Different adaptive strategies of three mangrove species to nutrient enrichment

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Abstract Mangrove species are undergoing environmental changes from nutrient-poor to enrichment due to the large nutrient input. The potential difference in adaptive strategies between the slow- and fast-growing species may lead to great changes in species interaction and ecosystem stability. This study aims to test whether the slow-growing species Aegiceras corniculatum (L.) Blanco and Kandelia obovata Sheue, Liu & Yong sp. nov. are distinctly different from a fast-growing species Laguncularia racemosa (L.) Gaertn. f. in response to soil nutrient enrichment. With the increase of soil nutrients, L. racemosa shifted from a more conservative to a more acquisitive strategy. The potential causes included the increases in specific leaf area, nutrient resorption efficiency, and photosynthetic capacity as indicated by the increase of leaf δ¹³C and unchanged leaf succulence, as well as the relocation of photosynthetic products as indicated by the shift toward fast-growing at the cost of constructive and defense compounds. In contrast, A. corniculatum and K. obovata maintained conservative strategies at any soil nutrient levels with only a slight increase in growth. These findings implied that L. racemosa will be more competitive over the slow-growing species in nutrient-rich soils through altering adaptive strategies.

Keywords Aegiceras corniculatum · Acquisitive strategy · Conservative strategy · Fast-growing · Growth-defense trade-off · Kandelia obovata · Laguncularia racemosa · Slow-growing
Introduction

Subtropical mangrove forests in China are generally low in plant diversity. *Aegiceras corniculatum* (L.) Blanco and *Kandelia obovata* Sheue, H.Y. Liu & J.W.H. Yong often predominate. These species have developed nutrient conservative strategies to cope with nutrient-poor environment of intertidal zone (Reef et al. 2010), represented by a slow growth rate (Chapin III 1980) and other features such as a high rate of leaf nutrient resorption (Lin et al. 2010; Reef et al. 2010), high photosynthetic nitrogen-use efficiency (Feller et al. 2009), long leaf life span, and sclerophyllous leaf (Komiyama et al. 2008). In addition to these conservative species, there are some fast-growing mangrove species such as *Laguncularia racemosa* (L.) Gaertn. f. and *Sonneratia apetala* Buch.-Ham and they may exhibit a competitive advantage over those slow-growing species (Li et al. 2020).

Mangroves are undergoing dramatic environmental change, particularly in estuaries where eutrophication has been occurring as a consequence of rapid development of aquaculture industry (Zhang et al. 2015). In response to this new environment, mangrove species may exhibit an increase in growth rate, leaf surface area, photosynthetic carbon gain, N resorption rate, or leaf area index of canopy (Love-lock et al. 2007; Feller et al. 2015; Weaver and Armitage 2020). Although it is generally believed that the response of plants to environment is inconsistent, the comparison between species with contrast functional strategies is limited. The understanding of the differences in the response of fast- and slow-growing species to nutrient enrichment is a base to predict the stability of mangrove stands in future environment.

The trait-based analysis offers a quantitative and reliable framework to evaluate plant strategies in response to environmental changes (Reich et al. 2014; Funk et al. 2017). A global plant economic spectrum consistent with trait coordinate relationships indicates a slow-to-fast gradient in plant adaptive strategy (Wright et al. 2004; Reich 2014). At the leaf level, leaf N and P, specific leaf area (SLA), or leaf mass per area (LMA), photosynthetic assimilation capacity, and dark respiration rate are defined as fundamental economic traits (Wright et al. 2004). In general, a high leaf N content accompanied by a large SLA allows leaves to achieve a great rate of photosynthesis, resulting in a fast growth rate of plants, indicating a fast-growing or acquisitive strategy (Reich et al. 1999; Hikosaka and Shigeno 2009). By contrast, a small SLA and slow photosynthesis result in a slow growth rate, and these species are generally called slow-growing or conservative species (Roche et al. 2004; Wright et al. 2004; Wellstein et al. 2017). Accordingly, if a species changes its adaptive strategy from slow- to fast-type, its trait-based coordination will shift along the economic spectrum or alter its slope or intercept (Heberling and Fridley 2012).

The plant growth rate is also related to its defense strength, forming a growth-defense trade-off relationship (Lind et al. 2013; Züst and Agrawal 2017). Long-term living in a stressful environment, mangrove species are generally rich in defense compounds (Lovelock et al. 1992; McKee 1995b; Oku et al. 2003; Parida et al. 2004; Bartwal et al. 2013). For example, the total reactive phenolics in mangrove leaves are 11.1%–48.8% (Basak et al. 1998), much higher than those of terrestrial plants (< 10%; Barbehenn et al. 2005). If nutrient availability increases, plants may adjust nutrient allocation by increasing plant growth and reducing the concentrations of defense compounds. Such a trade-off could be an additional way to estimate the changes in plant adaptive strategy.

Here we compared three common mangrove species with contrast growth rates in subtropical China using the variation, coordination, and integrative analysis of plant traits to test whether the responses of *A. corniculatum, K. obovata*, and *L. racemosa* to nutrient enrichment are distinctly different.

Materials and methods

Experimental design and sampling

*Aegiceras corniculatum* and *K. obovata* are among the most widely distributed species in China, and typically grow slowly (Wang et al. 2001; Liao and Zhang
2014), while L. racemosa is generally growing fast in natural forests (McKee 1995a, b).

The soils used to cultivate saplings were collected from a mangrove stand near the city of Xiamen, China (0.69 ± 0.10 g N kg⁻¹ and 0.60 ± 0.05 g P kg⁻¹). The soils were mixed with sands at the ratio of 3:1 to reduce the nutrients to a level as low as in the pristine mangrove forests like Shankou Mangrove Reserve, where the nutrient concentration ranges between 0.24–0.58 g N kg⁻¹ and 0.12–0.19 g P kg⁻¹ (He et al. 2006). The soil nutrients in human-disturbed mangroves can be as high as 0.8–2.70 g N kg⁻¹ (Alongi et al. 2001) and 0.21–0.45 g P kg⁻¹ (Han and Gao 2013). Based on these backgrounds, we applied a slow-release fertilizer (N-P-K of 15: 9: 11) at 0, 111.08, 258.52, and 349.46 g on the well-mixed soils to generate a nutrient gradient that spanned the range from poor to rich. The slow-release fertilizer can continuously release nutrients until 12 months. The soil N in pots after two months were 0.40, 0.70, 1.00, and 1.50 g kg⁻¹; and the corresponding concentrations of P were 0.34, 0.65, 1.08, and 1.25 g kg⁻¹. Here the P has been above the natural levels, thereby we conducted the comparison in plant traits among soil nutrients based only on the N gradient. Salinity was maintained at about 15‰ by mixing fresh water with salt, and the new water was added each day to replenish water lost through transpiration. The pore water salinity was adjusted every week and the soil moisture was maintained at around 85%.

Two-year-old saplings were provided by Quanzhou Mangrove Nursery where the saplings were cultivated with hypocotyls. The saplings of comparable size were planted in square pots and grown at natural photoperiod and light intensities on a land enclosed with a stainless fence. The pots were arranged in the center of the cultivation house to minimize the heterogeneity of light intensity. Fast- and slow-growing species were planted separately with four saplings in each pot. Five replicates (pots) were set up for each treatment of each species. To eliminate the interference from pot size (Boot and Mensink 1990), we used large containers (40×40×40 cm) according to the suggestion by Poorter et al. (2012) that plant dry biomass does not exceed 1 g L⁻¹.

After 2 years of cultivation, tree height was determined from the soil surface to the top branches of the canopy. All leaves were freeze-dried to a constant weight after harvested and cleaned. Leaf N and P reflect the allocation of available nutrients to the photosynthetic tissues, leaf C represents the investment in structural tissues (Poorter and Bergkotte 1992), SLA is defined as the light-capturing surface area per unit of dry biomass (Poorter et al. 2009), δ¹³C indicates plant water use efficiency (Farquhar et al. 1989), and total leaf biomass (the dry matter of all leaves of each individual) are strongly associated with plant growth (Violle et al. 2009). The average leaf biomass of each pot of each species represented one replicate. Around 10 to 20 healthy sun-lit leaves of each individual were selected for trait analysis and the average value of all leaves in each pot of each species represented the trait value of each replicate.

Trait measurement

The fine powders of leaf samples were determined for element concentrations after ground and sieved. Leaf C and N were analyzed with a VarioMax Elemental Analyzer (FIA, Elementar, Hanau, Germany) and P with an inductively coupled plasma optical emission spectrometer (ICP-OES, Optima 5300 DV, Perkin Elmer, Waltham, MA, USA). The SLA was calculated as the leaf area per mass (cm² g⁻¹). Leaf area was measured with a YMJ-B Portable Leaf-Area Analyzer (Zhejiang Top Cloud-Agri Technology). Leaf δ¹³C was analyzed in the isotope analysis lab of Tsinghua University. Leaf nitrogen resorption efficiency (NRE) is defined as the percentage of N in senescent leaves and in green mature leaves (Aerts 1996). Leaf succulence is the water content on a leaf area basis. Due to the lack of adequate leaves of K. obovata (usually does not grow well when cultivated in the pot for over two years), leaf δ¹³C, NRE, and succulence were analyzed only for L. racemosa and A. corniculatum. The soil in pots was determined for the nutrient concentrations with an FIA and an ICP-OES following the method for leaves.

The analysis procedures of defense chemical traits were conducted using the method of Lin et al. (2007). Briefly, a dry sample of 200 μg was ultrasonically extracted with 4 ml of MCW (methanol: chloroform: water = 12:5:1) for 1 h, then centrifuged at 5000 rpm for 15 min. The supernatant was collected and then mixed with 1/4 volume of deionized water and 1/6 volume of chloroform for liquid separation. The nonpolar phase and the polar phase were used for the determination of soluble phenol,
soluble sugar, and lipid content with the Folin-Ciocalteu method (Ainsworth and Gillespie 2007), the dinitrosalicylic acid method (Teixeira et al. 2012), and the gravimetric method (Inouye and Lotufo 2006), respectively. The remaining precipitate was washed with methanol, water, and MCW extract consecutively, then dried at 60 °C. After extracted with hydrochloric acid (10 ml of 2 M), the supernatant was collected. The remaining precipitate was washed with hot water and then dried at 60 °C after uric acid (2 ml of 72%) was added. The remaining precipitate was added with 10 ml of water standing for 24 h after standing at room temperature for 3 h. The supernatant was collected by centrifugation at 5000 rpm for 15 min. The remaining precipitate was washed with hot water three times and dried at 60 °C before being weighed. The cellulose content was calculated by measuring the reduced sugar content in the supernatant with the dinitrosalicylic acid method, with the difference in the weight of precipitate as verification again. The remaining precipitate was burned at 550 °C for 2 h in a muffle furnace. The ash was weighed after cooling to room temperature. The lignin content was calculated by the difference between the remaining precipitate and the ash content.

Statistical analysis

To unify the expression, soil N concentrations of 0.40, 0.70, 1.00, and 1.50 g kg⁻¹ were used to represent level 1, 2, 3, and 4 of soil nutrient gradients. All data were analyzed with SPSS 16.0 for Windows. To detect the variation of plant traits with soil nutrients and the differences among species, a two-way ANOVA was conducted firstly with soil nutrients and species as fixed factors. A further one-way ANOVA with Tukey as a Post-hoc comparing method was conducted separately among species and among soil nutrient levels to identify which particular differences were significant. An independent t-test was conducted between A. corniculatum and L. racemosa for NRE, leaf P, succulence, and δ¹³C. Trait coordination was identified with correlation analysis following the method of Wright et al. (2004). Here we focused on the co-variation of SLA with the other traits, then the difference in the response strategy among species was indicated by a shift of trait co-variation along the regression line or a difference in the slope. Using the mean of nearby points method, we built a new replacement for all the missing data (or outliers) to meet the requirement of the principal component analysis (PCA). PCA was conducted with the rotation by Varimax to identify the shift of the growth-defense spectrum. All traits were analyzed with

![Fig. 1 Variation of leaf traits across soil nutrient gradients (Means ± S.E.). Closed circle, Aegiceras corniculatum; Closed triangle, Kandelia obovata; Open square, Laguncularia racemosa. Missing data are either missing or removed outliers.](image-url)
PCA excluding NRE, succulence, and δ^{13}C due to the lack of the corresponding data of *K. obovata*. The lignin was also excluded due to its very low loading value.

**Results**

**Trait variation**

Generally, soil nutrient enrichment increased the N, P, and SLA of leaves of all the tested species, but there was only a slight increase in these traits for *K. obovata* (Fig. 1B, C, D). In addition, *L. racemosa* showed a substantial increase in total leaf biomass, tree height, and leaf δ^{13}C (Fig. 1E, F, I) and a decrease in leaf C, cellulose, total phenolics, and soluble sugar (Fig. 1A, 2A, B, C). However, a profound change in most traits occurred when soil N increased above 0.70 g kg^{-1} (the 2nd level). The statistical results are presented in Supplementary Table 1.

There was no difference in most traits between *A. corniculatum* and *K. obovata* including tree height, SLA, leaf C, total phenolics, soluble sugar, and lignin at any soil nutrient levels (Fig. 1A, D, F, 2B, C, D). In addition, *L. racemosa* had an overall greater value in total leaf biomass, tree height, NRE, succulence, and leaf δ^{13}C (Fig. 1E-I), and a lower leaf C, N, cellulose, and lipid than *A. corniculatum* and *K. obovata* (Fig. 1A, B, 2A, E). The differences in most traits became larger when soil N was above 0.70 g kg^{-1} (the 2nd level). The statistical results are presented in Supplementary Tables 2, 3.

**Trait coordination**

The slow-growing mangrove species *A. corniculatum* and *K. obovata* did not show significant trait correlations for almost all the tested traits except SLA vs. NRE and SLA vs. total leaf biomass of *A. corniculatum*. In contrast, the fast-growing species *L. racemosa* showed significant trait correlations for all the tested traits. The statistical results are presented in Supplementary Table 4. Because there was no significant difference in SLA among species, the differences in trait coordination between *A. corniculatum* and *L. racemosa* were only detected in the slope with *L. racemosa*, with a deeper slope of SLA-C, SLA-tree height, SLA-δ^{13}C, and SLA-NRE than *A. corniculatum* (Fig. 3A, E, F, H).

**Integrative response strategy**

Two independent axes of PCA analysis described ca. 68% of the total variation of all the tested traits with axis 1 and 2 accounting for ca. 38% and 29%, respectively. The first axis was mainly determined by leaf C, tree height, and leaf total biomass, revealing a trade-off between growth and structural investment; and the second axis was mainly composed of two clusters with SLA, leaf P, and leaf N on one end and cellulose, total phenolics, and soluble sugar on the other end, indicating a trade-off between nutrient accumulation and defense investment (Fig. 4). With soil nutrients increased, *L. racemosa* showed a clear shift to a fast-growing strategy at the cost of C and defense investment, while *A. corniculatum* and *K. obovata* exhibited increases in nutrient accumulation in leaves but fewer changes in growth and C investment (Fig. 4).
Discussion

The fast-growing feature of *L. racemosa* and the slow-growing feature of *A. corniculatum* and *K. obovata* were confirmed by tree height and leaf total biomass, but the difference in growth among species was much less when soil nutrient was poor (0.40 g N kg\(^{-1}\) and 0.34 g P kg\(^{-1}\)). This is in agreement with another comparative result among three mangrove species although those species are not distinctly different in original growth performance, where the different performance in relative growth rate, leaf production, and branch growth, as well as quantity and composition of secondary compounds among species, was only detected at higher nutrient or light availability. Such differences were greatly minimized at lower nutrient or light levels (McKee 1995a). These results suggest that the soil nutrient conditions should be considered when identifying the difference in adaptive strategies among species.

We found that the three mangrove species showed different responses to soil nutrient enrichment. The fast-growing species *L. racemosa* exhibited more plastic responses compared with the slow-growing species *A. corniculatum* and *K. obovata* in general.

*Laguncularia racemosa* adjusted from a more conservative to a more acquisitive strategy when soil nutrients increased from poor to rich. The increase of plant growth might be attributed to an increases in nutrient uptake by roots, nutrient resorption by leaves, photosynthetic capacity, or relocation of photosynthetic products. We had no direct evidence of increased nutrient uptake and CO\(_2\) assimilation, but our results of the increased NRE, SLA, and leaf δ\(^{13}\)C indicated a potentially improved photosynthesis. A larger SLA could be more efficient in a light interception for photosynthesis (Dijkstra and Lambers 1989). The increases in soil nutrients and leaf NRE could promote photosynthesis by providing more nutrients for ribulose1,5-bisphosphate (RuBP) carboxylation (Evans 1989). Theoretically, the increase of the carboxylation capacity and/or the decrease of the ratio of internal to external partial pressure of CO\(_2\) of leaves can lead to the increase of leaf δ\(^{13}\)C (Farquhar et al. 1989). In our study, the increase of leaf δ\(^{13}\)C (less negative) was more likely derived from the increase of the carboxylation capacity, because the unchanged leaf succulence indicated a constant internal conductance to CO\(_2\) diffusion (Maxwell et al. 1997) and an increase of carboxylation capacity could cause a decrease in \(^{13}\)C fractionation during consuming internal CO\(_2\) (Cordell et al. 1999). Further evidence came from the observation that nutrient enrichment had a significant effect on maximum rates of photosynthetic electron transport in the mangroves in Florida, particularly in the N-limited stand (Feller et al. 2003). Moreover, the least-cost theory, which states that the investment in photosynthetic capacity and water transport is optimized, means that a given photosynthetic rate is achieved at the lowest cost (Wright et al. 2003; Prentice et al. 2014). Improving the carboxylation capacity (consuming more N) of leaves instead of regulating stomatal conductance may be an effective

![Fig. 3](image-url)
way to enhance photosynthesis when plants have sufficient N supply but limited stomatal opening.

The substantial increase in the growth of *L. racemosa* was accompanied by a remarkable decline in leaf C, cellulose, total phenolics, and soluble sugar, indicating that the fast-growing was at the expense of constructive and defense investments. Such changes in ecological strategy have been also found in other cases, such as the herb species *Arabidopsis thaliana*, which exhibits a latitudinal gradient of ecological strategy with an increase of stress tolerance in higher latitudes (colder climates) at the expense of seed production (Vasseur et al. 2018).

Although the nutrient status was potentially improved, the nutrients did not accumulate substantially in the leaves of *L. racemosa* (a lower leaf N than other two species). That is, *L. racemosa* adopted a strategy of accelerating growth rather than nutrient accumulation. Similarly, plant species in a forest in South Africa increased leaf size (diameter of the largest circle within the leaf), SLA, and leaf area/stem length, but decreased foliar N and K with increasing nutrient availability (Power et al. 2019). This might be due to the enhanced consumption of N by the improved photosynthesis.

By contrast, the slow-growing species *A. corniculatum* and *K. obovata* exhibited a relative “inert” response to soil nutrients. This was reflected firstly by unchanged NRE, succulence, and δ¹³C, which was consistent with our previous observation in *A. corniculatum* (Wei et al. 2020). It was also reflected by a much less increase in tree height and leaf total biomass, and a less reduction of leaf C, cellulose, total phenolics, and soluble sugar than *L. racemosa*. This implied a weak growth-defense trade-off of *A. corniculatum* and *K. obovata*. Such inert response to soil nutrients was also found in other mangrove species. For example, four of five species, i.e., *Heritiera fomes* Buch.-Ham., *Xylocarpus mekongensis* Pierre, *Ceriops decandra* (Griff.) Ding Hou and *Avicennia officinalis* L., showed no response in height growth after three months of fertilization, but this study did not provide any information regarding their differences in adaptive strategies (Miah and Moula 2019).

A recent study confirmed that intraspecific correlations between growth and defense varied within and among populations (Hahn et al. 2021). The performance of *A. corniculatum* and *K. obovata* in our study provides further evidence of the neutral correlations between growth and defense traits.

Although there was a relative greater increase in leaf N and P resulted in a strategy shift from defense to nutrient accumulation, the extent of the shift was much less than the performance of *L. racemosa*. The accumulation of nutrients in leaves was also observed in the dry-site species in Australia, where the species showed a greater proportional increase in N than in photosynthetic rate (Wright et al. 2003). The underlying mechanisms have not been revealed although some possible hypotheses have been proposed such as exploiting a higher light (Roderick et al. 2000) or permitting a lower stomatal conductance to limit water loss through transpiration (Wright et al. 2003).
In addition, *L. racemosa* is originally distributed throughout the Americas, Caribbean, and the West Coast of Africa (Sereneski-Lima et al. 2021) and was introduced to China in 1999 for coastal restoration owing to its fast-growing feature (Chen et al. 2013). Although it is an alien species, *L. racemosa* can be living with native species stably (Huang and Lu 2019) and was not defined as an invasive species (Lu and Liao 2019). Meta-analysis results from 362 individual traits of 75 species pairs showed that invasive species are generally more plastic in their response to greater resource availability than non-invasive alien species (Davidson et al. 2011). Therefore, our results represented the differences between slow-growing and fast-growing species.

**Conclusion**

Our study confirmed that the two slow-growing species *A. corniculatum* and *K. obovata* differed from the intrinsic fast-growing species *L. racemosa* in response to soil nutrient enrichment. All species showed shorter tree height and higher defense compounds in nutrient-poor soils, but in nutrient-rich soils, *L. racemosa* exhibited a more acquisitive strategy than *A. corniculatum* and *K. obovata* which maintained conservative strategies. The close correlation between SLA and leaf $\delta^{13}C$ implied a potential mechanism involved in the adjustment of photosynthetic capacity by *L. racemosa*, which could be a key theory to explain the distinction in adaptive strategy between slow- and fast-growing mangrove species. Such contrast responses could lead to an alteration of ecosystem stability when resource availability changes, particularly for subtropical mangrove forests with low species diversity.

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**Author contributions** LW conceived and designed the experiments. HH, MYB, and YW analyzed the data. LW wrote the manuscript. All the authors contributed to the final version of this manuscript.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Conflict of interest** The authors declare no competing financial interests.

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