

Morphological traits and chlorophyll content of *Laguncularia racemosa* leaves in two ecosystem types along the coastline of Guyana

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ABSTRACT

Coastline ecosystems are resilient, and the mangrove species that inhabit them are well-suited to deal with harsh environmental stresses. Mangrove leaves are specialised plant structures that enable them to preserve their photosynthetic capability and functionality despite frequent changes in their habitats. Along the coastline of Guyana, we studied the morphological characteristics and chlorophyll content of 400 leaves taken from *Laguncularia racemosa* (L.) C.F. Gaertn., 1807 (Myrtales Combretaceae) trees found in Number 6 Village and Wellington Park mangrove ecosystems. The nearest individual sampling method was utilised to sample leaves throughout the wet and dry seasons. Our results demonstrate that *Laguncularia racemosa* leaves are mesophyllous, and leaf characteristics such as length, width, area, perimeter, mass, leaf specific area, and relative water content differed between the two ecosystem types, in both seasons. Significant correlations between leaf parameters were documented ($p < 0.05$, $R > 0.75$), with the Number 6 Village ecosystem during the dry season and the Wellington Park ecosystem during the wet season having greater values. Differences in chlorophyll content were also seen in the two types of ecosystems, but not seasonally. The results of our study suggest, to some extent, that plant structures can exhibit site-specific characteristics to preserve their survivability in different ecosystem types.

KEY WORDS

Ecosystem; Guyana; *Laguncularia racemosa*; leaves; mangroves.

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INTRODUCTION

Tropical mangrove forests constitute one of the most prolific ecosystems on the planet, despite their restricted geographical distribution (Bui & Lee, 2014). Mangroves are significant ecosystems owing to the ecological services they offer to populations as well as their particular significance for biodiver-

sity (Borges et al., 2017). They withstand environments that are constantly changing and physically demanding, both spatially and temporally, as well as disturbances such as insect infestations, lightnings, storm surges, and tropical cyclones (Nedd et al., 2021). However, despite serving as valuable models for studying physical environment-ecological interactions, coastal mangrove regions have

been cut for human activities, reducing the capability of the mudbanks to become linked to the coastline. This leads to large-scale erosion, susceptibility to strong tides and storms, and a decline in mangrove vegetation (Best et al., 2022).

In this study, we have concentrated on the leaf morphological characteristics and chlorophyll content of the *Laguncularia racemosa* (L.) G.F. Gaertn., 1807 (Myrtales Combretaceae). The morphological, reproductive, and physiological adaptations of *L. racemosa* or ‘white mangrove’ allow it to live in saline coastal regions. The leaves are simple, opposite, elliptical, moderately succulent, and range in length from 1–3 inches (2.54–7.62 cm) (Lonard et al., 2020). The presence of two glands on the petiole right below the leaf base, where excess salt is expelled, is one distinctive feature of the white mangrove as a result of the ecophysiological process of salt exclusion (Victório et al., 2023). Given the high adaptability rate of mangroves, we believe that the study of plant structures such as their leaves is important since any changes in the characteristics of leaves may reflect the type and extent to which environmental stresses act upon them, their coping mechanisms, and the overall health status of the trees themselves.

While there are a few published papers on the subject of mangrove leaves, little is known about the traits of *L. racemosa* leaves in various ecosystem types. However, the overall chlorophyll content and mangrove leaf characteristics may be affected by the type of ecosystem in which they thrive as well as seasonal variations (Kanniah et al., 2021). Changes in the biological structure and function of natural habitats, caused by spatial and ecological disturbances, may lead to habitat disruption and fragmentation in mangrove forests, impacting the overall development and rehabilitation of these ecosystems (Toosi et al., 2022). Changes in the leaf morphological traits can impact light interception capability, photosynthetic efficiency, and plant development, which is deeply connected to nutrition availability, water uptake, productivity, quality, and resilience (Weraduwege et al., 2015). Additionally, chlorophyll content concentrations in mangrove leaves might directly inhibit photosynthetic activity and also represent physiological plant stress, which is evident in certain disturbed forests (Zoletto & Cicuzza, 2022).

Ecosystem types that possess high disturbances

have more plants with damaged and underdeveloped leaves due to stressors including sea level rise, coastal storm damages, herbivore attacks, and pollution (Hespen et al., 2021). Disruptions to the leaf cellular structure can also result in considerable variations in chlorophyll concentration, which endanger the vitality, nutrient cycling, energy flow, and productivity in mangrove ecosystems (Jiang et al., 2022). Seasonality alters several processes in the environment and frequently necessitates adaptive plant responses. Droughts can periodically result in inadequate water and mineral absorption by roots, reduced plant growth, and reduced litter disintegration (Smith-Martin et al., 2019). Moreover, continuous rainfall during the wet and dry seasons has a direct effect on mangrove phenotypic plasticity (Pastor-Guzman et al., 2018). In response to the aforementioned, the purpose of our study was to examine and compare the morphological characteristics and chlorophyll content of *L. racemosa* leaves within two different ecosystem types, for two distinct seasons. Through our findings, we believe that the scientific community will become more cognisant of the extent to which mangrove species exhibit differences in their plant structures in response to seasonal and environmental stressors that affect their functionality in coastline ecosystems.

MATERIAL AND METHOD

Study area

This study was conducted in the dry (August 2022) and wet (December 2022) seasons in mangrove forests located at No. 6 Village, West Coast, Berbice (N 6019'28.40228", W 57033'37.49807") and Wellington Park, East Coast, Corentyne (N 6010'53.69905", W 57014'9.4088") (Figs. 1-3).

The Number 6 Village mangrove forest is a restored ecosystem comprised of very young mangrove trees that have not yet attained maturity (Fig. 3). Our study describes a restored mangrove ecosystem as a replanted ecosystem that is constantly managed and is presently recovering from perturbations to the structure and function of a pre-disturbance ecosystem (Bechtold et al., 2013). After complete degradation, this site was artificially replanted 11 years ago as a part of the Guyana Mangrove Restoration Project (MOA,

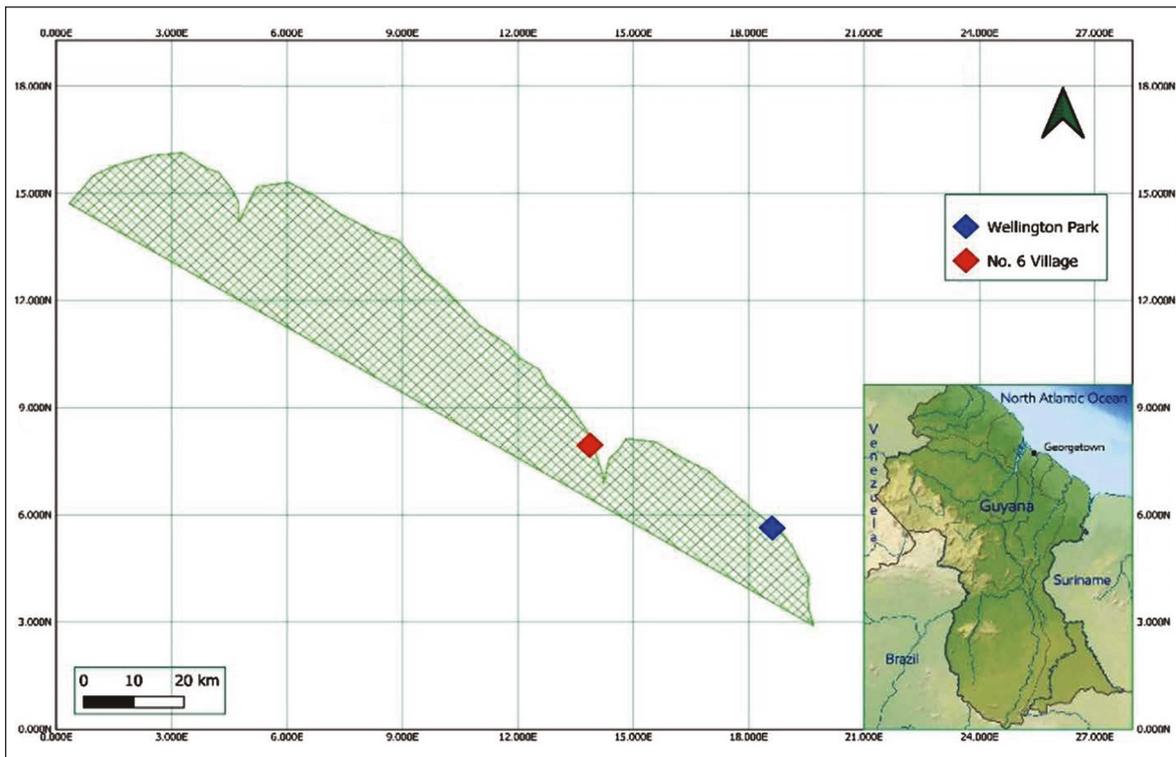


Figure 1. Map of the Guyana coastline showing the locations of the study sites.



Figures 2, 3. Site characteristics of Wellington Park (Fig. 2), and Number 6 Village mangrove forest (Fig. 3).

2016). Due to strict management and monitoring by forest rangers and field officers, this site has attained the status of a ‘young forest’ (Dookie et al., 2022). Within this area, we recorded very low disturbances inclusive of garbage dumping, fishing

activities, grazing livestock, and insect infestation (Table 1).

The mangrove forest located in Wellington Park is classified as a degraded site (Fig. 2). A degraded ecosystem is faced with progressive and gradual

damage caused by ongoing, large, stressful events or small, periodic disturbances that occur with such regularity that natural recovery severely lags or has no time to occur (Ghazoul & Chazdon, 2017). The Wellington Park mangrove forest was previously rehabilitated as part of the Guyana Mangrove Restoration Project (GMRP), which replanted 54,000 seedlings in an attempt to reinforce Guyana’s coastline (EPA, 2022) (Fig. 1). Nevertheless, considerable erosion was documented in this region in 2016, which resulted in a significant decrease in vegetative density. Visible extensive erosion caused by natural forces, as well as visible environmental damage to the mangrove environment, have contributed to the considerable decrease of mangrove forests in this restoration site, impacting sediments, water, vegetative cover, and wildlife species (Fig. 2). Additional noteworthy disturbances found within this site were more anthropogenic than natural and included infrastructure construction, rubbish dumping, burning, grazing, coastal and marine litter, and fishing activities (Oyedotun & Hamer, 2020) (Table 1).

Mangrove Leaf Sampling

To sample leaves from *L. racemosa* trees, the nearest individual sampling method was applied (Barbour et al., 1987). Ten trees were selected along a 200 m transect line 10 m inland from the coastline. The tree closest to the centre of ten (10) random points marked inside the designated transect line was selected (Fig. 4). The distance between every sample point and the nearest tree, as well as their height and diameter at breast height (DBH), were measured. Ten completely developed, healthy,

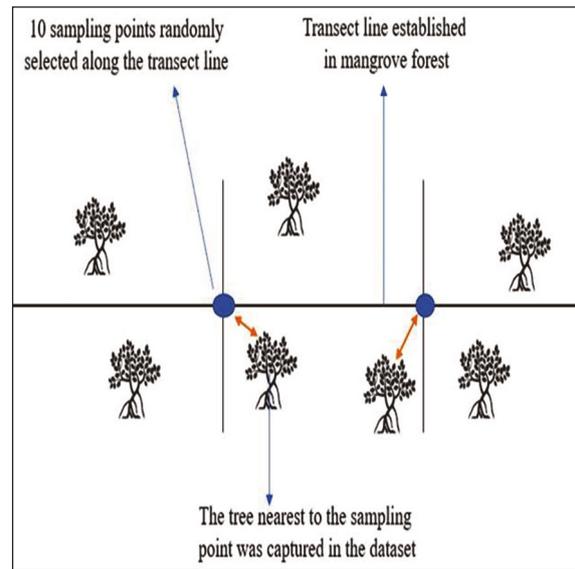


Figure 4. Layout of the nearest individual sampling method (adapted from Elzinga et al.,1998).

green leaves were then gathered between the third and sixth nodes of each tree, on five to seven branches that were substantially exposed to sunlight. Leaves were taken from trees in WP with heights that ranged from 7.35 ± 0.10 m to 7.37 ± 0.10 m while in NO6, leaves were taken from trees with similar heights ranging from 7.18 ± 1.01 m to 7.23 ± 0.10 m. Furthermore, DBH values of trees found in both WP and NO6 mangrove forests conformed to the > 5–10 cm diameter class. DBH values in WP ranged from 9.75 ± 0.22 cm to 9.78 ± 0.22 cm while NO6 DBH values ranged from 7.76 ± 0.17 cm to 7.79 ± 0.17 cm (Table 2).

		TYPES OF DISTURBANCES																
		ANTHROPOGENIC												NATURAL				
EXTENT OF DISTURBANCES	Ecosystem Type	Seashell mining	Lumbering (sawdust)	Infrastructure Development	Garbage Dumping	Fishing activities	Aquaculture	Burning	Sand Mining	Cutting	Agriculture	Grazing	Bark Stripping	Insect Infestation	Erosion	Storms/ Tides	Plant infestation	
		Number 6 Village	1	1	1	3	3	1	2	1	2	1	3	2	4	2	2	2
		Wellington Park	4	4	3	3	5	3	3	3	3	3	4	3	3	5	5	2

Table 1. Types and extent of disturbances occurring within the Number 6 Village and Wellington Park mangrove forests. Key: 1 - Very Low, 2 - Low, 3 - Moderate, 4 - High, 5 - Very High.

Leaf Measurements

The following measurements were taken using traditional methods on the 400 leaves collected in both seasons:

a) Leaf length (LL) and width (WW) (cm): were taken using a ruler on gridded paper.

b) Leaf area (AREA) (cm²): this was calculated using an established allometric equation (Montgomery, 1911). The leaves of *L. racemosa* are oval-elliptical, as such, let A = area, L = length, and W = width:

$$A = \pi \frac{L}{2} \frac{W}{2} = \frac{\pi}{4} LW$$

c) Perimeter (Peri) (cm) and thickness (TK) (mm): the perimeter of the leaves was estimated by measuring the outline of the leaf on graph paper using a string while the thickness was measured using a micrometre screwgauge on the central lamina area.

d) Leaf slenderness (SLEN) =

$$\frac{\text{Leaf Length (LL)}}{\text{Leaf Width (LW)}}$$

e) Leaf density (Density) (g/cm³) (Witkowski & Lamont, 1991) =

$$\text{leaf specific mass} \times \frac{1}{\text{leaf thickness (cm)}}$$

f) Sclerophylly index (IE) =

$$\frac{\text{leaf dry mass (g)}}{2} \times \text{leaf area (dm}^2\text{)}$$

Where sclerophylly (IE > 0.6) and mesophylly (IE < 0.6) (Rizzini, 1976).

g) Leaf specific mass (LSM):

$$\frac{\text{leaf dry mass (g)}}{\text{leaf area (cm}^2\text{)}}$$

h) Specific leaf area (SLA) =

$$\frac{\text{leaf area (cm}^2\text{)}}{\text{leaf dry mass (g)}}$$

i) Fresh mass, turgid mass, dry mass, and Relative water content (RWC):

i) In the field, leaves were weighed to determine their fresh mass (FW).

ii) After floating the leaves in deionised water for four (4) hours, they were reweighed to estimate the turgid mass (TW).

iii) The samples were then wrapped in aluminium foil and oven-dried for 19 minutes at 105 °C, followed by 24 hours at 80 °C after which they were reweighed to determine their dry mass (DW).

iv) The RWC was then determined using the following formula: (Sadeghi-Shoa et al., 2014), Relative Water Content (RWC) =

$$\frac{TFW-DW}{TW-DW} \times 10$$

where TFW = total fresh weight, DW = dried weight and TW = turgid weight.

j) Chlorophyll content

j) Leaf samples were weighed and immediately submerged in 10 mL of dimethyl sulphoxide (DMSO) in 15 mL Falcon tubes enveloped in aluminium foil.

jj) The tubes were then left to incubate at 65 °C for 4 hours.

jjj) After 4 hours, the samples were removed and allowed to cool after which 3 mL individual samples were then deposited into cuvettes with DMSO as the control.

jjv) Samples were then read spectrophotometrically at 645, 663, and 470 nm and the chlorophyll contents were calculated using the Arnon method (1949):

Let A = Absorbance at specific wavelengths, V = final volume of chlorophyll extract in DMSO and W = fresh weight of tissue:

$$\text{Chlorophyll a (C}_a\text{) \{mgg}^{-1}\text{}} = [(12.7A_{663} - 2.69A_{645}) V/W]$$

$$\text{Chlorophyll b (C}_b\text{) \{mgg}^{-1}\text{}} = [(22.9A_{645} - 4.68A_{663}) V/W]$$

$$\text{Total chlorophyll (C}_T\text{) (mgg}^{-1}\text{)} = C_a + C_b = [(20.2D_{645} + 8.02D_{663}) V/W]$$

Statistical analysis

All datasets acquired were subjected to log10 transformations after which they were analysed parametrically at a level of significance level of $p < 0.05$, utilising Microsoft Excel and RStudio programming software (2023.06.1 + 524). The study employed one-way analysis of variance (ANOVA) tests to evaluate the variations in average leaf measurements and chlorophyll content of *L. racemosa* leaves in relation to the ecosystem type. Tukey's Honest Significant Difference (HSD) tests were conducted for post hoc analysis in order to identify the ecosystem type that exhibited significant differences for each leaf parameter. Paired T-tests were performed on datasets to assess the prevalence of seasonality in leaf dimensions and chlorophyll content. Pearson correlation coefficients were utilised to assess the degree of association between the leaf measurements in both seasons for the two ecosystems. The study conducted multiple regression analyses to deduce the level of significance in the linear relationships between leaf dimensions and chlorophyll content concerning location. Principal component analyses (PCA) were conducted on the datasets constructed for both seasons to visualise trends and interrelationships established between the leaf parameters for both ecosystem types.

RESULTS

Leaf parameters

Leaf measurements collected from the Number 6 Village (NO6) and Wellington Park (WP) mangrove forests were described using a total of fourteen (14) parameters: length (LL), width (WW), thickness (TK), perimeter (Peri), area (AREA), fresh mass (FM), turgid mass (TM), dry mass (DM), slenderness (SLEN), leaf specific mass (LSM), leaf specific area (SLA), density (DENSITY), Sclerophylly Index (IE), and relative water content (RWC)—in the wet season (WS) and the dry season (DS) (Figs. 5, 6).

Ecosystem type

In Table 2, the average values reported for the dry season revealed that NO6 possessed leaves that had greater LL, WW, TK, Peri, AREA, DW, FW, TW, SLA, RWC, and IE than WP. However, leaves in WP had larger SLA and densities than NO6. Furthermore, in the wet season, the leaves from WP had larger average LL, WW, TK, AREA, DW, FW, TW, LSM, SLA, RWC, and IE than the leaves found in NO6. The leaves in NO6, however, had greater perimeters and densities than WP (Tab. 2).

SEASON TYPE	LOCATION	TREE PARAMETERS		LEAF PARAMETERS (Mean ±SE)													
		Height (m)	DBH (cm)	Length (cm)	Width (cm)	Thickness (mm)	Perimeter (cm)	Fresh mass (g)	Turgid mass (g)	Dry Mass (g)	Area (cm ²)	Slenderness	Leaf Specific (LSM) Mass	Leaf Specific (SLA) Area	Density (g/cm ³)	IE	RWC
DRY	Wellington Park	7.35 ±0.10	9.75 ^a ±0.22	7.97 ^b ±0.13	4.71 ^b ±0.72	0.88 ^b ±0.03	20.96 ^b ±0.30	1.12 ^b ±0.03	1.28 ^b ±0.03	0.30 ^b ±0.01	30.00 ^b ±0.84	1.70 ^b ±0.02	0.01 ^b ±0.01	104.85 ^a ±2.86	0.01 ^a ±0.01	0.04 ^b ±0.01	82.90 ^b ±1.50
	No. 6 Village	7.18 ±0.10	7.76 ^b ±0.17	9.03 ^a ±0.11	5.03 ^a ±0.08	1.12 ^a ±0.01	22.49 ^a ±0.32	1.38 ^a ±0.04	1.46 ^a ±0.04	0.39 ^a ±0.01	36.29 ^a ±1.00	1.82 ^a ±0.02	0.01 ^a ±0.01	93.26 ^b ±1.54	0.01 ^b ±0.01	0.08 ^a ±0.01	91.77 ^a ±0.89
WET	Wellington Park	7.37 ±0.10	9.78 ^a ±0.22	9.41 ^a ±0.14	5.07 ±0.09	0.95 ±0.02	23.46 ^a ±0.37	1.53 ±0.05	1.70 ±0.05	0.39 ^a ±0.01	38.19 ^a ±1.15	1.89 ±0.02	0.01 ±0.01	101.42 ±1.85	0.01 ±0.01	0.08 ^a ±0.01	86.26 ^a ±1.41
	Number 6 Village	7.23 ±0.10	7.79 ^b ±0.17	8.49 ^b ±0.11	4.75 ±0.08	0.93 ±0.03	21.27 ^b ±0.39	1.44 ±0.06	1.65 ±0.07	0.35 ^b ±0.01	23.18 ^b ±0.90	1.81 ±0.02	0.01 ±0.01	100.86 ±2.66	0.02 ±0.01	0.06 ^b ±0.01	82.65 ^b ±1.14

Table 2. Average values for leaf and tree measurements obtained from Wellington Park and Number 6 Village forests. Letters in the table show significant pairwise associations using the Tukey Honest Significant Difference (HSD) Test ($p < 0.05$).

A one-way ANOVA test reported significant differences in all fourteen leaf measurements in the dry season. The Tukey HSD test further indicated that the NO6 ecosystem possessed larger values in 12 out of 14 leaf measurements [LL, WW, TK, Peri, AREA, FW, DW, TW, LSM, RWC, IE, SLEN], while the WP ecosystem only possessed leaves with larger LSM and Density values. However, in the wet season, the number of significant differences in leaf measurements in both ecosystem types decreased, as the one-way ANOVA test reported significant results only in LL, Peri, DW, AREA, IE, and RWC. Additionally, the Tukey HSD test indicated that all significant leaf parameters in the wet season were located in WP.

Seasonality

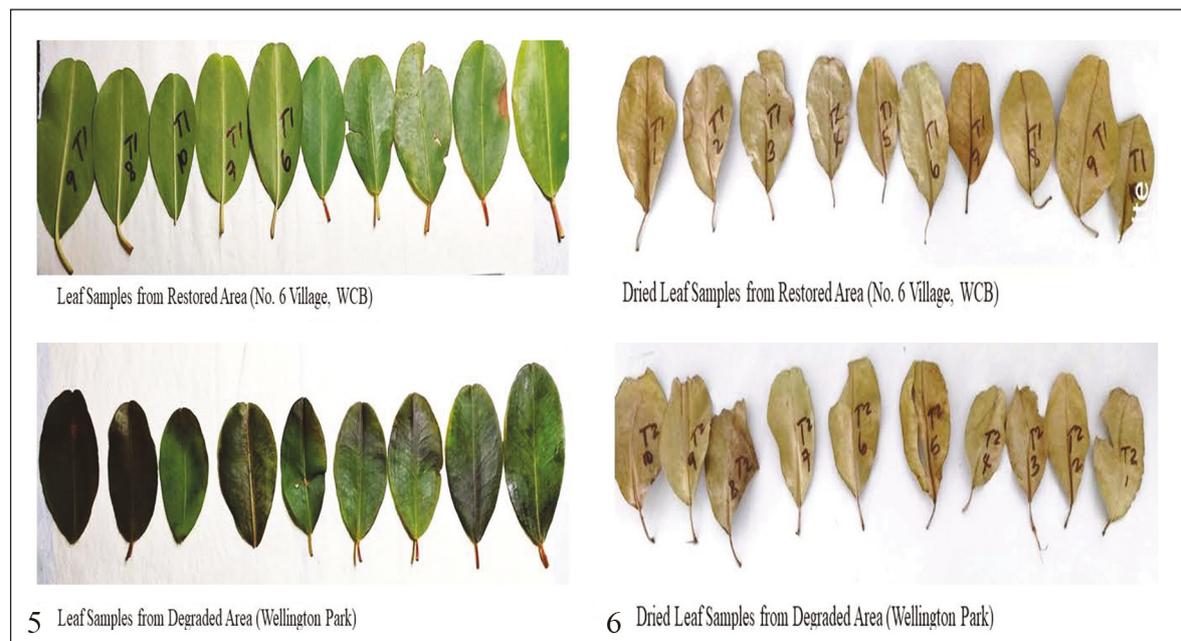
A paired T-test indicated that within the WP ecosystem, statistically significant differences in seasonality ($p < 0.05$) were reported for LL, Peri, AREA, FW, TW, DW, SLEN, and IE values. However, in the NO6 ecosystem, significant differences ($p < 0.05$) were reported for a greater number of leaf parameters including LL, WW, TK, Peri, TW, DW, AREA, IE, and RWC values.

Correlation among leaf parameters

The WP ecosystem showcased several strong, positive correlations ($p < 0.05, R > 0.75$) that were established between leaf parameters such as FW, TW, Area, LL, DW, IE, WW, IE, Peri, and FW for both seasons. Furthermore, strong, negative correlation values ($p < 0.05, R > -0.75$) were reported for SLA - LSM and DENSITY – TK. In the wet season, it was observed that the number of positive correlations between leaf measurements decreased. Further examination of correlation coefficients established in the NO6 ecosystem within both seasons revealed that the strength of positive associations was higher ($R > 0.85$) than WP, but declined in the wet seasons. Parameters such as FW, TW, IE, Area, WW, DW, LL, and Peri maintained strong positive correlations in NO6 while strong, negative correlations were also established between SLA – LSM and DENSITY – SLA ($R > -0.75$).

Multiple Regression Analysis

The established models generated for both seasons predicted that changes in the parameters of the leaves located in the NO6 and WP ecosystems were



Figures 5, 6. Leaf samples from the Number 6 Village and Wellington Park forests after they were Fig. 5 = freshly sampled, and Fig. 6 = dried in the oven to determine their dry masses.

significantly associated with their location in the wet season [$\text{Pr}(>|t|)$ values < 0.05 , adjusted $R^2 = 0.04$, overall p -value = 0.002], but not the dry season [$\text{Pr}(>|t|)$ values > 0.05 , adjusted $R^2 = 0.08$, overall p -value = 0.09].

Principal Component Analysis (PCA)

In the dry season, PC1 and PC2 explained 70.8% of the parameters' total variance. PC1 explained 53.86% of the variance and is mainly represented by the AREA, FW, and DW, while PC2 explained 16.94% of the variance and is mainly represented by LL. PC1 revealed that the NO6 ecosystem shared high values for the variables AREA, WW, IE, FW, DW, LL, TW, Peri, TK, and RWC, and low values for the variables DENSITY and SLA. Furthermore, the WP ecosystem shared high values for the variables SLA, DENSITY and SLEN, and low values for variables like TK, DW, TW, FW, LSM, IE, Peri, WW, AREA, and LL (Fig. 7). Additionally, PC2 showcased values that were directly opposite those that were reported for PC1 for both ecosystems.

In the wet season, PC1 and PC2 explained 74.43% of the parameters' total variance; PC1 explained 65.30% and PC2 explained 16.05% and were mainly represented by the AREA and IE. PC1 revealed that the NO6 ecosystem shared high values for the variables AREA, IE, WW, LL, Peri, FW, TW, DW, TK, and RWC, and low values for the variables DENSITY, SLEN, and SLA (Fig. 8). Additionally, the WP ecosystem shared high values for the variables SLA, SLEN, and DENSITY, and low values for the variables DW, IE, AREA, WW, FW, TW, TK, Peri, LL, and LSM. PC2 showcased opposite those reported for the variables in PC1 for both ecosystems.

Chlorophyll Content of Leaves

Average values (mmg^{-1}) indicated that in the dry season, the WP ecosystem possessed higher chlorophyll content (C_a : 97.24 ± 0.34 , C_b : 73.57 ± 0.19 , C_T : 170.76 ± 0.23), when compared to the NO6 ecosystem (C_a : 75.81 ± 0.17 , C_b : 51.77 ± 0.03 , C_T : 127.54 ± 0.16). This trend was also evident in the wet season with the WP ecosystem possessing higher values in chlorophyll content (C_a : 104.04 ± 0.52 , C_b : 259.82 ± 2.01 , C_T : 190.59 ± 2.06), when compared to the dry season, and to the NO6 ecosystem (C_a :

78.04 ± 0.64 , C_b : 62.13 ± 0.61 , C_T : 140.12 ± 0.43). A one-way ANOVA test reported statistically significant differences ($p < 0.05$) between locations in chlorophyll a and total chlorophyll content for the dry season only. The Tukey test revealed that the chlorophyll a and total chlorophyll contents were higher in WP than in the NO6 ecosystem.

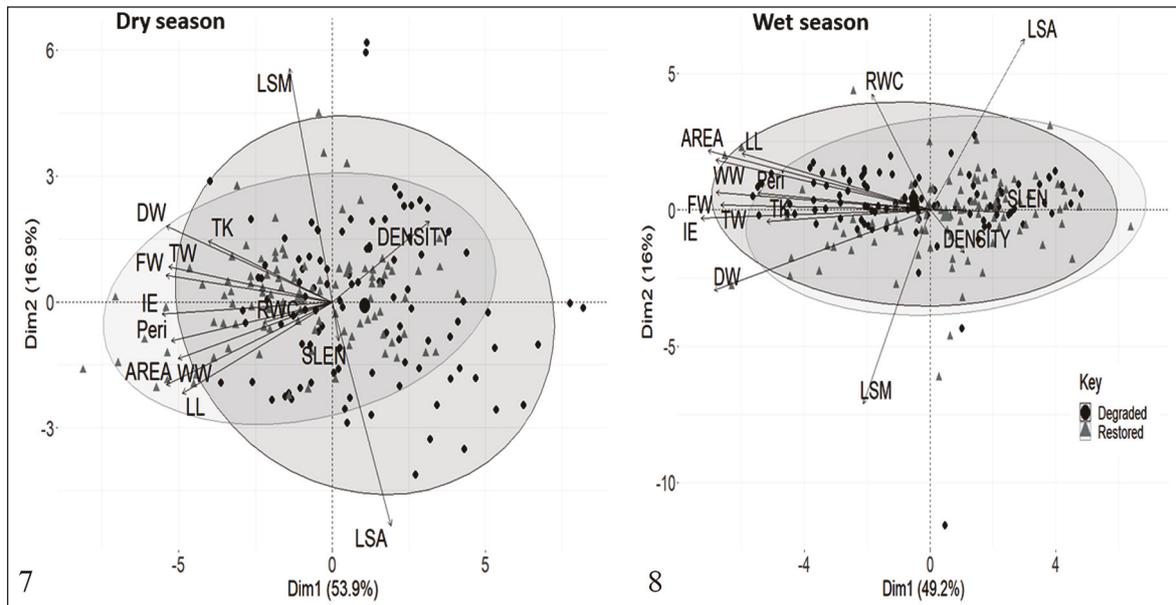
Paired T-tests reported insignificant differences ($p > 0.05$) in seasonality for chlorophyll content (a, b, and total) of leaves found in both mangrove ecosystems.

The established models generated for both seasons using multiple regression analysis predicted that changes in the chlorophyll content of the leaves located in the NO6 and WP ecosystems were significantly associated with their location in the dry season [$\text{Pr}(>|t|)$ values < 0.05 , adjusted $R^2 = 0.39$, overall p -value = 0.002], and the wet season [$\text{Pr}(>|t|)$ values < 0.05 , adjusted $R^2 = 0.16$, overall p -value = 0.05].

DISCUSSION

Ecosystem Type

Laguncularia racemosa trees located in NO6 and WP mangrove ecosystems displayed differences in leaf morphological features. This may be due to direct environmental effects on plant growth from physical conditions, or from an indirect environmental influence which can result from a developmental response (Li et al., 2015). Water deficiency and excess, temperature, nutrient availability, and light are among the environmental factors that impact plant development (Li et al., 2019). The variety in leaf size and shape may also be attributable to climatic conditions, which may affect the length, width, perimeter, thickness, and area as seen in both ecosystems. The height of the trees can additionally affect leaf traits due to the needs of vascular transport of sugars, the leaves of taller trees tend to be smaller and more uniformly sized than the leaves of shorter trees, which are often broader (Jensen & Zwieniecki, 2013). Additionally, the age of the trees is a further potentially significant aspect since the shift from juvenile to adulthood in several plant species is accompanied by a change in leaf size and form (Kuusk et al., 2018). The trees in the WP area were taller than those in the NO6 and may also indicate their degree of maturity, with the trees in WP,



Figures 7, 8. Ordination Biplot of leaf parameters in PC1 and PC2 and their value contribution to the plane construction in the dry Season (Fig. 7), and wet season (Fig. 8) for both ecosystem types.

having reached a “mature” stage in contrast to those in NO6, which comprise “new growth” trees. In contrast to what was observed in WP, the DBH is known to influence leaf size, and leaf dry mass, since bigger trees tend to have greater leaf shapes and sizes (Ma et al., 2022). Trees in the NO6 area were replanted by humans, which would have decreased the needed spacing between them as the trees grew in size, resulting in competition for resources. As a result, younger trees in NO6 were shaded by the older trees’ canopies, which lowered the rate of transpiration, water loss, and sunlight availability to the leaves, leading them to produce larger leaf sizes. On the contrary, extreme water loss and greater thermal gradients were more pronounced in WP with its dry soils, high disturbance levels, and sparse understory. This may have led to a decline in leaf size as an adaptation to water shortages, high saline levels, and higher transpiration rates under variable tidal circumstances (Naskar & Palit, 2014).

Soil enrichment can be enhanced by leaf litter decomposition, which may occur more often in the NO6 ecosystem since there are a greater number of trees, i.e., more leaves contributing to forest floor litter (Vinh et al., 2020). SLA values observed for both environments indicated that *L. racemosa* trees were able to appropriately acquire resources and sustain biomass production conservation mechanisms under

variable light circumstances. LMA varies across climatic gradients and species, with higher average levels in hotter, drier, and more intensely illuminated environments (Flores et al., 2014), the opposite of what was reported in our investigation for both ecosystem types. Estimated sclerophylly values indicated that *L. racemosa* leaves in both habitat types and seasons were mesophyllous in nature, contrary to the findings of Quadros et al. (2021) as changes in leaf mass may be correlated with alterations in water chemistry that are driven by physiological mechanisms for altering water use efficiency. Kodikara et al. (2020) reported that soil dehydration and hypersaline circumstances can impede the dry weight of leaves, which was noticeable in the WP environment during the dry season. Leaf expansion provides additional light-capturing surfaces, but the increase in surface area is accompanied by proportionally significant increases in the mass of structural components, especially the leafstalk, the midrib, and the supporting components in the leaf lamina (Guo et al., 2021). Larger leaves, such as those in the NO6 ecosystem, require more complicated and effective hydraulic systems and more mechanically stiff tissues for leaf lamina mechanical support; these requirements are likely to increase the dry mass necessary to physiologically and mechanically maintain the photosynthetic tissues.

Seasonality

Leaves exposed to rain experience changes in their leaf surfaces due to degrading waxes, which alters leaf orientation angles, causing local distortion, bending, and flapping (Roth-Nebelsick et al., 2022). Spatial-temporal fluctuations in dissolved nutrients can also influence leaf growth, as nutrient ratios may exhibit seasonal switching of nutrients which can result in shortages during wet and dry seasons (Rao et al., 2018). Variations in leaf measures in the WP forest indicated that the wet season is much more favourable than the dry season for leaf productivity. Due to precipitation, higher values of photosynthesis and respiration in the ecosystem are more evident within mangrove ecosystems during the wet season. Nevertheless, in dry seasons, decreases in cloudiness can result in a greater radiation supply in the forest canopy, decreased precipitation rates, and an increase in soil salinity. This can favour an increase in foliar abscission, affecting the ecosystem's carbon source and sink functions (Freire et al., 2021). As a result, leaves may alter in size and mass during the dry season to preserve water, which was evident in the WP ecosystem.

Seasonal variations in leaf mass may also lead to alterations in the total relative water content of leaves. In response to variations in water concentration and availability, the reactions to water stress of tree species in various forest ages vary substantially, with trees in younger sites, such as those in the NO6 area, being more resilient than those in the older, WP forest (Unawong et al., 2022). Furthermore, changes in tree density, canopy openness, vertical stratification, and the quantity of forest litter create fluctuations in air temperature and humidity, causing older forests to be warmer and drier than developing forests (Bretfeld et al., 2018). Changes in the leaf masses of plants may also be caused by canopy water interception as a result of higher rainfall during the wet season and dew accumulation, which can alter the overall leaf surface water content even though vegetation mass varies over a longer time frame (McDowell et al., 2018). As the dry season develops the surface soil dries resulting in variances in rates of soil water extraction between sites and over time within the soil profile (Spanner et al., 2022). The effects of salinity stress on leaf cell expansion often result in a reduction in leaf area. During salinity stress, a decrease in the relative leaf area ratio may be adaptive

due to the leaf's stronger cell walls or volume into which salts might be sequestered (Rozentsvet et al., 2022). Salt-tolerant plants such as mangroves limit the hydraulic conductivity of their roots which causes reduced growth rates and low stomatal conductance in the leaves, resembling a drought response (Dittmann et al., 2022).

Correlation, Regression, and PCA

The correlation values derived for leaf parameters in the NO6 and WP mangrove ecosystems were comparable to those reported by Shi et al. (2019), indicating that the proportional association between leaf area and the product of leaf length and width stays consistent. The leaf width-to-length ratio has been shown to correlate with leaf relative water content and the scaling exponent of the leaf dry mass against the leaf area relationship (Lin et al., 2022). As such, any changes to the leaf length, width, area, or perimeter can directly affect other parameters such as SLA, density, mass, and IE. Seasonality can influence the dry leaf mass, resulting in variations in leaf shape to adjust for the dry season, which also influences leaf length, width, area, and SLA (Li et al., 2015). SLA has an inverse connection with LMA, which takes into account the density, thickness, dry mass, and area of leaves, and can fluctuate depending on the plant's resource acquisition (de la Riva et al., 2016). The inverse relationship between density, SLA, and LSM held strong, negative values in this study and was consistent with the findings of Liu et al. (2020). These principal components generated were similar to those mentioned by dos Santos Garcia et al. (2022), who proposed that morphological differences observed between leaf parameters could be attributed to shifts due to environmentally induced plasticity from disturbance levels, leaf water uptake as a strategy to tolerate salinity levels, and water storage in tissues.

Leaf Chlorophyll Content

It is commonly assumed that plants should change their chlorophyll contents to adapt to their circumstances and enhance photosynthesis. The creation of chlorophyll requires a sequence of enzymatic processes, with excessive or inadequate temperatures hindering the enzyme reaction and ir-

reversibly damaging the original chlorophyll (Dunstan et al., 2018). A shortage of water in the leaves affects chlorophyll production, stimulates chlorophyll breakdown, and accelerates leaf yellowing. Precipitation has a direct impact on the amount of chlorophyll a in leaves, which increases dramatically during the rainy season, as seen in the WP ecosystem (Comparini et al., 2020). The quantity of chlorophyll pigments in the leaf is connected to physiological stress caused by interstitial salinity, inundation periods, water availability, variations in the incidence of solar irradiance, humidity, and climatic impact, all of which influence leaf development (Castellanos-Basto et al., 2021). One possible reason for the higher chlorophyll levels of leaves identified in the WP ecosystem is the age of the leaves found on the trees (Albert et al., 2018). Trees in NO6 are described as being more resource-conservative, whereas trees in WP forest are described as being more resource-acquisitive, which may suggest higher photosynthetic and light capture rates to enhance their growth rate despite environmental constraints.

Furthermore, the thickness of a leaf primarily impacts the length of light's optical path through it as well as the number of anatomical structures that reflect, absorb, and transmit light. Water deficits are frequently connected with leaf thickness and alter leaf characteristics such as leaf moisture content, water potential gradients, and transpiration, which can be related to leaf surface area expansion (Borsuk & Brodersen, 2019). In contrast to what is seen in the majority of ecosystems, leaves in NO6 and WP exhibited no variations between seasons. Flores-de-Santiago et al. (2018) noted that chlorophyll concentrations may be species-specific, as such, despite the differences within the types of ecosystems, *L. racemosa* can be classified into one single class, relating specifically to chlorophyll composition. Minimal variations in chlorophyll concentration during the transition from the dry to the rainy season may also imply that the trees maintain their photosynthetic potential despite environmental changes that may be countered by the season change, such as the availability of water. Our results also imply that *L. racemosa* trees found in NO6 and WP ecosystems exhibit, to an extent, a degree of homeostasis, which allows them to maintain constant chlorophyll concentration in their leaves (Rosado & Mattos, 2016).

CONCLUSIONS

Laguncularia racemosa leaves displayed morphological differences in both ecosystem types and seasons. Significant variances and correlations were observed in parameters including mass, length, width, area, perimeter, SLA, IE, and RWC. These variations and correlations were more apparent in the Number 6 Village ecosystem in the dry season and the Wellington Park ecosystem in the wet season. Our research additionally showed that the chlorophyll concentration of leaves varied between the two ecosystems, but not seasonally, with the Wellington Park ecosystem demonstrating more prominent fluctuations in chlorophyll a and total chlorophyll content. The results of this study suggest that plant structures such as leaves, although belonging to the same species, may exhibit site-specific modifications between different mangrove ecosystems.

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