Climatic Rather than Edaphic Variables Determine Leaf C, N, P Stoichiometry of Deciduous *Quercus* Species

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Abstract

Purpose

Leaf elemental stoichiometry is indicative of plant nutrient limitation, community composition, ecosystem function. Understanding the variations of leaf carbon (C), nitrogen (N), and phosphorus (P) stoichiometry at genus-level across large geographic regions and identifying their driving factors are important to predict species' distribution range shifts affected by climate change.

Methods

Here, we determined the patterns of leaf concentrations ([]) and ratios (/) of C, N, P of five deciduous oaks species (*Quercus*) across China covering ~ 20 latitude (~21–41° N) and longitude (~99–119° E) degrees, and detected their relationships with climatic, edaphic variables.

Results

Leaf [C], [N] and N/P, C/P significantly increased, while leaf [P] and C/N decreased with the increasing latitude. Leaf stoichiometry except for leaf [C] had no significant trends along the longitude. Climatic variables, i.e. mean annual temperature, mean annual precipitation, the maximum temperature of the warmest month, temperature seasonality, aridity index, and the potential evapo-transpiration were the determinants of the geographic patterns of leaf C, N, P stoichiometry. The mean annual precipitation and the maximum temperature of the warmest month indirectly regulated leaf C/N, C/P and N/P via altering leaf [P]. Edaphic variables had non-significant effects on leaf C, N, and P stoichiometry at the broad geographic range.

Conclusions

Climatic variables have more important effects than edaphic properties on leaf C, N, P stoichiometry of the studied deciduous *Quercus* species, which imply the ongoing climate change will alter nutrient strategies and potentially shift the distribution range of this eurytopic species.

Introduction

Under the scenarios of climate change, the temperature and the precipitation regimes are predicted to increase and shift, respectively. Affected by climate change, some mid-latitude and semi-arid regions are projected to have ~ 1.5 to 2 times of the global warming rate in the next several decades; furthermore, most regions are projected to have more frequent and intensified precipitation extremes (IPCC 2021). The warming as well as the precipitation regime shifts have considerable effects on the cycles of carbon (C), water, and energy regionally and globally (IPCC 2021; Zeng et al. 2017), in consequence, integratively affect the vegetation activities (Gao et al. 2019), and ecosystems functions (Yuan and Chen 2015). For instance, the warming and the drought altered litter decomposition and organic matter mineralization via

changing soil physical-chemical properties and microbial activities, leading to variations of plant nutrient availability and leaf stoichiometry (Reich and Oleksyn 2004; Yuan and Chen 2015).

Leaf stoichiometry drives basic physiological and ecological processes and indicates plant nutrient status, community composition, ecosystem functions (Lü et al. 2017). Carbon, nitrogen (N), and phosphorus (P) are important elements affecting the sustainability and the balance of biogeochemical cycles in terrestrial ecosystems (Gruber and Galloway 2008). Plant N and P regulate productivity and C sequestration in terrestrial ecosystems. Both the concentrations ([]) and the ratios (/) of leaf C, N and P are closely related to the utilization, the allocation of photosynthetic products and nutrients, and to a certain extent, to the ecological strategies of plant species (Ye and Wang 2021).

The spatial variability of plant stoichiometry can be affected by multiple environmental factors either at regional or global scales. At the regional scale, plant [N] and [P] decreased, and [C] increased, with increasing mean annual temperature (MAT) across China's terrestrial biomes (Tang et al. 2018); while leaf [N] and [P] of 753 terrestrial plant species increased with decreasing MAT but leaf N/P did not show significant changes in China (Han et al. 2005). However, when much more plant species (1900) across China were taken into consideration, plant functional type exhibited the greatest effects on most leaf nutrients, and precipitation explained more variations than temperature for leaf [N] but not for leaf [P] (Han et al. 2011). At the global scale, leaf [N] and [P] increased from the tropics to the mid-latitudes and remained stable or decreased at higher latitudes, and leaf N/P increased with temperature (Reich and Oleksyn 2004).

Up to date, the main large-scale (regional and global) patterns of plant stoichiometry have mainly been explored at multispecies- or community-level, mostly based on meta-analyses of literature (Han et al. 2005, 2011; Tian et al. 2018, 2019), which highlighted the potential replacement of species along environmental gradients (Elser et al. 2009; Han et al. 2005). However, large-scale patterns of leaf stoichiometry of C, N, and P based on measurements at family- and genus-level are scarcely explored except for very few researches (Tian et al. 2019; Sun et al. 2017), which are vitally important to predict plant's physiological strategies from their evolutionary adaptation to environmental nutrient availability, although the underlying mechanisms remain unclear (Tian et al. 2019). Research considering leaf stoichiometry of C, N, P at genus-level is potential to produce detailed parameters necessary for plant physiological and ecosystem functioning predictive models in macro-ecology and biogeography (He et al., 2019; Tang et al. 2018).

Large-scale ecological sampling on plant species at genus-level helps to better understand variations on leaf stoichiometry of C, N, P and provides opportunities to investigate the impacts of climate change on species' range shift (e.g., expansion, contraction, or displacement) (Pecl et al. 2017; Rigling et al. 2013), and on the consequent alteration of forest compositions, structures and functions (Albrich et al. 2020; Wieczynski et al. 2019). Deciduous oak (*Quercus*, Fagaceae) is one of the eurytopic species growing from temperate to tropical regions of China (Sun et al. 2014; Zhou 1993), across which with drastic variability of climatic and edaphic variables (Liu et al. 2005). Here, we sampled the leaves of five deciduous

Quercus species from a broad geographic range (latitudinal and longitudinal gradients) across China, determined leaf [C], [N], [P], and C/N, C/P, N/P, and detected their relationships with climatic and edaphic variables. We aimed to explore the patterns of leaf stoichiometry of C, N, P at *Quercus*-level and to examine its potential linkage with climatic and edaphic variables. We hypothesized that: 1) the geographical patterns of leaf C, N, P stoichiometry of *Quercus* genus are similar to those at community-level at regional and global scales; 2) climatic variables determine the leaf patterns of C, N, P stoichiometry of the deciduous *Quercus* species, since climate governs the functional diversity and controls the geographic shifts of plants (Aleixo et al. 2019; Wiczynski et al. 2019). Specifically, we managed to identify how climatic and (or) edaphic variables influence leaf C, N, P stoichiometry of the deciduous *Quercus* species. Results have great implications for understanding the potential species' range shift, forest composition, and community dynamic in the contexts of phytogeography and climate change.

Materials And Methods

Field sampling and trait measurement

During the mid- and late-growing seasons from July to October 2019, the leaves of five deciduous *Quercus* species (*Quercus variabilis*, *Q. aliena*, *Q. fabrei*, *Q. acutissima*, *Q. serrata*) were sampled from 22 locations covering approximately 20 latitudes (~ 21–41° N) and 20 longitudes (~ 99–119° E) across China (Figure 1). The sampled latitudinal and longitudinal gradients have a MAT and a MAP ranging from 8.2 to 23.2°C and from 767 to 1866 mm, respectively (Fick and Hijmans 2017). According to the distribution of the deciduous *Quercus* species, we sampled the oaks and ensured that the sampling sites were evenly distributed across latitude and longitude. At each sampling location, the mature and healthy leaves were collected from at least three individual trees for each species growing in natural forests. Uniformity, the individual trees with diameter at breast height larger than 5 cm and tree height above 2 m were selected. Soils at 0 - 20 cm depth below each tree were sampled at the same time. The leaf and soil samples were put in sealed plastic bags with ices and transported back laboratory within 8 hours.

In the laboratory, a sub-sample of the leaves was oven-dried to constant weight, and ground for [C], [N], and [P] measurements. Leaf [C] and [N] were determined using an elemental analyzer (Costech Analytical Technologies, Valencia, USA). Leaf [P] was determined by the molybdenum-antimony anti-colorimetric method (Dong 1997). Leaf C/N, C/P and N/P were calculated accordingly to leaf [C], [N] and [P]. Soil samples were air-dried, ground, and sieved for the measurement of pH, the concentrations of soil organic matter (SOM), soil total N (SN), soil total P (SP), and soil water content (SWC), according to the standard procedures (Liu et al. 1996). Specifically, SWC was determined by oven drying about 20 g of fresh soil at 105°C for 48 h. The soil pH was measured in a 1: 2.5 soil: water (w/v) mixture using a glass-electrode meter (FiveEasyPlus™ FE28, Mettler Toledo, Switzerland). Soil organic matter (SOM) and total nitrogen (SN) concentrations were determined by using K₂Cr₂O₇ titration method and micro-Kjeldahl method,

respectively. The concentration of soil total phosphorus (SP) was determined by the molybdenum antimony colorimetric method after digestion with $\text{H}_2\text{SO}_4\text{-HClO}_4$.

Climatic variables

Climatic variables including MAT, the minimum temperature of the coldest month ($T_{\min}$), the maximum temperature of the warmest month ($T_{\max}$), mean temperature of the driest quarter (T_{dry}), mean temperature of the wettest quarter (T_{wet}), temperature seasonality (TS), MAP, precipitation of the driest month ($P_{\min}$), precipitation of the wettest month ($P_{\max}$), precipitation of the coldest quarter (P_{cold}), precipitation of the warmest quarter (P_{warm}), and precipitation seasonality (PS) during 1970-2000 at the sampling locations were obtained from the WorldClim Bioclimatic variables for WorldClim version 2 (Fick and Hijmans 2017). Temperature seasonality (TS) was the difference between the annual maximum and minimum temperature, i.e. the standard deviation of annual temperature multiplied by 100. Precipitation seasonality (PS) was the coefficient of variation calculated based on monthly rainfall data. The aridity index (AI, annual) is the ratio of MAP to the potential evapo-transpiration (PET), which was obtained from the global aridity index and potential evapo-transpiration climate database v2 (<https://cgiarcsi.community/category/data/>) (Trabucco and Zomer 2019).

Statistical analysis

Prior to analyses, the data of leaf C, N, P stoichiometry was tested for approximate normality (Shapiro–Wilk test) and $\log_{10}$ -transformed to achieve normality when necessary. The climatic and edaphic variables were standardized via equation (A) to a mean of 0 and standard deviation of 1 to reduce the magnitude and multicollinearity (Du et al 2020).

$$\text{Standardized value} = \frac{\text{Original value} - \text{mean value}}{\text{Standard deviation}} \quad (\text{A})$$

To eliminate the interference of species on the relationships between leaf traits and latitude and longitude, general linear-mixed effect models (GLMEMs) were employed with species as the random effects (Crawley, 2012). We used step and lmer function in lmerTest R package to establish best-fit models based on AICc of each model to find out which and how environmental factors control the geographical patterns of leaf C, N, and P stoichiometry. We selected the first five environmental factors that significantly affected leaf C, N, P stoichiometry to calculate their relative importance through relaimpo R package (Chevan and Sutherland 1991). In addition, the relationships between the most important factors and leaf C, N, P stoichiometry were analyzed by general linear models (GLMs). The correlations among leaf stoichiometry were estimated by idaFast function in R package pcalg (Kalisch et al. 2012). Finally, the structural equation model (SEM) was utilized to explore the pathway of environmental factors that influence leaf stoichiometry (Gerlach et al. 1979). Based on the goodness-of-fit criteria, including the probability level (P), comparative fit index (CFI), the ratio of χ^2 to degrees of freedom (χ^2 / df), and root mean squared error of approximation (RMSEA), we selected the model when $P > 0.05$, $\chi^2 / \text{df} \leq 2$, $\text{CFI} \geq 0.98$, and RMSEA having the lowest value (Schermelleh-Engel et al. 2003). The

significant pathway coefficients were determined using 95% bootstrap confidence intervals. The following three potential pathways were considered in a hypothesis-oriented model: 1) climatic or edaphic variables will primarily influence leaf [C], [N] or [P]; 2) leaf C/N, C/P and N/P that are controlled by leaf [C], [N] or [P] might relate directly to climatic or edaphic variables; 3) there are potential pathways among these leaf stoichiometric traits. All statistical analyses were performed using the R v.3.6.3 software (R Core Team 2019), except for SEMs, by IBM SPSS Amos 24 (SPSS Inc., Chicago, IL, USA). Significance was set at $P < 0.05$.

Results

Geographic patterns of leaf C, N, P stoichiometry

The mean values of leaf [C], [N], [P], C/N, C/P, and N/P of the studied deciduous *Quercus* were 474.8, 17.3 and 1.13 mg g⁻¹, and 28.9, 438.7, 15.9, respectively (Table 1). The patterns of all leaf stoichiometric traits of the studied deciduous oaks varied significantly as indicated by the coefficient of variation (Table 1). Specifically, leaf [C], [N], C/P, and N/P significantly decreased but leaf [P] and C/N increased with latitude ($P < 0.01$), however, only leaf [C] decreased significantly with increasing longitude ($P < 0.01$) (Figure 2).

Table 1

Statistics of leaf stoichiometric traits of the studied *Quercus* species along latitudinal and longitudinal gradients in this study and th reported mean values from other studies across China and globe. [C], leaf carbon concentration (mg g⁻¹); [N], leaf nitrogen concentration (mg g⁻¹); [P], leaf phosphorus concentration (mg g⁻¹); C/N, leaf carbon to nitrogen concentration ratios; C/P, leaf carbon to phosphorus concentration ratios; N/P, leaf nitrogen to phosphorus concentration ratios. SE, standard error; CV, coefficient of variation (%).

	The deciduous <i>Quercus</i> species in this study					1,900 plant species	1,280 plant species across globe
	Mean	SE	Minimum	Maximum	CV	in China (Han et al 2011)	(Reich and Oleksyn 2004)
[C]	474.8	1.3	416.4	519	4.11	-	-
[N]	17.3	0.3	9.6	29.4	23.3	22.3	20.1
[P]	1.13	0.02	0.73	1.87	21.22	1.68	1.77
C/N	28.9	0.4	16.7	44.9	21.46	-	-
C/P	438.7	6.2	257.4	676.3	21.42	-	-
N/P	15.9	0.3	8.1	32.5	32.28	13.3	13.8

Determinants of leaf C, N, and P stoichiometry

According to the stepwise regression models and relative importance analysis, we found that climatic rather than edaphic variables significantly affected the leaf stoichiometries of the deciduous oaks (Figure 3, **Table S1**). Specifically, both the MAP and AI controlled the variation of leaf [N], C/N and N/P ($P < 0.05$), while PET and TS determined the patterns of leaf [C] ($P < 0.05$). The MAT, Tmax, and TS were the driving factors on leaf [P] and C/P ($P < 0.001$).

For the temperature-related factors, leaf [C], [N], C/P, and N/P (Figure 4a, b, e, f) were positively while leaf [P] and C/N (Figure 4c **and d**) were negatively related to MAT; leaf C, N and P stoichiometry except for leaf [P] and C/N were negatively related to TS (Figure 4a, b, d, e); only leaf [P], C/P and N/P were significantly affected by Tmax (Figure 4c, e, f). For the moisture-related factors, leaf [C], [N], C/P, and N/P (Figure 4g, h, k, l) increased while leaf [P] and C/N (Figure 4i, j) decreased significantly with AI; leaf [C], [P], C/P, N/P (Figure 4g, h, k, l) increased but leaf [P] and C/N (Figure 4i, j) decreased significantly with MAP; only leaf [P], C/P and N/P (Figure 4i, k, l) were significantly affected by PET.

Pathway of climatic variables affecting leaf stoichiometry

According to the structural equation model, the climatic variables, i.e. Tmax and MAP exhibited significant effects on the variations of leaf C, N and P stoichiometry, in particular on those of leaf [P], of the studied deciduous *Quercus* species (**Figure 5**). Both Tmax and MAP had direct influences (negative) on leaf [P] instead of leaf [C] or [N] and indirect effects on the variations of leaf C/N, C/P and N/P. Furthermore, MAP showed direct effects on the variations of leaf N/P. The variations of leaf [N] and [P] directly affected leaf C/N (negative) and C/P (positive), and the variation of leaf N/P was directly regulated by leaf C/N and C/P (**Figure 5**). The Tmax and MAP indirectly regulated leaf C/N, C/P and N/P via altering leaf [P] across the geographic scale.

Discussion

Patterns of leaf C, N, and P stoichiometry at *Quercus*-level were partly consistent with those at community-level

Geographical variations of leaf traits especially those related to C and N cycles are helpful to predict the adaptation and the fate of wide distribution plant species under global change (Blonder et al. 2017; Martínez-Sancho et al. 2018). Our results showed that leaf [N], [P] and N/P of the studied deciduous *Quercus* species were lower than those of 1,900 plant species in China (Han et al. 2011) and 1,280 plant species across the globe (Reich and Oleksyn 2004) (Table 1). The decreasing leaf [C], [N], C/P, N/P the increasing leaf [P] and C/N with increasing latitude (Figure 2) indicated that the *Quercus* species might alter nutrient allocation strategies to adapt to environmental change. The patterns of leaf C, N, and P stoichiometry at genus-level (*Quercus*) across China in this study were partly consistent with those general biogeographic ones that leaf [N] and [P] increase and leaf N/P decrease with increasing latitude

(or decreasing MAT) at multispecies- and community-level (e.g., Reich and Oleksyn 2004; Han et al. 2005, 2011; Tian et al. 2018, 2019), which tested our hypothesis 1.

The increase of leaf C/N and the decrease of leaf [N] along the latitudinal gradient in this study (Figure 2) were consistent with the patterns of 109 dominant species across China's forests (Tang et al. 2021). The results identified the reduction of N use efficiency (Wang et al. 2014) and N availability (Tang et al. 2021) from tropical to temperate forests. Leaf C/P and N/P are vital for plant growth, since the distribution and the variation of P-rich ribosomal RNA occur at different growth rates (Elser et al. 2003; Lambers and Poorter 2004; Makino et al. 2003). The significant increases in leaf C/P and N/P of the studied deciduous *Quercus* species with latitude coincided with a field investigation from temperate to tropical forests (Zhang et al. 2018). The results implied that the deciduous *Quercus* species maintain higher growth rate in temperate than in tropical forests, since deciduous species growing at temperate tended to be more resource acquisitive and grew faster within short growing season than at tropic (Ramírez-Valiente et al. 2017; Qi et al. 2020). Furthermore, the higher leaf [N] and N/P but the lower leaf [P] at low than high latitudes (Figure 2) suggested intensified P limitation (Li et al. 2016; Zhang et al. 2018) from northern to southern China. This pattern can be explained by the soil substrate age hypothesis (SSAH) which suggests that P limitation occurs in tropical forests (low latitude) due to soil aging and leaching (Reich and Oleksyn 2004).

Climatic variables determine the spatial patterns of leaf C, N, P of *Quercus* at a large geographical scale

The geographical variations in plant nutrients are associated with climate gradations and likely reflect the responses and adaptations of plants to climate change (Hedin 2003; Wright et al. 2004). The north-to-south and west-to-east transects across China both reflect shifts from cold, dry to warm, humid conditions, although the temperature gradient is more obvious in the former and the moisture gradient is more pronounced in the latter (**Figure S1, S2**). In this study, the significant relationships between MAT, Tmax, TS, MAP, PET, AI and leaf C, N, P stoichiometry implied that the nutrient status of the studied deciduous *Quercus* species was more likely affected by the co-regulation of temperature- and moisture-related factors, due to the slowdown of litter decomposition and soil N mineralization at low precipitation and temperature (Finger et al. 2016; Li et al. 2020). The results were partly identified by the temperature-plant physiology hypothesis (Reich and Oleksyn 2004), as reported that the stoichiometry of *Quercus variabilis* leaves was driven mostly by the variations of temperature and aridity rather than soil conditions and leaf structure (Sun et al. 2015).

Soil is the primary source for most plant nutrients at standing and plotting levels (Asner and Martin 2016; Feng et al. 2021; Liu et al. 2017). The roles of soils on plant nutrients can not be ignored despite we did not find the dominance of edaphic variables on leaf C, N, P stoichiometry of the studied deciduous *Quercus* at broad geographic scales (Figure 3, 5). On large spatial scales, the roles of climatic variables may conceal or be more significant than those of edaphic factors on plant elemental stoichiometry (Ordoñez et al. 2009; Sun et al. 2012), because the physiological and metabolic processes of plants were more sensitive to climate change than to soil conditions, which were identified at regional (Feng et al.

2021; Liu et al. 2017) and global scales (e.g. Hartmann 2011; He et al. 2020). Soils provide the main nutrient elements to maintain plant growth, but have a weak capacity to alter species composition or vegetation types (Zhang et al. 2018). The alterations of hydrothermal conditions caused by the changes in climate might have resulted in the different patterns of leaf C, N, and P stoichiometry of the studied deciduous *Quercus* species.

Possible mechanisms of climatic variables controlling leaf C, N, P stoichiometry

Plants form different nutrient strategies to adapt to changes in soil and climate (McGroddy et al. 2004; Freschet et al. 2015). Results from SEM in this study (Figure 5) suggested that the studied deciduous *Quercus* species regulate nutrient strategy under different hydrothermal conditions, that is, directly alter leaf [P] and then indirectly alter leaf C/N, C/P and N/P under the changes in climate variables across the geographic scale. The increasing temperature (Han et al. 2005; Kang et al. 2011) as well as the increasing precipitation (Du et al. 2020) had negative effects on leaf [P], which supported our results that the increasing Tmax and MAP led to low leaf [P] (Figure 5), and further decreased the photosynthesis P utilization, photosynthesis rate (leaf [C]) and N use efficiency, as indicated by the negative effects on stoichiometric ratios such as C/N, C/P and N/P (Figure 5). The identified strong correlations between leaf [N] and photosynthetic rate, N use efficiency (Guo et al. 2016) coincidentally confirmed our results (Figure 5). Although local variations in leaf stoichiometry were affected largely by the heterogeneity of soil nutrients and soil ages (Reich and Oleksyn 2004), our results indicated that regional variations of leaf C, N and P stoichiometry were primarily affected by climatic factors. This finding coincided with Zhang et al. (2018), who demonstrated that the spatial patterns of leaf stoichiometry from temperate to tropical forests were more affected by climate factors than soil factors. Specifically, the low precipitation and temperature in northern China might inhibit the decomposition and mineralization of soil organic matter and reduce N inputs of the ecosystem (Finger et al. 2016; Li et al. 2020), leading to low leaf [N] and N/P of the studied *Quercus* species (Figure 4). The results revealed how climatic variables influence leaf C, N, P stoichiometry of the deciduous *Quercus* species, which provided evidence for predicting nutrient strategies, which have considerable impacts on plant growth and survival, and further leading to potential distribution shifts of the eurytopic species, under the ongoing climate change.

Conclusions

We analyzed the spatial patterns of leaf C, N, P stoichiometry of five deciduous *Quercus* species and their linkages to the environmental variables across a broad geographic range in China. We found that the deciduous *Quercus* species significantly decreased leaf [C], [N], C/P, and N/P, but increased leaf [P] and C/N, with the increasing latitude. Leaf stoichiometry except for leaf [C] had no significant trends along the longitudinal gradient. The climatic variables, i.e. mean annual temperature and precipitation, the max temperature of the warmest month, temperature seasonality, aridity index, and potential evapo-transpiration, rather than the edaphic variables, were the determinants of the geographic patterns of leaf C, N, P stoichiometry of the studied deciduous *Quercus* species. Affected by climate change, *Quercus* species will alter leaf [P] to regulate leaf C, N, and P stoichiometry. The patterns of leaf C, N, and P

stoichiometry at genus level (*Quercus*) and their association with climatic variables suggest that the eurytopic species will adjust nutrient strategies and potentially shift the distribution range affected by climate change.

Declarations

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Authors' contributions

Y.W. designed the study; Y.T., Y.W., S.B., Y.L., Z.F., J.F. and F.F. performed the experiments; Y.T. analyzed the data; Y.T. and Y.W. drafted the manuscript. All authors contributed critically to the revised manuscript.

Availability of data

The data that support the findings of this study are available in the supplementary material of this article.

Conflict of interest statement

The authors declare no conflicts of interest.

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Figures

Figure 1

Locations of 22 sampling sites for the five deciduous *Quercus* species along latitudinal and longitudinal gradients across China. AK, Ankang in Shaanxi; BJ, Beijing; BS, Baise in Guangxi; CX, Chuxiong in Yunan; DL, Dali in Yunnan; GL, Guilin in Guangxi; GY, Guiyang in Guizhou; GZ, Guangzhou in Guangdong; HT, Huitong in Hunan; HY, Huaiyuan in Henan; JA, Ji'an in Jiangxi; JJ, Jiujiang in Jiangxi; JS, Jingshan in Hubei; JZ, Jinzhong in Shanxi; LA, Lin'an in Zhejiang; MM, Maoming in Guangdong; NJ, Nanjing in Jiangsu; NP, Nanping in Fujian; PX, Pingxiang in Jiangxi; SG, Shaoguan in Guangdong; SY, Shaoyang in Hunan; TG, Tonggu in Jiangxi. QAI, *Quercus alinea*; QAc, *Quercus acutissima*; QF, *Quercus fabri*; QS, *Quercus serrata*; QV, *Quercus variabilis*. The numbers before the species abbreviations represent the long-term (1970-2000) mean annual temperature (MAT, °C) and precipitation (MAP, mm). respectively, of the sampling locations.

Figure 2

Latitudinal (yellow) and longitudinal (green) patterns of leaf C, N, and P stoichiometry of the deciduous Quercus species. [C], leaf carbon concentration (mg g⁻¹); [N], leaf nitrogen concentration (mg g⁻¹); [P], leaf phosphorus concentration (mg g⁻¹); C/N, leaf carbon to nitrogen concentration ratios; C/P, leaf carbon to phosphorus concentration ratios; N/P, leaf nitrogen to phosphorus concentration ratios.

Figure 3

Relative importance of environmental factors on leaf stoichiometric traits of the deciduous *Quercus* species presented by radar maps. MAT, mean annual temperature (°C); Tmin, the minimum temperature of the coldest month; Tmax, the maximum temperature of the warmest month; Twet, mean temperature of the wettest quarter; TS, temperature seasonality; MAP, mean annual precipitation (mm); Pmin, precipitation of driest month; Pcold, precipitation of coldest quarter; PET, annual potential evapo-transpiration; AI, aridity index; SWC, soil water content (%). The abbreviations of leaf stoichiometric traits can be found in Figure 2. “*” “**” “***” showed $P < 0.05$, 0.01 , < 0.001 , respectively.

Figure 4

The relationships between the temperature-related (a - f), the moisture-related (g - l) factors and leaf C, N, P stoichiometry of the deciduous *Quercus* species. The red, green, and black colors in a - f indicated the relationships of leaf C, N, and P stoichiometry with mean annual temperature (MAT), the maximum temperature of the warmest month (Tmax), and temperature seasonality (TS), respectively; while those in g - l indicated the relationships of leaf C, N, and P stoichiometry with mean annual precipitation (MAP),

potential evapo-transpiration (PET), and aridity index (AI), respectively. The abbreviation of leaf traits can be found in Figure 2.

$\chi^2 / df = 0.687, P = 0.737, RMSEA = 0.000, CFI = 1.000$

Figure 5

Structural equation model (SEM) of the influencing pathway of the varying climatic factors and leaf stoichiometry. The black and red lines represent the positive and negative effects ($P < 0.05$), and the values on the line represent the path coefficients in the model. Abbreviations of the leaf stoichiometric traits and environmental factors are the same as indicated in Figure 2 and Figure 3.

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