

Leaf chlorophyll content and foliar damage in relation to biomass accumulation of *Sonneratia caseolaris* in the Segara Anakan Mangrove Lagoon, Indonesia

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Abstract

Mangrove biomass production is influenced by both structural attributes and leaf level physiological processes. However, empirical field studies linking these components at the stand scale remain limited. This study explored associations among leaf chlorophyll content, foliar damage, biomass accumulation of *Sonneratia caseolaris* (L.) Engl., and sediment nutrient conditions in the Segara Anakan Mangrove Lagoon, Indonesia. Three sampling stations were established, and field surveys were conducted from May to June 2023. Aboveground and belowground biomass were estimated using established species-specific allometric equations. Chlorophyll concentrations were determined spectrophotometrically, and foliar damage was quantified by the Bioleaf application on a smartphone. Positive associations were observed between biomass estimates and chlorophyll concentrations in both intact and partially damaged leaves, reflecting potential photosynthetic capacity. However, correlation analyses were based on plot-level data ($n = 15$) with limited replication. Therefore, the results should be interpreted as indicative ecological patterns rather than statistical evidence of causal relationships. Stations with relatively higher biomass also exhibited higher sediment nitrogen concentrations, suggesting a possible role of nutrient availability in supporting structural growth. Despite a high proportion of visibly damaged leaves across stations, measurable chlorophyll levels were maintained, indicating that partial tissue damage does not necessarily correspond to complete physiological impairment. Overall, the findings suggest that leaf-level physiological indicators may contribute to understanding spatial variability in mangrove biomass when interpreted within ecological and methodological constraints. Integrating structural and physiological measurements may support improved assessment of mangrove condition in dynamic estuarine environments.

Key words: coastal, environmental stress, leaf damage, photosynthetic capacity.

Introduction

Mangrove forests are among the most productive ecosystems in tropical regions. These forests play a role in global carbon sequestration and coastal stability. Their high biomass production and efficient nutrient cycling contribute substantially to long-term carbon storage, both above and below ground (Alongi 2020). Biomass production in mangroves is not only influenced by structural factors, such as stand density and tree size, but also by physiological processes related to photosynthetic capacity (Zheng et al. 2025). Variability in leaf conditions, particularly chlorophyll content and tissue integrity, can have important implications for vegetation growth and ecosystem function in dynamic coastal environments (Zhen et al. 2021, Deng et al. 2023).

Chlorophyll content reflects photosynthetic capacity and plant health and links leaf physiology to biomass production (Sherin et al. 2022). In mangroves, photosynthesis is influenced by salinity, temperature, nutrients (Sudhir et al. 2022, Blanco-Sacristán et al. 2024), and leaf damage (Visakorpi et al. 2024). Although damage can reduce carbon assimilation, partially damaged leaves may remain functional (Moustaka et al. 2021, Su et al. 2023). Studies in coastal mangrove forests in Mexico show that *Rhizophora mangle* L. with smaller stem diameters have relatively higher chlorophyll content, indicating that in the early growth phase, photosynthesis is directed more towards maintaining leaf physiological function under environmental stress. As tree size increases, carbon allocation shifts to stem and root structure formation, so that the role of increased leaf chlorophyll in biomass accumulation becomes relatively smaller (Castellanos-Basto et al. 2021).

In addition, the vegetation of *Avicennia marina* (Forssk.) Vierh. along the Red Sea coast of Saudi Arabia experiences physiological stress due to high salinity and excess nutrient abundance. These conditions force the plant to allocate a greater portion of its energy to osmotic regulation processes rather than growth. Consequently, there is a direct and negative impact on stem and leaf development (Shaltout et al. 2021). The growth of *Avicennia germinans* (L.) L. mangrove on Harbor Island is influenced by leaf chlorophyll content, which reflects various environmental factors, such as soil nitrogen availability, climatic conditions (drought and rainfall), soil characteristics, and soil microbial activity; in addition, the level of light interception also plays an important role in determining its physiological performance (Peng et al. 2022).

The Segara Anakan Lagoon (SAL) is a semi-enclosed estuarine system influenced by tides and river flows, forming a dynamic hydrological system with high sedimentation rates (Cahyo et al. 2024) and fluctuating salinity (Kresnasari and Gitarama 2021). Research on mangrove biomass in SAL conducted by Hilmi et al. (2024) reported that *Sonneratia caseolaris* (L.) Engl. with stem diameters ranging from 4.1 to 16.6 cm, exhibited biomass values between 0.6 and 18.28 t·ha⁻¹. However, field-based studies examining the interaction between leaf-level physiological traits, structural biomass accumulation, and sediment nutrient availability remain limited in this system.

Therefore, this study investigates the relationships among leaf chlorophyll content, foliar damage, aboveground and belowground biomass, and sediment nutrients in *S. caseolaris*. By integrating physiological indicators with structural measurements under natural estuarine

conditions, this study aims to improve our understanding of how leaf functional status may be associated with biomass variability.

Materials and Methods

Study area

This study was conducted in the mangrove forest of Laguna Segara Anakan, Cilacap, Central Java, Indonesia (7°43'–7°48' S; 108°55'–109°02' E). This forest is a natural stand with a variety of vegetation. One of the dominant vegetation species in the area is *S. caseolaris*. There were three sampling stations, namely Station 1 (St 1), Station 2 (St 2) and Station 3 (St 3) (Fig. 1). The field survey and sample collection were carried out from May

to June 2023.

Sampling design

Three sampling stations (St 1–St 3) were established across the lagoon to represent spatial heterogeneity. At each station, five 10 × 10 m plots were installed. Within each plot, the dominant tree (largest diameter) was selected for physiological measurements to represent maximum biomass contribution. This sampling approach follows mangrove forest guidelines recommended by Komiyama et al. (2008) and Kauffman and Donato (2012), which emphasise the importance of ecological representativeness in the selection of dominant individuals while retaining natural variation among plots. The main parameters of the study were vegetation biomass, consisting of abo-

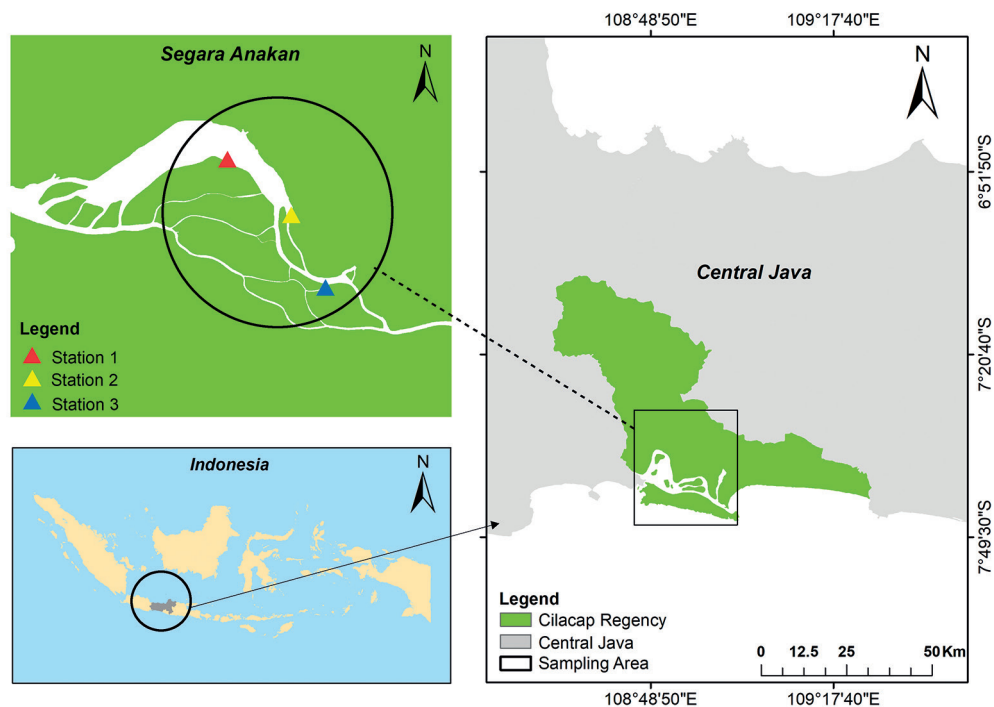


Fig. 1. Research location.

veground (AGB) and belowground biomass (BGB), chlorophyll content, and leaf damage.

Determination of biomass

AGB and BGB were estimated using a non-destructive method, namely, allometric equations. These equations were selected based on previous destructive studies conducted at the same location or under similar environmental conditions. The dominant tree in each plot was selected to represent the maximum biomass potential and to reflect optimal physiological condition at the station. Stem diameter at breast height was measured using a measuring tape, and both AGB and BGB were estimated using species-specific allometric equations. The AGB calculation formula is in equation (1); BGB is in equation (2); and the wood density of *S. caseolaris* is $0.34 \text{ g}\cdot\text{cm}^{-3}$.

$$Wt = 0.258 \cdot DBH^{2.287}, \quad (1)$$

where: Wt = aboveground biomass of an individual tree, kg; DBH = diameter at breast height, cm;

$$Wb = 0.295 \cdot \rho \cdot DBH^{1.94}, \quad (2)$$

where: Wb = root biomass, kg; ρ = wood density, $\text{g}\cdot\text{cm}^{-3}$; DBH = diameter at breast height, cm.

The equations were adopted from Kusmana et al. (2018).

Biomass calculated per individual tree ($\text{kg}\cdot\text{tree}^{-1}$) was summed per plot (100 m^2), scaled to hectare level ($\times 100$), converted to tonnes ($\div 1000$), and expressed as $\text{t}\cdot\text{ha}^{-1}$. Total biomass represents the sum of AGB and BGB.

Leaf sampling and chlorophyll analysis

From each dominant tree in each plot, 15

intact and damaged leaves were collected for chlorophyll content analysis. Leaves were sampled proportionally from the upper, middle, and lower canopy to reflect the vertical distribution of chlorophyll within the canopy. Chlorophyll content was determined using the Winternans and De Mots extraction method, followed by colorimetric analysis with a UV-Vis spectrophotometer, measuring absorbance at wavelengths of 649 nm and 665 nm (Winternans and De Mots 1965).

Foliar damage assessment

On the same tree, leaf damage was assessed by collecting approximately 10 % of the total leaves per individual, taking into account time constraints and technical feasibility (Pribadi 1998). Leaf damage was analysed using a smartphone-based application (BioLeaf; Machado et al. 2016). The number of dominant trees sampled differed among stations to account for variations in stand density and local habitat conditions. These differences were not standardised, as they were considered inherent characteristics of the SAL mangrove ecosystem. All measurement data were subsequently processed as station-level averages to ensure balanced weighting among locations.

Soil sampling

Supporting environmental parameters included total soil nitrogen, soil organic carbon, and soil phosphate concentrations. Soil sampling was conducted concurrently with biomass measurements within each plot. At the time of dominant tree measurement, surface soil samples (0–30 cm depth) were collected near the base of each sampled tree to represent the immediate rooting environment.

Statistical analysis

The relationships among biomass, chlorophyll content, and leaf damage were analysed using Pearson's correlation coefficient in Microsoft Excel. Correlation analyses were conducted using plot-level data ($n = 15$) to assess potential linear associations among variables. Given the inherent ecological variability of mangrove systems, and the limited sample size, results were interpreted cautiously and used to identify general ecological tendencies rather than to infer causality. Significance level was set at $\alpha = 0.05$.

Results

Biomass distribution among stations

Total biomass of *S. caseolaris* varied among the three sampling stations (Table 1). The highest mean biomass was recorded at St 1 ($7.69 \pm 2.06 \text{ t} \cdot \text{ha}^{-1}$), followed by St 3 ($4.15 \pm 2.67 \text{ t} \cdot \text{ha}^{-1}$) and St 2 ($3.20 \pm 0.97 \text{ t} \cdot \text{ha}^{-1}$). Biomass values represent the combined sum of aboveground and belowground components derived from species-specific allometric equations and subsequently converted to hectare scale as described in the Methods section.

Despite comparable tree size classes among stations, noticeable differences in accumulated biomass were observed, indicating spatial heterogeneity in stand development within the Segara Anakan

mangrove system.

Leaf chlorophyll content and foliar damage

Chlorophyll concentrations in intact leaves were highest at St 1 ($30.01 \pm 6.14 \text{ mg} \cdot \text{L}^{-1}$), slightly lower at St 2 ($29.13 \pm 3.66 \text{ mg} \cdot \text{L}^{-1}$), and lowest at St 3 ($24.03 \pm 1.53 \text{ mg} \cdot \text{L}^{-1}$) (Table 1). Damaged leaves showed lower chlorophyll concentrations than intact foliage at all stations, although substantial pigment levels were still maintained.

The proportion of damaged leaves was high across stations, ranging from 90 % to 92 %, while intact leaves accounted for only 8–10 % of sampled foliage (Table 1). Nevertheless, visible foliar damage did not correspond to a proportional decline in chlorophyll concentration, suggesting that damaged leaves retained measurable photosynthetic pigments.

Sediment nutrient characteristics

Sediment nutrient concentrations differed among stations (Table 2). Organic carbon ranged from 0.20 % at St 1 to 0.26 % at St 3. Nitrogen concentration was highest at St 1 (0.15 %) and lowest at St 3 (0.09 %). Phosphate concentration was similar at St 1 and St 2 (1.12–1.15 ppm) but markedly lower at St 3 (0.08 ppm). These variations indicate differences in nutrient availability among stations, particularly in nitrogen content, which may influence plant physiological performance and growth dynamics.

Table 1. Mean values and standard deviations of biomass, chlorophyll content in intact and damaged leaves, and the proportion of intact and damaged leaves.

Location	Biomass, $\text{t} \cdot \text{ha}^{-1}$	Intact leaf chlorophyll, $\text{mg} \cdot \text{L}^{-1}$	Damaged leaf chlorophyll, $\text{mg} \cdot \text{L}^{-1}$	Share of intact leaves, %	Share of damaged leaves, %
St 1	7.69 ± 2.06	30.01 ± 6.14	26.04 ± 5.67	9	91
St 2	3.20 ± 0.97	29.13 ± 3.66	21.90 ± 5.74	10	90
St 3	4.15 ± 2.67	24.03 ± 1.53	22.08 ± 5.33	8	92

Table 2. Mean values and standard deviations of sediment nutrient concentrations.

Element	Location		
	St 1	St 2	St 3
Organic carbon, %	0.20 ± 0.0009	0.25 ± 0.012	0.26 ± 0.033
Nitrogen, %	0.15 ± 0.004	0.13 ± 0.003	0.09 ± 0.002
Phosphate, ppm	1.12 ± 0.088	1.15 ± 0.176	0.08 ± 0.017

Correlation analysis

Pearson correlation coefficients among biomass, chlorophyll content, and leaf damage variables are presented in Table 3. Total biomass showed a weak positive association with chlorophyll concentration in intact leaves ($r = 0.24$) and a slightly higher but still weak positive association with chlorophyll concentration in damaged leaves ($r = 0.37$). The proportion of intact leaves exhibited a weak negative association with total biomass ($r = -0.10$), whereas the proportion of damaged leaves showed a similarly weak positive association ($r = 0.10$). Overall, the low magnitude of the coefficients suggests that biomass variation is influenced by multiple interacting environmental and physiological factors rather than by leaf chlorophyll concentration or visible foliar damage alone.

All correlation coefficients were low to moderate in magnitude, indicating weak linear associations among variables. These relationships should be interpreted cautiously, as biomass variability in

mangrove stands is influenced by multiple interacting physiological and environmental factors. The analysis was conducted using plot-level data ($n = 15$) to minimise potential bias and instability associated with small sample sizes and station-level averaging. Therefore, the results are best viewed as indicative ecological patterns rather than robust statistical evidence of causal relationships.

Discussion

Biomass patterns in relation to physiological performance

Total biomass differed noticeably among stations, with St 1 showing the highest value ($7.69 \pm 2.06 \text{ t} \cdot \text{ha}^{-1}$), followed by St 3 and St 2 (Table 1). This spatial variation cannot be interpreted solely as a function of chlorophyll concentration, because chlorophyll levels in intact leaves at St 2 were comparable to those at St 1, yet biomass remained considerably lower. These patterns indicate that stand-level

Table 3. Correlation between *S. caseolaris* stand biomass and chlorophyll content and leaf damage.

Parameter	Total biomass	Intact leaf chlorophyll	Damaged leaf chlorophyll	Share of intact leaves	Share of damaged leaves
Total biomass	1.00				
Intact leaf chlorophyll	0.24	1.00			
Damaged leaf chlorophyll	0.37	0.68	1.00		
Share of intact leaves	-0.10	0.34	-0.13	1	
Share of damaged leaves	0.10	-0.34	0.13	-1	1

biomass represents an integrated outcome of physiological processes operating over time rather than a direct reflection of instantaneous leaf pigment content (Shaltout et al. 2021).

Chlorophyll concentration reflects potential photosynthetic capacity, whereas biomass accumulates through sustained carbon assimilation and allocation to structural tissues. The moderate positive association between intact leaf chlorophyll and total biomass ($r = 0.24$; Table 3) suggests that photosynthetic capacity may contribute to growth, but it does not fully determine structural accumulation. Forest biomass, particularly in mangrove systems, is shaped by cumulative environmental conditions, nutrient availability, and resource allocation strategies across developmental stages.

The biomass values recorded in the present study were lower than those reported for mangrove stands in Hai Phong City, Vietnam (Pham et al. 2017) and Pulau Payung Beach, Banyuasin, Indonesia (Hermialingga et al. 2020). However, cross-site comparisons should be interpreted with caution, as mangrove biomass is strongly influenced by stand age, species composition, hydro-geomorphological setting (Mangora 2016), disturbance history, and methodological differences (Fatonah et al. 2023). Therefore, these comparisons are presented only to provide contextual reference rather than direct equivalence in productivity. Chlorophyll concentration is closely associated with photosynthetic capacity and carbon assimilation (Alongi 2020, Choudhary et al. 2024), which may contribute to biomass accumulation over time. Conversely, increased foliar damage and reduced chlorophyll levels may be associated with environmental stressors, such as salinity fluctuations, temperature extremes, sedi-

mentation pressure, or nutrient limitation (Talebzadeh and Valeo 2022).

Functional contribution of damaged leaves and compensatory responses

Although the analysis was conducted at the plot level, the moderate sample size and natural heterogeneity of the estuarine environment may limit statistical power. Future studies incorporating seasonal replication and experimental nutrient manipulation would strengthen causal inference regarding physiological–structural linkages in mangrove ecosystems. From a physiological perspective, chlorophyll concentration reflects the biochemical capacity for light capture and carbon fixation. Chlorophyll concentration is closely associated with photosynthetic carbon assimilation, which underpins biomass production (Sherin et al. 2022). Therefore, the present findings should be considered indicative of an ecological pattern rather than definitive evidence of causal relationships.

This pattern is consistent with the concept of compensatory photosynthesis. Under moderate herbivory or partial tissue loss, plants may enhance the photosynthetic capacity of remaining functional mesophyll tissue to offset reductions in leaf area. Such compensatory responses reflect physiological plasticity and tolerance mechanisms documented in woody perennials (Moustaka et al. 2021, Su et al. 2023). As long as vascular tissues remain functionally intact, assimilates can be transported to sinks organs, enabling continued contribution to biomass formation. However, damage to vascular tissues may disrupt nutrient transport and consequently limit chlorophyll synthesis. Increased chlorophyllase activity can further accelerate chlorophyll degradation, leading to

a visible shift in leaf colour from green to yellow. Such processes commonly occur during leaf senescence (Syvash and Zolotareva 2017), but may also be triggered by abiotic and biotic stressors (Talebzadeh and Valeo 2022), as well as nutrient deficiency (Naidoo 2016). A comparable pattern was reported from the coastal lagoon of Urias, Mexico, where mangroves in healthy condition exhibited higher chlorophyll concentrations than those subjected to environmental stress (Flores-de-Santiago et al. 2016).

In the context of estuarine mangrove ecosystems, where multiple stressors co-occur, the ability of *S. caseolaris* to maintain chlorophyll content despite visible leaf damage may reflect physiological tolerance under the observed environmental conditions. These findings suggest that visible leaf damage may not necessarily imply immediate functional impairment at the stand level.

Nutrient availability as a regulatory constraint

Sediment nutrient data (Table 2) provide further insight into the observed biomass differences. Nitrogen concentrations were highest at St 1 and lowest at St 3, while phosphate levels varied among stations. The lower biomass recorded at St 2, despite relatively high chlorophyll concentrations (Table 1), suggests that nutrient-mediated constraints may limit the conversion of assimilated carbon into structural biomass.

Nitrogen plays a central role in chlorophyll synthesis and enzyme production, including Rubisco, which governs carbon fixation efficiency. Under nitrogen limitation, photosynthetic potential may be maintained temporarily, but growth and structural tissue formation can be restrict-

ed. This interpretation aligns with Liebig's Law of the Minimum, whereby growth is limited by the scarcest essential resource rather than by overall resource abundance (Gorban et al. 2011, Ågren et al. 2012).

The observed patterns are consistent with the view that chlorophyll concentration may reflect potential assimilation capacity, whereas biomass represents realised growth influenced by nutrient-regulated allocation trade-offs. Similar nutrient-growth relationships have been documented in mangrove ecosystems subjected to variable nitrogen and phosphorus availability. Mangrove stands enriched with nitrogen and phosphorus tend to exhibit enhanced chlorophyll content and increased growth rates (Naidoo 2016, Aljahdali et al. 2021, Fathi 2022).

Environmental stress, shading, and chlorophyll stability

Environmental stress in this study was not directly quantified. Instead, sediment nutrient concentrations, particularly nitrogen, were used as indicators of site-level nutrient condition that may influence leaf physiological status and biomass accumulation. Therefore, interpretations regarding environmental stress should be considered indirect and exploratory.

Chlorophyll concentrations were highest at St 1 (Table 1), which may indicate more favourable microenvironmental conditions. Moderate canopy cover can reduce excessive irradiance, protecting chloroplast structure and limiting photoinhibition. In contrast, exposure to high light intensity in sparsely shaded areas may accelerate chlorophyll degradation and disrupt photosynthetic complexes (Apriliana et al. 2021, Wimpler et al. 2021).

The relatively stable chlorophyll levels observed despite high proportions of dam-

aged leaves suggest that *S. caseolaris* maintains protective physiological mechanisms, including antioxidant systems that mitigate reactive oxygen species accumulation under stress (Huang et al. 2019, Fathi et al. 2025). Leaf damage caused by physical injury, drought, or pathogens can increase ROS production excessively, which can damage cell membranes and organelles (especially chloroplasts), reduce chlorophyll levels, disrupt photosystem II (PS II), cause stomatal closure, and decrease stomatal conductance (Lu and Yao 2018). To mitigate the damaging effects and accumulation of excess ROS, plants have developed complex antioxidant defence systems, including enzymatic and non-enzymatic mechanisms that work together to reduce ROS and maintain cellular homeostasis (Haghpanah et al. 2025). The relatively stable chlorophyll content in *S. caseolaris* despite partial leaf damage may reflect a degree of physiological tolerance to environmental stress. Such physiological stability may contribute to sustained productivity under fluctuating environmental conditions, although direct measurements of carbon transfer were beyond the scope of this study. In this sense, chlorophyll concentration may function not only as an indicator of photosynthetic capacity but also as a proxy for stress resilience in mangrove stands.

Implications for mangrove productivity assessment

The integration of structural biomass measurements with leaf-level physiological indicators provides a more comprehensive framework for evaluating mangrove productivity. While biomass and diameter represent long-term growth accumulation, chlorophyll concentration offers a more im-

mediate reflection of physiological status. The correlations shown in Table 3 suggest that chlorophyll measurements, including those in partially damaged leaves, may provide early signals of productivity trends, although this requires validation with broader replication. In line with previous research, the low leaf damage reported by Kresnasari et al. (2024) refers to a scoring-level assessment, while this study quantifies the percentage of leaf damage. As long as the main photosynthetic tissues, such as mesophyll, chloroplasts, and vascular system (xylem-phloem) remain intact, the undamaged parts of the leaves continue to absorb light through chlorophyll pigments, fix carbon, enhance defence enzyme activity, and transport photosynthetic products to other tissues (Su et al. 2023).

For forestry-oriented monitoring, combining physiological and structural parameters may enhance stand health assessment, particularly in dynamic estuarine environments where nutrient supply and environmental stress fluctuate over time.

Limitations and future directions

Although the analysis was conducted at the plot level, the moderate sample size and natural heterogeneity of the estuarine environment may limit statistical power. Future studies, incorporating seasonal replication and experimental nutrient manipulation, would strengthen inference regarding physiological–structural linkages in mangrove ecosystems.

Despite these limitations, the consistency between observed patterns and established ecological theory, including compensatory photosynthesis and nutrient limitation frameworks, supports the plausibility of proposed mechanisms.

Conclusions

This study identified spatial variation in *S. caseolaris* biomass within the SAL and explored its associations with leaf-level physiological traits and sediment nutrient conditions. Observed patterns suggest that biomass variability may be related to differences in chlorophyll concentration and nitrogen availability among stations, however, these relationships were derived from limited station-level replication and should be interpreted cautiously.

The presence of measurable chlorophyll concentrations in partially damaged leaves indicates that visible foliar damage does not necessarily correspond to complete physiological dysfunction. These findings are consistent with the possibility that mangrove leaves retain functional capacity despite partial tissue loss, although direct measurements of carbon assimilation were beyond the scope of this study.

Overall, the results provide exploratory evidence that integrating structural biomass estimates with leaf-level physiological indicators may contribute to understanding spatial variability in mangrove stands. Given the limited number of analytical units, further studies, incorporating broader replication, seasonal observations, and experimental approaches, are required to strengthen inference regarding physiological–structural linkages in estuarine mangrove ecosystems. These relationships do not represent direct measurements of photosynthetic efficiency or carbon flux but rather indicate potential physiological–structural linkages.

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