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## Mangrove forest structure, water quality, and carbon storage at Palmares, Northern Pacific coast of Costa Rica

Jimena Samper-Villarreal<sup>1\*</sup>;  <http://orcid.org/0000-0002-7513-7293>

Adriana Omaña-Angulo<sup>1</sup>;  <http://orcid.org/0009-0008-9580-4541>

Jorge Cortés<sup>1,2</sup>;  <https://orcid.org/0000-0001-7004-8649>

1. Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Universidad de Costa Rica, 11501-2060 San José, Costa Rica; jimena.sampervillarreal@ucr.ac.cr (\*Correspondence), adrianaomana@gmail.com
2. Escuela de Biología, Universidad de Costa Rica, 11501-2060 San José, Costa Rica; jorge.cortes@ucr.ac.cr

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### ABSTRACT

**Introduction:** Mangroves provide many ecosystem services, yet they continue to be degraded and decline in numbers. Effective management strategies need baseline information to assess habitat condition and potential decline. In Costa Rica, mangroves on the North Pacific are the least studied.

**Objective:** To provide the first characterization of forest structure and carbon content of the Palmares mangrove. **Methods:** A total of 58 square plots (5 × 5 m) were sampled between March 2022 and April 2023. In each plot, mangrove species, stem height, and circumference were quantified. Samples were collected to estimate interstitial water salinity, fine root content, and sediment grain size, bulk density, and carbon content. Mangrove biomass and organic carbon (OC) were calculated using allometric equations. Water quality was assessed at six sites in the main channel during the dry and rainy seasons of 2023.

**Results:** Six mangrove species were identified at Palmares. *Rhizophora* spp. (55 % of plots) and *Avicennia* spp. (29 %) were the most abundant, while *Laguncularia* and *Conocarpus* were rare. Average tree height was 8 ± 7 m, width 11 ± 12 cm, and density 1 833 ± 1 757 stems ha<sup>-1</sup>. *Rhizophora* spp. were taller and wider than *Avicennia* spp. Interstitial water salinity at Palmares was 34 ± 14, which was higher during the dry season and in *Avicennia* spp. plots. Sediment was mainly composed of silt-clay (52 %), which was higher in *Rhizophora* spp. plots. Sediment bulk density was 0.8 ± 0.3 g cm<sup>-3</sup> and fine roots < 1 %. Above-ground biomass OC averaged 224 ± 335 Mg ha<sup>-1</sup> and was higher in *Rhizophora* spp. plots. Sediment OC was 8 ± 3 % and inorganic carbon 3 ± 1 %. OC was higher in sediment of *Rhizophora* spp., higher silt-clay, larger mangroves, and lower densities. There was no clear pattern of variation in water parameters along the main channel.

**Conclusions:** This first characterization of Palmares mangrove can serve as a baseline for further studies and effective management and conservation strategies.

**Key words:** Eastern Tropical Pacific; Bahía Huevos; blue carbon; carbon sequestration.

### RESUMEN

#### Estructura del bosque de manglar, calidad del agua y almacenamiento de carbono en Palmares, Pacífico Norte de Costa Rica

**Introducción:** Los manglares brindan muchos servicios ecosistémicos, pero continúan degradándose y desapareciendo. Las estrategias de manejo efectivas requieren de información de línea base para evaluar la condición del hábitat y su posible deterioro. En Costa Rica, los manglares del Pacífico Norte son los menos estudiados.



**Objetivo:** Realizar la primera caracterización de la estructura del bosque y el contenido de carbono en el manglar de Palmares.

**Métodos:** Se muestrearon en total 58 parcelas cuadradas (5 × 5 m) entre marzo de 2022 y abril de 2023. En cada parcela, se anotó la especie de mangle y se midió la altura y circunferencia del tallo. Se recolectaron muestras para estimar la salinidad del agua intersticial, el contenido de raíces finas, así como el tamaño de grano, la densidad aparente y el contenido de carbono del sedimento. Se calculó la biomasa del manglar y el carbono orgánico (OC) utilizando ecuaciones alométricas. Se evaluó la calidad del agua en seis sitios dentro del canal principal, durante la estación seca y la estación lluviosa de 2023.

**Resultados:** Se encontraron seis especies de mangle en Palmares. *Rhizophora* spp. (55 % de las parcelas) y *Avicennia* spp. (29 %) fueron las más abundantes, mientras que *Laguncularia* y *Conocarpus* fueron poco comunes. La altura promedio de los árboles fue de 8 ± 7 m, el diámetro de 11 ± 12 cm y la densidad de 1 833 ± 1 757 tallos ha<sup>-1</sup>. *Rhizophora* spp. fueron más altos y anchos que *Avicennia* spp. La salinidad del agua intersticial en Palmares fue de 34 ± 14, con valores más altos durante la estación seca y en las parcelas de *Avicennia* spp. El sedimento estaba compuesto principalmente por limo-arcilla (52 %), con mayor proporción en las parcelas de *Rhizophora* spp. La densidad aparente del sedimento fue de 0.8 ± 0.3 g cm<sup>-3</sup> y el contenido de raíces finas fue < 1 %. El promedio de OC en la biomasa aérea fue 224 ± 335 Mg ha<sup>-1</sup>, siendo mayor en las parcelas de *Rhizophora* spp. El contenido de OC en el sedimento fue de 8 ± 3 % y el de carbono inorgánico fue 3 ± 1 %. OC en el sedimento fue mayor en las parcelas de *Rhizophora* spp., con mayor proporción de limo-arcilla, árboles más grandes y menor densidad. No se observó un patrón claro de variación en los parámetros del agua a lo largo del canal principal.

**Conclusiones:** Esta primera caracterización del manglar de Palmares puede servir como una línea base para futuros estudios y para estrategias efectivas de manejo y conservación.

**Palabras clave:** Pacífico Tropical Oriental; Bahía Huevos; carbono azul; secuestro de carbono.

## INTRODUCTION

Mangroves are very important habitats found in tropical and subtropical coastlines. These coastal forests provide us with many ecosystem benefits, including coastal protection, sediment stabilization, nutrient assimilation, and nursery habitat for many ecologically and commercially important species (Kathiresan & Bingham, 2001). Mangroves are also a Blue Carbon sink, storing large amounts of organic carbon in their biomass and sediment for up to thousands of years (McLeod et al., 2011). Like many other coastal habitats, mangroves are highly threatened and great extensions of them have been degraded or lost, mainly due to anthropogenic activities (Valiela et al., 2001). Key stressors to mangrove ecosystems include changes in land use for agriculture, salt production, and shrimp aquaculture, as well as coastal development, deforestation, sediment compaction, and pollution (Leal & Spalding, 2024). Recently, it has been reported that more than half of mangroves worldwide are threatened, with 20 % at high risk of collapse and categorized as Endangered or Critically Endangered

Ecosystems (International Union for Conservation of Nature [IUCN], 2024). As mangrove forests are degraded or lost they can no longer provide the same benefits and can also potentially shift from carbon sinks to carbon sources (Donato et al., 2011; Kauffman et al., 2017).

Understanding the current habitat condition of mangroves is important for effective management, conservation, and restoration initiatives. Costa Rican mangroves are fully protected by law as public lands, yet they are still under anthropogenic pressure with marked challenges for their effective management (Pizarro et al., 2004; Sistema Nacional de Áreas de Conservación [SINAC], 2019). In Costa Rica, 99 % of mangroves are located on the Pacific coast, mainly due to a more rugged coastline providing abundant calmer areas where mangroves can grow, along with a much larger tidal range and corresponding landward intrusion of salt water compared to the Caribbean coast (Cortés, 2016a; Cortés, 2016b; Pizarro & Angulo, 1994).

In the Pacific of Costa Rica, mangroves have previously been categorized into those

found in the North, Central, and South sectors of this coast, based on precipitation intensity and spatial patterns (Jiménez & Soto, 1985). There is greater yearly precipitation in the Southern Pacific, with this region containing the most extensive and most structurally complex mangrove in Costa Rica, the Terraba-Sierpe mangrove (Jiménez & Soto, 1985; Mainardi, 1996; Pizarro & Angulo, 1994). This mangrove and those in the Gulf of Nicoya in the Central Pacific have been extensively studied, with many long-term mangrove monitoring stations found within them (SINAC, 2023). In contrast, the Northern Pacific coast of Costa Rica is a drier region, and mangroves are generally considered to be composed of shorter stands (Jiménez & Soto, 1985; Zamora-Trejos & Cortés, 2009). Nonetheless, taller stands can also be found in the North Pacific, including of *Pelliciera rhizophorae* Triana & Planch. (Loria-Naranjo et al., 2015; Samper-Villarreal et al., 2012). This mangrove species has a very limited global distribution and a declining population, classifying it as Vulnerable in the IUCN Red List (Rueda et al., 2024).

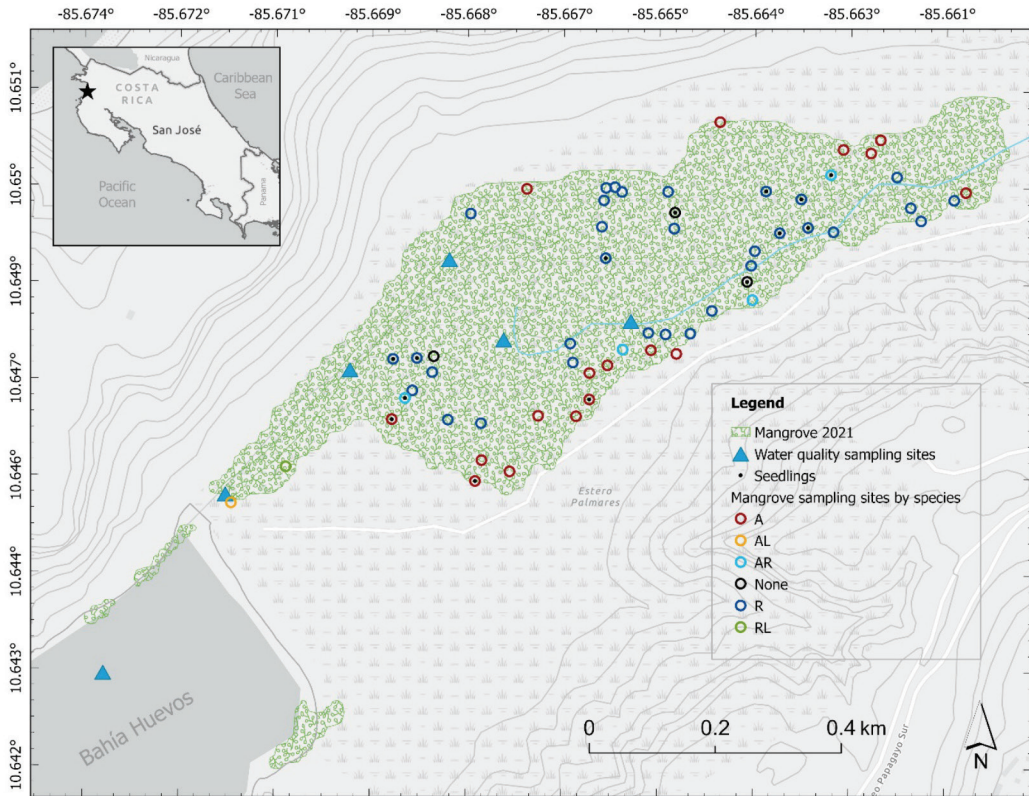
Overall, mangroves in the North Pacific of Costa Rica have been studied less than those in the Central and South Pacific of the country (Zamora-Trejos & Cortés, 2009). Given the importance of these coastal habitats and their continued degradation and loss due to anthropogenic activity it is key to have a solid understanding of mangrove composition in Costa Rica. In this study, we aimed to provide the first characterization of forest structure and carbon content in the Palmares mangrove on the Northern Pacific coast of Costa Rica to provide baseline information for future initiatives.

## MATERIALS AND METHODS

**Study site:** The Palmares mangrove (10°38'52.45" N & 85°40'5.92" W) is located within Bahía Huevos on the Northern Pacific coast of Costa Rica (Fig. 1). This region is characterized by a dry season from December to April and a wet season from May to November, with total precipitation between 1 400 and

1 500 mm yr<sup>-1</sup> (Córdoba-Muñoz et al., 1998). During most of the year, marine water temperature in this region is similar to and can go beyond 30 °C. However, wind action drives coastal upwelling during the dry season, causing colder and nutrient rich marine water to rise to the surface and water temperatures to decrease to ~ 18 °C (Alfaro & Cortés, 2012). The Palmares mangrove has ~ 1.5 km maximum length and 0.5 km maximum width. In a neighboring bay, mangrove forest structure and cover change over time were reported for Iguanita and Panamá (Benavides-Varela et al., 2016; Samper-Villarreal et al., 2012). In contrast, there are no previous studies for the Palmares mangrove, except for limited basic information on its mangrove and associated flora and fauna (Zamora-Trejos & Cortés, 2009). Five mangrove species have been previously reported to occur in the Palmares mangrove: *Rhizophora mangle* L., *Rhizophora racemosa* G. Mey., *Avicennia germinans* (L.) L., *Avicennia bicolor* Standl., and *Conocarpus erectus* L. (Córdoba-Muñoz et al., 1998). For this mangrove, reported ecosystem benefits include flood, storm and coastline protection, water filtration, nutrient recycling, sediment capture, and recreational and fishing activities (Córdoba-Muñoz et al., 1998). At the same time, reported stressors include tourism and excessive fishing (Córdoba-Muñoz et al., 1998). As all mangroves in Costa Rica, the Palmares mangrove is protected by law (Pizarro et al., 2004), yet there is currently no management plan in place.

**Sampling design:** Mangrove forest structure, sediment grain size, carbon content, and interstitial water salinity were assessed in a total of 58 square plots (Fig. 1). Site selection was based on preliminary aerial imagery and field observations. Forest structure sampling sites were distributed throughout the mangrove, within logistical constraints, to encompass the full range of variations noted in species composition, transitional and marginal vegetation, potential variations in salinity and tidal inundation at increasing distances from the main channel or river, and in seaward (mouth of



**Fig. 1.** Field sampling sites at the Palmares mangrove in Bahía Huevos, Northern Pacific coast of Costa Rica (the black star in the insert indicates the location of the mangrove on this coast). A = *Avicennia*. L = *Laguncularia*. R = *Rhizophora*. Mangrove layer source: Sistema Nacional de Áreas de Conservación (SINAC, 2021).

the estuary) to landward areas (Northeastern section of the mangrove). This forest structure sampling approach was intentional to sample the various strata within the mangrove and to support a detailed mapping effort (Pérez-Briceño et al. In prep.). Mangrove forest structure and carbon content can be assessed using sampling plots of various shapes and dimensions, each with their own strengths and challenges (Kauffman & Donato, 2012; Howard et al., 2014). Square plots with 5 m sides were selected for this study based on preliminary field observations and to aid the complementary mapping effort. This shape and size of sampling plot have been previously applied to assess forest structure in mangroves on the Pacific coast of Costa Rica (e.g. Cambroner-Bolaños et al., 2025; Samper-Villarreal & Silva-Benavides, 2015).

Mangrove forest structure, sediment grain size, carbon content, and interstitial water salinity were assessed in each plot. Following sampling, distance of each plot from the main channel or river and from the mouth of the estuary was estimated using ArcGIS Pro (v.3.1.0). Mangrove plots were sampled at low tide in subsequent field outings between March 2022 and April 2023. Additionally, water quality was assessed during high tide at six sites along the main channel (Fig. 1), once during the dry season (February 3<sup>rd</sup>) and a second time during the rainy season (October 21<sup>st</sup>) of 2023. Total water depth ranged between 1.5 m and 2.1 m.

**Forest structure:** Within each plot, circumference was measured for all living mangroves at approximately 1.3 m above sediment

level, except for *Rhizophora* spp. for which it was measured above the highest prop root (Cintrón & Schaeffer-Novelli, 1984). When tree trunks were naturally divided beneath 1.3 m in height, each stem was measured independently (Cintrón & Schaeffer-Novelli, 1984; Howard et al., 2014; Smith III, 1992). Circumference was divided by  $\pi$  to calculate diameter at breast height (DBH). Circumference and height were measured for each tree stem  $\geq 2.5$  cm. Tree height was measured directly using a tape measure for trees under 2 m tall, while height for taller trees was measured using a clinometer (Suunto). Height was estimated by comparing the trees to known heights nearby in a limited number of instances when neither of the previous measuring techniques were logistically feasible. Mangrove seedlings were counted within a 1 x 1 m quadrat within each plot, and circumference and height measured using a tape measure (except in two plots where only height was measured). Trees and seedlings were identified to the lowest possible taxon in the field. As *Rhizophora mangle* and *Rhizophora racemosa* were challenging to differentiate in the field, unless they were flowering at the time of sampling, they have been grouped together as *Rhizophora* spp. for subsequent analyses (Fromard et al., 1998).

Total above ground mangrove biomass (kg) per plot was calculated using allometric equations from those available for the species in the region (Cifuentes-Jara et al., 2018; Kauffman & Donato, 2012). Above ground biomass was

calculated using equations developed for mangroves on the mainland in the tropical nation of French Guiana (Fromard et al., 1998) (Table 1). Only one stem of *A. bicolor* was found within the plots with a DBH of 17.2 cm, therefore we applied the same equation as for *A. germinans* of DBH > 4 cm (Table 1). DBH of 3 % of stems were smaller and 8 % larger than the DBH range used for the development of the above ground biomass allometric equation (Fromard et al., 1998). The general equation for below ground biomass estimation was used (Table 1), due to a lack of detailed equations available for each species in the region (Kauffman & Donato, 2012). Main tree stem wood densities ( $\text{g cm}^{-3}$ ) used for this calculation were 0.830 for *Rhizophora*, 0.661 for *Avicennia*, and 0.600 for *Laguncularia* (Kauffman & Donato, 2012).

**Interstitial salinity, sediment grain size, and fine roots:** Salinity was measured from ~ 30 ml water samples collected by digging a hole at the center of each plot (up to 25 cm depth) and allowing it to fill with interstitial water. In three of the plots interstitial water was not available for sampling at these sediment depths. Interstitial salinity was measured using a manual refractometer (ATAGO). A sediment sample of approximately 100 g was collected manually in each plot and dried at 60 °C for 48 hr or until constant dry weight. Each dried sediment sample was weighed, wet sieved through a 0.063 mm pore sieve to remove fine sediment and dried again. Mangrove roots were manually

**Table 1**  
Allometric equations used for mangrove biomass estimation at Palmares.

Mangrove species	Allometric relationship	Equation mean DBH range	Reference
Above ground biomass			
<i>Rhizophora</i> spp. ( <i>R. mangle</i> / <i>R. racemosa</i> )	$B = 0.1282 \times (\text{DBH})^{2.60}$	1.3 ± 0.3 to 32.0	(Fromard et al., 1998)
<i>Avicennia germinans</i> (1 cm < DBH < 4 cm)	$B = 0.2004 \times (\text{DBH})^{2.10}$	1.5 ± 0.2 to 3.5 ± 0.2	(Fromard et al., 1998)
<i>Avicennia germinans</i> (DBH > 4 cm)	$B = 0.1400 \times (\text{DBH})^{2.40}$	4.5 ± 0.2 to 42.0	(Fromard et al., 1998)
<i>Laguncularia racemosa</i>	$B = 0.1023 \times (\text{DBH})^{2.50}$	1.5 ± 0.3 to 9.6	(Fromard et al., 1998)
Below ground biomass			
All species	$B = 0.199 \times (d)^{0.899} \times (\text{DBH})^{2.22}$	5.0 to 48.9 <sup>a</sup>	(Komiya et al., 2005)

B: Biomass (kg). DBH: Diameter at Breast Height (cm). d: wood density ( $\text{g cm}^{-3}$ ). <sup>a</sup> For 104 tree samples of which 26 unspecified DBH were used to estimate root weight.



separated during wet sieving, dried at 60 °C for 48 hr or until constant dry weight and weighed. The retained sediment was dried and sieved using an automatic shaker at 90 rpm for 15 min. Sieve pore sizes were 4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm. Following wet sieving and removal of mangrove roots, fine sediment content was calculated as the weight difference between the initial dry weight of the sample and the final dry weight of the sieved sediment > 0.063 mm.

**Surficial sediment and biomass carbon content:** In each plot a 30 ml surficial sediment sample was collected using a 60 ml (2.8 cm diameter, 4.5 cm depth) plastic syringe (Howard et al., 2014). Samples were dried at 60 °C for 48 hr or until constant dry weight and weighed to quantify sediment dry bulk density. Dried sediment samples were homogenized using a mortar and pestle. Fine roots were not removed prior to homogenization. The Loss on Ignition method was used to quantify organic and inorganic matter within each sample (Heiri et al., 2001). Briefly, a subsample of approximately 1.5 g was placed into pre-weighed dried crucibles. These were placed in a muffle furnace for four hours at 550 °C, allowed to cool in a desiccator and weighed. Then, they were placed in the furnace for two hours at 950 °C, allowed to cool and weighed again. Organic carbon (OC) percentage was calculated using the relationship for mangroves  $y = 0.415x + 2.8857$  (Howard et al., 2014). Inorganic carbon (IC) percentage was calculated by multiplying by 1.36 (Heiri et al., 2001). OC concentrations of 47 % for above ground biomass (Cifuentes-Jara et al., 2018) and 39 % for below ground biomass (Kauffman & Donato, 2012) were used to convert biomass to above and below ground OC biomass per plot ( $\text{kg m}^{-2}$ ) and converted to megagrams per hectare ( $\text{Mg OC ha}^{-1}$ ).

**Water quality:** Vertical Secchi depth was measured once at each site on the shaded side of the boat. Secchi depth was determined as the distance at which the black and white components of the Secchi disk were no longer discernable upon submersion in the water

column. A 3.8 l subsurface water sample was collected in a dark polypropylene bottle. Water temperature was measured immediately in the field by placing a manual thermometer in each bottle. Salinity was measured using a manual refractometer from a subsample of each water bottle. Approximately 1.3 l of each water sample was filtered using a vacuum pump through 47 mm glass microfiber filters with 60  $\mu\text{m}$  pores. For suspended matter (SM) quantification, filters were previously dried at 60 °C for 48 hr or until constant dry weight and weighed prior to filtration. After filtration, filters were dried again and reweighed. SM was calculated as the filter weight variation related to the total water volume sampled. Chlorophyll concentration was quantified by placing an additional 60  $\mu\text{m}$  pore sieve at the top of the filtering system. Chlorophyll-a concentrations were measured using a UV-Visible Spectrophotometer (Thermo Scientific) and relating it to the total filtered water volume. Filtered water from chlorophyll was retained to quantify water nutrient (phosphate, silicate, ammonium, nitrite, and nitrate) concentrations using a Flow Injection Autoanalyzer (Lachat Instruments) and relating it to the total volume of water filtered.

**Data analyses:** Variables were compared between plots with only *Avicennia* spp. and those with only *Rhizophora* spp. and between dry and rainy seasons using the Student t-test. Pearson correlations were used to assess relationships between variables. All analyses were done in R v.4.4.2 (R Core Team, 2024). Results are presented as mean  $\pm$  standard deviation.

## RESULTS

**Forest structure:** Six mangrove species were identified at Palmares: *Rhizophora mangle* and *Rhizophora racemosa* (Rhizophoraceae, hereafter referred to as *Rhizophora*), *Avicennia germinans* and *Avicennia bicolor* (Acanthaceae, hereafter *Avicennia*), *Laguncularia racemosa* (L.) L. (hereafter *Laguncularia*) and *Conocarpus erectus* (Combretaceae). Of these species, *C. erectus* was only found outside of sampled

plots. *Avicennia* was usually encountered farther away from the water channels, decreasing in size the farther away. Larger *Rhizophora* trees were found closer to the main channels, with a transition zone of smaller and denser *Rhizophora* between the *Avicennia* and *Rhizophora* (Fig. 2). A total of 179 living mangrove trees were found within the plots, corresponding to 252 tree stems. Of the total number of stems, 56 % were *Avicennia*, 42 % *Rhizophora*, and only 2 % were *Laguncularia*. At Palmares, 55 % of plots only contained *Rhizophora*, 29 % only had *Avicennia*, 7 % had both *Rhizophora* and *Avicennia*, 2% contained both *Rhizophora* and *Laguncularia*, while 2 % had *Avicennia* and *Laguncularia* (Fig. 1). The remaining plots did not have any living mangrove trees and consisted mainly of only prop roots, non-mangrove vegetation or salt pans.

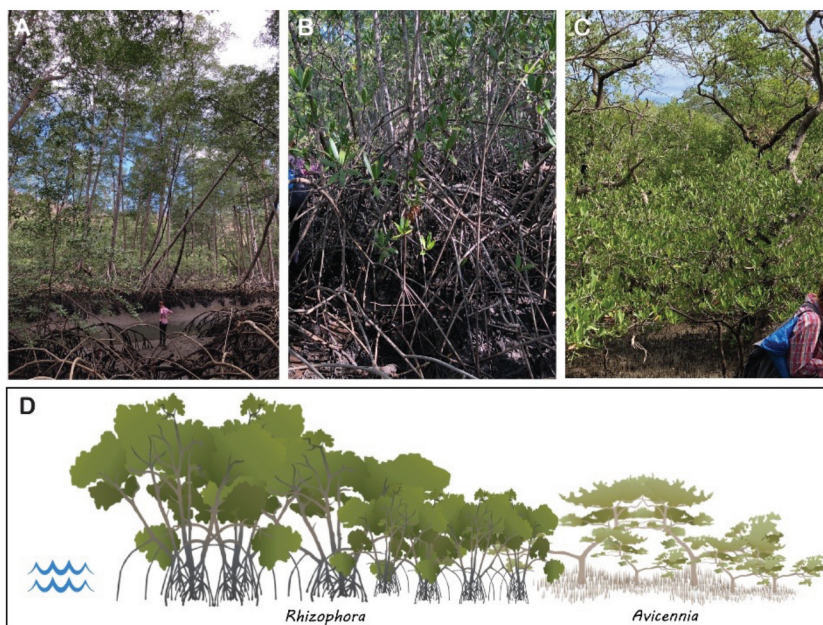
Tree stem height for the mangrove stand was  $7.9 \pm 7.4$  m (min. 1.4 m to max. 40 m) and DBH was  $11.0 \pm 12.3$  cm (min. 0.8 to max. 63.7 cm). There were greater frequencies of

stems at lower DBH (Table 2) with great height and DBH variability among species (Table 3). *Rhizophora* stems were taller and thicker than *Avicennia* (respectively  $t = -6.6$ ,  $p < 0.001$  &  $t = -5.2$ ,  $p < 0.001$ , Fig. 3). *Rhizophora* stem height was  $11.5 \pm 9.5$  m ( $n = 106$ ) and DBH of  $15.7 \pm 15.0$  cm ( $n = 107$ ). *Avicennia* stems were  $5.2 \pm 3.5$  m tall and  $7.4 \pm 8.3$  cm ( $n = 141$ ) wide. Meanwhile, *Laguncularia* had stems of  $10.9 \pm 0.6$  m in height and  $12.0 \pm 3.3$  cm ( $n = 4$ )

**Table 2**

Stem frequency by Diameter at Breast Height (DBH) category per genus at Palmares mangrove.

DBH (cm)	<i>Avicennia</i>	<i>Rhizophora</i>	<i>Laguncularia</i>
< 10	107	52	1
10-20	21	19	3
20-30	10	20	0
30-40	2	7	0
40-50	0	5	0
50-60	1	2	0
60-70	0	2	0



**Fig. 2.** Field photos from Palmares mangrove. **A.** Tall *Rhizophora* near the water channel. **B.** Shorter and denser *Rhizophora* further from the water channel. **C.** *Avicennia* further away from the channel. **D.** Diagram of the species and height pattern noted in the field (Ian Symbols).



Table 3

Stem height and Diameter at Breast Height (DBH) at Palmares mangrove by distance from main channel or river (D).

	Distance (m)				
	< 50	100	150	200	250
All					
Height (m)	10.7 ± 8.7	6.5 ± 5.9	8.6 ± 8.2	6.3 ± 4.9	3.6 ± 1.7
DBH (cm)	15.4 ± 15.4	8.4 ± 9.1	11.8 ± 11.0	10.0 ± 12.0	4.0 ± 4.3
n	83	93	36	21	19
<i>Rhizophora</i>					
Height (m)	12.2 ± 9.8	10.2 ± 10.3	10.6 ± 9.2	12.0 ± 5.5	na
DBH (cm)	17.5 ± 17.2	12.2 ± 13.2	14.5 ± 11.9	12.3 ± 5.6	na
n	59	17	25	6	0
<i>Avicennia</i>					
Height (m)	6.3 ± 3.0	5.6 ± 4.1	4.2 ± 2.6	4.1 ± 2.2	3.6 ± 1.7
DBH (cm)	9.8 ± 8.6	7.5 ± 7.8	5.6 ± 4.9	9.0 ± 13.8	4.0 ± 4.3
n	20	76	11	15	19

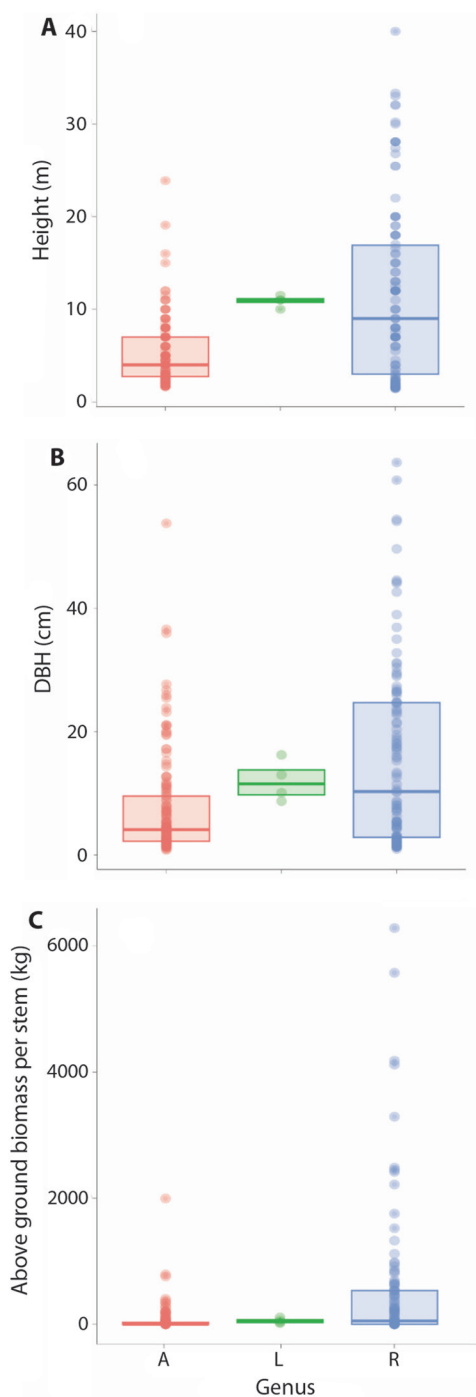
na = does not apply.

diameter. Mangrove stem density was  $1\,833 \pm 1\,757$  stems  $\text{ha}^{-1}$ , with a maximum of  $8\,800$  stems  $\text{ha}^{-1}$ . Basal area at Palmares was highly variable with an average of  $38.9 \pm 39.2$   $\text{m}^2$   $\text{ha}^{-1}$  for plots of all species compositions,  $48.5 \pm 46.4$   $\text{m}^2$   $\text{ha}^{-1}$  for *Rhizophora* plots, and  $29.5 \pm 21.7$   $\text{m}^2$   $\text{ha}^{-1}$  for plots with only *Avicennia*. There was no correlation between basal area and stem density in plots composed of only *Rhizophora* ( $r = -0.08$ ,  $p = 0.7$ ) or *Avicennia* ( $r = -0.4$ ,  $p = 0.2$ , Fig. 4). Basal area was not correlated with distance from the mouth of the estuary ( $r = -0.01$ ,  $p = 0.9$ ) yet it decreased marginally at greater distances from the main channel or river ( $r = -0.2$ ,  $p = 0.07$ , Fig. 4).

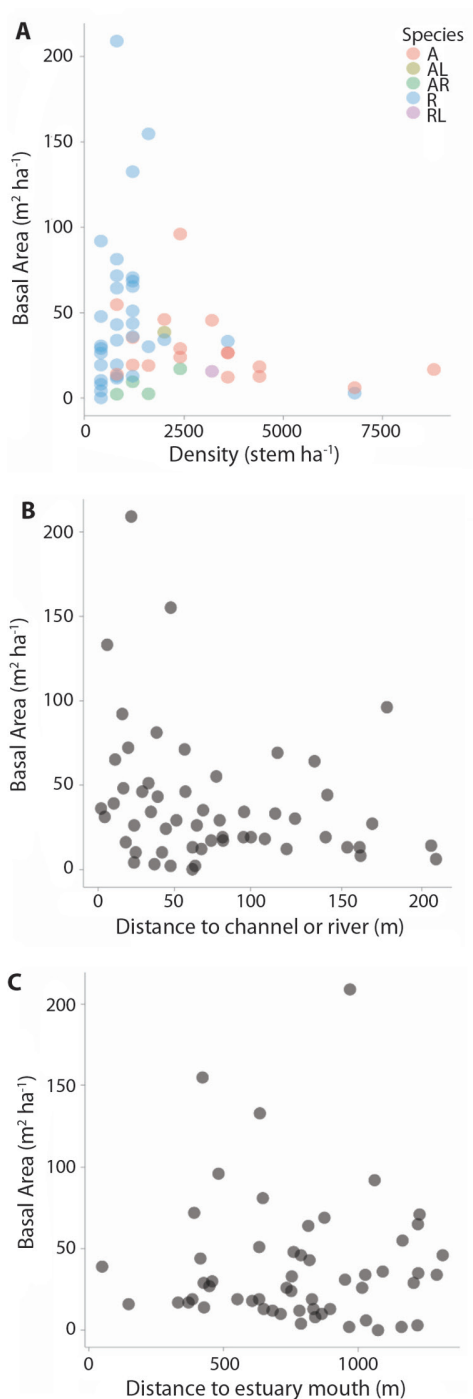
At Palmares, above ground biomass was  $475.9 \pm 712.2$   $\text{Mg}$   $\text{ha}^{-1}$  (76.4 % of plots < 500  $\text{Mg}$   $\text{ha}^{-1}$ ) and below ground biomass was  $166.6 \pm 199.5$   $\text{Mg}$   $\text{ha}^{-1}$  (83 % of plots had < 300  $\text{Mg}$   $\text{ha}^{-1}$ ). Above ground biomass was higher in *Rhizophora* stems ( $528.5 \pm 1\,096.9$  kg) compared to *Avicennia* stems ( $61.4 \pm 201.9$  kg,  $t = -4.3$ ,  $p < 0.001$ , Fig. 3). *Rhizophora* below ground biomass per stem ( $170.4 \pm 308.7$  kg) was also higher than for *Avicennia* stems ( $32.2 \pm 95.8$  kg,  $t = -4.5$ ,  $p < 0.001$ ). Seedlings were found in 24 % of sampling plots and at varying distances from the estuary mouth and from the main channel or river (Fig. 1). Ten plots only

had *Rhizophora* seedlings, three plots only had *Avicennia* seedlings, and one plot had both *Rhizophora* and *Avicennia*. Seedling density was  $4 \pm 5$  seedling  $\text{m}^{-2}$  when found, with a minimum of 1 and a maximum of 22 seedlings  $\text{m}^{-2}$ . Seedling diameter was  $1.0 \pm 0.5$  cm and height  $50.3 \pm 37.9$  cm.

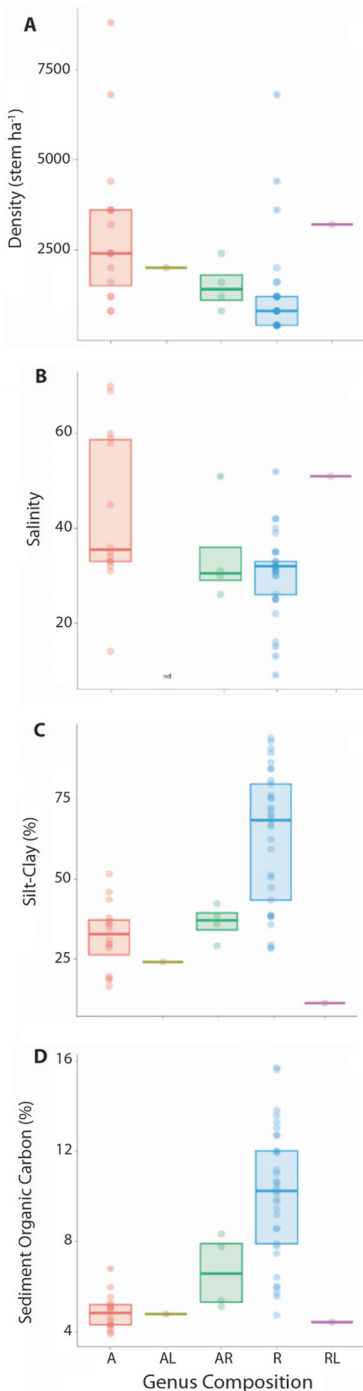
**Carbon storage in biomass and surficial sediment:** Above ground biomass OC in the mangrove stand was  $223.7 \pm 334.7$   $\text{Mg}$   $\text{ha}^{-1}$ . Mangrove above ground biomass OC was < 250  $\text{Mg}$   $\text{ha}^{-1}$  in 76.4 % of plots and ranged from a minimum of 0.05  $\text{Mg}$   $\text{ha}^{-1}$  to a maximum of 1 833  $\text{Mg}$   $\text{ha}^{-1}$  (only in one plot). Below ground biomass OC was  $65.0 \pm 77.8$   $\text{Mg}$   $\text{ha}^{-1}$ , with 80 % of plots having < 100  $\text{Mg}$   $\text{ha}^{-1}$  and ranging from a minimum of 0.04 to a maximum of 419  $\text{Mg}$   $\text{ha}^{-1}$  (one plot). Organic matter (OM) in surficial sediment was 13.1 ± 8.3 % (ranging from a minimum of 2.5 % to a maximum of 30.9 %). Sediment OC content was  $8.3 \pm 3.4$  % (3.9 to 15.7 %). Sediment OC content in plots composed of *Rhizophora* ( $10.1 \pm 2.9$  %,  $n = 33$ ) was higher compared to those of *Avicennia* ( $4.9 \pm 0.8$  %,  $n = 16$ ,  $t = -9.6$ ,  $p < 0.001$ , Fig. 5). Sediment OC was greater in plots with higher silt-clay content ( $r = 0.85$ ,  $p < 0.001$ ), taller stems ( $r = 0.42$ ,  $p < 0.01$ ), wider



**Fig. 3.** Mangrove tree stem metrics by genus at Palmares mangrove, Northern Pacific coast of Costa Rica. **A.** Average height. **B.** Diameter at Breast Height-DBH. **C.** Above ground biomass per stem A = *Avicennia*. L = *Laguncularia*. R = *Rhizophora*.



**Fig. 4.** Mangrove basal area at Palmares mangrove, Northern Pacific coast of Costa Rica in reference to: **A.** Stem density per species composition, **B.** Distance from main channel or river, and **C.** Distance from mouth of the estuary. A = *Avicennia*. L = *Laguncularia*. R = *Rhizophora*.



**Fig. 5.** Mangrove parameters by plot genus composition at Palmares, Northern Pacific coast of Costa Rica. **A.** Average tree stem density. **B.** Interstitial salinity. **C.** Sediment silt-clay. **D.** Sediment organic carbon content. A = *Avicennia*. L = *Laguncularia*. R = *Rhizophora*.

DBH ( $r = 0.36$ ,  $p < 0.01$ ), and with lower stem densities ( $r = -0.43$ ,  $p < 0.001$ , Fig. 6). Meanwhile, sediment OC did not vary with interstitial water salinity ( $r = -0.1$ ,  $p = 0.4$ ). Sediment inorganic carbon (IC) content was  $3.1 \pm 1.2$  % (ranging from a minimum of 0.9 to a maximum of 5.3 %). While IC content was low overall it was higher in *Rhizophora* plots ( $3.7 \pm 0.9$  %) compared to *Avicennia* plots ( $2.0 \pm 0.8$  %,  $t = -6.6$ ,  $p < 0.001$ ). Mangrove fine roots consisted of  $0.8 \pm 1.2$  % ( $n = 58$ ).

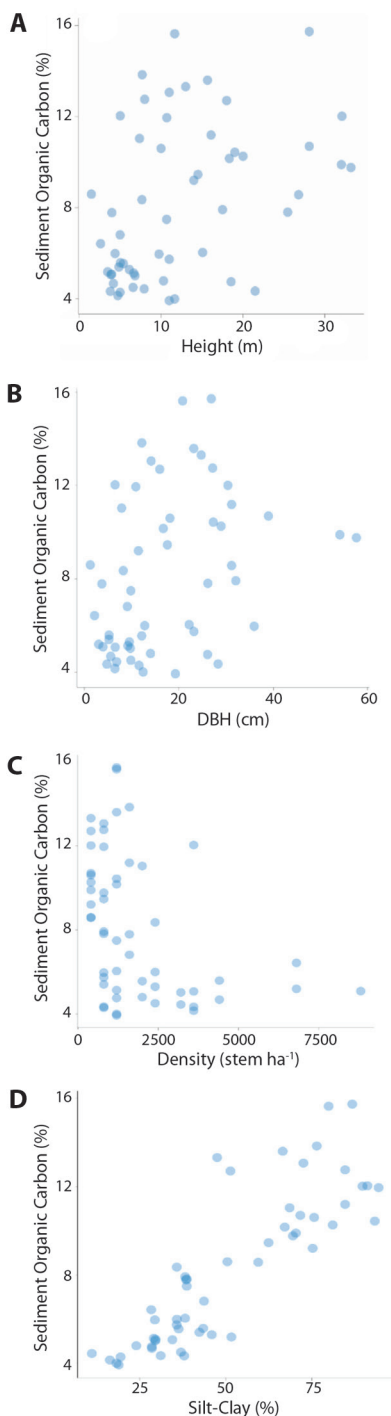
**Interstitial salinity:** Mean interstitial water salinity at Palmares was  $34 \pm 14$  ( $n = 55$ ). Salinity was higher at greater distances from the main channel or river ( $r = 0.4$ ,  $p < 0.01$ ). Salinity during the dry season ( $48 \pm 22$ ,  $n = 12$ ) was higher than during the rainy season ( $31 \pm 10$ ,  $n = 43$ ,  $t = 5.1$ ,  $p < 0.001$ ). Plots with only *Avicennia* had higher salinity ( $43.5 \pm 16.8$ ,  $n = 14$ ) than plots with only *Rhizophora* ( $30.9 \pm 9.2$ ,  $n = 34$ ,  $t = 2.6$ ,  $p = 0.02$ , Fig. 5).

**Sediment grain size and bulk density:** Mangrove sediment at Palmares mainly consisted of fine sediment particles (52 % silt-clay) and sand of various sizes (Table 4). Silt-clay content was higher in plots with only *Rhizophora* ( $63.3 \pm 20.8$  %) compared to those with only *Avicennia* ( $32.2 \pm 10.3$  %,  $t = -7.0$ ,  $p < 0.001$ , Fig. 5). Surficial sediment bulk density at Palmares was  $0.8 \pm 0.3$  g cm<sup>-3</sup>.

**Channel water column quality:** Secchi depth and chlorophyll concentration were higher in the dry season (Table 5). In contrast, water temperature and suspended matter were higher in the rainy season (Table 5). There was no variation in water column salinity or nutrient concentrations between samplings (Table 5). There was no clear pattern of variation in water parameters among the six water quality stations along the main channel.

## DISCUSION

This study provides the first characterization of the Palmares mangrove in Bahía



**Fig. 6.** Sediment organic carbon content related to multiple parameters per plot at Palmares mangrove, Northern Pacific coast of Costa Rica. **A.** Average stem height. **B.** Diameter at Breast Height-DBH. **C.** Stem density. **D.** Silt-clay content.

Huevos, Northern Pacific coast of Costa Rica. A total of six out of seven mangrove species in Costa Rica were found in this forest (Jiménez & Soto, 1985; Pizarro et al., 2004). This is the first report of *Laguncularia racemosa* at Palmares, most likely due to the detailed sampling carried out in this study compared to the limited previous reports of species present and how scarce this species is within the stand. This adds one more species to those previously reported for this mangrove (Córdoba-Muñoz et al., 1998). The only Costa Rican mangrove species absent at Palmares was *Pelliciera rhizophorae* Triana & Planch. (Tetrameristaceae), commonly known as the “tea mangrove” or “mangle piñuela” with characteristic trunk and flowers (Duke, 2020; Pizarro et al., 2004). This species has a limited distribution worldwide with decreasing populations, therefore it is characterized as Vulnerable in the IUCN Red List (Rueda et al., 2024). In the Pacific, this species is found in coastlines from Ecuador to the Northern Pacific coast of Costa Rica (Loría-Naranjo et al., 2015; Rueda et al., 2024). The distribution of this species in Costa Rica extends further North than Palmares, up to Santa Elena and Potrero Grande mangroves (Loría-Naranjo et al., 2015). Meanwhile, the “buttonwood mangrove” (*C. erectus*) was only found outside of the sampled plots and was not commonly sighted. This species along with the “white mangrove” *L. racemosa*, were very rare at Palmares, which was mainly composed of *Rhizophora* spp. and *Avicennia* spp. The limited presence of *Conocarpus* and *Laguncularia* and lack of *Pelliciera*, may be linked to higher interstitial salinity at Palmares, as these are mangrove species that are more commonly found at lower salinities (Jiménez, 1984; Lonard et al., 2021a; Lonard et al., 2021b; Loría-Naranjo et al., 2015). Similar to Palmares, nearby mangrove stands mainly composed of *Rhizophora* are found at Iguanita, Potrero Grande, and Santa Elena (Loría-Naranjo et al., 2015; Samper-Villarreal et al., 2012). Meanwhile, nearby mangroves that are mainly composed of *Avicennia* include Panama and Puerto Soley (Samper-Villarreal et al., 2012; Soto & Jiménez, 1982). Many factors influence species distribution within mangrove



**Table 4**  
Sediment grain size percentage at Palmares mangrove.

Sediment grain size	Percentage
Pebbles (> 4.0 mm)	1.3 ± 2.2
Very fine pebbles (2-4 mm)	1.4 ± 1.4
Very coarse sand (1-2 mm)	2.0 ± 1.9
Coarse sand (0.5-1 mm)	3.3 ± 2.6
Medium Sand (0.25-0.5 mm)	10.3 ± 8.3
Fine sand (0.125-0.25 mm)	16.7 ± 11.1
Very fine sand (0.063-0.125 mm)	13.3 ± 7.8
Silt-clay (< 0.063 mm)	51.6 ± 23.5

forests, including interstitial salinity, tidal and precipitation regimes, topography, sediment composition and compaction, nutrient concentrations and seed or propagule dispersal (Hogarth, 1999; Kathiresan & Bigman, 2001).

The vegetative distribution at Palmares was composed overall of taller *Rhizophora* spp. near the water channels, transitioning into smaller and denser *Rhizophora* spp. farther away, followed by *Avicennia* spp. that declined in height farther inland (Fig. 1 and Fig. 2). This pattern coincides with previously reported distributions for mangroves in the North Pacific of Costa Rica and has been linked to variations in interstitial salinity (Jiménez & Soto, 1985; Soto & Jiménez, 1982). At Palmares, *Rhizophora* trees were larger and contained more biomass than *Avicennia*. *Rhizophora* trees were also larger than *Avicennia* at Morales in the Central Pacific (Cambronero-Bolaños et al., 2025).

Factors potentially leading to marked height reduction in mangroves include increased salinity, diminished tidal regimen, higher sediment compaction, variations in nutrient availability, and diminished oxygenation (Hogarth, 1999; Kathiresan & Bigman, 2001; Naidoo, 2006). At greater distances from the main channel at Palmares, interstitial salinity was higher and basal area lower. This variation with distance from the main channel indicates a decrease in tidal inundation further inland, most likely related to variations in microtopography as the entire mangrove is categorized at an elevation of 0 m.a.s.l. (Fig. 1). Associated variations in environmental conditions including salinity, desiccation, and sediment compaction could also explain the high heterogeneity in the findings. While mangroves are able to tolerate wide salinity ranges, the various species have different mechanisms and thresholds of salinity tolerance (Parida & Jha, 2010). *Rhizophora* thrives in areas near sea water with frequent water exchange, while *Avicennia* is able to grow in areas with salinities higher than sea water (Morrow & Nickerson, 1973). The salinity of the main channel at Palmares (30) was five units below the seawater average of 35. Thereby, larger *Rhizophora* trees near the channel may be linked to lower interstitial salinities. While *Avicennia* mangroves are able to withstand higher salinities than other species, their morphologic and physiological stress does increase with salinity, leading to diminished heights

**Table 5**

Water quality sampled during the dry (February) and wet (October) season in the main channel at Palmares mangrove.

Water column parameter	February 2023	October 2023	statistical analysis
Secchi depth (m)	1.2 ± 0.2	0.8 ± 0.1	t = 4.2, p < 0.01
Temperature (°C)	26 ± 1	30 ± 1	t = -9.6, p < 0.001
Salinity	29 ± 2	30 ± 0	t = -1.6, p = 0.2
Chlorophyll (mg m <sup>-3</sup> )	3.0 ± 1.0	1.5 ± 0.3	t = 3.6, p = 0.01
SM (mg l <sup>-1</sup> )	23.8 ± 9.4	44.4 ± 9.5	t = -3.8, p < 0.01
Phosphate (μmol l <sup>-1</sup> )	0.4 ± 0.04	0.4 ± 0.05	t = -1.9, p = 0.1
Silicate (μmol l <sup>-1</sup> )	18.2 ± 8.7	25.8 ± 11.5	t = -1.3, p = 0.2
Ammonium (μmol l <sup>-1</sup> )	7.0 ± 1.7	8.4 ± 1.4	t = -1.6, p = 0.1
Nitrite (μmol l <sup>-1</sup> )	3.7 ± 0.4	3.6 ± 0.9	t = 0.2, p = 0.8
Nitrate (μmol l <sup>-1</sup> )	4.7 ± 2.0	4.4 ± 0.4	t = 0.3, p = 0.8

SM = Suspended matter.

and increasing their probability to perish (Naidoo, 2006; Suárez & Medina, 2005). Further North at Puerto Soley, mangrove tree height diminishes at higher salinities (Soto & Jiménez, 1982). At Palmares, stress from higher salinities would explain both the greater abundance of *Avicennia* farther from the channels and their decreasing height farther inland. However, future studies on channel and interstitial water along with microtopography should be conducted at higher temporal and spatial resolutions in this mangrove.

High salinity is not uncommon in mangroves on the North Pacific of Costa Rica, which is a region with much lower precipitation and a marked dry season. In the North Pacific coast, high salinity is considered a stress factor that leads to decreased structural complexity of the mangrove forests (Jiménez & Soto,

1985). Salinities at Palmares were similar to other mangroves in the North and Central Pacific coast of Costa Rica, with the exceptional high salinity of 155 at Puerto Soley (Table 6). Palmares salinities were higher than in the South Pacific coast of Costa Rica and magnitudes higher than in the Caribbean coast (Table 6), which fits with overall precipitation patterns (Jiménez & Soto, 1985). Therefore, while the Palmares mangrove is under salinity stress, which may be exacerbated in the dry season when salinities are higher at this site, mangroves further North have much higher interstitial salinities (Jiménez & Soto, 1985; Soto & Jiménez, 1982). Average stem height at Palmares was similar to other mangroves overall, yet maximum heights at Palmares of 40 m were comparable to the highest mangroves reported for Costa Rica at Iguanita and

**Table 6**

Summary of forest structure variables and interstitial salinity of multiple mangroves stands in Costa Rica. Maximum reported values are presented in parentheses.

Coordinates	Location <sup>ref</sup>	Salinity	Height (m)	DBH (cm)	Density (stems ha <sup>-1</sup> )
	<i>North Pacific</i>				
11°03'32" N & 85°40'00" W*	Puerto Soley <sup>ab</sup>	(155)	5.5 to 17.3 (19)	nd	1 708
10°54'49" N & 85°47'00" W*	Santa Elena <sup>c</sup>	32 ± 2	7.0 ± 0.4 (13)	13.9 ± 1.2 (39.2)	1 724
10°51'00" N & 85°48'00" W*	Potrero Grande <sup>c</sup>	31 ± 5	8.8 ± 0.6 (20)	16.1 ± 1.5 (77.4)	1 120
10°45'N & 85°40' W	Santa Rosa <sup>d</sup>	nd	10.0	nd	1 050
<b>10°38'09" N &amp; 85°40'03" W*</b>	Palmares <sup>x</sup>	<b>34 ± 14 (70)</b>	<b>7.9 ± 7.4 (40)</b>	<b>11.0 ± 12.3 (63.7)</b>	<b>1 833 ± 1 757 (8 800)</b>
10°37'05" N & 85°37'07" W*	Iguanita <sup>e</sup>	36.3 ± 1.5 38.2 ± 3.3	17.1 ± 1.3 (40.7)	18.1 ± 1.6 (53.2)	672
10°35'25" N & 85°39'56" W*	Panamá <sup>e</sup>	nd	11.2 ± 0.4 (27.8)	16.1 ± 1.2 (125.8)	84
	<i>Central Pacific</i>				
10°05'32" N & 84°58'27" W	Morales <sup>f</sup>	42 ± 8 (58) 35 ± 12 (75)	5.4 ± 3.3	4.7 ± 4.2	4 288
09°58' N & 84°45' W	Barranca <sup>d</sup>	nd	9.5	nd	1 100
	<i>South Pacific</i>				
08°47' N & 83°29' W	Térraba-Sierpe <sup>ghi</sup>	27.1 ± 0.3 30.1 ± 0.3	23.5 to 33.7 (40)	9.9 ± 0.4 12.2 ± 0.5 14.7 ± 1.5	1 368 ± 87 1 409 ± 114 201 ± 57
	<i>Central Caribbean</i>				
10°00'23" N & 83°03'54" W	Moin <sup>di</sup>	nd	10.5 ± 2.6 & 16.0 (~ 18)	20.0 ± 1.6 (~ 60)	708 ± 151 & 1 137
	<i>Southern Caribbean</i>				
09°35'23" N & 82°35'54" W	Gandoca <sup>jk</sup>	8.2 ± 4.1 (14)	12.8 ± 2.6 (~ 21)	21.4 ± 1.5 (~ 80)	687 ± 66

\*Coordinate source: Zamora-Trejos & Cortés (2009). nd = no data. References: <sup>a</sup> Jiménez & Soto (1985); <sup>b</sup> Soto & Jiménez (1982); <sup>c</sup> Loría-Naranjo et al. (2015); <sup>d</sup> Pool et al. (1977); <sup>e</sup> Samper-Villarreal et al. (2012); <sup>f</sup> Cambronero-Bolaños et al. (2025); <sup>g</sup> Espinosa-Sepúlveda (1992); <sup>h</sup> Loría-Naranjo et al. (2019); <sup>i</sup> Silva-Benavides (2009); <sup>j</sup> Manrow-Villalobos & Vilchez-Alvarado (2012); <sup>k</sup> Cortés et al. (2010); <sup>x</sup> This study.



Térraba-Sierpe (Table 6). At Térraba-Sierpe in the South Pacific, mangroves can grow up to 40 m tall, which is linked to greater precipitation and diminished saline stress (Silva-Benavides, 2009). Meanwhile, the estimated maximum mangrove height for Costa Rica is 45.8 m and worldwide mangroves can grow to 65 m tall in equatorial Africa (Simard et al., 2019). The presence of taller trees at Palmares is most likely not linked to increased fresh water input and instead may be linked to hydrodynamic regime within Bahía Huevos. The Iguanita mangrove nearby also has very tall trees of up to 41 m and it is located in the inner region of Bahía Culebra (Samper-Villarreal et al., 2012). Nonetheless, mangrove height estimations in mangrove forests have many logistical challenges such as limited visibility of the tree base or canopy from greater distances and challenges in straight distance measurements among mangrove prop roots and stems which can lead to tree height miscalculations (Saliu et al., 2021). In mangroves, tree height measurements using clinometers can yield an 8 % error while tree height estimations based on comparison to known height (i.e. thumb and stick estimates) can yield up to 15 % error (Saliu et al., 2021). In contrast, tree circumference or diameter measurements are much more reliable. At Palmares, average stem widths were also similar to reported values and maximum values of 64 cm and were only surpassed by mangroves at Potrero Grande, Panamá, and Gandoca (Table 6). Meanwhile, stem densities were higher than reported for other mangroves except recently for Morales in the Central Pacific (Table 6). Higher stem densities at Palmares compared to other locations may be influenced by the methodology used, in which stems were measured independently when tree trunks divided beneath 1.3 m in height (Cintrón & Schaeffer-Novelli, 1984). Other potential confounding factors in comparisons among mangrove stands include variations in species compositions and inclusion of associates mangrove species in various studies at some sites (Manrow-Villalobos & Vilchez-Alvarado 2012; Pool et al., 1977). Furthermore, overall variability in geomorphic

and tidal conditions differ greatly between the Caribbean and Pacific coasts of Costa Rica and among the various mangrove stands along the Pacific coast.

Above ground biomass and corresponding OC estimates at Palmares were higher than at other locations yet there is great variability within the mangrove. At Palmares, above ground biomass was estimated as  $475.9 \pm 712.2$  Mg ha<sup>-1</sup> and above ground biomass OC was  $223.7 \pm 334.7$  Mg ha<sup>-1</sup>. These estimates are at the higher ranges compared to other locations around the globe, with above ground biomass estimates that can range from as little as 8 Mg ha<sup>-1</sup> up to around 460 Mg ha<sup>-1</sup> (Komiya et al., 2008). In the Caribbean of Costa Rica, where maximum mangrove heights are smaller and stands are less dense than Palmares, above ground biomass has been reported as 330.2 Mg ha<sup>-1</sup> at Gandoca and 257.1 Mg ha<sup>-1</sup> at Moín (Manrow-Villalobos & Vilchez-Alvarado, 2012). Compared to Palmares, in the Golfo de Nicoya at Morales, the above ground biomass was  $104 \pm 127$  Mg ha<sup>-1</sup> and organic carbon stored corresponding to  $48 \pm 59$  Mg ha<sup>-1</sup> applying similar allometric equations (Cambronero-Bolaños et al., 2025). Also, within the Golfo de Nicoya in the Central Pacific, mangroves dominated by *Rhizophora* with densities of up to 1 200 trees ha<sup>-1</sup> and heights of 10 m had above ground biomass OC of 106.6 Mg ha<sup>-1</sup> (Cordero-Murillo et al., 2023). Meanwhile, Térraba-Sierpe has above ground biomass OC reported as  $72.5 \pm 3.2$  Mg ha<sup>-1</sup>, ranging from 9 to 241 Mg ha<sup>-1</sup> and with no clear zonation pattern explaining the variation (Sabrina-Geppert, 2012). General zonation of mangroves in the Southern Pacific coast of Costa Rica is composed of smaller trees near the main channels and increasing heights further inland (Jiménez & Soto, 1985). At Térraba-Sierpe biomass OC assessments were carried out near the main channels (Sabrina-Geppert, 2012), therefore mangrove biomass values may potentially differ if taller trees are assessed in future studies. These studies were carried out in different climatic and geomorphological conditions, with greater precipitation in the Gulf of Nicoya and Térraba-Sierpe,

and limited tidal variation in the Caribbean coast (Jiménez & Soto, 1985; Cortés, 2016a; Cortés, 2016b). Beyond environmental setting, there are potential variations in biomass estimations that may be linked to the caveats in the use of different allometric equations.

Allometric equations are used to estimate biomass from diameter, height and wood density values instead of measuring mangrove biomass directly as this would be highly destructive to mangrove stands. Biomass OC is subsequently calculated from the biomass values obtained. Estimating mangrove biomass from allometric equations comes with limitations and potential issues. These issues are particularly relevant when the equations were developed from a limited number of samples or diameter classes or were developed for mangroves in other regions with potentially differing climates and geomorphological setting, or for different species than the ones being studied (see Adame et al., 2017; Chave et al., 2005; Chave et al., 2014; Chou et al., 2022; Komiyama et al., 2005; Komiyama et al., 2008;). Above ground biomass for Palmares was estimated using allometric equations developed specifically for mangroves in the tropics of French Guiana (Fromard et al., 1998) while other studies applied global allometric equations (Chave et al., 2005; Komiyama et al., 2005), and some included species associated with mangroves (Manrow-Villalobos & Vilchez-Alvarado, 2012). At Palmares, 8 % of stems had larger DBH than those used to develop the allometric equation in French Guiana (Fromard et al., 1998), potentially leading to an overestimation of biomass in larger DBH categories. In Terraba-Sierpe, biomass OC estimations varied depending on which allometric equation was used (Sabrina-Geppert, 2012). Another potential source of variation is the number of plots sampled with less than six individuals present, which can lead to unintended errors when extrapolating findings to the forest if only a limited number of plots were sampled or from only some of the forest strata. However, in this first descriptive characterization of Palmares, we carried out a highly intensive field campaign, sampling a total of 58 plots within

the various strata of a relatively small mangrove (~ 1.5 km x 0.5 km), therefore potential misinterpretation errors when extrapolating to the rest of the mangrove stand should be minimal. There are many caveats that should be taken into consideration when comparing forest structure and biomass among stands with varying species compositions, and of studies that applied different field methods, including those that sampled the entire stand width and those sampling only a limited number of sites or strata.

At Palmares, surficial sediment OC content was greater when silt-clay percentages were higher, trees were larger and had lower stem densities. A great number of biotic and abiotic factors influence OC storage in mangrove sediment, including salinity, geomorphology, temperature, species composition, and associated organisms (MacKenzie et al., 2021). Meanwhile, tree height, width and stand density are intercorrelated as mangrove tree stem diameter increases as the stand density decreases in mangrove forests (Cintrón & Schaeffer-Novelli, 1984). Sediment OC content was two times higher in *Rhizophora* plots (10 %) compared to *Avicennia* ones (5 %). This also coincides with *Rhizophora* plots having two times the amount of silt-clay compared to *Avicennia* plots (63 % and 32 % respectively). At Terraba-Sierpe, sediment OC content was 7.1 to 11.8 % and increased from the channel further inland, potentially linked to lower organic matter accumulation near the channel from tidal action (Sabrina-Geppert, 2012). In contrast to zonation patterns in the North Pacific of Costa Rica, at Terraba-Sierpe in the South Pacific trees are generally smaller closer to the channels and increase in height further inland (Jiménez & Soto, 1985). At Terraba-Sierpe, sediment OC content increased from 8.5 % in the top 15 cm to 10-11% further down the core (Sabrina-Geppert, 2012). Sediment organic matter at Palmares (maximum of 30.9 %) was higher than reported for Puerto Soley, where it ranged from 2.2 to 20.8 % and where the silt-clay content of 8.7-23.4 % was lower than at Palmares (Soto & Jiménez, 1982). Terraba-Sierpe, is



mostly composed of fine sediment particles and *Rhizophora* is found in finer sediment while *Avicennia* is found in coarser sediment (Barrantes-Leiva & Cerdas-Salas, 2015). Sediment bulk density at Palmares ( $0.8 \text{ g cm}^{-3}$ ) also appears to be slightly higher than at Morales in the Central Pacific ( $0.6 \text{ g cm}^{-3}$ ) (Cambronero-Bolaños et al., 2025), and higher than reported for Terraba-Sierpe in the South Pacific ( $0.4$  to  $0.5 \text{ g cm}^{-3}$ ) (Sabrina-Geppert, 2012). At Palmares, only surficial sediment samples were collected, and sediment OC pool estimation has not been carried out as part of this study. Samples to 1 m depth within the mangrove have been collected at Palmares to provide sediment OC stock estimates and assess variability along sediment profiles (Samper-Villarreal et al., In prep.).

The findings from this study at the Palmares mangrove provide a baseline for future studies and management initiatives. Mangroves provide many ecosystem services of high monetary worth in Costa Rica (Hernández-Blanco et al., 2018). These coastal wetlands are legally protected in the country, with many also located within protected areas (Pizarro et al., 2004). However, mangroves are still under great stress from anthropogenic activities on the Pacific coast of Costa Rica, and many of them have been degraded or lost (Pizarro et al., 2004). In contrast to the Iguanita mangrove nearby in Bahía Culebra (Samper-Villarreal et al., 2012), the Palmares mangrove is not located within a protect area. Nonetheless, the land surrounding the mangrove is part of a tourism development project, therefore access to Palmares is controlled and limits many usual threats to mangroves, such as mangrove deforestation. Potential threats to this mangrove noted in the field include lightning strikes, and potential hydrologic regime modifications that could lead to higher salinities and desiccation as several unvegetated salt pans were observed. Additionally, jet skis can leak fuel and oil into the air and water, can disturb, injure or kill wildlife, particularly at high speeds in shallow waters, and cause noise disturbance to wildlife in coastal environments (Davenport & Davenport, 2006). Detailed mapping and temporal

analysis of mangrove cover change over time is currently needed at Palmares (Pérez-Briceño, In Prep.). In nearby mangroves, detailed mapping of mangrove coverage over time revealed potential natural and anthropogenic barriers to mangrove landward migrations (Benavides-Varela et al., 2016). Furthermore, increasing sea level is one of the key stressors to mangroves (Gilman et al., 2008; Godoy & de-Lacerda, 2015). At this time, a detailed assessment of the migration potential of the Palmares mangrove in response to anticipated sea level rise is needed.

**Ethical statement:** The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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