Acta Geochim (2017) 36(3):525–530
DOI 10.1007/s11631-017-0225-8

ORIGINAL ARTICLE

Ecological stoichiometry of nitrogen, phosphorous, and sulfur in China's forests

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Received: 23 February 2017 / Revised: 27 April 2017 / Accepted: 16 August 2017 / Published online: 28 August 2017

Abstract Much attention has been paid to the stoichiometry of carbon (C), nitrogen (N), and phosphorus (P) because of their significance for plant growth and climate change. However, other nutrients, such as sulfur (S), are often ignored. In this study, we analyzed the stoichiometry of N, P, and S in leaves of 348 plant species in China's forests. The results show higher N content and higher molar ratios of N/P and P/S in Angiospermae than in Gymnospermae. At the family level, Ulmaceae absorbed more N and P from soils than other families, and Cupressaceae absorbed more S than other families. In addition, except for bamboo and other tropical forests, leaf N and P content of China's forests generally increased from low to middle latitudes and then slightly decreased or plateaued at high latitudes. Plant ecotypes, taxonomic groups, environmental conditions, atmospheric S precipitation, and soil-available N and P significantly affected the distribution and stoichiometry of leaf N, P, and S in China's forests. Our study indicates that China's forests are likely limited by P and S deficiencies which may increase in the future.

11th international symposium on geochemistry of the earth's surface.

Electronic supplementary material The online version of this article (doi:10.1007/s11631-017-0225-8) contains supplementary material, which is available to authorized users.

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Keywords Forest · Stoichiometry · Nitrogen · Phosphorous · Sulfur · China

1 Introduction

Terrestrial plants are the products of biochemical reactions, and their normal growth depends not only on the availability of light, water, and carbon (C), but also on the balance of various nutrients (Peñuelas and Sardans 2009). Among the essential macronutrients, nitrogen (N), phosphorus (P), and sulfur (S) are important for plant growth and terrestrial C sequestration (Shi et al. 2016). The contents and ratios of these nutrients in plants vary significantly with global environmental change (Han et al. 2011; Oulehle et al. 2011), which may have significant impacts on plant growth and on C balance in forests and other terrestrial ecosystems (Oulehle et al. 2011). S deposition plays an important role in forest C and N cycles (Oulehle et al. 2011), and S also plays a major role in plant metabolism by coupling N and P (Shi et al. 2016). The S stoichiometry with N and P cycling in forests is, however, poorly known. Current studies of the ecological stoichiometry of forests and other terrestrial ecosystems have mainly focused on the ratio of C/N/P (Han et al. 2005) with little emphasis on the ratios of N/S and P/S (Han et al. 2011; Shi et al. 2016).

Forests occupy more than one-fifth of the global land surface and play an important role in the regulation of the global C balance and climate change (Song et al. 2013). China has 1.43×10^8 ha of forested land ranging from tropical and subtropical forests in the south to temperate and boreal forests in the north (Song et al. 2013). This study examined the ecological stoichiometry of N, P, and S through tree leaves and climate data.

2 Materials and methods

2.1 General characteristics of the forests

Based on climatic conditions and plant physiology, China's forests can be generally divided into eight types from high latitudes to tropics (Song et al. 2013): cold-temperate and temperate coniferous (CTC), coniferous and broad-leaf mixed (CB), deciduous broad- or small-leaf (DBS), subtropical evergreen and deciduous broad-leaf (SEDB), subtropical and tropical bamboo (STB), tropical and subtropical coniferous (TSC), subtropical (sclerophyllous) evergreen broad-leaf (SEB), and tropical (T). Plant composition, aboveground net primary productivity and other properties vary significantly among the forest types (Song et al. 2013).

2.2 Data collection

Leaf N, P, and S concentration data in tree species within China's forests were obtained from published literature (Hou 1982). For each species, the content of a nutrient was calculated from the average of several samples. The details of each sampling site are reported in the published literature (see Appendix S1 in the Supplementary Material). Based on the geographical climate of the sampling sites, the obtained species data were collected from eight forest types. The collected data were used to analyze the effects of taxonomic groups (phylum and family) and climate variables (mean annual precipitation or MAP, and mean annual temperature or MAT) on the stoichiometry of N, P, and S contents in China's forest (see Appendix S1 in Supplementary Material).

2.3 Statistical analyses

The data were statistically analyzed by an analysis of variance, and Duncan's test was used to compare means using R software (R 3.3.2 for Windows).

3 Results and discussion

3.1 Distribution of N, P, and S in different forests

The distribution of N, P, and S in tree leaves varied greatly among the eight forest types (Table 1). Previous studies have established that leaf N and P generally increase from low latitudes (tropic zone) to middle latitudes (cooler and drier zone) and then slightly decrease at high latitudes (cold temperate zone) (Reich and Oleksyn 2004). According to our results, the leaf N and P of China's forests showed similar trends, except for T and STB (Table 1). In China, many tropical plants and bamboos have a high growth rate. We supposed these plants' fast metabolisms require more N and P, resulting in N and P enrichment in biomes.

Compared with global and regional values, the average available P content in China's soils is quite low (Han et al. 2005). Consequently, the leaf P content of China's forests ($1.1\ mg \cdot g^{-1}$) (Table 1) is significantly lower than that of global forests ($1.42\ mg \cdot g^{-1}$) (Reich and Oleksyn 2004). Han et al. (2011) reported leaf S content in China's forests up to $1.58\ mg \cdot g^{-1}$, whereas our results show a lower content ($1.1\ mg \cdot g^{-1}$). This is likely due to the data's having been obtained before the 1980s and the increasing trend in SO_2 emissions in China after that time.

The molar ratios of N/P, N/S, and P/S among the eight forests were in the range of 27.3–61.7, 25.9–78.0, and 1.0–4.2, respectively. The molar ratios of N/P, N/S, and P/S were significantly higher in SEB, CB, and CB forests, respectively than those in other forests. However, lower P concentration at a given leaf N concentration in Chinese flora contributes to a higher average molar ratio of N/P in China's forests ($N/P = 38.8 \pm 2.7$, $n = 161$) (Table 1) than in global forests ($N/P = 33.7 \pm 0.74$, $n = 331$) (Reich and Oleksyn 2004). For example, the values of N/P in TSC, DBS, SEDB, and SEB forests were significantly higher than those in global forests (Table 1).

In general, the leaf N/P molar ratio (35.4) can be an indicator of the potential limitation of N or P during forest growth (Aerts and Chapin 2000). In this study, the N/P molar ratio ($N/P = 38.8$) was higher than 35.4, implying that China's forests are more likely limited by P. Although the data in our study were limited, the average molar ratios of N/S ($N/S = 41.7 \pm 2.3$, $n = 91$) and P/S ($P/S = 1.7 \pm 0.2$, $n = 269$) (Table 1) were similar to values reported in previous, more robust studies of China's forests ($N/S = 38.7 \pm 0.55$ and $P/S = 1.68 \pm 0.2$, $n = 391$) (Han et al. 2011). Therefore, our results support the previous findings that forests' molar ratios of N/S and P/S have stabilized at an adaptive value under stable environmental conditions (Reich and Oleksyn 2004).

3.2 Variation of N, P, and S among different taxonomic groups of forests

The N, P, and S contents in leaves varied markedly among the different taxonomic groups of forests, especially at the phylum and family levels (Table 2), a finding that supports previous study (Zhang et al. 2012). It has been reported that S concentration was more significantly affected by taxonomy than N and P concentrations in plant leaves (Zhang et al. 2012). However, our analysis found no significant difference in P and S contents or in the N/S ratio between

Table 1 Contents of N, P, and S, and molar ratios of N/P, N/S, and P/S in eight forest types of China

Forest type	N		P		S		N/P	N/S	P/S
	n	mg·g^{-1}	*n*	mg·g^{-1}	*n*	mg·g^{-1}	Molar ratio	Molar ratio	Molar ratio
CTC	13	14.2 ± 1.7bc	27	1.2 ± 0.1ab	25	1.0 ± 0.1b	33.6 ± 5.6b	51.0 ± 8.0b	1.9 ± 0.3b
CB	22	13.6 ± 0.9b	26	1.6 ± 0.2a	5	0.6 ± 0.1c	27.3 ± 3.2c	78.0 ± 7.6a	4.2 ± 0.5a
DBS	13	20.4 ± 1.6a	29	1.1 ± 0.1b	28	2.7 ± 0.5a	38.8 ± 6.5b	46.2 ± 5.4b	1.0 ± 0.3c
SEDB	9	14.7 ± 1.1b	67	0.9 ± 0.1c	68	1.0 ± 0.1bc	57.8 ± 7.9a	34.6 ± 6.1c	1.6 ± 0.3b
SEB	28	14.6 ± 1.0b	80	0.9 ± 0.1c	83	0.8 ± 0.1c	61.7 ± 9.0a	41.6 ± 3.1bc	2.1 ± 0.5b
TSC	27	11.8 ± 0.9c	56	0.9 ± 0.1bc	56	1.0 ± 0.1bc	46.3 ± 8.2b	37.6 ± 5.2c	1.5 ± 0.2b
STB	3	16.3 ± 2.5ab	3	1.6 ± 0.3a	1	1.0	27.3 ± 9.6c	38.1	1.3
T	54	14.8 ± 0.8b	63	1.5 ± 0.1a	10	1.3 ± 0.3b	28.8 ± 4.3c	25.9 ± 13.6c	1.3 ± 0.4bc
Total	169	14.5 ± 0.4	351	1.1 ± 0.1	276	1.2 ± 0.1	38.8 ± 2.7	41.7 ± 2.3	1.7 ± 0.2

Different lowercase letters indicate significant differences within the same column at $p = 0.05$ level based on Duncan's test

CTC cold-temperate and temperate coniferous forest, *CB* coniferous and broad-leaf mixed forest, *DBS* deciduous broad- or small-leaf forest, *SEDB* subtropical evergreen and deciduous broad-leaf forest, *SEB* subtropical (sclerophyllous) evergreen broad-leaf forest, *TSC* tropical and subtropical coniferous forest, *STB* subtropical and tropical bamboo forest and *T* tropical forest. *n* represents number of plant species. For each species, the content of a nutrient is the average of several samples

Table 2 Contents of N, P, and S, and molar ratios of N/P, N/S, and P/S in different arbor groups of China's forests

Taxonomic group	N		P		S		N/P	N/S	P/S
	n	mg·g^{-1}	*n*	mg·g^{-1}	*n*	mg·g^{-1}	Molar ratio	Molar ratio	Molar ratio
Phylum									
Gymnospermae	61	12.4 ± 0.6c	98	1.1 ± 0.1a	76	1.0 ± 0.1b	34.9 ± 4.0b	43.1 ± 4.5a	1.7 ± 0.2c
Family									
Pinaceae	49	12.4 ± 0.6c	77	1.1 ± 0.1a	55	0.8 ± 0.1b	34.0 ± 4.4b	48.2 ± 5.4a	1.9 ± 0.2a
Cupressaceae	7	9.4 ± 1.5c	12	1.1 ± 0.2ab	11	1.8 ± 0.4a	31.4 ± 13.0b	16.1 ± 3.2b	0.9 ± 0.2d
Taxodiaceae	4	17.0 ± 4.0ab	8	0.8 ± 0.1b	9	0.8 ± 0.2b	57.5 ± 13.6a	48.0 ± 10.7a	1.5 ± 0.4cd
Angiospermae	106	15.7 ± 0.6b	245	1.1 ± 0.1a	194	1.3 ± 0.1b	41.0 ± 3.6ab	40.9 ± 2.4a	1.8 ± 0.2b
Family									
Fagaceae	44	14.4 ± 0.6b	94	0.9 ± 0.1b	84	0.8 ± 0.04b	48.6 ± 4.4a	43.8 ± 2.9a	1.6 ± 0.2cd
Theaceae	7	13.5 ± 2.3bc	12	0.7 ± 0.1b	8	0.8 ± 0.1b	68.8 ± 26.1a	31.6 ± 4.7a	1.1 ± 0.4d
Ulmaceae	6	25.5 ± 4.4a	14	1.3 ± 0.2a	12	1.3 ± 0.4b	36.9 ± 7.9b	47.3 ± 12.4a	1.8 ± 0.5bc
Lauraceae	7	12.8 ± 1.6bc	11	1.0 ± 0.1ab	5	1.4 ± 0.7b	38.5 ± 17.1b	–	1.6 ± 0.7cd

Different lowercase letters indicate significant differences within the same column at $p = 0.05$ level based on Duncan's test

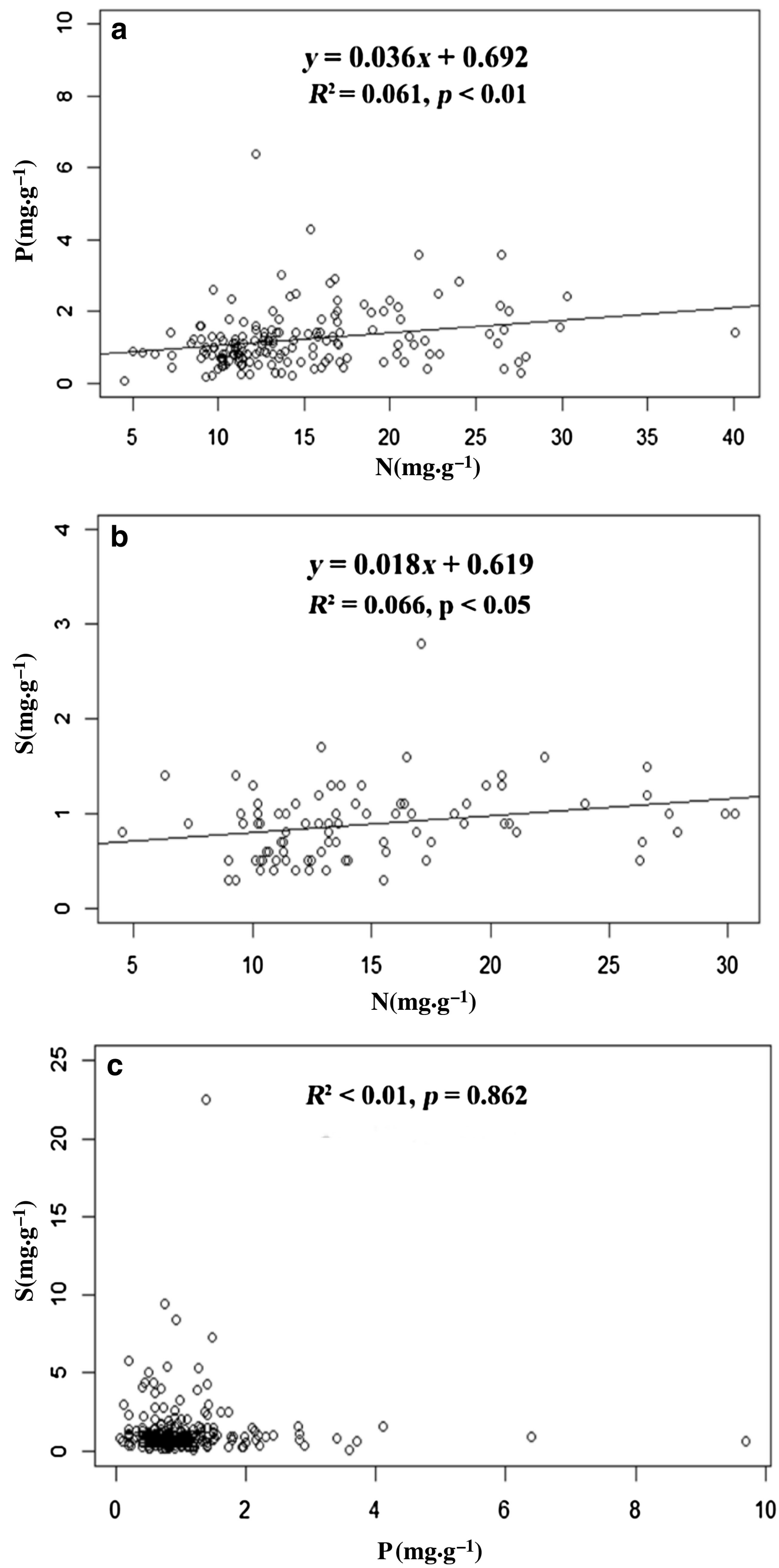
n represents number of plant species. For each species, the content of a nutrient is the average of several samples

Gymnospermae and Angiospermae. On the other hand, N content and the molar ratios of N/P and P/S in Angiospermae were higher than those in Gymnospermae. This might be caused by the different supplies of soil-available N and P (Han et al. 2005, 2011), the spatial heterogeneity of atmospheric S precipitation (Oulehle et al. 2011), and N, P, and S absorption variations of different plants (Zhang et al. 2012). Among the seven families, the highest N and P contents were found in Ulmaceae, and the S content was significantly higher in Cupressaceae than in other families. Since plants with high N and P contents in leaves usually have high growth rates (Fyllas et al. 2009), the high N and P contents in Ulmaceae plants might be due to their high growth rates. Additionally, the low N content in Cupressaceae might necessitate S supplements to meet metabolism requirements (Oleksyn et al. 2002).

3.3 Abiotic controlling of ecological stoichiometry of N:P:S in forests

Our results show leaf P and S had a positive correlation with N ($p < 0.01$ and $p < 0.05$, respectively) (Figs. 1a, b, 2). Meanwhile, leaf N and P decreased and the molar ratio of N/P increased with increasing MAT and MAP (Fig. 2),

Fig. 1 Correlations of N and P (**a**), N and S (**b**), and P and S (**c**) in plants of China's forests. Each dot represents one sample



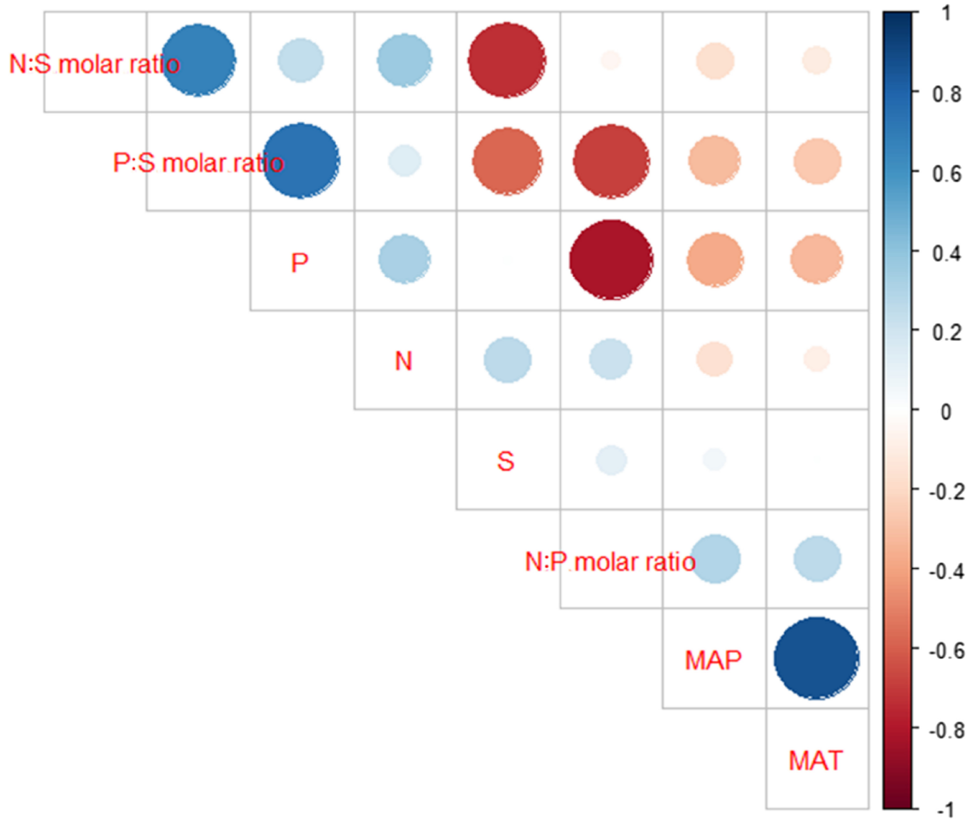


Fig. 2 Corrplot of N, P, S, N/P, N/S, P/S, MAT, and MAP intercorrelations in China's forests

which confirm the findings of Han et al. (2005) and Reich and Oleksyn (2004). However, the leaf S content in our study had no relationship with MAT and little relationship with MAP. Such responses are considered plant adaptations to MAP and MAT (Reich and Oleksyn 2004), but the effect of the S stoichiometric constraint is not clear. For instance, the high rainfall in the tropics may reduce availability of N and P and have little impact on S in soils, decreasing leaf N and P contents under higher MAT and MAP (Chadwick et al. 1999).

Our results also suggest that the significantly higher N and S contents in DBS forests were probably due to the higher percentage of Ulmaceae and Salicaceae in those forests. Similarly, the significantly higher N/P in SEB forests was likely due to the higher percentage of Theaceae. The significantly higher ratios of N/P and P/S in CB forests were very likely due to the higher percentage of Pinaceae.

3.4 Implications for forest management

Our results show the leaf P content of China's forests was lower than the global value and China's forests were mainly limited by P; forests with low leaf P content could benefit from the application of P fertilizer (TSC, SEDB, and SEB forests). Meanwhile, leaf S content of China's forests has decreased. With the reduction in emissions of atmospheric SO_2 since the beginning of the twenty-first century in China, S deficiency may become an increasingly important problem for China's forests because S tends to be leached under humid environmental conditions. The effects of P fertilizer application in low P areas, the effects of S deficiency on forest growth, and the stoichiometry of N, P, and S in forests need to be better understood in order to develop sustainable forest management practices.

4 Conclusions

In summary, the distribution of leaf N, P, and S contents significantly varied among the eight types of China's forests. Leaf N and P generally increased from the tropic zone to cooler and drier zones, and then slightly decreased at the cold temperate zone, except for bamboo and other tropical forests. Overall, the distribution and stoichiometry of leaf N, P, and S in China's forests were not only affected by plant ecotypes, taxonomic groups, and environmental conditions, but also by atmospheric S precipitation and the supplies of soil-available N and P. Most importantly, China's forests are more likely limited by P and S deficiency, which should be considered in future forest management.

Acknowledgements We acknowledge support from the National Natural Science Foundation of China (41522207, 41571130042) and the State's Key Project of Research and Development Plan of China (2016YFA0601002).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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