Journal of Animal & Plant Sciences, 35(4): 2025, Page: 1175-1188
ISSN (print): 1018-7081; ISSN (online): 2309-8694
https://doi.org/10.36899/JAPS.2025.4.0101

RELATIONSHIPS BETWEEN ENVIRONMENTAL FACTORS AND PLANT FUNCTIONAL TRAITS IN MANGROVE ECOSYSTEMS: CHARACTERIZATION BY FT-IR SPECTROSCOPY

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ABSTRACT

Mangrove ecosystems are of crucial importance in maintaining biodiversity and environmental stability. However, these ecosystems are increasingly threatened by anthropogenic and natural factors. The implementation of conservation strategies that take advantage of the unique functional traits of mangroves is therefore essential for their protection. This study employs the technique of Fourier transform infrared spectroscopy (FT-IR) to analyze the relationship between environmental factors and the functional properties of the leaves of white mangrove (*Laguncularia racemosa*), black mangrove (*Avicennia germinans*) and red mangrove (*Rhizophora mangle*). This analysis provides biochemical fingerprints that reveal the influence of environmental factors on ecosystem functioning, with significant correlations found between spectral bands and environmental variables. Temperature exhibited a correlation with band 1 (3323-3398 cm^{-1}), linked to carbohydrates, proteins, alcohols and phenolic compounds. Salinity and bulk density influenced bands 3 (1717-1729 cm^{-1}) and 4 (1614-1655 cm^{-1}), associated with amide I, pectin, phospholipids and cholesterol esters. The influence of surface soil pH on band 7 (1130-1165 cm^{-1}) reflected the presence of polysaccharides, while subsoil pH aligned with band 6 (1203-1237 $cm^{-1)}$, indicative of lignin and xylans. Furthermore, an association was observed between organic matter content and bands 5 (1462 cm^{-1}) and 8 (999-1103 cm^{-1}), indicating the role of cellulose and pectin in cell structure. Additionally, interstitial soil pH influenced bands 9 (815-884 cm^{-1}) and 10 (719 cm^{-1}), linked to cellulose and amide V stability, respectively. The findings demonstrate the significant impact of environmental factors (temperature, salinity and pH) on the chemical composition of mangrove ecosystems, and the results provide fundamental information on their biochemical adaptations. This supports the development of conservation strategies to improve the resilience and sustainability of these ecosystems.

Keywords: mangrove, environmental changes, FT-IR

INTRODUCTION

Mangroves are coastal ecosystems of significant ecological importance due to the multiple ecosystem services they provide, including protection against coastal erosion, carbon storage, and their role as critical habitats for numerous species of flora and fauna (Venkateswarlu and Venkatrayulu, 2023). These plant ecosystems, typically distributed in tropical and subtropical regions, contribute significantly to climate regulation and global biodiversity conservation. However, these ecosystems are under increasing threat due to anthropogenic pressures, including urbanization, land-use change, and unsustainable exploitation of natural resources. Climate change exacerbates this vulnerability through sea level rise, increased temperatures, and salinity variability (Agraz-Hernández *et al*., 2006; Akram *et al*., 2023).

In semi-arid regions, where extreme temperature and salinity conditions are prevalent, mangroves face even more pronounced environmental challenges (Rodríguez-Medina *et al*., 2020; SEMARNAT, 2010). These adverse conditions affect both their structural development and metabolic processes, making them an ideal system for investigating the adaptation and resilience mechanisms that allow them to survive in such hostile environments (Akram *et al*., 2023). In Mexico, mangroves occupy approximately 775,555 hectares, distributed along the Pacific, Gulf of Mexico, and Caribbean coasts, positioning the country as one of the nations with the greatest diversity and extent of these ecosystems (Rodríguez-Medina *et al*., 2020; Semarnat, 2010).

In the state of Sonora, mangroves are predominantly situated along the eastern coastline of the

Gulf of California. These areas are characterized by extreme environmental conditions, including elevated temperatures, high salinity, and limited freshwater availability, which impose significant restrictions on plant life (Torres *et al*., 2022). The Laguna Tóbari site, located in northwestern Mexico, is characterized by a notable diversity of mangrove flora, comprising three principal species: *Laguncularia racemosa* (white mangrove), *Avicennia germinans* (black mangrove), and *Rhizophora mangle* (red mangrove). These species have been classified as low risk according to the International Union for Conservation of Nature (IUCN) Red List (NOM-059-SEMARNAT-2010, 2010; Torres *et al*., 2021). However, the ability of these species to persist in adverse conditions is strongly dependent on their capacity to undergo highly specialized metabolic and structural adaptations, which enable them to cope with both abiotic and biotic stressors (Arreola-Lizárraga *et al*., 2018; Torres *et al*., 2021; Vargas-Terminel *et al*., 2023).

The ability of mangroves to adapt to these extreme conditions can be studied through advanced analytical techniques such as Fourier transform infrared spectroscopy (FT-IR). This technique is based on the absorption of infrared radiation by the molecules of the analyzed material, generating a characteristic spectrum that provides detailed information about its molecular composition (Baker *et al*., 2014; Liu and Kim, 2017; Yun *et al*., 2024). FT-IR analysis evaluates the impact of environmental factors such as salinity, soil pH and temperature extremes on mangrove adaptive responses (Krilov *et al*., 2009; Meera *et al*., 2023). Chemical alterations in lipids, proteins, and carbohydrates reflect biochemical mechanisms underlying their ability to tolerate adverse conditions. Among the main biochemical responses is the production of protective compounds, such as tannins and anthocyanins, which help plants mitigate the effects of water and salt stress (Dittmann *et al*., 2022). In addition, it has been observed that salinity can induce modifications in the protein structures of leaves, affecting both their functionality and adaptive capacity (Barreto *et al*., 2021). In mangrove leaves, FT-IR allows the identification of key functional groups, such as lipids, proteins and phenolic compounds, which are directly associated with physiological responses to environmental stress factors. Lipids play a key role in stabilizing cell membranes, while proteins and phenolic compounds act as antioxidants and protectors against oxidative damage generated by extreme conditions (Lu *et al*., 2020; Roy *et al*., 2023). For example, spectral bands associated with proteins can reveal changes in their structure due to salt stress, while phenolic compounds reflect adaptive responses to drought and salinity (Lu *et al*., 2020; Šamec *et al*., 2021). These findings are essential for understanding how abiotic factors, such as soil chemistry and water availability, influence the physiology and biochemistry of mangrove leaves.

MATERIALS AND METHODS

Study Area (Geographical Location): Mangrove forests in the American Pacific reach their northernmost limit in subtropical latitudes (Ochoa-Gómez *et al*., 2019; Torres *et al*., 2022). Given the subtropical, arid and little-explored conditions observed along the Sonoran coast in the Gulf of California (Bautista-Olivas *et al*., 2018), an annual study was conducted in the coastal lagoon of El Tóbari, which exhibits an arid gradient (Figure 1). The mangrove forest in this lagoon is composed of species including *Laguncularia racemosa* [L.] Gaertn (Lr), *Avicennia germinans* [L.] Stearn (Ag) and *Rhizophora mangle* [L.] (Rm), all of which are categorised as vulnerable according to Mexican regulations (NOM-059-SEMARNAT-2010, 2010).

The El Tóbari lagoon extends over approximately 255 hectares covered by mangroves (Rodríguez-Zúñiga *et al*., 2013), and its water dynamics are influenced by ocean currents (Beman and Francis, 2006). With an average depth of 1.5 m, the lagoon is characterized by a warm, arid climate, where the mean annual temperature reaches 25°C and precipitation is 375 mm per year (Torres *et al*., 2022). The system receives its freshwater supply mainly through rainfall runoff and agricultural irrigation surpluses from the Yaqui Valley (Rodríguez-Zúñiga *et al*., 2013).

Sampling design: Three study sites were established in the lagoon of Tobari, in the state of Sonora, Mexico, in September of 2021. Each comprising three 20 × 20 m monitoring units (Figure 1 A). Sampling was conducted in accordance with a cross-and-angled pattern within each unit, with three samples collected at each point (Figure 1B). From these samples, leaves were collected from the top, middle, and bottom of the plants, yielding a total of 1 kg of leaves per section. A total of 90 samples were obtained for each sampling point. The collected samples were transported to the National Technological Institute of Mexico/ Technological Institute of Yaqui Valley, to the Coastal Zones Laboratory. The collected leaves were subjected to a drying process utilizing a hot air flow at 45 °C for a period of 48 hours in a tray dryer. This was done in order to prevent band overlapping in the FT-IR spectra, particularly in the 3500-3000 cm^{-1} and 1600 cm^{-1} regions, which is caused by the presence of water. Subsequently, the dried samples were pulverized in a hammer mill and sieved using an 80-point sieve per square inch. For FT-IR measurements, the sieved samples were compressed into pellets.

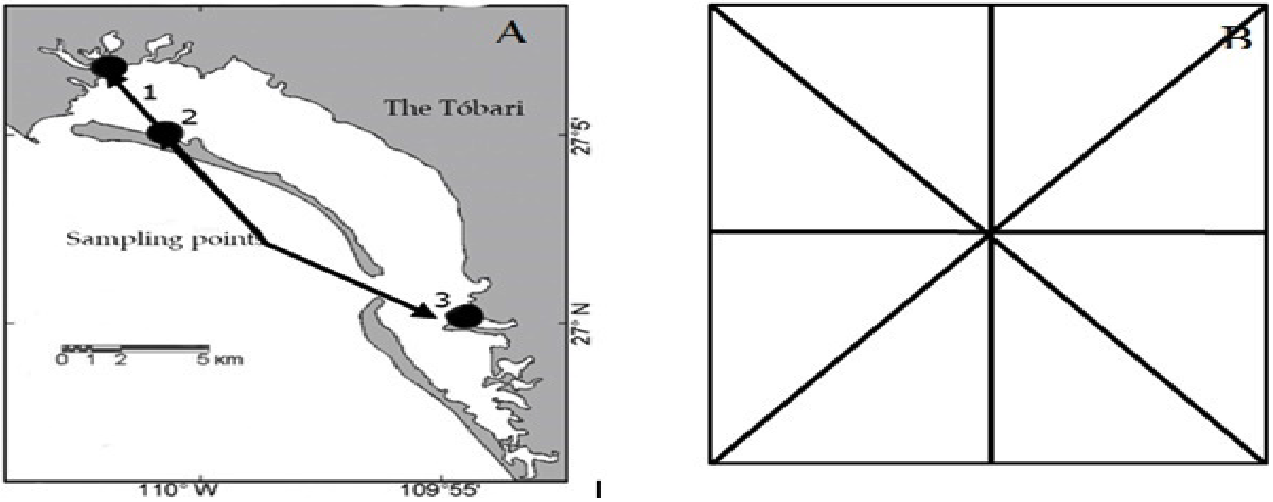

Fig 1. Study area: Tóbari (points 1, 2 and 3) in the Gulf of California, Sonora, México (A). Sampling performed (B)

FT-IR Leaf Analysis: The spectral data were processed using the OMNIC software from THERMO FISHER. The compressed sample was scanned without any preparation at a resolution of 0.01 cm^{-1}, using air as the blank reference spectrum to minimize the presence of carbon dioxide and water vapor. The data were further processed using the Savitsky-Golay second derivative in Origin Lab 8.5 software (Topală and Rusea, 2018; Topala and Tataru, 2018).

Soil Physico-Chemical Analysis: Two soil samples were collected at a depth of 20 cm using a soil auger (0.0033 m2). The following parameters were determined: texture (Klute, 1986), soil pH by electrometry, and organic matter (OM) (Heiri *et al*., 2001). Additionally, bulk density and soil moisture content were assessed (Casasola and Warner, 2009).

At each sampling station, two piezometers were installed at depths of 0.5 and 1.5 m to measure interstitial and subsurface salinity. A total of 36 piezometers were installed (Casasola and Warner, 2009). The flood level was measured monthly using the piezometer at a depth of 1.5 metres. Precipitation data for the study period were obtained from the Sonora Automatic Weather Station Network (Cesave-Siafeson, 2021). The water level was determined based on tidal predictions provided by CICESE (2021) (http://predmar.cicese.mx/programa/).

Salinity and flood level: The monthly recording of salinity and flood level data was conducted. In each monitoring plot, two piezometers were installed for the measurement of salinity in both interstitial water (at a depth of 0.5 m) and groundwater (at a depth of 1.5 m), in accordance with the guidelines set forth by Casasola and Warner (2009). This resulted in a total of 36 piezometers being utilized in the study. The flood level was evaluated on a monthly basis utilising the piezometer situated at a depth of 1.5 metres. The piezometers were constructed using one-inch diameter PVC pipes, with slots of alternating widths every 2 cm in the buried section. The pipes were covered with a 250 μm mesh, fixed with plastic clips. Precipitation data for the duration of the study were obtained from a weather station situated approximately 3 km from the coastal lagoons and managed by the Sonoran Automatic Weather Stations Network (http://www.siafeson.com/remas2/). The data on precipitation were aggregated on a monthly basis. The water levels recorded during the study period were obtained from CICESE (2021) tidal predictions (http://predmar.cicese.mx/programa/).

Statistical analysis was conducted using Kolmogorov-Smirnov and Levene tests to check for variance and normality. To observe differences in sediment, pneumatophore, salinity, and flooding level physicochemical data sets across plots, a general univariate model using ANOVA and Tukey tests was employed (Steel *et al*., 1996).

RESULTS

Chemical analysis of mangrove leaves by FT-IR and its interrelation with environmental variables: The canonical correspondence analysis (Fig 2.), shows the relationships between the bands obtained by FT-IR and the environmental variables of the mangrove. Temperature (1) is mainly associated with band 1 (3323-3398 cm-1), which is assigned to N-H and O-H stretching, indicators of the presence of carbohydrates, proteins, alcohols, and phenolic compounds (Table 1). Salinity and bulk density (4) show a strong correlation with band 4 (1614-1655 cm-1), which is assigned to the C=O stretching of amide 1, which is related to the presence of proteins and pectin. In addition, salinity is also associated with band 3 (1717-1729 cm-1), corresponding to stretches of saturated C=O esters, associated with phospholipids and cholesterol esters. The pH in the surface soil (3) has a strong correlation with band 7 (1130-1165 cm-1), which corresponds to C=O stretching of polysaccharides (Table 1). This link suggests that pH could be influenced by the concentration of these compounds in the soil. Subsurface soil pH (2) shows a significant association with band 6 (1203-1237 cm-1), which is assigned to C-O stretching, an indicator of lignin and xylans, suggesting that deeper soil pH might be related to more complex organic matter degradation.

Organic matter (5) in the soil is strongly associated with band 5 (1462 cm-1), which corresponds to OH-bending in cellulose, indicating the presence of decomposing plant matter in the soil. A correlation was also observed with band 8 (999-1103 cm-1), corresponding to C-OH, C-C, and C-H in pectin, suggesting the influence of organic matter on the cell wall structure of plants in the mangrove. Interstitial soil pH (6) is associated with band 9 (815-884 cm-1), which corresponds to C-O bending in cellulose, suggesting that interstitial pH is related to the stability of cellulose structures in soil. Likewise, band 10 (719 cm-1), which maps to N-H bending in the amido V band of proteins, correlates with environmental variables, suggesting that proteins also play a role in mangrove response to environmental factors. Finally, band 11 (551-607 cm-1), corresponding to the C-H fingerprint region in C-O or C-C bending and stretching, is related to several of the environmental variables, indicating the complexity of interactions between the environment and the chemical composition of the mangrove soil. These results, taken together, demonstrate that mangrove environmental conditions, such as temperature, salinity, bulk density, and different soil pH levels, significantly influence the chemical composition detected by FT-IR, reflecting the biochemical adaptations that occur in this ecosystem in response to its environment.

The protein structure of mangrove leaves was analysed by FT-IR in the amide I region. Table 2 shows the characterisation of the predominant secondary structure of mangrove proteins by FT-IR spectroscopy in the amide I region. This revealed a prevalence of the beta sheet conformation in several samples from different plants and locations. This suggests structural conservation with slight variations depending on site and species. Wavelengths associated with beta sheets range from 1615 cm-1 to 1635 cm-1, indicating subtle differences in protein conformation influenced by the local environment. Furthermore, some samples exhibit structural variations, including the presence of alpha-helices in 'Rm. Furthermore, the presence of Siari' (1655 cm-1) and disordered structures in 'Lr. Furthermore, the presence of alpha-helices in 'Rm. Siari' (1646 cm-1) and disordered structures in 'AG' are also observed. This suggests specific adaptations to local mangrove conditions, as evidenced by the presence of alpha-helices in Siari at 1643 cm-1. These wavelength differences, even within similar structures, reflect the influence of the physico-chemical environment on protein conformation, thereby underscoring the structural diversity observed in mangrove proteins in Laguna del Tóbari, Sonora, Mexico.

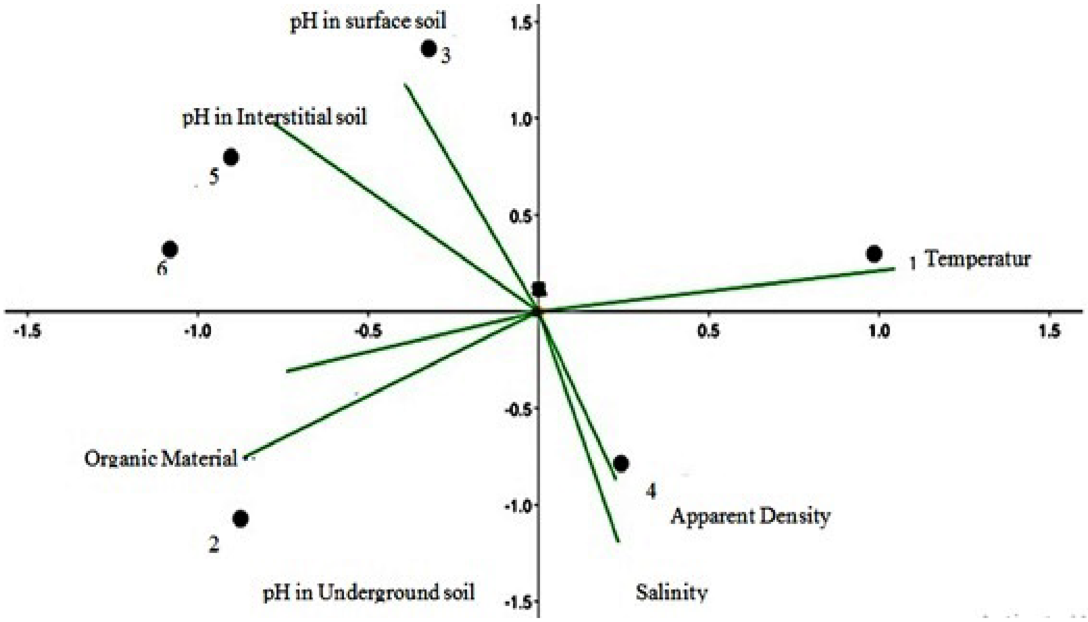

Fig 2. Analysis of canonical correspondence of soil properties and FT-IR spectral bands. The dots indicate the band number.

Table 1 Spectral Assignment: Correspondence between FT-IR Bands obtained from the mangrove leaves of the Tovari lagoon, Sonora. and Characteristic Functional Groups

Experimental Data		Literature		
Band Number	Wavelength (cm^{-1})	Allocation	Taxpayer	Reference
1	3323-3398	Stretch N-H and OH	Carbohydrates, proteins, alcohols, phenolic compounds	(Kumar *et al.*, 2016; Topală and Rusea, 2018)
2	2917	Asymmetrical CH_2 Stretch	Lipids	(Türker-Kaya and Huck, 2017)
3	1717-1729	Saturated ester C=O	Phospholipids and cholesterol esters	(Meade *et al.*, 2010)
4	1614-1655	Amide C=O Stretch 1	Protein and pectin	(Topală and Rusea, 2018)
5	1462	OH Folding	Cellulose	(Santiago-Cintrón and Hinchliffe, 2015; Topală and Rusea, 2018)
6	1203-1237	C-O Stretch	Lignin and xylan	(Bobby *et al.*, 2012; Wilson *et al.*, 2000)
7	1130-1165	Stretch C=O	Polysaccharides	(Meade *et al.*, 2010; Topală and Rusea, 2018)
8	999-1103	C-OH, C-C, C-H	Pectin	(Bobby *et al.*, 2012)
9	815-884	C-O Bent	Cellulose	
10	719	N-H Bending	Amide V Protein Band	(Topală and Rusea, 2018)
11	551-607	Fingerprint region	C-H flexion and C-O or C-C stretch	(Yang and Yen, 2002)

Table 2. Characterization of the Predominant Secondary Structure in Mangrove Proteins by FT-IR Spectroscopy in the Amida I Region in Laguna del Tobari, Sonora, Mexico.

Plant	Wavelength (cm^{-1})	Protein Structure
Rm. Huivulai	1629	Beta Sheet
Rm. Atanasia	1631	Beta Sheet
Rm. Siari	1655	Alpha Helix
Lr. Huivulai	1622	Beta Sheet
Lr Atanasia	1615	Beta Sheet
Lr. Siari	1646	Disorderly
AG. Huivulai	1635	Beta Sheet
Lr. Atanasia	1632	Beta Sheet
AG. siari	1643	Disorderly

Physicochemical in Soils: The temperature and temperature graphs reflect the climatic conditions of a mangrove, where warm temperatures, which gradually increase from winter to summer, create an environment conducive to the flora and fauna characteristic of this ecosystem. Precipitation, concentrated at a significant peak in August, is vital to maintaining mangrove health, as it recharges freshwater bodies and reduces salinity, allowing for an essential balance between salt and fresh water (Fig 3.). During the long dry season, the mangrove faces challenges of high salinity and reduced availability of fresh water, forcing species to adapt to these extreme conditions, demonstrating the resilience of this unique ecosystem.

Table 4 illustrates the significant dissimilarities in the physicochemical attributes between surface (S) and interstitial (I) water. The pH of the surface water exhibits a range between 8.2 and 8.6, indicative of more alkaline conditions, while the interstitial water displays a pH range between 7.3 and 7.8, suggestive of a slightly higher acidity. The temperature of the surface water exhibits a range of 25.3°C to 30°C, displaying greater variability compared to the interstitial water, which presents a narrower range of 25°C to 26°C. This indicates a higher thermal stability in the interstitial water. The oxidation-reduction potential (ORP) indicates that the surface water exhibits a range of -140.6 mV to -238.5 mV, whereas the interstitial water displays a more reducing environment, with a range of -250.4 mV to -380.4 mV. These findings indicate that interstitial water is more thermally stable, more acidic, and exhibits a more reducing environment compared to surface water. With regard to pH, the sediments from Atanasia are observed to be the most acidic, with a value of 5.9, while those from Siari exhibit a slightly higher pH of 6.6, and those from Huivulai are situated between the two with a pH of 6.1. These differences in pH are statistically significant, as indicated by an F-value of 4.1 and a P-value of 0.03, which suggests that sediment acidity varies markedly between sites. Additionally, the bulk density (BD) of the sediments exhibits a comparable pattern, with Atanasia exhibiting the highest density of 0.81 g/cm³, in contrast to Siari and Huivulai, which have lower values of 0.73 g/cm³ and 0.74 g/cm³, respectively. These differences in bulk density are highly significant, with an F value of 14 and a P value of less than 0.05, indicating that the sediments at Atanasia are more compact and potentially richer in dense minerals.

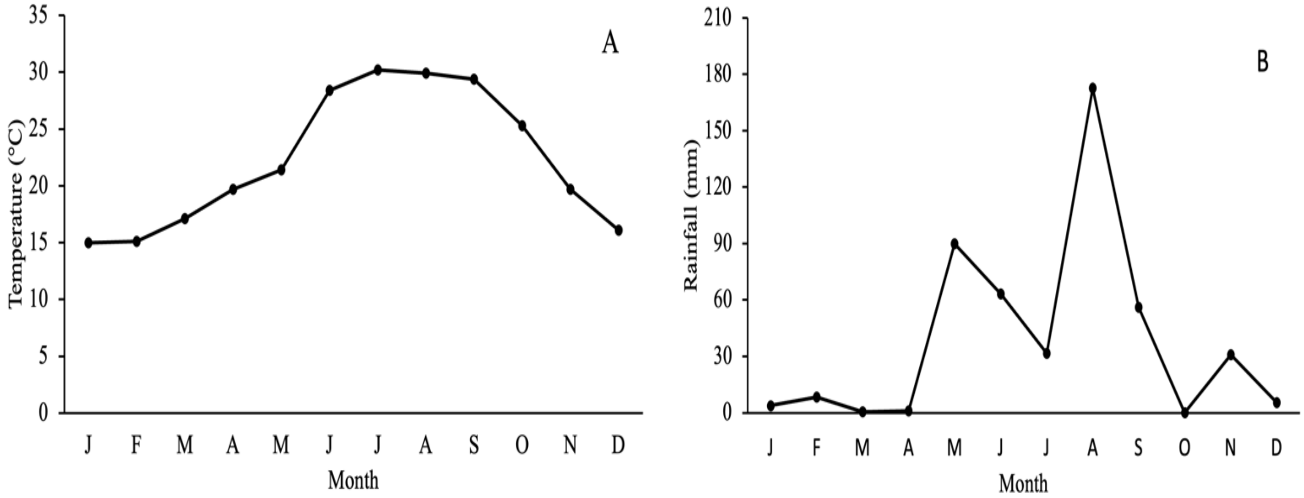

Fig. 3. Annual Temperature and Precipitation Standards of the Tobari Lagoon A) Temperature. B) Precipitation

With regard to organic matter (OM) content, Atanasia once again exhibits the highest value (5.9%), while Huivulai displays the lowest value (4.5%) and Siari is situated between these two extremes with a value of 5.4%. The observed differences in organic matter content are statistically significant, as indicated by an F-value of 3.8 and a P-value of 0.001. This suggests that Atanasia may have a greater accumulation of plant matter or organic remains in its sediments. Moreover, the textural composition of the sediments exhibits notable variations in the proportions of sand, silt, and clay between the sites. The highest sand content is observed in Huivulai, at 68.9%, indicating a coarser and less water-retentive sediment. In contrast, Siari has the highest silt content at 35.4%, which may contribute to a higher moisture-holding capacity. Conversely, Atanasia exhibits the highest clay content at 33.6%, indicating a finer and stickier texture. These textural differences are significant in the case of sand ($F = 19$, $P < 0.05$) and silt ($F = 26$, $P < 0.05$), but not so much in the case of clay, where the differences do not reach statistical significance ($F = 1.8$, $P = 0.08$) (Fig. 5). The combined results indicate that the sediments from Atanasia are denser, more acidic and richer in organic matter, with a more clayey texture. In contrast, the sediments from Huivulai are sandier, while those from Siari are siltier. These differences reflect environmental variations and may be due to differences in sediment source or water dynamics at these sites.

The total tree density is higher in Huivulai (2250 trees ha $^{-1}$) compared to Siari (1650 trees ha $^{-1}$) and Atanasia (1725 trees ha $^{-1}$). Furthermore, Huivulai has the highest density of *Laguncularia racemosa* (Lr) with 775 trees ha $^{-1}$, while Siari has the highest density of *Rhizophora mangle* (Rm) with 325 trees ha $^{-1}$. Atanasia exhibits a lower diversity of species, with a dominant presence of *Avicennia germinans* (Ag) and *Laguncularia racemosa* (Lr), but no *Rhizophora mangle* (Rm). In terms of total basal area, Siari has the largest value at 66.9 m² ha^{-1}, driven primarily by *Laguncularia racemosa* (42.3 m² ha^{-1}), in comparison to Huivulai and Atanasia, which have significantly smaller values. The basal areas were found to be 23.8 m² ha^(−1) and 25.7 m² ha^(−1), respectively. It is noteworthy that at Huivulai and Atanasia, *Rhizophora mangle* is completely absent, which has the effect of reducing the basal area at these sites. The mean height of trees at the Siari site is the highest, with the *Laguncularia racemosa* reaching 5.3 m in height. In comparison, the trees at the Huivulai and Atanasia sites are shorter, with an average height of 3.4 m and 2.6 m for Lr, respectively. The species *Avicennia germinans* is observed to have a consistently greater height at Siari (4.2 m) in comparison to the other sites. The highest diameter at breast height (Dbh) for *Laguncularia racemosa* is observed at Siari (15.1 cm), indicating that trees at this site are more robust. In contrast, the Dbh of Lr at Huivulai and Atanasia is significantly lower, with values of 7.8 cm and 8.4 cm, respectively. The presence of *Rhizophora mangle* is exclusive to Siari, with a diameter at breast height (Dbh) of 6.5 cm (Table 6). These findings suggest that Siari not only exhibits the highest diversity of mangrove species but also the largest and most robust trees, as evidenced by its greater basal area, height, and Dbh. In contrast, Huivulai and Atanasia display a less diverse structure and smaller trees, with a notable absence of *Rhizophora mangle* at these sites.

Table 4. Physical Chemistry of Surface and Interstitial Water.

		Siari	Huivulai	Atanasia	Range	F	P
pH	S	8.2±0.2	8.3±0.2	8.6±0.2	8.2-8.6	0.5	0.8
	I	7.5±0.2	7.4±0.2	7.4±0.1	7.3-7.8	1.5	0.43
Temp	S	26±1.5	30±2.3	29.5±1	25.3-30	0.8	0.6
	I	25.7±1.1	25.8±1.3	26±1.2	25-26	0.2	0.99
Cond	S	51.1±2.5	53.4±2.8	57.8±1.6	48.4-57.8	1.4	0.18
	I	52.3±2.1	56.1±1.4	62.2±2.2	52.3-68.7	9.4	<0.05
Sal	S	33.8±1.7	35.1±2	38.4±1.3	31.3-37.1	1.7	0.12
	I	34.1±1.4	37±0.9	42.3±1.8	34.1-46.9	11	<0.05
ORP	S	-140.6±24.3	-161.2±29.2	-164.3±18.5	-140.6 to -238.5	1.1	0.38
	I	-250.4±35.7	-374.7±40.7	-324.5±16.2	-250.4 to -380.4	2.4	0.02

Table 5. Sediment physicochemicals

		Siari	Huivulai	Atanasia	F	p
	pH	6.6±0.1	6.1±0.1	5.9±0.2	4.1	0.03
	BD	0.73±0.03	0.74±0.02	0.81±0.03	14	<0.05
	OM	5.4±0.3	4.5±0.4	5.9±0.5	3.8	0.001
Texture	Sand	21.2±3.1	68.9±1.8	35.8±3.1	19	<0.05
	Silt	35.4±2.2	7.6±1.2	30.6±2.1	26	<0.05
	Clay	43.4±2.3	23.4±0.9	33.6±1.8	1.8	0.08

Table 6. Structural attributes of the mangrove forest in Bahía del Tóbari.

		Tóbari		
		Siari	Huivulai	Atanasia
Density	Ag	1175	1475	1525
(Trees·ha^{-1})	Lr	150	775	200
	Rm	325	0	0
	Total	1650	2250	1725
Basal area	Ag	15.3±1.7	12±1.4	10.2±0.9
(m^{2}·ha^{-1})	Lr	42.3±2.9	11.8±1.8	15.5±0.1
	Rm	9.3±1.4	0	0
	Total	66.9±6.0	23.8±3.2	25.7±1.0
Height	Ag	4.2±0.2	3±0.1	2.5±0
(m)	Lr	5.3±0.6	3.4±0.1	2.6±0.1
	Rm	3.4±0.3	0	0
Dbh	Ag	8.6±0.6	7.4±0.5	6.9±0.3
(cm)	Lr	15.1±1.6	7.8±0.9	8.4±0.2
	Rm	6.5±0.6	0	0

DISCUSSION

Relationship between FT-IR bands and mangrove environmental variables: El the canonical correspondence analysis shown in Figure 2, a relationship can be observed between the spectral bands obtained by FT-IR and the environmental variables of the mangroves, which is fundamental to understanding the adaptation of these plants to their environment. Figure 2 reveals that temperature correlates closely with band 1 (3323-3398 cm-1), which represents N-H and O-H stretches associated with carbohydrates, proteins, alcohols and phenolic compounds. This finding indicates that elevated temperatures may modify the concentration of these compounds, which in turn could influence the generation of reactive oxygen species (ROS) and the ability of plants to resist heat stress stress (Zandalinas *et al.*, 2022). Tables 4 and 5 demonstrate how alterations in water properties and sediment characteristics can intensify the impact of thermal stress on plants, influencing nutrient availability and water quality. These changes in the environment contribute to the observed alterations in plant growth, development, physiology, and performance, as detailed in Table 6. In order to cope with these alterations, plants implement a range of metabolic strategies, including the production of compatible solutes, which stabilise proteins and cellular structures, and the modification of the antioxidant system in order to maintain redox balance and cellular homeostasis (Hasanuzzaman *et al*., 2013; Valliyodan and Nguyen, 2006). These adaptive mechanisms are of vital importance for the survival and success of mangroves subjected to heat stress, thereby emphasising the necessity of elucidating the interactions between soil chemistry, environmental conditions and plant physiological responses (Pimentel-Victório *et al*., 2023; Ramírez-Rodríguez *et al*., 2005).

There is a correlation between salinity and soil bulk density with band 4 (1614-1655 cm-1) of the spectrum (Table 1 and Fig. 2), which corresponds to the C=O stretching of amide 1. This is a marker for proteins and pectin. This correlation indicates that both proteins and pectin are essential for maintaining cell structure under conditions of high salinity, thereby contributing to the stability of plant cells in saline environments. Furthermore, salinity is linked to band 3 (1717-1729 cm-1), which reflects the stretching of saturated C=O esters, associated with phospholipids and cholesterol esters. This suggests that salinity may impact the lipid composition of cell membranes. A comparative study between a halophyte (*Suaeda salsa*) and a glycophyte (*Spinacia oleracea*) exposed to different NaCl gradients revealed that salinity alters the composition and extensibility of root cell walls. The presence of elevated concentrations of NaCl has been demonstrated to increase the rigidity of cell walls, thereby enhancing cell stability in the context of salt stress. Furthermore, it was observed that pectin and cellulose form essential mechanical lattices in cell walls in these environments (Liu *et al*., 2022). In coffee plants (*Coffea arabica*), changes in pectin and hemicelluloses were observed, with an increase in uronic acid, monolignol and lignin in all fractions analyzed. At the cellular level, irregularities were observed in the cytoplasm and chloroplasts, including the absence of starch granule (de Lima *et al*., 2014). Prior research on the impact of salinity on the proteins of marine organisms indicates a tendency for these proteins to form supercoiled regions with a high content of acidic residues. Amino acids such as leucine, methionine and lysine have been observed to have a high preference for α-helices, while acidic residues (aspartic acid) are more commonly found in supercoiled regions (Paul *et al*., 2008). This is due to the under-representation of hydrophobic and positively charged amino acids, and the over-representation of acidic residues (Fleming and Richards, 2000). Research has demonstrated that halophilic proteins have a more flexible and ordered secondary structure to avoid aggregation and loss of function in saline environments. The flexibility of the protein is also influenced by the high occurrence of negatively charged residues, particularly aspartate (Paul *et al*., 2008; TeykİN *et al*., 2022). In response to salt stress, plants express genes that encode proteins to help them tolerate stress. An increase in salinity leads to an increase in phosphoglycerate kinase in chloroplasts, which may indicate an increase in photosynthetic carbon uptake (Reyes *et al*., 2008). An example of this is the overexpression of the ATP synthase subunit β to support the energetic requirements of secondary transport mechanisms (Cornah *et al*., 2003).

The application of spectral analysis has enabled the establishment of a correlation between the FT-IR bands and specific environmental parameters. This facilitates the interpretation of how the chemical characteristics of mangrove leaves respond to factors such as salinity and soil density. Bands 3 and 4 of the FT-IR spectra confirm the occurrence of structural and compositional changes in plants subjected to salt stress, thereby underscoring the impact of salinity on both the cell wall matrix and cell membrane composition. These changes serve to reinforce cell stability and adaptation in saline environments. The data presented in Table 6 demonstrate that alterations in salinity and other environmental factors exert a profound impact on not only the biochemical composition of plants, but also their physical structure. For instance, alterations in tree density and basal area demonstrate the capacity of the mangrove forest to adapt to elevated salinity levels and fluctuations in nutrient supply, as evidenced by the correlation between spectral and physicochemical data (Chowdhury *et al*., 2019).

A strong correlation is evident between surface soil pH and band 7 (1130-1165 cm-1), which is associated with C=O stretching of polysaccharides. This relationship indicates that pH may be influencing the concentration of polysaccharides in the soil, which could potentially affect soil structure and nutrient availability. In contrast, subsurface soil pH is related to band 6 (1203-1237 cm-1), which corresponds to C-O stretching. This indicates the presence of lignin and xylans. This indicates that subsurface soil pH may be associated with more complex organic matter degradation, which has implications for carbon cycling and nutrient dynamics in mangroves (Kida and Fujitake, 2020). Conversely, the presence of organic matter in the soil is strongly correlated with band 5 (1462 cm-1), which corresponds to the OH-bending mode of cellulose. This observation indicates the existence of decaying plant matter. This emphasizes the significance of organic matter in the formation of mangrove soil structure and its interconnection with mangrove leaves, as cellulose represents a pivotal element of plant cell walls. Moreover, the correlation with band 8 (999-1103 cm-1), corresponding to the C-OH, C-C and C-H groups in pectin, indicates that organic matter also exerts an influence on the cell wall structure of plants, which could affect their capacity to resist environmental stress (Topală and Rusea, 2018).

At last, band 9 (815-884 cm-1), which is linked to C-O bending in cellulose, is associated with the pH of the interstitial soil. This suggests that pH may influence the stability of cellulose structures in soil roots, thereby affecting the structure of mangrove leaves as they attempt to adapt to adverse conditions. The results demonstrate that the chemical composition of mangrove leaves is significantly influenced by a range of environmental factors, including temperature, salinity, bulk density and soil pH. This underscores the biochemical adaptations that occur in this ecosystem in response to its environment, highlighting the importance of considering multiple environmental factors when studying mangrove ecology (Pimentel-Victório *et al*., 2023).

Leaves contain a complex matrix of organic compounds, and their FT-IR spectra exhibit distinctive spectral properties within the range of 4000 to 400 cm-1. The composition of a plant's leaves can provide valuable insight into both the plant's response to its environment and the ecological effects of that response. The biochemical changes observed in mangrove plants in Tobari lagoon manifest as distinctive vibrational patterns, which correspond to the functional groups present. These patterns result in the formation of spectral absorption features that serve as distinctive "fingerprints" for a multitude of compounds how anthocyanins and polyphenols (Silverstein *et al*., 2005; Topala and Tataru, 2018).

It is crucial to acknowledge that the secondary structure of proteins represents the most stable spatial configuration they can assume under specific conditions. This structural form is directly contingent upon the amino acid sequence of the protein in question. It is therefore unsurprising that proteins of the same species can have different amino acid sequences (Cuevas-Velázquez and Covarrubias-Robles, 2011). The secondary structure of the protein is directly influenced by the environment (Zhong and Johnson Jr, 1992). Environmental changes, including those affecting factors such as pollution, pH, salinity and bulk density, can prompt the plant to adapt and alter the secondary structure of proteins in order to maintain normal functioning (Hollóczki and Gehrke, 2019).

Protein structure in mangrove leaves and its relationship with environmental conditions: The characterization of the predominant secondary structure of mangrove leaf proteins by FT-IR spectroscopy in the Amide I region indicates a prevalence of the beta-sheet conformation in several samples from different plants and locations. This indicates that the proteins in mangroves exhibit structural conservation, with slight variations dependent on the specific site and species. Wavelengths associated with beta-sheets range from 1615 cm-1 to 1635 cm-1, indicating that subtle differences in protein conformation are influenced by the local environment. , for example, in the case of Rm. Furthermore, the presence of alpha-helices was identified, exhibiting a distinctive band at 1655 cm-1. This helical structure indicates that the protein in question exhibits a more ordered and stable conformation than that observed in other samples. Similar outcomes have been documented in mollusc proteins, wherein temperature and pH modify the secondary structure of proteins, thereby conferring enhanced resilience to environmental fluctuations (Cadena-Cadena *et al*., 2019). In contrast, the proteins of Lr. Siari and AG. Siari exhibited disordered structures, with bands located at 1646 cm^{-1} and 1643 cm^{-1}, respectively. The appearance of disordered structures in these proteins indicates a more flexible and less regular conformation. These variations in protein structure are not merely technical, but reflect specific adaptations to the environmental conditions of the mangroves in which they are found (Bhat *et al*., 2020; Topală and Rusea, 2018).

The difference in secondary structure observed between proteins is a consequence of the impact of the physico-chemical environment on protein conformation. These environments encompass factors such as nutrient availability, salinity and temperature, which can influence protein structure and, consequently, protein function (Matarredona *et al*., 2020). The adaptability of proteins to these conditions indicates that, in addition to their basic structural function, they may play a pivotal role in the adaptive response to local environmental conditions. For instance, alterations in protein secondary structure encompass fluctuations in α-helix and β-fold composition, which are associated with shifts in enzyme activity (Wang *et al*., 2024). This indicates that modifications in protein secondary structure may be pivotal for mangrove survival and functionality in diverse environmental contexts.

These findings have significant implications for our understanding of how mangrove organisms adapt to their specific habitats, even when they are in the same area (Fig. 1). The structural diversity observed in the proteins not only provides insight into the biochemical adaptations of these organisms, but may also offer clues about their ability to cope and thrive in extreme environmental conditions (El Sabagh *et al*., 2021). The proteins found in mangrove ecosystems within the Tóbari Lagoon demonstrate a sophisticated interplay between biological entities and their surrounding environment. This underscores the significance of biochemical adaptations in ensuring survival and ecological functionality.

The physico-chemical differences between surface and interstitial water: The pH, which varies significantly between surface and interstitial water, not only reflects differences in acidity, but also has direct implications for the solubility and availability of essential nutrients, such as phosphorus and micronutrients, which are sensitive to changes in pH. A reduction in pH levels within the interstitial water may facilitate the availability of specific nutrients, yet simultaneously enhance the toxicity of heavy metals, which in turn may impact the health of mangrove flora and fauna. (de Oliveira-Barbirato *et al.*, 2021). The thermal stability of interstitial water, in contrast to the greater temperature variability in surface water, indicates that the subsurface may function as a thermal buffer, providing a more constant environment for benthic organisms and plant roots. Such stability is of great consequence for the survival of species that are sensitive to thermal fluctuations, particularly in an environment that is exposed to temperature extremes (Ferreira *et al.*, 2024).

The lower Oxide Reduction Potential (ORP) observed in interstitial water is indicative of more reducing conditions, which is a characteristic feature of anaerobic environments such as mangrove soils. These conditions foster anaerobic microbial activity, including the decomposition of organic matter and the production of gases such as hydrogen sulphide (Shilla and Shilla, 2020). The occurrence of anaerobic decomposition processes not only influences soil chemistry but also affects water quality and the availability of essential plant nutrients, including nitrogen and Sulphur (Paśmionka *et al.*, 2021) .

The variability in sediment bulk density observed in mangrove ecosystems highlights the presence of soil heterogeneity, which in turn gives rise to the formation of a diverse array of microhabitats (Gloria *et al.*, 2024). The compaction of sediments may impede water infiltration and restrict soil oxygenation, which could in turn affect root activity and microbial communities (Das *et al.*, 2023). Conversely, soils of a less dense and more porous nature facilitate greater water and air circulation, which may enhance aerobic microbial activity and nutrient mineralisation. (Das *et al.*, 2023; Gloria *et al.*, 2024)

The collective impact of these differences in physico-chemical properties on mangrove ecology is profound, influencing species distribution and diversity, trophic interactions and biogeochemical cycling. It is therefore essential to understand these differences in order to effectively manage and conserve mangroves, as each microhabitat within the mangrove may require specific conservation and restoration strategies, considering its uniqueness and its role in the overall ecosystem.

Conclusions: The chemical composition of mangrove leaves, as determined by FT-IR, demonstrates a robust interrelationship with mangrove environmental variables, including temperature, salinity, pH, and soil bulk density. These environmental factors exert a significant influence on the molecular structures present in the mangrove soil, as evidenced by the spectral bands that have been detected. The observed correlations indicate that the physico-chemical environment of the mangrove affects not only the availability of nutrients, but also the composition and stability of organic and inorganic compounds in the ecosystem. The pH of the soil, both surface and interstitial, plays a pivotal role in regulating chemical structures and organic matter degradation. This may have implications for biodiversity and the adaptation processes of mangrove species to local conditions. Additionally, salinity and bulk density are strongly correlated with specific compounds, including proteins and polysaccharides. This suggests that these factors may be associated with plant health and resilience in high-salinity environments. Moreover, the variations in protein structure observed in mangrove leaves demonstrate the adaptive capacity of these plants in response to alterations in environmental conditions. The prevalence of specific secondary structures, such as beta sheets, coupled with the detection of alpha-helices and disordered conformations in select samples, points towards a structural adaptation that may be associated with resilience to environmental stress and the capacity of plants to thrive in diverse microenvironments within the mangrove ecosystem. Taken together, these results emphasize the intricate interplay between environmental conditions and mangrove chemistry, and highlight the value of FT-IR spectroscopy as a means of elucidating these processes. The ability of mangrove plants to adapt to fluctuations in the physico-chemical milieu is critical to their persistence, and understanding these adaptations at the molecular level may provide new insights for the conservation and management of these fragile ecosystems.

Author Contributions: F.C.C and J.R.T conceived and designed research. J. R.T and F.J.C.L. conducted experiments. J.L.A.M and F.J.C.L. analyzed data. L.A.M and I.M.F wrote the manuscript. All authors interpreted the data and approved the final version.

Conflicts of Interest: “The authors declare no conflict of interest.”

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