

Publication status: This preprint has not been published elsewhere.

Leaf metabolites and carbon harvesting: Insights into spatial extremities of a mangrove ecosystem in Mumbai, India

Sahir Q. Mansuri, Vijendra P. S. Shekhawat

<https://doi.org/10.1590/2675-2824074.25165>

Submitted on: 2026-03-26

Posted on: 2026-03-27 (version 1)

(YYYY-MM-DD)

Leaf metabolites and carbon harvesting: Insights into spatial extremities of a mangrove ecosystem in Mumbai, India

Sahir Q. Mansuri¹, Vijendra P. S. Shekhawat¹

S.Q.M.:  <https://orcid.org/0009-0000-1675-9079>

V.P.S.S.:  <https://orcid.org/0000-0001-6926-2736>

¹ RD and SH National College and SWA Science College - Department of Botany and Biotechnology Department of Botany, Off Linking Road, Bandra (w) Mumbai Bandra West MAHARASHTRA 400050

* Corresponding author: shekhawatvps@gmail.com

ABSTRACT

Mangrove physiological traits are largely driven by ecogeomorphic conditions and environmental stressors. These traits provide adaptive strategies to enable growth and productivity in challenging coastal and marine settings. Moreover, plant biodiversity is a key component to determine the habitat richness, functioning and larger ecosystem dynamics and has a central role in carbon sequestration processes. The urban mangrove green cover at Carter Road in Mumbai harbors key species like *Sonneratia alba* Sm., *Sonneratia apetala* Buch.-Ham., *Rhizophora mucronata* Poir., and *Avicennia marina* (Forssk.) Vierh. They were evaluated for essential phytochemicals like proline and chlorophyll in ambient ecosystem conditions. Proline was highest in *R. mucronata* ($22.42 \pm 0.40 \mu\text{mol g}^{-1}$) and lowest in *S. apetala* ($18.93 \pm 0.14 \mu\text{mol g}^{-1}$). Chlorophyll a, Chl b, Chla+b and Chl a/b varied significantly at the two positional extremes –landward and seaward, with considerably higher values recorded at the landward edge. Chl a content (mg g^{-1}) at the landward edge ranged from 1.60 ± 0.03 to 1.31 ± 0.12 and were much higher in comparison to the seaward fringe (0.71 ± 0.06 to 0.58 ± 0.02). Positional increments were also observed for Chl b and Chl a+b. Linear mixed effect model was significant for positional distinctiveness of soil carbon parameters like soil organic carbon (SOC%), bulk density and soil strata organic carbon (SOC_{Org}). The SOC (%) gave maximum values of surface soil (0-10 cm) at seaward ($1.41 \pm$

0.06) and landward (2.08 ± 0.31) positions with corresponding SOC_{org} (Mg C ha^{-1}) values of 18.05 ± 1.711 and 22.367 ± 2.35 respectively, indicating significant carbon deposits landwards. The standing biomass carbon for aboveground and belowground biomass was $357.00 \pm 33.09 \text{ Mg C ha}^{-1}$ and $99.39 \pm 9.21 \text{ Mg C ha}^{-1}$ respectively. This study provides insights into modulation of Chlorophyll content impacting the ecosystem productivity and its carbon storage propensities.

KEYWORDS: Mangroves, mangrove physiology, chlorophyll, biomass, ecosystem carbon pools, Carbon stock, urban landscapes

Article in press

INTRODUCTION

Mangroves are globally recognized as one of the most carbon-rich coastal ecosystems, playing a substantial role in climate change mitigation through their carbon sequestration capacity (Donato et al., 2011; Alongi, 2014). Occupying less than 1% of the tropical coastal area, mangrove forests store carbon at significantly higher rates and quantities than many terrestrial or boreal forests, with their soils serving as the largest carbon reservoir within these ecosystems (Alongi, 2014; Alongi, 2020). This is facilitated by their unique adaptations to thrive in saline, anoxic soils with extreme sunlight and temperatures regimes of tropics and sub-tropic climate. Their aboveground plant morphological characteristics like pneumatophores, leaves, lianas etc., along with intricate root systems trap and stabilize organic matter and sediments, are noteworthy and unique to these coastal giants (Murdiyarto et al., 2010; Alongi, 2014; Twilley et al., 2017). Mangrove leaves are generally thick, leathery, and possess a well-developed cuticle layer which reduces water loss through transpiration. They often have recessed or sunken stomata, minimizing exposure to salt spray and reducing water vapor diffusion (Alongi, 2014; Singh, 2020). *A. marina*, have salt glands on the leaf surface for maintaining ionic balance by actively excreting excess salt (Alongi, 2014; Naidoo, 2016). The ability of mangroves to maintain photosynthetic activity under conditions otherwise detrimental is facilitated by biochemical adaptations such as antioxidant enzyme activities and osmolytes to mitigate oxidative damage induced by salt and other abiotic stressors (Naidoo, et al., 2016; Chen et al., 2024). The leaf morphology and physiology of mangroves are intricately adapted to their challenging habitats, with structural features that minimize water loss and salt intrusion, and physiological mechanisms that sustain photosynthesis and growth under fluctuating environmental stresses (Ball, 1986; Lovelock, 2006; Naidoo, et al., 2016; Alongi, 2025).

Chlorophyll, the primary photosynthetic pigment, underpins the remarkable productivity of mangrove ecosystems, which thrive in the challenging intertidal zones of tropical and subtropical coastlines (Tomlinson, 1986; Alongi, 2020). Variations in chlorophyll concentration, which can span from 269.8 to 800.7 $\mu\text{mol}/\text{m}^2$ across different species and locations, serve as a critical indicator of plant vitality and photosynthetic capacity, directly reflecting the health and productivity of these unique forests (Indian Institute of Space Science, 2019; Porra, 2002). Despite their inherent resilience, the photosynthetic machinery of mangroves, specifically their chlorophyll content and function, is highly susceptible to various environmental stressors. Elevated temperatures, often exceeding 35°C, can significantly impair photosynthetic performance and reduce leaf formation rates, leading to compromised plant health and growth (Field, 1995; Naidoo, 2025). High salinity, a ubiquitous feature of mangrove habitats, also directly impacts chlorophyll efficiency, leading to decreased carbon assimilation and stunted growth, a phenomenon observed in dwarf mangroves (Ball and Farquhar 1984; Tuffers et al., 2001; Naidoo, 2009; Naidoo, 2025). Monitoring chlorophyll dynamics is essential for assessing mangrove ecosystem health,

predicting their response to ongoing environmental changes, and informing effective conservation and restoration strategies (Liu et al., 2019).

Additionally proline, an osmo-protectant amino acid, accumulates in mangrove tissues in response to prevailing marine environmental conditions, acting as a biochemical marker for stress tolerance (Parveen et al., 2024). Under such stress conditions, proline accumulation is a mitigation strategy to reinstate osmotic imbalance and circumvent oxidative damage, enabling mangroves like *A. marina* to maintain photosynthetic activity (Aljahdali et al., 2021). Proline stabilizes proteins and membranes, scavenge free radicals, and maintain cellular osmotic balance, thereby enhancing stress tolerance in the tissues (Das et al., 2016). The elevated proline levels in mangroves like *A. marina* have been correlated with increased antioxidant enzyme activities (Aljahdali and Alhassan, 2020). Additionally, proline accumulation reflects the physiological status of mangroves under environmental stress and can serve as a sensitive biochemical indicator for early detection of stress (Chen et al., 2022; Nizam et al., 2022; Parveen et al., 2024). The dual assessment of chlorophyll and proline can indicate the physiological status and productivity potential in mangroves, highlighting the species-specific adaptive strategies to maintain ecosystem productivity under fluctuating environmental pressures (Afele et al., 2021).

The growth and productivity of mangroves is influenced by a suite of biotic and abiotic factors including species composition, age, tidal inundation, salinity gradients, nutrient availability, and climatic variables such as temperature and precipitation (Alongi, 2014; Alongi, 2018; Kauffman et al., 2020; Alongi, 2025). Many other morphological and physiological traits of mangrove coastal forests add to their exceptional growth rates and biomass accumulation, surpassing many terrestrial ecosystems (Donato et al., 2011; Alongi, 2018). Physiological adaptations like high water use efficiency (Ball, 1986), enable them to sustain high net primary productivity (NPP), with reported values reaching up to $1300 \text{ g C m}^{-2} \text{ year}^{-1}$ in some tropical regions (Alongi, 2018). Furthermore, mangroves contribute to coastal productivity through complex food web interactions and nutrient cycling, supporting biodiversity and fisheries, which in turn reinforce their resilience and carbon dynamics (Alongi, 2018; Padhy et al., 2021).

Growth trajectories of mangrove stands typically follow a sigmoidal pattern, with rapid biomass accumulation in early decades reaching a plateau as forests mature, often around 30 to 50 years (Kauffman et al., 2020; Alongi and Zimmer 2024). Notably, the allocation of biomass and thus carbon, between aboveground and belowground components is substantial, with belowground biomass contributing significantly to carbon storage, and this can be overtly enhanced by the soil carbon due to slower decomposition rates in waterlogged sediments (Alongi, 2014; Alongi, 2018; Kauffman et al., 2020). Sediment organic carbon stocks often exceed aboveground biomass carbon, constituting up to 90% of total ecosystem carbon, with carbon burial rates in sediments estimated at 138 to over 400 g

C m⁻² year⁻¹ depending on geomorphic setting and regional differences (Alongi 2014; Alongi 2018; Breithaupt et al., 2022). Carbon burial is also facilitated by high sedimentation rates and anoxic conditions that inhibit microbial decomposition (Marois and Mitsch, 2015; Breithaupt et al., 2022). Restoration and afforestation efforts have demonstrated better potential to recover carbon stocks comparably to natural forests over time, making mangrove rehabilitation a viable strategy for enhancing blue carbon sinks (Song et al., 2023; Alongi and Zimmer, 2024). Finally, Yao et al. (2025) elaborated on a host of workable suggestions for marine carbon storage (mCS) and carbon dioxide removal (mCDR) at regional scales enunciating vitality of marine ecosystems in the changing climate scenarios.

Mangroves contribute disproportionately to global blue carbon stocks, accounting for a substantial fraction of carbon burial and exchange in coastal zones, despite their limited spatial extent (Howard et al., 2014; Alongi, 2020). Additionally, the carbon stored in mangrove ecosystems comprises both recently fixed organic biomass carbon and older (soil+biomass) stable carbon pools acting as long-term carbon sinks (Alongi, 2020; Breithaupt et al., 2022). World-wide, threats from anthropogenic activities and climate change-induced sea-level rise pose significant challenges to mangrove carbon storage potential (Friess et al., 2019; Alongi, 2020). Mumbai, a prominent metropolitan on India's west coast, harbours substantial mangrove forests that are under increasing scrutiny due to rapid urbanization and environmental pressures (Kulkarni et al., 2010; Vaz, 2014). Many anthropogenic activities interfering mangroves are widely reported in Mumbai. They include dumping of municipal and industrial waste, domestic sewage, solid waste, and heavy metal contamination etc. prominently at Thane creek, Mithi river, Dahisar, Kanjurmarg among many others (Patil et al., 2014; Everard et al., 2014; Pachpande and Pejaver, 2015; Patil et al., 2015; Shinde and Dhonde, 2017; Shinde et al., 2018; Sharma et al., 2022; Patil and Kanhere, 2024). These activities considerably degrade the mangrove ecosystems and reduce the carbon sequestration potential (Vaz, 2014; Everard et al., 2014; Sharma et al., 2022; Akram et al., 2023).

A recent study on Mumbai mangroves by Bhattacharjee et al. (2025) indicated a whopping 40% reduction in total green mangrove cover in last three decades, which is a significant decline, especially for a city with huge reclaimed land and high population density. The current study was based on the premise that urban mangroves maybe experiencing extreme stress attributed to a.) anthropogenic pollution; and b.) geomorphological uniqueness with rocky barricade seawards; and c.) proportionally copious oceanic volume offering a humongous exposure to the various stressors; that can have a deep impact on ecophysiological responses and productivity of the ecosystem. Understanding the biomass dynamics and carbon storage potential of these urban mangroves is of paramount importance for effective conservation and management of such landscapes.

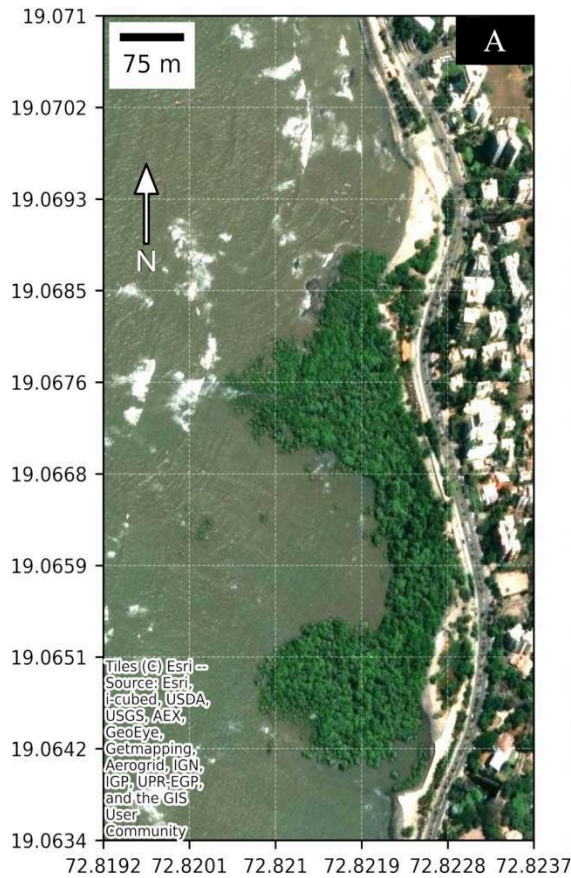
Keeping this in view, the current investigation was aimed to carry out some ecophysiological and geocological exploration on species like *Sonneratia alba* Sm., *Sonneratia apetala* Buch.-Ham., *Rhizophora mucronata* Poir., and *Avicennia marina* (Forssk.) Vierh., aimed at creating a comprehensive profile of urban mangrove ecosystems. The relative densities of the mangrove trees observed for the species in this study at Carter Road were in the order *Avicennia marina* > *Rhizophora mucronata* > *Sonneratia apetala* > *Sonneratia alba* that were consistent with the findings of Kantharajan et al. (2018). Additionally, species like *A. marina*, *R. mucronata* and *S. apetala* have been reported for their more relative resistance to either withstand or circumvent diverse pollution and other factors prevailing in urban setups, for instance, heavy metals, microplastics, organic pollutants, etc. pertinent to growth and productivity of mangrove plants (MacFarlane et al., 2003; Shete et al., 2009; Ghosh et al., 2020; Afefe et al., 2021; Nasrin et al., 2021; Mansuri and Shekhawat, 2025). Moreover, morpho-anatomical and physiological distinctiveness that represent an array of variability with contrasting adaptations (Giesen et al., 2006) like root aeration, salt regulation and growth forms, guided the selection of such suitable species in this study (Tomlinson, 1986, Tatongjai et al., 2021). The main goal of the study was to understand the variations in the physiological adaptability of these species in the changing geomorphic conditions at the landward and seaward extremities of the ecosystem that could provide insights into the modulation of chlorophyll content impacting the ecosystem productivity and its carbon storage propensities.

METHODS

STUDY SITE

Situated along the western coastline of Mumbai, mangroves at the Carter Road (19.06477° N, 72.82195° E) are a vital ecological-urban interface that hosts few mangrove species like *Sonneratia alba* Sm., *Sonneratia apetala* Buch.-Ham., *Rhizophora mucronata* Poir., largely dominated by *Avicennia marina* (Forssk.) Vierh. The ecosystem exhibits a clear zonation in its vertical extent with tallest plants on the landward edge and reducing forest canopy height seawards (Figure 1). Field measurements and modelling studies have demonstrated that this mangrove belt reduced the wave heights by over 50% (Samiksha et al., 2019). This protection is particularly vital given the increasing vulnerability of the Mumbai coastline to climate-induced sea-level rise and extreme weather events, especially cyclones (Mohanty, 2020).

Mansuri & Shekhawat



Landward

Seaward



Figure 1. Site description: (A) map of the mangrove site at Carter Road, Mumbai. tick marks; legends: top left - scale and north arrow bottom left – attribution); (B) mangrove trees at the landward edge of the ecosystem experiencing minimal tidal influence; (C) mangrove tree at the seaward edge of the ecosystem with a rocky barricade offering restricted tidal drainage; (D) northern margin of the ecosystem with visible decline in canopy height.

LEAF PHYSIO-BIOCHEMICAL STUDIES

Different properties of leaf pertaining to physiological characteristics were measured that include weight, moisture, chlorophyll content and proline content. The leaf moisture % fresh

weight (LM % F_w) was determined by measuring the fresh weight followed by drying the leaves to constant weight with their difference used to calculate the total moisture weight and its percentage in the leaf.

$$\text{Leaf moisture (LM \% } F_w) = \frac{(FW-DW)}{FW} \times 100 \quad \dots\dots (\text{eq. 1})$$

FW = Fresh weight and DW = Dry weight.

Proline was extracted from fresh leaf samples with their weighed aliquots (50 mg) immediately mixed with maximum 1 ml of ethanol:water (40:60 v/v) and incubated overnight at 4 °C. Standard curve for proline was prepared for determination of proline concentrations in leaf samples using following equation (Bates et al., 1973):

$$\text{Proline } (\mu\text{mol g}^{-1} F_w) = \frac{(A_{ex}-\text{blank})}{\text{slope}} \times \frac{V_{ex}}{V_{aq}} \times \frac{1}{F_w} \quad \dots\dots (\text{eq. 2})$$

Where A_{ex} = absorbance of extract; V_{ex} = volume of extract; V_{aq} = volume of aliquot; and F_w = fresh weight.

Chlorophyll extraction protocols are well established with variations in the solvents but the larger deviations in the calculations for determination of Chlorophyll concentrations were noticed in many established protocols like Arnon's equations (Arnon, 1949), Lichtenthaler's equations (Lichtenthaler, 1987) and Porra's equation (Porra, 2002; Chazaux et al., 2022; Esteban et al., 2018). The evidenced corrections provided by Chazaux et al. (2022) were found suitable especially due to the improved accuracy. Chlorophyll extraction was performed the same day from freshly collected leaves of different zones i.e. seaward (S) and landward (L). Minimum quantity of pre-chilled (-20 °C) 85% acetone buffered with Tris-HCl (pH 8) was added to 150 mg leaf samples, followed by grinding till homogeneity and centrifugation at 4500 rpm for 5 minutes. The supernatant was stored on ice in the dark. The total volume was made up to 25 ml in the volumetric flasks while in dark and thawed for 20 minutes before spectrophotometric measurements. Chlorophyll a, Chlorophyll b and Chlorophyll a+b were measured at 663.6 nm and 646.6 nm (Chazaux et al., 2022). The buffered 85% acetone was used as blank and fresh blanks were added in between measurements considering the volatility of acetone. In between measurements for both wavelengths, intermittent corrections were performed at higher wavelengths to remove the scattering effects that are not related to the analytes of interest. Following equations were used for determination of chlorophyll concentrations ($\mu\text{g ml}^{-1}$):

$$\text{Chl}_a = (12.18 \times A_{663.6 \text{ nm}} - 2.36 \times A_{646.6 \text{ nm}}) \quad \dots\dots (\text{eq. 3})$$

$$\text{Chl}_b = (20.19 \times A_{646.6 \text{ nm}} - 4.59 \times A_{663.6 \text{ nm}}) \quad \dots\dots (\text{eq. 4})$$

$$\text{Chl}_{a+b} = (17.83 \times (A_{646.6 \text{ nm}} + 7.58 \times A_{663.6 \text{ nm}})) \quad \dots\dots (\text{eq. 5})$$

The values obtained from the equations were converted to mg.g^{-1} for actual concentration in the leaf samples.

For spectrophotometric accuracy the equipment was calibrated with blank solutions before each set of measurements. Cuvettes were cleaned in between measurements with dry fibreless tissues to avoid artifacts and remove fingerprints. Blanks were refilled intermittently due to presence of organic solvents. All the glassware was washed after pre-incubation in dilute acids overnight.

Table 1. Leaf physiological parameters in four mangrove species at Carter Road.

	Species				ANOVA (one-way)*	
	<i>S. alba</i>	<i>A. marina</i>	<i>R. mucronata</i>	<i>S. apetela</i>	p	F
Leaf Moisture (%) F_w	80.943 ^a ±1.188	82.528 ^a ±7.002	71.722 ^a ±1.102	71.596 ^a ±1.606	0.130	2.527
#Proline ($\mu\text{mol g}^{-1}F_w$)	21.050 ^a ±0.487	21.587 ^a ±0.408	22.429 ^a ±0.402	18.934 ^a ±0.141	<0.0005	15.160

*ANOVA between species groups; #significant differences between species.

SOIL, BIOMASS AND CARBON

The total area of the study site was measured using google maps with ‘measure distance’ feature that provides fairly accurate estimate of area. Transect method was used for sampling the area (250 m length) along the coast with three plots of 10 × 10 m (Kauffman and Donato, 2012).

Soil samples were collected from seaward and landward sediments using an open face peat auger. Soil samples were retrieved from subplots at random from maximum 50 cm depth with 10 cm interval (0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40-50 cm) with minimum gap of 2 m between subplots. Soil samples were incubated the same day at 50 °C for 24 hours and weighed multiple times till a constant weight is measured twice consecutively to confirm complete drying. Soil samples were crushed using mortar and pestle in an air conditioned laboratory maintained at 22 °C. Soil was sieved through 2 mm steel mesh and biological, plastic or cloth like material were discarded. Three different samples within the subplot (same depth) were mixed to give a single sample for respective depth of each subplot. Hence, a subplot gave 1 complete representative sample of a particular depth and total 5 samples (up

to 50 cm). Sample collection was conducted in January and February 2022 with regular Soil Organic Carbon (SOC %) estimations using Walkley and Black method (Walkley and Black, 1934; Dookie et al., 2022). Soil C_{org} was estimated from SOC (%), BD (g cm⁻³) and sample thickness (cm) (Howard et al., 2014).

$$\text{Carbon density (SCD)} = \text{SOC (\%)} \times \text{Bulk density (g cm}^{-3}\text{)} \dots\dots\dots \text{(eq. 6)}$$

They involved determination of soil carbon density (SCD) (g C cm⁻³) of the cores multiplied with the depth (10 cm) for strata core carbon (SCC).

$$\text{Strata core carbon (SCC, g C cm}^{-2}\text{)} = \text{SCD} \times \text{sample thickness} \dots\dots\dots \text{(eq. 7)}$$

Further, core carbon values were converted to soil strata C_{org} or the SOC_{org} for each depth and,

$$\text{SOC}_{org} \text{ (Mg C ha}^{-1}\text{)} = \text{SCC} \times \frac{1 \text{ Mg}}{10^6 \text{ g}} \times \frac{10^8 \text{ cm}^2}{\text{ha}} \dots\dots\dots \text{(eq. 8)}$$

scaled to the project area (6.564 ha) to give SOC_{org}, up to 50 cm depth that were summed to give a total SOC_{org} of the ecosystem.

Standing aboveground biomass (AGB) and belowground biomass (BGB) were calculated by measuring the tree diameter at breast height (DBH) 1.3 m above the ground (Komiyama, 2008) along with correction for BGB by Adame et al. (2017).

$$W_{top} = 0.251 \cdot \rho \cdot \text{DBH}^{2.46} \dots\dots\dots \text{(eq. 9)}$$

$$W_{root} = 0.199 \cdot \rho \cdot \text{DBH}^{2.22} \dots\dots\dots \text{(eq. 10)}$$

Where W_{top} and W_{root} represent above ground tree weight and belowground root weight respectively in kilogram (kg)

For more reflective estimates wood density (ρ) of *A. marina* was retrieved from the regional scientific study (Shashikala, 2020), since it is the most dominant species. Tree densities of plots were employed to determine aboveground and belowground biomass in the plot area (Mg ha⁻¹). The biomass values were converted to carbon values using a factor of 0.464 (Murdiyarsa et al., 2010).

DATA ANALYSIS

Data compilation and basic statistical methods like ANOVA, correlation and descriptive statistics were performed using MS excel. XLSTAT and Google Colab were employed for detailed statistical measures and analysis like the Tukey's Post-hoc test to compare all pairs of group means after a significant ANOVA test to identify specific groups that differ from each other. For example, each response (Chlorophyll content), we tested main effects of species, position (L or S) and the position × species interaction at α = 0.05. Assumptions

were evaluated via visual inspection of residuals and homogeneity of variances; where appropriate, values were analysed on the original scale.

Further, to investigate chlorophyll parameters for species-based differences among positional groups, each chlorophyll parameter was modelled with an Ordinary Least Squares (OLS) regression for species, position, and their interaction (species \times position). For every species, the estimated marginal mean (EMM) difference (L – S) was computed as a linear contrast of the fitted coefficients, where EMM refers to the mean response adjusted for other variables in the model. The standard error (SE) of each contrast was obtained from the model's coefficient covariance matrix via the contrast vector. A two-sided z statistic as $z = \text{estimate}/\text{SE}$ was formed and calculated p-values using the normal distribution; 95% confidence intervals were estimated $\pm 1.96 \times \text{SE}$. This approach tested whether the L – S EMM difference for each species is different from zero ($\alpha = 0.05$).

In another instance of soil parameters SOC (%), bulk density (BD) and soil strata carbon (strata SOC_{Org}), since ANOVA assumes independence and the soil data was clustered i.e. repeated measures from similar groups at the site, random effects were assessed with Linear Mixed Effect (LME) model to account for dependencies among soil parameters while reducing the influence of specific confounding variables like bulk density. Soil parameters were analysed using a LME model with estimated marginal means (EMM) for each combination of depth and position. Likelihood ratio tests (LRTs) assessed the model fit. Depth, position (L and S) and their interaction were included as fixed effect while core was included as a random intercept to account for repeated measurements within each sampling location. For each parameter, the full model was compared against reduced models to test effects of depth, position, and their interaction. LR statistics (LR_{stats}), chi-square p-values, fixed-effect estimates, and standard errors were calculated. LR_{stats} values more than one assume a good fit for the alternate hypothesis. Model convergence and singularity were checked, and any singular reduced models were excluded from LRT reporting. Landward-Seaward comparisons were drawn in few instances with differences of EMMs (L–S) of the parameter at any given soil depth.

Finally, the correlation heatmaps were prepared by taking mean of means for all the chlorophyll parameters across species and all soil parameters across depth profile with consistent positional groups (Landward and Seaward).

RESULTS

LEAF PHYSIOLOGY

The physio-biochemical properties like leaf moisture (%), fresh weight, proline content and chlorophyll content of mangrove leaf samples from four different species were estimated (Table 1). Mean leaf moisture percentage fresh weight (LM% F_w) for *A. marina* (82.53%), *S. alba* (80.94%), *R. mucronata* (71.72%), and *S. apetella* (71.60%) are presented (Table 1).

The omnibus ANOVA was not significant, ($F = 2.53$, $p = 0.13094$) for species, and Tukey's HSD found no significant pairwise differences at $\alpha = 0.05$. Visually, the boxes overlap among species, aligning with the non-significant result (Figure 2).

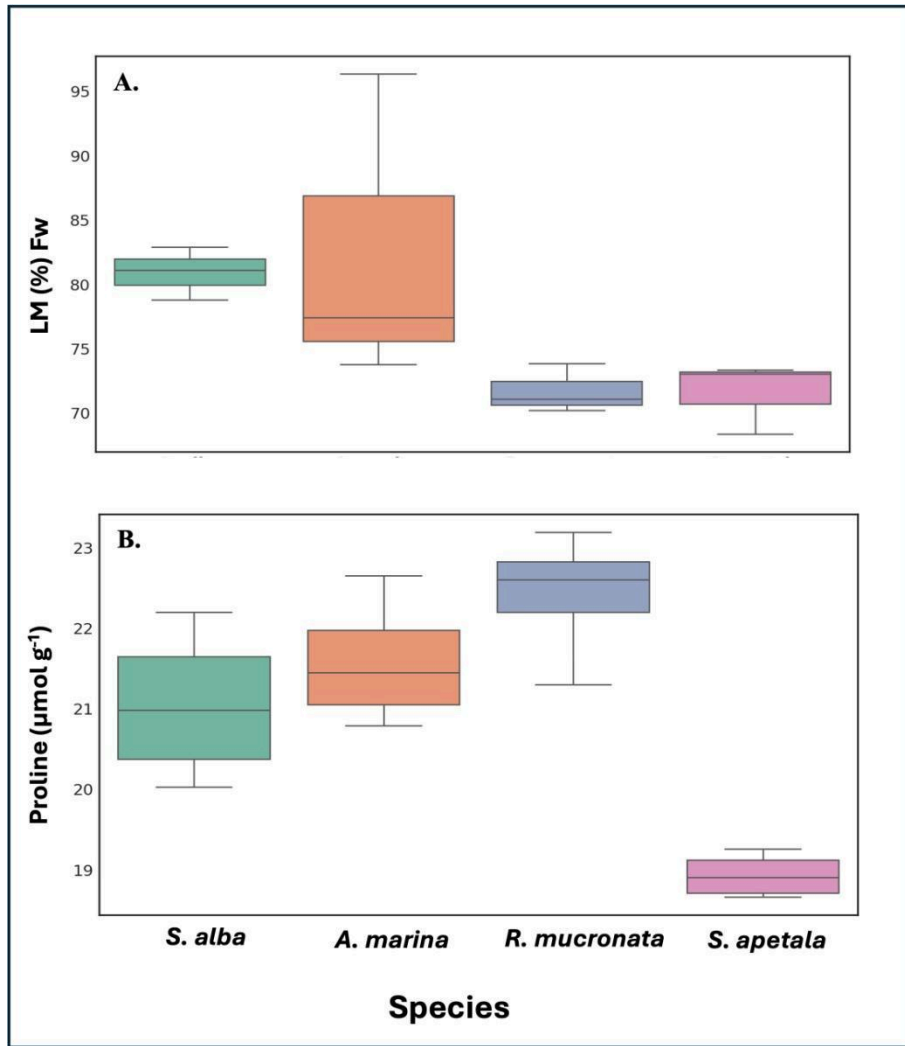


Figure 2: Boxplot for ambient A. LM(%) Fw or leaf moisture (%) fresh weight and B. proline content ($\mu\text{mol g}^{-1}$) in four mangrove species at Carter Road.

The ambient proline (Pro) content ($\mu\text{mol g}^{-1}$) of *R. mucronata* was highest (22.43 ± 0.40) followed by *A. marina* (21.59 ± 0.41) and *S. alba* (21.05 ± 0.49). *S. apetala* gave lowest Proline content at 18.93 ± 0.14 (Table 1). One-way ANOVA indicated a significant effect of species with $F = 15.16$ (Table 1). Tukey HSD post-hoc tests revealed significantly lower Pro content in *S. apetala* than *S. alba* ($p < 0.01$), *A. marina* ($p < 0.01$), and *R. mucronata* ($p < 0.001$), while other comparisons among species remained insignificant. Presumably, *S. apetala* accumulated less proline in the given set of ecosystem conditions than the other three

species (Figure 2). The latter group did not differ meaningfully from one another under the ambient ecosystem conditions.

Chlorophyll content (Chl a, Chl b, Chla+b) mg g^{-1} and Chl a/b ratio when assessed using two-way ANOVA with position (Landward vs. Seaward) and species showed position effects with Chl a ($p < 0.001$), Chl b ($p < 0.001$), Chl a+b ($p < 0.001$) and Chl a/b ($p < 0.001$) and marginally significant effect of species on Chl a ($p < 0.05$) only, but no position-dependent modulation across species (Table 2). All interaction effects (position \times species) were insignificant – Chl a ($F = 2.86$), Chl b ($F = 0.33$), Chl a+b ($F = 1.13$) and Chl a/b ($F = 0.20$) (Table 2). Tukey's HSD post-hoc multiple comparisons were performed primarily on the species and no significant differences were recorded. The inspection of EMMs for the Chl a/b ratio (Figure 3) showed two significant species contrasts seaward (largest absolute difference $\sim 0.29 \text{ mg g}^{-1}$ between *R. mucronata* and *S. apetalla*).

Table 2. Two-way ANOVA results for chlorophyll content in the four species and their respective positions along the seashore ($p < 0.05$).

	Species		Position		Interaction	
	F_{stat}	p	F_{stat}	p	F_{stat}	p
Chl a	3.68	< 0.05	377.06	< 0.000001	2.86	0.065
Chl b	0.35	0.78	71.72	< 0.000001	0.33	0.80
Chla+b	1.04	0.39	192.44	< 0.000001	1.12	0.36
Chl a/b	2.00	0.149	18.59	< 0.0001	0.19	0.89

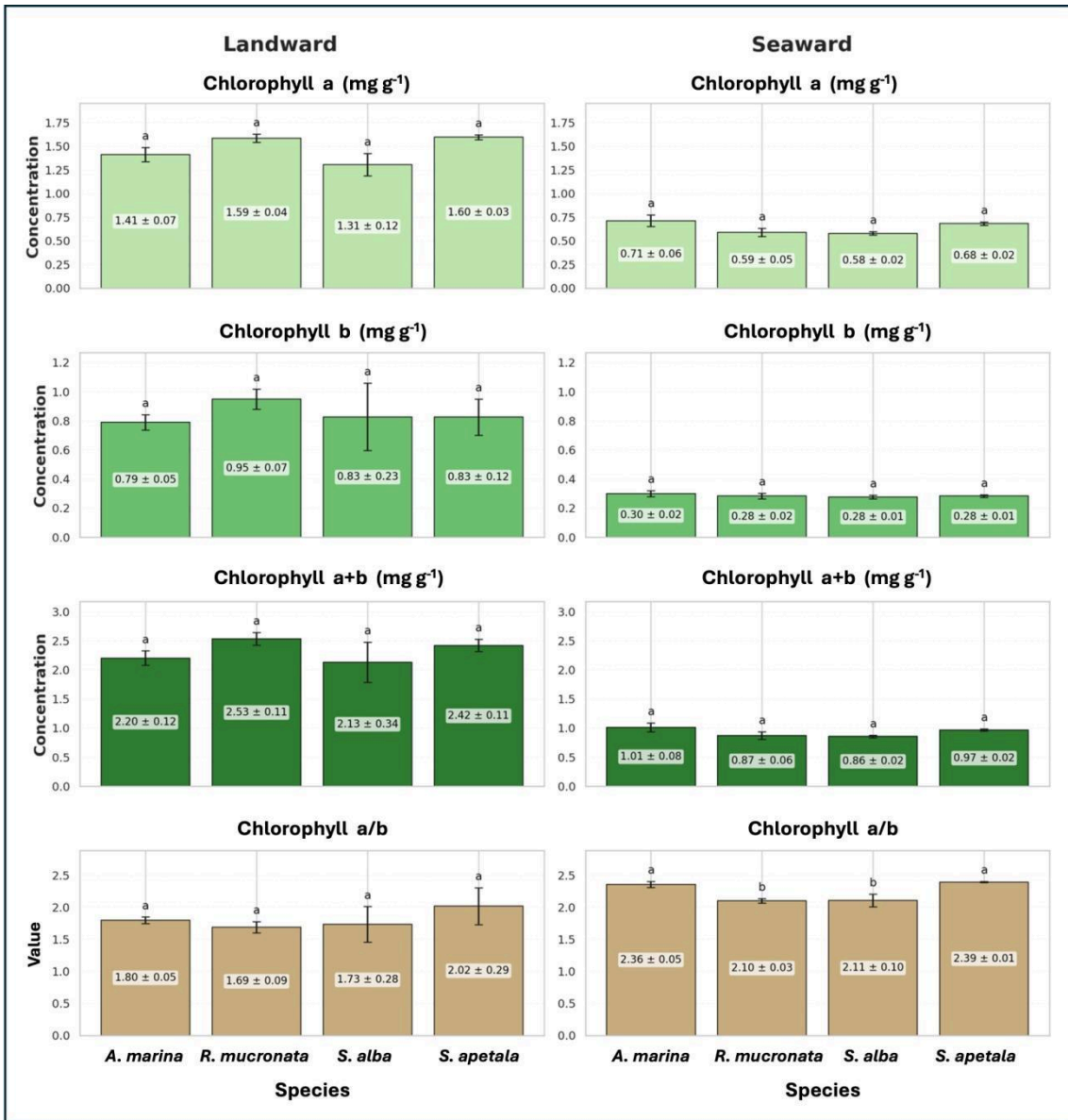


Figure 3. Mean chlorophyll content (mg g⁻¹) in four mangrove species at Carter Road, Mumbai. Left and right panel: landward and seaward mangrove vegetation respectively. Top to bottom: chlorophyll a; chlorophyll b; chlorophyll a+b and ratio of chlorophylls (a/b). Inside bars: mean values; and letters above error bars: Tukey’s post hoc comparisons.

ORDINARY LEAST SQUARES MODEL FOR CHLOROPHYLL

Modelling studies for chlorophyll concentrations (Chl a, Chl b and Chl a+b, mg g⁻¹) with ordinary least squares (OLS) showed statistically significant (L – S) EMM differences ($p < 0.05$) for all four species (Figure 4 and 5). For the ratio (Chl a/b), two species (*A. marina* and *R. mucronata*) exhibited significant (L – S) EMM differences, whereas *S. alba* and *S. apetalla* were not statistically distinguishable from zero. Positive differences indicate higher

values on the landward side while negative differences indicate higher values seaward (Figure 5). Overall, concentration metrics consistently differed by shoreline position across species, while the Chl a/b ratio showed species-specific effects. The differences in chlorophyll concentrations were dominated by position, with limited and variable species-level separation, and minimal evidence of zone-dependent modulation across species indicating that position-related differences were broadly similar across species.

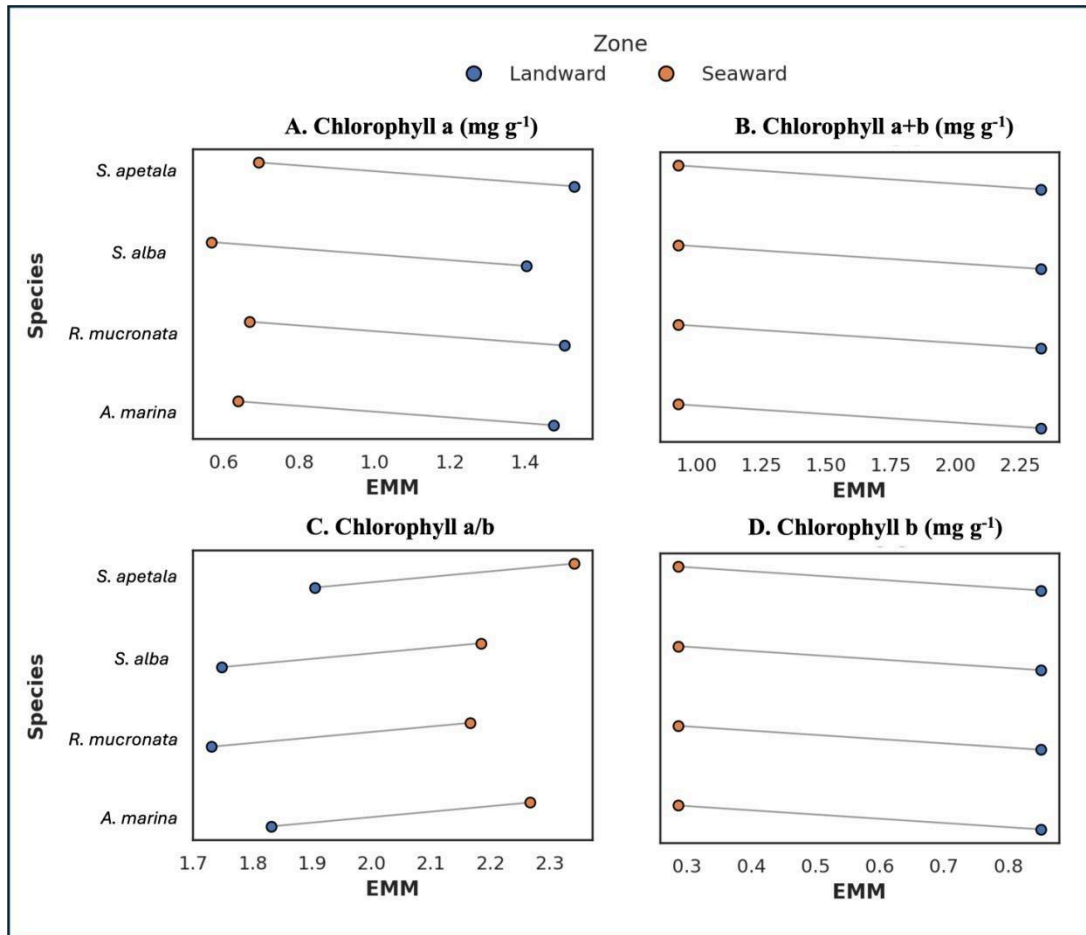


Figure 4. Cleveland dot-plots displaying estimated marginal means (EMMs) modelled with OLS for chlorophyll parameters by species within each shoreline position (Landward, Seaward). Panels correspond to parameters (A) Chl a; (B) Chl b; (C) Chl a+b; and (D) Chl a/b. species on the y-axis and EMMs on the x-axis with 95% confidence intervals. Species are ordered by their EMM within each panel to emphasize relative ranking. Legend indicates shoreline position: blue -landward and orange -seaward. The model used to estimate EMMs (fixed: species × position, grouped with position (see legend) and intervals reflect within-panel uncertainty for the marginal means. Limited overlap or separation suggests meaningful differences.

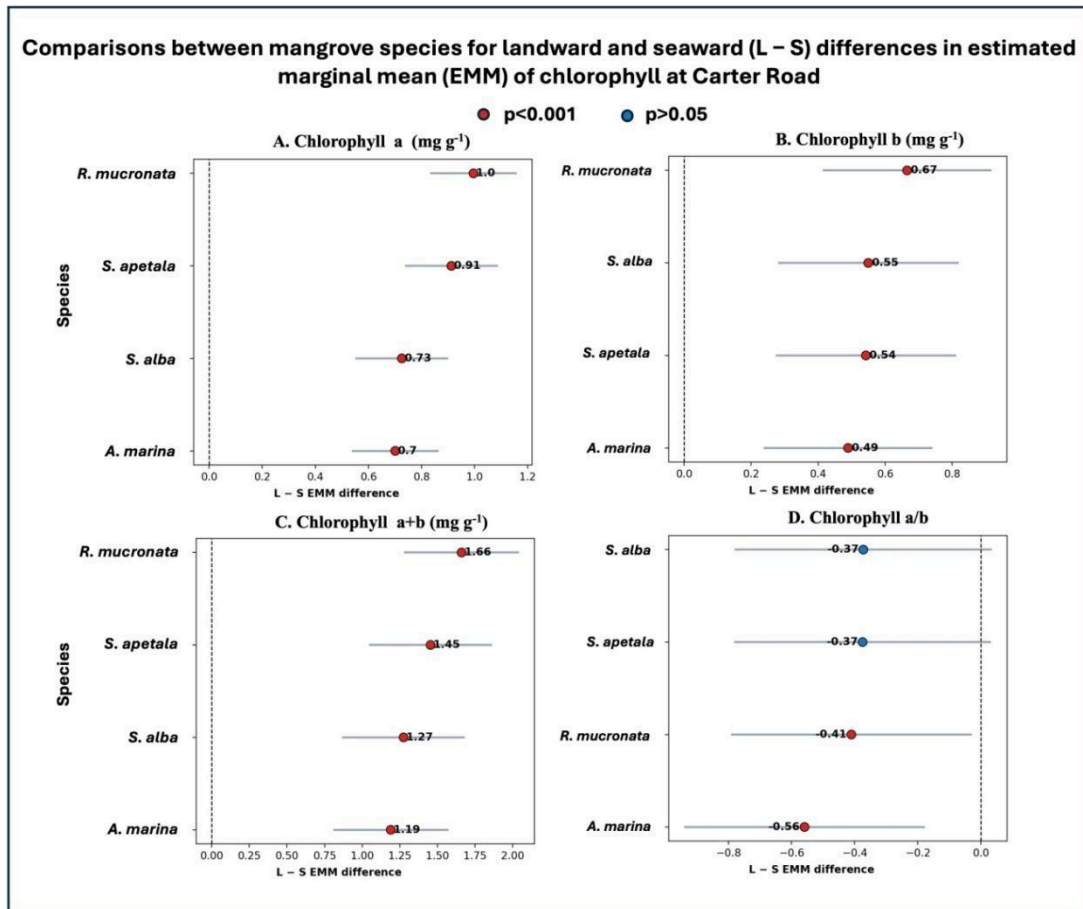


Figure 5: Landward – Seaward estimated marginal mean (EMM) differences with CIs and p-values. Each panel corresponds to a chlorophyll outcome: (A) Chl a; (B) Chl b; (C) Chl a+b (mg g⁻¹); and (D) Chl a/b ratio. For each species, the point shows the EMM difference (landward minus seaward) with a 95% confidence interval (horizontal bar). Labels give the difference value and two-sided p-value from a normal-approximation z test; a dashed vertical line marks zero (no difference). Legends: red = statistically significant differences ($p < 0.001$), blue = Not significant ($p \geq 0.05$). Positive values indicate higher EMMs in Landward relative to seaward; negative values indicate higher EMMs in seaward. Species are ordered by the difference within each panel to emphasize magnitude and direction.

SOIL CARBON PARAMETERS

The data for soil parameters soil organic carbon (SOC %), bulk density (BD) and soil strata C_{Org} (will be addressed as SOC_{Org} further) up to 50 cm depth was estimated (Table 3). Trends of these parameters with increasing depth in either seaward or landward soil samples were insignificant in one way ANOVA. However, two way ANOVA for pairwise comparisons without replication between depth and position were significant for position only. For

example, SOC (%) ($F=81.51$) of seaward soil samples was in the range -1.41 ± 0.06 to 1.11 ± 0.10 (0-10 to 40-50 cm depth) in comparison with the landward sediments (2.08 ± 0.31 to 1.49 ± 0.20) (Table 3). The soil strata C_{Org} ($F = 53.26$) was considerably higher in the landward sediments (20.79 ± 2.45 to 24.07 ± 2.41 Mg C ha⁻¹) with drastically lower seaward trends (1.12 ± 0.06 to 1.41 ± 0.12 Mg C ha⁻¹). Bulk density ($F=0.85$) was insignificant across position (L and S) as well as across the depth profile ($F=0.19$) (Table 3). Tukey's post-hoc analysis concurrently was insignificant for depth wise comparison of means. Hence, the depth pattern was evaluated with a more robust LME model that has better ability to predict the treatment groups to configure the associations and relative trends.

Table 3. Soil parameters up to 50 cm depth in the seaward and landward coastal sediments.

	Sample locations with soil depth (cm)									
	Seaward					Landward				
	0-10	10-20	20-30	30-40	40-50	0-10	10-20	20-30	30-40	40-50
Soil OrganicCarbon	1.41	1.30	1.26	1.19	1.11	2.08	1.93	2.02	1.70	1.49
SOC (%)	± 0.06	± 0.08	± 0.08	± 0.12	± 0.10	± 0.31	± 0.30	± 0.36	± 0.24	± 0.20
Bulkdensity	1.28	1.19	1.15	1.15	1.11	1.12	1.16	1.29	1.33	1.41
(g cm⁻³)	± 0.07	± 0.07	± 0.05	± 0.06	± 0.03	± 0.06	± 0.05	± 0.12	± 0.10	± 0.12
Soil strata SOC_{Org}	18.05	15.54	14.60	13.72	12.44	22.37	20.79	24.07	21.95	20.04
(Mg C ha⁻¹)	± 1.71	± 1.87	± 1.57	± 1.97	± 1.38	± 2.36	± 2.45	± 2.41	± 2.51	± 1.48
Soil pH	7.35	7.48	7.45	7.52	7.80	6.62	6.88	6.77	6.96	7.44
	± 0.08	± 0.07	± 0.04	± 0.08	± 0.07	± 0.11	± 0.11	± 0.11	± 0.11	± 0.11
Moisture (%)	---	---	---	---	---	60.13	54.97	28.57	28.50	17.35
						± 1.78	± 2.83	± 4.30	± 2.63	± 1.75

Values represent mean \pm SEM

LINEAR MIXED EFFECT MODEL FOR SOIL PARAMETERS

The mixed-effects framework (LME), showed patterned differences with considerable decline in SOC (%) indicating significant stratification with depth ($LR_{stat}=40.4$) and positional differences ($LR_{stat}=9.59$), as well as their interaction effects ($LR_{stat}=7.28$) (Table 4). Estimated marginal means (EMMs) indicated declining SOC (%) with depth on the seaward side, for example, 0–10 cm vs 40–50 cm showed a significant decrease ($p < 0.01$) (Figure 6). Positional differences tended to favour higher SOC (%) landward, with a landward–seaward contrast at 20–30 cm of 0.753 percentage points (EMM difference) ($p < 0.05$). These results

indicate broadly higher soil organic carbon (SOC %) on the landward side and a depth decline that is consistent across positions, suggesting that landward areas may play a key role in carbon storage within this ecosystem.

Table 4. Result of linear mixed effect model for soil parameters

	Depth		Position		Depth×Position	
	LR _{stat}	p	LR _{stat}	p	LR _{stat}	p
Soil organic carbon (SOC) (%)	40.4	<0.000001	9.598	<0.001	7.275	<0.01
Bulk density (g cm⁻³)	---	<0.01	19.966	<0.00001	19.485	<0.001
Soil strata C_{Org} (MgC ha⁻¹)	31.684	<0.000001	18.026	<0.00001	13.686	<0.01

Similar trends were observed for BD with strong position effects and could be seen with evidence that depth profiles differ by position (Table 4). Position effects ($LR_{stat}=19.96$) and the depth × position interaction influences ($LR_{stat}=19.49$) were both quite significant ($p < 0.001$). The depth-only reduced model was singular ($p < 0.01$), preventing a clean LRT for an overall effect of depth; however, the interaction implies that BD's depth pattern is not parallel between positions ($p < 0.001$). EMM position contrasts were generally modest at any single depth, suggesting that while the overall position effect is clear, the depth-dependent divergence is better captured as a profile difference rather than isolated pairwise depths.

The SOC_{Org} (Mg C ha⁻¹) varied significantly across both depth and location as indicated in two-way ANOVA (Table 4). The SOC_{Org} displayed consistent and robust structure (Figure 5) with depth ($LR_{stat} = 31.68$), position ($LR_{stat} = 18.026$), and depth × position ($LR_{stat}=13.68$).

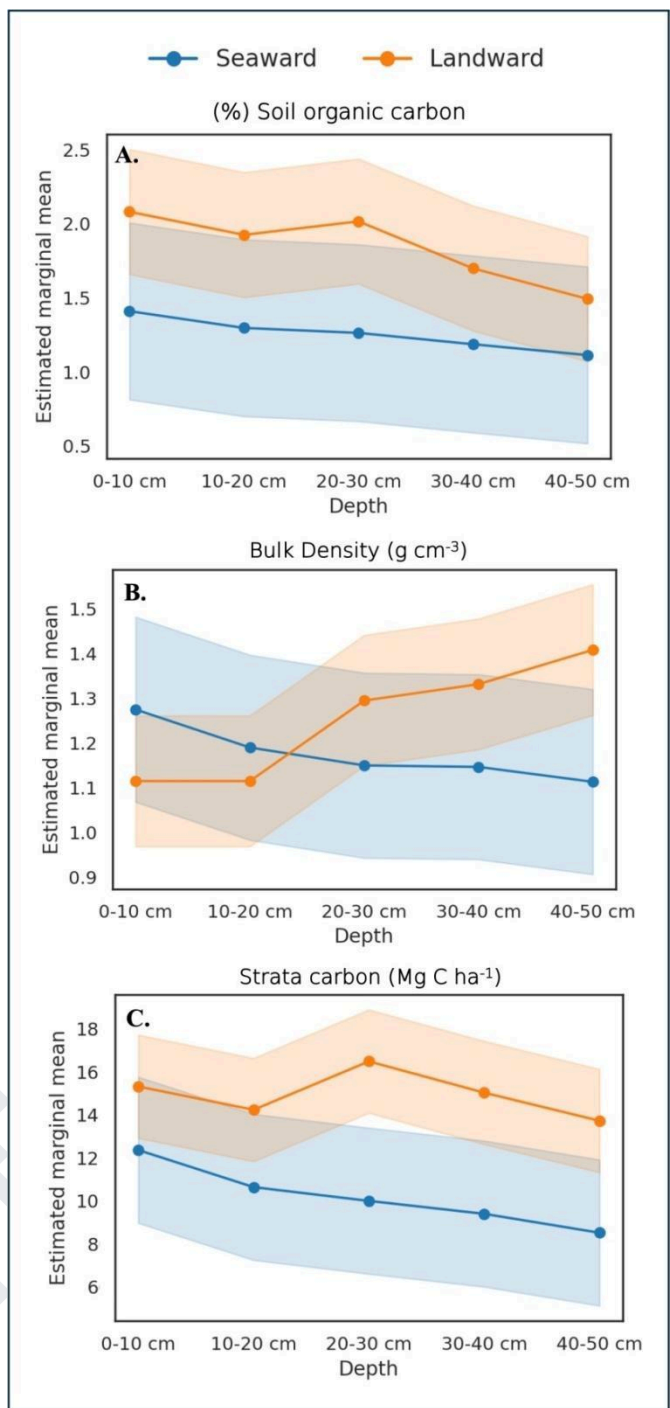


Figure 6. Line charts for comparison of EMMs of sediment parameters. On x axis: soil depth (0 to 50 cm); and y axis: (A) SOC (%); (B) Bulk density (g cm⁻³); and (C) Soil strata carbon (SOC_{Org} - Mg C ha⁻¹).

This indicates that absolute levels differ between seaward and landward zones, and the way carbon accumulates with depth is also driven by relative position of the vegetation in

the ecosystem. Soil pH was consistently incremental across the depth profile for both seaward (7.35 ± 0.08 to 7.80 ± 0.07) and landward (6.62 ± 0.11 to 7.44 ± 0.11). Strong one way ANOVA suggests that pH values were meaningfully significant for same depth across the two locations (seaward ($F = 16.096$; $p < 0.0001$) and landward ($F = 18.641$; $p < 0.0001$) on Carter road mangroves.

LEAF PIGMENT AND SEDIMENT RELATIONS

The correlation between the key chlorophyll and soil parameters was quite distinct for certain relationships (Figure 7). For instance, pH showed drastically strong positive correlation in landward samples with chlorophyll concentrations (Chl a: $r = 0.98$; Chl b: $r = 0.85$ and Chl a+b: $r = 0.90$) whereas Chl a/b with extreme negative correlation ($r = -0.76$). Seaward samples had very weak correlations for these parameters. pH also had an absolute negative association ($r = -1.0$) with seawards strata SOC_{org} and remained consistent though moderately weak landwards. Another notable switch between the two positions (L & S) was the negative correlation of Chl a+b concentration with Chl a/b ratio ($r = -0.63$) and SOC (%) ($r = -0.37$) in the landward samples whereas seaward showed moderately positive relations (Figure 7). The strata SOC_{org} had consistent strong positive associations with Chl a across the ecosystem boundaries (L: $r = 0.61$ and S: $r = 0.97$).

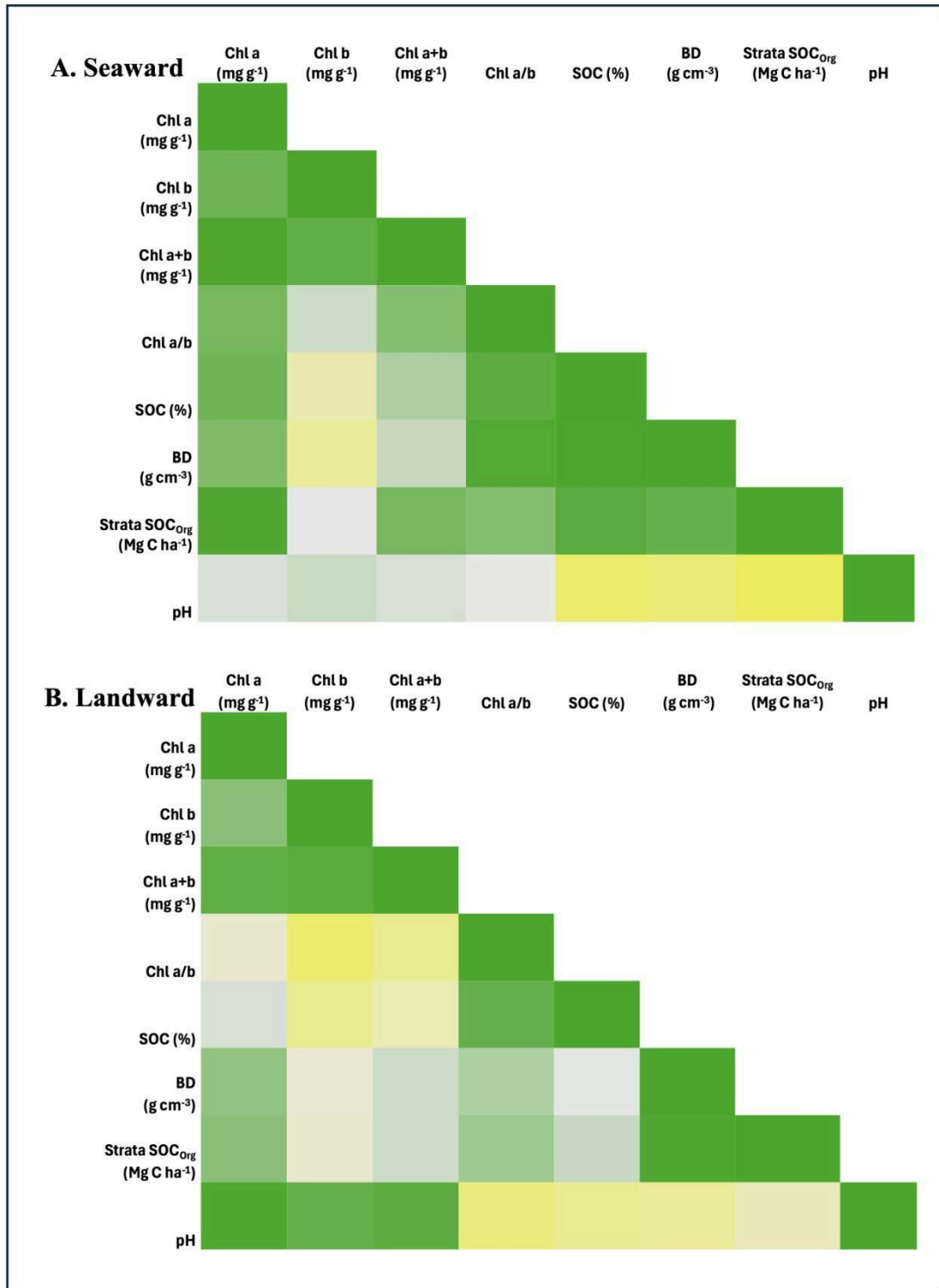


Figure 7. Correlation of chlorophyll and sediment parameters at the ecosystem boundaries (A) seaward and (B) landward. Colours indicate strength of association – Green: $r=1$ and Yellow: $r=-1$ and Grey: $r=0$

TREE BIOMASS AND CARBON

The tree density of 2717.5 individuals per hectare was recorded at the study site with dominance of *A. marina*. Trees on the landward edge were taller with visibly thicker girth and DBH while trees on seaward fringe were much shorter. Overall, larger proportion of the ecosystem had trees with DBH range (10 to 40 cm) mostly at landward edge (Table 6). The (mean \pm SEM) values of AGB and BGB stood at 769.41 ± 71.33 Mg ha⁻¹ and 214.20 ± 19.86 Mg ha⁻¹ respectively with their biomass carbon pools - $AGBC_{Org} = 357.00 \pm 33.10$ MgC ha⁻¹ and $BGBC_{Org} = 99.39 \pm 9.21$ MgC ha⁻¹ (Figure 8).

DISCUSSION

LEAF PHYSIOLOGY

Leaf moisture (LM % F_w) was >70% for all the species in the order *A. marina* > *S. alba* > *R. mucronata* = *S. apetella* (Figure 2). The proline content of species in the natural environment was significantly different in the order *R. mucronata* > *A. marina* > *S. alba* > *S. apetala*. Local and regional environmental factors, especially stressors like tidal inundation, solar radiations, fresh water inputs, salinity among many others, can collectively influence the production of photochemicals and osmoprotectants in mangrove plants (Flores-de-Santiago et al., 2016; Dookie et al., 2023). In high salinity conditions, mangroves accumulate compatible solutes (e.g., sugars, sugar alcohols, proline, glycine) as osmoprotectants (Bryant et al., 2024; Naidoo, 2025) with a primary mandate to maintain turgor pressure necessary to protect the photosynthetic apparatus including cellular structures such as chloroplasts and thylakoid membranes, from damage, and indirectly supporting chlorophyll function and stability (Bryant et al., 2024; Parveen et al., 2024). Such mechanisms are also known to provide heat tolerance in saline environments (Bryant et al., 2024). Proline, an amino acid as well as a compatible solute, is synthesised either in the cytosol or chloroplast based on either of its roles. Additionally, it is a common physiological response to osmotic stress triggered by salinity, drought, and other abiotic challenges (Verbruggen and Hermans, 2008; Meena et al., 2019; Nizam et al., 2022; Parveen et al., 2024). Mangroves in hypersaline dwarf zones with less tidal flushing and higher soil salinity, often exhibit higher Na⁺ concentrations in leaves accompanied by increased proline accumulation to counteract the osmotic and ionic challenges (Mehta and Vyas, 2023; Naidoo, 2025). Other known factors of proline accumulation in plants include, metal toxicity and high UV radiation zones (Kishor et al., 1995; Hayat et al., 2012; Meena et al., 2019; Nizam et al., 2022; Alharbi et al., 2024). The biochemical synthesis of proline, usually under stress, is orchestrated by enzymes Δ 1-pyrroline-5-carboxylate synthetase (P5CS) and Δ 1-pyrroline-5-carboxylate reductase

(P5CR) from glutamate as the parent molecule (Delauney and Verma, 1993; Liu and Wang, 2020). Abscisic acid is also known to stimulate proline synthesis under salt and osmotic stress (Nizam et al., 2022). There can be variation in the proline accumulation by mangrove species in different stress conditions (Meena et al., 2019; Nizam et al., 2022). Presumably, in our study, *S. apetela* accumulated less proline in the given set of ambient ecosystem conditions, tropical climate with urban influence, than the other three species (Figure 3). The latter group did not differ meaningfully from one another under the ambient ecosystem conditions. Liu and Wang (2020) provide a good explanation of the heat stress mediated connectedness between transpiration rates with proline synthesis and accumulation which is feedback-regulated by proline. Similarly, another study by Wang et al. (2022) demonstrated effects of low temperatures on proline accumulation in five different mangrove species wherein *A. marina* gave a relatively quicker and stronger response for proline accumulation than most species, however the levels subsided with prolonged stress. Afele et al. (2021) explored the ambient proline concentration of *A. marina* (18.57 mg g⁻¹ DW) and *R. mucronata* (23.98 mg g⁻¹ DW). Two other studies indicate accumulation of proline under upwelling stress factors and another under ambient heavy metal stress (Li et al., 2022; Alharbi et al., 2023).

Chlorophyll content can be useful to determine whether plants are able to protect their photosynthetic apparatus due to marine as well as anthropogenic stressors (Sharma et al., 2025). Chl a content of *S. alba* was consistently lower than one or more species whereas *R. mucronata* and *A. marina* exceed significantly with similar trends for Chl a+b in either locations (Figure 3). Moreover, for Chl b, *A. marina* and *S. apetella* exceed *S. alba* and it seems that *S. alba* on the landward edge invests less in total pigment suggesting a smaller photosynthetic apparatus or different leaf economics. *A. marina* and *S. apetella* show higher accessory pigment (Chl b), supporting stronger light-harvesting capacity or acclimation to canopy/light conditions inland. A study by Afele et al. (2021) observed higher chlorophyll content in *A. marina* than *R. mucronata* supporting former's greater tolerance and wider distribution. Avicenniaceae family is often considered more tolerant to salinity stress than Rhizophoraceae (Hutchings and Saenger, 1987; Afele et al., 2021). The Lythraceae family, is comprised of terrestrial, aquatic and mangrove species (*Sonneratia* spp. – *S. caseolaris*, *S. lanceolata*, *S. alba* and *S. apetala*) – with notable presence of these mangroves in the coastal regions with varying salinity (Tomlinson, 1986; Ball and Pidsley, 1995; Simpson, 2010; Tatongjai et al., 2021). Among these, *S. alba*, is known for its maximum growth even at 50% sea water (Ball and Pidsley, 1995). *S. apetella* showed the strongest high-light acclimation at the shore fringe (highest a/b), consistent with greater irradiance and reflectance at the seaward edge. *R. mucronata*'s lower a/b suggests a more shade-like antenna composition or different stress response at the fringe (Figure 3). Based on two-way ANOVA, species showed a significant effect across all measures, indicating consistent differences among each other (Table 2). Location had a strong and highly significant effect on Chl a, Chl b, and Chl a+b,

reflecting clear landward–seaward contrasts (EMM differences), and was also significant for the Chl a/b ratio (Figure 5). Interaction effects were significant for the Chl a/b ratio and Chl b, suggesting that species differences vary by location, conversely the interaction effects for Chl a and Chl a+b were marginal (around the 0.05 threshold), implying broadly similar species ranking across locations with only weak evidence of location-specific shifts (Table 2 and Figure 4). It will be appropriate to infer that species identity and location contribute meaningfully to chlorophyll variation, with the strength and nature of interactions most pronounced for the Chl a/b ratio and Chl b.

Factors like salinity have thus far revealed a significant reduction in Chlorophyll content (Chl a and Chl b) (Marae et al., 2024; Naidoo, 2025). High salinity can lead to increased levels of reactive oxygen species (ROS), causing cellular damage (Meena et al., 2019; Nizam et al., 2022). Mangroves activate ROS scavenging systems, and carotenoids play a crucial protective role against this oxidative stress, which can indirectly influence the stability of other photosynthetic pigments like chlorophyll (Hasanuzzaman, 2021; Zhou et al., 2022, Parveen et al., 2024). Although, there have been reports where higher salinity correlated with higher chlorophyll content in climax communities of *Ceriops decandra* and *Excoecaria gallocha* (Sarker et al., 2021; Ahmed et al., 2022; Parveen et al., 2024). In another study, *A. marina* exhibited higher values of these photochemical molecules in lower salinity zones (littoral and intertidal) than their landward counterparts (Marae et al., 2024). Dookie et al. (2023) observed relatively higher chlorophyll content in *Avicennia germinans* growing in degraded habitats when compared with natural or restored ones.

Conversely, in our study, lower chlorophyll content was observed in the seaward plants that may be attributed to the rocky barricade with restricted drainage seawards and extremely younger population growing in tropical heat. This barricade effect coupled with aridity in the tropical sun may contain the salts in the sediments that can increase salinity levels on the seaward edge. Moreover, being an urban hotspot of Mumbai, Carter road has significant influence of urban runoff, discharge, plastic wastes and maybe petroleum too, due to extensive port activity in Mumbai. These can disturb the sediment nutrient balance of trace metals, iron, sulphur, nitrogen and many others indispensable for forest productivity (Alongi, 2014; Chen et al., 2018). Nitrogen-limitation can directly impact chlorophyll production, especially in extremely saline sediments (Naidoo, 2025). Another study by Duke and Watkinson (2002) on *A. marina* and *R. mangle* plants, explained the occurrence of deteriorating chlorophyll mutations due to poly aromatic hydrocarbon (PAH) that have a lethal effect on the population of the young seedlings. Mangrove population at the landward edge of Carter road has higher chlorophyll content and seems more resilient and dominant with mature stands and higher species diversity that can provide nursing through intricate balance of sediment nutrition and distribution as well as bioavailability.

SOIL CARBON PARAMETERS

The LME model suggests meaningful vertical structuring and spatial (positional) differences in SOC (%) and carbon stocks that the simpler per-position one-way ANOVAs missed. The gains likely come from modelling all depths jointly, accounting for repeated measures within cores, and testing interactions directly. Caveats include the singular reduced model for BD's depth test and boundary convergence warnings, which are common in mixed models; nonetheless, key effects e.g. decline in SOC (%) with depth and landward elevation as well as interaction patterns for BD and mean soil strata C_{org} are supported by likelihood ratio tests and EMM contrasts (Table 3). Based on the finding it can be concluded that SOC (%) decreases with depth and is higher landward (e.g., + 0.671% at 0–10 cm, $p = 0.072$, and + 0.753 % at 20–30 cm, $p < 0.05$), BD depth profiles differ by position (interaction $p < 0.001$), and soil strata C_{org} shows position differences with depth-dependent profiles (all the effects and interactions $p < 0.01$). In practical terms, the landward edge tends to have higher carbon stocks (Figure 8), and the depth gradients are not parallel across positions— that may be consistent with geomorphic or hydrological controls varying across the transect.

CHLOROPHYLL AND SEDIMENT RELATIONS

Most associations of SOC (%), BD and soil strata SOC_{org} with chlorophyll parameters transitioned to weaker or negative associations while moving from seaward fringe to landward edge (Figure 7). These relationships provide valuable insights into the possible integrated patterns of ecophysiology driven blue carbon sequestration of this mangrove ecosystem at the two spatial extremities. Albeit fluctuating, but relationships of Chl a/b with soil parameters make it an important positively associated factor in the carbon burial processes, only seconded by Chl a concentrations.

ECOSYSTEM CARBON ACCUMULATION: SEDIMENT AND TREE BIOMASS

The tree density at Carter Road is quite high when compared with other sites in Mumbai like Thane Creek. *A. marina* covered the maximum canopy of the ecosystem with accompanying species relatively fewer in number. Mumbai mangroves have faced considerable fluctuations in the forest structure in past two decades. Vijay et al. (2005) reported tree densities of > 900 trees per hectare for Mumbai mangroves. Later, Patil et al. (2014) recorded 89, 218, 233, 159 and 150 trees per hectare for different regions within Thane Creek ecosystem which indicate a sharp decline in a decade. Further, our analysis recorded about 6.54 hectare green cover at the Carter road, Mumbai. Two decades old report indicate large forest extent in Mumbai with high tree densities (Vijay et al., 2005) that has been declining since then. Bhattacharjee et al. (2025) reported 40% loss of green cover in last three decades. Similar to our observation at the study site, *A. marina* is consistently identified as the predominant mangrove species

across Mumbai's coastal areas, including Thane Creek, Manori Creek, and Gorai Creek (Kantharajan et al., 2018; Azeez et al., 2022; Sawant et al., 2024; Patil and Kanhere, 2024).

Our estimates indicate a significant biomass carbon deposits in this ecosystem with mean values of $AGBC_{Org}$, $BGBC_{Org}$ and $Ecosystem C_{Org}$ to be much higher than the previous assessments in Mumbai region partly due to the different allometric equations used that were reportedly lower than most studies for similar forest structure (Singh et al., 2023). The DBH of trees at Carter Road were in the range (10 to 40 cm) or there were very small seedlings landwards and young stands with $DBH < 5$ cm seawards. There were too few stands ranging between 5 to 10 cm in each plot. Another study by Nar et al. (2024) recorded DBH between 17 cm to 58 cm, however, their time for measurement was not available, to compare the values or determine the rate of biomass carbon accumulation. Earlier studies reported DBH that typically ranged from 3 cm to 40 cm (IISST, 2019).

Table 5. Total Soil strata organic carbon in the study area.

Soil depth interval (cm)	SOC _{Org} (Mg C)	
	Seaward	Landward
0-10	118.51 ±11.23	128.37±9.31
10-20	101.98±12.27	108.50 ±18.00
20-30	95.85 ±10.30	101.59 ±14.81
30-40	90.08±12.87	100.31±13.53
40-50	81.65±9.03	88.85±9.45
Total	488.07	527.62
*Average of total	507.84	

Values represent mean ± SEM

* Average of landward and seaward SOC_{Org} values summed up to 50 cm depth.

Table 6. Total ecosystem carbon stock of mangroves at Carter Road.

Above Ground Biomass Carbon	Below Ground Biomass Carbon	*Soil Organic Carbon	Ecosystem Carbon
--------------------------------	--------------------------------	-------------------------	---------------------

	(AGBC _{Org})	(BGBC _{Org})	(SOC _{Org})	(C _{Org})
Organic Carbon(C _{Org}) #(Mg C ha ⁻¹)	357.00±33.01	99.39±9.21	91.78±9.84	548.17
Total carbon (Mg C)	2334.80	650.01	507.84	3492.65

#Values represent mean ± SEM.

*Average of landward and seaward SOC_{Org} values summed up to 50 cm depth

The aboveground and belowground biomass accounted (mean ± SEM) 769.41 ± 71.33 Mg ha⁻¹ and 214.20 ± 19.86 Mg ha⁻¹ respectively. The carbon counterparts of the biomass carbon pools - AGBC_{Org} = 357.00 ± 33.10 MgC ha⁻¹ and BGBC_{Org} = 99.39 ± 9.21 MgC ha⁻¹(Table 6). Mangrove carbon sequestration studies like the one by Singh et al. (2023) estimated mangrove biomass carbon and soil carbon at Thane creek with integrated allometry-remote sensing techniques and accounted AGBC_{Org} at 47.68 MgC ha⁻¹ with an increment from previous estimate of 21.66 MgC ha⁻¹ (Patil et al., 2015). The (BGBC_{Org}) was 18.06 MgC ha⁻¹(Patil et al., 2015) and 12.41 MgC ha⁻¹(Singh et al., 2023).

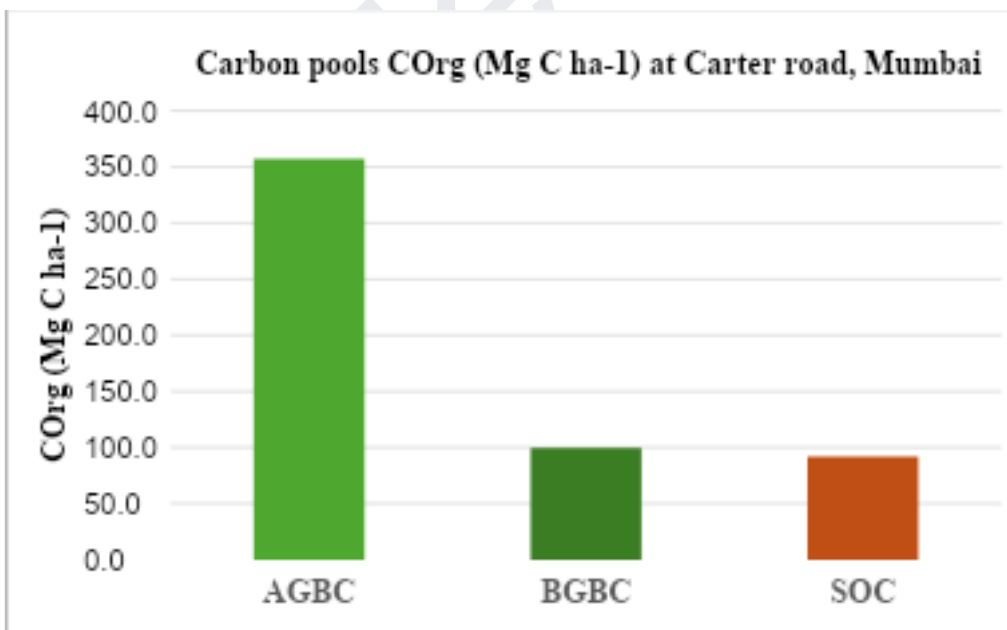


Figure 8. Bar graph for carbon pools (C_{org} Mg C ha^{-1}) of the mangrove ecosystems at Carter Road, Mumbai. (AGBC= aboveground biomass carbon; BGBC=belowground biomass carbon; SOC=soil organic carbon).

The average of SOC_{org} up to 50 cm depth was estimated about 91.79 ± 9.85 MgC ha^{-1} with seaward and landward SOC_{org} of 488.07 Mg C and 527.62 Mg C respectively (Table 5). The average landward and seaward SOC_{org} for the entire ecosystem summed up to 50 cm depth was 507.84 Mg and can give only rough estimate of ecosystem carbon stock since samples belonged to extreme ends of ecosystem along the shoreline and values can be highly skewed. Different mangrove locations at Thane creek had SOC (%) varying between 2.35 to 13.86% (Patil et al., 2014) and the mean sediment carbon stock, measured up to 40 cm depth, was 63.79 Mg C ha^{-1} and 30% concentrated in the top 0-10 cm layer (Singh et al., 2023). The total organic carbon in surface sediments across Mumbai mangroves ranged from 2.5% to 5.3%, with highest at Versova and lowest at Sewri (Kesavan et al., 2025). In this study, the ecosystem $AGBC_{org}$ and $BGBC_{org}$ values were 2334.80 Mg C and 650.01 Mg C respectively (Figure 8). The total ecosystem carbon stock, the sum of the three carbon pools $AGBC_{org}$, $BGBC_{org}$ and SOC_{org} , was 3492.65 Mg carbon (Table 6). Relatively, our estimates suggest a large carbon deposit at the Carter road mangroves with significant sediment and $AGBC_{org}$ reserves. The vibrance of this plant community may be attributed to species diversity at Carter Road that contribute to carbon burial along with supportive environmental and sediment conditions. Being an urban hotspot, its serenity attracts leisurely activities along the coast.

Overall, a robust physiology adds to the productivity of mangroves. Elevated chlorophyll levels typically correlate with higher photosynthetic rates, contributing to enhanced biomass accumulation and net primary productivity (Lovelock, 2006; Alongi, 2025) and indicate favourable growth conditions with increased carbon assimilation (Singh et al., 2023; Rodríguez-Reales et al., 2024). Empirical studies have demonstrated that mangrove productivity, measured in terms of biomass or carbon sequestration, aligns with chlorophyll content variations across species and sites, modulated by environmental gradients such as salinity, nutrient availability, and light intensity (Kumar et al., 2023; Alongi, 2025).

CONCLUSION

The small mangrove plant community at Carter Road exuberates wilderness by standing its ground in the face of coastal, climate and urban stressors. This pilot study of profiling mangroves at Carter Road was an attempt to understand the ecophysiological and geocological status of urban ecosystems that face unique position specific challenges. The ecosystem proline levels indicate the stressors experienced by the ecosystem. Such secluded ecosystems, with unique geomorphological characteristics and urban influence, can exhibit diverse strategies of adaptation and survival. The spatial variability in the chlorophyll and SOC (%) across the seaward and landward positions are meaningful indicators of resilience

to drive productivity and carbon storage, especially in the existing ecogeomorphological setting and urban influence. The carbon storage capability of this ecosystem is largely driven by the mangrove community with at least four distinct species and high tree density of *A. marina*. Several coastal locations in Mumbai, under huge urban influence, need to be explored and accounted for, to understand their role and importance in the rapidly declining mangrove cover of the city. Such investigations are necessary to inform policies and promote re-establishment of species rich patches of mangrove ecosystem that can add to the coastal resilience of the city.

ACKNOWLEDGMENT

We warmly thank the anonymous reviewers for their excellent review and suggestions to improve this manuscript.

AUTHOR CONTRIBUTIONS

S.Q.M.: Conceptualization; Investigation; Methodology; Data curation; Formal Analysis; Writing – original draft.

V.P.S.S.: Conceptualization; Investigation; Project Administration; Supervision; Resources; Writing – review & editing.

FUNDING

This research work did not receive a specific grant from any funding agency. The DBT-STAR grant to the department is sincerely acknowledged.

AI USE DISCLOSURE

AI tools were not used for any form of data analysis, writing or interpretations. This work employed the AI feature of Google Colab to generate visualisations during the preparation of this manuscript. Such outputs were carefully reviewed and edited by the authors to ensure accuracy and clarity. Authors take full responsibility for the content of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available from the corresponding author upon reasonable request

REFERENCES

- Abdul Azeez, S., Gnanappazham, L., Muraleedharan, K. R., Revichandran, C., John, S., Seena, G. & Thomas, J. 2022. Multi-decadal changes of mangrove forest and its response to the tidal dynamics of thane creek, Mumbai. *Journal of Sea Research*, 180, 102162. DOI: <https://doi.org/10.1016/j.seares.2021.102162>
- Adame, M. F., Cherian, S., Reef, R. & Stewart-Koster, B. 2017. Mangrove root biomass and the uncertainty of belowground carbon estimations. *Forest Ecology and Management*, 403, 52–60. DOI: <https://doi.org/10.1016/j.foreco.2017.08.016>
- Afeke, A. A., Khedr, A.-H. A., Abbas, M. S. & Soliman, A. S. 2021. Responses and Tolerance Mechanisms of Mangrove Trees to the Ambient Salinity along the Egyptian Red Sea Coast. *Limnological Review*, 21(1), 3–13. DOI: <https://doi.org/10.2478/limre-2021-0001>
- Ahmed, S., Sarker, S. K., Friess, D. A., Kamruzzaman, M., Jacobs, M., Islam, M. A., Alam, M. A., Suvo, M. J., Sani, M. N. H., Dey, T., Naabeh, C. S. S. & Pretzsch, H. 2022. Salinity reduces site quality and mangrove forest functions. From monitoring to understanding. *Science of the Total Environment*, 853, 158662 DOI: <https://doi.org/10.1016/j.scitotenv.2022.158662>
- Akram, H., Hussain, S., Mazumdar, P., Chua, K. O., Butt, T. E. & Harikrishna, J. A. 2023. Mangrove Health: A Review of Functions, Threats, and Challenges Associated with Mangrove Management Practices. *Forests*, 14(9). DOI: <https://doi.org/10.3390/f14091698>
- Alharbi, B. M., Abdulmajeed, A. M., Jabbour, A. A. & Hashim, A. M. 2023. Eco-physiological responses of *Avicennia marina* (Forssk.) Vierh. to trace metals pollution via intensifying antioxidant and secondary metabolite contents. *Metabolites*, 13 (808). DOI: <https://doi.org/10.3390/metabo13070808>
- Alharbi, K., Gharib, H., Mohamed, E., Elsamahy, B., Khedr, R., Darwish, A., AL-Hharbi, N., Albishi, T., Rashed, A., Mohamed, A. & Abdelaal, K. 2025. Effect of Some Biostimulants on Agronomic, Physiological, and Quality Traits of Wheat Plants (*Triticum aestivum* L.) under Water Deficit Stress Conditions. *Polish Journal of Environmental Studies*, XX(X), 1–17. DOI: <https://doi.org/10.15244/pjoes/194229>
- Aljahdali, M. O. & Alhassan, A. B. 2020. Ecological risk assessment of heavy metal contamination in mangrove habitats, using biochemical markers and pollution indices: A case study of *Avicennia marina* L. in the Rabigh lagoon, Red Sea. *Saudi Journal of Biological Sciences*, 27 (4), 1174–1184. DOI: <https://doi.org/https://doi.org/10.1016/j.sjbs.2020.02.004>

- Aljahdali, M. O., Alhassan, A. B. & Zhang, Z. 2021. Environmental Factors Causing Stress in *Avicennia marina* Mangrove in Rabigh Lagoon Along the Red Sea: Based on a Multi-Approach Study. *Frontiers in Marine Science*, 8. DOI: <https://doi.org/10.3389/fmars.2021.646993>
- Alongi, D. M. 2014. Carbon cycling and storage in mangrove forests. *Annual Review of Marine Science*, 6, 195–219. DOI: <https://doi.org/10.1146/annurev-marine-010213-135020>
- Alongi, D. M. 2018. *Blue carbon: Coastal sequestration for climate change mitigation*. Springer.
- Alongi, D. M. 2020. Carbon balance in salt marsh and mangrove ecosystems: A global synthesis. *Journal of Marine Science and Engineering*, 8(10), 1–21. DOI: <https://doi.org/10.3390/jmse8100767>
- Alongi, D. M. 2025. Global Meta-Analysis of Mangrove Primary Production: Implications for Carbon Cycling in Mangrove and Other Coastal Ecosystems. *Forests*, 16(5). DOI: <https://doi.org/10.3390/f16050747>
- Alongi, D. M., & Zimmer, M. 2024. Blue carbon biomass stocks but not sediment stocks or burial rates exhibit global patterns in re-established mangrove chronosequences: a meta-analysis. *Marine Ecology Progress Series*, 733, 27–42. DOI: <https://doi.org/10.3354/meps14560>
- Arnon, D. I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Betavulgaris*. *Plant physiology*, 24(1), 1–15. DOI: <https://doi.org/10.1104/pp.24.1.1>
- Ball, M. C. 1986. Photosynthesis in mangrove. *Wetlands (Australia)*, 6, 12–22.
- Ball, M. C., & Farquhar, G. D. 1984. Photosynthetic and stomatal responses of two mangrove species, *Aegiceras corniculatum* and *Avicennia marina*, to long term salinity and humidity conditions. *Plant Physiology*, 74(1), 1–6. DOI: <https://doi.org/10.1104/pp.74.1.1>
- Ball, M.C. & Pidsley, S.M. 1995. Growth Responses to Salinity in Relation to Distribution of Two Mangrove Species, *Sonneratia alba* and *S. lanceolata*, in Northern Australia. *Functional Ecology*, 9, 77-85. DOI: <https://doi.org/10.2307/2390093>
- Banerjee, S., Ghosh, S., Singh, K., Ghodke, M. & Sudarshan, M. 2021. Detection of metals and associated bacteria from Mumbai mangroves and their impact analysis. *Regional Studies in Marine Science*, 48, 102007. DOI: <https://doi.org/https://doi.org/10.1016/j.rsma.2021.102007>

- Bates, L. S., Waldren, R. P. & Teare, I. D. 1973. Rapid determination of free proline for water-stress studies. *Plant and Soil*, 39(1), 205–207. DOI: <https://doi.org/10.1007/BF00018060>
- Bhattacharjee, S., Sharma, M. & Tiwari, A. 2025. Change and continuity of coastal mangroves in greater mumbai, India: towards the sustainable governance of blue-green infrastructure. *Land*, 14, 1732. DOI: <https://doi.org/10.3390/land14091732>
- Breithaupt, J. L. & Steinmuller, H. E. 2022. Refining the global estimate of mangrove carbon burial rates using sedimentary and geomorphic settings. *Geophysical Research Letters*, 49 (18), e2022GL100177. DOI: <https://doi.org/10.1029/2022GL100177>
- Bryant, C., Harris, R. J., Brothers, N., Bone, C., Walsh, N., Nicotra, A. B. & Ball, M. C. 2024. Cross-tolerance: Salinity gradients and dehydration increase photosynthetic heat tolerance in mangrove leaves. *Functional Ecology*, 38(4), 897–909. DOI: <https://doi.org/10.1111/1365-2435.14508>
- Chazaux, M., Schiphorst, C., Lazzari, G. & Caffarri, S. 2022. Precise estimation of chlorophyll a, b and carotenoid content by deconvolution of the absorption spectrum and new simultaneous equations for Chl determination. *Plant Journal*, 109(6), 1630–1648. DOI: <https://doi.org/10.1111/tpj.15643>
- Chen, G., Gao, M., Pang, B., Chen, S. & Ye, Y. 2018. Top-meter soil organic carbon stocks and sources in restored mangrove forests of different ages. *Forest Ecology and Management*, 422, 87–94. DOI: <https://doi.org/10.1016/j.foreco.2018.03.044>
- Chen, B., Ding, Z., Zhou, X., Wang, Y., Huang, F., Sun, J., Chen, J. & Han, W. 2022. Integrated full-length transcriptome and microRNA sequencing approaches provide insights into salt tolerance in mangrove (*Sonneratia apetala* Buch.-Ham.). *Frontiers in Genetics*, 13. DOI: <https://doi.org/10.3389/fgene.2022.932832>
- Chen, Y., Zhang, S., Guo, J. & Shen, Y. 2024. Spatiotemporal evolution and impact mechanisms of gross primary productivity in tropics. *Forests*, 15(6), 913 DOI: <https://doi.org/10.3390/f15060913>
- Das, S. K., Patra, J. K. & Thatoi, H. 2016. Antioxidative response to abiotic and biotic stresses in mangrove plants: A review. *International Review of Hydrobiology*, 101(1–2), 3–19. DOI: <https://doi.org/10.1002/iroh.201401744>
- Delauney, A. J. & Verma, D. P. S. 1993. Proline biosynthesis and osmoregulation. *The Plant Journal*, 4 (2), 215–223. DOI: <https://doi.org/10.1046/j.1365-313X.1993.04020215.x>
- Dhanalakshmi, M., Akter, S., Gogoi, P., Deshmukhe, G., Landge, A. T., Bhushan, S., Layana, P., Shivkumar, Wanjari, R. N. & Nayak, B. B. 2024. The effect of the tidal cycle on the phytoplankton community assemblage in a mangrove-dominated tropical tidal creek.

Environmental Monitoring and Assessment, 196(9). DOI: <https://doi.org/10.1007/s10661-024-12954-y>

- Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., Stidham, M. & Kanninen, M. 2011. Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, 4(5), 293–297. DOI: <https://doi.org/10.1038/ngeo1123>
- Dookie, S., Jaikishun, S. & Ansari, A. A. 2022. Soil and water relations in mangrove ecosystems in Guyana. *Geology, Ecology, and Landscapes*, 8 (3), 1–25. DOI: <https://doi.org/10.1080/24749508.2022.2142186>
- Dookie, S., Jaikishun, S. & Ansari, A. A. 2023. *Avicennia germinans* leaf traits in degraded, restored, and natural mangrove ecosystems of Guyana. *Plant-Environment Interactions*, 4(6), 324–341. DOI: <https://doi.org/10.1002/pei3.10126>
- Duke, N. C. & Watkinson, A. J. 2002. Chlorophyll-deficient propagules of *Avicennia marina* and apparent longer term deterioration of mangrove fitness in oil-polluted sediments. *Marine Pollution Bulletin*, 44(11), 1269–1276. DOI: [https://doi.org/10.1016/S0025-326X\(02\)00221-7](https://doi.org/10.1016/S0025-326X(02)00221-7)
- Esteban, R., García-Plazaola, J. I., Hernández, A. & Fernández-Marín, B. 2018. On the recalcitrant use of Arnon's method for chlorophyll determination. *New Phytologist*, 217(2), 474–476. DOI: <https://doi.org/10.1111/nph.14932>
- Everard, M., Jha, R. R. & Russell, S. 2014. The benefits of fringing mangrove systems to Mumbai. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(2), 256–274. DOI: <https://doi.org/10.1002/aqc.2433>
- Field, C. D. 1995. Impact of expected climate change on mangroves. *Hydrobiologia*, 295 (1-3), 75–81. DOI: <https://doi.org/10.1007/BF00029113>
- Flores-de-Santiago, F., Kovacs, J. M., Wang, J., Flores-Verdugo, F., Zhang, C., and González-Farías, F. 2016. Examining the influence of seasonality, condition, and species composition on mangrove leaf pigment contents and laboratory based spectroscopy data. *Remote Sensing* 8 (3), 226. DOI: <https://doi.org/10.3390/rs8030226>
- Friess, D. A., Rogers, K., Lovelock, C. E., Krauss, K. W., Hamilton, S. E., Lee, S. Y., Lucas, R., Primavera, J., Rajkaran, A. & Shi, S. 2019. The state of the world's mangrove forests: past, present, and future. *Annual Review of Environment and Resources*, 44 (1), 89–115. DOI: <https://doi.org/10.1146/annurev-environ-101718-033302>
- Giesen, W., Wulffraat, S., Zieren, M. & Scholten, L. 2007. Mangrove guidebook for Southeast Asia, 1st ed. RAP Publication, Bangkok.
- Hasanuzzaman, M., Raihan, Md. R., Masud, A. A., Rahman, K., Nowroz, F., Rahman, M., Nahar, K. & Fujita, M. 2021. Regulation of reactive oxygen species and antioxidant

- defence in plants under salinity. *International Journal of Molecular Sciences*, 22, 9326. DOI: <https://doi.org/10.3390/ijms22179326>
- Hayat, S., Hayat, Q., Alyemeni, M. N., Wani, A. S., Pichtel, J. & Ahmad, A. 2012. Role of proline under changing environments: A review. *Plant Signaling and Behavior*, 7(11), 1-11. DOI: <https://doi.org/10.4161/psb.21949>
- Parveen, H. K., Muhammed, J., Sneha, V. K., Busheera, P. & Augustine, A. 2024. OMICS strategies: Revealing the enigma of salinity tolerance in mangroves. *Crop Design*, 3(2), 100052. DOI: <https://doi.org/https://doi.org/10.1016/j.cropl.2024.100052>
- Howard, J., Hoyt, S., Isensee, K., Telszewski, M. & Pidgeon, E. 2014. *Coastal Blue Carbon: Methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses*. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature. Arlington, Virginia, USA. 180 pp
- Hutchings, P. A., & Saenger, P. (1987). *Ecology of mangroves*. University of Queensland Press.
- IISST. 2019. *Monitoring The Health of Mangroves of Maharashtra State Using Near Real Time satellite Remote Sensing Data*. Mumbai, Indian Institute of Space Science and Technology & Department of Space, Govt. of India: 48 pp. <https://mangroves.maharashtra.gov.in/Site/SiteInfo/Pdf/IIST.pdf>
- Kantharajan, G., Pandey, P. K., Krishnan, P., Ragavan, P., Jeevamani, J. J. J., Purvaja, R. & Ramesh, R. 2018. Vegetative structure and species composition of mangroves along the Mumbai coast, Maharashtra, India. *Regional Studies in Marine Science*, 19, 1–8. DOI: <https://doi.org/10.1016/j.rsma.2018.02.011>
- Kauffman, J. B. & Donato, D. C. 2012. *Protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests*. Center for International Forestry Research (CIFOR), Working Paper 86. DOI: <https://doi.org/10.17528/cifor/003749>
- Kauffman, J. B., Adame, M. F., Arifanti, V. B., Schile-Beers, L. M., Bernardino, A. F., Bhomia, R. K., Donato, D. C., Feller, I. C., Ferreira, T. O., Jesus Garcia, M. del C., MacKenzie, R. A., Megonigal, J. P., Murdiyarso, D., Simpson, L. & Hernández Trejo, H. 2020. Total ecosystem carbon stocks of mangroves across broad global environmental and physical gradients. *Ecological Monographs*, 90(2), 1–18. DOI: <https://doi.org/10.1002/ecm.1405>
- Kesavan, S., Martin Xavier, K. A., Nair, M. M., Gurjar, U. R., Sukla, S. P., Jaiswar, A. K., Bhusan, S., Abdul Azeez, S. & Deshmukhe, G. 2025. Assessment of secondary microplastics trapped in mangrove ecosystem of a highly populated tropical megacity,

- India. *Journal of Hazardous Materials Advances*, 17, 100587. DOI: <https://doi.org/10.1016/j.hazadv.2024.100587>
- Kesavan, S., Xavier, K. A. M., Deshmukhe, G., Jaiswar, A. K., Bhusan, S. & Shukla, S. P. 2021. Anthropogenic pressure on mangrove ecosystems: Quantification and source identification of surficial and trapped debris. *Science of The Total Environment*, 794, 148677. DOI: <https://doi.org/10.1016/j.scitotenv.2021.148677>
- Kishor, P. B. K., Hong, Z., Miao, C.H., Hu, C.-A. A. & Verma, D. P. S. 1991. Overexpression of A1-pyrroline-5-carboxylate synthetase increases proline production and confers osmotolerance in transgenic plants. *Plant Physiology*, 108(1995), 1387–1394.
- Komiyama, A., Ong, J. E. & Pongpan, S. 2008. Allometry, biomass, and productivity of mangrove forests: A review. *Aquatic Botany*, 89(2), 128–137. DOI: <https://doi.org/10.1016/j.aquabot.2007.12.006>
- Kulkarni, V. A., Jagtap, T. G., Mhalsekar, N. M. & Naik, A. N. 2010. Biological and environmental characteristics of mangrove habitats from Manori creek, West Coast, India. *Environmental Monitoring and Assessment*, 168 (1–4), 587–596. DOI: <https://doi.org/10.1007/s10661-009-1136-x>
- Kumar, T. & Das, P. K. 2023. Estimation of gross primary productivity of Indian Sundarbans mangrove forests using field measurements and Landsat 8 Operational Land Imager data. *Tropical Ecology*, 64(1), 167–179. DOI: <https://doi.org/10.1007/s42965-022-00256-8>
- Li, X., Wang, Y., Zhang, Y., Xiang, J., Yang, Z., Gu, F. & Wu, M. 2022. Evaluating the physiological and biochemical responses of different mangrove species to upwelling. *Frontiers in Marine Science*, 9, 989055. DOI: [doi: 10.3389/fmars.2022.989055](https://doi.org/10.3389/fmars.2022.989055)
- Liu, C., Liu, Y., Lu, Y., Liao, Y., Nie, J. & Yuan, X. 2019. Use of a leaf chlorophyll content index to improve the prediction of above-ground biomass and productivity. *PeerJ*, 6, e6240. DOI: <https://doi.org/10.7717/peerj.6240>
- Liu, J. & Wang, Y. S. 2020. Proline metabolism and molecular cloning of Amp5CS in the mangrove *Avicennia marina* under heat stress. *Ecotoxicology*, 29(6), 698–706. DOI: <https://doi.org/10.1007/s10646-020-02198-0>
- Lovelock, C. E., Ruess, R. W. & Feller, I. C. 2006. Fine root respiration. *Tree Physiology*, 26(12), 1601–1606. DOI: <https://doi.org/10.1093/treephys/26.12.1601>
- Mansuri, S.Q. & Shekhawat, V.P.S., 2025. Evaluating mangrove sediments for anthropogenic marine pollution of heavy metals and microplastics in Mumbai, India. *Soil Sediment Contamination*. 1-29. DOI: <https://doi.org/10.1080/15320383.2025.2575051>

- Marae, S. S., Hegazy, A. K., Rostom, M., Hussein, Z. S. & Awad, H. E. A. 2024. Molecular variations and photosynthetic pigment content of *Avicennia marina* growing in subtropical habitat types. *Egyptian Journal of Botany*, 64(4), 16–27. DOI: <https://doi.org/10.21608/ejbo.2023.225319.2432>
- Marois, D. E. & Mitsch, W. J. 2015. Coastal protection from tsunamis and cyclones provided by mangrove wetlands – a review. *International Journal of Biodiversity Science, Ecosystem Services & Management*, 11 (1), 71–83. DOI: <https://doi.org/10.1080/21513732.2014.997292>
- Meena, M., Divyanshu, K., Kumar, S., Swapnil, P., Zehra, A., Shukla, V., Yadav, M. & Upadhyay, R. S. 2019. Regulation of L-proline biosynthesis, signal transduction, transport, accumulation and its vital role in plants during variable environmental conditions. *Heliyon*, 5(12), e02952. DOI: <https://doi.org/10.1016/j.heliyon.2019.e02952>
- Mehta, D. & Vyas, S. 2023. Comparative bio-accumulation of osmoprotectants in saline stress tolerating plants: A review. *Plant Stress*, 9, 100177. DOI: <https://doi.org/10.1016/j.stress.2023.100177>
- Mohanty, A. 2020. *Preparing India for extreme climate events: mapping hotspots and response mechanisms*. New Delhi: 1–68 pp. https://www.ceew.in/sites/default/files/CEEW-Preparing-India-for-extreme-climate-events_10Dec20.pdf
- Murdiyarso, D., Donato, D., Kauffman, J. B., Kurnianto, S., Stidham, M. & Kanninen, M. 2010. Carbon storage in mangrove and peatland ecosystems. Center for International Forestry Research (CIFOR), *Working Paper 48*, 35. DOI: <https://doi.org/10.17528/cifor/003233>
- Naidoo, G. 2009. Differential effects of nitrogen and phosphorus enrichment on growth of dwarf *Avicennia marina* mangroves. *Aquatic Botany*, 90(2), 184–190. DOI: <https://doi.org/10.1016/j.aquabot.2008.10.001>
- Naidoo, G. 2016. The mangroves of South Africa: an ecophysiological review. *South African Journal of Botany*, 107, 101–113. DOI: <https://doi.org/10.1016/j.sajb.2016.04.014>
- Naidoo G. 2025. Dwarfing in Mangroves: A Review. *Physiologia Plantarum*. 177(4):e70411. DOI: <https://doi.org/10.1111/ppl.70411>.
- Nar, D., Chaubey, S. S. & Gavas, S. 2024. Assessment of carbon sequestration potential of *Avicennia marina*. *Advanced Engineering Science*, 56, 4–6.
- Nasrin, S., Mahmood, H. & Rahman, M.M., 2021. Parental influences on salt adaptive divergence of *Sonneratia apetala* (Buch.-Ham.) seedlings along the salinity gradient in

- the Sundarbans of Bangladesh. *Environmental Challenges* 4, 100121. DOI: <https://doi.org/10.1016/j.envc.2021>.
- Nizam, A., Meera, S. P. & Kumar, A. 2022. Genetic and molecular mechanisms underlying mangrove adaptations to intertidal environments. *IScience*, 25(1), 103547. DOI: <https://doi.org/10.1016/j.isci.2021.103547>
- Pachpande, S. C. & Pejaver, M. 2015. Natural Carbon sequestration by dominant mangrove species *Avicennia marina* var. *acutissima* ex Staf & Moldenke ex Moldenke found across Thane creek, Maharashtra, India. *International Journal of Scientific & Engineering Research*, 6(2), 1162–1165.
- Padhy, S. R., Bhattacharyya, P., Nayak, S. K., Dash, P. K. & Mohapatra, T. 2021. A unique bacterial and archaeal diversity make mangrove a green production system compared to rice in wetland ecology: A metagenomic approach. *Science of The Total Environment*, 781, 146713. DOI: <https://doi.org/10.1016/j.scitotenv.2021.146713>
- Patil, S. S. & Kanhere, C. 2024. Ecological disturbances and adaptation of mangroves in high-disturbance urban areas of Navi Mumbai in India. *Agro Environmental Sustainability* 2(4), 186–196. DOI: <https://doi.org/10.59983/s2024020404>
- Patil, V., Singh, A., Naik, N. & Unnikrishnan, S. 2014. Estimation of carbon stocks in *Avicennia marina* stand using allometry, CHN analysis, and GIS methods. *Wetlands*, 34(2), 379–391. DOI: <https://doi.org/10.1007/s13157-013-0505-y>
- Patil, V., Singh, A., Naik, N. & Unnikrishnan, S. 2015. Estimation of mangrove carbon stocks by applying remote sensing and GIS techniques. *Wetlands*, 35(4), 695–707. DOI: <https://doi.org/10.1007/s13157-015-0660-4>
- Porra, R. J. 2002. The chequered history of the development and use of simultaneous equations for the accurate determination of chlorophylls a and b. *Photosynthesis Research*, 73(1–3), 149–156. DOI: <https://doi.org/10.1023/A:1020470224740>
- Rodriguez-Reales, R. R., Gómez, J. P., Bohórquez-Herrera, J. & Martínez-Habibe, M. C. 2024. Influence of soil salinity on the structural attributes and aboveground biomass carbon in a mangrove community of Mallorquin swamp in Barranquilla, Colombia. *Scientific Reports*, 15(1), 28684. DOI: <https://doi.org/10.1038/s41598-025-10278-6>.
- Samiksha, S. V., Vethamony, P., Bhaskaran, P. K., Pednekar, P., Jishad, M. & James, R. A. 2019. Attenuation of Wave Energy Due to Mangrove. *Energies*, 12.
- Sarker, S. K., Reeve, R. & Matthiopoulos, J. 2021. Solving the fourth-corner problem: forecasting ecosystem primary production from spatial multispecies trait-based models. *Ecological Monographs*, 91(3). DOI: <https://doi.org/10.1002/ecm.1454>

- Sawant, S., Bonala, P., Joshi, A., Shindikar, M., Patil, A., Vyas, S. & Deobagkar, D. 2024. Integration of machine learning and remote sensing for assessing the change detection of mangrove forests along the Mumbai coast. *Journal of Earth System Science*, 133(4), 186. DOI: <https://doi.org/10.1007/s12040-024-02378-0>
- Sharma, L.K., Sharma, S. & Bhaveshkumar, K.I. 2025. Mangrove phenological shifts over eco-climatic stressors in the Gulf of Kutch using Sentinel-1&2 time series data. *Regional Studies in Marine Science*, 85, 104133. DOI: <https://doi.org/10.1016/j.rsma.2025.104133>
- Sharma, D., Rao, K. & Ramanathan, A.L. 2022. A systematic review on the impact of urbanization and industrialization on Indian coastal mangrove ecosystem in Madhav, S., Nazneen, S. and Singh, P. (eds.) *Coastal Ecosystems - Environmental importance, current challenges and conservation measures*. Springer, 175-199 pp.
- Sharma, S. & Parthasarathy, D. 2018. Urban ecologies in transition: contestations around waste in Mumbai in Jenia Mukherjee (ed). *Sustainable Urbanization in India*. Springer nature, 207-233 pp.
- Shashikala, S. 2020. *Wood anatomical studies of important mangrove species from Maharashtra sea coast for the identification*. Wood Properties and Uses Division Institute of Wood Science and Technology (Indian Council of Forestry Research and Education) - Ministry of Environment, Forest and Climate Change, Govt. of India. 82 pp.
- Shete, A., Gunale, V.R. & Pandit, G.G. 2009. Organochlorine pesticides in *Avicennia marina* from the Mumbai mangroves, India. *Chemosphere*, 76(11), 1483–1485. DOI: <https://doi.org/10.1016/j.chemosphere.2009.06.055>
- Shinde, P. S. & Donde, S. S. 2017. Effect of heavy metal pollution on mangrove (*Avicennia marina*) carbon sequestration at Mithi River. *Pollution Research*, 36(4), 943–948.
- Shinde, P., Donde, S. & Ram, A. 2018. Water pollution association with Mangrove carbon sequestration in Mithi river. *Ecology, Environment and Conservation*, 24, S152–S158.
- Simpson, M.G. (Ed.), 2010. Acknowledgments, in: *Plant Systematics* (Second Edition). Academic Press, San Diego,. DOI: <https://doi.org/10.1016/B978-0-12-374380-0.50028-2>
- Singh, J. K. 2020. Structural characteristics of mangrove forest in different coastal habitats of Gulf of Khambhat arid region of Gujarat, west coast of India. *Heliyon*, 6(8), e04685. DOI: <https://doi.org/10.1016/j.heliyon.2020.e04685>
- Singh, S. G., Vennila, A., Singh, R., Bharti, V. S., Shukla, S. P. & Purushothaman, C. S. 2023. Standing carbon stock of Thane Creek mangrove ecosystem: An integrated approach

- using allometry and remote sensing techniques. *Regional Studies in Marine Science*, 67, 103207. DOI: <https://doi.org/10.1016/j.rsma.2023.103207>
- Song, S., Ding, Y., Li, W., Meng, Y., Zhou, J., Gou, R., Zhang, C., Ye, S., Saintilan, N., Krauss, K. W., Crooks, S., Lv, S. & Lin, G. 2023. Mangrove reforestation provides greater blue carbon benefit than afforestation for mitigating global climate change. *Nature Communications*, 14(1),756. DOI: <https://doi.org/10.1038/s41467-023-36477-1>
- Tatongjai, S., Kraichak, E. & Kermanee, P. 2021. Comparative anatomy and salt management of *Sonneratia caseolaris* (L.) Engl. (Lythraceae) grown in saltwater and freshwater. *PeerJ*, 9. DOI: <https://doi.org/10.7717/peerj.10962>
- Tomlinson, P. B. 1986. *The botany of mangroves*. Cambridge University Press. https://assets.cambridge.org/97811070/80676/frontmatter/9781107080676_frontmatter.pdf
- Tuffers, A. V., Naidoo, G. & von Willert, D. J. 2001. Low salinities adversely affect photosynthetic performance of the mangrove *Avicennia marina*. *Wetlands Ecology and Management*, 9(3), 225–232. DOI: <https://doi.org/10.1023/A:1011164924907>
- Twilley, R. R., Rovai, A. S. & Riul, P. 2018. Coastal morphology explains global blue carbon distributions. *Frontiers in Ecology and the Environment*, 16(9), 503–508. DOI: <https://doi.org/https://doi.org/10.1002/fee.1937>
- Vaz, E. 2014. Managing urban coastal areas through landscape metrics: An assessment of Mumbai's mangrove system. *Ocean and Coastal Management*, 98, 27–37. DOI: <https://doi.org/10.1016/j.ocecoaman.2014.05.020>
- Verbruggen, N. & Hermans, C. 2008. Proline accumulation in plants: a review. *Amino Acids*.35(4), 753-9. DOI:<https://doi.org/10.1007/s00726-008-0061-6>.
- Vijay, V., Biradar, R. S., Inamdar, A. B., Deshmukhe, G., Baji, S. & Pikle, M. 2005. Mangrove mapping and change detection around Mumbai (Bombay) using remotely sensed data. *Indian Journal of Marine Sciences*, 34(3), 310–315.
- Walkley, A. & Black, I. A. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Science*, 37(1), 29-38.
- Wang, S. M., Wang, Y. S., Su, B. Y., Zhou, Y. Y., Chang, L. F., Ma, X. Y. & Li, X. M. 2022. Ecophysiological responses of five mangrove species (*Bruguiera gymnorrhiza*, *Rhizophora stylosa*, *Aegiceras corniculatum*, *Avicennia marina*, and *Kandelia obovata*) to Chilling Stress. *Frontiers in Marine Science*, 9, 1–8. DOI: <https://doi.org/10.3389/fmars.2022.846566>

- Yao, W., Morganti, T. M., Wu, J., et al. 2025. Exploring site-specific carbon dioxide removal options with storage or sequestration in the marine environment – The 10 Mt CO₂ yr⁻¹ removal challenge for Germany. *Earth's Future*, 13(4), 1–32. DOI: <https://doi.org/10.1029/2024EF004902>
- Zhou, Y., Wen, L., Liao, L., Lin, S., Zheng, E., Li, Y. & Zhang, Y. 2022. Comparative transcriptome analysis unveiling reactive oxygen species scavenging system of *Sonneratia caseolaris* under salinity stress. *Frontiers in Plant Science*, 13. DOI: <https://doi.org/10.3389/fpls.2022.953450>

Article in press

This preprint was submitted under the following conditions:

- The authors declare that the necessary Terms of Free and Informed Consent of participants or patients in the research were obtained and are described in the manuscript, when applicable.
- The authors declare that the preparation of the manuscript followed the ethical norms of scientific communication.
- The authors declare that they are aware that they are solely responsible for the content of the preprint and that the deposit in SciELO Preprints does not mean any commitment on the part of SciELO, except its preservation and dissemination.
- The authors declare that the data, applications, and other content underlying the manuscript are referenced.
- The deposited manuscript is in PDF format.
- The authors declare that the research that originated the manuscript followed good ethical practices and that the necessary approvals from research ethics committees, when applicable, are described in the manuscript.
- The authors declare that once a manuscript is posted on the SciELO Preprints server, it can only be taken down on request to the SciELO Preprints server Editorial Secretariat, who will post a retraction notice in its place.
- The authors agree that the approved manuscript will be made available under a [Creative Commons CC-BY](#) license.
- The submitting author declares that the contributions of all authors and conflict of interest statement are included explicitly and in specific sections of the manuscript.
- The authors declare that the manuscript was not deposited and/or previously made available on another preprint server or published by a journal.
- If the manuscript is being reviewed or being prepared for publishing but not yet published by a journal, the authors declare that they have received authorization from the journal to make this deposit.
- The submitting author declares that all authors of the manuscript agree with the submission to SciELO Preprints.