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Light and competition alter leaf stoichiometry of introduced species and native mangrove species

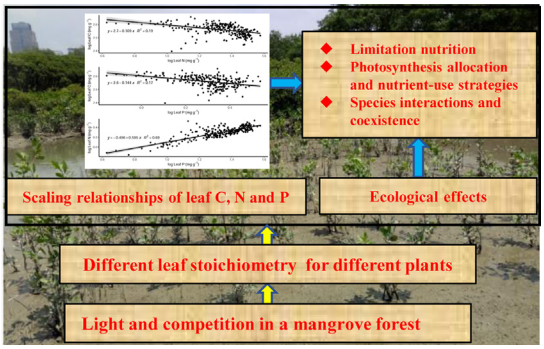
Dehuang Zhu [a,b], Dafeng Hui [c], Mengqi Wang [d], Qiong Yang [d], Shixiao Yu [a,b,*]

[a] *Department of Ecology, School of Life Sciences/State Key Laboratory of Biocontrol, Sun Yat-sen University, Guangzhou 510275, China*
[b] *Shenzhen Research Institute, Sun Yat-sen University, Guangzhou 518054, China*
[c] *Department of Biological Sciences, Tennessee State University, Nashville 37209, USA*
[d] *Guangdong Neilingding Futian National Nature Reserve, Shenzhen 518040, China*

HIGHLIGHTS

- Leaf C, N, and P concentrations and their ratios had scaling relationships in the mangrove forests.
- Light and competition significantly influenced the leaf stoichiometry of mangrove plants.
- There was N limitation in the mangrove forests.
- Leaf stoichiometry of the mangrove forests supported the growth rate hypothesis.

GRAPHICAL ABSTRACT



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ABSTRACT

Ecological stoichiometry is the study of the balance of ecosystem energy and nutrient cycling, especially carbon (C), nitrogen (N), and phosphorus (P). C, N, and P are the key elements for plant growth and metabolism. Systematic research on leaf stoichiometry in mangrove forest ecosystems is still lacking. To understand the leaf stoichiometry of introduced species and native species in mangrove forests, we selected four species (one introduced species, *Sonneratia apetala*, and three native species, *Avicennia marina*, *Aegiceras corniculatum*, and *Kandelia obovate*) and measured leaf C, N, and P contents under different light conditions. The results showed that there were significant negative scaling relationships of leaf C versus N and C versus P but positive scaling relationships of leaf N versus P in the four mangrove species. Light and competition had significant effects on leaf stoichiometry, especially under the full light condition. *S. apetala* influenced leaf elements in a mixture with native species. Interspecific competition reduced leaf N and P contents in *A. corniculatum* and *K. obovate* but increased leaf N and P contents in *A. marina*. Leaf N and P contents of the four species showed similar responses to both intraspecific and interspecific competition. The ratio of leaf C:N:P (108:11:1) in the mangrove forests was lower than that in other ecosystems, and species with a higher growth rate had a higher leaf P content and lower N:P ratio, supporting the growth rate hypothesis. Leaf N:P was 11.04, indicating that there was N limitation in the mangrove forests. This systematic research of leaf stoichiometry of mangrove forests improves our understanding of mangrove growth and nutrient use strategies in response to different environmental stresses.

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[*] Corresponding author at: Department of Ecology, School of Life Sciences/State Key Laboratory of Biocontrol, Sun Yat-sen University, Guangzhou 510275, China.
E-mail address: lssysx@mail.sysu.edu.cn (S. Yu).

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1. Introduction

Ecological stoichiometry is the study of the composition of multiple key elements, particularly carbon (C), nitrogen (N), and phosphorus (P), and ecological interactions in organisms and provides new perspectives for understanding energy flow and nutrient cycling in ecosystems (Cross et al., 2007; Elser et al., 2000a, 2000b; Reich et al., 2006; Sistla and Schimel, 2012). C, N, and P are the key chemical elements for plant growth and metabolism in terrestrial and aquatic ecosystems (Aerts and Chapin, 1999; Elser et al., 2007; Michaels, 2003; Vrede et al., 2004). C, N, and P concentrations and their stoichiometry in plant organs are linked to ecological processes and the structure and functions of ecosystems (Elser et al., 2010; Sardans et al., 2012; Zechmeister-Boltenstern et al., 2015). Compared with roots and shoots, leaves are considered the most active organ. Leaf C, N, and P are important constituents of chlorophyll, and leaf chlorophyll is linked to photosynthetic capacity and net primary production (Croft et al., 2017; Elser et al., 2010; Gitelson et al., 2006). In addition, soil fertility (Achat et al., 2018) and light availability (Fajardo and Siefert, 2019; Keenan and Niinemets, 2016; Miatto et al., 2016) may directly affect the contents of elements in leaves.

C, N, and P stoichiometry reflects the growth of plants, and the growth rate represents the overall life history strategy of plants. The P content and C:N:P ratio in organisms depend largely on changes in the allocation to P-rich ribosomal RNA (rRNA) at different growth rates, which is the basis of growth rate hypothesis (GRH, Elser et al., 2003; Makino et al., 2003). The GRH proposes that fast-growing organisms often have a higher P content and lower N:P ratios than the slow-growing organisms due to elevated demand for P for the synthesis of P-rich rRNA under rapid growth (Elser et al., 2000a, 2000b; Karpinets et al., 2006). The N:P ratio is an indicator used to assess assessing the nutrient efficiency and limitation of plants in different ecosystems (Cernusak et al., 2010; Güsewell, 2004; Herbert et al., 2003; Koerselman and Meuleman, 1996; Mao et al., 2016). The C:N ratio is an important parameter of C and N cycling in ecosystems (Zaehle et al., 2014). Many studies have been conducted to investigate the stoichiometry of plants in aquatic and terrestrial ecosystems (Du et al., 2019; Guiz et al., 2017; Li et al., 2018; Mayor et al., 2014; Xia et al., 2014; Zhang et al., 2018a). Previous studies have supported the GRH for plants (Lovelock et al., 2007a; Niklas and Cobb, 2005; Yan et al., 2015; Zechmeister-Boltenstern et al., 2015). However, very few studies have assessed leaf stoichiometry in mangrove ecosystems (Lovelock et al., 2007a; Feller et al., 2007; Feller et al., 2003a, 2003b; Reef et al., 2010). Reef et al. (2010) reported that the mean C:N:P ratio was 1062:31:1 in the leaves of two mangrove species, that is, *Avicennia marina* and *Ceriops australis*; this value is significantly higher than that measured in aquatic vascular plants and other terrestrial forests (Demars and Edwards, 2007; McGroddy et al., 2004). Mangrove leaf stoichiometry needs to be further investigated. Previous studies also found that C:N:P stoichiometry differs among different ecosystems, and environmental factors such as light may have direct effects on the stoichiometry. Under different light conditions, plants may allocate different amounts of C and nutrients to leaves to meet the requirements for their growth and development (Xie et al., 2018). Our understanding of leaf C:N:P stoichiometry in response to different light conditions in mangrove forests is not well developed. Homeostasis of the elements in plankton (Andersen and Hessen, 1991), herbaceous (Yu et al., 2015), and natural forest (Zhang et al., 2018b) ecosystems has been reported. However, it is still not clear whether homeostasis exists in mangrove forest ecosystems.

Mangrove forests consist of shrubs and trees that grow along tropical and subtropical coastlines, and they are the most diverse and productive intertidal ecosystems (Alongi, 2002; Giri et al., 2011). However, mangrove forests are degrading due to the development of aquaculture, pasture, rapid urbanization, and climate change (Richards and Friess, 2016). Afforestation is proposed to reduce C emissions and mitigate climate change in many countries. In mainland China, mangrove afforestation has been conducted for more than two decades (Chen et al., 2009; Ren et al., 2009). The common tree species used in mangrove afforestation in China include two native species, *Kandelia obovate* and *Sonneratia caseolaris*, and one introduced species, *Sonneratia apetala*. *S. apetala* is a shade-intolerant, fast-growing, and highly adaptable tree that originated from Bangladesh, Myanmar, and India (Jayatissa et al., 2002; Peng et al., 2016). The effect of *S. apetala* is of wide concern (He et al., 2018; Lunstrum and Chen, 2014; Peng et al., 2016; Wu et al., 2020), especially its impact on the growth of the native species (e.g., *K. obovata*, *A. marina*, *Aegiceras corniculatum*). No previous study has provided information on the stoichiometry of *S. apetala* and the native species. In addition, how species competition influences plant stoichiometry remains poorly understood in the mangrove forests, especially the impacts of *S. apetala* on the stoichiometry of the native species in a mixed planting system. Studies on ecological stoichiometry in mangrove forests will improve our understanding of mangrove growth, nutrient use strategies, and responses to different environmental stresses, which will provide a scientific basis for the conservation and management of mangrove forests.

In this study, we conducted a manipulative field experiment to determine the effects of specific competition (different planting systems-monoculture or mixed species with introduced species and native species) and light intensity on leaf C, N, and P contents and their stoichiometry in a mangrove forest. We proposed four hypotheses: (1) *S. apetala* and native species will have different scaling relationships between leaf C versus N, C versus P, and N versus P; (2) the light condition will significantly affect leaf stoichiometry; (3) compared to monoculture, species in the mixture will have different C:N:P ratios as intraspecific competition and *S. apetala* will change nutrient uptake and influence leaf stoichiometry of native species; and (4) there will be a positive relationship between the growth rate and the N:P ratio, as suggested by the growth rate hypothesis.

2. Materials and methods

2.1. Study sites

The field experiment was conducted in the Futian National Nature Reserve (22°32′N, 113°45′E) located on the north of Shenzhen Bay, Guangdong Province, China. The reserve is the smallest mangrove reserve (368 ha) in China. The mean annual temperature is 22.6 °C, the total annual precipitation is 1794 mm, and mean annual evaporation is 1500–1800 mm in this reserve (Lunstrum and Chen, 2014; Yang et al., 2014). The main tidal characteristics in the study area are irregular semidiurnal tides that are often affected by typhoons from summer to autumn. In Shenzhen Bay, species richness of the mangrove community is poor (Ren et al. 2011). The dominant species are *K. obovata*, *A. marina*, and *A. corniculatum*, and some exotic species such as *S. apetala* and *S. caseolaris*. Four species (*A. marina, K. obovata, A. corniculatum* and *S. apetala*) account for >80% of the mangrove community area in Shenzhen Bay, and their populations are decreasing (Polidoro et al., 2010). Therefore, we selected these four species in this study.

2.2. Experimental design

In July 2017, we set u plots consisting of two age classes (14 and 26 years) in *S. apetala* plantations. Each plot was 10 m × 10 m. Five plots were established in the 14-year-old plantation compares with four plots for 26-year-old plantation, that is, a total of nine plots. The seedling experiment was conducted in a bare mudflat in the reserve. We manipulated the light environment to represent light intensity under the canopy of the 14-year-old and 26-year-old plantations of *S. apetala*. Each light condition plot was 10 m × 10 m, and there was a 5 m gap between two adjacent plots. The average heights of the *S. apetala* plantation in the 14-year-old and 26-year-old plantations were 9.45 m and 14.5 m. Light intensity was measured 10 times using a digital illumination photometer in the mudflat and in the 14-year-old and 26-year-old plantations of *S. apetala*. The light intensity in 14-year-old and 26-year-old *S. apetala* plantation canopies were 22.81% and 8.62% of the mudflat, respectively. One-year seedlings of four species (*S. apetala*, *K. obovata*, *A. marina,* and *A. corniculatum*) were selected for the experiment. At the beginning of the experiment, the mean seedling height was 75 ± 13.45 cm, 39 ± 3.56 cm, 51.11 ± 5.76 cm, and 37.29 ± 5.46 cm for *S. apetala*, *K. obovata*, *A. marina*, and *A. corniculatum*, respectively.

We used a split plot design with light condition (including full light, medium light, and low light) as the main plot factor and planting system (including monoculture each with one of the four individual species, mixture with three different species combinations, and mixture with four species combinations for a total of eleven planting types) as the spilt plot factor. Three blocks were used for the light condition treatments. The three light treatments were implemented using black polypropylene shade netting (no shading, 25% shading, and 10% shading) to simulate light environment in the mudflat, and under the 14-year-old and 26-year-old of *S. apetala* plantation canopies. The shade nets were mounted 200 cm above the ground for the mangrove growth. At each light level, both monoculture and mixed planting systems were applied. In the monoculture planting system, 15 seedlings of each of the four mangrove species were planted in the plots as the control in May 2018. In the mixed planting system, two individuals of *S. apetala* or native species for the intraspecific treatment were planted together; this was repeated 15 times; one individual of *S. apetala* and one individual of the three native species (e.g., one individual of *S. apetala* and one individual of *K. obovata*) for the interspecific treatment were planted together; this was repeated 15 times. In total, 810 plant seedlings (3 light levels × [4 species in the monoculture +8 species in the mixture for the intraspecific treatment +6 species in the mixture for the interspecific treatment =18 species] × 15 replicates) were used in this study. The experiment lasted for a total of 310 days.

2.3. Sampling and elemental analysis

In April 2019, all of the mangrove plants were harvested. Each harvested tree was separated into leaves, shoots, and roots. Each component was transported to the laboratory and oven-dried at 80 °C for 72 h for biomass measurement. The above- and below-ground biomass were calculated. The relative growth rate (RGR) of total biomass was calculated as $RGR = (\log W_2 - \log W_1) / (t_2 - t_1)$, where W_2 and t_2 are final biomass and time, and W_1 and t_1 are original biomass and time, respectively. Five seedlings were randomly selected in each treatment, and one healthy and fully expanded leaf was selected from each seedling to measure leaf C, N, and P concentrations. Specific leaf area (SLA), the leaf dry-mass content (LDMC), and leaf thickness (LT) were measured using five leaves from one plant. SLA was estimated using the fresh leaf area divided by the oven-dried mass (Pérez-Harguindeguy et al., 2013). LDMC was calculated as leaf oven-dried mass divided by the water-saturated fresh mass (Pérez-Harguindeguy et al., 2013). Leaf thickness (LT) was measured at the widest point of the main vein of each leaf using a micrometer, avoiding important secondary veins (Pérez-Harguindeguy et al., 2013). The chlorophyll content (Chl) and total carotenoid content (Caroten) were calculated. Absorption of the extraction solution was determined at 663 nm and 646 nm for chlorophyll *a* (Chl a) and chlorophyll *b* (Chl b) and at 470 nm for total carotenoids content (Caroten) using a spectrophotometer (Wellburn, 1994). All of the leaf samples were ground to a fine powder using a ball mill (200T, WTFER, China) and an agate mortar grinder (RM200, Retsch, Haan, Germany). Total leaf nitrogen was analyzed with the semi−Kjeldahl method (Parkinson and Allen, 1975); total leaf phosphorus was determined by digestion with H_2SO_4–H_2O_2 solution (Parkinson and Allen, 1975); and leaf carbon was measured with the potassium dichromate (KCr_2O_7) method (Kalembasa and Jenkinson, 1973).

2.4. Statistical analysis

To determine the law of C:N:P ratios in the four species, we used allometric functions with Standardized Major Axis (SMA) regression analysis (Legendre and Legendre, 2012):

$$\text{Log Y} = \log a + b * \log \text{X}, \tag{1}$$

where Y and X are C, N, and P concentrations or their ratios; parameter *b* represents the allometric exponent; and parameter *a* reflects the allometric constant. Parameters *a* and *b* were estimated using the package “smatr” in R 3.5.1(Warton et al., 2012).

To evaluate the effect of *S. apetala* on the leaf stoichiometry of native species, we used one-way ANOVA. The interactions of light and planting system on the stoichiometry were detected using two-way ANOVA. We quantified the leaf elements (C, N and P) and stoichiometry of *S. apetala* and native species in response to intraspecific and interspecific competition using response ratios (lnRR):

$$\ln\frac{X_t}{X_c} = \ln X_t - \ln X_c, \tag{2}$$

where X_t and X_c represent the values of the leaf elements or stoichiometry in the experimental treatment and the control, respectively, at the same light level.

Correlation analysis was applied to develop relationships between functional traits and leaf stoichiometry in the different species. The variables were log- or Box-Cox transformed to meet the normality requirement. All of the data analyses were performed using R 3.5.0 (R Core Team, 2018).

3. Results

3.1. Allometric relationships of leaf elements

Three elements (i.e., C, N, and P) in leaves showed allometric relationships for the all tree species (Table 1). For instance, the scaling exponents (i.e., the slope for the reduced major axis regression curve) for C versus N, C versus P, and N versus P significantly differed from 1.0 (i.e., −0.11, −0.14, and 0.60, respectively), whereas the scaling exponents of C versus N and C versus P were similar for the all species. The scaling exponents of leaf N versus P was 0.60 (95% CI = 0.55–0.64, $p < 0.001$), which was close to 2/3 (Fig. 1).

For each plant species, the scaling exponents of C versus N and C versus P were negative, whereas the scaling exponent of leaf N versus P was positive (Table 1). However, there were no significant differences in allometric exponents and allometric constants of C versus N in *A. corniculatum* and C versus P in *A. marina.*

3.2. Effects of light and competition on leaf ecological stoichiometry

For all of the plant species, light condition had significant effects on leaf stoichiometry (Table 2). With the exception of the leaf C and N:P ratio, competition also had significant impacts on the leaf ecological stoichiometry. However, the interaction between light and competition had no effects on the leaf stoichiometry.

For each plant species, leaf stoichiometry of *A. marina* was affected by light but was not affected by competition and interaction between light and competition (Table A1). With the exception of leaf N:P ratio, competition and the interaction between light and competition had significant impacts on the leaf stoichiometry of *A. corniculatum*. For *S. apetala*, only leaf P and N:P ratio were significantly influenced by competition and the interaction between light and competition. Light had

Table 1
Summary of reduced major axis regression analyses (slope and y-intercepts, log $\alpha$and b, respectively) of leaf carbon (C), nitrogen (N), and phosphorus (P) stoichiometry for four mangrove species.

	Species	n	log α (95%CI)	b (95%CI)	r^2	p
C versus N	Am	60	3.00 (2.87, 3.14)	−0.33 (−0.43, −0.23)	0.44	<**0.001**
	Ac	60	2.53 (2.43, 2.64)	0.02 (−0.07, 0.11)	0.01	0.612
	Ko	58	2.65 (2.63, 2.69)	−0.05 (−0.07, −0.02)	0.22	<**0.001**
	Sa	83	2.74 (2.68, 2.80)	−0.13 (−0.17, −0.09)	0.31	<**0.001**
	All	261	2.70 (2.67, 2.75)	−0.11 (−0.14, −0.08)	0.19	<**0.001**
C versus P	Am	60	2.49 (2.42, 2.56)	0.13 (−0.06, 0.33)	0.03	0.176
	Ac	60	2.59 (2.57, 2.62)	−0.14 (−−0.25, −0.03)	0.09	**0.016**
	Ko	58	2.61 (2.60, 2.62)	−0.07 (−0.12, −0.04)	0.22	<**0.001**
	Sa	83	2.58 (2.56, 2.60)	−0.08 (−0.14, −0.02)	0.08	**0.009**
	All	261	2.60 (2.59, 2.62)	−0.14 (−0.18, −0.11)	0.17	<**0.001**
N versus P	Am	60	1.56 (1.42, 1.70)	−0.40 (−0.79, −0.02)	0.07	**0.041**
	Ac	60	0.96 (0.91, 1.01)	1.13 (0.93, 1.33)	0.69	<**0.001**
	Ko	58	0.93 (0.89, 0.96)	1.50 (1.35, 1.65)	0.87	<**0.001**
	Sa	83	1.08 (1.00, 1.15)	0.91 (0.72, 1.10)	0.54	<**0.001**
	All	261	−0.50 (−0.56, −0.43)	0.60 (0.55, 0.64)	0.69	<**0.001**

Note: Am: *Avicennia marina*, Ac: *Aegiceras corniculatum*, Ko: *Kandelia obovata*, Sa: *Sonneratia apetala*, All: all of the plant species. Bold values indicate significant difference ($P < 0.05$).

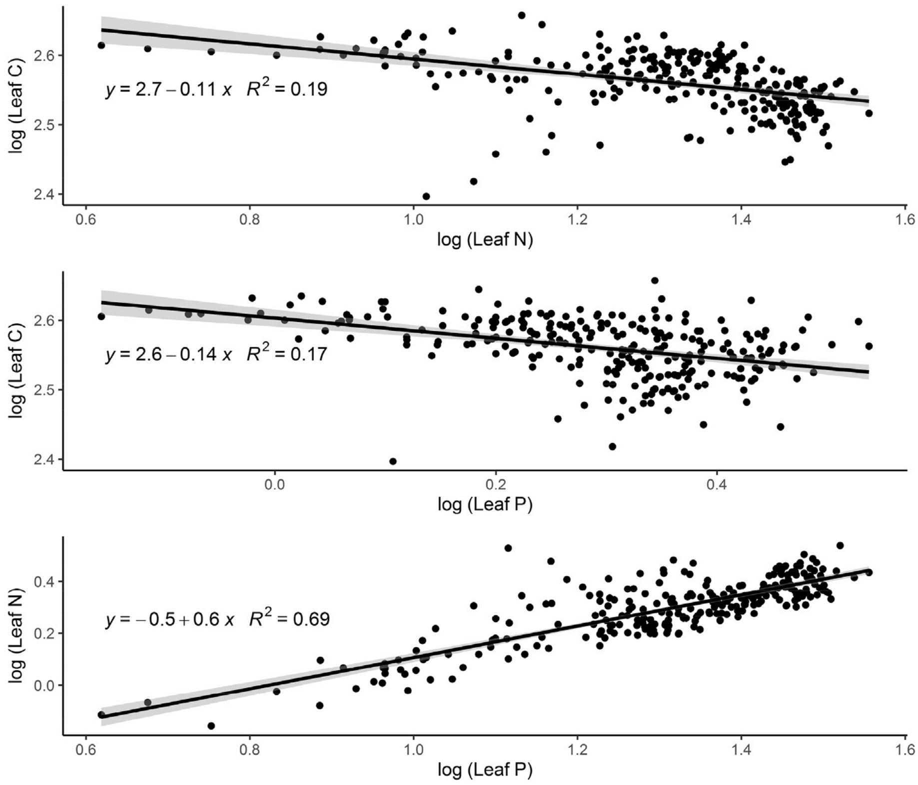

Fig. 1. Bivariate plots among the leaf carbon (C), nitrogen (N), and phosphorus (P) in the mangrove forests. Major axis regression for significance of R^2.

Table 2
F-values and significance levels for two-way ANOVAs testing the effects of light (3 levels) and competition (2 levels) and their interactions on leaf stoichiometry for mangrove species.

	Light		Competition		Light × Competition	
	F	p	F	p	F	p
Leaf C	8.97	<**0.001**	1.34	0.256	1.12	0.354
Leaf N	74.48	<**0.001**	6.15	<**0.001**	0.59	0.788
Leaf P	23.39	<**0.001**	9.35	<**0.001**	0.90	0.517
C:N	71.86	<**0.001**	5.68	<**0.001**	0.79	0.615
C:P	25.23	<**0.001**	7.57	<**0.001**	0.95	0.475
N:P	65.06	<**0.001**	1.51	0.201	0.81	0.593

Note: Bold values indicate significant difference ($P < 0.05$).

significant impacts on the leaf stoichiometry of *A. corniculatum, K. obovate*, and *S. apetala* (Table A1).

For each plant species, the response ratios of the leaf N and P contents (ln RR_{LN} and ln RR_{LP}) of *A. marina* and *S. apetala* were mainly negative under all light conditions, whereas *A. corniculatum* and *K. obovata* showed the opposite tendency (Figs. 2 and 3). The response ratios of leaf C (ln RR_{Lc}) of *A. marina*, *K. obovate*, and *S. apetala* were mainly positive under all light conditions, whereas negative effects were observed for *A. corniculatum* (Fig. A1). Both intraspecific and interspecific competition had basically the same effects on leaf C, N, and P for all species. The ln RR_{LN} and RR_{LP} of *A. corniculatum* and *K. obovate* under medium and low light were significantly higher than those under the full light condition. *A. marina* and *S. apetala* showed the opposite results. The

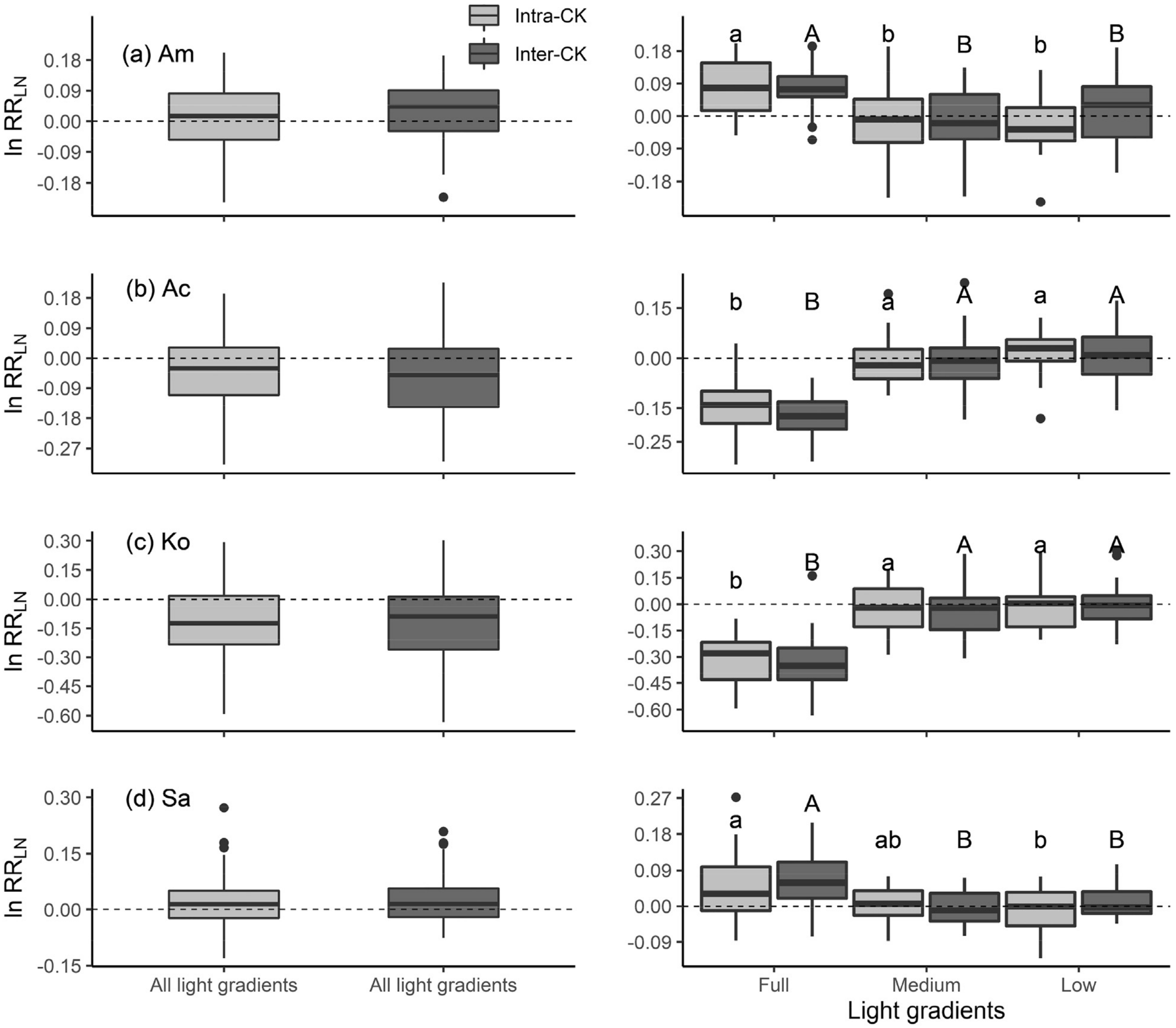

Fig. 2. Response ratios of leaf nitrogen content (ln RR$_{LN}$) of four mangrove species under all light conditions and each light level (Full, Medium, Low). (a) Am: *Avicennia marina*, (b) Ac: *Aegiceras corniculatum*, (c) Ko: *Kandelia obovata*, (d) Sa: *Sonneratia apetala*. Different letters represent the significant differences of each species under the same light environment at $P < 0.05$.

response ratios of the leaf C of *A. marina, K. obovate* and *S. apetala* under the full light condition were significantly lower than those under medium and low light, and the ln RR$_{Lc}$ of *A. corniculatum* was higher in the full light than that under medium and low light (Fig. A1).

3.3. Relationships between functional traits and leaf stoichiometry

There were significantly positive correlations between RGR and leaf stoichiometry; with the correlation coefficient ranged from 0.35 to 0.85. With the exception of leaf P and N:P ratio, and leaf C:P and N:P ratios, the correlations of all functional traits were positive for all of the plants (Table 3). Specifically, the correlation coefficient between RGR and N:P ratio was significantly positive 0.36. Leaf elements and their ratios also had significant correlations with other functional traits such as biomass, R:S ratio, SLA, and the chlorophyll content (Table A2). Leaf N, P, C:N and C:P ratios showed strong correlations with the total biomass and R:S; the correlation coefficients ranged from −0.85 to 0.83. Therefore, leaf stoichiometry responded to the regulation of functional traits in mangrove species. The RGR of *S. apetala* was higher than that of the native species, and the RGR of *A. corniculatum* was also higher than that of *A. marina* or *K. obovate* (Fig. A2). Nevertheless, *A. corniculatum* and *S. apetala* had higher RGRs but significantly lower ratios of leaf N:P than *A. marina* or *K. obovate* under the medium and low light conditions (Fig. 4).

4. Discussion

4.1. Allometric relationship of leaf stoichiometry

Different species have different leaf stoichiometric scaling relationships. For all of the species, leaf C, N, and P showed allometric scaling relationships in this study. Specifically, the scaling exponents of leaf C versus N and leaf C versus P were negative, indicating that less leaf N and P contents were allocated to the production of proteins and P-rich cellular components when more C was allocated to leaves for growth (Vrede et al., 2004). Interestingly, the scaling exponent of leaf N versus P was approximately 2/3, supporting the elastic self-similarity model (McMahon, 1973; Niklas and Enquist, 2002a; Niklas and Enquist, 2002b). For each species, the scaling exponents of leaf C versus N and leaf C versus P were also negative, whereas that of leaf N versus P was positive. It is noteworthy that N typically scaled approximately isometrically with P in *A. corniculatum* and *S. apetala* according to the

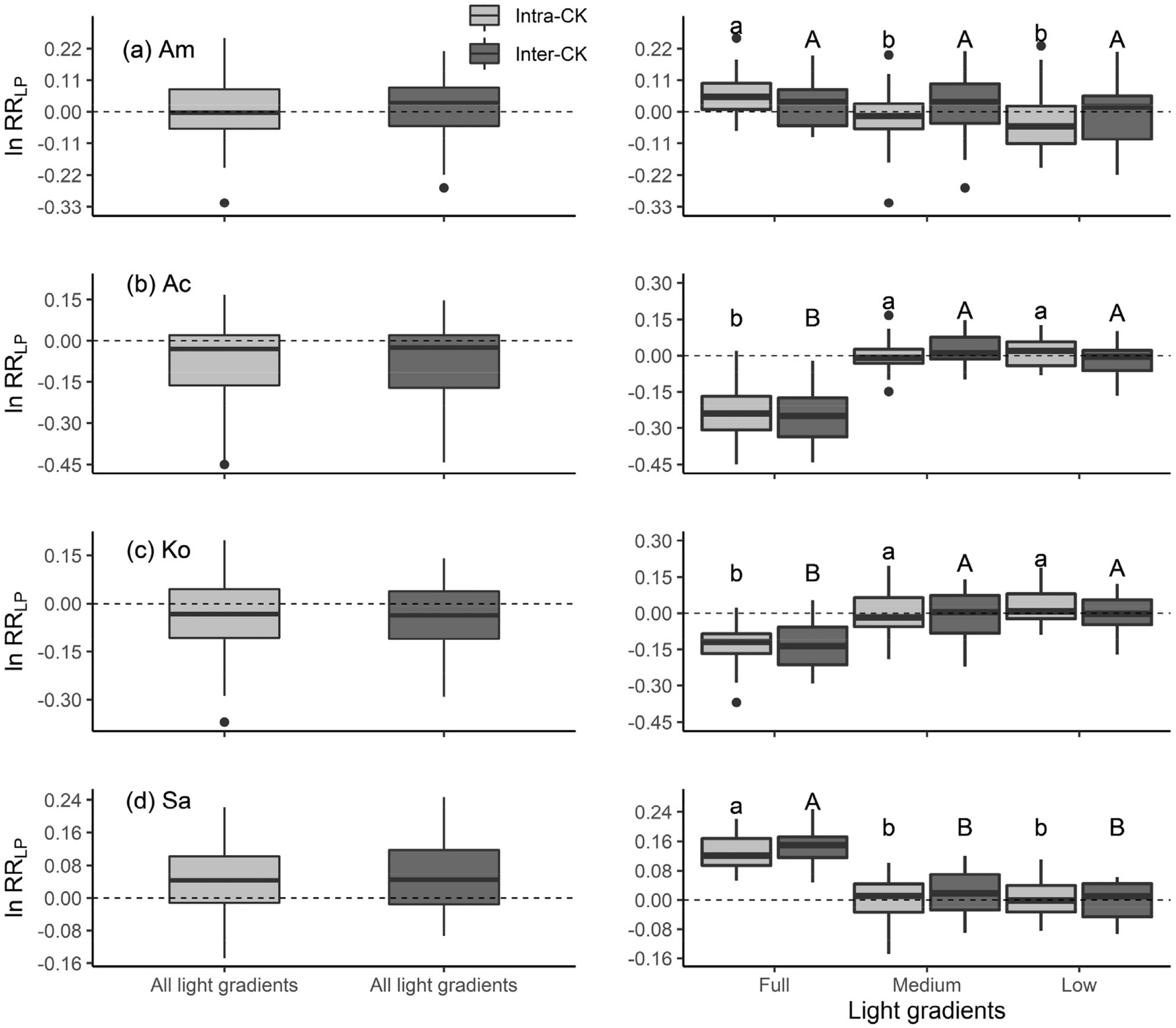

Fig. 3. Response ratios of leaf phosphorus content (ln RR_{LP}) of four mangrove species under all light conditions and each light level (Full, Medium, Low). (a) Am: *Avicennia marina*, (b) Ac: *Aegiceras corniculatum*, (c) Ko: *Kandelia obovata*, (d) Sa: *Sonneratia apetala*. Different letters represent the significant differences of each species under the same light environment at $P < 0.05$.

Table 3
Correlation coefficient of relative growth rate (RGR) and leaf C:N:P stoichiometry of mangrove species.

	RGR	Leaf C	Leaf N	Leaf P	C:N	C:P	N:P
RGR	1.00						
Leaf C	0.35**	1.00					
Leaf N	0.85***	0.55***	1.00				
Leaf P	0.73***	0.27*	0.74***	1.00			
C:N	0.80***	0.69***	0.95***	0.65***	1.00		
C:P	0.75***	0.51***	0.79***	0.94***	0.76***	1.00	
N:P	0.36***	0.46***	0.57***	0.12	0.62***	0.01	1.00

Note.
* Indicates a significant correlation at the 0.05 level.
** Indicates a significant correlation at the 0.01 level.
*** Indicates a significant correlation at the 0.001 level.

proportional term N ∝ P, which differed from N ∝ $P^{3/4}$ for leaves reported by Reich and Oleksyn (2004). *A. corniculatum* and *S. apetala* allocated more N and P to leaves, resulting in isometric relationships for leaf N versus P. In brief, the scaling exponents of C versus N and C versus P were negative across all species except *A. corniculatum* (C versus N) and *A. marina* (C versus P), whereas that of N versus P were positive for the four mangrove species except *A. marina*. The above findings seemed to partially support our first hypothesis.

The leaf stoichiometry of plants also responds to environmental changes. In this study, the coefficient of variation (*CV*) of leaf C, N, and P concentrations and their ratios showed large differences among of four species (Table A3). In general, leaf stoichiometry of *S. apetala* had smaller *CV* than the native species, indicating that *S. apetala* has greater adaptation to a changing environment. Compared to leaf N, P, C:N, C:P, and N:P, the variation of leaf C was smaller. This indicated that plants fix C through photosynthesis and maintain a relatively stable C level. The *CV* of the leaf N:P of *A. corniculatum* and *K. obovate* was lower than that of *A. marina*, indicating that the nutrient efficiency of *A. marina* is susceptible to light and competition. Overall, the leaf stoichiometry of the mangrove species had less variation, indicating the mangrove forests may have evolved over the long term and adapted to the changing biological (e.g., neighbor competition) and abiotic (e.g., light) conditions (Frost et al., 2005; Jeyasingh et al., 2009). Indeed, viviparous mangrove species have strong adaptability to intertidal environments, which might result in low variation of leaf stoichiometry (Kadoya and Inoue, 2015).

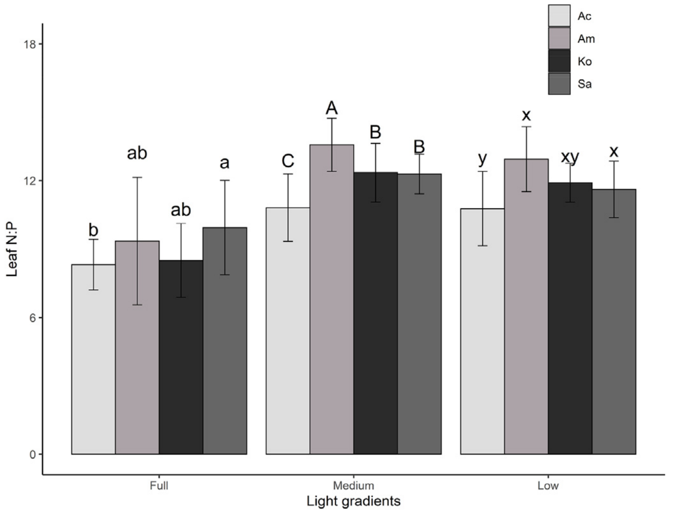

Fig. 4. Ratios of leaf nitrogen (N): leaf phosphorus (P) of four mangrove species under each light level (Full, Medium, Low). (a) Am: *Avicennia marina*, (b) Ac: *Aegiceras corniculatum*, (c) Ko: *Kandelia obovata*, (d) Sa: *Sonneratia apetala*. Different letters combinations represent the significant differences between *S. apetala* and native species under the same light environment at $P < 0.05$.

4.2. Response of leaf stoichiometry to light and competition

Light is one of the most important resources for plant growth and regulates plant photosynthesis (Niinemets and Valladares, 2004; Valladares and Niinemets, 2008). Leaf C, N and P are the major elements in chlorophyll and enzymes and play critical roles in leaf photosynthesis and respiration. In turn, different photosynthetic rates will influence leaf C contents and leaf stoichiometry. In this study, we found that light had significant impacts on leaf stoichiometry in the mangrove ecosystem as light influenced leaf photosynthesis, supporting our second hypothesis. The lnRR of each species showed significant differences under different light conditions. This provides further evidence that light mediates leaf trait variation (Sack et al., 2006; Williams et al., 2020).

Competition also influenced leaf stoichiometry. Regardless of intraspecific competition (monoculture with one species) or interspecific competition (a mixture with different species), the responses of leaf C, N, and P were similar. For *A. corniculatum* and *K. obovata*, there were negative responses of leaf N and P to competition, indicating less allocation of leaf N and P to photosynthesis (Chen et al., 2013), whereas leaf C showed positive responses ($\ln RR > 0$) for *A. corniculatum*. However, *S. apetala* and *A. marina* showed the opposite trend for leaf N, P, and C. The responses of leaf C, N and P in each species were significantly affected by light and competition. In interspecific treatments, the responses of leaf N and P of *A. corniculatum* and *K. obovata* were mostly negative. This finding indicated that *S. apetala* reduced the accumulation of N and P of *A. corniculatum* and *K. obovata*, which subsequently decreased the photosynthesis of the native species, and might eventually inhibit the growth of native species (Jiang et al., 2019). Conversely, the responses of leaf N and P of *A. marina* mixed with *S. apetala* were mostly positive, likely because *A. marina* is shade-intolerant (Chen and Ye, 2014; Jiang et al., 2019; Minchinton, 2001). The leaf stoichiometry of *A. corniculatum* and *K. obovata* was also affected by the interaction of light and competition (Table A1). In addition, we found that the total biomass and RGR of native species were significantly lower in the mixture with *S. apetala* than in the monoculture. Overall, *S. apetala* regulated the growth of the native species by changing leaf stoichiometry. Our results supported our third hypothesis.

4.3. Relationships between functional traits and leaf stoichiometry

Leaf stoichiometry reflected the growth and nutrition of plants. In this study, functional traits had strong relationships with the leaf stoichiometry of mangrove species (Table 3, Table A2). There was a positive correlation between the total biomass of mangrove species and leaf C but negative correlations with leaf N and P. This occurred because with greater C investment in biomass, leaf C contents was increased, but leaf N and P contents were diluted and decreased. R:S had a negative relationship with total biomass. Compared to total biomass, R:S had contrary correlations with leaf stoichiometry. We also found that thinner leaves had a higher SLA in this study, indicating that less C was allocated to leaves for plant growth (Abrams and Mostoller, 1995). Leaf C, N, and P had significant relationships with leaf chlorophyll as they are constituents of chlorophyll. Carotenoids also had strong positive correlations with leaf N and P, indicating higher leaf N and P would produce more carotenoids for light-harvesting and photoprotective functions (Young, 1991).

Across all the species, RGR had significant positive correlations with leaf stoichiometry (Table A2). The introduced species *S. apetala* had higher RGR than the native species. Nevertheless, the ratios of leaf N:P of *K. obovate* and *A. marina* were higher than those of *S. apetala* and *A. corniculatum* under medium and low light conditions, which supported the GRH (Elser et al., 2003; Elser et al., 1996; Makino et al., 2003). Our results are consistent with those obtained in previous mangrove studies (Lovelock et al., 2007a). Different ecosystems have different plant C:N:P ratios. In this study, the mean leaf C:N:P ratio was 108:11:1 in the mangrove forest, lower than in previous studies conducted in aquatic ecosystems, for example, mean ratios of 700:35:1 for marine plants (Atkinson and Smith, 1983) and 291:17:1 for aquatic macrophytes (Xia et al., 2014). Our result was also lower than that in studies conducted in a Queensland mangrove forest and central Red Sea mangroves (Reef et al., 2010; Alongi, 2011; Almahasheer et al., 2016). The availability of nutrients to the mangrove forests is controlled by biotic and abiotic factors such as tidal levels, elevation, soil nutrients, plant species, and different stages of development. Leaf N:P is considered an indicator of the nutrient limitation of plants (Güsewell, 2004; Koerselman and Meuleman, 1996). Leaf $N{:}P < 14$ generally indicates N limitation and leaf $N{:}P > 16$ suggests P limitation, whereas leaf $14 < N{:}P < 16$ represents N and P co-limitation in wetland plants (Koerselman and Meuleman, 1996). In previous studies, mangrove stands were limited by P (Lovelock et al., 2006; Almahasheer et al., 2016), and others were limited by N (Feller et al., 2003b; Lovelock et al., 2007b; Naidoo, 2009). Both N and P limitation have been observed in the mangrove forests in Belize and Panama (Feller et al., 2003a; Lovelock et al., 2004). The mean leaf N:P of 11.04 in this study is lower than that of terrestrial plant species in China (Han et al., 2005) and global plants (Reich and Oleksyn, 2004) but higher than that of wetland plants in Germany (Minden and Kleyer, 2014). This result indicated that there was N limitation exists in the mangrove forests, consistent with previous studies (Feller et al., 2003b; Naidoo, 2009). The higher leaf P in mangrove plants was related to the low-lying stagnant water environment enriched with P.

5. Conclusions

Knowledge of the leaf stoichiometry of mangroves will help us understand the leaf nutrient status and growth of mangrove trees. In this study, there were significant negative scaling exponents of leaf C versus N, C versus P, but positive scaling exponents for leaf N vs. P in the four mangrove species. The scaling exponent of leaf N versus P was approximately 2/3 for all the species, and leaf N typically scaled approximately isometrically with P of *A. corniculatum* and *S. apetala*. Compared to leaf N and P, leaf C was relatively stable. Leaf nutrients (C, N, and P) were significantly affected by light. Both intraspecific and interspecific competition reduced the leaf N and P contents of *A. corniculatum* and *K. obovate* but increased the leaf N and P contents of *A. marina* and *S. apetala*. In particular, *S. apetala* had a significant impact on the growth of native species and further affected their leaf stoichiometry. In addition, there were significant correlations between the functional traits and leaf stoichiometry. In the mangrove ecosystem, species with a higher RGR had a higher leaf P content and lower N:P, supporting the GRH hypothesis. The leaf C:N:P ratio was 108:11:1 in this study, which is lower than that in wetlands and other terrestrial ecosystems. Leaf N:P was 11.04, indicating N limitation in the mangrove forests. The results generated in this systematic study improved our understanding of C, N, and P stoichiometry of the mangrove species and the impact of introduced species on the growth of native species, thus providing useful information for the restoration and management of mangrove forest ecosystems.

CRediT authorship contribution statement

Dehuang Zhu: Formal analysis, Writing - review & editing.**Dafeng Hui:**Writing - review & editing.**Mengqi Wang:**Project administration, Resources.**Qiong Yang:**Project administration, Resources.**Shixiao Yu:** Writing - review & editing.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.140301.

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