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Leaf nitrogen and phosphorus stoichiometry of *Quercus* species across China

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ABSTRACT

Leaf stoichiometry patterns and their controlling factors at different scales, such as the global flora or single species/genus, are still poorly understood. Here, we analyzed a national-level dataset of leaf nitrogen (N) and phosphorus (P) concentrations and their stoichiometry for 13 *Quercus* species from 41 study sites in China, aiming to document the patterns of leaf N and P concentrations and N:P ratio to investigate how these patterns vary with geographic and climatic variables. The averages of leaf N and P concentrations and N:P ratio were 17.27 mg g^{-1}, 1.54 mg g^{-1} and 13.96, respectively, across all *Quercus* species studied. Significant differences in leaf N and P concentrations were detected, while no significant difference in leaf N:P ratio was found among species. Leaf N and P concentrations and N:P ratio showed single-peak curves or linear patterns along the geographic and climatic gradients. Principal component analysis (PCA) revealed that the first PCA axis, which reflected the temperature and evaporation variations along the altitude and longitude, had good relationships with leaf N and P concentrations and N:P ratio. The second PCA axis, which reflected temperature and moisture variations along the latitude, only showed a significantly correlation with leaf N concentration. Leaf N:P ratio was well constrained to a relatively stable range for *Quercus* species and was less influenced by environmental variables. Leaf N and P concentrations were mainly driven by heat and water distribution induced through geographic variations. Leaf stoichiometry-geography relationships are more complicated than stoichiometry-climate relationships.

1. Introduction

Leaf stoichiometry, especially nitrogen (N) and phosphorus (P), plays vital roles in studying vegetation composition, ecosystem function and nutrient limitation (Elser et al., 2000; Allen and Gillooly, 2009; Venterink and Gusewell, 2010). The patterns of leaf N and P concentrations and N:P ratio, as well as the biotic or abiotic factors controlling them, have been well documented in the past decades (Gusewell, 2004; Reich and Oleksyn, 2004; Han et al., 2005; Renteria and Jaramillo, 2011). It has been reported that leaf N and P concentrations are correlated with geographic and climatic variables (Ordonez et al., 2009; Chen et al., 2011). Several hypotheses have been developed to interpret these correlations. Plant physiology hypothesis proposes that plant metabolic processes are temperature sensitive, and increases in nutrient (e.g., N, P) concentration can compensated for decreases in metabolic rate at low temperature or high latitude (Reich and Oleksyn, 2004; van de Waal et al., 2010; Chen et al., 2011). Biogeochemical hypothesis assumes that soil nutrient availability, which is influenced by rainfall through leaching effects, drives the variation of leaf nutrient concentration (McGroddy et al., 2004; Kang et al., 2011).

Whether a stable range of stoichiometry exists for a given genus/species is still under debate (McGroddy et al., 2004; Townsend et al., 2007; Elser et al., 2010). Recent studies have focused on leaf stoichiometry of a given genus (He et al., 2008; Gotelli et al., 2008), or species (Yu et al., 2010; Kang et al., 2011) and its correlations with climatic factors, to compare with the global flora, which neglected the inter-family and inter-specific differences. These studies are necessary to understand how plants respond to climate change in future by identifying the current patterns of nutrient-climate relationship (Wright et al., 2004; Kang et al., 2011; Sardans et al., 2012). Recent studies have discovered a non-linear leaf N-latitude relationship at genus (Reich and Oleksyn, 2004) or species (Kang et al., 2011) levels, which differs from the linear latitudinal decline for the global or regional flora observed previously (Reich and Oleksyn, 2004; He et al., 2008). However, it is still uncertain on relationship between leaf stoichiometry and climatic, geographic variables for a single genus or species.

Quercus species are keystone species in a wide range of habitats from Mediterranean semi-desert woodlands to subtropical rainforest, dominanting broad-leaved evergreen forests in Europe, North America and Southeast Asia (Huang et al., 2000). In China, *Quercus* species have attracted much attention because of their great

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importance in producing timber, charcoal, and dye products (Feng, 2008). Moreover, many *Quercus* species are under threat of extinction in the wild, largely due to land-use change, livestock grazing and unsustainable harvesting (Peng et al., 2007). According to Flora Republicae Popularis Sinicae (FRPS) (Huang et al., 2000), *Quercus* genus contains 51 species and 14 varieties distributed from subtropical to temperate zones in China. Such a wide geographical distribution provides a rare opportunity to examine nutrient status and stoichiometry for the genus at a regional scale. To our knowledge, no study has attempted to document the patterns of variation in leaf N and P concentrations in *Quercus* species in relation to geographical and climatic factors across China. In the present study, we compiled a national dataset of leaf N and P concentrations and the geographic and climatic variables for *Quercus* species in China through published literatures. Our objectives were (1) to determine whether a stable range of leaf N and P stoichiometry exists for *Quercus* species (2) to assess the relationships between leaf stoichiometry and environmental factors, and (3) to explore the effects of environmental factors underlying the pattern of leaf nutrient status at individual genus level.

2. Materials and methods

The genus *Quercus* is composed of the subgenus *Quercus* and *Cyclobalanopsis*, and the genus *Cyclobalanopsis* is further subdivided in FRPS. Thirteen *Quercus* species were selected in present study, including *Q. wutaishanica* (*Q. liaotungensis*), *Q. acutissima*, *Q. mongolica*, *Q. aliena* var. *acutiserrata*, and *Q. variabilis*, etc. (Appendix A).

2.1. Dataset

Data were collected from published studies on leaf N and P concentrations (mass ratio) and N:P ratio for the 13 *Quercus* species. Leaves samples used for determining leaf N, P and N:P ratio were all collected from mature trees in natural forests during the growing season (July–October). Geographic and climatic variables were recorded with the leaf samples in these studies (Appendix A), including altitude (ALT), latitude (LAT), longitude (LON), mean annual temperature (MAT), mean temperature in July (MT_{max}), mean temperature in January (MT_{min}), mean of annual sunshine hours

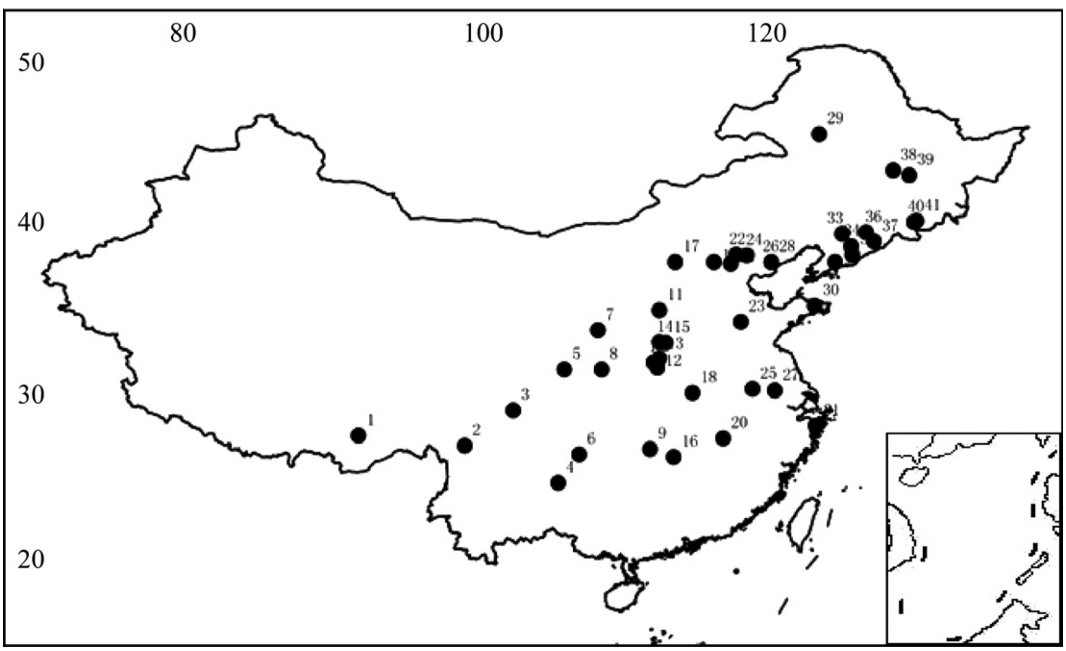

Fig. 1. Distribution of study areas. The small square stands Nansha Islands in China.

Table 1
Leaf N and P concentrations and N:P ratio for all *Quercus* species.

Species	N			P			N:P		
	Mean (mg g^{-1})	SD (mg g^{-1})	CV (%)	Mean (mg g^{-1})	SD (mg g^{-1})	CV (%)	Mean	SD	CV (%)
All species	17.27 (*n* = 105)	6.26	36	1.54 (*n* = 70)	0.63	41	13.96 (*n* = 67)	5.15	37
Q. wutaishanica	23.52 (*n* = 12)	4.15	18	1.74 (*n* = 8)	0.62	36	14.57 (*n* = 9)	4.97	34
Q. acutissima	16.23 (*n* = 11)	5.76	35	1.41 (*n* = 13)	0.43	30	14.00 (*n* = 10)	4.38	0.31
Q. mongolica	21.03 (*n* = 12)	4.64	22	2.08 (*n* = 12)	0.65	31	11.63 (*n* = 11)	4.77	41
Q. aliena var. *acutiserrata*	20.29 (*n* = 10)	8.23	41	1.53 (*n* = 10)	0.46	30	13.34 (*n* = 10)	4.6	34
Q. variabilis	18.33 (*n* = 12)	5.72	31	1.18 (*n* = 11)	0.7	59	16.56 (*n* = 10)	3.84	23
Q. aquifolioides	11.14 (*n* = 25)	2.87	26	–	–	–	–	–	–
Q. fabric	18.96 (*n* = 4)	4.38	23	1.30 (*n* = 4)	0.45	35	16.78 (*n* = 5)	4.65	28
Q. dentate	18.75 (*n* = 6)	4.48	24	1.64 (*n* = 5)	0.62	38	12.11 (*n* = 5)	4.24	35
Q. serrata var. *brevipetiolata*	21.56 (*n* = 3)	1.69	8	1.41 (*n* = 3)	0.37	26	15.81 (*n* = 3)	3.39	21
Q. aliena	22.10 (*n* = 3)	2.82	13	1.87 (*n* = 3)	0.64	34	12.58 (*n* = 3)	3.55	28
Q. pannosa	15.13 (*n* = 3)	4.67	31	–	–	–	–	–	–
Q. guajavifolia	12.88 (*n* = 3)	1.22	9	–	–	–	–	–	–
Q. griffithii	9.10 (*n* = 1)	–	–	1.5 (*n* = 1)	–	–	6.07 (*n* = 1)	–	–
F	7.79			2.48			1.70		
P	0.000			0.018			0.110		