JEE Journal of Ecological Engineering

Journal of Ecological Engineering, 2026, 27(6), 395–410
https://doi.org/10.12911/22998993/217735
ISSN 2299–8993, License CC-BY 4.0

Received: 2026.01.03
Accepted: 2026.04.16
Published: 2026.05.01

Potential carbon stock distribution of mangrove and its effect on abiotic stressor: A case study in Pemali River estuary, Central Jawa, Indonesia

Nabela Fikriyya[1*], Muhammad Fauzan[1], Mahardhika Nur Permatasari[1], Any Kurniawati[2], Adinda Kurnia Putri[1], Sesilia Rani Samudra[1], Aghni Fitri Karimah[1]

[1] Study Program Aquatic Resource Management, Faculty of Fisheries and Marine Science, Jenderal Soedirman University, 53122, Purwokerto, Indonesia

[2] Study Program Marine Science, Faculty of Fisheries and Marine Science, Jenderal Soedirman University, 53122, Purwokerto, Indonesia

* Corresponding author, e-mail: nabela.fikriyya@unsoed.ac.id

ABSTRACT

The Pemali River estuary in Brebes is a mangrove rehabilitation area. Mangrove cover has increased significantly over the past two decades. However, it still faces anthropogenic pressures that may affect carbon storage and physiological responses. This study aimed to evaluate the mangrove carbon stock distribution by stand age and examined its relationship with proline accumulation, a biomarker of abiotic stress. Field data were collected from July to September 2025 at three stations representing different mangrove stand ages (>15 years, 10–15 years, and <5 years). Vegetation structure was assessed based on species composition and stem diameter, while biomass was estimated using specific allometric equations. Sediment analysis included organic carbon, nitrate, and phosphate, while leaf proline levels were analyzed using a colorimetric method. The relationship between carbon stocks, proline levels, and environmental parameters were evaluated using multivariate analysis (PCA). The results showed that *Rhizophora mucronata* dominated all stations. Older mangrove stands (>15 years) had the highest biomass and carbon stocks, estimated at 805.42–945.28 mg/kg. Sediment organic C was also highest in older mangroves (0.93–2.24%) and decreased in younger areas. Proline concentrations ranged from 0.018–0.434 mg/g, peaking in *Acanthus ilicifolius* under low pH and dry conditions. PCA showed sediment organic C correlated with salinity, DO, temperature, and sediment nutrients. Proline was negatively correlated with pH, TDS, and salinity, and positively with water phosphate.

Keywords: abiotic stress, mangrove carbon, PCA, Pemali Estuary, prolin.

INTRODUCTION

Mangrove ecosystems play a crucial role in maintaining coastal stability, not only as natural barriers against abrasion and storms, but also as efficient carbon sinks, contributing to global climate change mitigation. Mangroves can store about 10% of the total marine blue carbon (Yadav et al., 2015), thus locking CO_2 in biomass and sediments and reducing the concentration of greenhouse gases in the atmosphere (Choudhary et al., 2024). Mangroves store carbon in their aboveground biomass, roots, and especially sediments – where carbon accumulates over the long term (Redi et al., 2019). Indonesia is recognized as the country with the largest mangrove carbon storage potential. Global analyses indicate that Indonesia alone stores more than 30% of the world's mangrove carbon stocks, the highest proportion among all countries (Hamilton and Friess, 2018). As such the condition, distribution, and sustainability of mangrove ecosystems are a strategic issue in coastal management. However, Indonesia's coastline is inseparable from anthropogenic pressures, which have led to the degradation of mangrove ecosystems in various regions.

Land conversion to fishponds, settlements, industrial activities, and tourism has reduced area and the services it provides. This includes a reduction in carbon sequestration capacity (Choudhary et al., 2024). This situation also affects the Pemali River area in Brebes, a key estuary on the north coast of Central Java. Between 2000 and 2008, the mangrove area decreased by 650.54 ha (Brebes et al., 2020) or approximately 68.46 ha per year. This was due to ecological and anthropogenic factors (Suyono et al., 2019). Periodic rehabilitation efforts by the Mangrove Sari Coastal Forest Conservation Community Group (KMPHP) have shown positive results. The mangrove area increased by 815.76 ha in 2008 (Aminah et al., 2020), by 101.25 ha from 2008 to 2013 and by 184.23 ha from 2013 to 2018 (Annisa et al., 2019).

The latest monitoring data shows a 79.83% increase in mangrove cover in the Pemali estuary between 2014 and 2024. This contrast with other estuaries on the north coast of Java, which experienced mangrove loss. This success in Pemali was driven by sediment accretion and community-based rehabilitation programs, such as silvofishery (Candraningtyas et al., 2025). However, pollution inputs to the area are still found, originating from anthropogenic activities, such as fish ponds, industry, settlements, and tourism (Heriati et al., 2021). The water quality of the Pemali River is rated lightly to moderately polluted, especially in the rainy season. Parameters like BOD, COD, coliform, nutrient runoff, and heavy metals, exceed standards (Haque, 2011).

These environmental pressures can trigger abiotic stress on mangroves, including high salinity, eutrophication, heavy metal pollution, and hydrological changes. One important physiological response in mangroves under stress is the accumulation of proline, an osmoprotectant amino acid that maintains cell structure stability, reduces oxidative damage, and supports osmotic balance (Ghosh et al., 2022; Meena, et al., 2019). Proline increases indicate plant stress tolerance, including in mangroves. Species like *Kandelia obovata* and *Bruguiera gymnorrhiza* show higher proline under cold stress, and *Laguncularia racemosa* does so under heavy metal stress (Cabañas–Mendoza et al., 2023; Wang et al., 2022). In *B. parviflora* proline and polyphenol rise with salinity, confirming the adaptive role of proline (Parida et al., 2002).

The ecological and social context of the Pemali River Estuary is unique. There has been a significant increase in mangrove cover due to successful rehabilitation. However, this area continues to experience pollution pressures that can affect carbon storage capacity and mangrove physiological responses. Numerous studied have been conducted in the Pemali River Estuary such as gastropod composition (Kusuma et al., 2020), and macrozoobenthos structure community (Sinaga et al., 2019). In addition, carbon stock estimation has been investigated by Nainggolan et al., (2022) and Ahmed et al., (2023), focusing on variations in stand age and sediment depth. Nevertheless, these studies have not yet integrated carbon estimates with abiotic environmental factors. Variations in mangrove age resulting from rehabilitation may lead to differences in carbon stocks between locations. It is important to assess their distribution.

Globally, this research supports SDGs 14 (Life Below Water) and 15 (Land). These goals emphasize sustainable conservation of terrestrial and marine biological resources. Few studies link carbon stock, abiotic stress, and proline accumulation are still limited. Therefore, this study assessed the distribution of carbon stocks in the mangrove ecosystem in the Pemali River Estuary and examined its relationship with proline as an abiotic stress response. Findings offer insight into mangrove resilience and carbon stock potential in the rehabilitation area.

METHODS

The study was conducted from July to September 2025 in the Pemali River estuary mangrove ecosystem area in Brebes. Data collection was carried out using stratified sampling based on different age types: >15 years (station 1), 10–15 years (station 2), and <5 years (station 3), each consisting of three plots (Figure 1). This selection based on the assumption that larger tree size is associated with greater carbon storage capacity (Mardliyah et al., 2019), therefore, it is necessary to examine differences in carbon storage across different stand ages. Mangrove vegetation data collection was carried out in plots measuring 10 × 10 m for trees, 5 × 5 m for poles, and 2 × 2 m for

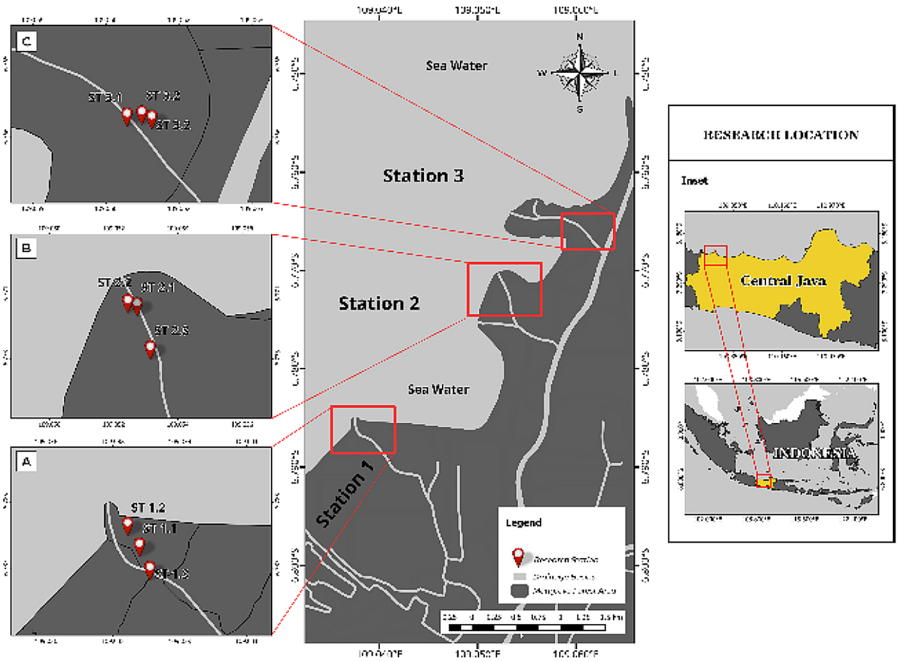

Figure 1. Sampling locations

seedlings. The data collected included the number of individuals, the number of species, and DBH (diameter at breast height), which were analyzed using the Shannon-Wiener H', Simpson Dominance, and Density. Data collection for aboveground carbon estimation used a specific allometric equation (Table 1) from DBH values (Smith and Whelan, 2006). Carbon estimates were calculated using a conversion factor of 0.46 multiplied by biomass (Hapsari et al., 2024).

In situ measurements of water physicochemical parameters, including DO, pH, temperature, and salinity, were then compared with the Water Quality Standards stipulated in Government Regulation No. 22 of 2021. Nitrate and phosphate testing was conducted at the Environmental Agency (DLHKP) UPTD Environmental Laboratory in Kebumen, Central Java. Sediment samples were then collected three times at each station, which were then composited and analyzed for nitrate, phosphate, and organic carbon at the Aquatic Productivity and Environment Laboratory of the Bogor Agricultural Institute (Proling Lab). The nitrate (H_2SO_4, H_2O_2, digestion, phenate, spectrophotometry), phosphate (H_2SO_4, H_2O_2, digestion, ascorbic acid, spectrophotometry), and organic carbon (Walkey and Black) methods were used.

Proline content as an indicator of mangroves was assessed at each station and for each species by collecting 3–5 individuals. From each individual, five leaves were sampled and subsequently composited into single sample, which was then extracted and analyzed for proline content. Thus, each species at each station was represented by one composite sample as the analytical unit. The proline content was tested using the Bates (1973) colorimetric method. This assay is simple, reliable, and quantitative, it does not require sophisticated instrumentation or expensive reagents (Ábrahám et al., 2010). Moreover, it represents an expected and validated approach in the aquatic plant stress studied (Afefe et al., 2021). The following steps were applied according to (Afefe et al., 2021):

Homogenization and filtration: 250 to 500 mg of fresh leaf tissue (taken from the youngest, fully developed leaves) was ground in a chilled mortar with liquid nitrogen until crushed and homogenized with 5 mL of 3% sulfosalicylic acid (to precipitate the protein). The homogenate was then filtered through a Whatman® n2 filter paper.

Reaction with ninhydrin: 2 ml of the filtered sample was mixed with 2 ml of glacial acetic acid and 2 ml of acidic ninhydrin (prepared) in a test tube. After stirring, the sample was incubated at 100 °C for 1 hour, resulting in the formation of a colored complex. After one hour, the reaction was stopped by placing the tubes in an ice bath.

Extraction: 4 mL of toluene was added to each tube and vortexed for 15–20 seconds. The

Table 1. Allometric aboveground biomass (Hilmi et al., 2024)

Species	Allometric equation
Avicennia marina	$W_{top} = 0.308{*}D^{2.11}$
Rhizophora mucronata	$W_{top} = 0.143{*}D^{2.519}$
Avicennia alba	$W_{top} = 0.2901{*}D^{2.2605}$
Rhizophora sp	$W_{top} = 0.128{*}D^{2.260}$
Bruguiera parviflora	$W_{top} = 0.7749{*}D^{2.4167}$
General equation	$W_{top} = 0.251{*}P{*}D^{2.46}$

Note: D is the diameter at breast height (DBH) and for species lacking species-specific allometric, used general equation.

organic and inorganic phases were then separated, resulting in the chromophore being dissolved in the toluene.

Spectrophotometric measurement: The maximum absorbance of the chromophore when dissolved in toluene was achieved at a wavelength of 520 nm. Therefore, the organic phase of each sample and the chromophore-containing standard were collected, and the absorbance at 520 nm was measured spectrophotometrically.

Statistical analysis was performed using Paleontological Statistics (PAST) software version 4.13, using PCA to examine the relationship between belowground carbon and water parameters and proline content and water parameters, as well as regression to examine the relationship between aboveground and belowground carbon.

RESULTS AND DISCUSSION

The species richness of mangrove

On the basis of the research results (Table 2), four species were found spread across three stations. Station 1 contained only the species *Rhizophora mucronata*, with the highest number of individuals, 161, in the Tree category. This species was also found throughout all stations and at all developmental stages. *R. mucronata* is highly tolerant of variations in salinity and substrate, capable of growing in landward to seaward zones (Basyuni et al., 2019; Gunawan and Iskandar, 2017; Purwanto et al., 2022). Therefore, it is quite easy to find in the area even under quite extreme conditions, such as station three, which is dry and not flooded. Furthermore, this species is easily cultivated by the community, so it is also often found in this area, which is included in the rehabilitation area. The second most abundant species is *Avicennia marina*, with 137 individuals at station 2 and also distributed at station 3, and found in the tree and sapling growth stages. Station 4 encompasses the area with the highest number of species, specifically 4, all of which are in the sapling category, as they are areas less than 5 years old (Table 2).

Both stations were dominated by a single species, which from an ecological perspective may increase vulnerability to local extinction and ecosystem degradation, thereby requiring anticipatory management actions by local communities and government authorities. This finding is consistent with Hillebrand et al. (2008), who stated that high dominance (low evenness) tends to reduce local biodiversity and makes communities more susceptible to disturbances, environmental changes, and biological invasions.

Overall, the H’ value for each station is 0 (Table 3) because only one species was found, except for Station 3, which had a value of 0.76, which is considered low. This is consistent with the Dominance value of 1, indicating the area is dominated by a single species, *R. mucronata*. This is common in the mangrove ecosystems that are heavily dominated by a single species, so the Dominance value also reaches 1 (the maximum), indicating absolute dominance by a single species, such as *R. mucronata*. Conversely, Station 3 has an H’ value of 0.76, which is considered low, indicating the presence of several species, but their distribution is still uneven or unbalanced. The persistently high Dominance value for *R. mucronata* confirms that despite the presence of more than one species, one species still dominates the community. This pattern is consistent with findings in various mangrove ecosystems in Southeast Asia and Indonesia, where disturbed or less heterogeneous areas tend to have low diversity and high dominance (Amores et al., 2024; Rahman et al., 2023; Sari et al., 2022).

The e’ (evenness) value ranges from 0 to 1. The closer it is to one, the more even the distribution. If e’ approaches 0, there is a single dominant species. Table 3 shows undefined values except for station 3, as only one species was found. At station 3, a value of 0.76 was obtained. At stations 1 and 2, the e’ value is undefined because there is only one species present – mathematically, evenness cannot be calculated if there is only one species (Diniyatushoaliha et al., 2024). At station 3, the e’ value of 0.76 (Table 3) indicates a moderate

Table 2. Mangrove composition of Pemali estuary

Station	Growth stage	Species	Family	Order	Quantity
1	*Rhizophora mucronata*	Tree	Rhizophoraceae	Myrtales	161
	Rhizophora mucronata	Sapling	Rhizophoraceae	Myrtales	3
	Rhizophora mucronata	Seedling	Rhizophoraceae	Myrtales	10
2	*Avicennia marina*	Tree	Acanthaceae	Scrophulariales	137
	Avicennia marina	Sapling	Acanthaceae	Scrophulariales	34
	Rhizophora mucronata	Seedling	Rhizophoraceae	Myrtales	10
3	*Rhizophora mucronata*	Sapling	Rhizophoraceae	Myrtales	105
	Avicennia marina	Sapling	Acanthaceae	Scrophulariales	33
	Sonneratia caseolaris	Sapling	Lythraceae	Myrtales	6
	Acanthus ilicifolius	Sapling	Acanthaceae	Scrophulariales	2

to high level of evenness, meaning that although there are still dominant species, the distribution of individuals between species is relatively even (Kartika et al., 2024; Sadono et al., 2020). This value aligns with the low diversity category and the remaining dominance, but not absolute.

On the basis of Table 3, the majority of density values are classified as very dense, except at station 1, during the sapling development stage, where only three individuals were found. This pattern aligns with findings in various mangrove areas in Indonesia, where most natural or conservation mangrove areas exhibit high density, especially if dominated by one or two key species, such as *R. mucronata* or *Avicennia marina* (Arfan et al., 2024; Jaelani et al., 2025). A study in Surabaya, for example, reported that 83% of the mangrove area was classified as very dense, dominated by *A. marina* and *R. mucronata* (Jaelani et al., 2025). Furthermore, in terms of richness, the majority of stations had a value 0 because only one species was found, while at station 3, four species were found, which is still relatively low compared to more homogeneous mangrove areas.

The potential distribution carbon stock

Table 4 shows aboveground biomass and carbon estimates measured from mangrove stems. Biomass was calculated based on two categories: tree and sapling, with total biomass being the sum of the two. Carbon estimation is calculated based on the total biomass produced, referring to the conversion of carbon present in biomass. The range of Biomass values is 50.19–2054.96 and the range of carbon is 23.09-945.28 (Table 4). The highest biomass value is found at station 1.2 followed by 1.1 and 2.3. All three are influenced by several factors such as the number of individuals, DBH, and age of the plants. For example, station 1.2 (2054.96) has a fairly high number of individuals, namely 54 (Figure 2a) with an average

Table 3. Mangrove structure community of Pemali estuary

Station 1								
No	Growth stages	Quantity	H’	D	e’	Di	Category	Richness
1.	Tree	161	0	1	None	5366.67	Very dense	0
2.	Sapling	3	0	1	None	400	Rare	0
3.	Seedling	10	0	1	None	8333.33	Very dense	0
Station 2								
No	Growth stages	Quantity	H’	D	e’	Di	Category	Richness
1.	Tree	137	0	1	None	4566.67	Very dense	0
2.	Sapling	34	0	1	None	4533.33	Very dense	0
3.	Seedling	14	0	1	None	11666.67	Very dense	0
Station 3								
No	Growth stages	Quantity	H’	D	e’	Di	Category	Richness
1.	Sapling	146	0.76	1	1	19466.67	Very dense	0.60

Table 4. Biomass estimation, Aboveground carbon & Belowground carbon

Stasiun	Aboveground biomass				Belowground C-organik (%)
	Tree	Sapling	Total (t/ha)	Biomassa estimation (mg/Kg)	
1.1	1747.06	3.86	1750.92	805.42	1.21
1.2	2054.96	-	2054.96	**945.28**	1.39
1.3	1418.61	7.22	1425.83	655.88	**2.24**
2.1	1323.30	38.17	1361.47	626.28	**2.21**
2.2	806.94	66.98	873.91	402.00	1.75
2.3	1448.42	-	1448.42	666.27	0.93
3.1	36.04	14.14	50.19	23.09	0.55
3.2	46.98	85.35	132.33	60.87	0.60
3.3	30.98	20.40	51.38	23.63	0.50

DBH of 8.55 (Figure 2b). Similarity, stations 1.1 (1750.92) and 2.3 (1448.42), despite having relatively low number of individuals (47 and 26, respectively), exhibited some of the highest average DBH values, namely 1.1 (6.23 cm) and 2.3 (10.27 cm), respectively. Even though both of them are located in mangrove areas older than 10 years. The average DBH increases with age, indicating that larger trees are found at older stations. Younger mangroves (Station 3.1–3.3) have very small DBH (average at 2 cm) because they are still in the early stages of growth. DBH and tree size can compensate for the smaller number of individuals (Komiyama et al., 2008). In addition, at stations 1.1 and 1.2 are dominated by *R. mucronata* which according to (Doodee et al., 2025), often shows high biomass and carbon stocks, especially in old forests, with biomass values above the global average and high total organic carbon (TOC), such as in Ferney, Mauritius.

Global research confirms that stand structure (number of trees per hectare, DBH, and tree height) is the main factor determining mangrove biomass (Kamruzzaman, et al., 2017; Komiyama et al., 2008). In addition, stand age also plays an important role – generally, the older the mangrove, the greater the biomass because the trees grow larger and biomass accumulation increases (Komiyama et al., 2008). This relationship is also observed in various mangrove ecosystems in Southeast Asia and the world, where stands with large and old trees, although few in number, still contribute significant biomass (Ahmed et al., 2023; Komiyama et al., 2008). This is consistent with the research findings showing that mangrove biomass at station 1, with mangroves aged more than 15 years, in all three plots was quite high, at 1750.92, 205.96, and 1454.96, compared to station 3, which was less than 5 years old, with values ranging from 50.19 to 132.33 (Table 4). The high biomass value at station 3.2, at 132.33, is likely due to the majority of *R. mucronata*. In addition to its high habitat tolerance, *R. mucronata* also exhibits rapid growth, characterized by good diameter, height, and number, thereby contributing significantly to mangrove biomass.

The estimated aboveground carbon value reflects the ability of the mangrove ecosystem to absorb and store carbon, which is derived from the biomass value. Table 4 shows that the estimated carbon value obtained is directly proportional to the biomass value, which is influenced by the number of individuals, DBH, and plant age. The older the mangrove, the greater its potential to absorb and capture carbon, thus significantly mitigating climate change. Mature mangroves (Station 1.1–1.3, >15 years old), had a higher DBH and higher carbon estimates compared to young mangroves (<5 years old at Station 3), even with a relatively similar number of individuals (Figure 2a). Mature mangroves have larger sizes, leading to a significant increase in biomass, resulting in significantly greater carbon storage capacity. This finding aligns with Alongi et al., (2016), who found that the carbon storage capacity of the stem increases along with age, consistent with the understanding that mangroves require years to develop and accumulate significant biomass. Furthermore, Li et al., (2023); Xiang et al., (2022) found that the peak carbon sequestration rate occurs at 15–20 years of age, then declines with age.

The belowground carbon value, calculated from sediments in the mangrove area, with values ranging from 0.50 to 2.24 (Table 4). On the basis

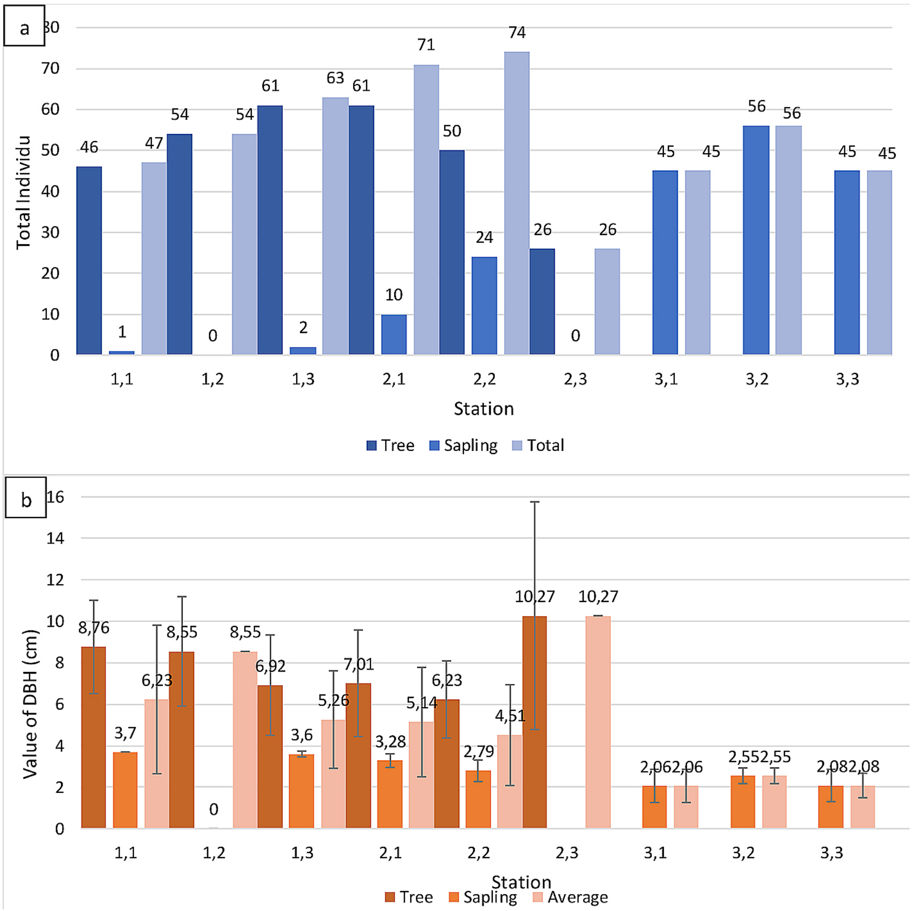

Figure 2. Data of each station and diameter stem: (a) number of mangrove individuals, (b) average DBH

of Table 4, it can be seen that the highest value is found at station 1.3, with stations 1 and 2 having values that are not significantly different. The value of belowground carbon in sediments is influenced by a combination of abiotic and anthropogenic factors. On the basis of the PCA analysis, it can be seen that organic C in mangrove sediments is positively correlated with temperature, DO, salinity, nitrate, and phosphate in sediments and negatively correlated with nitrate in water (Figure 3). Temperature, dissolved oxygen, and salinity are the main regulators of organic C content in mangrove sediments. Higher DO can increase photosynthetic activity and microorganism growth, thereby enriching organic matter in sediments (Asante et al., 2024). Salinity also plays an important role in regulating the process of decomposition and carbon accumulation, higher salinity can increase organic C stabilization (Kida and Fujitake, 2020; Rahman et al., 2021; Zou et al., 2023).

On the basis of Figures 4b and 4c, it can be seen that both aboveground and belowground have a tendency for carbon distribution patterns to become smaller with decreasing age. Age is a crucial benchmark in carbon storage capacity, which not only affects tree capacity, but also sediment capacity. This is in line with Jones et al., (2019); Xiang et al., (2022) Li et al., (2023) and Fengfeng et al., (2024), soil and root carbon increase with age, but tend to be stable or slightly decrease after reaching maturity. On the basis of the regression analysis, both have a positive relationship, there is an increase in belowground carbon along with increasing aboveground carbon. On the basis of the coefficient of determination (R^2) value, it is only around 38.42%, indicating that the relationship between the two variables is not very strong and there are other factors that have not been measured in this study (Figure 4a). This is in line with Hu et al., (2021) and Alongi and Zimmer, (2024) who found that global meta-analyses showed no significant relationship between mangrove biomass carbon stocks (aboveground) and blue carbon stocks in sediments (belowground). This is due to differences in the timescale of carbon accumulation between vegetation and sediment, as well as the influence of different environmental factors. These include sediment type

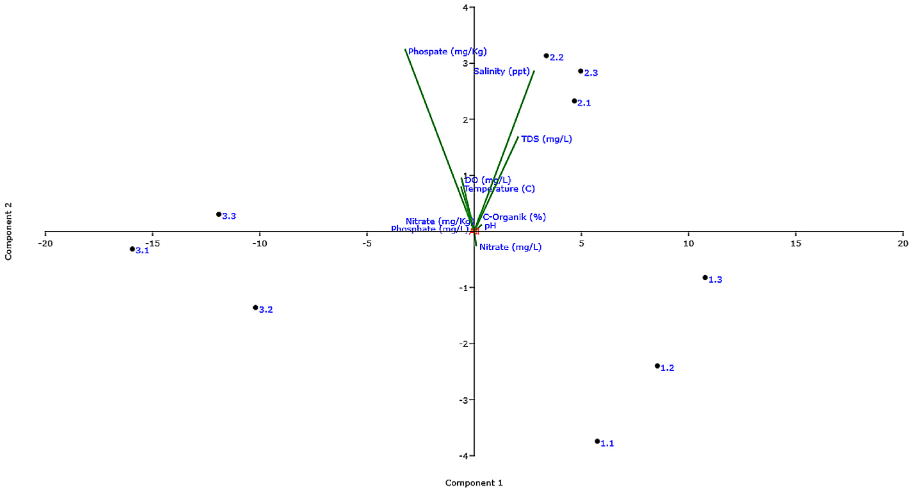

Figure 3. Principal component analysis (PCA) showing the relationships between belowground carbon stock, proline content and selected abiotic parameters across mangrove station in the Pemali River

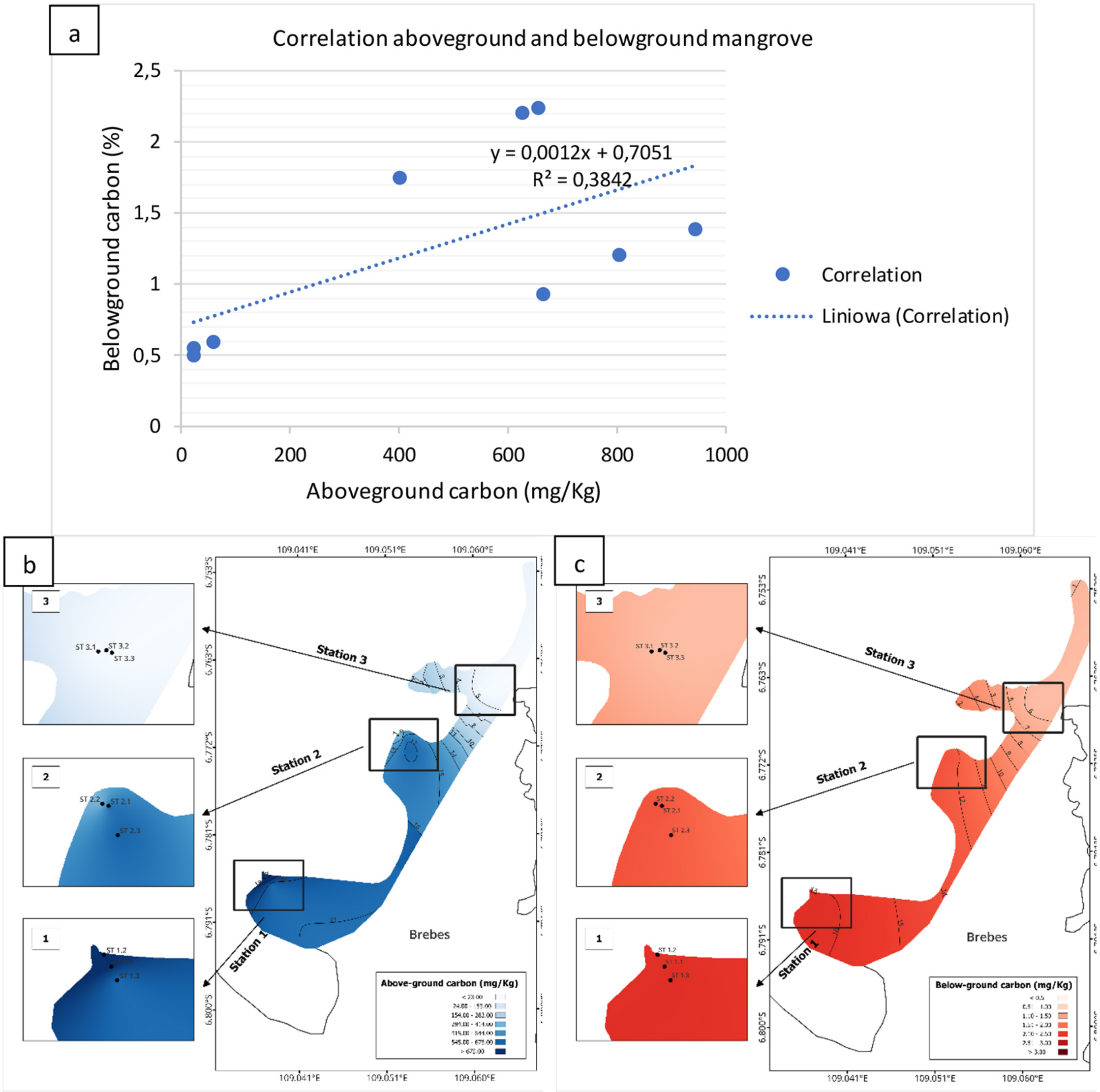

Figure 4. Distribution of mangrove carbon stocks across the study area: (a) regression analysis showing the relationship between aboveground and belowground carbon stocks, (b) spatial distribution of aboveground mangrove, (c) spatial distribution of belowground mangrove

soil depth, and geomorphological setting as well as hydrological flow dynamics, tidal regimes, organic matter content, and nutrient availability (N, P, and K). According to Allais et al., (2024), hydrological conditions can influence the deposition, stabilization, flushing, and oxygenation of organic matter, whereas sediment type and grain size contribute to the control of physical stabilization and dilution of organic matter.

Accumulation proline as a biomarker of stress and its relationship with water quality

Proline is an amino acid that acts as an osmoprotectant, maintaining osmotic balance, stabilizing protein structures, and as a heavy metal chelator to aid detoxification. The consistent increase in proline accumulation under various abiotic stress conditions makes it a physiological indicator or biomarker of plant stress levels and tolerance (Ghosh et al., 2021; Meena et al., 2019). Proline accumulation in the Pemali River Estuary ranged from 0.018 to 0.434 (Figures 5a, 5b, 5c). The highest proline content was found in *Acanthus illifolius* at the sapling stage, at 0.434, found at station 3, in a non-waterlogged environment, indicating its sensitivity to environmental changes (Figure 5c). The lowest value was found at station 2 in *Avicennia marina* at the seedling stage. Although still in the sapling growth phase, this species was categorized as high, indicating that proline accumulation is more influenced by abiotic factors. *Rhizophora mucronata* had a range of 0.026–0.127, with the highest values occurring in the sapling (0.127) and seedling (0.113) development stages (Figure 5a). Meanwhile, *A. marina* had a range of 0.018–0.391, with the lowest and highest values occurring in the sapling (Figure 5b). The *Sonneratia caseolaris* proline content was found only in the sapling stage, with a range of 0.018–0.188 (Figure 5c). This indicates that the proline content is not related to plant age, but rather to the stressors experienced, as evidenced by stations aged <5 years having quite high proline levels for all types of growth and species.

On the basis of the PCA analysis, proline levels were positively correlated with phosphate content in water and negatively correlated with pH, TDS, and salinity (5d). The relationship between proline and pH was negative, and the pH values at the study site varied from 4.57 to 6.5, with the lowest value at station 3 indicating more acidic conditions suspected of waste or intensive human activity (Figure 6b). This value is below the quality standard of 7–8.5. Low pH values in mangrove areas can inhibit the absorption of essential nutrients (N, P, K), causing physiological stress and disrupting mangrove growth (Celis-Hernández et al., 2021; Sha et al., 2018) and increasing the solubility of heavy metals and sulfur compounds, potentially toxic to plants (Robin et al., 2022; Sha et al., 2018). Compared with the increase in proline levels with decreasing pH, this indicates that the mangroves are under stress. This is evidenced by the highest proline value found in the *A. ilicifolius* species (0.434), which was found at the lowest pH of 4.57. This level accumulates in plant tissue as a stress response. Proline accumulation is widely recognized as an adaptive response to stress (Cheng et al., 2017; He et al., 2025) and functions as an antioxidant in mangroves (Parveen et al., 2024). Increased proline levels gave been reported to be positively correlated with enhanced plant resistance to osmotic stress under aluminum exposure (Ma and Yang, 2022), as well as with improved tolerance and detoxification of heavy metals (Hg, Cd, Pb) in *Kandelia obovata* (Cheng et al., 2017).

Similarly, TDS (total dissolved solids) has a negative correlation, meaning the values are inversely related. High TDS values are followed by low proline values, and vice versa. However, based on the literature, the two should have a positive correlation. TDS (reflects the number of dissolved ions, especially salts (such as NaCl), in water. High TDS causes osmotic stress in plants, similar to salinity conditions, which are associated with increased proline accumulation (Meena et al., 2019) (Moukhtari et al., 2020). TDS values tended to be higher at station 1 and 2 (23.1–25.9 mg/L),). TDS values tended to be high at stations 1 and 2 (23.1–25.9 mg/L), but were much lower at station 3 (15.2–17.2 mg/L), which may indicate differences in dissolved material input (Figure 6a). However, these values were much lower than the water TDS range according to Bloomfield et al., (2020) which is 1.000–10.000 mg/L.

Salinity values ranged from 19.5–35 ppt, which tended to decrease from stations 1 to 3 and were still within the water quality standard range, except for station 1.3, which tended to have marine salinity (Figure 6a). This area is an open area, making it more susceptible to seawater runoff. Stations 1 and 2 ranged from 30–35 ppt, indicating marine conditions, while station 3 only had 19.5–22.9 ppt, more reminiscent of brackish

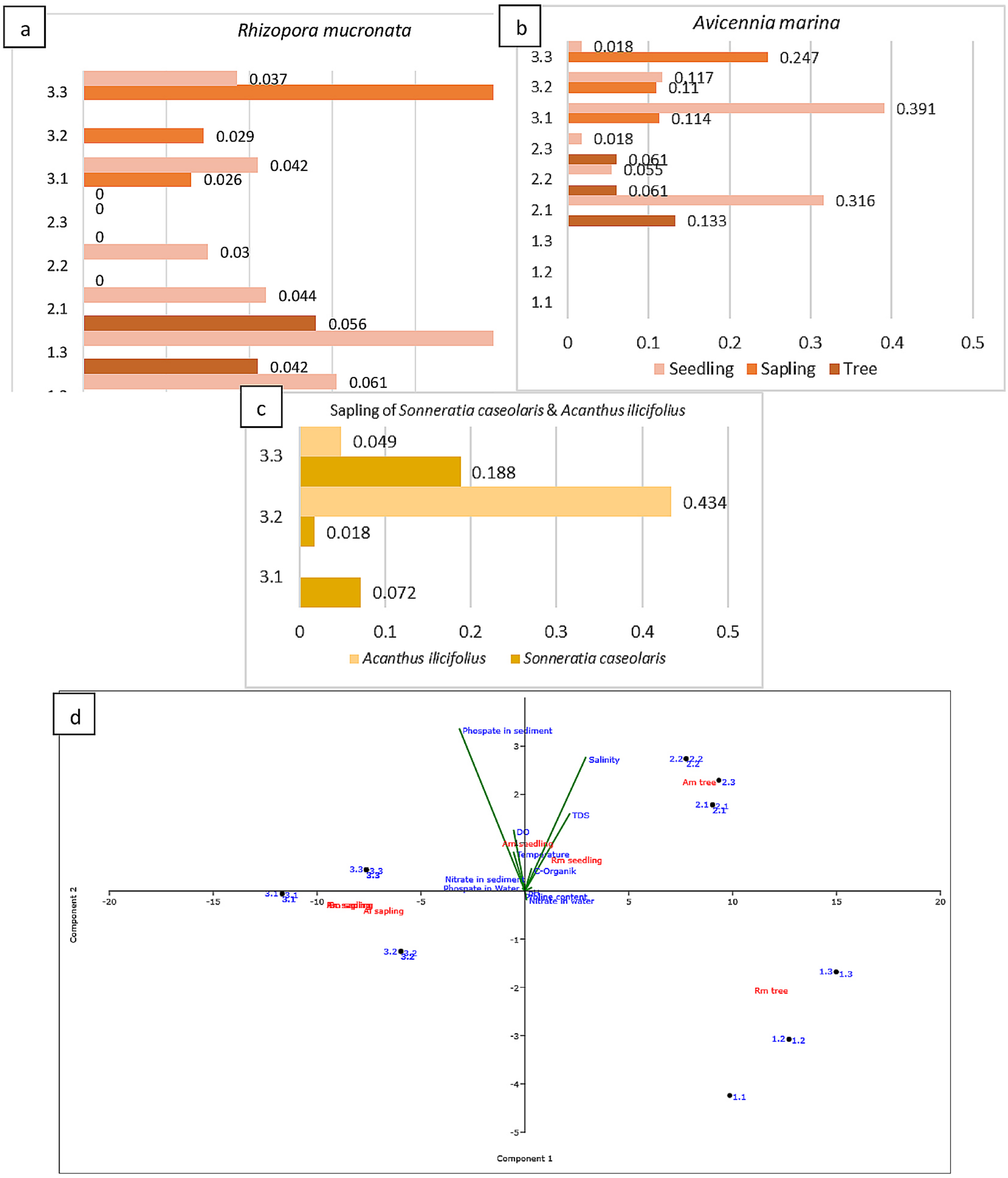

Figure 5. Accumulation of proline in mangrove species across the study area: (a) *Rhizophora mucronata,* (b) *Avicennia marina,* (c) sapling of *Sonneratia caesolaris* and *Acanthus illifolius,* (d) Principal component analysis (PCA) illustrating the relationships between the proline content and selected abiotic parameters

waters. This generally indicates an environmental gradient from marine to transitional waters, affecting the physicochemical parameters at each station. This gradient is very common in mangrove ecosystems and plays a significant role in shaping the physicochemical parameters and community structure of mangroves (Wang et al., 2024). On the basis of the PCA analysis, salinity was negatively correlated with proline levels, with the lowest salinity value at station 3 and the highest proline in that area. Although the salinity in this area still met quality standards, it stimulated proline production to prevent oxidative damage.

The phosphate levels in the water were positively correlated with proline levels, with higher proline levels occurring at stations with higher phosphate content. However, the opposite should be true. Primary research shows that proline increases significantly under phosphate-deficient conditions, as an adaptive response to nutrient stress through gene activation. P5CS1 is controlled by the transcription factor PHR1/PHL1 and ABA hormone signaling (Aleksza et al., 2017). The proline biosynthesis pathway is primarily controlled by the P5CS and P5CR genes, with P5CS expression being strongly upregulated under stress conditions, thereby promoting proline accumulation (Liu and Wang, 2020; Mehta and Vyas, 2023). The observed increase in proline under higher phosphate concentrations in the present study may therefore reflect a more complex physiological response. Numerous studies have shown that proline accumulation is more induced by water stress, salinity, temperature extremes, or exposure to xenobiotics rather than by phosphate levels alone (Pecka et al., 2025; Raza et al., 2023; Spormann et al., 2023). Phosphate levels in water (0.06–1.1 mg/L) showed striking and fluctuating differences between stations (Figure 6c). The lowest and highest values were found at Station 3, namely 0.06 mg/L (3.3) and 1.1 mg/L (3.1). Phosphate in the sediment also varied significantly, ranging from 2.18–20.4 mg/kg, with relatively low levels at Station 1 (2.18–3.18 mg/kg), moderate levels at Station 2 (8.18–9.18 mg/kg), and the highest levels at Station 3 (15.37–20.4 mg/kg) (Figure 6d).

The nutrient concentration data in water and sediment showed variation between stations and plots. Nitrate in water ranged from 0.32–1.15 mg/L, with the highest values at Station 1.1 and the lowest at station 3.1, which is above the water quality standard for marine tourism and marine biota, at 0.06 mg/L (Figure 6c). This value indicates nutrient enrichment, which has the potential to cause eutrophication. Meanwhile, the sediment concentration was relatively stable but higher, at 1.4–1.86 mg/kg, suggesting nutrient deposition in the sediment (Figure 6d). This pattern is common in mangrove ecosystems, where water is more sensitive to external inputs and biogeochemical processes, while sediment tends to store nutrients more stably (Toan et al., 2025). In general, these data indicate that Station 1 tends to receive greater nitrate input, while Station 3 has high phosphate accumulation in both water and sediment. This condition may reflect differences in nutrient sources, anthropogenic activities, or ecological processes such as nutrient deposition and release from sediments that vary across locations. This is in line with Al-araji's (2019) statement that sources of phosphate include human and animal waste as well as fertilizers.

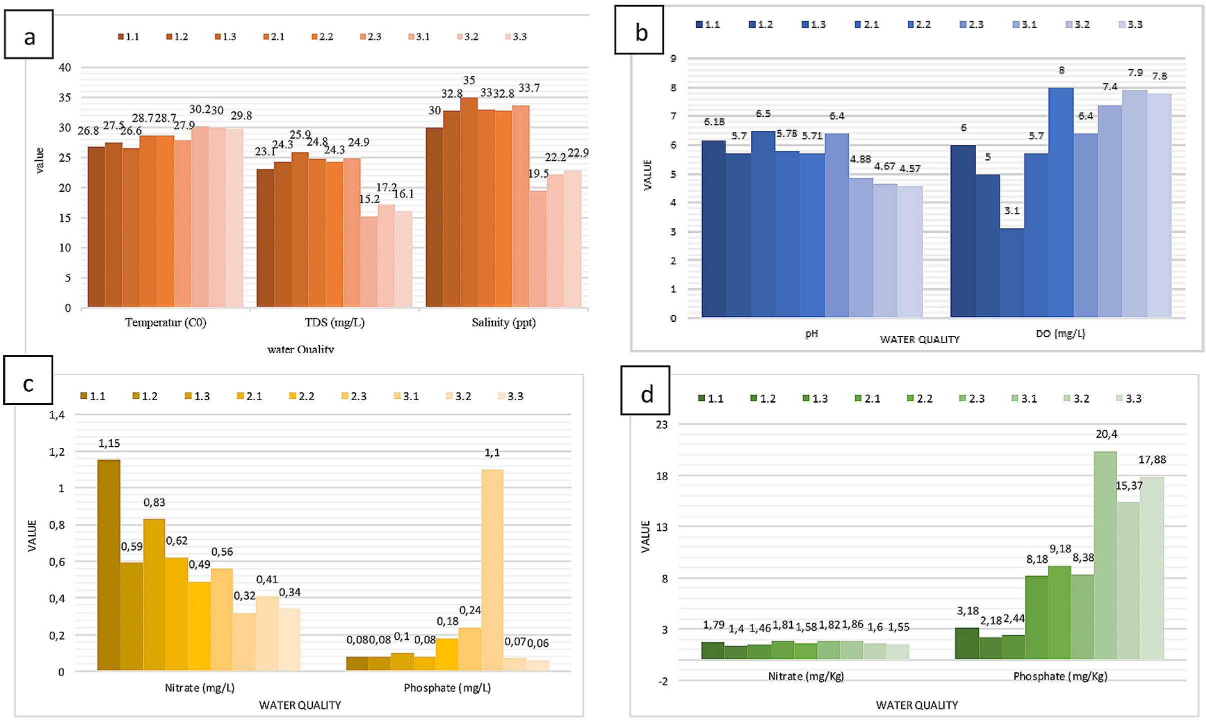

Figure 6. Water quality parameters of Pemali estuary: (a) temperature, TDS, salinity, (b) pH and DO, (c) nitrate and phosphate concentration in water, (d) nitrate and phosphate concentration in sediment. Standard mutu of Indonesia government regulations Number 22 years 2021: temperature (28–30 °C); pH (7–8.5); dissolved oxygen (DO) (> 5 mg/L); salinity (s/d 34 ppt); nitrate (0.06 mg/L); total dissolved olids (TDS) of estuary (1000–10.000 mg/L.)

Another value that has no relationship with proline is temperature, although the majority of results are lower than the quality manual (28–30 °C), namely 26.6–30.2 °C (Figure 6a). This value shows quite a clear variation between locations. However, according to Soeprobowati et al., (2022) this range is still optimal for mangrove life. According to Tamimi et al., (2021), the physiological function of mangrove decreases at a temperature of 38 °C, as indicated by a decrease in the photosynthesis process. Furthermore, the dissolved oxygen (DO) concentration ranged from 3.1–8 mg/L, exhibiting significant fluctuations, which indicated differences in aeration levels or biological productivity between locations (Figure 6b).The lowest value of 3.1 mg/L at station 1.3, which does not meet the water quality standard of >5 mg/L. Station 1.3 is a tourist area. Low DO values (e.g., 3.1 mg/L) are often found in the areas with limited water circulation, high organic decomposition, or prolonged water stagnation, while high values (up to 8 mg/L) typically occur in the areas with good aeration, high light exposure, and high photosynthetic productivity (Mattone and Sheaves, 2017).

CONCLUSIONS

Overall, the Muara Pemali mangrove area has low diversity, with only 1–3 species found, as it is a rehabilitation area dominated by *Rhizophora mucronata*. Estimated biomass and carbon values (aboveground) are influenced by several factors, including the number of individuals, DBH, and vegetation age. The area with the oldest vegetation age has the highest carbon content, namely station 1 (>15 years), and the highest is station 1.2, with the highest number of individuals and DBH values. Furthermore, aboveground and belowground values have a positive correlation and a pattern of carbon distribution that decreases with age. On the basis of the PCA analysis, it was shown that organic carbon in mangrove sediments was positively correlated with temperature, DO, salinity, nitrate, and phosphate in the sediments and negatively correlated with nitrate in the water. The highest levels of the secondary metabolite proline were found in *Acanthus illifolius* species in non-waterlogged environmental conditions, indicating that the species is sensitive to environmental changes. The results highlight the need to protect existing mangrove stands and implement rehabilitation strategies that integrate stand age, species composition, local environmental conditions, and physiological indicators alongside carbon-based assessment to support sustainable conservation policies. Future studies are expected to focus on specific contamination sources, such as heavy metals, while integrating molecular responses, including analyses of gene expression and stress-related enzymes, to strengthen the understanding of physiological mechanism underlying variations in proline accumulation and carbon storage.

Acknowledgments

The author would like to thank Universitas Jenderal Soedirman and LPPM for funding this research through the Competency Development Research (RPK) scheme under contract number 14.511/UN23.34/PT.01/V/2025. The author also extends gratitude to Sayyidah Nurul Hilaliyyah and Muhammad Fakhri Dwi Nugroho for their assistance in data collection.

REFERENCES

1. Ábrahám, E., Hourton-cabassa, C., Erdei, L., Szabados, L. (2010). Methods for Determination of Proline in Plants. In R. Sunkar (Ed.), *Plant Stress Tolerance* (pp. 317–331). Humana Press. https://doi.org/10.1007/978-1-60761-702-0
2. Afefe, 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. https://doi.org/10.2478/limre-2021-0001
3. Ahmed, S., Kumar, S., Friess, D. A., Sullibie, C., Naabeh, S., Pretzsch, H., Jacobs, M., Sarker, S. K., Friess, D. A., Kamruzzaman, M., Jacobs, M., Sillanpää, M., Naabeh, C. S. S., Pretzsch, H. (2023). Mangrove tree growth is size-dependent across a large-scale salinity gradient. *Forest Ecology and Management*, *537*(July 2022), 120954. https://doi.org/10.1016/j.foreco.2023.120954
4. Ahmed, Y., Kurniawan, C. A., Efendi, G. R., Pribadi, R. (2023). Estimasi Cadangan Karbon Mangrove Berdasarkan Perbedaan Tahun Tanam Rehabilitasi Mangrove (2005, 2008, 2011, 2014 dan 2017) di Kawasan Ekowisata Mangrove Pandansari, Kabupaten Brebes. *Buletin Oseanografi Marina, 12*(1), 9–19. https://doi.org/10.14710/buloma.v12i1.40871
5. Al-araji, K. H. Y. (2019). Evaluation of Physical chemical and biological characteristics of

underground wells in Badra City, Iraq. *Baghdad Science Journal*, *16*(3), 560–570. https://doi.org/http://dx.doi.org/10.21123/bsj.2019.16.3.0560

6. Aleksza, D., Horváth, G., Sándor, G., Szabados, L. (2017). Proline accumulation is regulated by transcription factors associated with phosphate starvation1[OPEN]. *Plant Physiology*, *175*, 555–567. https://doi.org/10.1104/pp.17.00791
7. Allais, L., Thibodeau, B., Khan, N. S., Crowe, S. A., Cannicci, S., Not, C. (2024). Salinity, mineralogy, porosity, and hydrodynamics as drivers of carbon burial in urban mangroves from a megacity. *Science of The Total Environment*, *912*, 168955. https://doi.org/https://doi.org/10.1016/j.scitotenv.2023.168955
8. Alongi, D. M., Murdiyarso, D., Fourqurean, J. W., Kauffman, J. B., Hutahaean, A., Crooks, S., Lovelock, C. E., Howard, J., Herr, D., Fortes, M., Pidgeon, E., Wagey, T. (2016). Indonesia's blue carbon: a globally significant and vulnerable sink for seagrass and mangrove carbon. *Wetlands Ecology and Management*, *24*(1), 3–13. https://doi.org/10.1007/s11273-015-9446-y
9. Alongi, D., 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*. https://doi.org/https://doi.org/10.3354/meps14560
10. Amores, A., Maxey, E., Aguilar, S., Pentason, J. (2024). Distribution of mangrove species diversity along environmental variables using canonical correspondence analysis in Brgy. Penaplata, Samal City, Philippines. *American Journal of Life Sciences*, *12*(5), 86–94. https://doi.org/10.11648/j.ajls.20241205.11
11. Annisa, A. Y. N., Pribadi, R., Pratikto, I. (2019). Analisis perubahan luasan hutan mangrove di kecamatan Brebes dan wanasari, kabupaten Brebes menggunakan citra satelit landsat tahun 2008, 2013 Dan 2018. *Journal of Marine Research*, *8*(1), 27–35. https://doi.org/10.14710/jmr.v8i1.24323
12. Arfan, A., Maru, R., Nyompa, S., Sukri, I., Juanda, M. F. (2024). Analysis of mangrove density using ndvi and macrobenthos diversity in ampekale tourism village South Sulawesi, Indonesia. *Jurnal Sylva Lestari*, *12*(2), 230–241. https://doi.org/10.23960/jsl.v12i2.788
13. Asante, F., Sam, C., Correia, A., Campioli, M., Yeboah, J., Ofori, S., Dahdouh-Guebas, F Asare, N. (2024). Unravelling the impact of environmental variability on mangrove sediment carbon dynamics. *The Science of the Total Environment*, *74837*. https://doi.org/https://doi.org/10.1016/j.scitotenv.2024.174837
14. Basyuni, M., Nasution, K., Slamet, B., Sulistyono, N., Bimatara, Y., Putri, L., Yustaini, E., Hayati, R., Lesmana, I. (2019). Introducing of a silvofishery pond on sapling and seedling density based in Lubuk Kertang Village, North Sumatera. *IOP Conf. Series: Earth and Environmental Science*, *012115*, 260. https://doi.org/10.1088/1755-1315/260/1/012115
15. Brebes, K., Tengah, J., Aminah, S., Azizah, R., Nuraini, T., Djunaedi, A., Nuraini, R. A. T., Djunaedi, A. (2020). Komposisi dan kelimpahan fitoplankton di perairan pandansari, desa kaliwlingi, kabupaten Brebes, Jawa Tengah. *Journal of Marine Research*, *9*(1), 81–86. https://doi.org/10.14710/jmr.v9i1.25793
16. Cabañas–Mendoza, M. del R., Andrade, J. L., Sauri-Duch, E., Hernández-Terrones, L., Fuentes, G., Santamaría, J. M. (2023). Lead tolerance of *Laguncularia racemosa* is associated to high proline accumulation and high antioxidant capacities. In *BioMetals 36*(4), 887–902. https://doi.org/10.1007/s10534-023-00488-8
17. Candraningtyas, C. F., Hafiffah, A. S., Widowati, D., Mardiyanto, M. B., Saputri, A. B., Setyawan, A. D. W. I. (2025). *Spatial and temporal dynamics of mangrove cover change in five estuaries along the North Coast of Central Java, Indonesia (2014–2024). International Journal of Bonorowo Wetlands, 15*(1), 49–60. https://doi.org/10.13057/bonorowo/w150106
18. Celis-Hernández, O., Villoslada-Peciña, M., Ward, R., Bergamo, T., Pérez-Ceballos, R., Girón-García, M. P. (2021). Impacts of environmental pollution on mangrove phenology: Combining remotely sensed data and generalized additive models. *The Science of the Total Environment*, 152309. https://doi.org/10.1016/j.scitotenv.2021.152309
19. Cheng, S., Fung, N., Tam, Y., Li, R., Shen, X., Niu, Z., Chai, M., Yu, G. (2017). Temporal variations in physiological responses of Kandelia obovata seedlings exposed to multiple heavy metals. *Marine Pollution Bulletin*. https://doi.org/10.1016/j.marpolbul.2017.03.060
20. Choudhary, B., Dhar, V., Pawase, A. S. (2024). Blue carbon and the role of mangroves in carbon sequestration: Its mechanisms, estimation, human impacts and conservation strategies for economic incentives. *Journal of Sea Research*, *199*(September 2023), 102504. https://doi.org/10.1016/j.seares.2024.102504
21. Diniyatushoaliha, A., Al Idrus, A., Bahri, S. (2024). Biodiversity indices of mangrove community in gili sulat, east lombok. *Jurnal Biologi Tropis*, *24*(3), 791–799. https://doi.org/10.29303/jbt.v24i3.7571
22. Doodee, M., Rughooputh, S., Jawaheer, S. (2025). Mangrove biomass productivity and sediment carbon storage assessment at selected sites in Mauritius: the effect of tidal inundation, forest age and mineral availability. *Environmental Research Communications*, *7*. https://doi.org/https://doi.org/10.1088/2515-7620/adacac

23. Fengfeng, Liu, Y., Qi, Y., Deng, N., Xiang, H., Qi, C., Peng, P., Jia, L., Zhang, X. (2024). Tree age affects carbon sequestration potential via altering soil bacterial community composition and function. *Frontiers in Microbiology*, *15*. https://doi.org/10.3389/fmicb.2024.1379409
24. Ghosh, U., Islam, M., Siddiqui, M., Cao, X., Khan, M. (2021). Proline, a multifaceted signalling molecule in plant responses to abiotic stress: understanding the physiological mechanisms. *Plant Biology*, *24*(2), 227–239. https://doi.org/https://doi.org/10.1111/plb.13363
25. Gunawan, H., Iskandar, S. (2017). Dynamics of mangrove community in revegetation area of Karangsong, north coast of Indramayu District, West Java, Indonesia. *Biodiversitas Journal of Biological Diversity*, *18*(2), 659–665. https://doi.org/10.13057/biodiv/d180230
26. Hamilton, S. E., Friess, D. A. (2018). Global carbon stocks and potential emissions due to mangrove deforestation from 2000 to 2012. *Nature Climate Change*. https://doi.org/10.1038/s41558-018-0090-4
27. Hapsari, K. A., Borrero Avellaneda, W. J., van Maanen, B., Restrepo, J. C., Polanía, J., Sibaja Castillo, D. J., Gómez Vargas, L. F., Rodríguez-Rodríguez, J. A., Urrego, D. H., Jos, W., Restrepo, J. C., Polanía, J., Jose, D., Castillo, S., G, L. F. (2024). Structure and carbon stocks of accessible mangroves under different conservation status in the Colombian Caribbean. *Forest Ecology and Management*, *564*(121984), 1–13. https://doi.org/10.1016/j.foreco.2024.121984
28. Haque, A. (2011). *Analisis Penentuan Status Mutu Air dengan Menggunakan Metode Indeks Pencemaran (Ip) pada Musim Penghujan dan Musim Kemarau (Studi Kasus: Sungai Pemali, Brebes - Jawa Tengah)* [Univeritas Diponegoro]. https://eprints.undip.ac.id/view/divisions/sch=5Fenv/2011.type.html
29. He, G., Xie, H., Tan, B., Chen, M., Wu, Z., Dai, Z. (2025). Effects of microplastics and heavy metal stress on the growth and physiological characteristics of pioneer plant Avicennia marina. *Marine Pollution Bulletin*, *216*(April), 117929. https://doi.org/10.1016/j.marpolbul.2025.117929
30. Henna Parveen, 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. https://doi.org/10.1016/j.cropd.2024.100052
31. Heriati, A., Solihuddin, T., Husrin, S., Salim, H. L., Mustikasari, E., Kepel, T. L., Ati, R. N. A. (2021). Mangrove Ecosystem Development on North Coast of Java. *IOP Conference Series: Earth and Environmental Science*, *925*(1). https://doi.org/10.1088/1755-1315/925/1/012020
32. Hillebrand, H., Bennett, D. M., Cadotte, M. W. (2008). Concepts & synthesis emphasizing new ideas to stimulate research in ecology consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, *89*(6), 1510–1520. https://doi.org/10.1890/07-1053.1
33. Hilmi, E., Hendrayana, Samudra, S. R., Fikriyya, N., Junaidi, T., Cahyo, T. N., Putri, N. A., Ummah, A. N. (2024). Species-specific and landscape carbon storage analysis of mangrove forest in Segara Anakan Lagoon, Cilacap, Central Java, Indonesia. *Biodiversitas*, *25*(8), 2784–2755. https://doi.org/10.13057/biodiv/d250848
34. Hu, Y., Fest, B., Swearer, S., Arndt, S. (2021). Fine-scale spatial variability in organic carbon in a temperate mangrove forest: Implications for estimating carbon stocks in blue carbon ecosystems. *Estuarine Coastal and Shelf Science*, *259*(107469). https://doi.org/https://doi.org/10.1016/j.ecss.2021.107469
35. Jaelani, L. M., Safitri, D. S., Kristian, N. E., Alina, A. N., Syariz, M. A., Sanjaya, H., Abdul Rasam, A. R. (2025). Mapping mangrove species distribution and density using Sentinel-2 satellite imagery and spectral analysis. *Journal of Human, Earth, and Future*, *6*(1), 1–11. https://doi.org/10.28991/HEF-2025-06-01-01
36. Jones, I., DeWalt, S., Lopez, O., Bunnefeld, L., Pattison, Z., Dent, D. (2019). Above- and below-ground carbon stocks are decoupled in secondary tropical forests and are positively related to forest age and soil nutrients respectively. *The Science of the Total Environment*, *697*, 133987. https://doi.org/10.1016/j.scitotenv.2019.133987
37. Kamruzzaman, M., Minhaj-Uj-Siraj, M., Ahmed, S., Osawa, A. (2017). Regeneration status of mangrove species under mature stands in the oligohaline zone of the Sundarbans, Bangladesh. *Regional Studies in Marine Science*, *16*, 15–20. https://doi.org/10.1016/j.rsma.2017.07.007
38. Kartika, A. F., Fikriyya, N., Nurul Zulkarnaen, R. (2024). Vegetation diversity in mangrove forest area of Mojo village, Ulujami district, Pemalang regency, Central Java. *Buitenzorg: Journal of Tropical Science*, *1*(2), 1–9. https://doi.org/10.70158/buitenzorg.v1i2.8
39. Kida, M., Fujitake, N. (2020). Organic carbon stabilization mechanisms in mangrove soils: A review. *Forests*, *11*, 981. https://doi.org/https://doi.org/10.3390/f11090981
40. Komiyama, A., Ong, J. E., Poungparn, S. (2008). Allometry, biomass, and productivity of mangrove forests: A review. *Aquatic Botany*, *89*(2), 128–137. https://doi.org/10.1016/j.aquabot.2007.12.006
41. Kusuma, E. W., Tri Nuraini, R. A., Hartati, R., Azizah, R., Nuraini, T., Hartati, R. (2020). Komposisi jenis gastropoda di mangrove desa Kaliwlingi

dan Sawojajar, Jawa tengah. *Journal of Marine Research*, *9*(2), 167–174. https://doi.org/10.14710/jmr.v9i2.26558

42. Li, L., Liu, W., Ai, J., Cai, S., Dong, J. (2023). Predicting mangrove distributions in the Beibu Gulf, Guangxi, China, using the MaxEnt Model: Determining tree species selection. *Forests*, *14*(1). https://doi.org/10.3390/f14010149
43. 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. https://doi.org/10.1007/s10646-020-02198-0
44. Ma, L., Yang, S. (2022). Growth and physiological response of Kandelia obovata and Bruguiera sexangula seedlings to aluminum stress. *Environmental Science and Pollution Research*, *29*, 43251–43266. https://doi.org/10.1007/s11356-021-17926-0
45. Mardliyah, R., Ario, R., Pribadi, R. (2019). Estimasi simpanan karbon pada ekosistem mangrove di desa Pasar Banggi Dan Tireman, Kecamatan Rembang Kabupaten Rembang. *Journal of Marine Research*, *8*(1), 62–68.
46. Mattone, C., Sheaves, M. (2017). Patterns, drivers and implications of dissolved oxygen dynamics in tropical mangrove forests. *Estuarine, Coastal and Shelf Science*, *197*, 205–213. https://doi.org/10.1016/j.ecss.2017.08.028
47. Meena, M., Divyanshu, K., Kumar, S., Swapnil, P., Zehra, A., Shukla, V., Yadav, M., Upadhyay, R. (2019). Regulation of L-proline biosynthesis, signal transduction, transport, accumulation and its vital role in plants during variable environmental conditions. *Heliyon*, *5*(July), e02952. https://doi.org/10.1016/j.heliyon.2019.e02952
48. Mehta, D., Vyas, S. (2023). Comparative bioaccumulation of osmoprotectants in saline stress tolerating plants: A review. *Plant Stress*, *9*(August 2022), 100177. https://doi.org/10.1016/j.stress.2023.100177
49. Moukhtari, E., Cabassa-Hourton, C., Farissi, M., Savouré, A. (2020). How does proline treatment promote salt stress tolerance during crop plant development? *Frontiers in Plant Science*, *11*. https://doi.org/10.3389/fpls.2020.01127
50. Nainggolan, F. A., Pribadi, R., Trianto, A. (2022). Struktur komposisi dan simpanan karbon di sedimen hutan mangrove Pandansari, Kaliwlingi, Brebes. *Journal of Marine Research*, *11*(3), 529–538. https://doi.org/10.14710/jmr.v11i3.33393
51. Parida, A., Das, A., Das, P. (2002). NaCl stress causes changes in photosynthetic pigments, proteins, and other metabolic components in the leaves of a true mangrove, *Bruguiera parviflora*, in hydroponic cultures. *Journal of Plant Biology*, *45*, 28–36. https://doi.org/10.1007/bf03030429
52. Pecka, J., Kraus, K., Zelen, M., Hniliˇ, H. (2025). Exogenous Proline Modulates Physiological Responses and Induces Stress Memory in Wheat Under Repeated and Delayed Drought Stress. *Agronomy, 15*(6)*,*1–17.
53. Purwanto, R. H., Mulyana, B., Satria, R. A., Yasin, E. H. E., Putra, I. S. R., Putra, A. D. (2022). Spatial distribution of mangrove vegetation species, salinity, and mud thickness in mangrove forest in Pangarengan, Cirebon, Indonesia. *Biodiversitas*, *23*(3), 1383–1391. https://doi.org/10.13057/biodiv/d230324
54. Rahman, A., Islam, M. A., Idris, M. H., Bhuiyan, M. K. A., Chowdhury, M. M., Abualreesh, M. H., Abu, H. M. K. (2023). Species diversity and assemblage of mangroves at Setiu Wetland, Terengganu, Malaysia. *Borneo Journal of Resource Science and Technology*, *13*(1), 173–190. https://doi.org/10.33736/bjrst.5109.2023
55. Rahman, M., Donoghue, D., Bracken, L. (2021). Is soil organic carbon underestimated in the largest mangrove forest ecosystems? Evidence from the Bangladesh Sundarbans. *Catena*, *200*(105159). https://doi.org/https://doi.org/10.1016/j.catena.2021.105159
56. Raza, A., Charagh, S., Abbas, S., Hassan, M., Saeed, F., Haider, S., Sharif, R., Anand, A., Corpas, F., Jin, W., Varshney, R. (2023). Assessment of proline function in higher plants under extreme temperatures. *Plant Biology*. https://doi.org/10.1111/plb.13510
57. Redi, A., Sitabuana, T. H., Hanifati, F. I., Arsyad, P. N. K. (2019). Urgensi pembentukan peraturan daerah provinsi Bali tentang perlindungan dan pengelolaan hutan mangrove berlandaskan kearifan lokal. *Jurnal Muara Ilmu Sosial, Humaniora, Dan Seni*, *3*(1), 32. https://doi.org/32 https://doi.org/10.24912/jmishumsen.v3i1.3517
58. Robin, S. L., Marchand, C., Mathian, M., Baudin, F., Alfaro, A. (2022). *Distribution and bioaccumulation of trace metals in urban semi-arid mangrove ecosystems*. *10*. https://doi.org/10.3389/fenvs.2022.1054554
59. Sadono, R., Soeprijadi, D., Susanti, A., Wirabuana, P. Y. A. P., Matatula, J. (2020). Species composition and growth performance of mangrove forest at the coast of Tanah Merah, East Nusa Tenggara. *Biodiversitas Journal of Biological Diversity*, *21*(12). https://doi.org/10.13057/biodiv/d211242
60. Sari, A., Tuwo, A., Saru, A., Rani, C. (2022). Diversity of fauna species in the mangrove ecosystem of Youtefa Bay Tourism Park, Papua, Indonesia. *Biodiversitas Journal of Biological Diversity*, *23*(9). https://doi.org/10.13057/biodiv/d230915
61. Sha, C., Wang, M., Jiang, Y., Lin, G. (2018). Interactions between pH and other physicochemical properties of mangrove sediments: A review. *Chinese Science Bulletin*. https://doi.org/10.1360/n972018-00369

62. Sinaga, N. N., Herawati, H., Hamdani, H., Sahidin, A. (2019). Structure of Macrozoobenthos (Gastropods) Community in Mangrove Forest Ecotourism Pandansari Kabupaten Brebes, Central Java. *Asian Journal of Fisheries and Aquatic Research*, *4*(3), 1–6.
63. Smith, T. J., Whelan, K. R. T. (2006). Development of allometric relations for three mangrove species in South Florida for use in the Greater Everglades Ecosystem restoration. *Wetlands Ecology and Management*, *14*(5), 409–419. https://doi.org/10.1007/s11273-005-6243-z
64. Soeprobowati, T. R., Anggoro, S., Puryono, S., Purnaweni, H., Sularto, R. B., Mersyah, R. (2022). Species Composition and Distribution in the Mangrove Ecosystem in the City of Bengkulu, Indonesia. *Water*, *14*(21), 3516. https://doi.org/10.3390/w14213516
65. Spormann, S., Nadais, P., Sousa, F., Pinto, M., Martins, M., Sousa, B., Fidalgo, F., Soares, C. (2023). Accumulation of proline in plants under contaminated soils—are we on the same page? *Antioxidants*, *12*. https://doi.org/10.3390/antiox12030666
66. Suyono, S., Ginistyo, G., Zuhri, N. (2019). Mangrove reforestation as abrasion prevention in Brebes, Central Java. In *Unovsersitas Ppancasakti Tegal*. https://repository.upstegal.ac.id/88/
67. Tamimi, B. M., Radziah, C., Mohd, C. (2021). Temperature stress on physiological and morphological traits in *Rhizophora apiculata* temperature stress on physiological and morphological traits in *Rhizophora apiculata*. *Baghdad Science Journal, 18*(4), 1492–1500. https://doi.org/https://dx.doi.org/10.21123/bsj.2021.18.4(Suppl.).1492 Temperature
68. Toan, N., Ngoc, P., Dung, L., Tue, N., Quy, T., Nhuan, M. (2025). Nitrate, ammonium, and phosphate patterns from mangrove sediment cores near extensive aquaculture areas in the Red River Delta, Vietnam. *One Ecosystem*, *10*. https://doi.org/10.3897/oneeco.10.e150217
69. Wang, S.-M., Wang, Y.-S., Su, B., Zhou, Y., Chang, L., Xiao-Yu, Li, X.-M. (2022). Ecophysiological responses of five mangrove species (*Bruguiera gymnorrhiza, Rhizophora stylosa, Aegiceras corniculatum, Avicennia marina,* and *Kandelia obovata*) to chilling stress. *Front. Mar. Sci., 9*. https://doi.org/10.3389/fmars.2022.846566
70. Wang, W., Xin, K., Chen, Y., Chen, Y., Jiang, Z., Sheng, N., Liao, B., Xiong, Y. (2024). Spatio-temporal variation of water salinity in mangroves revealed by continuous monitoring and its relationship to floristic diversity. *Plant Diversity*, *46*(1), 134–143. https://doi.org/10.1016/j.pld.2023.06.006
71. Xiang, W., Xu, L., Lei, P., Ouyang, S., Deng, X., Chen, L., Zeng, Y., Hu, Y., Zhao, Z., Wu, H., Zeng, L., Xiao, W. (2022). Rotation age extension synergistically increases ecosystem carbon storage and timber production of Chinese fir plantations in southern China. *Journal of Environmental Management*, *317*, 115426. https://doi.org/10.1016/j.jenvman.2022.115426
72. Yadav, A., Ram, A., Majithiya, D., Salvi, S., Sonavane, S., Kamble, A., Ghadigaonkar, S., Jaiswar, J. R. M., Gajbhiye, S. N. (2015). Effect of heavy metals on the carbon and nitrogen ratio in *Avicennia marina* from polluted and unpolluted regions. *MPB*, *101*(1), 359–365. https://doi.org/10.1016/j.marpolbul.2015.10.020
73. Zou, H., Li, X., Li, S., Xu, Z., Yu, Z., Cai, H., Chen, W., Ni, X., Wu, E., Zeng, G. (2023). Soil organic carbon stocks increased across the tide-induced salinity transect in restored mangrove region. *Scientific Reports, 13*. https://doi.org/https://doi.org/10.1038/s41598-023-45411-w