A trade-off between leaf carbon economics and plant size among mangrove species in Dongzhaigang, China

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Abstract

1. The relationship between plant size and trait characteristics is a fundamental aspect of the global spectrum that encompasses plant form and function. However, it remains unclear whether plant size affects interspecific variation in leaf structural traits at a specific ontogenetic stage. 2. In this research, we investigated the leaf structural traits, plant height, and diameter at breast height (or basal diameter) of 10 shrub and tree species. This study was carried out along an intertidal gradient within a mangrove forest located in Southeast China. 3. We found that leaf traits differed significantly between shrubs and trees in their response to intertidal gradients, which contributes to the advancement of our understanding of plant adaptive strategies and the evolution of traits within varying environmental contexts. Among all species, leaf carbon economics (leaf dry mass content, leaf mass per area, and leaf density) decreased significantly with increasing plant height and diameter. For each growth form and intertidal zone, the plant size-trait patterns were consistent with those in the pooled dataset. 4. Collectively, these findings suggest that mangrove plants undergo a size-dependent shift from resource conservation to resource acquisition strategies with increasing stature. Therefore, plant size serves as an indicator of the "slow-fast" spectrum of plant performance and the dichotomy between conservation and acquisition strategies.

Introduction

Leaf functional traits are effective indicators of the ecological strategies employed by species and their adaptive performance within a specific environmental context. (Iida *et al.* , 2014; Asao *et al.*, 2020; Mueller *et al.*, 2024). They have the potential to encapsulate plant strategies that pertain to water-use efficiency, growth dynamics, and nutrient acquisition (Roskilly *et al.* , 2019; Visakorpi *et al.*, 2023). For example, an increase in leaf mass per area (LMA) and leaf thickness (LT) indicates greater investments in leaf C structures and a longer leaf lifespan, which, in turn, enhance the mean nutrient residence time in leaves (Wright *et al.* , 2004; Díaz*et al.*, 2016). Understanding leaf trait variation is crucial for delineating niche differentiation, elucidating competitive exclusion dynamics, and interpreting the mechanisms of community assembly (Valverde-Barrantes *et al.* , 2017; Bergmann *et al.*, 2020). Nevertheless, the relationships between leaf functional traits and plant size remain unclear. The leaf economics spectrum (LES) represents a well-established framework within the realm of plant functional ecology that describes trait covariation relevant to carbon and nutrient economics across plant species (Wright *et al.* , 2004; Mueller *et al.*, 2024). For instance, less costly structural leaf phenotypes, such as low LMA and low leaf dry matter content (LDMC), are commonly linked to a suite of traits that enhance rapid growth and resource acquisition, including elevated leaf nutrient concentrations and increased metabolic rates (Guimarães *et al.* , 2022; Yan *et al.*, 2023). Conversely, the opposite traits (high LMA and LDMC) are associated with conservative economics, which are slower growth rates, reduced resource uptake, and decreased tissue turnover (Joswig *et al.* , 2022). Leaf economics and plant size represent two pivotal dimensions—exemplifying a decoupled correlation—that are fundamental to life-history strategies across the global spectrum of plant form and function (Díaz *et al.* , 2016; He *et al.*, 2024). However, the findings differ among studies, and the field is far from resolved. Several studies have related the traits of LES (e.g., leaf area, LA; specific leaf area, SLA; and leaf nitrogen concentration, LNC) to growth rates (dos Santos and Ferreira, 2020; Simpson*et al.*, 2020). In principle, since tree size affects access to resources and, thereby, growth rates (Piponiot *et al.* , 2022), it is expected that tree size is associated with leaf economic traits (Iida*et al.* , 2014; He and Yan, 2018). For example, larger trees tend to preempt light resources to smaller trees that, in turn, enables faster growth among trees of larger stature (Maynard *et al.* , 2022). Previous studies have shown that LA and LNC increased among larger plants (He and Yan, 2018; Zheng *et al.*, 2022), which is interpreted as the result of plants adopting acquisitive economic strategies in response to higher growth rates through acclimation and plasticity. However, larger trees exhibit heightened vulnerability to environmental stressors such as drought and higher solar irradiance (Rozendaal *et al.* , 2006; Bennett*et al.*, 2015; McGregor *et al.*, 2021). Consequently, leaf traits often undergo corresponding shifts toward more conservative economic strategies as plant size increases, as exemplified by reductions in SLA and LA, along with an increase in LDMC (Kenzo*et al.* , 2015; Dayrell *et al.*, 2018; Park *et al.*, 2019). Therefore, what we have learned about the effects of plant size on leaf economics is not consistent across studies. Numerous recent studies have explored size-trait relationships in terrestrial plants (Park *et al.* , 2019; Thomas *et al.*, 2020; Zheng *et al.*, 2022). However, coastal mangroves have not been well studied. Mangroves constitute an ecological assemblage of trees and shrubs that have adapted to thrive in the intertidal zones of tropical and subtropical coastal regions. The intertidal zone experiences considerable fluctuations in moisture and temperature between the highest tides, when it is submerged, and the lowest tides, when it is exposed to air and sun (Weitzman *et al.* , 2021). This zone is distinguished by a gradient that ranges from high to low and is influenced by the continental shelf's structure, variations in tidal fluctuations, and the succession of plant communities (Yu*et al.* , 2023). The interplay of sediment formation matrices, sedimentation rates, and the extent and duration of tidal waterlogging among intertidal zones leads to a diverse array of sediment characteristics, including nutrient composition, salinity, oxygen levels, and temperature (Hayes *et al.* , 2017; Ma*et al.*, 2020). Considering that salinity and temperature are paramount environmental factors influencing mangrove functional traits (Medina-Calderón *et al.* , 2021; Lang *et al.*, 2022), mangroves could have specialized structural traits along intertidal gradients (Yu *et al.* , 2023) and thus provide a unique opportunity to improve our understanding of plant size-trait relationships. In this study, we examined leaf traits and their relationships with plant size in a sample of 10 dominant mangrove species in Dongzhaigang, China. We hypothesize that: (1) leaf functional traits exhibit significant variation across growth forms and intertidal zones due to the differential responses of various growth forms to changing environmental conditions along the intertidal gradient (Islam *et al.* , 2024), and (2) smaller species are inclined to adopt increasingly conservative economic strategies characterized by high LD, LMA, and LDMC, as they are more susceptible to carbon starvation induced by shading (McDowell *et al.* , 2018).

2. Materials and Methods

2.1 Site description

The experiment was conducted at the Dongzhaigang National Nature Reserve (110°32´–110°37´E and 19°51´–20°01´N) in northeastern Hainan Province, China. The reserve is the earliest established mangrove reserve in China, covering 3337.6 ha. This area is characterized by a semi-enclosed estuary with a muddy bottom, nourished by four small rivers. It experiences semidiurnal tidal cycles, averaging a tidal range of 1.6 to 1.8 meters. The climate is characterized as a tropical maritime monsoon with an average annual rainfall of 1676.4 mm and a mean annual temperature ranging from 23.3 to 23.8°C (Li *et al.* , 2016). A total of thirty-five species of mangrove plants have been documented across 25 genera and 18 families. This included 24 species of true mangroves, which belong to 14 genera and 10 families, as well as 11 species of minor mangroves, categorized under 11 genera and 8 families (Jiang *et al.* , 2023). Deforestation ceased in 1986 when the bay was declared a national nature reserve. The dominant mangrove species are *Avicennia marina* , *Aegiceras corniculatum* ,*Bruguiera sexangula* , *Ceriops tagal* , and *Rhizophora stylosa* .

2.2 Field survey

The field survey was conducted during the peak of the rainy season. We selected five tree species and five shrub species for this study based on previous field investigations and literature research (Bai *et al.* , 2021; Yu *et al.*, 2023). Among our sampled species, five were located in the low intertidal zone, and five were in the high intertidal zone (Table 1). Four plots (10 m×10 m, >1 km apart) were established for each species. The height and diameter at breast height (DBH) or basal diameter of each individual tree and shrub were recorded. For each species, we collected 30 current-season, fully expanded, light-exposed mature and healthy green leaves from three adult individuals per plot and mixed them as a composite sample. All leaves were placed in plastic bags and immediately stored in a cooler with ice. Subsequently, we transported the samples to the laboratory for the measurements of leaf structural traits.

2.3 Leaf traits

The fresh leaf chlorophyll content (LCC) was estimated with a portable optical chlorophyll meter (SPAD-502, Konika-Minolta Inc., Tokyo, Japan). The leaf area (LA) was determined with a leaf area meter (LI-3000c, Lincoln, Nebraska, USA). Additionally, leaf thickness (LT) was measured using a digital micrometer (Digimatic micrometer, Mitutoyo, Japan). This measurement was derived from the average of three randomly selected positions on each leaf, deliberately avoiding the prominent veins to ensure accuracy on flat leaf surfaces. Leaf fresh mass (LFM) was weighted using a balance (0.0001 g, Meilen, Meifu Electronics Co. Ltd., Shenzhen, China). Following the rehydration procedure, the leaves were carefully dabbed with tissue paper to eliminate any residual surface moisture prior to measuring the leaf saturated mass (LSM). Samples were subsequently oven-dried to a constant mass at 65degC for at least 48 h and then weighed to obtain the leaf dry mass (LDM). Leaf volume (LV) was estimated using LA multiplied by LT. The leaf mass per area (LMA), the reciprocal of the specific leaf area (SLA), was calculated using the LDM divided by the LA. Leaf density (LD) was calculated by dividing LMA by LT. The leaf dry matter content (LDMC) was calculated as the ratio of LDM to LSM. Finally, water saturation deficit (WSD), a critical parameter widely utilized for assessing plant tolerance to temporary water shortages, was calculated as follows (Lal*et al.* , 2009):

$$\text{WSD}\,(\%) = \frac{(LSM - LFM)}{(LSM - LDM)} \times 100\%$$

2.4 Statistical analyses

All the statistical analyses were conducted using R (version 4.3.0, R Core Team 2023). Normality, homoscedasticity, and model fit were assessed using residual plots, Shapiro-Wilk test, and Levene's test. First, we conducted two-way analysis of variance (ANOVA) using general linear model procedures to test for the main effects of intertidal gradients and growth forms and their interactions on leaf traits. When the effects of treatments were significant, mean comparisons were performed using the '*emmeans* ' package. Second, phylogenetic signals of all traits were calculated with Blomberg's K statistic (Blomberg *et al.* , 2003) using the '*picante* ' package. This test compares the variance of the phylogenetically independent contrast of the study trait against those obtained with data randomly reshuffled in the phylogeny. A K value close to 1 indicates a significant phylogenetic effect, while a value close to 0 suggests no phylogenetic signal. In this study, the K values were less than 1, and the corresponding p values were greater than 0.05 for all traits, suggesting a lack of phylogenetic conservatism (Appendix Table S1). To investigate multivariate trait relationships, we performed principal component analysis (PCA) on all 11 leaf traits and plant sizes using the '*vegan* ' package. Finally, we used simple regression analyses to examine the effects of plant height and diameter on

LCC, LD, LDMC, WSD, and LMA and used general linear models to test the difference in regression slopes between intertidal zones and growth forms.

3. Results

Leaf structural traits varied significantly among the 10 sampled mangrove species (Table 2). The most variable traits were LV, LFM, LSM, and LDM, with a coefficient of variation (CV) approximately 60%. In contrast, LCC, LT, LDMC, LD, and LMA were the least variable, with CVs < 30%. LA and WSD were moderately variable (CV= 48.81% and 42.00%, respectively). The LCC, LA, LT, LV, LFM, LSM, LDM, and LMA increased significantly, and the WSD decreased from the low to high intertidal zones (Table 3 and Figure 1, $p < 0.05$). However, no significant differences between intertidal gradients were found for LDMC and LD. Compared with shrubs, trees had greater LA, LV, LFM, LSM, and LDM and lower LMA (Table 3 and Figure 1, $p < 0.05$), while growth form had no significant effect on the other traits. Additionally, we found significant interactive effects between growth forms and intertidal gradients on all traits, except for LMA. Trees in high intertidal zones had greater LCC, LA, LV, LFM, LSM, and LDM and lower LT than shrubs (Table 3 and Figure 1, $p < 0.05$), while differences in these traits between the growth types were not apparent in low intertidal zones. The LDMC, LD, and WSD were higher for shrubs than for trees only in low intertidal zones (Table 3 and Figure 1,$p < 0.05$), but these differences were not significant in high intertidal zones. The PCA results showed that Axis 1 and Axis 2 explained 48.9% and 23.2% of the total variance, respectively (Figure 2). Two independent dimensions of trait variation stood out within this plane. One dimension (upper left to lower right in Figure 2) ran from short and small DBH species with 'conservative' leaves (high LMA, LDMC, and LD) to tall and large DBH species with 'acquisitive' leaves (low LMA, LDMC, and LD). The other ran from large LA species tending to have thick and heavy leaves to small LA species tending to have thin and light leaves (lower left to upper right in Figure 2). Among all morphological and physiological characteristics, LMA, LDMC, LD, LCC, and WSD were negatively correlated with plant height and diameter (Figure 3). Similar patterns of LMA, LDMC, LD, LCC, and WSD in relation to plant height and diameter were found when intertidal zones and growth forms were analyzed individually, with LMA, LDMC, LD, LCC, and WSD decreasing with plant height and diameter (Appendix Figures S1 and S2). When regression slopes between different growth forms and intertidal gradients were tested, only LCC between high and low tides responded differently to plant diameter ($p < 0.05$, Appendix Table S2).

4. Discussion

We examined the impacts of plant form and intertidal gradient on leaf structural traits and analyzed the relationships between leaf structural traits and plant size among 10 dominant mangrove species. Our findings indicate that most leaf traits were significantly affected by growth form, intertidal gradient, and their interactions, consistent with our first alternative hypothesis. We also found a negative relationship between leaf economic traits (LMA, LDMC, and LD) and plant size, consistent with our second alternative hypothesis.

4.1 Growth forms and intertidal gradients affect leaf traits

We found that most leaf structural traits of mangrove species differed significantly along intertidal gradients. Specifically, the LCC, LA, LT, LV, LFM, LSM, LDM, and LMA increased significantly, and the WSD decreased with elevation. These results differed from those of a previous study of mangrove plants along an intertidal gradient in mangrove wetlands in Hainan, China, which reported that LMA and LT decreased significantly from low to high intertidal zones (Yu *et al.* , 2023). Salinity and pH are recognized as the principal sediment characteristics influencing the functional traits of mangrove leaves (Reddy *et al.* , 2021).

Elevated salinity levels have been shown to impede mangrove tree growth (Ahmed *et al.* , 2022). Concurrently, sediment pH indirectly influences the functional traits of mangrove leaves by modulating soil nutrient availability and salinity levels (Hartemink and Barrow, 2023). Several studies have shown that the LDMC, LT, and LMA of mangroves increase with increasing salinity and decreasing pH (del Campo *et al.* , 2022), indicating greater conservation of plants in highly stressed soils (Wright *et al.* , 2004; Díaz *et al.*, 2016). Yu *et al.*(2023) reported that sediment pH increased significantly and salinity decreased significantly from low to high intertidal zones in the Hainan Dongzhaigang Reserve. In principle, LDMC, LT, and LMA could decrease along elevational gradients. Conversely, we found that LDMC, LT, and LMA increased significantly along the elevational gradient. The possible reason for this difference is that LCC and WSD, in addition to conventional traits related to LES, are important physiological parameters that determine the survival and growth of mangrove plants (Biber, 2006). Our findings that trees had greater LA, LV, LFM, LSM, and LDM and lower LMA than shrubs were partially consistent with a study by Wang*et al.* (2019), who reported that LA, LDM, and LMA were greater in trees than in shrubs. LA reflects a plant's light capture potential (Strauss *et al.* , 2020). Tree canopies are typically exposed to high irradiance, while understory shrubs may face constraints in terms of the availability of light resources (Kenzo *et al.* , 2015; He and Yan, 2018). Therefore, higher LA in trees may be an adaptation to high light intensity to maintain greater photosynthetic capacity and productivity. Moreover, higher LV, LFM, LSM, and LDM can enhance photosynthetic capacity under high irradiance. This is achieved by increasing the nitrogen content and expanding the photosynthetic machinery volume per unit leaf area (Oguchi *et al.* , 2005; Liu *et al.*, 2019), which may explain the greater LV, LFM, LSM, and LDM in trees. LMAs are the primary driving factors of drought tolerance (Fletcher *et al.* , 2018). Our findings indicate that mangrove shrubs may experience more limited access to water resources than trees, as evidenced by the greater WSD observed for shrubs. Additionally, a high LMA suggests a reduction in intercellular space and increased resistance to gas diffusion within the mesophyll (Peguero-Pina *et al.* , 2017). This characteristic could be advantageous by enhancing plant tolerance to cell collapse, a consequence of drought stress (Bussotti and Pollastrini, 2015; Evans, 2021). The diffusion resistance of shrubs with a high LMA may increase to decrease leaf transpiration. Hence, determining the variation in leaf traits between different growth forms is essential for elucidating the mechanisms that underpin the ecological strategies of plant species. These strategies are crucial for successful adaptation and occupancy of diverse habitats (Wang *et al.* , 2022; Islam *et al.*, 2024). Exploring the effects of intertidal gradients on leaf functional traits between plant growth forms is helpful for understanding species diversity maintenance in forests (del Campo *et al.* , 2022; Yu *et al.*, 2023). Our study revealed that the responses of leaf structural traits to growth form vary across intertidal zones. Leaf functional trait variation with growth form effectively reflects a plant's adaptation strategy, which shapes differences in their demand and utilization of resources such as light, precipitation, temperature, and nutrients (Islam *et al.* , 2024). Thus, leaf traits differ among growth forms in response to intertidal elevation gradients with changes in moisture, temperature, salinity, and wave energy (Wang *et al.* , 2019). Our study has shed light on the different effects of intertidal gradients on leaf traits between different plant growth forms. This enhanced understanding is expected to deepen our insight into plant adaptive strategies and the evolutionary dynamics of plant traits as they adapt to the mosaic of environmental conditions. In addition, our findings reveal a major mechanism maintaining plant diversity in mangrove forests.

4.2 A trade-off between leaf economics and plant size

Despite a wealth of research into trait relationships in plants (Prieto*et al.* , 2018; Simpson *et al.*, 2020; Zhou *et al.*, 2022), our understanding of leaf trait relationships in mangroves lags behind that of terrestrial species. Plant height and diameter are important variables for characterizing plant size. **Our study revealed that large mangrove species (tall and large diameter) tended to have low leaf structural investment (low LMA, LD, and LDMC). This is contrary to several studies that have shown positive relationships between LMA and tree size across developmental stages for** conspecific individuals **(Nouvellon *et al.*, 2010;** He and Yan, 2018**;** Liu*et al.*, 2020**). There are three possible**

interpretations for this difference. First, the size-trait may have different drivers, which may co-occur within species while being decoupled among species (Zhou *et al.*, 2022). Thus, the negative size-trait relationships found across species disappeared when the analysis focused on intraspecific patterns. Second, decreases in LMA are often interpreted as a strategic adaptation by plants to enhance their light-harvesting efficiency (del Campo *et al.*, 2022). The canopies of taller plants experience greater solar irradiance compared to those of their shorter counterparts (Maynard*et al.*, 2022). These differences in the light exposure of plant crowns may be instrumental in the observed variability in LMA. Finally, decreases in LMA may result from decreases in leaf water stress (e.g., WSD) with increasing plant size. Our study underscores the importance of elucidating the underlying mechanisms behind trait-trait relationships, both within and among species. These mechanisms are essential for deepening our insight into the intricate adaptive strategies employed by plants in their quest for survival and success.Our results were also inconsistent with previous research on global plant size-trait relationships (Díaz *et al.*, 2016; Joswig *et al.*, 2022**;** Maynard *et al.*, 2022**).** A previous study pinpointed a crucial collection of functional traits that summarize the spectrum of forms and functions within the plant kingdom, with leaf economics (e.g., LMA) and plant size (e.g., tree height) being the**two** dominant **dimensions** underpinning life-history strategies (Maynard *et al.* , 2022). The distinct orthogonality of these two axes implies that they are shaped by different environmental drivers. For example, a comprehensive global assessment examining 17 traits across an extensive sample of over 20,000 species demonstrated that variations in size-related traits are strongly associated with latitudinal gradients, which are indicative of constraints on water or energy availability (Joswig *et al.* , 2022). In contrast, economic traits show a near-exclusive response to soil conditions, highlighting the unique influence of soil factors on these characteristics. Therefore, **these interspecific size-trait relationships are confounded by environmental drivers at a global scale.Consistent with previous research** (Kenzo *et al.* , 2006; Louis *et al.*, 2012)**, we found that** LCC significantly decreased with plant height. High LCC leaves are related to low dark respiration rates and light compensation points, permitting better acclimation to poor light for small trees and shrubs (Guimarães*et al.* , 2022). Negative correlations between LCC and plant height indicate that a high LCC contributes to light-harvesting efficiency at low irradiances. Despite substantial differences in leaf traits among growth forms and intertidal gradients, negative relationships between leaf traits (LMA, LDMC, LD, LCC, and WSD) and plant size (height and DBH) were detected within different growth forms and intertidal zones. Our results disagree with the findings of Li *et al.* (2021), who utilized leaf trait networks derived from global data to assert that the interdependence of leaf economic traits was more pronounced in shrubs than in trees. Plants in environments with limited resource availability are likely subjected to more intense selective pressures, leading to a tighter correlation between traits to ensure efficient resource acquisition and utilization**(Flores-Moreno *et al.*, 2019;** Liu*et al.*, 2019**). For instance,** leaf economic and hydraulic traits are found to be independent in humid regions **(Li *et al.*, 2015)** but exhibit strong coupling in arid regions **(Yin *et al.*, 2018).** In comparison to **terrestrial plants,** mangroves may face more constrained availability of water resources **since water uptake under saline conditions is energetically expensive**

(Santini *et al.*, 2015). Consequently, mangroves adopt a cost-effective strategy that promotes a strong correlation between leaf traits and plant size across growth forms and intertidal gradients, facilitating efficient functioning.

5. Conclusions

We examined the responses of leaf structural traits to growth form and intertidal gradient as well as the associations between leaf traits and plant size across mangrove species in Dongzhaigang, China. Our findings revealed that leaf traits differed significantly among growth forms in response to intertidal gradients. These findings contribute to a deeper understanding of plant adaptive strategies and trait evolution in response to diverse environmental conditions. Negative relationships between leaf traits (LMA, LDMC, LD, LCC, and WSD) and plant size (height and diameter) were found for each growth form and intertidal zone, as well as for the pooled data set. **These findings suggest that mangrove trees undergo a size-dependent shift from resource-conservative to resource-acquisitive strategies with increasing stature. It is imperative to emphasize that additional studies are warranted to elucidate intraspecific trait variability at local scales. Such research would significantly enhance our understanding of community assembly dynamics and the mechanisms by which plant communities influence ecosystem processes (Kumordzi *et al.*, 2014). Exploring the variability of intraspecific traits at local scales, both among communities and across environmental gradients, represents a promising and intriguing pathway for future scientific investigations.**

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Author contributions

All authors contributed intellectual input and assisted in manuscript preparation. D.J. and Q.Y. conceived the study. D.J., T.N., Q.H., J.Y., and E.F. collected the data. D.J. analyzed the data with assistance from Q.Y. D.J. prepared the initial draft with input from all authors in the final manuscript.

Conflict of interest

The authors declare no conflicts of interest.

Data availability statement

Data and R code supporting this study are provided as Supporting Information accompanying this manuscript.

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Appendix

Table S1 Blomberg's K for each leaf trait.

Table S2 Results of analysis of covariance (ANCOVA) with leaf traits (LCC, LDMC, LD, WSD, and LMA) as dependent variables, plant height and diameter as covariates, and intertidal gradients and growth forms as the factors. Values in bold indicate significant effects ($p < 0.05$).

Figure S1 Relationships between leaf traits and plant size, fitted by regression for shrubs and trees. The coefficients of determination (R^2) and p are shown in each panel. The trait abbreviations are provided in Table S1.

Figure S2 Relationships between leaf traits and plant size, fitted by regression for low- and high-elevation intertidal zones. The coefficients of determination (R^2) and p are shown in each panel. The trait abbreviations are provided in Table S1.

Table 1 List of species, genera, families, intertidal gradients, growth forms, plant heights, and diameters at breast height (DBHs) or basal diameters (means ± SE) in the study.

Species	Genera	Families	Intertidal zone	Growth form	Plant height (m)	DBH/basal d
Avicennia marina	Avicennia	Acanthaceae	Low	Shrub	1.86±0.26	5.37±0.74
Kandelia candel	Kandelia	Rhizophoraceae	Low	Shrub	2.39±0.13	5.83±0.87
Aegiceras corniculatum	Aegiceras	Primulaceae	Low	Shrub	1.32±0.40	4.48±0.82
Sonneratia caseolaris	Sonneratia	Lythraceae	Low	Tree	8.83±1.66	16.03±2.36
Sonneratia apetala	Sonneratia	Lythraceae	Low	Tree	7.92±1.57	14.40±3.84
Ceriops tagal	Ceriops	Rhizophoraceae	High	Shrub	1.72±0.14	4.77±0.41
Lumnitzera racemosa	Lumnitzera	Combretaceae	High	Shrub	2.13±0.15	6.56±1.26
Rhizophora stylosa	Rhizophora	Rhizophoraceae	High	Tree	3.25±0.30	4.55 ±0.24
Bruguiera sexangula	Bruguiera	Rhizophoraceae	High	Tree	3.12±0.82	6.20 ±2.34
Bruguiera gymnorrhiza	Bruguiera	Rhizophoraceae	High	Tree	3.25±0.34	5.34 ±0.53

Leaf trait	Abbreviation	Mean	Min	Max	CV (%)
Leaf chlorophyll content (SPAD)	LCC	64.91	43.28	86.33	16.62

Leaf area (cm^2)	LA	18.44	7.62	41.36	48.81
Leaf thickness (mm)	LT	0.55	0.36	0.82	23.64
Leaf volume (cm^3)	LV	1.03	0.34	2.76	61.17
Leaf fresh mass (g)	LFM	1.05	0.36	2.62	60.00
Leaf saturated mass (g)	LSM	1.18	0.43	2.90	59.32
Leaf dry mass (g)	LDM	0.30	0.10	0.75	63.33
Leaf dry mass content (%)	LDMC	25.38	14.42	34.34	16.58
Leaf density ($g\ cm^{-3}$)	LD	0.29	0.14	0.40	20.69
Water saturation deficit (%)	WSD	14.00	5.14	23.40	42.00
Leaf mass per area ($g\ m^{-2}$)	LMA	159.39	89.26	242.71	22.84

Table 2 Leaf traits (units), their mean values, ranges, and coefficients of variation (CVs) in this study.

Leaf trait	Intertidal gradient *F, P*	Growth form *F, P*	Intertidal gradient × Growth form *F, P*
LCC	**8.71****	0.11	**7.67****
LA	**43.31*****	**47.03*****	**48.97*****
LT	**13.61*****	0.39	**6.26***
LV	**29.58*****	**17.24*****	**13.04*****
LFM	**39.26*****	**19.42*****	**16.58*****
LSM	**35.62*****	**18.01*****	**17.94*****
LDM	**37.50*****	**14.01*****	**26.19*****
LDMC	0.45	1.92	**12.89*****
LD	0.33	2.77	**13.98*****
WSD	**4.71***	1.77	**15.07*****
LMA	**18.67*****	**4.66***	0.85

Table 3 Effect of intertidal zone gradient, growth form, and their interactions on leaf traits. The trait abbreviations are shown in Table 2. Significant results ($p < 0.05$) are shown in bold. ***: $p < 0.001$,**: $p < 0.01$,*:$p < 0.05$.

Figure legends

Figure 1 Leaf structural traits of shrubs and trees within low- and high-elevation intertidal zones. Trait abbreviations are provided in Table 2. Statistically significant differences between shrubs and trees are shown with asterisks (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$). n.s. = not significant.

Figure 2 Principal component analysis (PCA) conducted on 11 leaf traits and plant height and diameter among 10 mangrove species in Dongzhaigang, China. Trait abbreviations are provided in Table 2.

Figure 3 Relationships between leaf traits and plant size. The coefficients of determination (R^2) and p are shown in each panel. The trait abbreviations are provided in Table 2.

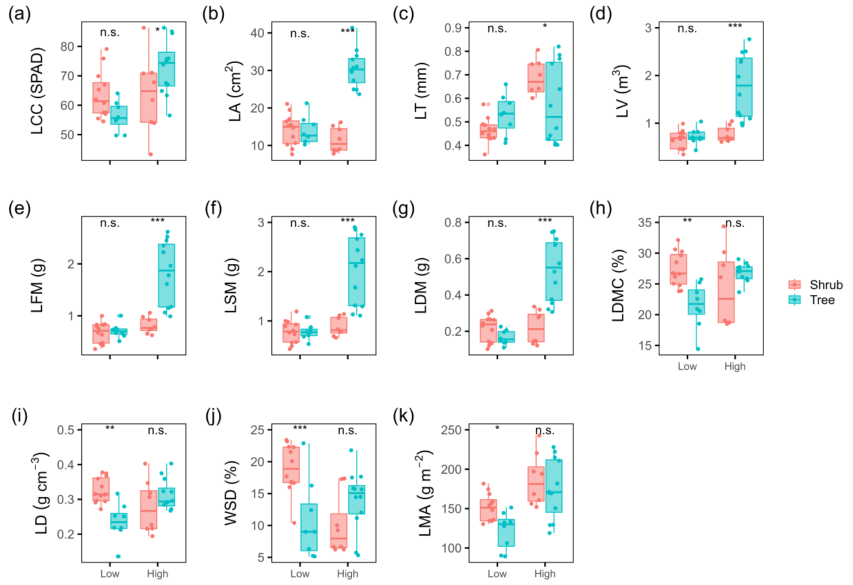
(a)
LCC (SPAD)
n.s.
*
(b)
LA (cm^2)
n.s.
***
(c)
LT (mm)
n.s.
*
(d)
LV (m^3)
n.s.
***
(e)
LFM (g)
n.s.
***
(f)
LSM (g)
n.s.
***
(g)
LDM (g)
n.s.
***
(h)
LDMC (%)
**
n.s.
Shrub
Tree
(i)
LD (g cm^{-3})
**
n.s.
(j)
WSD (%)
***
n.s.
(k)
LMA (g m^{-2})
*
n.s.
Low
High

Fig. 1

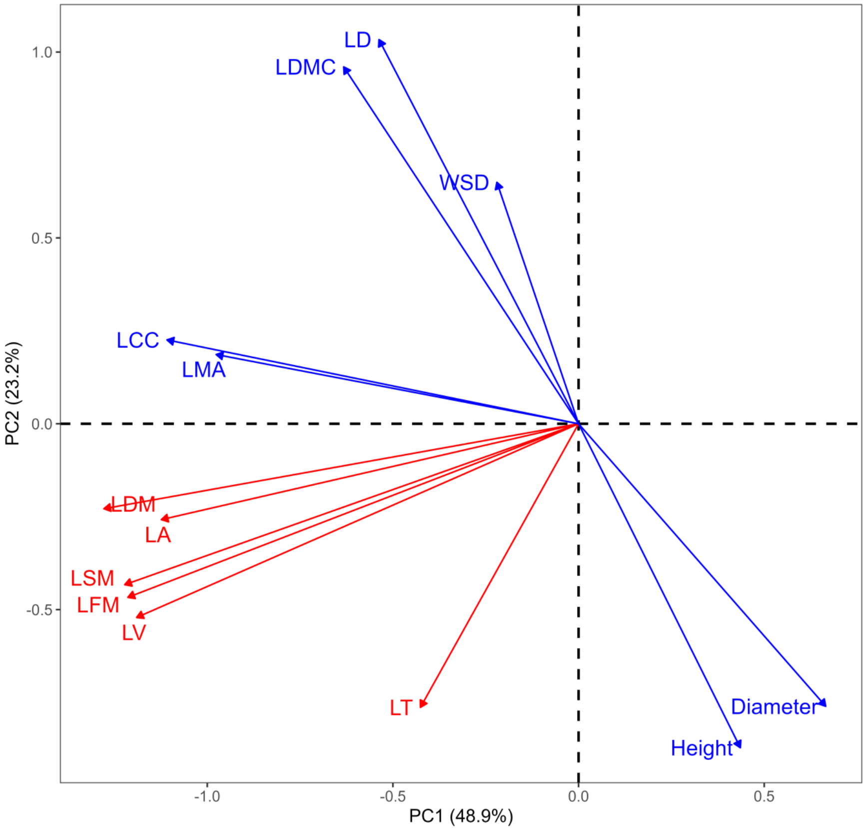
LD
LDMC
WSD
LCC
LMA
LDM
LA
LSM
LFM
LV
LT
Diameter
Height
PC2 (23.2%)
PC1 (48.9%)
1.0
0.5
0.0
-0.5
-1.0
-0.5
0.0
0.5

Fig. 2

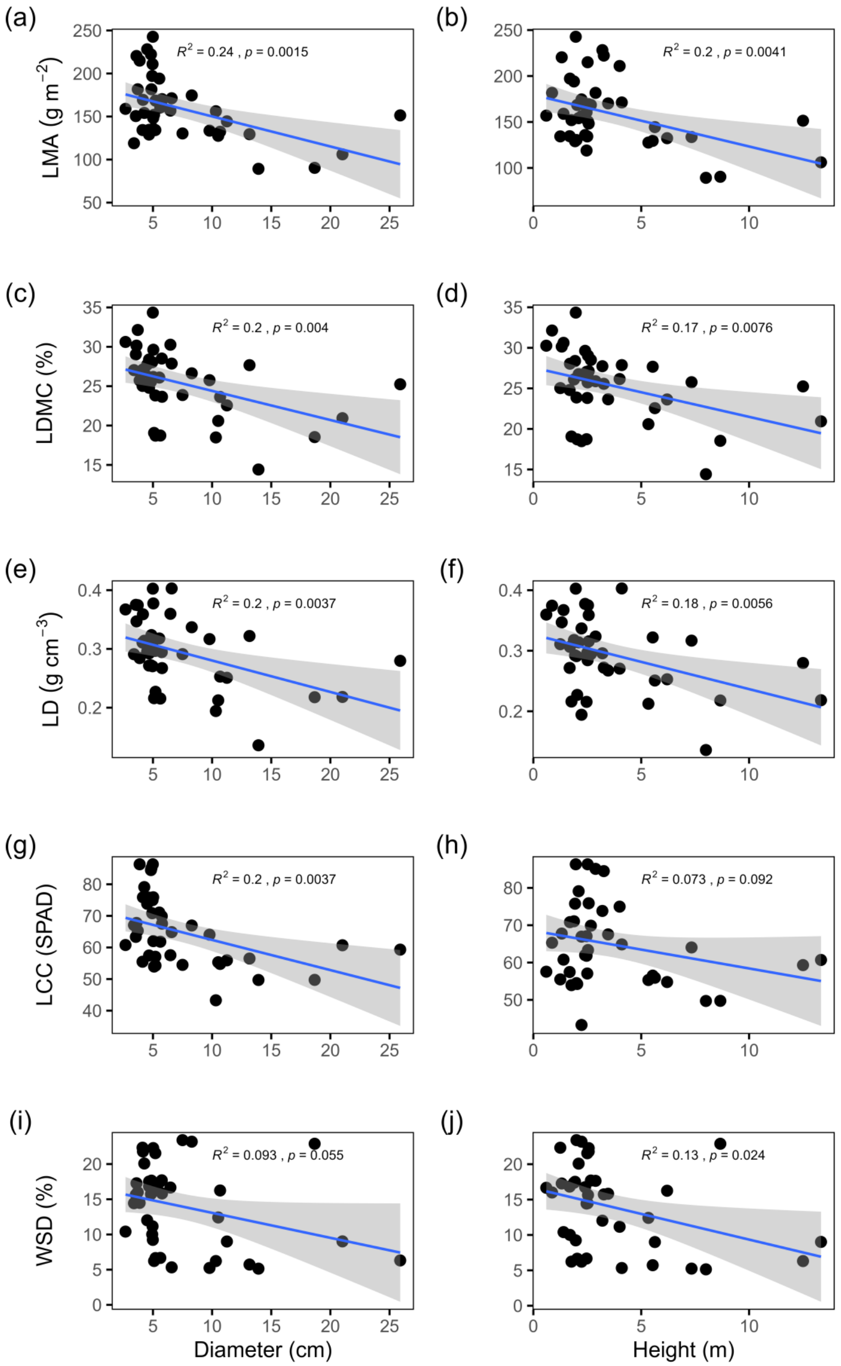

Fig. 3

Appendix

Table S1 Blomberg's K for each leaf trait.

Leaf traits	K	p
LCC	0.10	0.26
LA	0.44	0.07
LT	0.02	0.62
LV	0.21	0.28
LFM	0.28	0.16
LSM	0.26	0.21
LDM	0.38	0.11
LDMC	0.03	0.56
LD	0.01	0.76
WSD	0.02	0.59
LMA	0.30	0.15
Height	0.03	0.62
Diameter	0.30	0.35

Note: leaf chlorophyll content (SPAD, LCC), leaf area (cm^2, LA), leaf thickness (mm, LT), leaf volume (cm^3, LV), leaf fresh mass (g, LFM), leaf saturated mass (g, LSM), leaf dry mass (g, LDM), leaf dry mass content (%, LDMC), leaf density (g cm^{-3}, LD), water saturation deficit (%, WSD), leaf mass per area (g m^{-2}, LMA), plant height (m, Height), diameter at breast height or basal diameter (cm, Diameter).

Table S2 Results of analysis of covariance (ANCOVA) with leaf traits (LCC, LDMC, LD, WSD, and LMA) as dependent variables, plant height and diameter as covariates, and intertidal gradients and growth forms as the factors. Values in bold indicate significant effects ($p < 0.05$).

	LCC (SPAD)	LDMC (%)	LD (g cm^{-3})	WSD (%)	LMA (g m^{-2})
	F, P	*F, P*	*F, P*	*F, P*	*F, P*
Diameter	**10.68****	**9.59****	**9.56****	**3.77***	**11.14*****
Growth form	**5.71***	<0.01	0.06	0.58	0.04
Diameter × Growth form	0.79	2.83	1.85	0.06	0.04
Height	**3.41***	**8.16****	**8.57****	**5.26***	**9.06****
Growth form	**6.00***	0.43	0.16	0.02	0.76
Height × Growth form	1.33	2.65	1.63	0.20	0.04
Diameter	**11.44****	**8.97****	**9.19****	**4.92***	**14.57*****
Tidal level	**3.80***	0.28	0.42	**9.84****	**10.12****
Diameter × Tidal level	**5.74***	<0.01	0.04	2.01	1.10
Height	**3.24***	**7.78****	**8.66****	**6.54***	**11.71****
Tidal level	**5.13***	0.06	0.16	**8.99****	**11.50****
Height × Tidal level	0.02	1.20	2.06	0.04	0.05

Note: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$

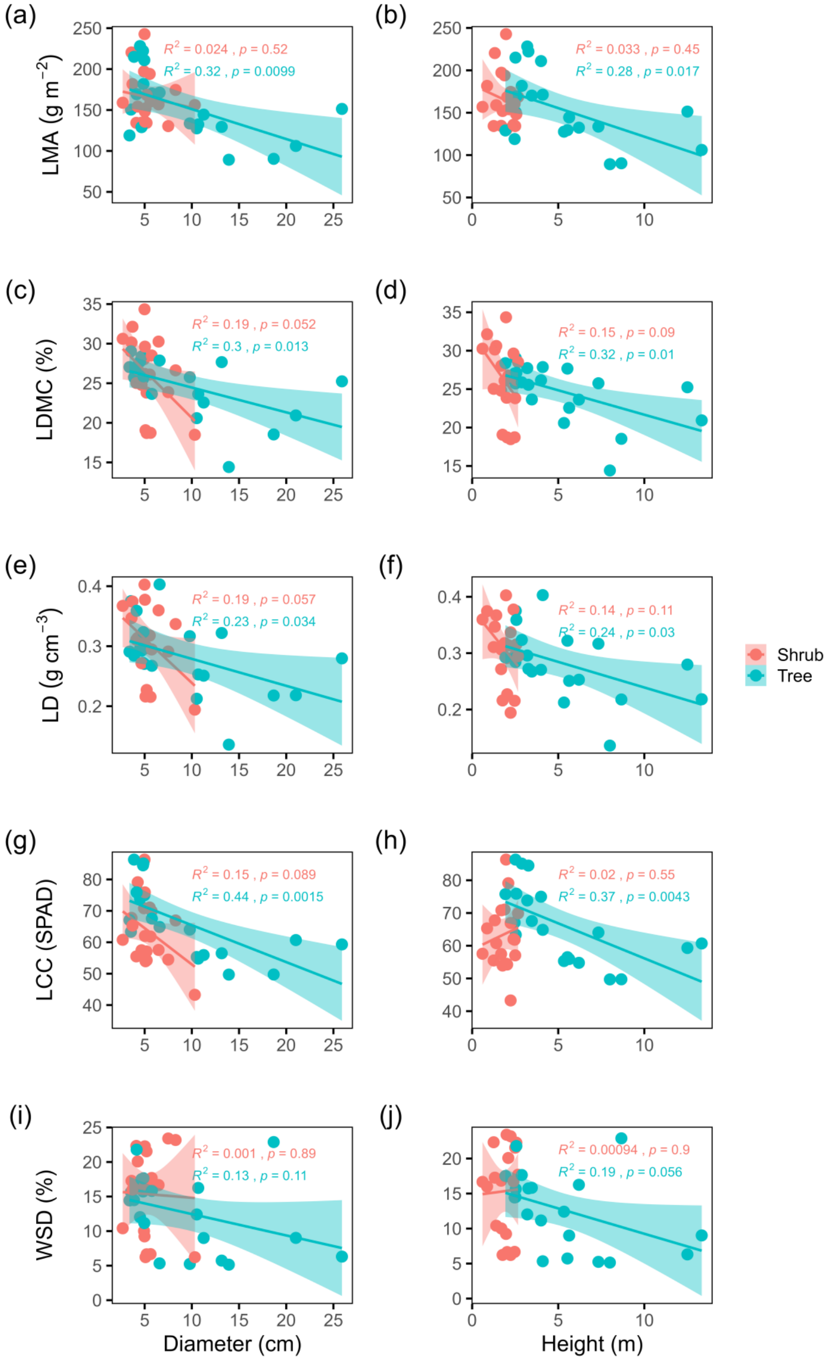

Figure S1 Relationships between leaf traits and plant size, fitted by regression for shrubs and trees. The coefficients of determination (R^2) and p are shown in each panel. The trait abbreviations are provided in Table S1.

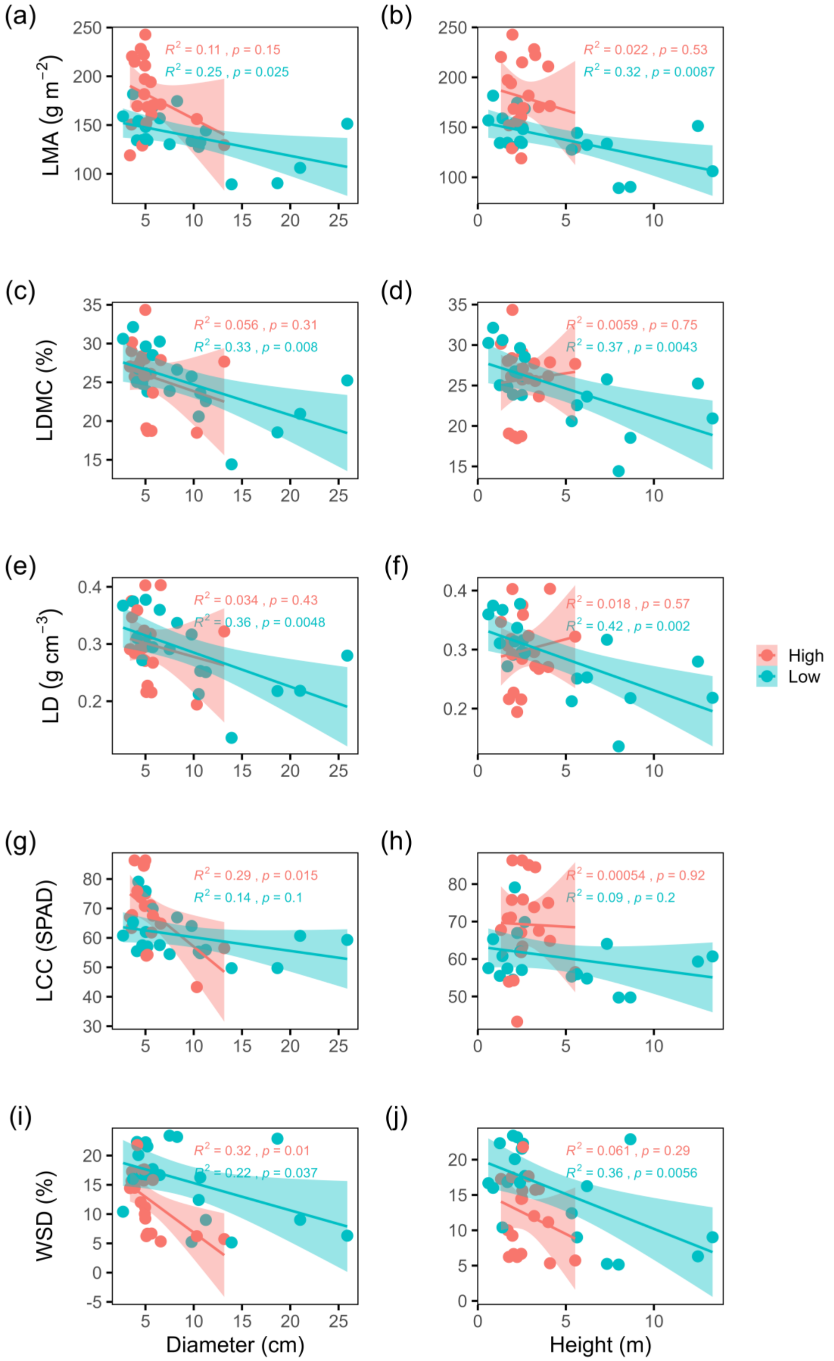

Figure S2 Relationships between leaf traits and plant size, fitted by regression for low- and high-elevation intertidal zones. The coefficients of determination (R^2) and p are shown in each panel. The trait abbreviations are provided in Table S1.