 | 42 | 1.06 | 27 | 13.0 | 0.38 |
| Broadleaf | 258 | 17.9 | 390 | 1.05 | 255 | 15.1 | 0.55* |
| Phylogeny | | | | | | | |
| Seed plant | 536 | 18.9 | 720 | 1.22 | 529 | 14.3 | 0.52* |
| Fern | 18 | 12.4 | 25 | 0.81 | 18 | 17.6 | 0.46 |
| Gymnosperm | 27 | 11.7 | 43 | 1.05 | 27 | 13.0 | 0.38 |
| Angiosperm | 509 | 19.4 | 677 | 1.23 | 502 | 14.3 | 0.51* |
| Monocotyledon | 109 | 16.5 | 133 | 1.32 | 109 | 13.1 | 0.35* |
| Dicotyledon | 426 | 19.6 | 586 | 1.20 | 419 | 14.6 | 0.55* |
| Photosynthetic pathway | | | | | | | |
| $C_3$ herb | 206 | 21.2 | 242 | 1.56 | 204 | 13.6 | 0.46* |
| $C_4$ herb | 38 | 19.4 | 38 | 1.47 | 36 | 13.0 | 0.15 |
| All species | 554 | 18.6 | 745 | 1.21 | 547 | 14.4 | 0.54* |

Spearman's rank correlation coefficient ($r_s$) between species-specific leaf N and P was calculated for each functional group (*n*, sample size). Correlations with *, $P < 0.001$; those without, $P > 0.05$.

## Results

### Patterns of leaf N, P and N : P ratio across all species

Leaf N, P and N : P mass ratio exhibited large variations, primarily ranging *c.* 8–50 mg g$^{-1}$ for N; 0–5 mg g$^{-1}$ for P, and 5–40 for N : P ratio (Fig. 2). Geometric means for all species were 18.6 and 1.21 mg g$^{-1}$, and 14.4, respectively; the corresponding arithmetic means were 20.2 and 1.45 mg g$^{-1}$, and 16.3, respectively (Table 1). Across all species, leaf N and P were highly positively correlated (Fig. 2a; Table 1).

### Patterns of leaf N, P and N : P ratio across functional groups

Leaf N and P varied markedly across the functional groups (Table 1; Fig. 3). For leaf N, geometric means ranged from 11.7 mg g$^{-1}$ for conifers to 22.2 mg g$^{-1}$ for deciduous trees. Those for P varied from 0.81 mg g$^{-1}$ for ferns to 1.56 mg g$^{-1}$ for $C_3$ herbs. In contrast, mean N : P ratios showed a relatively narrow range, from 13.0 (conifers, gymnosperms, $C_4$ herbs) to 17.6 (ferns), with 12 out of 15 groups taking a value between 13 and 15 (Table 1; Fig. 3). Statistical comparisons between functional groups further confirmed the relative constancy of N : P ratios across different functional groups (Table 2). Among nine comparison pairs, only one (monocotyledons vs dicotyledons) showed a significant difference ($P < 0.05$) in N : P ratio, in contrast with eight in leaf N, and four in leaf P ($P < 0.05$). Spearman's rank correlation coefficients between leaf N and P concentrations also reflected the comparative stability of N : P ratios (Table 1). Eleven out of 15 functional groups showed a significant positive correlation ($P < 0.001$).

### Relationships between leaf N, P, N : P and latitude (MAT)

Leaf N and P were significantly correlated with latitude and MAT across all species (Fig. 4a,b,d,e), while the leaf N : P ratio was weakly correlated with latitude and MAT ($P = 0.257$ and $P = 0.221$) (Fig. 4c,f). In general, leaf N and P increased and the N : P ratio decreased as latitude increased and MAT decreased.

## Discussion

### Overall patterns of N and P stoichoimetry in China's flora

This work presents, to the best of our knowledge, the first analysis of leaf N and P stoichiometry of a large number of terrestrial plant species across China. Our analysis indicated that leaf N of all 753 species had a geometric mean of 18.6 mg g$^{-1}$ (arithmetic mean 20.2 mg g$^{-1}$), nearly identical to that reported by Elser *et al.* (2000b) for 397 terrestrial plant species (geometric mean 17.6 mg g$^{-1}$; arithmetic mean

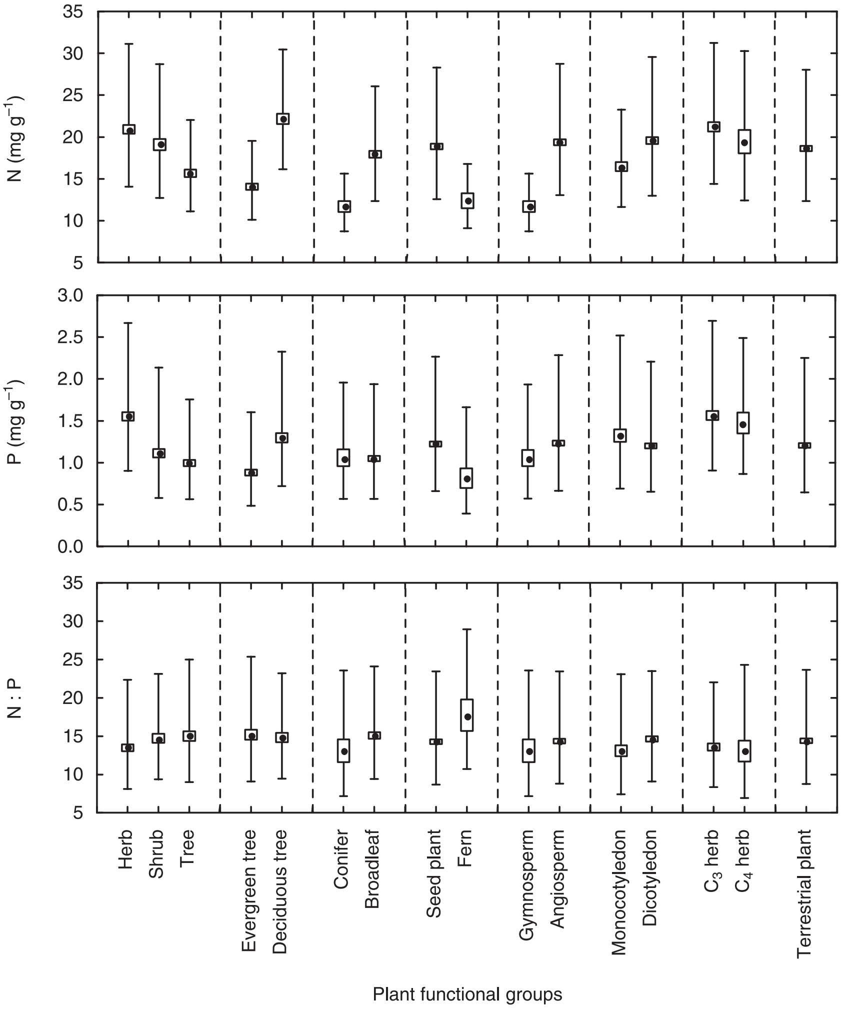

**Fig. 3** Box-and-whisker plots showing geometric mean, geometric standard deviation and geometric standard error for leaf nitrogen (mg g$^{-1}$), phosphorus (mg g$^{-1}$), and N : P mass ratio.

**Table 2** Results of ANOVA for comparisons between different functional groups

| | Nitrogen | | Phosphorus | | N : P | |
|---|---|---|---|---|---|---|
| Comparison pair | *F*(*m*, *n*) | *P* | *F*(*m*, *n*) | *P* | *F*(*m*, *n*) | *P* |
| Herb vs shrub | 4.51<br>(1, 379) | <0.05 | 37.65<br>(1, 487) | <0.001 | 2.78<br>(1, 373) | 0.10 |
| Herb vs tree | 54.33<br>(1, 390) | <0.001 | 79.77<br>(1, 501) | <0.001 | 4.03<br>(1, 385) | 0.05 |
| Shrub vs tree | 20.00<br>(1, 283) | <0.001 | 3.64<br>(1, 430) | 0.06 | 0.11<br>(1, 280) | 0.74 |
| Evergreen vs deciduous | 136.41<br>(1, 276) | <0.001 | 43.63<br>(1, 416) | <0.001 | 0.16<br>(1, 273) | 0.69 |
| Conifer vs broadleaf | 33.48<br>(1, 283) | <0.001 | 0.00<br>(1, 430) | 0.96 | 2.31<br>(1, 280) | 0.13 |
| Fern vs seed plant | 19.29<br>(1, 552) | <0.001 | 10.80<br>(1, 743) | <0.05 | 3.12<br>(1, 545) | 0.08 |
| Gymnosperm vs angiosperm | 43.26<br>(1, 534) | <0.001 | 2.73<br>(1, 718) | 0.10 | 1.02<br>(1, 527) | 0.31 |
| Monocotyledon vs dicotyledon | 16.52<br>(1, 533) | <0.001 | 2.58<br>(1, 717) | 0.11 | 4.30<br>(1, 526) | <0.05 |
| $C_3$ vs $C_4$ herb | 1.63<br>(1, 242) | 0.20 | 0.44<br>(1, 278) | 0.51 | 0.24<br>(1, 238) | 0.62 |

Data in each group were log-transformed (base *e*).
*m*, *n* denote degrees of freedom between and within groups, respectively.

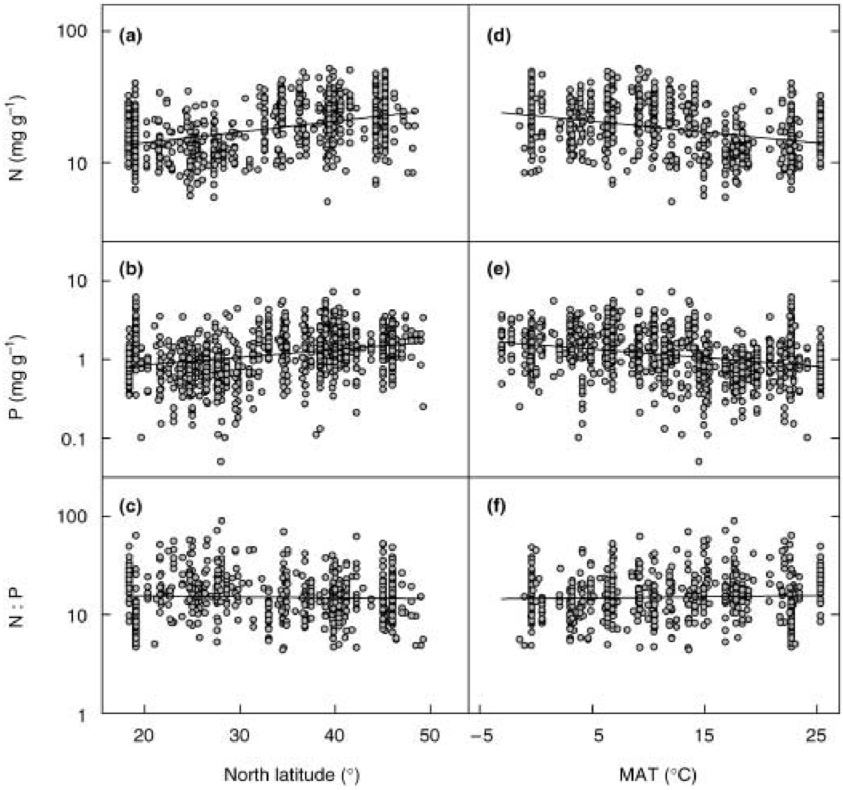

**Fig. 4** Relationships between leaf nitrogen, phosphorus and N : P mass ratio of plants, latitude and mean annual temperature (MAT) in China. Each data point represents a log-transformed, species-specific average of all observations of N, P or N : P within each sampling site (see Appendix 2). Linear regressions are shown for (a) latitude and leaf N ($r^2 = 0.179$, $P < 0.001$, $n = 813$); (b) latitude and leaf P ($r^2 = 0.101$, $P < 0.001$, $n = 1177$); (c) latitude and leaf N : P ($r^2 = 0.002$, $P = 0.257$, $n = 780$); (d) MAT and leaf N ($r^2 = 0.141$, $P < 0.001$, $n = 813$); (e) MAT and leaf P ($r^2 = 0.100$, $P < 0.001$, $n = 1177$); (f) MAT and leaf N : P ($r^2 = 0.002$, $P = 0.221$, $n = 780$).

**Table 3** Statistics of leaf nitrogen, phosphorus and N : P mass ratio for all species analysed by this study; Elser *et al*. (2000b); and Reich & Oleksyn (2004)

| Data source | N (mg g$^{-1}$) | P (mg g$^{-1}$) | N : P |
|---|---|---|---|
| This study | | | |
| Mean | 18.6 (20.2) | 1.21 (1.46) | 14.4 (16.3) |
| SD | 8.41 | 0.99 | 9.32 |
| *n* | 554 | 745 | 547 |
| Reich & Oleksyn (2004) | | | |
| Mean | 18.3 (20.1) | 1.42* (1.77*) | 11.8* (13.8*) |
| SD | 8.71 | 1.12 | 9.47 |
| *n* | 1251 | 923 | 894 |
| Elser *et al*. (2000b) | | | |
| Mean | 17.7 (20.6) | 1.58* (1.99*) | 11.0* (12.7*) |
| SD | 12.23 | 1.49 | 6.82 |
| *n* | 398 | 406 | 325 |

Both geometric and arithmetic (in parentheses) means are presented to facilitate comparisons between different studies.
*Significant difference in means of P or N : P between this study and the others ($P < 0.001$). No significant differences in N were between studies ($P > 0.05$).

20.6 mg g$^{-1}$); and by Reich & Oleksyn (2004) for 1251 world plant terrestrial species (excluding China's plants) (geometric mean 18.3 mg g$^{-1}$; arithmetic mean 20.1 mg g$^{-1}$).

Leaf P of China's flora, however, was significantly lower than the global averages (Table 3). The geometric mean leaf P was 1.21 mg g$^{-1}$ for China's flora, 15% lower than the value reported by Reich & Oleksyn (2004) and 23% lower than that reported by Elser *et al.* (2000b) (Table 3).

A larger geometric mean N : P mass ratio (14.4) thus resulted for China's flora – data from Elser *et al.* (2000b) and Reich & Oleksyn (2004) yielded a geometric mean N : P ratio of 11.0 and 11.8, respectively – primarily caused by lower leaf P in Chinese vegetation than in global vegetation (Table 3). Because leaf N : P mass ratio is an indicator of the relative limitation of N vs P (N : P ratios <14 often indicate N limitation and N : P ratios >16 frequently signify P limitation; Koerselman & Meuleman, 1996; Aerts & Chapin, 2000), the higher N : P ratio in this study than in others (Elser *et al.*, 2000b; Reich & Oleksyn, 2004) might imply that China's flora are relatively more limited by P (geometric mean N : P ratio of Chinese flora = 14.4) than the world flora analysed by Reich & Oleksyn (2004).

Why, then, did lower leaf P (and higher N : P ratios) occur in China's flora? A potential cause for such a low leaf P may be the low soil P content in China. Plant and soil P are generally coupled at ecosystem scales (Aerts & Chapin, 2000; Hedin, 2004). Overall soil P contents across most areas of China were below the global average (National Soil Survey Office of China, 1997, 1998; Shen & Chen, 1998). A comparison between the mean soil P content of China and the USA also suggested that soil P was much lower in China than in the USA: 561 ppm for China (National Soil Survey Office of China, 1998) vs 699 ppm for the USA (US Geological Survey, 2001). Furthermore, our

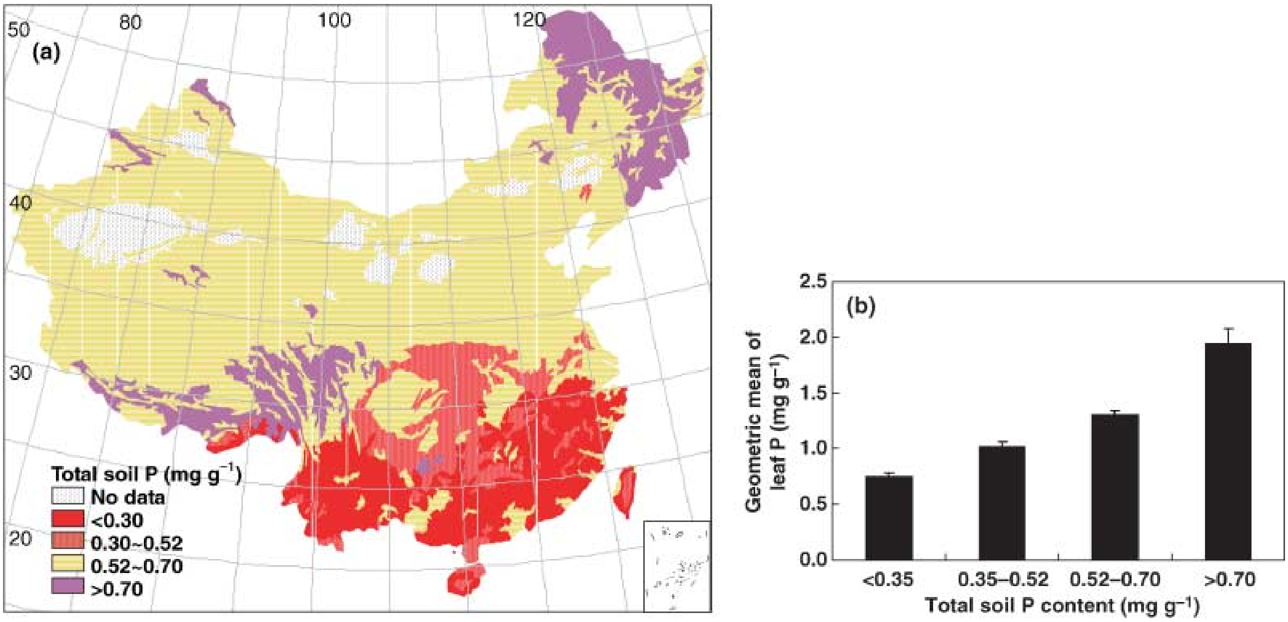

**Fig. 5** Soil phosphorus contents and their relationship with mean leaf P content of plants in China. (a) Distribution of soil P contents. P content is divided into four classes: <0.35, 0.35–0.52, 0.52–0.70 and >0.70 mg g$^{-1}$, based on the map of soil P potential of China (Jiang *et al*., 1986). (b) Geometric mean leaf P contents (mg g$^{-1}$) by each soil P content class (mg g$^{-1}$) and standard error bars. Numbers of species were 210, 262, 654 and 66 for the four soil P classes. Differences in geometric mean leaf P content between different soil P classes were all statistically significant at the 0.05 level (ANOVA, Student–Newman–Keuls (S–N–K) *post hoc* test).

analysis indicated that regional leaf P increased significantly with increasing regional soil P content (Fig. 5), suggesting that plants are probably P-limited in most soils of China.

Another possibility for this low leaf P is that more plant samples were collected from the southern than in the northern areas, because soil P is usually low in the south. To explore this possibility, we simply divided the plant samples into two groups: samples from north of 30°N (north group); and those from south of 30°N (south group). The 30°N parallel corresponds roughly to the boundary between subtropical and temperate climates in China (Fang, 2001; Fang *et al.*, 2002). Plant samples from the Tibetan Plateau were included in the north group because the plateau is >4000 m high and has a temperate climate. The results showed that the ratio of samples from the south group to that from the north group for leaf N and P was 0.64 (450 vs 707) and 0.77 (834 vs 1087), respectively, showing a higher proportion of samples from the north than the south group. This suggests that the lower leaf P content and the higher leaf N : P ratios in Chinese plants compared with the global data sets are probably not caused by preferential sampling of southern species (which tend to have low leaf P).

## Variations in N and P stoichoimetry across functional groups

Large differences in leaf N and P occurred across functional groups of Chinese flora (Tables 1, 2; Fig. 3). We found that leaf N and P levels were significantly higher in herbs than in woody plants, and in deciduous than in evergreen species, consistent with higher N and P in short-lived, fast-growing species than in long-lived, slow-growing species, as identified previously (Pate & Dell, 1984; Foulds, 1993; Aerts, 1996; Thompson *et al.*, 1997; Güsewell & Koerselman, 2002). Moreover, higher N and P occurred in seed plants than in ferns, and higher N in angiosperms than in gymnosperms, suggesting that these phylogenic groups differed in leaf chemistry. However, unlike Marschner (1995), we did not find significant differences in leaf N and P between $C_3$ and $C_4$ species ($P > 0.2$). Although $C_4$ plants may have an advantage over $C_3$ plants in N- (even P-)poor conditions, Güsewell (2004) argued that the advantages conferred by photosynthetic pathways may not be specifically related to N or P limitation, thus leaf N and P may not contrast between these two photosynthetic pathways.

Because of the highly positive correlations between leaf N and P (Table 1), N : P ratios across different functional groups varied less than N or P alone (Fig. 3; Table 2). The relative constancy of N : P ratio across functional groups may reflect a fundamental feature of the plant kingdom with respect to leaf N and P stoichiometry. The strong correlation between concentrations of N and P may result from the most basic biochemical processes – metabolic activities shared among terrestrial plants, such as photosynthesis and respiration (Duarte, 1992).

### Relationships between N, P, N : P and latitude (MAT)

While leaf N, P and N : P ratios at the level of species and functional groups reflect adaptations of plants to their local nutrient limitations (Grime *et al.*, 1997; Aerts & Chapin, 2000), there may exist global trends in leaf N, P and N : P reflecting biogeographical gradients in N and P supplies that constrain nutrient adaptations at the local scale. In recent analyses of leaf nutrient distributions, Reich & Oleksyn (2004) identified two broad trends in leaf N, P and N : P distributions in global vegetation: (1) leaf P, and to a lesser degree leaf N, decreases as latitude decreases (or MAT increases); (2) leaf N : P ratio increases as latitude decreases (or MAT increases). Because similar trends also occurred within different taxonomic groups, these global trends were thought to be independent of taxonomic groups or shifts in species composition (Hedin, 2004; Reich & Oleksyn, 2004). Similarly to Reich & Oleksyn (2004), we have identified correlations between leaf N, P, N : P ratio and latitude (MAT) in Chinese flora (Fig. 4). However, these correlations, especially those between N : P ratio and latitude (MAT), when characterized with simple linear regression lines, had gentler slopes than those reported by Reich & Oleksyn (2004). The nonsignificant linear regressions between leaf N : P ratio and latitude or MAT (Fig. 4c,f) may be caused in part by the smaller geographical extent of China (latitudes ranged from 18 to 49°N for our data set compared with 43°S to 70°N recorded by Reich & Oleksyn, 2004; Appendix S2, available online as supplementary material), and in part by the existence of the Tibetan Plateau, which is located at the relatively low latitudes but has lower temperatures than some higher latitudes in China.

In conclusion, general patterns of N and P stoichoimetry in Chinese terrestrial plant species were in agreement with the trends identified by recent analyses of the global flora that did not include Chinese species. However, some patterns unique to Chinese flora also emerged: (1) leaf P across all 753 species was considerably lower than the global averages that excluded Chinese species, resulting in a markedly higher N : P ratio, probably reflecting a greater degree of P limitation for Chinese vegetation than for vegetation elsewhere; and (2) there was a trend of increasing N : P ratio with decreasing latitude, but this trend might not be comparable with that of the global data set identified by Reich & Oleksyn (2004), probably because of the smaller latitudinal extent of China and the cold Tibetan Plateau in the lower latitudes.

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## Supplementary material

The following supplementary material is available for this article online.

### Appendix S1

Data set of leaf nitrogen (N) and phosphorus (P) concentrations in wild terrestrial plants of China, compiled by J. Y. Fang, Y. Zhang and W. X. Han, Department of Ecology, College of Environmental Sciences, Peking University, 2000.

### Appendix S2

Leaf nitrogen (N) and phosphorus (P) averaged by species within sample area (for Fig. 4), compiled by J. Y. Fang, W. X. Han and Y. Zhang, Department of Ecology, College of Environmental Sciences, Peking University, 2000.

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