

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 input of external nutrients. 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 *Laguncularia racemosa* (L.) Gaertn. f. in response to soil nutrient enrichment. With the increase of soil nutrients, *L. racemosa* shifted from more conservative to more acquisitive strategy, which might be attributed to the increases in specific leaf area, nutrient resorption efficiency and photosynthesis capacity (indicated by the increase of leaf $\delta^{13}\text{C}$ and unchanged leaf succulence), as well as the relocation of photosynthetic products (indicated by the shift towards 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 other species in nutrient-rich soils.

Additional Remark Abstract

- The explicit purpose of the study

Previous studies generally overlooked the potential difference in response plasticity between functional types of plants to environmental changes. This study aimed to compare the response of the slow- and fast-growing mangrove species to nutrient enrichment.

- The location of the study

This study was carried out in a glasshouse in the campus of the Institute of Urban Environment, Chinese Academy of Sciences, Xiamen, China.

- A brief summary of the methodology used

The two-year saplings of three mangrove species were planted in pots under a range of nutrient levels. The adaptive strategy comparison was based on the variation, coordination and integrative analysis of plant traits.

- Key results

The slow-growing mangrove species maintained conservative strategies, while the intrinsic fast-growing mangrove species shifted from more conservative to more acquisitive strategy with the increase of soil nutrients.

- Main point/s of significance

This study found an overlooked ecological phenomenon that the fast-growing species is more plastic in response to soil nutrient enrichment than the slow-growing species, and their difference in adaptation strategies is enhanced with soil nutrients. These findings suggest that *L. racemosa* is more competitive in nutrient-rich soils.

1 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 are often predominated. These species have developed nutrient conservative strategies in adaptive to the nutrient-poor environments of the intertidal zone (Reef et al. 2010), represented by slow growth rate (Chapin III 1980) and other features such as 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 (Komiya et al. 2008) etc. In addition to these conservative species, some fast-growing mangrove species such as *Laguncularia racemosa* (L.) Gaertn. f. and *Sonneratia apetala* Buch.-Ham also emerged in the mangrove forests in China and they may exhibit a competitive advantage over those slow-growing species (Li et al. 2020).

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

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 nitrogen (N) and phosphorus (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 with a large SLA allows leaves to achieve a great rate of photosynthesis, resulting in a fast growth rate of plants, involved in 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).

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 increase, plants may adjust nutrient allocation by increasing plant growth and reducing the concentrations of defense compounds. Such trade-off could be an additional way to estimate the changes of plant adaptive strategy.

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

2 Materials And Methods

2.1 Experimental design

Of these species, *A. corniculatum* and *K. obovata* are among the most widely distributed species in China, and typically growing 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. Due to the high nutrient concentrations in the initial soils ($0.69 \text{ g kg}^{-1} \pm 0.10 \text{ g kg}^{-1}$ of N and $0.60 \text{ g kg}^{-1} \pm 0.05 \text{ g kg}^{-1}$ of P), we mixed the soils with sands at the ratio of 3: 1 and homogenized them to reduce the nutrients to the level as low as in the pristine mangrove forests like Shankou Mangrove Reserve, where the N ranges 0.24 g kg^{-1} - 0.58 g kg^{-1} , and P 0.12 g kg^{-1} - 0.19 g kg^{-1} (He et al. 2006). The soil nutrients in human-disturbed mangroves can be as high as 0.8 g kg^{-1} - 2.70 g kg^{-1} of N (Alongi et al. 2001) and 0.21 g kg^{-1} - 0.45 g kg^{-1} of P (Han and Gao 2013). Based on these background, we applied a slow-release fertilizer (N-P-K of 15: 9: 11, 12 months) at 0 g, 111.08 g, 258.52 g, and 349.46 g on the well-mixed soils to generate a nutrient gradient that spanning the range from poor to rich. The soil N in pots after two months were 0.40 g kg^{-1} , 0.70 g kg^{-1} , 1.00 g kg^{-1} , and 1.50 g kg^{-1} ; and the corresponding concentrations of P were 0.34 g kg^{-1} , 0.65 g kg^{-1} , 1.08 g kg^{-1} , and 1.25 g kg^{-1} , respectively. The P here has been above the natural levels, thereby we conducted the comparison in plant traits among soil nutrients based only on N gradient. Salinity was maintained at $\sim 15\text{‰}$ by mixing freshwater with salt, and the new water added each day to replenish water lost through transpiration.

The two-year-old saplings were provided by Quanzhou Mangrove Nursery where the saplings were cultivated with hypocotyls. The saplings with comparable size were planted in square pots and grown at natural photoperiod and light intensities in 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 biomass does not exceed 1 g L⁻¹.

2.2 Sampling and measurement

After 2 years of cultivation, tree height was determined from the soil surface to the top branches of the canopy. All leaves of each individual were freeze-dried to a constant weight after been 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), $\delta^{13}\text{C}$ 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 was obtained to represent the trait value of each replicate. After been ground and sieved, the fine powders of leaf samples were determined for element concentrations in leaves. 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). 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 $\delta^{13}\text{C}$ was analyzed in the isotope analysis lab of Tsinghua University. Leaf nitrogen resorption efficiency (NRE) is defined as the percent 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 pot over two years), leaf $\delta^{13}\text{C}$, NRE and succulence were analyzed only for *L. racemosa* and *A. corniculatum*. The soils in pots were determined the nutrient concentrations with a FIA and an ICP-OES respectively following the method for leaves.

The analysis procedures of defense chemical traits were followed by the method of Lin et al. (2007). Briefly, 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 supernatants were 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, the dinitrosalicylic acid method, and the gravimetric method, respectively. The remaining precipitates were washed with methanol, water, and MCW extract consecutively, then dried at 60°C. After been extracted with hydrochloric acid (10 ml of 2 M), the supernatant was collected. The remaining precipitates were washed with hot water and then dried at 60°C after uric acid (2 ml of 72%) added. The remaining precipitates were added with 10 ml of water standing for 24h after standing at room temperature for 3 h. The supernatant was collected by centrifugation at 5000 rpm for 15 min. The remaining precipitates were 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 precipitates as verification again. The remaining precipitates were burned at 550°C for 2 h in a muffle furnace. After been cooling to room temperature, the ash was weighed and the lignin content was calculated.

2.3 Statistical analysis

To unify the expression, soil N concentrations of 0.40 g kg⁻¹, 0.70 g kg⁻¹, 1.00 g kg⁻¹, and 1.50 g kg⁻¹ were used to represent level 1, level 2, level 3, and level 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 Turkey as Post-hoc comparing method was conducted separately among species and among soil nutrient levels to identify which particular differences are significant. An independent t-test was conducted between *A. corniculatum* and *L. racemosa* for NRE, leaf P, succulence, and $\delta^{13}\text{C}$. Trait coordination was identified with the 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 of the slope. By using mean of nearby points method, we build 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 growth-defense spectrum. All traits analyzed with PCA excluded NRE, succulence, and $\delta^{13}\text{C}$ due to the lack of the corresponding data of *K. obovata*, and the lipid also excluded due to its very low loading value.

3 Results

3.1 The extent of intraspecific trait variation

Generally, soil nutrient enrichment increased the leaf N, P, and SLA of all the tested species despite only a slight increase of these traits for *K. obovata* (Fig. 1b, c, d). In addition, *L. racemosa* also showed a substantial increase in total leaf biomass, tree height, and leaf $\delta^{13}\text{C}$ (Fig. 1e, f, i) and a decrease in leaf C, cellulose, total phenolic, and soluble sugar (Fig. 1a, 2a, b, c). But a profound change of most traits occurred when soil N increased to above 0.70 g kg⁻¹ (the 2nd level). The statistical results are presented in Supplement Table 1.

There was no difference in most traits between *A. corniculatum* and *K. obovata* including tree height, SLA, leaf C, total phenolic, soluble sugar and lignin at any soil nutrient levels (Fig. 1a, d, f, 2b, c, d). While *L. racemosa* had an overall greater value in total leaf biomass, tree height, NRE, succulence and leaf $\delta^{13}\text{C}$ (Fig. 1e-i), and a lower leaf C, N, cellulose and lipid than *A. corniculatum* and *K. obovata* (Fig. 1a, b, 2a, e). The statistical results are presented in Supplement Table 2, 3.

3.2 Trait coordination

The slow-growing mangrove species *A. corniculatum* and *K. obovata* did not show significant trait correlations for most economic traits except SLA vs. leaf N and SLA vs. total leaf biomass of *A. corniculatum* as well as SLA vs. leaf N of *K. obovata*. In contrast, the fast-growing species *L. racemosa* showed significant trait correlations for all the tested traits. The statistical results are presented in Supplement 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* having the deeper slopes of SLA-C, SLA-tree height, SLA- $\delta^{13}\text{C}$, and SLA-NRE than *A. corniculatum* (Fig. 3a, e, f, h).

3.3 Integrative response strategy

Two independent axes described ca. 68% of the total variation of all the tested traits with the Axis 1 and 2 accounted for ca. 38% and 29%, respectively. The first axis was mainly determined by leaf C, tree height, and leaf total biomass, revealed a trade-off between growth and structural investment; and the second axis was mainly composed of two clusters with SLA, leaf P and N on one end and cellulose, total phenolics and soluble sugar on the other end, indicated a trade-off between nutrient accumulation and defense investment (Fig. 4). With soil nutrient increased, *L. racemosa* showed a clear shift to 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 less changes in growth and C investment (Fig. 4).

4 Discussions

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 kg^{-1} of N and 0.34 g kg^{-1} of P). This is in agreement with another comparative results 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, but 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 identify 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 slow-growing species *A. corniculatum* and *K. obovata* in general.

Laguncularia racemosa adjusted from more conservative to more acquisitive strategy when soil nutrients increased from poor to rich. The increase of plant growth might be attributed to the increases in nutrient uptake by roots, nutrient resorption by leaves, and photosynthetic capacity, and the 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 $\delta^{13}\text{C}$ indicated a potentially improved photosynthesis. A larger SLA could be more efficient in light interception for photosynthesis (Dijkstra and Lambers 1989). The increases of 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 $\delta^{13}\text{C}$ (Farquhar et al. 1989). In our study, the increase of leaf $\delta^{13}\text{C}$ (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). A 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, based on the least-cost theory, which states that the investment in photosynthetic capacity and water transport is optimized, meaning 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 way to enhance photosynthesis when plants had 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 of ecological strategy have been also found in other cases, such as a herb species *Arabidopsis thaliana* exhibited a latitudinal gradient of ecological strategy with an increase of stress tolerance in higher latitude (colder climates) at the expense of seed production (Vasseur et al. 2018).

Although the nutrient status was potentially improved, the nutrients did not accumulated substantially in the leaves (a lower leaf N than the other species). That is, *L. racemosa* adopted a strategy by 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 potassium 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 nutrient. This was reflected firstly by unchanged NRE, succulence and $\delta^{13}\text{C}$, 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 provide 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, but 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 unrevealed 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 invasive species (Lu and Liao 2019). Based on the meta-analysis results from measuring 362 individual traits of 75 species pairs that invasive species are nearly always more plastic in their response to greater resource availability than non-invasive alien species (Davidson et al. 2011). Therefore, our results can represent the differences between slow-growing and fast-growing species.

5 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 at nutrient-poor soils, but in nutrient-rich soils, *L. racemosa* exhibited more acquisitive strategy and *A. corniculatum* and *K. obovata* maintained conservative strategies. The close correlation between SLA and leaf $\delta^{13}\text{C}$ implied a potential mechanism involved in the adjustment of photosynthesis 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 changed, particularly for subtropical mangrove forests with low species diversity.

Declarations

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Conflicts of interest/Competing interests

The authors declare no competing financial interests.

Availability of data and material

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Authors' 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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Figures

Figure 1

Variation of leaf traits across soil nutrient gradients (Mean $\pm$ S.E.). Closed circle, *Aegiceras corniculatum*; Closed triangle, *Kandelia obovata*; Open square, *Laguncularia racemosa*. Missing data are either missing or removed outliers.

Figure 2

Variation of leaf chemical traits across soil nutrient gradients (Mean $\pm$ S.E.). The symbols are the same as above.

Figure 3

The correlation between SLA and the other traits (log-transformed data). The symbols are the same as above. The lines refer to the lineal regression results.

Figure 4

The principal component analysis (PCA) for the traits of the three species at different soil nutrient levels. Closed red, *Aegiceras corniculatum*; Closed dark red, *Kandelia obovata*; and Open green, *Laguncularia racemosa*. Circle, Triangle, Square, and Diamond are representing the trait values across soil nutrient gradient.

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