

Different Adaptive Strategies of Three Mangrove Species to Nutrient Enrichment: Revealed by Trait-based Analysis

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Abstract

Mangrove species are undergoing environmental changes from nutrient-poor to nutrient 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 functioning. This study aims to test whether the response strategies to soil nutrient availability differ between the slow- and fast-growing mangrove species. The comparison was carried out among three common mangrove species including two slow-growing species *Aegiceras corniculata* and *Kandelia obovata*, and one intrinsic fast-growing species *Laguncularia racemosa*. All tested species showed conservative strategies (such as slow-growing and high concentrations of leaf tolerance/resistance traits) when living in the nutrient-poor soils. But when soil nutrient increased, *L. racemosa* shifted to a fast-growing strategy, accompanied by a substantial reduction of tolerance traits including the concentrations of carbon, cellulose, total phenolics, and soluble sugar in leaves. In contrast, *A. corniculatum* and *K. obovata* maintained still conservative strategies even under nutrient enrichment. All the species increased leaf nitrogen, phosphorus, lipid, lignin and specific leaf area (SLA) with soil nutrient availability, but *L. racemosa* showed a greater nutrient acquisition capacity indicated by a steeper regression line of SLA vs. nutrient resorption efficiency than *A. corniculatum*. Further, the steeper regression line of SLA vs. leaf $\delta^{13}\text{C}$ of *L. racemosa* indicated a higher water use efficiency than *A. corniculatum*. The dependence of the adaptive strategies of these species to soil nutrient status improved the standing of plant-plant interactions at different soil nutrient status.

Additional Remark Abstract

- The explicit purpose of the study

Previous studies generally overlooked the comparison of the responses of the different functional types of plants to environmental changes. This study aimed to compare the response of the slow- and fast-growing mangrove species to nutrient availability.

- 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

A simulation experiment was applied. The saplings of three mangrove species were planted in soils with a gradient of nutrient levels. The adaptive strategy comparison was based on the trait analysis at leaf and tree levels.

- Key results

The slow-growing mangrove species maintained conservative strategies, while the intrinsic fast-growing mangrove species shifted its adaptive strategies from a conservative strategy in the nutrient-poor soils to a fast-growing strategy in the nutrient-rich soils.

- Main point/s of significance

This study found an overlooked ecological phenomenon that *Laguncularia racemose* shifted its adaptive strategy with soil nutrient status, and relatively, the other two species maintained still conservative strategies even when soil nutrient increased. These findings improved our standing of the interactions between the coexisting species. In a multiple-species community, a stronger competitive capacity of *Laguncularia racemose* compared with *Aegiceras corniculata* and *Kandelia obovate* will be only shown under a certain soil condition.

Introduction

Subtropical mangrove forests are generally low in plant diversity with only a few species dominated. Mangrove species often form conservative strategies in adaptive to a nutrient-poor, saline, anoxic environment. These strategies include slow growth rate (Chapin III 1980), high leaf nutrient resorption rate (Lin et al. 2010; Reef et al. 2010), high photosynthetic nitrogen-use efficiency (Feller et al. 2009), long leaf life span and sclerophyllous (Komiyama et al. 2008), etc.. However, mangroves are now undergoing dramatic environmental changes particularly in estuaries where eutrophication has been occurring as a consequence of the rapid development of aquaculture industry (Zhang et al. 2015). So now it is urgent to find out how these slow-growing mangrove species respond to nutrient enrichment, and whether their responses are different from those fast-growing species.

The trait-based methodology offers a method to quantitatively estimate the responses of plants to environmental changes (Funk et al. 2017). Comparatively, the trait integrative analysis might be more related to plant performance than single-trait analysis (Rosado and de Mattos 2017; Guo et al. 2018; da Silveira Pontes et al. 2010). Additionally, the trait coordinate analysis has been becoming an alternative method to detect plant ecological strategy along a slow-to-fast economic spectrum (Wright et al. 2004; Reich 2014). In general, high nitrogen (N) accompanied with large SLA allows the leaves to achieve a great rate of photosynthesis, resulting in a fast growth rate of plants (Reich et al. 1999; Hikosaka and Shigeno 2009). In contrast, a small SLA and slow photosynthesis result in a low growth rate, but which are advantageous in low resource conditions or harsh environments (Roche et al. 2004; Wright et al. 2004; Wellstein et al. 2017).

Plant traits are mostly easy to measure and often have a tight link to environment factors, which therefore have triggered interest to explore new phenotypic traits, such as the surface area, density, toughness, and carbon stable isotope abundance $\delta^{13}\text{C}$ of leaves (Tanaka-Oda et al. 2010; Chauvin et al. 2018; Moles 2018). Mangrove plants are generally rich in phenolic compounds with about 20% of the carbon (C) fixed by photosynthesis channeling into the phenylpropanoid (Asha et al. 2012). The total

reactive phenolics in mangrove leaves vary from 11.1% to 48.8% (Basak et al. 1998), much higher than those of terrestrial plants. For instance, sugar maple (*Acer saccharum* Marshall) and red oak (*Quercus rubra*) contain total phenolics < 10% (Barbehenn et al. 2005). Phenolics and other tolerance-related compounds such as lipid and soluble sugar are accumulated when living in stressful environments (Lovelock et al. 1992; McKee 1995b; Oku et al. 2003; Parida et al. 2004; Bartwal et al. 2013). However, these chemical traits are rarely taken account of in plant response studies (Chauvin et al. 2018).

In this study, we compared both the common functional traits and the tolerance traits among three common mangrove species to determine their difference in adaptive strategies to nutrient enrichment.

Materials And Methods

2.1 Experimental design

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

The soils used to plant 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 concentrations to the level as low as in the pristine mangrove forests like Shankou Mangrove Reserve, where the N ranges $0.24 \text{ g kg}^{-1} - 0.58 \text{ g kg}^{-1}$, and P $0.12 \text{ g kg}^{-1} - 0.19 \text{ g kg}^{-1}$ (He et al. 2006). The soil nutrient concentrations in human-disturbed mangroves can be as high as $0.8 \text{ g kg}^{-1} - 2.70 \text{ g kg}^{-1}$ of N (Alongi et al. 2001) and $0.21 \text{ g kg}^{-1} - 0.45 \text{ g kg}^{-1}$ of P (Han and Gao 2013). Based on the ranges mentioned above, we applied a slow-release fertilizer at 0 g, 111.08 g, 258.52 g, and 349.46 g on the well-mixed soils to generate a nutrient gradient spanning the range of nutrient-poor to nutrient-rich. This fertilizer contains N, P, and K with a mass ratio of 15: 9: 11, and the nutrient release can last 12 months. Two month later, we measured the soil nutrient concentrations in pots: the N 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} . The P in here has been above the natural concentrations, and only the N covered the range from nutrient poor to rich levels. Salinity was maintained at $\sim 15\text{‰}$ by mixing freshwater with salt. Then the new water was 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 an enclosed land 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 mangrove 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 to determine leaf traits. 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 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*, 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 a ICP-OES respectively following the method for leaves.

The analysis procedures of tolerance-related chemical traits were followed by the method of Lin et al. (2007). Briefly, 200 μg of dry samples were ultrasonically extracted with 4 ml of MCW (methanol: chloroform: water = 12:5:1) for 1 h, then centrifuged at 5000 rpm for 15 min to collect the supernatants. The supernatants were 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, respectively. Specifically, the soluble phenol content was determined by the Folin-Ciocalteu method, the soluble sugar was determined by the dinitrosalicylic acid method, and the lipid content was determined by the gravimetric method. 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) and 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%) was added. The remaining precipitates were standing at room temperature for 3 h, and then were added with 10 ml of water standing for another 24 h. After the extraction, 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 by 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

All data were examined for normality (with Skewness and Kurtosis) and homogeneity (with Levene's test) in SPSS 16.0 for Windows. To analyze the variation of traits with soil nutrient availability, the interactions of traits between soil nutrient levels and trait values were tested by multivariate generalized linear models. The one-way ANOVA was used to compare the difference in traits among the treatments for each species (LSD or Games-Howell was used for Post-hoc comparison). Following the integrative analysis, we conducted principal component analysis (PCA; pair-wise correlation analyses) with all the tested traits. The correlation analysis was used to examine the pairwise relationships between traits. To unify the expression, we used the N concentrations of 0.40 g kg⁻¹, 0.70 g kg⁻¹, 1.00 g kg⁻¹, and 1.50 g kg⁻¹ to represent level 1, level 2, level 3, and level 4 of soil nutrient gradients.

Results

The adaptive strategies were indicated by the traits at both the leaf and tree levels. The conservative strategy is presented by the slow-growing and high in tolerance traits. *A. corniculatum* and *K. obovata* maintained conservative strategy even the soil N concentration increased as high as 1.50 g kg⁻¹, while *L. racemosa* shifted from slow- to fast-growing along the soil nutrient gradient.

3.1 Variation of traits

There was no difference in tree height between *A. corniculatum* and *K. obovata* (df = 6, $p = 0.981$), but *L. racemosa* was about two times taller than *A. corniculatum* and *K. obovata* (df = 6, $p < 0.001$) when soil nutrient increased. Soil nutrient concentration was not related to leaf N (df = 6, $p = 0.149$), leaf P (df = 6, $p = 0.992$), and SLA (df = 6, $p = 0.992$), but significantly related to leaf C, leaf biomass, and tree height (df = 6, $p < 0.001$). There was a greater total leaf biomass (df = 2, $p < 0.001$) but lower leaf C (df = 2, $p < 0.001$) and leaf N (df = 2, $p < 0.001$) of *L. racemosa* than those of *A. corniculata* and *K. obovata*. No differences in SLA (df = 2, $p = 0.670$) and leaf P (df = 2, $p = 0.228$) were found among the three species regardless of the levels of soil nutrients (Fig. 1). Increase of soil nutrients did not lead to significant changes in all tested traits (df = 3, $p > 0.05$) of *A. corniculata* and *K. obovata* (Fig. 1). In contrast, all the tested traits of *L. racemosa* were substantially increased except leaf C which declined remarkably (df = 3, $p < 0.001$; Fig. 1). Similar, there was no variation in chemical traits of *A. corniculata* and *K. obovata* (Fig. 2), while the significant reduction in cellulose, total phenolics, and soluble sugar were found in *L. racemosa* (df = 19, $p < 0.001$). The substantial decrease of cellulose occurred when soil N increased from 0.70 g kg⁻¹ to 1.00 g

kg⁻¹, and total phenolics and soluble sugar decreased sharply when soil N increased from 0.40 g kg⁻¹ to 0.70 g kg⁻¹ (Fig. 2).

3.2 Trait integrated analysis

PCA results indicated an axis of tolerance-growth tradeoff and a nutrient accumulation axis, accounted for 32.47% and 31.79% of total variations in traits, respectively (Fig. 3). All species showed a conservative strategy when growing in nutrient-poor soils, but the three species responded in different ways to nutrient increases. *L. racemosa* shifted its adaptive strategy to fast-growing along the soil nutrient gradient, while *A. corniculata* and *K. obovata* continued to accumulate nutrients in their leaves with the increase of nutrient availability.

3.3 Trait correlation

Following the global leaf spectrum method, we conducted the correlation analysis of SLA with the other traits (Fig. 4-6). The significant correlations were found in SLA vs. tree height ($r^2 = 0.628$, $p = 0.007$), SLA vs. leaf C ($r^2 = -0.845$, $p < 0.001$), SLA vs. leaf N ($r^2 = 0.642$, $p = 0.004$), SLA vs. leaf P ($r^2 = 0.721$, $p = 0.001$), SLA vs. cellulose ($r^2 = 0.704$, $p = 0.001$), SLA vs. soluble sugar ($r^2 = -0.799$, $p < 0.001$), SLA vs. $\delta^{13}\text{C}$ ($r^2 = 0.772$, $p < 0.001$) for *L. racemosa*. But for the slow-growing species *A. corniculatum*, the significant correlations were found only for SLA vs. leaf N (*A. corniculatum* $r^2 = 0.697$, $p = 0.006$; *K. obovata* $r^2 = 0.989$, $p = 0.011$), SLA vs. leaf P (*A. corniculatum* $r^2 = 0.762$, $p = 0.010$), and SLA vs. lipid (*A. corniculatum* $r^2 = 0.557$, $p = 0.031$).

Discussion

Our study confirmed the different responses of the three mangrove species to nutrient enrichment, indicated by trait variation, trait integrative analysis, and trait coordination results.

Trait integrative analysis showed a tolerance-growth tradeoff along soil nutrient gradients (Fine et al. 2006; Bauerle et al. 2007). Along this trend, *L. racemosa* shifted towards a fast-growing direction when soil nutrient increased, while *A. corniculatum* and *K. obovata* continued to conserve nutrients in leaves. The shift in ecological strategies has been found in a herb species *Arabidopsis thaliana*, a latitudinal gradient of ecological strategies was observed with increased stress tolerance in higher latitude (colder climates) at the expense of seed production (Vasseur et al. 2018). In our case, the substantial increase in growth of *L. racemosa* when soil nutrient increased 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 stress tolerance.

Surprisingly, *L. racemosa* had lower leaf nutrients and no difference in SLA from *A. corniculatum* and *K. obovata* across all the soil nutrient levels although all the species increased leaf nutrients and SLA with soil nutrient availability. A similar observation was in a forest in South Africa, where plant species

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). These observations indicated that some plant species, probably the fast-growing species such as *L. racemosa* in our case, adopted a strategy by accelerating growth rather than nutrient accumulation.

The close relationship between SLA and the most leaf traits of *L. racemosa* may indicate a plastic response of fast-growing species to soil nutrient availability. While the irrelevance between the most traits of *A. corniculatum* and *K. obovata* indicated a relative “inert” response of slow-growing species. The positive correlation between SLA and $\delta^{13}\text{C}$ of *L. racemosa* showed a steeper regression line compared to that of *A. corniculatum*, implied that *L. racemosa* promoted water use efficiency when soil nutrient increased (Vitousek et al. 1990).

The increase of leaf $\delta^{13}\text{C}$ could be derived from the increase of the carboxylation capacity and the mesophyll resistance to CO_2 diffusion (Evans and Von Caemmerer 2013) because the stomatal conductance of mangroves is generally limited by saline condition. However, there was fewer opportunities that the mesophyll resistance increased because the leaf succulence was reduced with soil nutrient availability for all the tested species. Thereby, the increase of leaf $\delta^{13}\text{C}$ was more likely due to the increase of carboxylation capacity, which can consume internal CO_2 , causing a decrease in ^{13}C fractionation, and consequently resulting in a less negative leaf $\delta^{13}\text{C}$ (Cordell et al. 1999). The least-cost theory states that the investment in photosynthetic capacity and water transport is optimized, such that a given photosynthetic rate is achieved at the lowest cost (Wright et al. 2003; Prentice et al. 2014). According to that, promoting the carboxylation capacity (consuming more N) by *L. racemosa* instead of regulating stomatal conductance may be an effective way to enhance photosynthesis when plants under sufficient N supply but limited stomatal opening. This explained at least partly that how the fast-growing species *L. racemosa* assimilated more C to stimulate plant growth although which need to be further examined by empirical experiments.

Conclusion

Our study confirmed that the two slow-growing species *A. corniculatum* and *K. obovata* did show different response strategy to soil nutrient enrichment from the intrinsic fast-growing species *L. racemosa*. Three mangrove species all showed conservative strategy (slow-growing and high in tolerance traits) when living in nutrient-poor soils. But when living in nutrient-rich soils, *L. racemosa* exhibited fast-growing at the expense of the tolerance chemical compounds; in contrast, *A. corniculatum* and *K. obovata* maintained still conservative strategy across the nutrient gradient. The contrasting response strategies between slow- and fast-growing mangrove species could lead to a fundamental alteration of ecosystem stability when resource availability changed, particularly for those subtropical mangrove forests with low diversity of species. The correlation between SLA and leaf $\delta^{13}\text{C}$ implied a potential mechanism involved in the adjustment of photosynthesis capacity, which could be a key theory to explain

the distinction in adaptive strategy between slow- and fast-growing species and thereby worth to be examined by future experiments.

Declarations

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Conflicts of interest/Competing interests

The authors declare no competing financial interests.

Availability of data and material

We agree to archive the data associated with this manuscript should the manuscript be accepted.

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

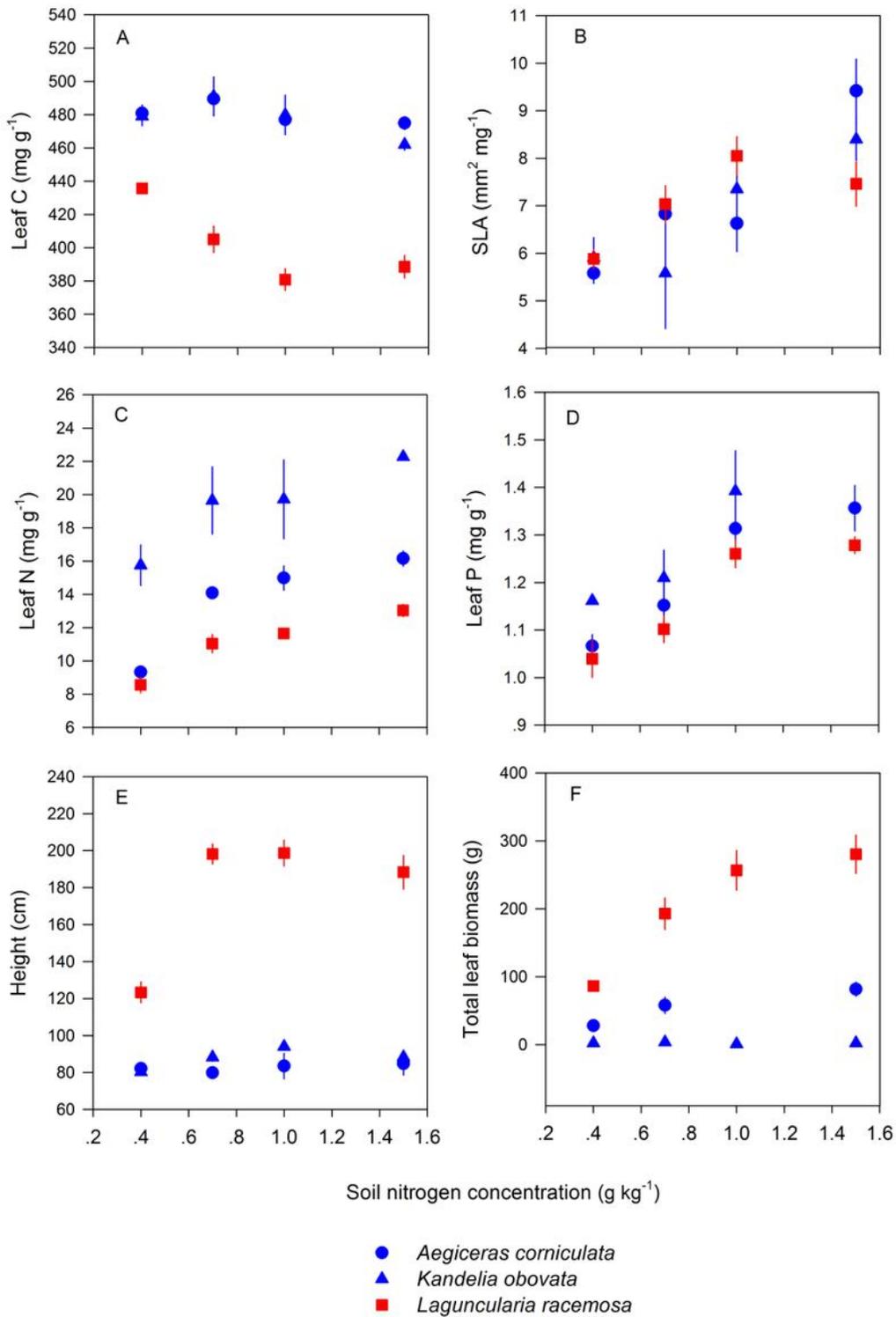


Figure 1

Variation of leaf traits (A-F) across soil nutrient gradients. Circle, *Aegiceras corniculatum*; Triangle, *Kandelia obovata*; Square, *Laguncularia racemosa*. The leaf P of *K. obovata* was missing due to the lack of adequate leaf numbers.

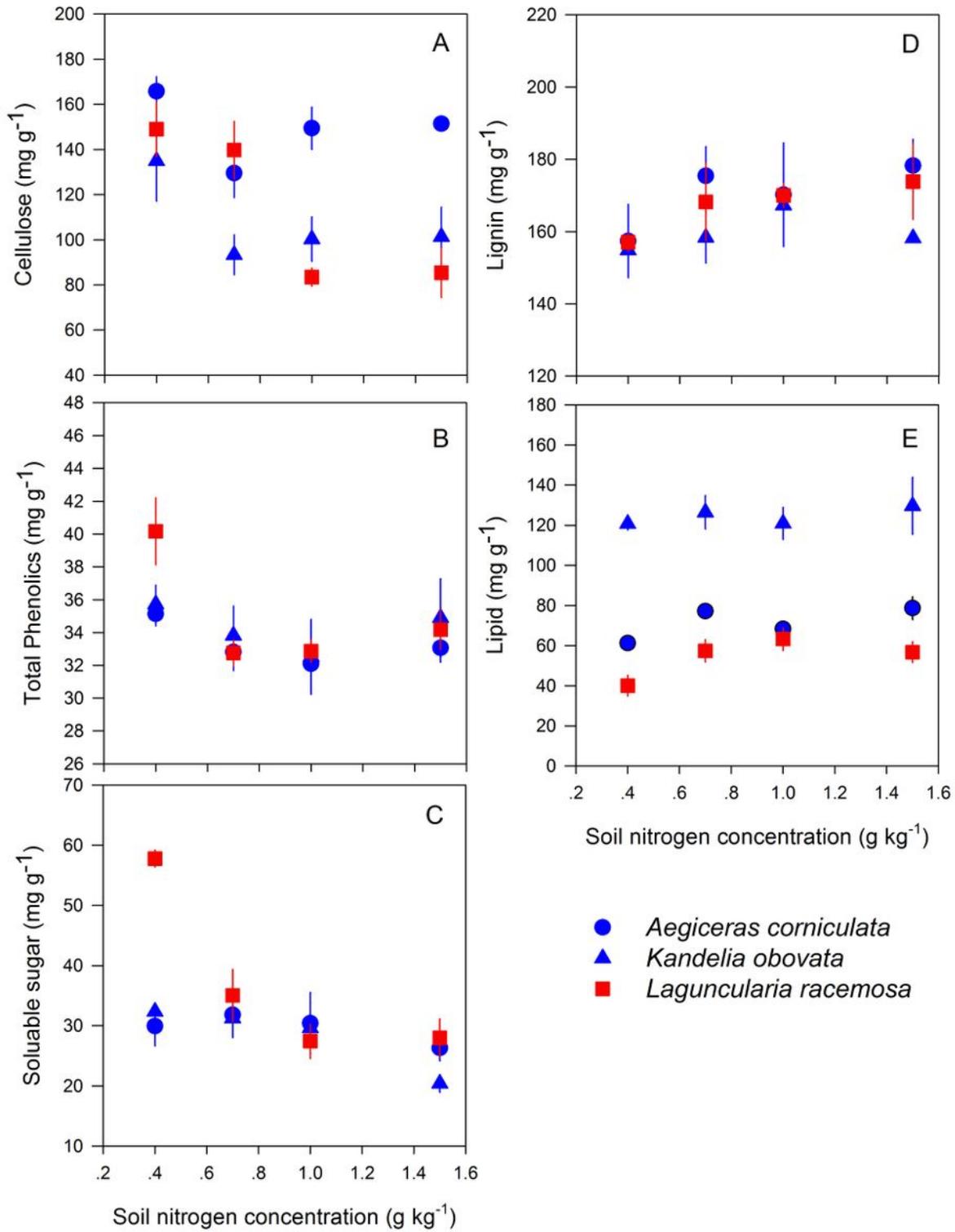


Figure 2

Variation of leaf chemical traits across soil nutrient gradients.

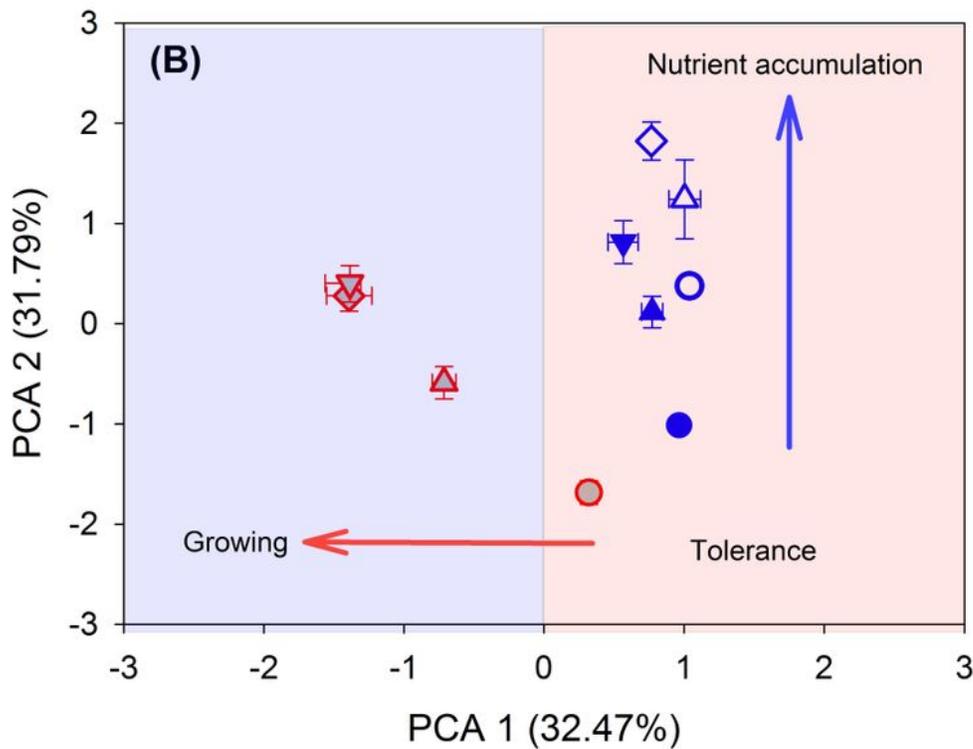
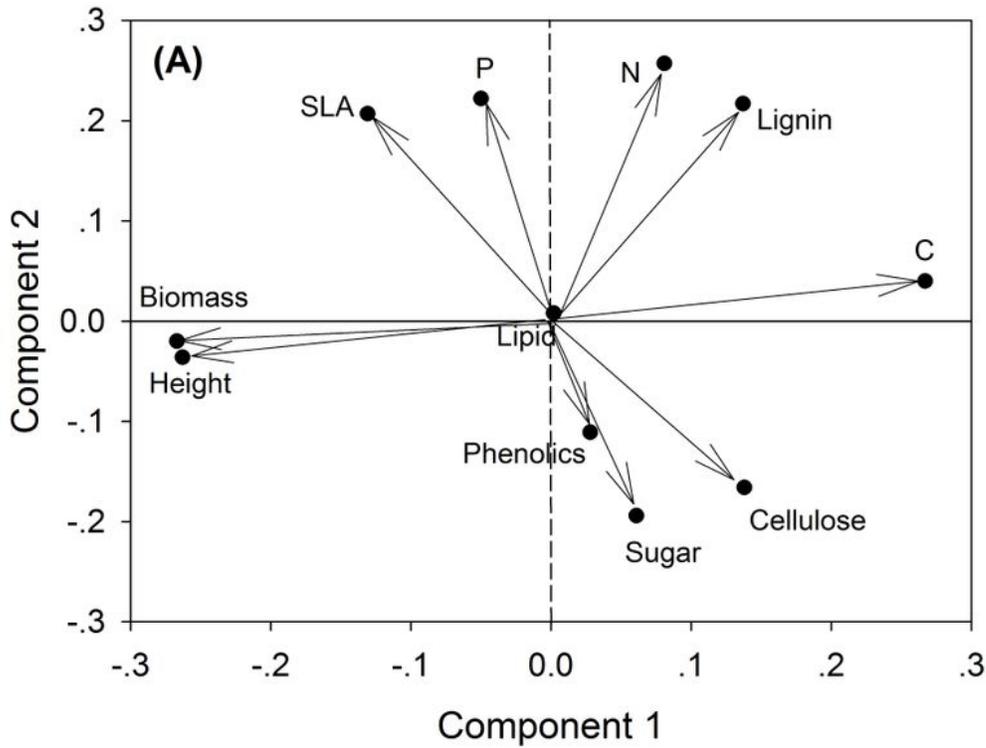


Figure 3

Projection of two main axes of principal component analysis (PCA) for the traits of the three species at different soil nutrient levels. Closed and open symbols refer to *Aegiceras corniculatum* and *Kandelia obovata* respectively, and grey-filling symbols to *Laguncularia racemosa*. Circle, Triangle (up), Diamond, and Triangle (down) are representing the trait values across soil nutrient gradient. The arrows indicate the shift trends of adaptive strategies.

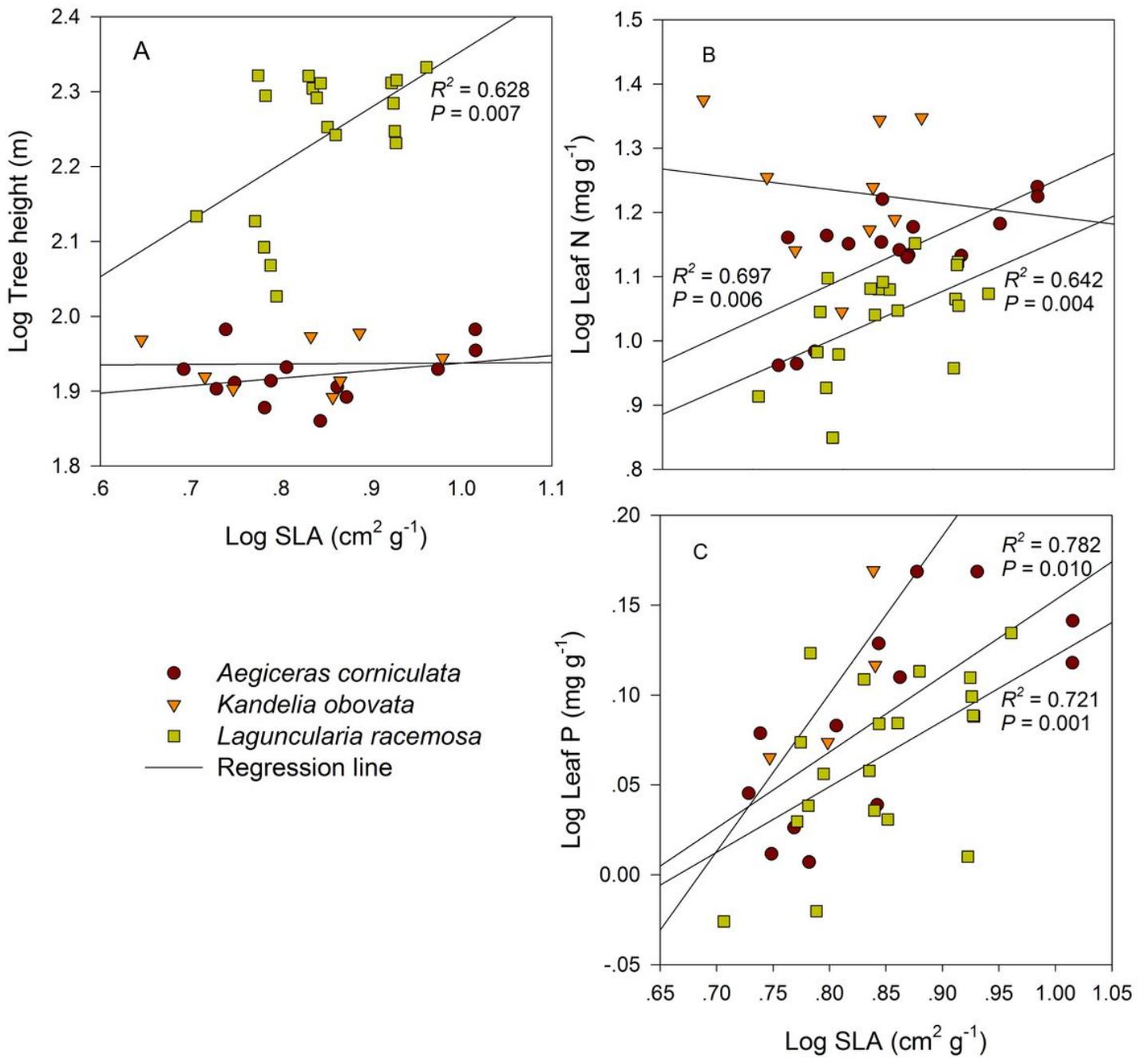


Figure 4

The correlation of SLA and tree height, leaf N and P of three mangrove species (log-transformed data). The statistical results were shown only for those significant correlations.

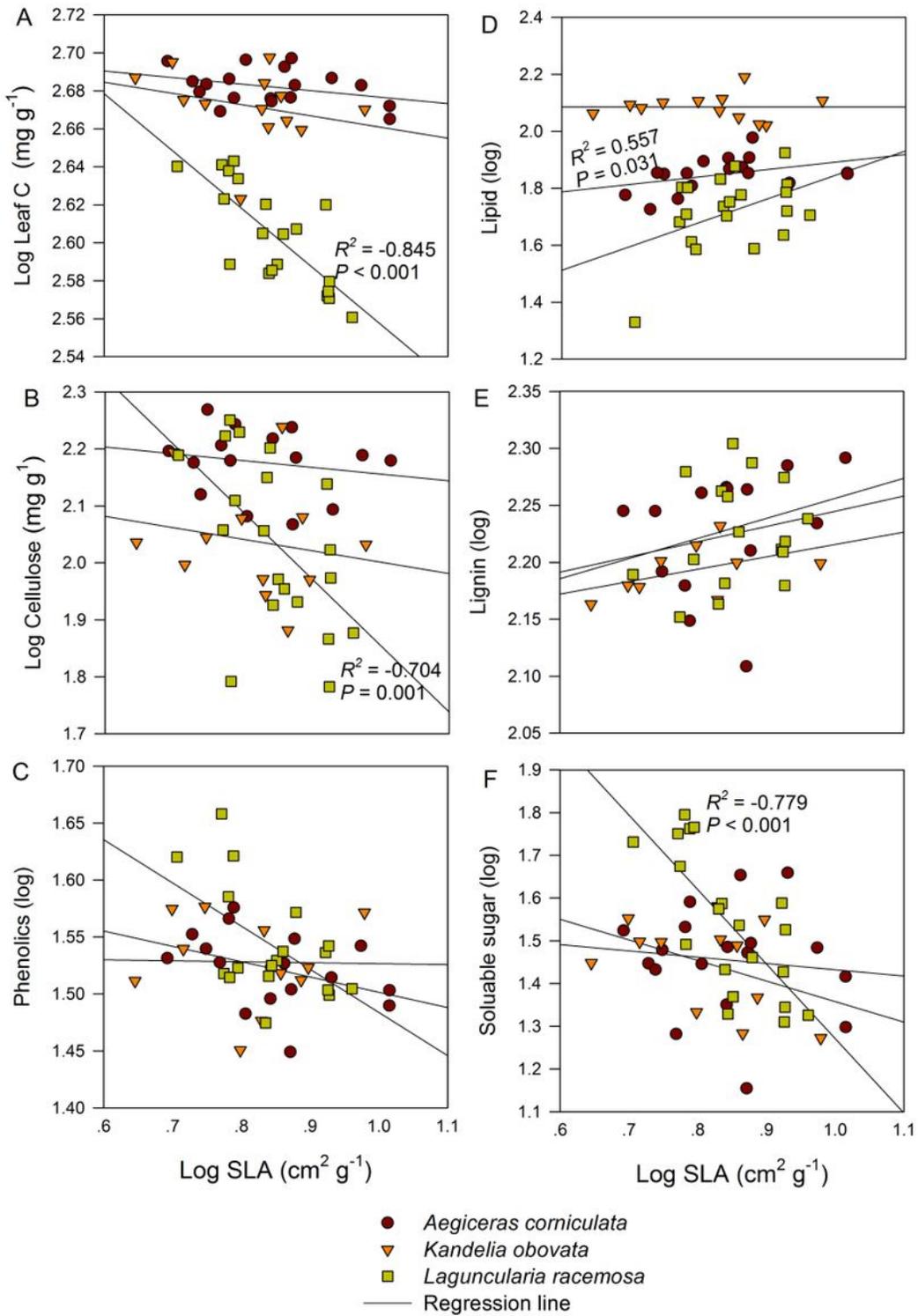


Figure 5

The correlation of SLA to the leaf chemical traits of three mangrove species (log-transformed data). The statistical results were shown only for those significant correlations.

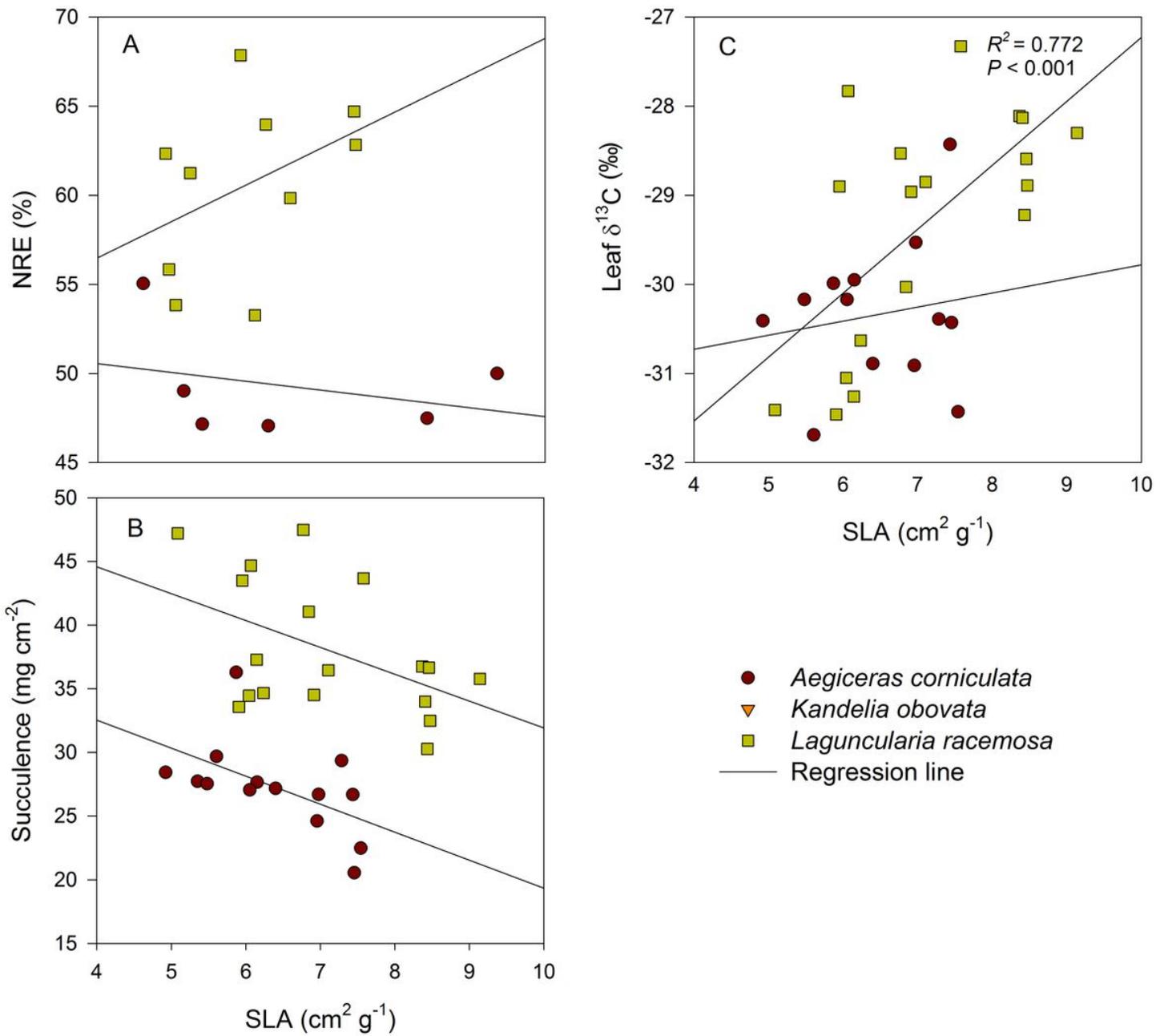


Figure 6

The correlation of SLA to the nitrogen resorption efficiency (A), leaf succulence (B), and leaf $\delta^{13}\text{C}$ (C) of *Aegiceras corniculatum* and *Laguncularia racemosa*. The statistical results were shown only for those significant correlations.