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Species-specific spatial and temporal variation in foliar nitrogen and phosphorus in mangrove plants

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ABSTRACT: Foliar nitrogen (N) and phosphorus (P) concentrations and stoichiometry affect the productivity and functioning of plants, and they play an important role in biogeochemical processes. We investigated spatial and temporal variation in foliar nutrient concentrations and N:P stoichiometry in mangroves of China, and partitioned the relative importance of taxonomic, climatic and edaphic factors in explaining the variations. To assess spatial patterns, we collected mature leaves of 3 broadly distributed mangrove species in China spanning a latitudinal gradient. To assess temporal variation in leaf stoichiometry, we selected 1 site and sampled leaves of 4 species monthly over 12 mo. Positive relationships were found between foliar nutrient concentrations and latitude or soil nutrient concentrations in individual species. Species accounted for 76, 46 and 18% of the spatial variation in foliar N, P and N:P mass ratio, respectively, while soil nutrients and climate accounted for only small portions of the variation (≤8.3%). Different species showed no consistent patterns across temporal variation in foliar nutrient concentrations or stoichiometry, and species accounted for 94, 86 and 26% of the variations in foliar N, P and N:P ratio, respectively, throughout the year, while climatic factors accounted for only a very small portion of the variations (≤0.5%). Our results suggest that species affect foliar nutrient concentrations and stoichiometry in mangroves more strongly than environmental factors, and that stoichiometric homeostasis in mangroves may play an important role in mitigating the effects of environmental changes in coastal areas.

KEY WORDS: Nutrients · Stoichiometry · Coastal · Mangroves · Leaf trait · N:P ratio

1. INTRODUCTION

Leaf nutrient concentrations play an important role in the growth and functioning of plants as well as the biogeochemical cycling of terrestrial and marine ecosystems. For instance, nitrogen (N) and phosphorus (P) are important in protein synthesis and enzymatic activity, and they are among the most limiting nutrients for plant growth in terrestrial and coastal ecosystems (Chapin 1980, Reich et al.1997, Reef et al. 2010). Often, N:P stoichiometry reflects the balance of N and P, and the leaf N:P ratio is considered an indicator of the relative limitation of N vs. P (N:P mass ratios <14 often indicate N limitation, and N:P mass ratios >16 frequently signify P limitation) (Koerselman & Meuleman 1996, Aerts & Chapin 2000).

Foliar N and P concentrations are affected by many abiotic and biotic factors, among which soil nutrient status (Townsend et al. 2007), latitude/climate (Reich & Oleksyn 2004, Han et al. 2005, Chen et al. 2013) and taxonomy and functional group/plant growth form are considered to be among the primary factors (Zhang

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et al. 2012, Hao et al. 2015). Changes in plant N and P concentrations and N:P ratios affect ecological processes through the physiological responses and functioning of plants and also through the responses of herbivores and food-web cycling (Güsewell 2004). In addition, changes in these nutrients are directly related to the ecosystem biogeochemical cycling through primary productivity, litterfall decomposition and flux rates (Almahasheer et al. 2018, Tang et al. 2018). Understanding the spatiotemporal patterns of leaf elemental composition and the factors affecting variations is important to develop global biogeochemical cycling models (Ren et al. 2006, Tang et al. 2018).

Mangroves grow in intertidal areas along tropical and subtropical coastlines, where they provide important ecosystem services including shoreline protection, biodiversity and fisheries support (by providing breeding, spawning and nursery habitat for many species including commercially valuable fish), as well as being important in carbon, N and P sequestration and storage (Ewel et al. 1998, Breithaupt et al. 2014, Wang et al. 2019). In addition, located at the ecotones between terrestrial and oceanic ecosystems, mangroves are considered a major source of organic carbon to the oceans through the outflux of mangrove-derived or terrigenous organic matter along with nutrients, and thus play an important role in marine biogeochemistry (Dittmar et al. 2006, Tait et al. 2017). Mangrove ecosystems vary vastly in nutrient availability depending on the geomorphological setting they inhabit and which nutrients may be derived from human impacts (Reef et al. 2010). For instance, mangroves growing on oceanic islands or open coasts typically receive low nutrient supply and are considered to be oligotrophic ecosystems (McKee 2001, Anton et al. 2020), while mangroves growing along highly impacted coasts or river estuaries often experience high nutrient flow and eutrophication (Sanders et al. 2014, Gritcan et al. 2016). Correspondingly, foliar N and P concentrations and N:P ratios in mangroves show large variations among sites throughout the world (Lovelock et al. 2007). However, only a few studies have reported large-scale (regional or global) spatial variation in foliar nutrient concentrations and stoichiometry in mangroves (e.g. Lovelock et al. 2007, Anton et al. 2020), or their temporal dynamics (Wang et al. 2003, Bernini et al. 2010). Therefore, the factors influencing foliar N and P concentrations and N:P stoichiometry in mangroves remain poorly understood.

In this study, we measured foliar N, P and N:P ratios of the only 3 broadly distributed mangrove species across southeastern China, and data relating to climate and soil nutrient status were also collected. In addition, we measured foliar N, P and N:P ratios monthly in 4 mangrove species located within the Dongzhai Harbor National Natural Reserve, Hainan province. We aimed to determine the spatial variation and temporal dynamics of foliar nutrient concentrations and N:P stoichiometry in the mangroves of China and partition the relative importance of taxonomic, climatic and edaphic factors in explaining the variations.

2. MATERIALS AND METHODS

2.1. Site description

To determine the spatial pattern of foliar nutrients in mangroves, 112 sites across the natural mangrove distribution area in southeastern China were selected for leaf and soil sampling, including 37 sites of *Aegiceras corniculatum*, 39 sites of *Kandelia obovata* and 36 sites of *Avicennia marina* communities (Fig. 1). For each species community, sites were selected to span as large a geographical range as possible from all 4 provinces (Hainan, Guangxi, Guangdong and Fujian) in China that have natural mangrove forests. Sites vary from latitude 18 to 27° N, ranging in mean

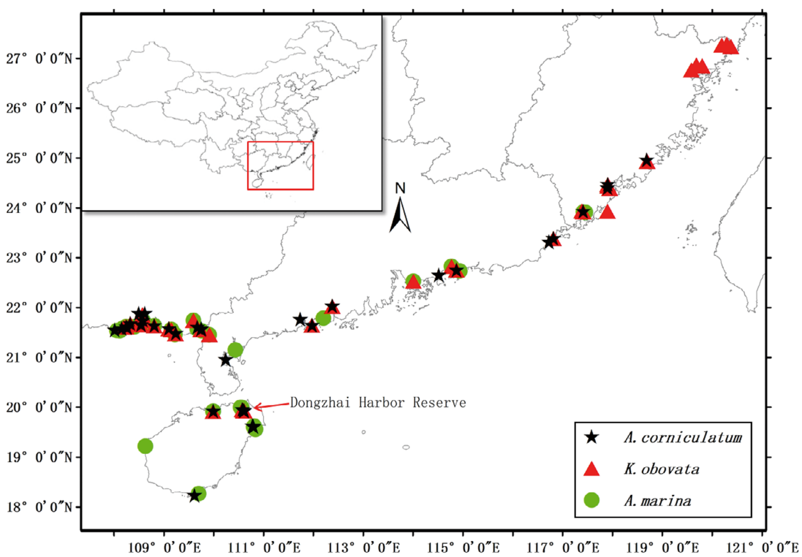

Fig. 1. Sampling sites (n = 112) across southeastern China for the spatial pattern investigation of foliar nutrients in 3 species of mangroves (*Aegiceras corniculatum*, n = 37 sites; *Kandelia obovata*, n = 39; *Avicennia marina*, n = 36)

annual temperature from 18.0 to 25.5°C, and average annual rainfall from 962 to 2537 mm. Tidal range varies from microtidal in the eastern part of Hainan (ca. 0.75–1 m) to macrotidal in Fujian (up to 4 m).

To determine the temporal dynamics of foliar nutrients, 4 mangrove communities in Dongzhai Harbor National Natural Reserve (19° 55′ N, 110° 36′ E) in Hainan province were selected for study. This area is characterized by a tropical monsoon climate. The mean annual air temperature is 23.5°C, with a maximum of 28.4°C in July and a minimum of 17.1°C in January. The mean annual rainfall is 1676 mm, with a rainy season between May and October. The tides are irregularly semi-diurnal, with an average range of about 0.89 m. More details about the mangroves in this reserve can be found in Xiong et al. (2017). Monospecific stands of the 4 most prevalent species in the reserve were selected for study: *A. marina*, *Ceriops tagal*, *Bruguiera sexangula* and *Rhizophora stylosa*.

2.2. Sampling and measurements

For the spatial pattern study, leaf samples were collected from at least 5 individual trees within an area of about 200 m^2 at each site and mixed as a composite sample. For trees with small crown and height (e.g. *A. corniculatum* and *C. tagal*), up to 10 trees were sampled. Around 20 mature leaves were collected on the upper crown of each tree. Here, the mature leaf was defined as being fully expanded and showing no signs of senescence. Top soil to 20 cm depth was collected with a steel corer (5 cm in diameter) from each site and measured for nutrient concentrations. Two soil cores were collected within the same area where trees were sampled and mixed as a composite sample. Leaf and soil sampling occurred from December 2018 to April 2019. Leaves and soils were air-dried until a constant weight was reached and ground using a ball mill before analysis. Foliar N and soil N concentrations were measured with an elemental analyzer (Elementar vario MAX CNS). Foliar P and soil total P concentrations were determined following the standard methods of the Chinese Ecosystem Research Network by digesting samples in mixed acids followed by colorimetric methods (Liu 1996).

For the temporal dynamics study, leaf samples were collected monthly from March 2015 to February 2016. Mature leaves were collected from the same 10 individual trees each time within an area of 400 m^2 in each sampled stand, and mixed as a composite sample. Leaf samples were measured for N and P concentrations in the same way as described above.

2.3. Climatic data collection

For the spatial pattern study, annual mean temperature, minimum temperature and mean annual rainfall of each of the 112 sites were extracted from the WorldClim Bioclimatic 2.5-minute dataset (www.worldclim.org/bioclim) (Fick & Hijmans 2017). For the temporal dynamics study, mean monthly temperature and monthly rainfall during the study period were obtained from a local meteorological station.

2.4. Statistical analyses

The relationships between foliar nutrients and latitude; foliar nutrients and soil nutrients; and foliar N and P were analyzed by linear regression within each species. The differences among species were analyzed by 1-way ANOVA followed by multiple comparison tests with Fisher's least significant difference test. The effects of species, climate and soil nutrient status on the spatial variation in foliar nutrients were determined by ANCOVA within a general linear model, with species as the fixed factor and climate and soil nutrient status as covariates. As there were 3 correlated variables of climatic factors and 2 correlated variables of edaphic factors, 6 runs of ANCOVAs were conducted to determine the influencing factors in the spatial variations of foliar N, foliar P or foliar N:P ratio. In each ANCOVA, either mean annual temperature, minimum temperature or rainfall was included as the climatic factor, and similarly, either soil N concentration or soil P concentration was included as the edaphic factor. The proportion of variations explained by each factor (if significant) was calculated as the proportion of the total sum of squares accounted for by each factor. Similarly, the effects of species and climate on monthly variation in foliar nutrients were also determined by ANCOVA, with species as the fixed factor and climate as the covariate. In each ANCOVA, either mean monthly temperature or monthly rainfall was included as the climatic factor. In the temporal analysis, samples from 3 months of the same season were grouped together to give a seasonal average, and the differences among the 4 seasons were analyzed by 1-way ANOVA. Data were tested for normality using a Shapiro-Wilk test and Levene's test to examine homogeneity of variance. Log transformation (leaf N) or reciprocal transformation (leaf P) were conducted to meet the statistical requirements for data normality or variance homogeneity. Statistical analyses were performed using SPSS software (version 16.0) at a significance level of 0.05.

3. RESULTS

3.1. Spatial variation in foliar N and P concentrations and N:P ratios in 3 mangrove species across China

Positive relationships between foliar N concentration and latitude was found in *Avicennia marina* ($p = 0.05$; $r^2 = 0.108$) and *Kandelia obovata* ($p < 0.01$; $r^2 = 0.183$) but not in *Aegiceras corniculatum* (Fig. 2a). Foliar P concentration was positively related to latitude only in *A. marina* ($p < 0.05$; $r^2 = 0.108$), but not in the other 2 species (Fig. 2b). Foliar N:P mass ratio was not related to latitude in any species (Fig. 2c). Foliar N concentration was positively related to soil total N concentration in *A. marina* ($p < 0.05$; $r^2 = 0.112$) and *A. corniculatum* ($p < 0.05$; $r^2 = 0.125$) but not in *K. obovata* (Fig. 3a). Positive relationships between foliar P and soil total P concentration were found in all 3 species ($p < 0.05$ or 0.01; $r^2 = 0.156$–0.238; Fig. 3b). However, when data of the 3 mangrove species were pooled, foliar N, P and N:P ratio were not related to latitude or soil nutrient concentrations. Foliar N and P were positively correlated across China either within species or among species (Fig. 4).

When data of the 3 species were pooled, species accounted for 76, 41 and 18% of the spatial variation in foliar N, foliar P and N:P ratio, respectively, while soil nutrient concentrations or climate only accounted for small portions of the spatial variation (≤8.3%) (Table 1). When averaged across different sites, *A. marina* had the highest foliar N and P concentrations and N:P ratio, *K. obovata* had intermediate values, and *A. corniculatum* had the lowest values ($p < 0.001$; Fig. 5).

3.2. Temporal variation in foliar N and P concentrations and N:P ratio in 4 mangrove species

Foliar N and P concentrations and N:P ratios varied among different months, but there was no consistency in the pattern of temporal variation among species (Fig. 6). When compared among 4 seasons, foliar N and P in *A. marina* had the highest values in spring (March, April and May) and the lowest values in autumn (September, October and November) ($p < 0.01$; $F = 12.076$; df = 3), while *Bruguiera sexangula* had significantly higher foliar N concentrations in autumn and winter than in the other 2 seasons ($p < 0.05$; $F = 5.512$; df = 3). No significant seasonal pattern was found in *Rhizophora stylosa* or *Ceriops tagal*.

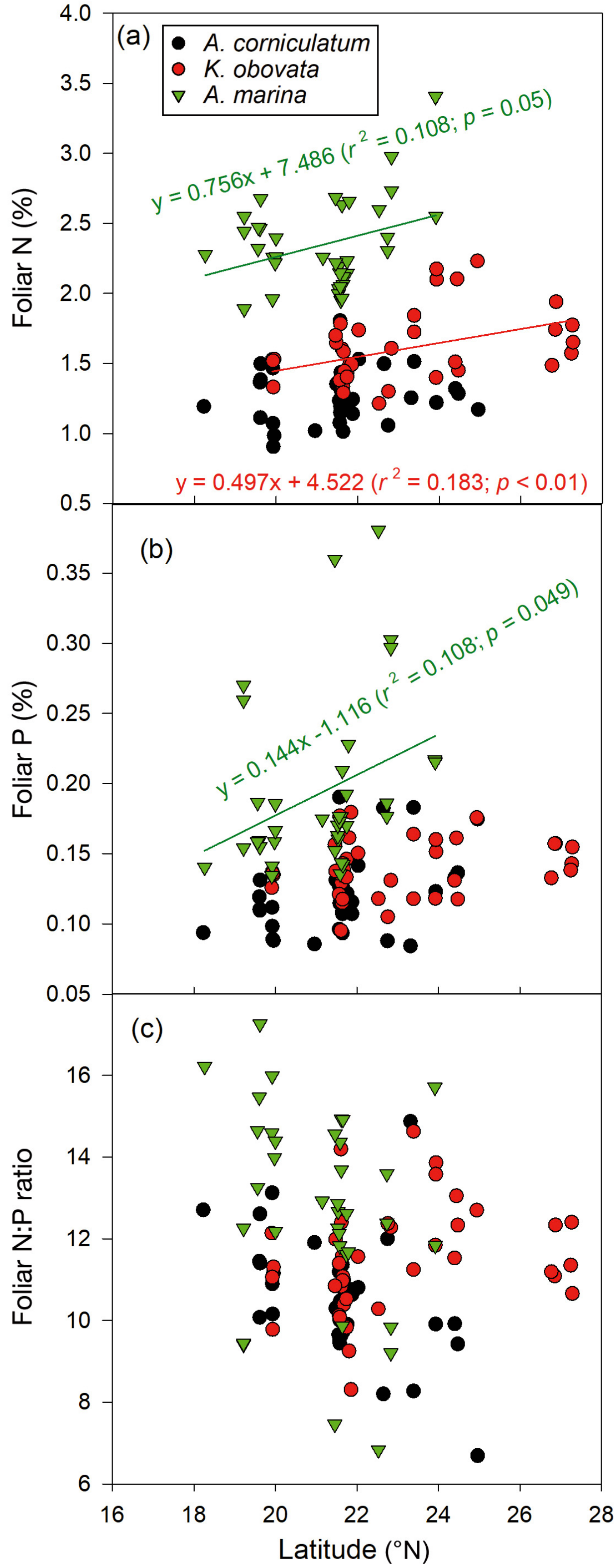

Fig. 2. Relationships between latitude and foliar (a) N concentration, (b) P concentration and (c) N:P ratio in 3 mangrove species (*Aegiceras corniculatum*, *Kandelia obovata*, *Avicennia marina*) across southeastern China. Significant relationships are shown

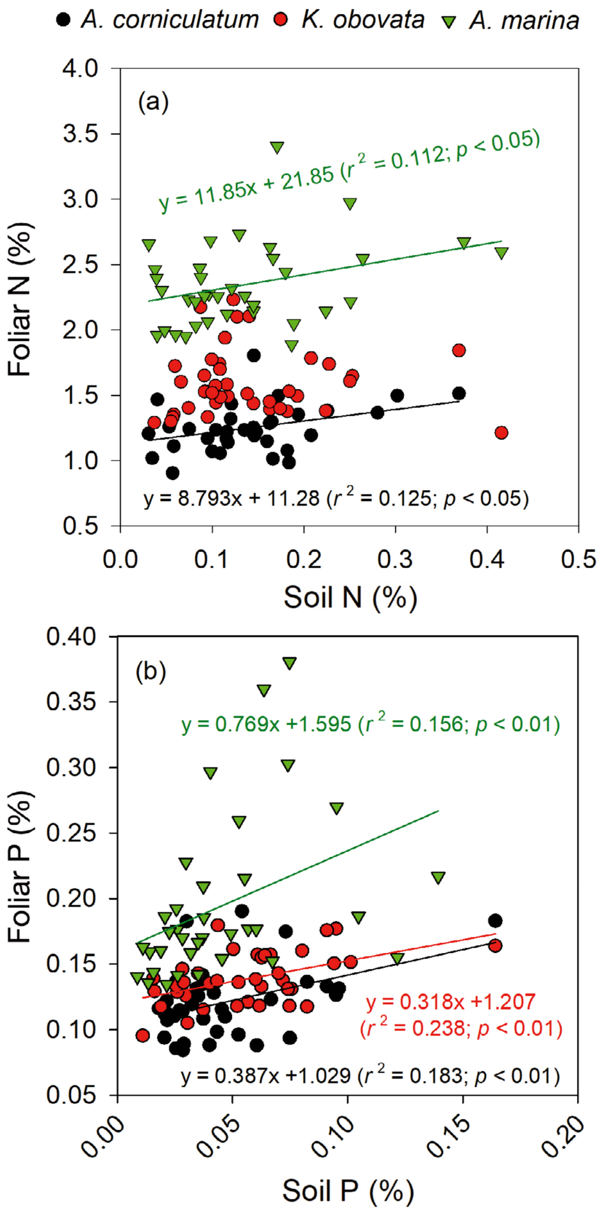

Fig. 3. Relationships between (a) foliar N and soil N and (b) foliar P and soil P in 3 mangrove species (*Aegiceras corniculatum*, *Kandelia obovata*, *Avicennia marina*) across southeastern China. Significant relationships are shown

When data from the 4 species were pooled, species accounted for 94.1, 85.6 and 26.1% of the monthly variation in foliar N, foliar P and foliar N:P ratio, respectively, whereas climatic factors (temperature or rainfall) only accounted for ≤0.5% of the variation (Table 2). When averaged across different months, *A. marina* had the highest foliar N and P concentrations and N:P ratio, *R. stylosa* and *B. sexangula* had intermediate values, and *C. tagal* had the lowest values ($p < 0.001$; Fig. 6).

4. DISCUSSION

Previous studies found that leaf N and P concentrations increased with increasing latitude (Reich & Oleksyn 2004, Han et al. 2005, Chen et al. 2013), which was explained by temperature-related plant physiological processes and the geographical pattern of substrate nutrient status along latitudes (Reich & Oleksyn 2004, Lovelock et al. 2007). In this study, positive relationships between foliar N or P concentrations and latitude were only found in individual species (Fig. 2), but not when all species were pooled. The relatively weak relationships are probably due to the small latitudinal extent (18–28° N) of mangrove distribution in China. Mean annual temperature decreased with increasing latitude ($p < 0.001$; $r^2 = 0.975$; data not shown), which partly explains the positive relationships between foliar N or P concentrations and latitude. Soil P concentrations increased with increasing latitude ($p < 0.05$; $r^2 = 0.142$; data not shown), and foliar nutrient concentrations were positively related to soil nutrients (Fig. 3), which also partly explains the positive relationship between foliar nutrient concentrations and latitude. Although we only sampled soil from the top 20 cm, this may not be the main reason for the relatively weak relationships between foliar nutrients and soil nutrients, because our previous study showed that around 50% of the fine root biomass of mangroves were located in the top 20 cm soil layer (Xiong et al. 2017).

Despite the small latitudinal scale of mangrove distribution in China, the ranges of foliar N (0.7–3.4%) and P (0.07–0.38%) concentrations measured in our study are similar to the ranges of mangroves reported from other areas across the world (compiled by Lovelock et al. 2007). However, the foliar N:P mass ratio in our study (between 7 and 17, with a mean of 12) was much lower than those reported in the literature for mangroves (between 16 and 98, with a mean of 37) (Lovelock et al. 2007). The foliar N:P ratio indicates the relative availability of N vs. P (Güsewell 2004). The range of N:P ratios found in our study indicates that mangroves in China are generally N limited relative to P because N:P mass ratios <14 and >16 correspond to N limitation and P limitation, respectively (Koerselman & Meuleman 1996, Aerts & Chapin 2000). A previous study also reported N limitation in *Kandelia obovata* from China as indicated by a foliar N:P molar ratio <31 (corresponding to N:P mass ratio <14) and higher N resorption than P resorption during leaf senescence (Wang et al. 2011). The general N limitation relative to P (or luxury P uptake) in mangroves of China

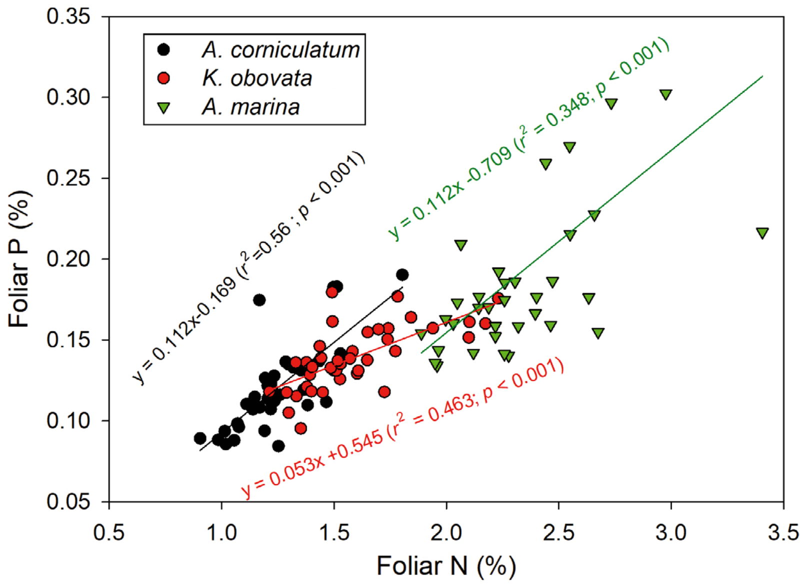

Fig. 4. Correlations between foliar N and P concentrations in 3 mangrove species (*Aegiceras corniculatum*, *Kandelia obovata*, *Avicennia marina*) across southeastern China. Significant relationships are shown

Table 1. Percent of variation in mangrove foliar N concentration, P concentration and N:P ratio across southeastern China explained by influencing factors (species, climate and soil nutrient concentrations), determined by ANCOVA. As multiple ANCOVAs were run for each response variable with different combinations of explaining factors, only the highest values are presented here. *p < 0.05; **p < 0.01; ***p < 0.001

Explaining factor	Foliar N concentration	Foliar P concentration	Foliar N:P ratio
Species	76***	41.3***	18.0***
Climate[a]	2.4***	4.3**	3.7*
Soil nutrients[b]	5.4***	8.3***	3.7*

[a]Mean annual temperature or minimum temperature or annual rainfall
[b]Soil N or P concentration

may be related to the fact that most mangroves in China are adjacent to mariculture ponds, and these ponds produce nutrient-rich wastewater and sediments that may pose pollution issues to intertidal areas (Chen et al. 2020, Pérez et al. 2020). P accumulates faster than N globally in freshwater ecosystems under anthropogenic impacts, leading to lower N:P ratios in water and macrophytes located in nutrient-enriched areas than in less impacted sites (Yan et al. 2016). A similar pattern of faster P accumulation relative to N was also found in the sediments of a highly impacted mangrove wetland (Sanders et al. 2014).

In contrast to the extensive studies on the spatial patterns of plant nutrients in terrestrial ecosystems, less attention has been given to the temporal dynamics of plant nutrients (Lü et al. 2017). One study examining the temporal dynamics of foliar nutrients in mangroves showed higher foliar N and P concentrations during the Northern Hemisphere cooler seasons (from November to April) than warmer seasons (from May to October) in *K. candel* (Wang et al. 2003) (this species in China was later confirmed as *K. obovata*). In our study, with 4 mangrove species examined, *A. marina* showed a similar seasonal pattern as *K. obovata* reported by Wang et al. (2003), while *Bruguiera sexangula* showed a different seasonal pattern, and other species (*Rhizophora stylosa* and *Ceriops tagal*) showed no significant seasonal changes (Fig. 6). The lower nutrient concentrations during the warmer seasons than cooler seasons are likely linked to higher growth rates in warmer seasons and thus a dilution of nutrients due to increasing biomass (Güsewell & Koerselman 2002). However, the inconsistent seasonal patterns among different species suggest that the physiological responses of mangrove plants to seasonal climate change may be constrained by specific species characteristics. Correspondingly, species effect was the major factor driving the temporal variations in foliar N and P in the 4 mangrove species studied (Table 2).

Our study showed that the majority of the spatial and temporal variations in foliar N and P concentrations of mangroves were explained by species, while climate and soil nutrients only explained a small portion of these variations (Tables 1 & 2). Our results are consistent with several studies on terrestrial plants, which also reported stronger effects of phylogeny/growth forms than environmental factors (Thompson et al. 1997, He et al. 2006, Zhang et al. 2019). Furthermore, one study in a karst area found that the relative influences of taxonomy and environmental factors on leaf element concentrations are dependent on phylogenetic scale, with phylogeny having a stronger effect at the subfamily level and environmental conditions having a stronger effect at the genus level (Hao et al. 2015). Given that the 69 recognized mangrove species worldwide belong to 20 families (Lovelock 1993), species difference also represents family-level difference in most cases and therefore species may play an important role in the variations of mangrove foliar nutrients at a regional scale. The role of taxonomy in leaf stoichiometry is likely linked to differences in structural or osmotic fractions of leaf tissues and selective uptake of certain nutrients by plants which are controlled by evolution (Watanabe et al. 2007, Zhang et al. 2012). Furthermore, different mechanisms of salt regulation in different mangrove species also play a role in element uptake, accumulation and resorption (Medina et al. 2015).

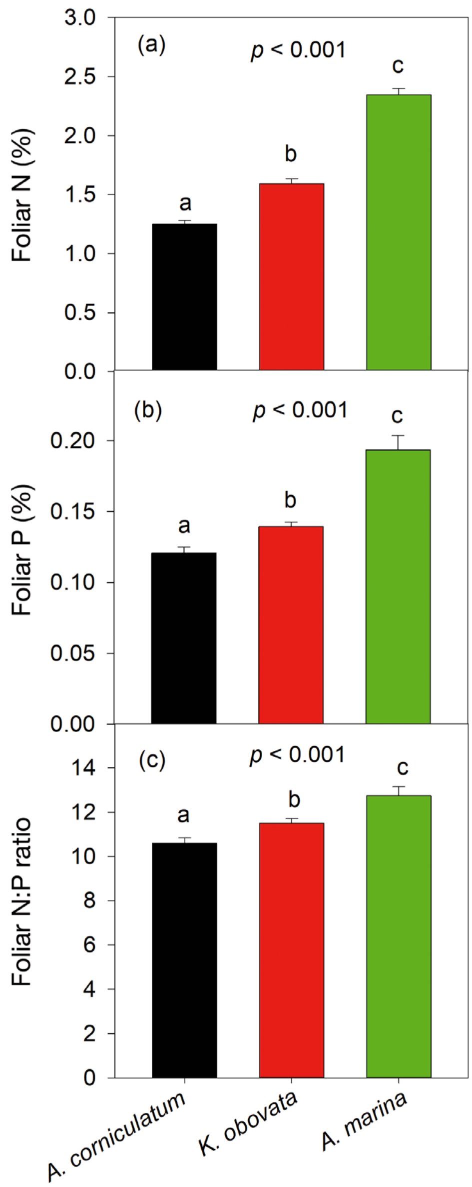

Fig. 5. Differences in foliar N and P concentrations and N:P ratios in 3 mangrove species (*Aegiceras corniculatum*, *Kandelia obovata*, *Avicennia marina*) across southeastern China. Data are means ± SE. Different letters indicate significant differences among species

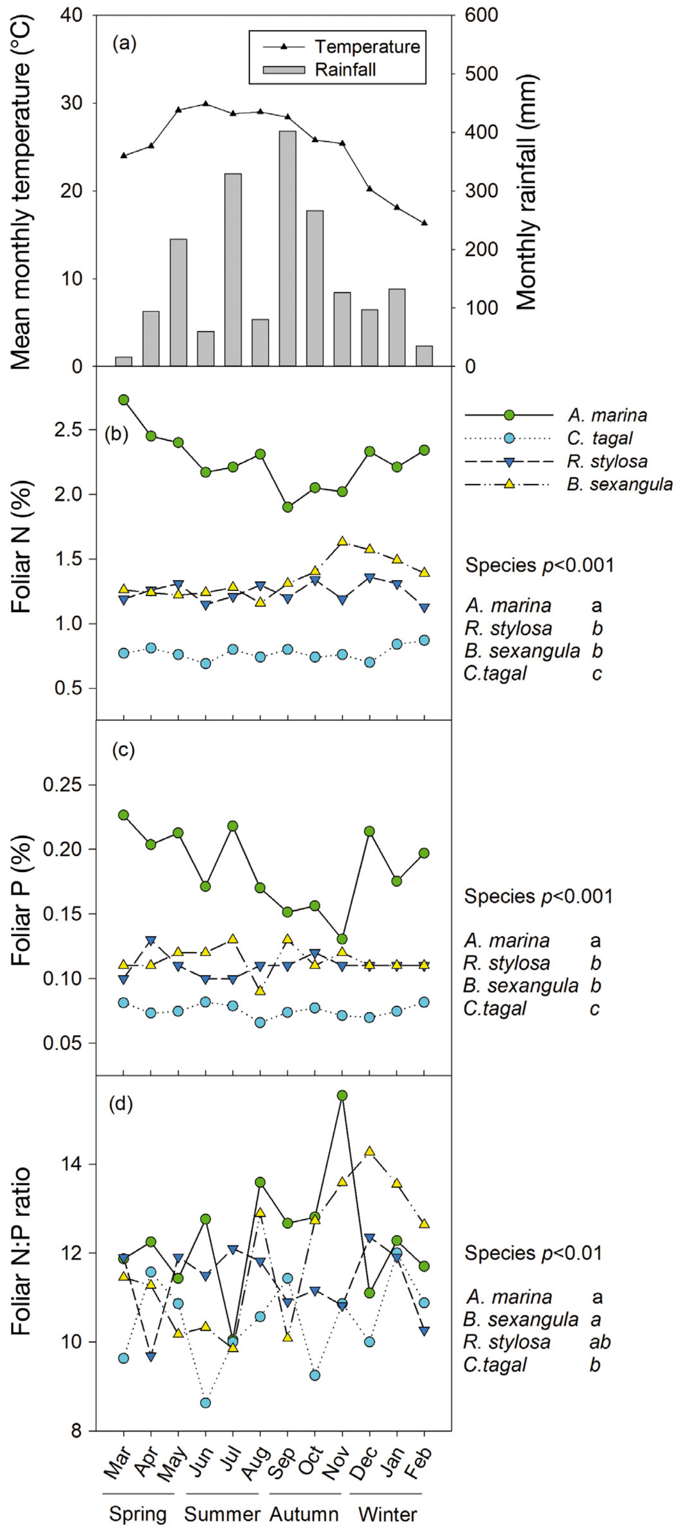

Fig. 6. Monthly dynamics of (a) climate, (b) foliar N concentration, (c) foliar P concentration and (d) foliar N:P ratio in 4 mangrove species (*Avicennia marina*, *Bruguiera sexangula*, *Ceriops tagal*, *Rhizophora stylosa*) located in Dongzhai Harbor Reserve, China. Different letters on the right side of panels b to d indicate significant differences among species

Table 2. Percent of variation in mangrove foliar N concentration, P concentration and N:P ratio in 4 species throughout 1 yr explained by influencing factors (species, climate), determined by ANCOVA. As multiple ANCOVAs were run for each response variable with different combinations of explaining factors, only the highest values are presented here. *p < 0.05; **p < 0.01; ***p < 0.001; ns: not significant

Explaining factor	Foliar N concentration	Foliar P concentration	Foliar N:P ratio
Species	94.1***	85.6***	26.1**
Climate[a]	0.5*	ns	ns

[a]Mean monthly temperature or monthly rainfall

Stoichiometric homeostasis is the ability of an organism to maintain a given elemental composition despite variations in the elemental composition of its environment or diet (Sterner & Elser 2002, Güsewell 2004). Eutrophication has been recognized as a major factor that affects water quality in aquatic ecosystems within coastal areas (Gritcan et al. 2016), and nutrient enrichment affects the within-stand nutrient cycling of mangroves, including primary productivity, nutrient-use efficiency, nutrient resorption, litter decomposition, nutritional quality of plant tissue and allocation to defense (Feller et al. 1999). The much stronger effects of species than environmental factors in affecting foliar nutrient concentrations and N:P stoichiometry in mangroves suggest that stoichiometric homeostasis in mangroves may mitigate the effects of nutrient enrichment. For example, Wei et al. (2020) found that saplings of *Aegiceras corniculatum* maintained constant nutrient resorption efficiency under eutrophic conditions. Studies in terrestrial ecosystems have shown that elementally or stoichiometrically homeostatic species tend to have a high and stable biomass, and ecosystems dominated by more homeostatic species have higher productivity and greater stability (Yu et al. 2010). Therefore, the strong elemental and stoichiometric homeostasis in mangroves may play an important role in maintaining ecosystem functioning despite predicted environmental changes such as climate warming and increasing nutrient loads to coastal areas.

We recognize that there are limitations in our study. Firstly, in the spatial pattern investigation, we did not measure within-site variations. At a site scale, gradients of soil nutrients and salinity are common in mangroves, and these environmental variations play an important role in mangrove nutrient cycling, especially in monospecific stands (Feller et al. 1999, 2003). Therefore, our conclusion that species shape the variation of foliar stoichiometry much more than environmental factors is only applicable at a regional scale but not a local scale. Secondly, in the seasonal pattern investigation, the temporal changes in soil nutrients were not measured, which might have an effect on the temporal dynamics of foliar nutrients. Seasonal dynamics of soil and plant nutrients have been commonly reported in terrestrial ecosystems, especially in temperate and arctic areas (Koller & Phoenix 2017), but they are rarely measured in mangroves, possibly because mangroves grow in tropics and subtropics with relatively stable climate among seasons.

5. CONCLUSIONS

By measuring foliar N and P concentrations of 3 broadly distributed mangrove species across China and examining the monthly dynamics in 4 mangrove species located in one area, we showed that species explained the majority of the spatial and temporal variation in foliar N and P concentrations while climatic factors and soil nutrients only explained a small portion of the variation. The much stronger effect of species than environmental factors in influencing foliar nutrient concentrations and stoichiometry suggests a homeostatic regulatory mechanism in mangrove plants, which may play an important role in mitigating the effects of climatic changes along with nutrient enrichment on the functionality of these coastal wetlands.

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