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Adaptive leaf morphology and anatomy of *Rhizophora apiculata* under environmental gradients in Tulic, Argao, Cebu, Philippines with implications for conservation

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Abstract. *Jarapan TJ, Flores M, Cuizon DR, Roble CM, Lanante AN, Yburan D, Enal CN, Emnacen M, Cortes ST, Almagro JJN, Retubado ZAZ, Lorca AS. 2025. Adaptive leaf morphology and anatomy of* Rhizophora apiculata *under environmental gradients in Tulic, Argao, Cebu, Philippines with implications for conservation. Biodiversitas 26: 2978-2991.* Mangrove forests provide critical ecosystem services, including coastal protection, biodiversity conservation, and carbon sequestration. However, they are increasingly threatened by environmental stressors, such as salinity fluctuations, habitat degradation, and climate change. Understanding species-specific adaptive responses to these stressors is essential for developing effective conservation strategies. This study investigated how coastal gradients and canopy light zones influence the morphological and anatomical leaf traits of *Rhizophora apiculata* in Tulic, Argao, Cebu, Philippines. A total of five quadrats of 5x5 m were placed in each of the landward, midward, and seaward zones. In each zone, environmental parameters including soil salinity, pH, and light intensity were recorded. Leaf samples were collected and analyzed for length, width, and anatomical features using the nail polish and potato impression method. Results demonstrated pronounced leaf plasticity in seaward individuals, with significant variations in width-related traits, while landward individuals exhibited limited morphological flexibility. The middle canopy zone showed strong adaptation to variable light conditions, with spongy mesophyll development and petiole length contributing notably to physiological performance. These findings suggest the role of leaf trait plasticity in enhancing the resilience of *R. apiculata* to changing environmental conditions. Incorporating trait-based approaches into mangrove conservation and restoration planning can strengthen ecosystem stability and sustain the protective and ecological functions of mangrove forests under different stressors.

Keywords: Coastal gradients, leaf parameters, leaf plasticity, light canopy, *Rhizophora apiculata*

INTRODUCTION

Mangrove forests rank among the world's most productive and vital ecosystems, providing essential ecological, economic, and social benefits (Lee et al. 2014; van Bochove et al. 2014; Srikanth et al. 2015; Friess 2016; Inocentes et al. 2025; Rosales et al. 2025). These ecosystems stabilize shorelines, mitigate the effects of natural disasters, and offer unique habitats while supplying critical resources, such as food, medicines, fuels, and building materials. However, mangroves face increasing threats from climate change, pollution, and deforestation, which stresses the need to better understand their adaptive mechanisms (Ellison et al. 2020; Sánchez et al. 2021; Cortes et al. 2024). To comprehend how mangroves persist amid these challenges, it is crucial to investigate species-specific adaptations that enhance their resilience. Among these mangrove plants, *Rhizophora apiculata* Blume known as spurred mangrove and locally as Bakauan lalaki in the Philippines exemplifies an exceptional set of adaptations that enable survival in environmentally challenging intertidal zones.

This adaptation allows *R. apiculata* and other mangrove species to thrive in habitats characterized by fluctuating salinity, waterlogging, and variable nutrient availability (Alongi 2014; Cheng et al. 2015; Amaliyah et al. 2017). One of the most notable adaptive mechanisms is leaf plasticity, mainly morphological and anatomical adjustments in leaf traits that enhance its survival and functionality under stress. Globally, investigations of mangrove leaf plasticity have documented its role in managing water loss, optimizing photosynthesis, and ensuring structural stability (Reef and Lovelock 2015; Naskar et al. 2021; Xin et al. 2024). Additionally, variations in stomatal density and leaf area have been linked to salinity gradients (Peel et al. 2017), while modifications in leaf size, shape, and thickness are critical for maintaining water balance and regulating salt uptake (Reef and Lovelock 2015; Mollick et al. 2021).

Despite this global understanding, the adaptive mechanisms of mangrove species particularly in relation to leaf plasticity remain underexplored in the Philippine context. These leaf adjustments not only sustain physiological functioning under high-salinity conditions, but also underscore the species' adaptability in response to localized environmental gradients (Romañach et al. 2018;

Naskar et al. 2021). A notable site for studying these dynamics is the Argao mangrove forest in southern Cebu, which harbors the dense timber stand in the region. Within this forest, *R. apiculata* is one of the dominant species (Lillo and Buot Jr. 2016). Argao mangrove forest has 22 mangrove species across 11 families and 14 genera, and *R. apiculata* plays a particularly critical role in maintaining the forest's ecological structure. Some species, such as *Rhizophora stylosa* Griffith, *Ceriops decandra* (Griff.) Ding Hou, and *Lumnitzera racemosa* Willd. also contribute significantly to the same. Ecologically, these species help protect against coastal erosion and storm surges, serve as a nursery for marine species, and sequester carbon, all of which are vital for climate change mitigation (Chow 2018). Furthermore, mangroves in Argao sustain local fisheries, promote tourism, and provide timber and medicinal plants, while also holding cultural and educational significance (Lillo et al. 2015; de Souza et al. 2017).

Focusing specifically on *R. apiculata*, its morphological features further illustrate its remarkable adaptability. The species is characterized by prominent stilt roots extending up to 5 m, which stabilize the plant in soft, muddy substrates and aid in gas exchange via specialized pneumatophores (Amaliyah et al. 2017). It has also dark green, smooth, leathery elliptical leaves with reddish stalks and long red stipules at the base. The flowers have cream-colored, linear petals in a cross shape, with yellow sepals, and they produce viviparous seeds (Mariano et al. 2019; Laith 2021). Given these characteristics, this study hypothesizes that *R. apiculata* exhibits significant leaf plasticity, with morphological and anatomical traits varying according to local environmental conditions. By examining these adaptive responses in Barangay Tulic. This research aimed to address a critical knowledge gap and contribute to targeted conservation and restoration strategies that can mitigate the impacts of climate change and human activity on these vital coastal ecosystems.

MATERIALS AND METHODS

Study site

The study was conducted in the mangrove forest of Barangay Tulic, specifically in Sitio Cancainap (Figure 1). The site is located at approximately 9°52'0" N, 123°35'0" E on the island of Cebu, the Philippines. Tulic is a coastal village in Argao, known for its extensive mangrove forests. The area is part of the larger Argao municipality, which is recognized for its rich biodiversity and ecological significance. The mangrove forest in Tulic is home to a diverse range of flora and fauna. One of the key species in this ecosystem is *R. apiculata*.

Procedures

The research was divided into three parts, i.e., (i) exploring the different environmental parameters such as soil salinity, soil pH, and canopy light intensity; (ii) collecting leaf samples for their morphological trait; (iii) analyzing the anatomical traits of the leaves.

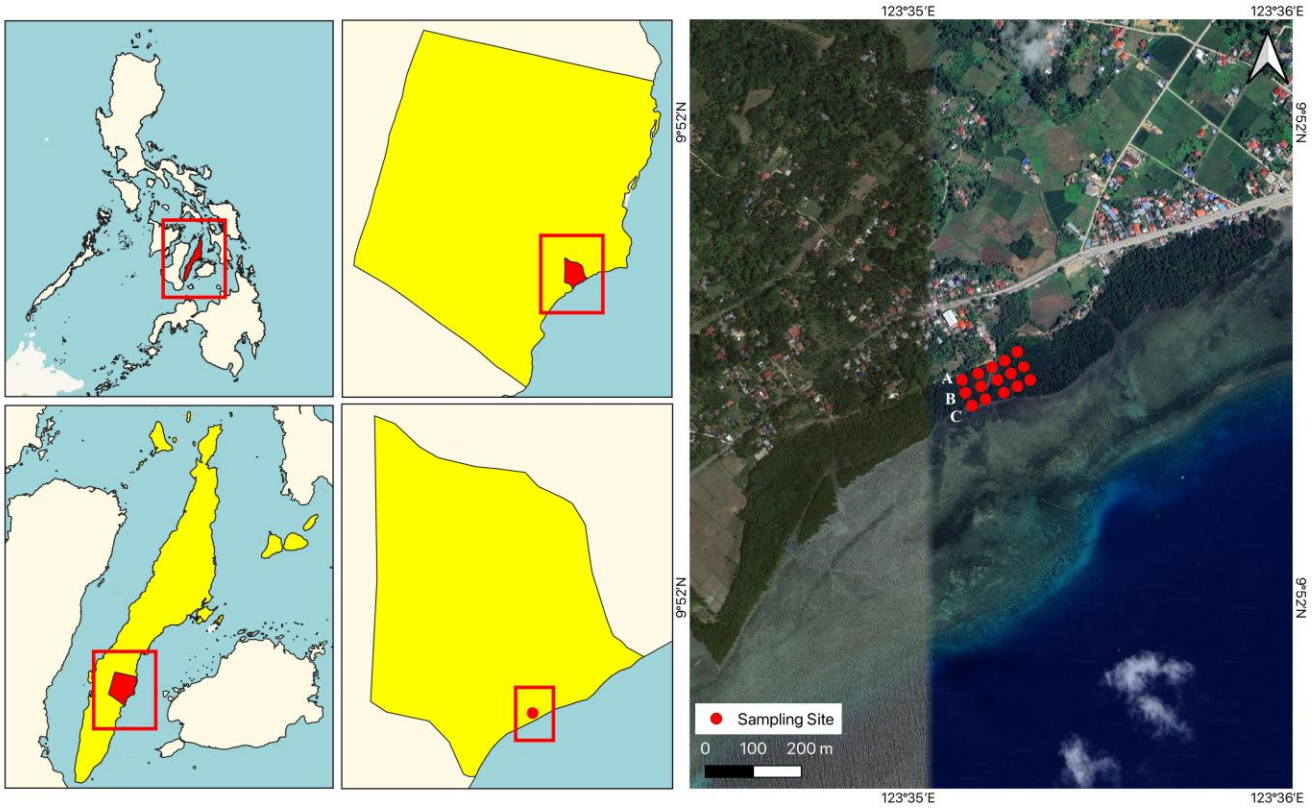


Figure 1. The mangrove forest in Tulic, Argao, Philippines, indicating the sample collection sites. A. Landward zone, B. Midward zone, C. Seaward zone

Environmental parameters

All samples were collected from different zonations, namely landward, midward, and seaward zones. Five quadrats were established in each zonation, each measuring 5×5 m. The chosen areas were then explored to obtain their environmental parameters. Soil salinity and pH were measured by a multi-parameter instrument, which was inserted into the soil, and the results were obtained after waiting for 3 minutes. It was discovered that different coastal gradients exhibit varying data, with the highest soil salinity in the seaward zone, followed by the midward zone due to its brackish water, and then the landward zone. However, soil pH across all coastal gradients was found to be neutral. Meanwhile, the measurement of light intensity was conducted using a lux meter to ensure accurate readings across various outdoor conditions. The lux meter was placed at the desired height and angle to measure the light intensity that the leaves were exposed in different canopy positions: top, middle, and bottom (Khan et al. 2020). Observations indicated that the top canopy receives the most direct sunlight and experiences the highest light intensity, the middle canopy receives filtered light due to shading from the top canopy, and the bottom canopy is the most shaded part, receiving diffuse light.

Morphological observation

Four hundred and fifty mature leaf samples in total were collected and observed. On the top canopy, three leaves were taken, followed by four leaves in the middle canopy and three leaves at the bottom canopy in every quadrant (Figure 2). The leaves were carefully detached using scissors at the petiole to avoid damage, stored in a labeled zip lock, and then transported to the laboratory at Cebu Technological University Main Campus, Cebu City, the Philippines for further analysis.

Mature leaves were scanned using a scanner with a true scale and measurement, such as a ruler and saved in JPEG file format (Mollick et al. 2021). Using the ImageJ, leaf morphological parameters, such as Leaf Length (LL) (cm), Leaf Width (LW) (cm), Leaf Middle Width (LMW) (cm), Leaf Upper Quarter Width (LUQW) (cm), Leaf Petiole Length (PL) (cm), Leaf Base Angle (LBA) (degree), Leaf Tip Angle (LTA) (degree), Leaf Area (LA) (cm^2), and Leaf Perimeter (LP) (cm) were obtained (Table 1; Figure 3) (Khan et al. 2020; Mollick et al. 2021). From the measured parameters, the ratios of Leaf Length/ Leaf Width (LL/LW), Leaf Length/ Petiole Length (LL/PL), Leaf Base Angle/Tip Angle (LBA/LTA), and Leaf Upper Quarter Width/Lower Quarter Width (LUW/LDW) were calculated (Mollick et al. 2021). The study incorporated various leaf morphological parameters to gain a deeper understanding of the multivariate relationships among them.

Anatomical observation

Microscopic images of leaf cross sections and stomata density were captured with 90 leaves. The assessment of stomatal density was conducted using the nail polish technique. A thin coat of clear nail polish was applied, allowed to dry, and then removed using transparent tape. This tape was then placed on a slide and viewed under a light microscope at 40x magnification. The stomatal density was determined by counting the stomata within a specified area (Peel et al. 2017). The thickness of the epidermis (µm), palisade mesophyll (µm), and spongy mesophyll (µm) were measured by obtaining smooth cross-sections of the leaves using the potato method. These sections were then stained with safranin, mounted in aqueous glycerin, and viewed under a microscope connected to a computer for image capture and analysis using ImageJ software (Khan et al. 2020). All leaf samples were then weighed and oven dried (Petruzzellis et al. 2019) for 24 hours at 60°C and then weighed again to obtain leaf dry weight (g).

Figure 2. *Rhizophora apiculata* in Argao, Philippines (right) and leaf shape (left) in three ecological zonations (landward, midward, seaward) and three canopy positions (top, middle, and bottom)

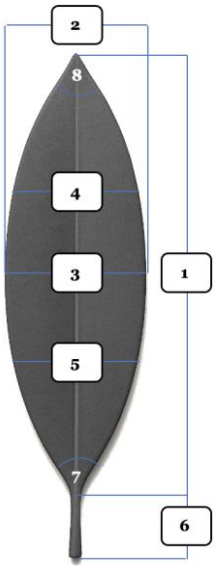


Figure 3. Morphological leaf parameters adapted from Mollick et al. (2021): 1. Leaf length, 2. Leaf width, 3. Leaf middle width, 4. Leaf upper quarter width, 5. Leaf down quarter width, 6. Petiole length, 7. Leaf base angle, 8. Leaf tip angle

Table 1. Leaf parameters used in this study

SI No.	Leaf parameters	Abbreviation	Description
1	Leaf Length (cm)	LL	Distance between leaf base to leaf tip of a leaf blade
2	Leaf Width (cm)	LW	Distance at the widest point of a leaf blade
3	Leaf Middle width (cm)	LMW	Distance at the middle point of a leaf blade
4	Leaf Upper Quarter Width (cm)	LUW	Distance at 3/4 length of a leaf blade
5	Leaf Down Quarter Width (cm)	LDW	Distance at 1/4 length of a leaf blade
6	Petiole Length (cm)	PL	Distance from leaf detachment part to base of a leaf blade
7	Leaf Area (cm^2)	LA	Amount of space inside the boundary of a leaf blade
8	Leaf Perimeter (cm)	LP	Circumference of a leaf blade
9	Leaf Base Angle (rad)	LBA	Rad at the base of a leaf blade
10	Leaf Tip Angle (rad)	LTA	Rad at the tip of a leaf blade
11	Leaf Index	LL/LW	Ratio of length to width of a leaf blade
12	Leaf Area/Perimeter	LA/LP	Ratio of area to perimeter of a leaf blade
13	Leaf Length/Petiole Length	LL/PL	Ratio of leaf length to petiole length of a leaf blade
14	Leaf Base Angle/Tip Angle	LBA/LTA	Ratio of base angle to tip angle of leaf blade
15	Leaf Upper Quarter Width/Down Quarter Width	LUW/LDW	Ratio of leaf upper quarter width to down quarter width of lead blade
16	Specific Leaf Area (cm^2/g)	SLA	Area-weight ratio
17	Leaf Thickness (cm)	LT	Distance between adaxial (upper) and abaxial (lower) sides of a leaf blade

Data analysis

Descriptive statistics (mean, standard deviation) summarized leaf traits to assess variability across sites (Peel et al. 2017). A Two-way ANOVA was used to analyze differences in leaf traits (dependent variable) across different environments (independent variable), allowing simultaneous analysis of multiple variables (Khan et al. 2020). Principal Component Analysis (PCA) reduced data complexity and identified adaptive traits linked to environmental conditions (Mollick et al. 2021). The Phenotypic Plasticity Index (PPI) was calculated to compare phenotypic plastic responses to different environmental parameters, using the formula as follows: PI = 1 - x / X, where (x) is the smallest value and (X) the largest value for each leaf trait. The PPI ranges from 0 (no plasticity) to 1 (maximum plasticity) (Gratani 2014; Khan et al. 2020; Mollick et al. 2021). Principal Component Analysis (PCA) was conducted to examine the relationships among multiple leaf parameters across coastal gradients and multiple leaf parameters across canopy light zones (Dong et al. 2020).

RESULTS AND DISCUSSION

Leaf morphological and anatomical variation across coastal gradient

The results of the two-way ANOVA which reveals significant differences in leaf parameters across the coastal gradients (Table 2). Morphological and anatomical parameters, such as LW, LUW, LDW, LBA, LTA, LL/LW, and LUW/LDW, exhibit the highest difference with a *p*-value ≤0.0001. The leaf parameters from the landward zone, such as LUW, LDW, SLA, LBA, LTA, LUW/LDW, UE, PM, SM, and LE, are significantly different from those of the rest of the coastal zones. Meanwhile, in the midward zone, LDW, LBA, LTA, UE, SM, and LE are significantly different from both seaward and landward. In the seaward zone, parameters such as LW, LDW, LBA, LTALL/LW, UE, SM, and LE are significantly different from those in other coastal zones. LDW, LBA, LTA, UE, SM, and LE parameters have significant differences across all coastal zones. Notably, LDW, LBA, LTA, UE, SM, and LE consistently differed across all three coastal zones suggesting that these parameters are the most sensitive to environmental variation across the gradient.

The results indicated that mangroves with their remarkable ability to inhabit harsh coastal environments, demonstrate significant differences in their leaf traits. This difference is a crucial adaptive mechanism that allows mangroves to survive and thrive under varying environmental conditions, such as changes in salinity, water availability, and light exposure. Leaf plasticity, which includes variations in morphological and anatomical traits, is integral to the overall resilience and ecological success of mangrove species (Gratani 2014; Khan et al. 2020).

A significant difference of ($p<0.05$) in the parameters suggests that the environmental conditions specific to the zone have a pronounced effect on leaf morphology and anatomy. Conversely, in the landward zone, characterized by lower salinity and higher exposure to sunlight, *R. apiculata* exhibits significant differences in LUW and PM. The broader leaves indicated by LUW suggest an adaptation to maximize light capture in environments with higher competition for sunlight. The thicker PM indicates an increased photosynthetic capacity, which is crucial for energy production in the more terrestrial conditions of the landward zone (Ren et al. 2019).

The midward zone characterized by its brackish water environment, provides a unique balance of freshwater and saltwater that significantly influences the leaf parameters. This is due to the freshwater from the Argao river. During high tide, the freshwater from Argao river is mixed with the seawater in Tulic, making the water brackish (Malaki et al. 2013). The thicker LDW, UE, and LE in this zone indicate adaptations for enhanced water retention and structural support, crucial for managing osmotic stress and

physical damage in a variable saline environment (Naskar and Palit 2015; Naskar et al. 2021). These morphological and anatomical adjustments underscore the adaptability of *R. apiculata* to the midward zone's conditions, optimizing its growth and survival.

Rhizophora apiculata demonstrates significant differences in several leaf traits due to the high salinity and tidal fluctuations characteristic in the seaward zone. The variations in LBA and LTA suggest structural adaptations for effective water drainage and reduced salt accumulation on the leaf surfaces, minimizing salt stress. Changes in the LL/LW indicate that the leaves in this zone are shaped to improve light interception and reduce physical damage from wind and water movements (Naskar and Palit 2015). Additionally, the thicker SM reflects an adaptation to enhance gas exchange and buoyancy, crucial for coping with the dynamic and saline conditions of the seaward zone (Lovelock et al. 2016). In general, these findings highlight the remarkable adaptability of *R. apiculata* to different coastal gradients, optimizing their leaf structures to thrive in varying environmental conditions, ensuring efficient resource utilization and resilience. Understanding these adaptive strategies is crucial for assessing mangrove ecosystem health and supporting conservation and management efforts.

Leaf morphological and anatomical variation across canopy light zones

A significant variation showed in leaf morphological traits across canopy light gradients, reflecting adaptive strategies that enhance photosynthetic performance under differing light intensities (Table 2). Specific parameters that reflect these adaptive changes include LL, LW, LMW, LDQW, PL, LA, and LP, particularly in leaves located in the bottom canopy, where significant morphological variation is necessary due to limited light. The LTA in the top canopy also shows significant differences ($p<0.05$), as leaf angles in higher light zones often adjust to reduce excessive light capture and heat load. Key anatomical features, including the upper and lower epidermis, spongy mesophyll, and palisade mesophyll, exhibit structural changes depending on light intensity (Figure 4). In high-light conditions, the palisade mesophyll, rich in chloroplasts, becomes more developed to increase photosynthetic capacity, while in shaded environments, the spongy mesophyll, which aids in gas exchange, often expands. The thickness and density of the upper and lower epidermis can also adjust to regulate light penetration and water conservation. Studies on functional trait responses to light variation highlight the importance of plasticity in traits such as SLA, LT, and PL, which are closely linked to photosynthetic capacity and energy use efficiency.

Mangroves have the ability to adapt to varying light conditions within a forest or canopy structure (Ahmed et al. 2022). This plasticity refers to the ability of leaves to alter their shape, size, and structural properties in response to environmental gradients, particularly the availability of light, which varies significantly from the top (sun-exposed) to the bottom (shade-dominated) canopy zones (Khan et al. 2020). In the top canopy, leaves are exposed to intense sunlight and typically exhibit smaller surface areas, thicker laminae, and steeper leaf tip angles to minimize photodamage and water loss through transpiration. Conversely, leaves in the lower canopy must capture as much diffuse light as possible, leading to larger, broader leaves with thinner laminae, longer petioles, and flatter leaf angles to enhance light interception and maximize photosynthetic efficiency (Naskar and Palit 2015; Khan et al. 2020). This morphological plasticity is crucial for optimizing carbon gain while minimizing water loss, a balance that depends on the interaction between structural leaf properties and light capture efficiency (Lambers and Oliveira 2019; Khan et al. 2020). Furthermore, plasticity allows for greater resource use efficiency and competitive advantage in heterogeneous environments, contributing to overall plant fitness and survival (Alam et al. 2018). This adaptation is especially significant in mixed-light environments, where competition for light is intense and leaf traits must adjust dynamically to optimize light harvesting (Eskelinen et al. 2022).

Interaction effects of coastal gradients and canopy light zones on leaf morphological and anatomical plasticity

The interaction between coastal gradients and canopy light zones plays a pivotal role in shaping the morphological and anatomical plasticity of plant leaves, particularly in mangroves, as demonstrated in Table 2 and Figure 5 and supported by a research finding (Vieira et al. 2014). Coastal gradients encompassing variations in salinity, tidal exposure, soil conditions, and nutrient availability create distinct environmental pressures that influence leaf traits (He et al. 2021). For instance, leaves in seaward zones exposed to higher salinity and tidal forces often adapt by becoming thinner, with specific angles to minimize salt buildup and resist mechanical stress from waves (Simard et al. 2019). In contrast, midward and landward zones, which are subject to less saline but more stable conditions, promote thicker leaves and larger areas to enhance photosynthetic efficiency and water retention (Vieira et al. 2014). These adaptations reflect the plants' capacity to modify leaf structures in response to spatial environmental shifts along the coastal gradient, allowing them to optimize resource use and maintain physiological functions under challenging conditions (He et al. 2021).

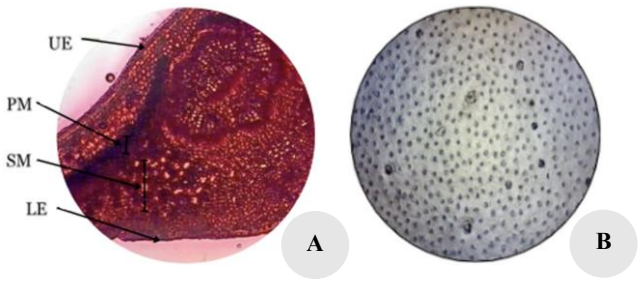
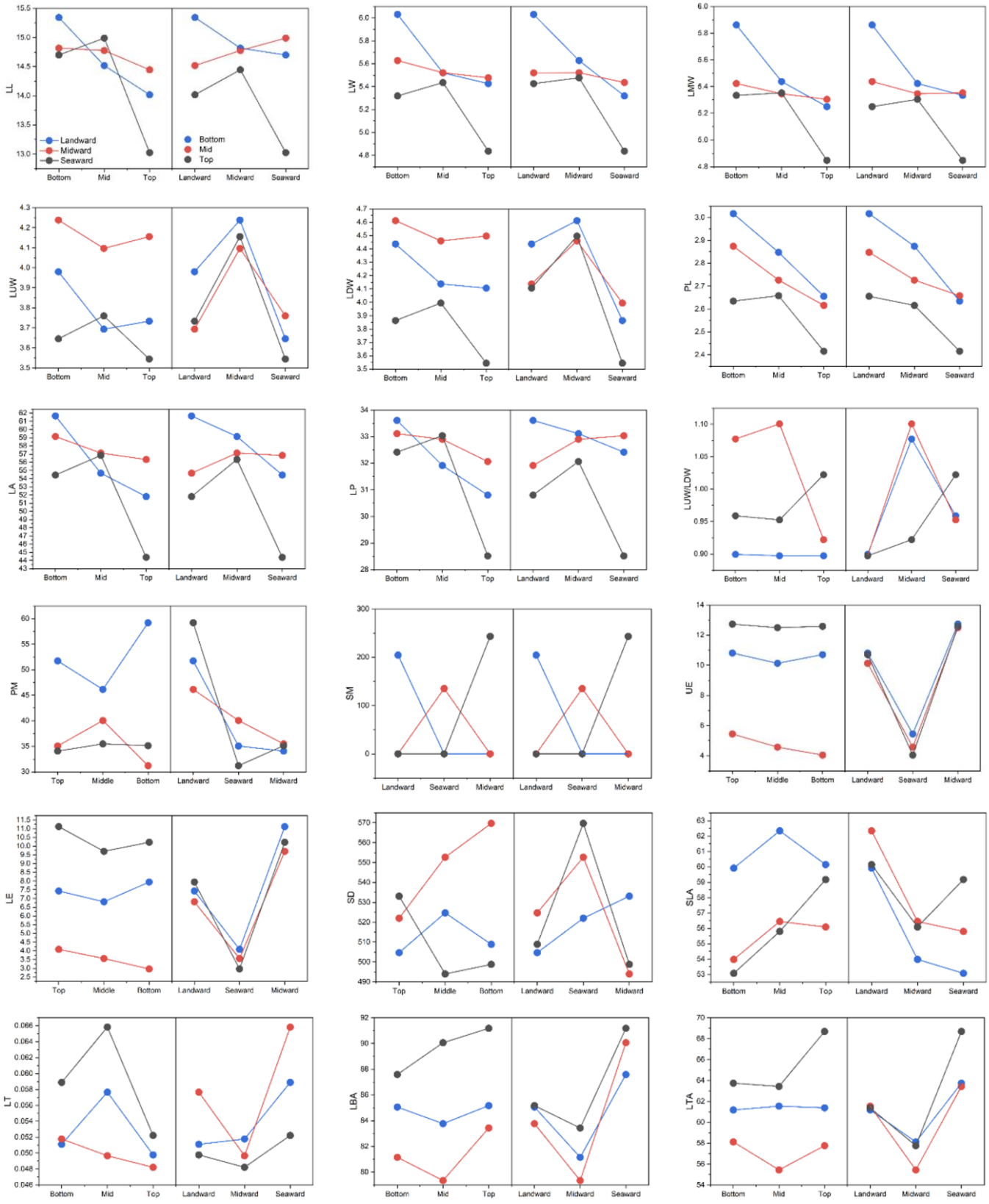


Figure 4. The anatomical traits of *Rhizophora apiculata* in Tulic, Argao, Philippines, with 10x10 magnification in (A) midrib leaf cross-section and with 4x10 magnification and an area of 0.19625mm^2 in (B) stomata. (Annotations based on Wijaya et al. 2024: UE: Upper Epidermal, PM: Palisade Mesophyll, SM: Spongy Mesophyll, LE: Lower Epidermal)

Table 2. Two-way analysis variance of morphological and anatomical parameters. The same letters (within each canopy) indicate no significant difference (Tukey, P>0.05) among coastal zones (LW: Landward, MW: Midward, SW: Seaward)

Parameters	Coastal gradients			*F*(*p*)	Canopy light position			*F*(*p*)	Interaction effect *F*(*p*)
	LW	MW	SW		Bottom	Middle	Top		
LL	14.61 ± 1.61[a]	14.69 ± 1.73[a]	14.31 ± 1.93[a]	3.07 (0.050)	14.95 ± 1.81[a]	14.76 ± 1.70[a]	13.83 ± 1.60[b]	17.91 (<0.0001)	4.75 (0.001)
LW	6.03 ± 0.65[a]	5.54 ± 0.77[a]	5.22 ± 0.83[b]	15.53 (<0.0001)	5.66 ± 0.89[a]	5.49 ± 0.67[a]	5.25 ± 0.76[b]	10.64 (<0.0001)	3.89 (0.004)
LMW	5.51 ± 0.71[a]	5.36 ± 0.77[ab]	5.20 ± 0.86[b]	7.18 (0.346)	5.54 ± 0.91[a]	5.38 ± 0.69[a]	5.13 ± 0.75[b]	7.181 (0.00085)	2.45 (0.045)
LUW	3.79 ± 0.50[a]	4.16 ± 0.65[b]	3.66 ± 0.67[b]	27.83 (<0.0001)	3.95 ± 0.73[a]	3.85 ± 0.57[a]	3.81 ± 0.64[a]	2.04 (0.131)	1.73 (0.143)
LDW	4.22 ± 0.54[a]	4.52 ± 0.80[b]	3.82 ± 0.81[c]	37.62 (<0.0001)	4.30 ± 0.92[a]	4.20 ± 0.70a[b]	4.05 ± 0.71[b]	4.31 (0.014)	2.24 (0.064)
PL	2.84 ± 0.62[a]	2.74 ± 0.63[ab]	2.58 ± 0.71[b]	6.56 (0.00156)	2.84 ± 0.66[a]	2.74 ± 0.68[a]	2.56 ± 0.61[b]	6.51 (0.002)	0.42 (0.793)
LA	55.91 ± 12.11[a]	57.50 ± 14.61[ab]	52.38 ± 14.39[b]	17.16 (0.0009)	58.41 ± 15.52[a]	56.21 ± 12.95[a]	12.25 ± 1.05[b]	11.75 (<0.0001)	3.76 (0.005)
LP	32.09 ± 3.46[a]	32.71 ± 4.04[ab]	31.49 ± 4.43[b]	4.83 (0.008)	33.05 ± 3.99[a]	32.62 ± 3.75[a]	30.46 ± 3.93[b]	18.47 (<0.0001)	4.46 (0.002)
SLA	60.95 ± 16.46[a]	55.60 ± 13.75[b]	55.99 ± 13.8[b]	5.79 (0.003)	55.65 ± 13.21[a]	58.19 ± 17.23[a]	58.47 ± 12.93[a]	1.55 (0.213)	0.61 (0.652)
LT	0.053 ± 0.04[a]	0.050 ± 0.007[a]	0.060 ± 0.053[a]	2.05 (0.130)	0.05 ± 0.01[a]	0.08 ± 0.06[a]	0.05 ± 0.01[a]	1.47 (0.231)	0.40 (0.808)
LBA	84.57 ± 9.75[b]	81.11 ± 10.01[c]	89.66 ± 12.51[a]	21.94 (<0.0001)	84.60 ± 10.42[a]	84.39 ± 11.29[a]	86.59 ± 12.28[a]	1.81 (0.164)	0.80 (0.524)
LTA	61.38 ± 5.65[b]	56.94 ± 5.36[c]	65.10 ± 10.74[a]	432.26 (<0.0001)	61.01 ± 6.70a[b]	60.14 ± 7.38[b]	62.61 ± 10.40[a]	4.16 (0.016)	2.57 (0.037)
LL/LW	2.60 ± 0.20[b]	2.67 ± 0.24[b]	2.77 ± 0.33[a]	16.23 (<0.0001)	2.67 ± 0.25[a]	2.69 ± 0.22[a]	2.66 ± 0.35[a]	0.58 (0.561)	0.70 (0.590)
LA/LP	1.72 ± 0.21[a]	1.74 ± 0.39[a]	1.66 ± 0.26[a]	3.38 (0.0349)	1.74 ± 0.28[a]	1.71 ± 0.22[a]	1.66 ± 0.39[a]	2.50 (0.083)	2.76 (0.027)
LL/PL	5.32 ± 1.05[b]	5.69 ± 1.72[ab]	6.01 ± 1.10[a]	6.50 (0.0017)	5.57 ± 1.75[a]	5.73 ± 1.70[a]	5.71 ± 1.51[a]	0.37 (0.693)	0.59 (0.667)
LBA/LTA	1.39 ± 0.19[a]	1.42 ± 0.19[a]	1.41 ± 0.22[a]	1.04 (0.355)	1.40 ± 0.18[a]	1.41 ± 0.19[a]	1.41 ± 0.24[a]	0.12 (0.880)	2.44 (0.046)
LUW/LDW	0.90 ± 0.08[b]	1.04 ± 0.45[a]	0.98 ± 0.12[a]	9.19 (0.0001)	0.98 ± 0.29[a]	0.98 ± 0.36[a]	0.95 ± 0.11[a]	0.76 (0.469)	3.16 (0.014)
UE	10.55 ± 3.4.1[a]	12.61 ± 2.35[b]	4.67 ± 2.08[c]	67.26 (<0.0001)	9.11 ± 4.16[a]	9.070 ± 4.40[a]	9.66 ± 4.41[a]	0.44 (0.647)	0.21 (0.932)
PM	52.36 ± 10.97[a]	34.88 ± 6.48[b]	35.43 ± 17.03[b]	20.23 (<0.0001)	41.84 ± 17.17[a]	40.55 ± 15.19[a]	40.28 ± 11.40[a]	0.14 (0.868)	2.08 (0.090)
SM	204.37 ± 65.43[a]	135.16 ± 44.29[b]	243.19 ± 51.27[c]	29.47 (<0.0001)	184.26 ± 73.38[a]	200.22 ± 67.67[a]	198.23 ± 70.32[a]	0.74 (0.478)	0.48 (0.747)
LE	7.39 ± 1.70[a]	10.35 ± 2.37[b]	3.54 ± 1.44[c]	99.78 (<0.0001)	7.04 ± 3.53[a]	6.69 ± 3.09[a]	7.54 ± 3.51[a]	1.57 (0.214)	0.86 (0.495)
SD	512.77 ± 93.15[a]	508.63 ± 62.74[a]	548.13 ± 61.02[a]	2.54 (0.085)	525.8 ± 72.78[a]	523.8 ± 85.97[a]	519.93 ± 67.86[a]	0.05 (0.953)	1.01 (0.407)

Note: Leaf Length (LL), Leaf Width (LW), Leaf Middle Width (LMW), Leaf Upper Quarter Width (LUW), Leaf Down Quarter Width (LDW), Petiole Length (PL), Leaf Area (LA), Leaf Perimeter (LP), Specific Leaf Area (SLA), Leaf Thickness (LT), Leaf Base Angle (LBA), Leaf Tip Angle (LTA), Leaf Index (LL/LW), Leaf Area/Perimeter (LA/LP), Leaf Length/Petiole Length (LL/PL), Leaf Base Angle/Tip Angle (LBA/LTA), Leaf Upper Quarter Width/Down Quarter (LUQW/LDQW), Upper Epidermis (UE), Palisade Mesophyll (PM), Spongy Mesophyll (SM), Lower Epidermis (LE), Stomata Density (SD). Letters (a), (b), and (c) next to the mean values (e.g., 14.61±1.61[a]) represent the results of a post-hoc Tukey's HSD test conducted after the two-way ANOVA. Same letter (e.g., all groups marked with a) → No significant difference between those groups. Different letters (e.g., a, b, or c) → Statistically significant difference (P<0.05) between those groups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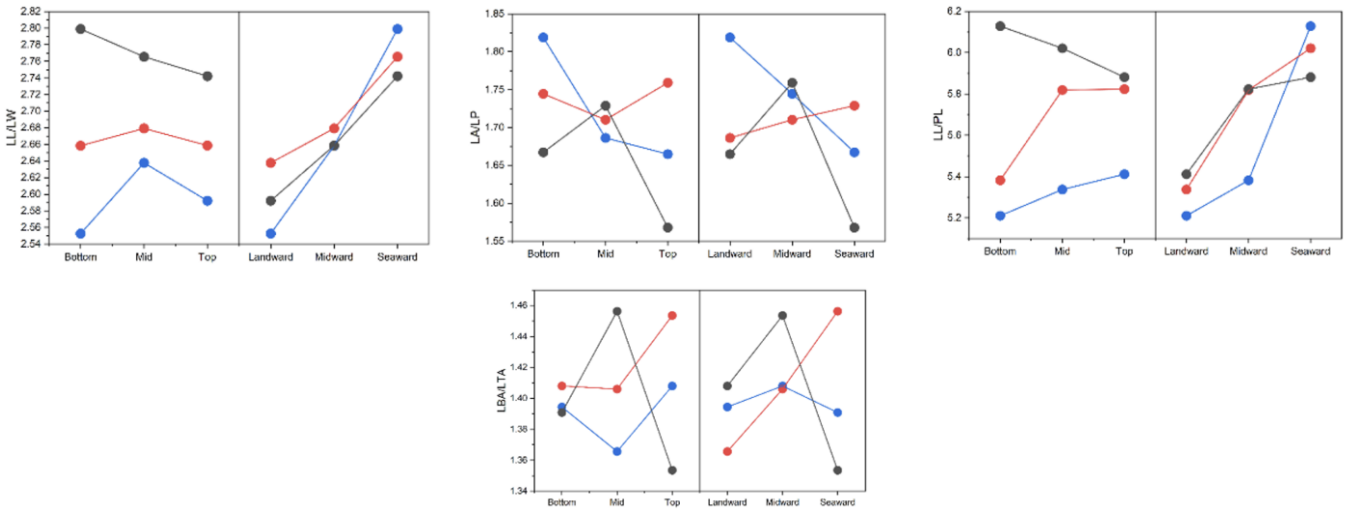

Figure 5. Coastal gradient and canopy light zone interactions across 22 leaf parameters

Canopy light zones further intensify the variability in leaf traits, driven by differences in light availability across the vertical canopy (Simard et al. 2019). Leaves exposed to direct sunlight, typically in the top canopy, exhibit thicker mesophyll layers and smaller surface areas to reduce water loss through transpiration and withstand high light intensities (Vieira et al. 2014). Conversely, leaves in the shaded lower canopy adapt by becoming broader and thinner, optimizing light capture to perform photosynthesis efficiently under low-light conditions (Simard et al. 2019). The interaction of these two factors, i.e., coastal gradients and canopy light zones, create a complex interplay where their combined influence leads to significant plasticity in certain traits (He et al. 2021), as indicated by measurable interaction effects (e.g., F-values with $p<0.05$). This synergy underscores the dynamic nature of plant adaptation, demonstrating how environmental factors work together to shape the functional and structural attributes of leaves. Understanding these interactions is vital for informing conservation strategies and managing ecosystems in coastal areas increasingly threatened by climate change and human activities (Vieira et al. 2014).

Recent studies emphasize the significant role of coastal gradients and canopy light zones in shaping leaf morphological and anatomical plasticity. Coastal gradients, such as salinity and tidal variations, drive adaptations like increased leaf thickness and reduced stomatal density, optimizing water retention, and minimizing osmotic stress in *Heritiera fomes* Banks (Khan et al. 2020). Concurrently, light availability across canopy zones influences leaf structure; plants exposed to higher light intensities develop thicker mesophyll layers to prevent photo damage (Fotis and Curtis 2017), while shaded leaves adapt by expanding surface areas to maximize light capture (Simpson et al. 2017). These combined environmental factors lead to distinct adaptations that enhance photosynthesis and stress tolerance in mangroves (Reef and Lovelock 2020). Such plasticity underscores the resilience of mangroves to environmental challenges and highlights the importance of understanding these dynamics for effective conservation strategies (Tobing et al. 2022).

Stomatal density of *Rhizophora apiculata* across coastal gradients and canopy light zones

Stomatal Density (SD) has no significant difference across all canopies light zones and coastal gradients (Table 2). Across canopy light zones, the bottom canopy has the highest stomatal density, specifically in the midward zone (Figure 5). Additionally, across coastal zones, the seaward zone has the highest stomatal density, specifically in the top canopy. The result shows that in the midward zone, the bottom canopy displays the highest stomatal density, suggesting a response to reduced light availability. This gives insights and aligns with studies that also focus on other *Rhizophora* species indicating that plants in shaded environments increase stomatal density to optimize CO_2 uptake for photosynthesis (Bai et al. 2023; Wijaya et al. 2024). Conversely, the top canopy in the seaward zone exhibits the highest stomatal density, likely reflecting adaptations to intense sunlight, high salinity, and tidal stress, this trait may support rapid gas exchange during brief stomatal openings, compensated by other water-saving anatomical or physiological traits. This agrees with research on mangrove zonation, highlighting that stomatal traits are influenced by environmental stressors to optimize gas exchange and maintain water balance (Peel et al. 2017; Rangkuti et al. 2025). These results underscore the species' ability to adjust physiological traits in response to varying microclimatic and environmental pressures within mangrove ecosystems.

According to Peel et al. (2017), *Rhizophora mangle* L. has lower stomatal density with lower salinity and higher stomatal density with increasing salinity due to the reduction of leaf size in saline environments. However, no significant variation in stomatal density across coastal gradients and canopy light zones may suggest that *R. apiculata* maintains a conserved stomatal strategy. This stability indicates that gas exchange regulation may rely

more on stomatal behavior or other anatomical adaptations rather than variation in stomatal number. The result could also be due to a lack of representative samples for the stomatal density, with only 90 leaves tested out of 450 total leaves. This topic requires further examination to address current limitations.

Association of morphological and anatomical parameters with coastal gradients

The association of 17 morphological parameters across three coastal gradients: landward, midward, and seaward is presented in Figure 6.A. The first two principal components (PC1 and PC2) explain a total of 53.4% of the variance, with PC1 contributing 41.3% and PC2 contributing 12.1%. Points represent individual leaf samples from each zone, color-coded to reflect their respective coastal gradients (black: landward, red: midward, green: seaward), while ellipses depict the 95% confidence intervals for each group, showcasing data spread within each gradient. The vectors represent the loadings of morphological traits, where the length of each vector indicates its contribution to PC1 and PC2. Traits such as LL, LW, LA/LP, LMW, LDQW, PL, and LUQW exhibit strong positive loadings on PC1, suggesting these parameters significantly drive variation across the coastal zones. Notably, midward samples cluster towards higher PC1 scores, highlighting enhanced development of these traits in the midward zone. This zone likely provides favorable conditions, such as a balanced combination of substrate texture, salinity, and tidal range, supporting optimal leaf development.

Landward samples are clustered towards lower PC2 scores, indicating adaptations, such as increased LTA in response to reduced water availability and terrestrial stresses. Meanwhile, seaward samples occupy an intermediate position, reflecting adaptations to higher salinity and tidal inundation through traits like increased LBA, which enhances water retention and nutrient absorption. These patterns align with findings that environmental factors, such as salinity and light availability, significantly influence leaf morphology and overall plant physiology (Yang et al. 2021). The association of leaf anatomical parameters with coastal gradients is presented in Figure 6.B.

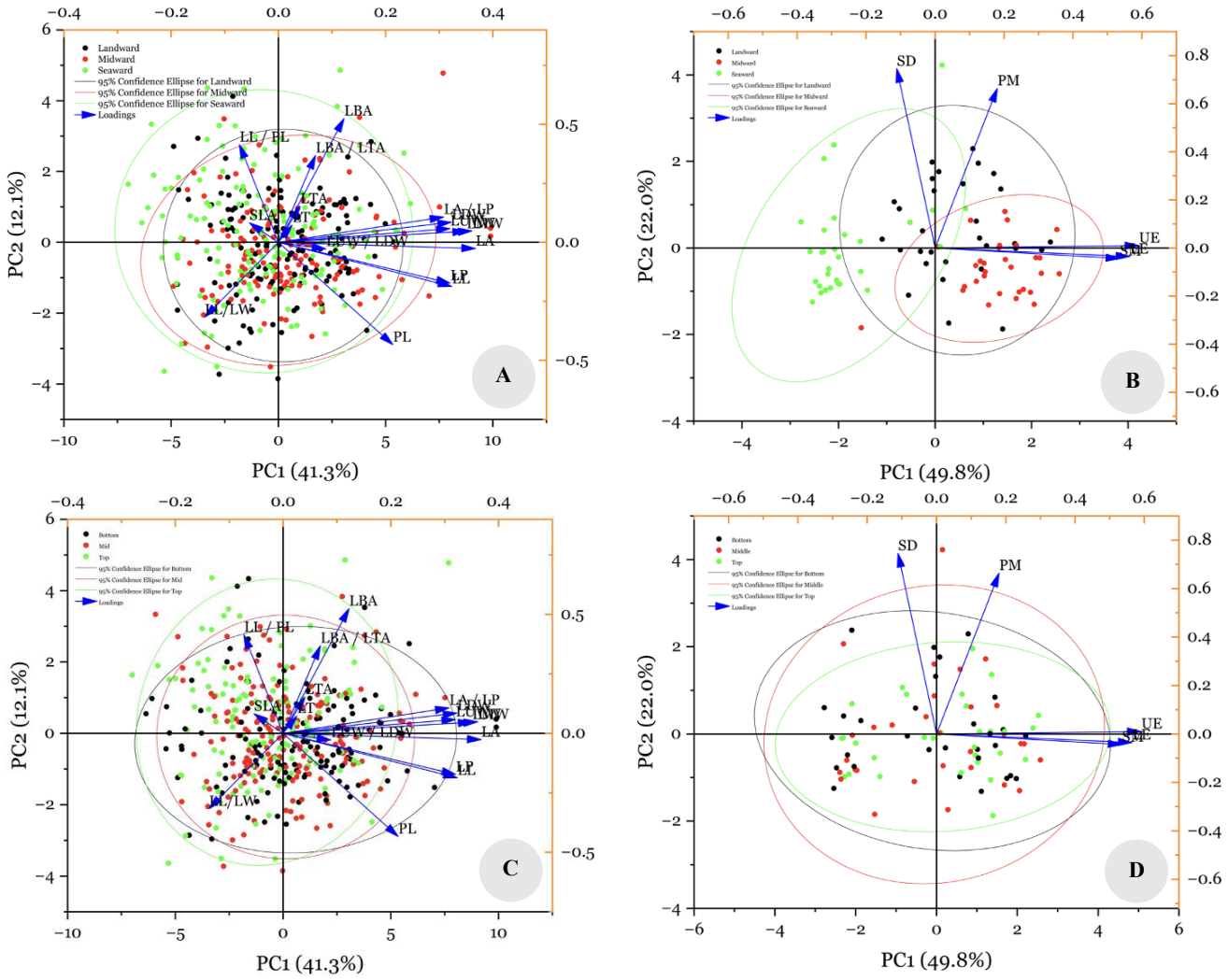

Figure 6. Relationships of leaf morphological and anatomical traits to: A and B. The coastal gradients, C and D. Canopy light zones

The PCA biplot shows that PC1 and PC2 explain 63.3% of the variance, with PC1 contributing 41.3% and PC2 contributing 22.0%. The ellipses represent the 95% confidence intervals for each coastal gradient, reflecting within-group variability. Four anatomical parameters, i.e., PM (palisade mesophyll), SM (spongy mesophyll), UE (upper epidermis), and LE (lower epidermis), show varying contributions to PC1 and PC2. The separation along PC1 indicates a strong environmental gradient affecting leaf anatomy. Landward samples have high positive values on PC1, driven by thicker UE and LE, likely adaptations to reduce water loss from and enhance structural protection against terrestrial stressors, such as reduced humidity and higher temperatures (Liu et al. 2020). In contrast, seaward samples show negative PC1 values, reflecting thinner epidermal layers and reduced SM. This adaptation may minimize energy use while mitigating salinity and tidal stresses (Naskar and Palit 2015). Midward samples cluster centrally, suggesting a transitional zone with mixed anatomical traits. PM exhibits a positive correlation with PC1, indicating increased palisade mesophyll thickness in landward zones, likely driven by higher light availability (John et al. 2013). The overlapping ellipses along PC2, which account for 22.0% of the variance, indicate substantial within-group variability, suggesting the influence of other factors such as nutrient availability or localized microclimatic variations on leaf anatomy (Yang et al. 2021).

Association of morphological and anatomical parameters with canopy light zones

The association of 17 morphological parameters across three canopy light zones: bottom, middle, and top is presented in Figure 6.C. The first two principal components (PC1 and PC2) explain a total of 53.4% of the variance, with PC1 contributing 41.3% and PC2 contributing 12.1%. Points represent individual leaf samples from each canopy position, color-coded to reflect their respective light zones (black: bottom, red: middle, green: top), while ellipses depict the 95% confidence intervals for each group, showcasing data spread within each zone. The vectors represent the loadings of morphological traits, where the length of each vector indicates its contribution to PC1 and PC2. Traits such as LL, LW, LA/LP, LMW, LDQW, PL, and LUQW exhibit strong positive loadings on PC1, reflecting their enhanced development in bottom canopy leaves. These adaptations optimize light capture and resource acquisition under low-light conditions, consistent with the shade avoidance syndrome, which promotes increased leaf area and broader structures to intercept more light (Casal and Fankhauser 2023).

In contrast, the LUQW/LDQW ratio shows a negative correlation with PC1, suggesting reduced development of this trait in bottom canopy leaves and more pronounced values in middle canopy leaves. This pattern indicates that the middle canopy strikes a balance between maximizing leaf surface area and efficient light capture. The lesser differentiation along PC2, with overlapping confidence ellipses, suggests that other environmental factors, such as water or nutrient availability, also contribute to morphological differences within canopy light zones. The association of four-leaf anatomical traits, i.e., Palisade Mesophyll (PM), Spongy Mesophyll (SM), Upper Epidermis (UE), and Lower Epidermis (LE) with canopy light zones is presented in Figure 6.D. The PCA biplot reveals that PC1 explains 49.8% of the variance, while PC2 accounts for 22.0%, representing a combined 71.8% of the total variation. The separation along PC1 highlights the significant influence of light availability on anatomical traits across the canopy. Palisade Mesophyll (PM) and Spongy Mesophyll (SM) show strong positive loadings on PC1, indicating their enhanced development in middle and top canopy leaves. The PM, located closer to the surface, absorbs light efficiently, while the SM facilitates gas exchange, aligning with the favorable light conditions in these zones. In contrast, Upper Epidermis (UE) and Lower Epidermis (LE) are more developed in bottom canopy leaves, likely as an adaptation to lower light conditions. A thicker epidermis may prevent light from penetrating too deeply, protecting internal tissues from photoinhibition or damage. Additionally, a well-developed SM in the bottom canopy maximizes gas exchange, supporting photosynthetic efficiency in shaded environments. The overlapping confidence ellipses along PC2 suggest substantial within-group variability, highlighting the influence of other environmental factors, such as microclimatic variations, water availability, or nutrient distribution, on leaf anatomy within the canopy.

Leaf morphological and anatomical plasticity index

Plants are exposed to heterogeneity in the environment where new stress factors, such as climate change, land use change, and invasiveness are introduced, and where inter- and intraspecies differences may reflect resource limitation or environmental stress factors (Gratani 2014). The leaf morphological and anatomical plasticity index of *R. apiculata* reflects its adaptive strategies to environmental stressors, particularly salinity. Phenotypic plasticity is considered one of the major means by which plants can cope with environmental factor variability. To measure the phenotypic plasticity a PI was applied as it provides a numerical value that represents the extent of variation in specific traits (such as leaf morphology and anatomy) under different environmental conditions on the maximum and minimum values measured for each leaf parameter, aiming to observe the sensitivity of each parameter across canopy light positions and coastal gradients. This allows for a standardized comparison across different studies and species. The plasticity index of various parameters from different canopies and zonation where the index ranges from 0.2 (least plasticity) to 1.0 (maximum plasticity) (Figure 7). The landward zone has the least plasticity with Leaf Downward Width (LDW) and Leaf Width (LW) particularly noticeable in the bottom and middle canopy. Seaward plants have the highest plasticity with LA and LL parameters. Meanwhile, the top canopy leaves have the least LL plasticity, apart from the seaward zone, but have higher LW and SLA. The middle canopy has the highest index for the PL and LT and the bottom canopy has higher LA plasticity.

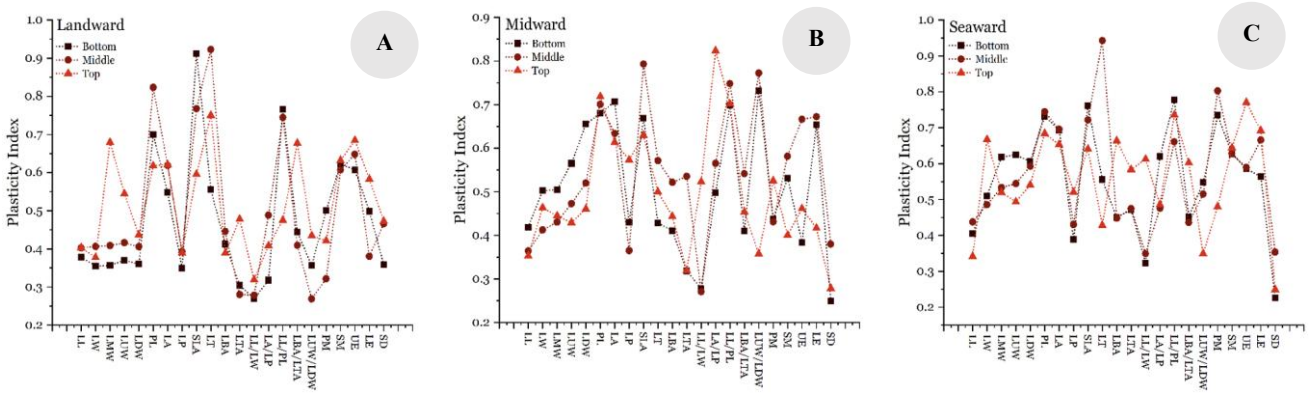

Figure 7. Plasticity index of various leaf morphological and anatomical parameters in: A. Top, B. Middle, C. Bottom canopy light zone

In the landward zone, LMW, LUW, LBA/LTA, and SM have the greatest plasticity index in the top canopy (ranging from 0.54 to 0.68). This could be due to the top canopy being exposed to higher light intensity, which can lead to greater variability in traits captured in high-light environments (Lambers and Oliveira 2019). The PL, LA, SLA, LT, LL/PL, SM, and UE have the greatest plasticity from the middle canopy (ranging from 0.6 to 0.92), and leaf traits in intermediate light conditions reflect adaptations that enhance photosynthetic performance while minimizing water loss (Naskar et al. 2021; Eskelinen et al. 2022). Longer Petioles (PL) may help leaves reach for available light, while larger Leaf Areas (LA) enhance photosynthetic capacity. The SLA and LL/PL have the highest index in the bottom canopy (0.91 and 0.77). This reflects the need for plants to maximize light capture in shaded environments. Sun-exposed populations develop well-developed palisade parenchyma, enhancing photosynthetic rates and reducing photoinhibition under high-light conditions (Magota et al. 2024).

In the midward zone, LL/LW, LA/LP, and PM are more prominent in the top canopy as the leaves are exposed to high light intensities. The adaptations such as higher leaf length and width ratios allow for better light capture and reduced shading of lower leaves. The thicker Palisade Mesophyll is also crucial in maximizing light absorption and energy production (Starzecki 2015). The SLA, LT, LBA, LTA, LL/PL, LBA/LTA, LUW/LDW, SM, UE, LE, and SD have the highest index in the middle canopy ranging from 0.38 to 0.79. The middle canopy experiences a mix of light and shade, leading to optimizing photosynthesis under variable light conditions. Higher specific leaf area and leaf thickness allow for efficient light capture while managing water retention. The presence of spongy mesophyll and well-developed epidermis aids in gas exchange and protection against environmental stressors (Baillie and Fleming 2020). The LL, LW, LMW, LUW, LDW, and LA are more prominent in the bottom canopy, ranging from 0.42 to 0.71. Light Availability is significantly lowered, and leaves tend to be broader and larger to maximize light interception from the Bottom Canopy. Larger traits help maximize light capture, which is critical in the bottom canopy for survival in low-light environments (Niinemets and Tobias 2019).

In the seaward zone, LW, LP, LBA, LTA, LL/LW, LBA/LTA, UE, and LE have the highest plasticity index in the top canopy (ranging from 0.52 to 0.77). The top canopy receives direct sunlight necessitating adaptations that allow leaves to efficiently capture light while minimizing photodamage, the plasticity in traits allows morphological adjustment to optimize light interception and reduce heat stress (Simard et al. 2019). The middle, which experiences a mix of direct and diffuse light canopy, is more pronounced with parameters, such as LL, PL, LT, and PM (0.44-0.94). The higher plasticity index indicates that plants in this zone can significantly alter their leaf traits to optimize photosynthesis under varying light conditions (Falster et al. 2018). The bottom canopy is more prominent on LMW, LUW, LDW, SLA, LA/LP, LL/PL, LUW, and LDW parameters with plasticity index ranging from 0.55 to 0.78 that focuses on optimizing leaf structure for light capture and minimizing water loss. At low light intensity, photosynthesis and plant growth are reduced. Plants respond to changing light conditions by adjusting a suite of morphological and physiological traits (Gommers et al. 2013).

Implication for conservation management

The morphological and anatomical plasticity of *R. apiculata* leaves across coastal gradients and light regimes is well-documented and carries significant implications for mangrove conservation practices. The high phenotypic plasticity observed in key leaf traits such as leaf width, petiole length, mesophyll thickness, and stomatal density illustrates the species' capacity to adapt to a wide range of abiotic conditions. This plasticity is essential in enhancing tolerance to environmental stresses, including salinity fluctuations, tidal flooding, and light variability, all of which are exacerbated by climate change and human disturbance (Gratani 2014; Wang et al. 2021). As environmental conditions continue to shift, the ability of *R. apiculata* to exhibit morphological adjustments is crucial for its survival, particularly in the fluctuating intertidal environments it inhabits.

The structural flexibility of *R. apiculata* leaves not only facilitates the optimization of photosynthetic performance but also plays a pivotal role in regulating water balance and improving resource-use efficiency. This flexibility is key for thriving in intertidal zones that experience constant environmental variability (Karabourniotis et al. 2021). Morphological variations, especially in the mesophyll and epidermal layers, suggest that the species' plastic responses are not merely transient but integral to ensuring long-term ecosystem stability (He et al. 2021). These findings underscore the importance of incorporating trait-based assessments into conservation strategies, as such traits are critical in understanding how species respond to environmental pressures over time.

From a restoration standpoint, the phenotypic plasticity observed in *R. apiculata* should inform conservation planning, particularly in the selection of propagules or donor populations that possess leaf traits aligned with the environmental conditions of target restoration sites. This approach can enhance the success of mangrove restoration efforts by increasing establishment success and ensuring that newly planted populations are well-suited to local environmental conditions (Ellison et al. 2020). Furthermore, regular monitoring of leaf traits can serve as an early warning system for environmental stress, helping to detect ecological shifts before they escalate into widespread ecosystem degradation (Muscarella et al. 2017). In this context, long-term monitoring of functional traits across microhabitats will be vital for adaptive management, enabling the promotion of genetic diversity and trait variability, which are essential for maintaining resilient ecosystems in the face of environmental change (del Campo et al. 2022).

The application of trait-based ecological theory to mangrove conservation offers a powerful predictive framework for anticipating species' responses to ongoing environmental changes (Li et al. 2018). This framework can be instrumental in designing effective conservation measures, such as establishing buffer zones, improving habitat connectivity, and preserving the evolutionary potential of mangrove populations. As coastal ecosystems become increasingly vulnerable to climate change, protecting not only the *R. apiculata* populations but also their capacity for adaptive variation will be essential for sustaining critical ecosystem services and biodiversity. However, it is crucial to recognize that, while mangroves like *R. apiculata* demonstrate remarkable plasticity in their leaf morphology to cope with varying salinity, light, and nutrient conditions, their ability to continue adapting to extreme environmental stresses, such as rising sea levels and pollution, may be limited over time.

Prolonged exposure to severe environmental conditions could diminish the adaptive capacity of *R. apiculata*, especially when compounded by factors such as genetic constraints, energy demands, and the aging of mangrove trees. These factors can restrict the species' ability to sustain its plasticity, potentially leading to reduced resilience and growth in the long term. Thus, while *R. apiculata* remains ecologically adaptable and serves as a keystone species in coastal defense and biodiversity preservation, conservation strategies must consider both the species' current plasticity and its future potential for adaptation under changing environmental conditions. Understanding and applying these insights will be critical in developing climate-adaptive, site-specific mangrove conservation measures that ensure the long-term health and functionality of coastal ecosystems.

In conclusion, this study highlights the remarkable capacity of *R. apiculata* to adjust its leaf morphological and anatomical traits in response to variations in coastal gradients and canopy light conditions. The species demonstrated significant phenotypic plasticity in key traits such as stomatal density, leaf length, and palisade and mesophyll thickness. These are traits that enable efficient resource utilization and sustained physiological performance under stressors like salinity, tidal fluctuation, and variable light availability. These adaptive responses underscore the ecological resilience of *R. apiculata* and its potential as a keystone species in mangrove conservation and restoration. The findings reinforce the importance of incorporating trait-based assessments into conservation planning, particularly as mangrove ecosystems face mounting pressures from climate change and human disturbance. Continued research on species-specific adaptive strategies will be critical for informing adaptive management and safeguarding the long-term stability and functionality of mangrove habitats.

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