



Research article

Morphoanatomic variation in tissues of *Rhizophora mangle* seedlings subjected to different saline regimes: cross-seeding experimentAlejandra Robles Sánchez^{a,c,*}, José Ernesto Mancera Pineda^a, Xavier Marquínez Casas^a, Jairo Humberto Medina Calderón^b^a Departamento de Biología, Facultad de Ciencias, Universidad Nacional de Colombia Sede Bogotá, Carrera 45 # 26-85, 11001, Colombia^b Universidad Nacional de Colombia Sede Caribe, San Andrés Isla, Carretera Circunvalar San Luis Free Town 52 - 44, 880008, Colombia^c Corporation Center of Excellence in Marine Sciences – CEMarin, Carrera 21 # 35-53, 111311, Colombia

ARTICLE INFO

Keywords:

Salinity
Hypodermis
Foliar mesophyll
Xylem vessels
Cavitation

ABSTRACT

Rhizophora mangle, one of the main neotropical mangrove species, has wide phenological variability associated with soil salinity. Since global warming is one of the main drivers of changes in salinity, understanding the influence of this variable at the species level would help improve the prediction of climate change in the ecological services provided by mangroves. To understand the physiological and/or anatomical responses to water stress generated by edaphic salinity and its relationship with phenological and structural diversity, we quantified the functional traits of leaf tissue subjected to a cross-seeding experiment between two forests with different ranges of natural salinity (0–18 PSU¹ and 20 to 70 PSU). A total of 180 propagules, 90 native and 90 from the other forest, were planted in each forest. Every three months for a year, soil salinity and growth, adaptability, and survival of propagules that were transformed into seedlings were measured. The traits evaluated between the two saline regimes presented significant differences, as stated in the working hypothesis. Likewise, there were modifications in the hypodermis and the xylem vessels in the exchanged seedlings, tissues related to water storage, and conduction. These responses allowed native euhaline forest seedlings to grow in oligohaline. The opposite occurred with seedlings originating in low salinities that did not survive in high salinities. Differences in adaptability between populations of *R. mangle* subjected to ranges of contrasting salinity may imply changes at the structural level, zoning, and abundance of the species front to the climate change processes.

1. Introduction

Rhizophora mangle, known as red mangrove, is widely distributed along the tropical and subtropical coasts of the Western Hemisphere (Arbeláez-Cortes et al., 2007), occupying the western coast of Africa between Angola and Mauritania. In America, it is widely distributed in the Caribbean from the Florida Peninsula to Brazil and on the Pacific from Mexico to the north coast of Chile (Arbeláez-Cortes et al., 2007). It is a pioneer species in ecological succession in mangrove forests (Davis, 1940), which can occur in two growth forms, tall and scrub plants, with stilt roots that allow aeration (Lugo and Snedaker, 1974; Ortíz Alvarez, 2010). *R. mangle* can grow at salinities ranging from 0 to 90‰ (Orihuela et al., 1991), given that it can maintain a high internal negative osmotic pressure, filtering salt absorption as it obtains fresh soil water (Scholander, 1968). There are differences at the physiological and

morphological levels in the two growth forms that may be due to fluctuations in salinity (Lin and da SL Sternberg, 1993).

Climate variability has a very significant control on mangrove productivity and landscape cover associated with changes in rainfall, humidity, sea level, and soil salinity (López-Medellín et al., 2011; Asbridge et al., 2016; Lovelock et al., 2017). Changes have been found in *R. mangle* at the physiological and anatomical level associated with the salinity gradient, such as its mechanism of exclusion of salt during water absorption (ultrafiltration at the roots), strong osmoregulation, ion compartmentalization in the leaves (Scholander, 1968; Werner and Stelzer, 1990) and increase in leaf thickness and the wet weight/dry weight ratio at sites of constantly high salinity (Camilleri and Ribí, 1983). In mangrove trees, there are changes in wood formation (Menezes et al., 2003) associated with water regimes, being more porous and less dense in the rainy season with greater availability of fresh water and less porous

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and denser in the dry season with higher interstitial salinity in the medium (Ramírez Correa et al., 2010). Regarding the changes in stomatal conductance and the relative content of water against two salinity ranges on San Andrés Island (Smith Channel Forest and Old Point Regional Mangrove Park-OPRMP), Rodríguez-Rodríguez et al. (2018) determined that stomatal conductance presented an inverse relationship with the saline range, where the lowest average values were reported in the highest salinity forest (PRMOP), while the highest values were found in the lowest salinity forest (Smith Channel). In the case of relative water content, this value was much higher for individuals who were under low salinity conditions. These morphoanatomical and physiological changes in the species caused by salinity are evidence of its wide phenological variability, as this variability is affected by the action of environmental factors (Mehlig, 2006).

In mangrove and glycophyte species, salinity, as an abiotic stress factor, generates changes at a physiological and morphological level, such as a reduction in stomatal conductance, reduction in the CO₂ uptake rate, decrease in the transpiration rate, and an increase in xylem stress, modification of succulence in the leaf, stomata that vary in number and size, increase in cuticle thickness, early lignification, development of tylose, inhibition of differentiation and modifications in the number and diameter of xylem vessels (Poljakoff-Mayber, 1975; Ball and Farquhar, 1984; Aziz and Khan, 2001; Parida and Jha, 2010), affecting the growth and metabolism of individuals (Ball, 2002), generating plants with shrub morphology under extremely adverse conditions (Feller, 1995).

Salinity is also closely related to the water use efficiency, the rate of CO₂ assimilation, and stomatal conductance in mangroves (Hao et al., 2009; Rodríguez-Rodríguez et al., 2018; Lopes et al., 2019), so it is expected that this abiotic factor, together with the availability of water can influence the zoning, structural development, and composition of mangrove communities (Lugo and Snedaker, 1974; Mancera-Pineda et al., 2009). Therefore, various studies have focused on the effect of salinity on mangrove growth and development (Melcher et al., 2001; Ewers et al., 2004; Vovides et al., 2014; Komiyama et al., 2019); however, few investigations have focused on the morphoanatomic adaptations or functional traits that mangrove species generate against this environmental factor (e.g., the study by Arrivabene et al. 2014 about functional traits in the leaf of *A. schaueriana*, *L. racemosa* and *R. mangle* where the influence of salinity on water storage was determined). This investigation was raised to improve knowledge about the variation in functional traits of *R. mangle* as a function of changes in interstitial salinity and the implications that can be generated at a structural level both at population and community levels in the mangrove forests of the insular Caribbean.

The expected consequences of global warming include alterations in rainfall patterns and a higher frequency of El Niño Southern oscillation-ENSO cold and warm extreme events (Cai et al., 2015; Chen et al., 2017). Therefore, global warming is one of the main drivers of changes in soil salinity in mangrove forests. Therefore, it is important to understand how a possible increase in interstitial salinity caused by climate change affects mangrove species and the goods and services they provide. The aim was to determine the morphoanatomical responses of leaf tissues in *R. mangle* seedlings subjected to two natural ranges of edaphic salinity. For this purpose, an experiment of cross seeding or exchange of seedlings between populations was designed, taking advantage of the natural conditions offered on San Andrés Island (Colombia). On this island, just 6 km away, are the Smith Channel and Old Point forests with interstitial salinity ranges from 0 PSU (practical units of salinity) to 18 PSU and 20 PSU to 70 PSU, respectively.

Our working hypothesis assumes that since salinity generates water stress that leads to tissue modification, the seedlings of each forest present anatomical traits adapted to each range of salinities and that in the exchanged seedlings, the storage and conduction tissues of water (hypodermis, xylem vessels) are modified, which influence the structure of each forest in terms of the size and abundance of individuals.

2. Material and methods

2.1. Study area

San Andrés Island (SAI) is located in the Caribbean Sea and is part of the archipelago of San Andrés, Providencia, and Santa Catalina. The island and the rest of the archipelago are of volcanic origin (Díaz et al., 1996). The island has an elongated shape in the NS direction with a length of 12.5 km and a maximum width of 3 km, and an area of 27 km², with some hills up to 86 m above sea level in the central part (Gavio et al., 2010; Gamboa et al., 2012). The areas adjacent to the coastline are generally flat, with elevations of 5 m (INGEOMINAS, 1996). The SAI is located in the dry and humid tropical climate transition zone, and the climate is semihumid due to the influence of trade winds, which mitigate dry conditions. The annual average temperature is 27.4 °C, with maximum values of 30 °C (May and June) and minimums of 25.5 °C (December to February). The average annual precipitation is 1797.8 mm, with a monomodal distribution between a dry season (January to April), which has strong winds, and a wet season (October to December), in which 80% of rainfall occurs (Gavio et al., 2010). From May to July, the rains are moderate (IDEAM, 1995).

The study was carried out in two mangrove forests of SAI (Figure 1): Old Point forest is located in the northeast (12°34'00.5" N; -81°42'19.3" W), has an area of 65 ha (Rodríguez-Rodríguez et al., 2018) and presents trees on average 7.9 ± 0.2 m high and 8.5 ± 0.3 cm of diameter at breast height (DBH) (Rodríguez-Rodríguez et al., 2018). Two types of forests are characterized in Old Point, a fringe forest where *R. mangle* is dominant over *L. racemosa* and *A. germinans* (relative densities of 79%, 15% and 6%, respectively) and a basin forest where *A. germinans* dominates over *L. racemosa* and *R. mangle* (relative densities of 58%, 23% and 20%, respectively) (Sánchez-Núñez, 2009). Since there are no constant watercourses on the island, the hydroperiod of these forests is determined by rainfall and tides (Medina Calderon, 2016). Within this ecosystem, the interstitial salinity variation ranges from 20 PSU to 70 PSU (Sánchez Núñez and Mancera Pineda, 2012; Medina Calderón, 2016), the nitrogen concentration is 1.88 ± 0.12 mg cm⁻³, phosphorus is 0.08 ± 0.004 mg cm⁻³, and organic matter is 105.7 ± 5.0 mg cm⁻³ (Rodríguez-Rodríguez

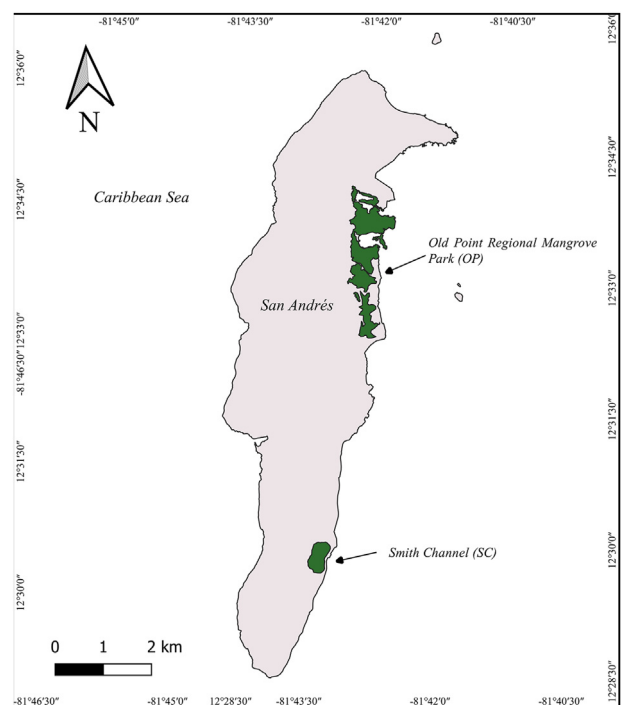


Figure 1. Location of Old Point and Smith Channel mangrove forests on San Andrés Island (SAI), Colombia.

et al., 2018). This mangrove is euhaline according to the Venice system (1959) classification.

Smith Channel forest is located to the southeast ($12^{\circ}30'11.3''$ N, $-81^{\circ}43'06.8''$ W), has an area of 17 ha (Rodríguez-Rodríguez et al., 2018) and trees have heights averaging 21.9 ± 0.7 m and 31.5 ± 1.2 cm of DBH, where *R. mangle* is dominant over *L. racemosa* (relative densities of 75% and 25%, respectively) (Sánchez Núñez and Mancera Pineda, 2012; Rodríguez-Rodríguez et al., 2018). The forest is isolated from the sea and tides by sand barriers and the island's main road, and its hydroperiod depends on rainfall and groundwater (Medina Calderon, 2016). Physiographically, it is classified as an inland mangrove swamp (Medina Calderon, 2016). The variation in interstitial salinity ranges from 0 PSU to 18 PSU, the nitrogen concentration is 2.16 ± 0.18 mg cm⁻³, phosphorus is 0.09 ± 0.014 mg cm⁻³ and organic matter is 97.5 ± 4.3 mg cm⁻³ (Rodríguez-Rodríguez et al., 2018). This mangrove is oligohaline according to the Venice system (1959) classification.

2.2. Planting populations by crossing

Cross seeding is understood as the exchange and seeding of *R. mangle* propagules between two mangrove forests with different salinity ranges (Old Point and Smith Channel). In January 2016, propagules were collected that did not have developed leaves and roots or the presence of herbivory or pathogens.

The collection was carried out in January since one of the flowering stages reported for the species in these two forests corresponds to October (Sánchez Nunez and Mancera Pineda, 2011); therefore, the propagules had approximately a month of dispersion. Immediately after, the planting proceeded as follows: 90 propagules of *R. mangle* developed in Smith Channel were planted in Old Point (OP + SC), and 90 propagules developed in Old Point were planted in Smith Channel (SC + OP). For each forest, 90 propagules were planted in their forest of origin as a control treatment (native seedlings OP + N and SC + N). The 90 propagules per group were sown in 6×4 m plots separated every 50 cm to avoid competition between individuals. The sowing of each propagule was vertical, where the hypocotyl axis was introduced at 5 cm deep to improve rooting and avoid the loss of individuals due to flooding. This seeding was monitored when the propagules were already in the seedling stage, four times during one year (Figure 2).

2.3. Height measurement of seedlings and collection and fixation of plant organs

In each plot, the height of the seedlings was measured three times (August 2016, November 2016, and March 2017). The collection of three individuals originating from the cross seeding and native seeding experiment was carried out in four seasons (May 2016, August 2016, November 2016, March 2017). Leaf samples were obtained from each seedling. The collected organs were fixed in FAA solution (10:5:85, formaldehyde:acetic acid:70% ethanol) for a period of 48 h, changed to 70% ethanol, and stored until morphoanatomical measurements were made. Because in seedlings OP + SC the mortality was almost 100% toward the second evaluation period of the experiment (August 2016), only results of this group were obtained up to this date.



Figure 2. Cross-seeding plot of individuals of *R. mangle* in the Old Point forest.

2.4. Measurement of physicochemical variables

In interstitial water from each forest, salinity was measured with a Schott conductivity meter (handilab LF-12), and pH was measured with a Schott pH meter (handylab pH 11). The collection of interstitial water for the physicochemical measurements was carried out at 30 cm deep by two methods: in the case of the Old Point forest with a rod connected to a hose and to a syringe to obtain the interstitial water by pressure (McKee et al., 1988). The rod was buried 30 cm into the ground, and then the sample was obtained by absorption from the syringe. The second method used in the Smith Channel forest, where the substrate is very compact, was the opening of a hole 30 cm deep with the help of a shovel, where the infiltration of the water was waited for the taking of the sample. Salinity values were reported in PSU. Three replicas of the physicochemical measurements were taken for each forest, and this process was repeated on each of the organ collection dates (May 2016, August 2016, November 2016, and March 2017).

2.5. Preparation of tissues for fresh histological measurement

The fresh tissue measurement process was carried out in the Laboratorio de Equipos Ópticos of the Department of Biology of the Universidad Nacional de Colombia - Bogotá. Two leaves from each individual were selected from each seedling at each sampling time for a total of 82 samples for the experiment.

Hand-cut tissue sections were taken from each of the organs (0.5 cm–1 cm for leaf) that were rinsed with 5% hypochlorite from 10 to 15 min. Then, the samples were washed and neutralized with acetic water (1 drop of glacial acetic acid per 100 ml of distilled water) to stabilize the pH for 10 min and finally washed with distilled water. After rinsing, the samples were stained with Astra blue - basic fuchsin, where first, the basic fuchsin stain was made for 5 min, they were washed with distilled water, and then they were stained with Astra-blue for 15 min and finally they were washed with distilled water (Robles Sanchez, 2019). Once the tissues were stained, they were observed with a Leica M205 stereoscope and photographed with an MC170HD camera using the Leica Application Suite (LAS) program.

2.6. Measurement of stained tissues

The total leaf thickness, hypodermis, palisade parenchyma, and spongy parenchyma were measured in the leaf. The lumen diameter of the xylem vessels and the thickness of their lignified walls were measured in the central rib of the blade (Figure 3). Measurements were determined with ImageJ version ij152-win-java8 and photoediting with Adobe Photoshop CC2017.

2.7. Statistical analysis

To establish whether the salinity ranges of Old Point and Smith Channel presented significant differences, a W Mann-Whitney-Wilcoxon test was performed (0.05% significance). In the case of pH, the Mann-Whitney-Wilcoxon U test (0.05% significance) was also carried out to determine if there were changes in this physicochemical variable.

The relationship between growth and salinity was determined for each group using the Spearman correlation coefficient and the growth rate by simple linear regression. Since the OP + SC group presented total mortality in the second sampling, it was not considered for this analysis. The survival percentage was calculated for the four groups.

Nonparametric statistical tests were carried out on morphoanatomical features because the data did not show normality or homogeneity of variances. For each group evaluated, the Spearman correlation coefficient test was carried out to determine the relationship between functional traits and interstitial salinity ranges and determine the significant differences between the tissues of the evaluated groups. The Kruskal-Wallis KW (0.05% significance) test was performed, and data were

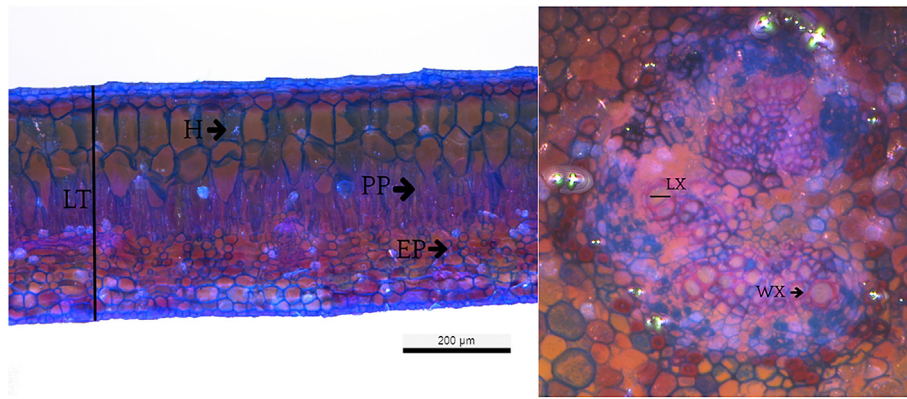


Figure 3. Seedling sections of the *R. mangle* leaf. H: Hypodermis thickness; LT: Leaf thickness; PP: Palisade parenchyma thickness; EP: Spongy parenchyma thickness; LX: Diameter of the lumen of the xylem vessels; WX: Wall thickness of xylem vessels.

plotted in box plots. Statistical analyses and graphics were performed with the R program (version 4.0.2).

3. Results

3.1. Physicochemical variables

3.1.1. Salinity

The evaluated interstitial salinity ranges presented significant differences according to the Mann-Whitney-Wilcoxon W test ($W = 144$, $p\text{-value} = 3.644 \times 10^{-5}$). At Old Point, the average salinity was $38.46 \text{ PSU} \pm 11.25 \text{ s.d. PSU}$, while at the Smith Channel, the salinity average was $9.5 \text{ PSU} \pm 2.74 \text{ s.d. PSU}$ during the study period (Figure 4A).

In the Smith Channel forest, the salinity ranged from 5.80 PSU to 11.73 PSU. A decrease in interstitial salinity was observed over time. At Old Point, the salinity varied between 23.93 PSU and 47.70 PSU, showing a difference between the maximum and minimum salinity of 23.77 PSU, four times greater than that of the Smith Channel. In this case, there was also a trend of decreasing interstitial salinity during the experiment (Figure 4B), presenting a slight variation in May and August, where salinity was higher in the second measurement than in the first (difference of 0.73 PSU).

3.1.2. pH

The pH values were not significantly different between sites and between seasons, ranging from 5.7 to 6.9 ($W = 47.5$, $p\text{-value} = 0.1655$).

3.2. Seedling survival and growth

3.2.1. Survival

The survival rate of SC + N seedlings decreased from 27.8% to 6.7%, while in SC + OP seedlings, decreased from 52.2% to 22.2%, where more than 20% of the initial seedlings were kept alive. In OP + N seedlings, the percentage decreased from 92.2% to 60%, showing a higher survival compared to the other groups. In the case of OP + SC seedlings, the survival rate in the first evaluation was 2.2%, and later, this population collapsed (Figure 5). These changes in survival occurred within 217 days.

3.2.2. Seedling growth

The Spearman correlation shows an inverse relationship between salinity and growth in the three groups evaluated, being weaker in OP + NV, indicating that the variability of growth in this group is due in 37% to the range of interstitial salinity of the Old Point forest. In the case of the Smith Channel forest groups, the Spearman correlation shows that more than 40% of the growth variability is explained by the forest interstitial salinity, being higher in SC + NV (47%) and lower in SC + OP (0.44%) (Table 1). Regarding the linear regression analyses (Table 1), the adjusted models of the equation show higher daily growth in SC + NV (0.73 mm/day) than in SC + OP (0.70 mm/day) and the lowest growth in OP + NV seedlings (0.35 mm/day). The linear regressions indicate that the daily growth rate is higher in SC + NV, although the average growth at the end of the experiment was higher in SC + OP (591.2 mm) after SC + NV (509 mm) and smaller in OP + NV (408.9 mm) (Figure 6).

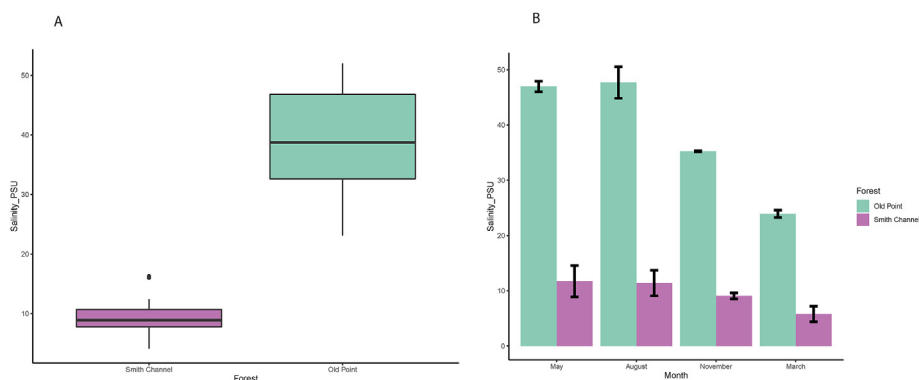


Figure 4. Interstitial salinity for each forest evaluated in the *R. mangle* cross-seeding experiment. A: Total salinity per forest; B: Interstitial salinity values for each forest at each of the measured seasons. The bars indicate the standard error of each group of data.

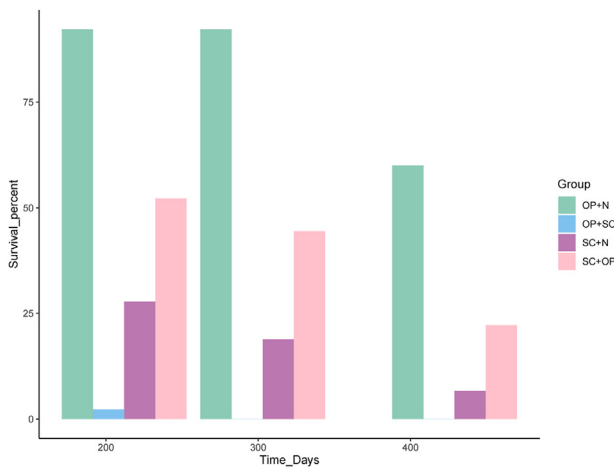


Figure 5. Survival percentages of each of the seedling groups evaluated in the cross-seeding experiment after 212, 303 and 429 days: SC + N: native seedlings Smith Channel; SC + OP: seedlings seeded on the Smith Channel; OP + N: native seedlings Old Point; OP + SC: seedlings seeded on the Old Point.

3.3. Morphoanatomical measures of *R. mangle*

3.3.1. Tissue comparison between groups

The KW test between the native groups showed significant differences in almost all the morphoanatomical traits evaluated except the thickness of the secondary walls of the leaf xylem vessels. In the case of the KW results for the four groups, there were significant differences in all the morphoanatomical traits evaluated, indicating that the cross-seeding experiment increased the variation within the traits (Table 2).

3.3.2. Spearman correlation between salinity and morphoanatomic traits

The results obtained by the Spearman correlation coefficient showed different relationships and with different levels between the traits and interstitial salinity depending on the group. In the Smith Channel oligohaline forest, in the SC + NV group, the wall thickness of the xylem vessels was the trait that was most affected by the interstitial salinity of the forest, where the relationship between both variables was inverse and where the coefficient showed that more than 40% of the variation of the trait depended on salinity. The traits thickness of the leaf, hypodermis thickness, and palisade parenchyma thickness presented a direct but weak relationship with the salinity range (less than 30%). The traits spongy parenchyma thickness and diameter of the lumen of the xylem vessels showed an inverse but weak relationship with salinity in the Smith Channel (less than 40%). In the SC + OP group, the traits of leaf thickness, hypodermis thickness, palisade parenchyma thickness, and spongy parenchyma thickness were those that were most affected by interstitial salinity, where the relationship was direct with more than

50% of the variability due to this environmental factor. In the case of the traits, the diameter of the lumen of the xylem vessels and wall thickness of the xylem vessels presented weak and inverse relationships with interstitial salinity (less than 30%). In the Old Point euhaline forest, in the OP + NV group, the palisade parenchyma thickness and the diameter of the lumen of the xylem vessels were those most affected by salinity, where the relationship was inverse and 45% greater. In the case of the traits leaf thickness, hypodermis thickness, palisade parenchyma thickness, and secondary wall thickness of the xylem vessels, the relationship with salinity was inverse and weak (less than 40%). In the OP + SC group, in the traits hypodermis thickness and secondary wall thickness of the leaf xylem vessels, the relationship was direct and 40% higher, while in the trait diameter of the lumen of the xylem, the relationship was direct but weak (less than 40%). For the traits secondary wall thickness of the leaf xylem vessels, parenchyma thickness, and spongy parenchyma thickness, the relationship was inverse but weak (less than 30%) (Table 3).

3.3.3. Morphoanatomical features evaluated by group and time

As the Spearman correlation test showed, the thickness of the leaf blade tended to be greater with increased salinity in SC + OP (Figure 7A), while in SC + N, this relationship was much weaker; therefore, in Figure 7A, a trend of tissue change as a function of salinity was not observed. The opposite occurred in the Old Point groups, where there was a weak inverse relationship between leaf blade thickness and salinity (Figure 7A). On the other hand, the variability in tissue thickness tended to be greater in the Old Point group than in the Smith Channel group and was much more marked in OP + SC when salinity presented the highest value (standard deviation of 523.16 to 47.70 PSU).

In the thickness trait of the hypodermis, the SC + NV, SC + OP, and OP + NV groups presented a pattern similar to that of the thickness of the leaf compared to the salinity ranges (Figure 7B), determining that this tissue could depend on the thickness of the leaf. In the case of the OP + SC group, the relationship between tissue thickness and salinity became direct, which was contrary to what happened with the thickness of the leaf (Figure 7B). For these traits, the groups planted in the Old Point forest continued to present the highest variability in the data (Figure 7B), with this greater variability in OP + SC (standard deviation of 90.42 to 47.70 PSU).

Within the photosynthetic parenchyma, in the palisade parenchyma, the SC + OP group presented a direct relationship of increased tissue thickness with increased salinity (Figure 7C). In contrast, the SC + NV, OP + NV, and OP + SC presented an inverse relationship to the salinity ranges (Figure 7C), being this weaker in SC + NV. Within this trait, the variation of the tissue measurement was greater in SC + NV at low salinities (standard deviation from 26.13 to 5.80 PSU).

In the spongy parenchyma trait, the SC + OP group presented the strongest and most direct relationship with salinity among the evaluated groups (Figure 7D). The SC + NV group presented a very slight

Table 1. Results of the statistical tests developed between salinity and growth of *R. mangle* seedlings subjected to the cross-seeding experiment.

Group		Simple linear regression				Spearman's correlation coefficient
		Coefficient	p-value	R-squared	Adjusted R-squared	
SC + NV	Intercept	204.0315	0.00200 **	0.1982	0.1804	-0.4711
	Pending	0.7347	0.00171 **			
	Adjusted equation model	204.0315 + 0.7347 * days				
SC + OP	Intercept	266.8657	1.36*10 ⁻¹¹ ***	0.2679	0.2606	-0.4451
	Pending	0.7023	2.54*10 ⁻⁸ ***			
	Adjusted equation model	266.86 + 0.7023 * days				
OP + NV	Intercept	257.5786	2*10 ⁻¹⁶ ***	0.1612	0.1573	-0.3733
	Pending	0.3473	6.31*10 ⁻¹⁰ ***			
	Adjusted equation model	257.5786 + 0.3473 * days				

*** or ** = significant difference in p-value.

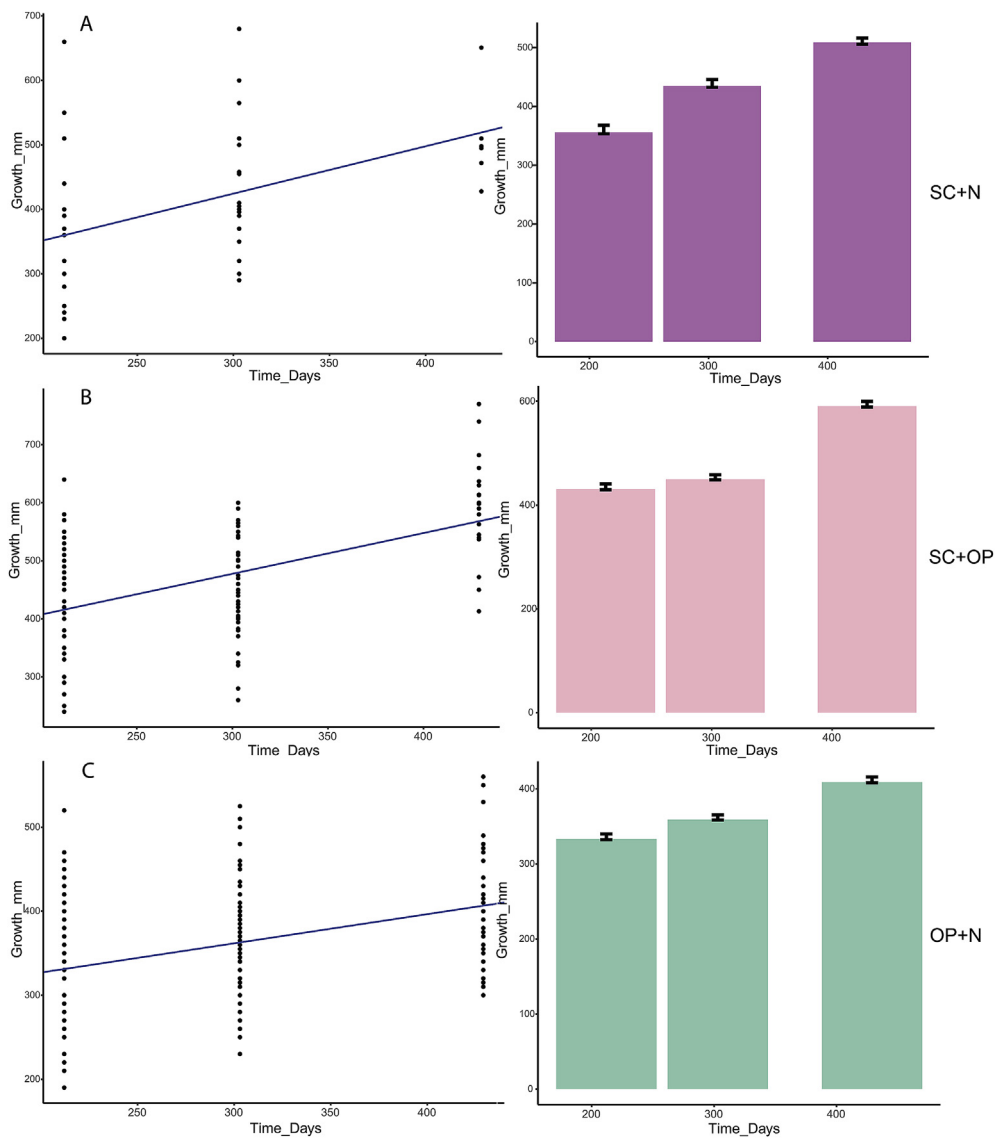


Figure 6. Graph of fitted line (Linear Regression) and growth averages for the groups evaluated in the experiment of cross-seeding of *R. mangle* populations between the Smith Channel and Old Point forests of the island of San Andrés A: Smith Channel native seedlings (SC + N); B: Seedlings sown in Smith Channel (SC + OP); C: Old Point native seedlings (OP + N). The bars indicate the standard error of each group of data.

relationship between the trait and salinity, of which a trend is not seen in Figure 7D. In the case of the Old Point groups, both OP + NV and OP + SC presented weak inverse relationships between the morphoanatomic traits and the salinity range (Figure 7D). This result shows an inverse pattern of the trait between both forests front to the salinity ranges. The greatest variation of the trait occurred in OP + SC (standard deviation from 40.83 to 47.70 PSU).

In xylem vessels, the lumen diameter trait showed an inverse relationship with the salinity ranges in the SC + NV, SC + OP, and OP + NV groups (Figure 7E), being this stronger in OP + NV, while in the case of OP + SC group, this relationship was direct but weak, indicating a different tissue response compared to the other groups. For the trait, the greatest variation in tissue measurement occurred in SC + OP at the highest salinity (standard deviation from 4.27 to 47.70 PSU).

Table 2. KW test for the determination of differences (significance of 5%) in the traits of the leaf between the evaluated groups of seedlings of the experiment of cross-seeding of *R. mangle*.

Organs	Functional Traits	Native Groups		All Groups	
		Chi ²	p Value	Chi ²	p Value
Leaves	Leaf Thickness	59.84	1.03*10 ^{-14***}	70.47	3.38*10 ^{-15***}
	Hypodermis	46.72	8.20*10 ^{-12***}	67.91	1.19*10 ^{-14***}
	Palisade Parenchyma	30.3	3.70*10 ^{-8***}	49.22	1.17*10 ^{-10***}
	Spongy Parenchyma	45.74	1.35*10 ^{-11***}	60.22	5.28*10 ^{-13***}
	Diameter Lumen Xylem Vessels	40.66	1.81*10 ^{-10***}	350.94	2.2*10 ^{-16***}
	Wall Xylem Vessels	3.528	6.03*10 ⁻²	71.54	1.99*10 ^{-15***}

KW: Kruskal Wallis. *** = significant difference.

Table 3. Results of the Spearman correlation test for the morphoanatomical traits measured of *R. mangle* against interstitial salinity in the cross-seeding experiment.

Group	Functional Traits					
	Foliar Leaf					
	Leaf Thickness	Hypodermis	Palisade Parenchyma	Spongy Parenchyma	Diameter Lumen Xylem Vessels	Wall Xylem Vessels
SC + NV	0.1931	0.1976	-0.0385	0.1331	-0.3306	-0.4007
SC + OP	0.6516	0.5946	0.5640	0.6118	-0.1091	-0.2600
OP + NV	-0.1982	-0.1947	-0.4746	-0.0371	-0.5345	-0.3536
OP + SC	-0.1514	0.4033	-0.2912	-0.2647	0.2620	0.5136

Bold = Correlation greater than 40%.

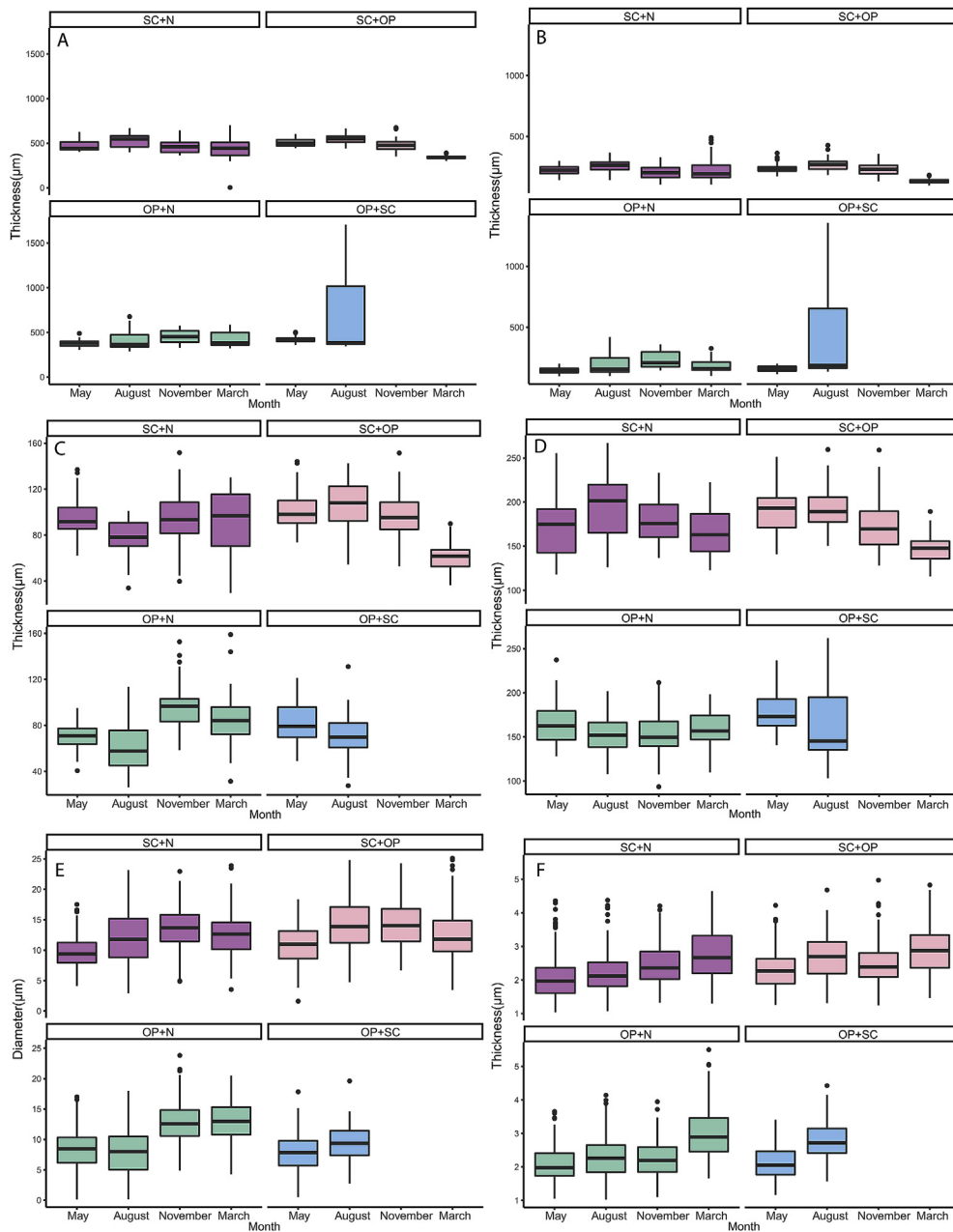


Figure 7. Morphoanatomical traits for each group and time of *R. mangle* evaluated in the cross-seeding experiment. A: Leaf thickness: SC + N: N = 216; SC + OP: N = 216; OP + N: N = 216; OP + SC: N = 80. B: Hypodermis: SC + N: N = 216; SC + OP: N = 216; OP + N: N = 216; OP + SC: N = 80. C: Palisade parenchyma: SC + N: N = 216; SC + OP: N = 216; OP + N: N = 216; OP + SC: N = 80. D: Spongy parenchyma: SC + N: N = 216; SC + OP: N = 216; OP + N: N = 216; OP + SC: N = 80. E: Diameter of the lumen of the xylem vessels: SC + N: N = 816; SC + OP: N = 852; OP + N: N = 864; OP + SC: N = 324. F: Wall thickness of the xylem vessels: SC + N: N = 816; SC + OP: N = 852; OP + N: N = 864; OP + SC: N = 324.

In the xylem vessel wall thickness trait, the same response was presented as that obtained in the xylem vessel lumen diameter trait, where SC + NV, SC + OP, and OP + NV presented an inverse relationship with the ranges of salinity (Figure 7F), being stronger in SC + NV, while in the

case of OP + SC, there was a direct and weak relationship between the trait and salinity (Figure 7F). The greatest variation in tissue thickness in this trait occurred in SC + OP and OP + NV (standard deviation of 0.71–5.80 PSU in SC + OP and at 23.93 PSU in OP + NV).

4. Discussion

4.1. Growth and survival against salinity variation

Functional traits are morphological, anatomical, biochemical, physiological, or phenological attributes characteristic of organisms that determine their biological efficacy and, therefore, their success according to environmental conditions (Valladares et al., 2007; Kattge et al., 2011). Thus, they have become a tool to understand and predict the distribution of species (Costa - Saura et al., 2016). In the case of *R. mangle*, the variation of functional traits is crucial to understand the adaptation of individuals of the species to abrupt changes in salinity. The data obtained for salinity in this study coincide with the values reported by different authors during different years in the same study area (Sánchez Núñez and Mancera Pineda, 2012; Medina Calderón, 2016; Rodríguez-Rodríguez et al., 2018), indicating that saline ranges have been maintained over time.

The salinity of the evaluated forests had an inverse and considerable relationship with the growth of *R. mangle* seedlings, which was corroborated by the Spearman correlation coefficient (between 37 and 47%). This relationship was stronger in SC + NV, which developed within the Smith Channel oligohaline forest, demonstrating that populations of *R. mangle* that are subjected to low salinity ranges can become more susceptible to abrupt changes in this regulator. Therefore, in the growth results (Figure 6, Table 1), the Smith Channel forest groups presented a higher growth rate (SC + NV = 0.73 mm/day, SC + OP = 0.70 mm/day) than the Old Point group (OP + NV = 0.35 mm/day). This demonstrates that low salinity ranges generate optimal conditions for the development of *R. mangle* in early growth stages since they allow a greater translocation of nutrients to the stem, increasing its elongation. This result agrees with Werner and Stelzer (1990), who indicated that the optimal salinity for the growth of *R. mangle* seedlings is 9.99 PSU, a salinity value that is present in the Smith Channel forest range. On the other hand, it has been determined that mangrove species during their initial stages of growth are more sensitive to environmental stress, and therefore, the increase in salinity can affect their growth (Ball, 2002; Jayatissa et al., 2008), which explains the low growth rate found in the OP + NV group within the Old Point euhaline forest.

In the first stage of seedling growth, a rapid response of individuals to interstitial salinity is very important, as this is crucial for their survival (Jayatissa et al., 2008). Among the survival results for *R. mangle*, there was a greater success of the individuals of the OP + NV group located in the Old Point forest compared to SC + OP, SC + NV, and OP + SC, the last being the most affected because it collapsed in the early stages of the experiment. The difference in the survival percentages determines that the population from which individuals OP + NV originate can adapt more efficiently to abrupt changes in salinity. This is confirmed by the SC + OP group made up of propagules originating in Old Point. More than 20% of its seedlings survived against the Smith Channel oligohaline condition, which was even more successful than SC + NV (6.7% survival). In the case of the propagules that originated in the Smith Channel forest, the 100% mortality that the OP + SC group presented toward 303 days and the low percentage of survival of SC + NV toward the end of the experiment. It was possible to infer that propagules originating in an oligohaline environment such as the Smith Channel forest have a low probability of adapting to abrupt changes in salinity.

Kodikara et al. (2018), in their research with the mangrove species *Rhizophora apiculata*, *R. mucronata*, *Avicennia marina*, *A. officinalis*, *Bru-guiera gymnorrhiza*, and *B. sexangula*, determined that salinities higher than 30 PSU delayed growth and decreased the survival percentage. The opposite occurs in *R. mangle* because survival was higher in the OP + NV group subjected to a range of high salinities (23.93 PSU to 47.70 PSU) while at low salinities, the groups presented very low survival rates. The low survival of the seedlings in the Smith Channel may be because, under conditions with low water stress due to salinity, the individuals of *R. mangle* enter into intraspecific or interspecific competition (with

L. racemosa) for resources (edaphic, light), which would lead to a reduction in the number of individuals of the species. Growth as a result of survival is key to understanding the structure of the two mangrove forests. A Smith Channel with a low salinity range (5.80 PSU to 11.73 PSU) and without connection to the sea presents slight water stress due to salinity, which allows a higher growth rate and the presence of taller trees (greater than 20 m according to Sánchez Nunez and Mancera Pineda, 2011; Sánchez Nunez and Mancera Pineda, 2012; Rodríguez-Rodríguez et al., 2018) but in number reduced by intra- and interspecific competition. In Old Point, where the interstitial salinity is high (23.93 PSU to 47.70 PSU) individuals of *R. mangle* develop low growth (approximately 7 m according to Rodríguez-Rodríguez et al., 2018). However, survival is greater because their propagules show greater adaptability to water deficit conditions in the environment. This is due to viviparism, since the propagule accumulates large amounts of Cl and Na from the mother tree before germination, which confers tolerance to the tissues during their dispersal stage (Zheng et al., 1999) and a lower risk osmotic, before the abrupt change in salinity, thus generating the development of a tolerance trait in the dispersal organ of the species.

4.2. Functional traits and adaptation to salinity

At the morphoanatomic level, the results of the KW test (Table 2) show the variation between the traits of the four groups evaluated (except for the wall thickness of the xylem vessels among the native groups), determining that the populations of *R. mangle* in the Smith Channel and Old Point do show morphoanatomic differences within the same species. The results of the Spearman correlation test show that the SC + NV group presented only one morphoanatomic trait that was moderately and directly affected by the salinity range of the Smith Channel forest (wall thickness of the xylem vessels). In the OP + NV and OP + SC groups, the salinity of the forest was only considerably affected (thickness of the palisade parenchyma and diameter of the lumen of xylem vessels inversely in OP + NV; thickness of the hypodermis and thickness of the wall of the xylem vessels directly in OP + SC). In the SC + OP group, the greatest number of traits were directly affected by salinity in the Smith Channel (leaf thickness, hypodermis thickness, and thickness of photosynthetic parenchyma) (Table 3). From this differential variation, by forest and by group, it can be pointed out that, in the propagules of the SC + NV group, when they originated and grew in an oligohaline environment, they were subjected to an increase in salinity of 5.93 PSU during the experiment, which did not mean an environmental stressor that alters photosynthetic processes and efficient use of water. In this case, the increase in salinity only inversely affected the wall thickness of the xylem vessels; that is, the increase in the salinity range generates thin vessels because the xylem system of the plant is not present and at risk of cavitation due to saline stress (Hacke et al., 2006; Reef and Lovelock, 2014).

In OP + NV, part of the photosynthetic tissues and the plant's hydraulic system was affected by the salinity range (23.77 PSU) of the Old Point forest, which was four times higher than that present in the Smith Channel. For this group, an inverse relationship was observed between salinity and the thickness of the palisade parenchyma because salinity stress affects the photosynthetic rate due to the reduction in the diffusion of CO₂ toward the chloroplasts and the closure of the stomata to avoid the loss of water. This causes modifications in the functioning and shape of the chloroplasts (alteration of the structure of the thylakoid membranes), affecting the capture and use of energy and leading the plant to reduce the thickness of its photosynthetic tissues to be able to stay in the environment (Parida et al., 2003, 2004). Regarding the trait diameter of the lumen of the xylem vessels, there was an inverse relationship with the range of salinity of the forest. This modification of lumen reduction in OP + NV vessels seeks to avoid cavitation (formation of air bubbles). Water tends to evaporate in vulnerable areas such as xylem pits (Tyree et al., 1994; Melcher et al., 2001; Hacke et al., 2006), which can generate an embolism block in the xylem vessel and affect hydraulic conductivity

(Woodruff et al., 2007; Zwieniecki and Holbrook, 2009; Wheeler et al., 2013), leading to the collapse of the individual.

In the OP + SC group, both traits were involved in the water resources. First, the thickness trait of the hypodermis presented a direct relationship with salinity because its propagules initially developed in an oligohaline medium. Salinity varied only 5.93 PSU. Then when sown in a euhaline environment with a broader range of variation (23.77 PSU), the water deficit becomes much higher; therefore, the plant must develop a succulent leaf (Tomlinson, 1994). This allows a greater thickening of the hypodermis through the elongation of the cell hyalines of this tissue to increase the water storage capacity and reduce osmotic shock through the accumulation within the vacuoles of excess solutes (Werner and Stelzer, 1990; Parida and Jha, 2010). The second feature was the wall thickness of the xylem vessels, which was directly related to salinity. In this case, as in the hypodermis, the tissue had an abrupt change in salinity between both forests, increasing the water deficit and the risk of embolism (Woodruff et al., 2007; Zwieniecki and Holbrook, 2009; Wheeler et al., 2013); thus, the strategy of the hydraulic system was to thicken the wall of the xylem vessels to reduce the risk of cavitation. Although within the OP + SC group the traits most strongly associated with salinity generated modifications to the change of environment, the individuals did not manage to survive throughout the experiment, which may be an indication that the propagules originating in oligohaline forests do not achieve their adaptation. In euhaline forests, their morphoanatomic traits from development do not show tolerance to high salinities.

The SC + OP group, which was generated in a euhaline forest (Old Point) and later settled in an oligohaline forest (Smith Channel), had the highest number of traits associated with interstitial salinity (11.73 PSU). First, the leaf thickness and hypodermis traits thickened toward higher salinity, which indicates that being individuals who originated in a euhaline forest, the minimum increase in salinity generates a signal of water stress and the need to accumulate water. The tissues thicken at higher salinity values even if the stress is lower in the Smith Channel. In the case of photosynthetic tissues, both presented thickening at high salinities, showing an opposite response to that presented by OP + NV (in palisade parenchyma); however, the origin of the propagules was the same. That is, when water stress caused by salinity is reduced, the photosynthetic rate increases because there is no danger of water loss during stomatal opening; therefore, the diffusion of CO₂ toward chloroplasts increases, and the process becomes more efficient, allowing well-developed photosynthetic parenchyma.

Altogether, the functional traits evaluated for the four groups show an advantage in the development, adaptation, and survival of individuals of *R. mangle* originating in euhaline forests such as Old Point. While individuals originating in oligohaline forests can develop greater growth and large trees, they are more susceptible to changes in interstitial salinity, reducing their survival during dispersal stages.

4.3. Functional traits and possible response to climate change

The difference in adaptability between *R. mangle* populations subjected to contrasting salinity ranges may imply changes in the structural, zoning, and abundance levels of the species in the face of climate change processes. In the case of the study carried out on the island of San Andrés, during the first months of 2016 (January–April), high temperatures were recorded according to the Oceanic Niño Index (ONI), a period during which evapotranspiration increased. Without rains, leading to higher salinity in the Smith Channel and Old Point forests (first stage of the sampling), then for three months (May to July), the temperature began to drop, a period in which the salinity was little variable compared to the first months. For the following, for six months, there was a reduction in temperature with increased rainfall - Niña Event (August–January). During this time, a considerable reduction in salinity occurred in both forests, and toward the last two months of the experiment (February–March), the temperature began to increase, during which time the

lowest salinities were reported in the Smith Channel and Old Point (NOAA, 2021).

The present study results show that the OP + SC group collapsed during the Niño period, corroborating that individuals of *R. mangle* originating in the Smith Channel may become more susceptible to drought events due to climate change since they do not tolerate the increase in abrupt interstitial salinity. In the case of the SC + OP group, the individuals managed to adapt and develop greater growth in both the Niño and Niña periods, demonstrating that the population of *R. mangle* present at Old Point can adapt to changes in the saline gradient. In the case of native groups, SC + NV presented high growth but low survival, confirming that the population of *R. mangle* present in the Smith Channel was more susceptible to environmental changes. In contrast, the OP + NV group presented greater survival and less affectation of functional traits by saline stress and survived against an adverse environmental event.

Evaluating a future scenario for the forests of the island of San Andrés, we must start from the premise that the stability of the mangrove forests depends on the interaction of physical, chemical, and biological factors. This operates at different scales (spatial, temporal, and organizational) (Feller et al., 2010), and the alteration in any of these factors affects the structure, functions, and ecosystem services that it provides to adjacent ecosystems (Jennerjahn et al., 2017). Among the effects of climate change, the rise in sea level is one of the most worrying since it is due to the thermal expansion of ocean water generated by high temperatures and the melting of polar ice caps (Qin et al., 2014 in Alongi, 2015).

If an increase in the sea occurs that exceeds the accretion capacity of the Old Point forest, it becomes a subtidal environment (Feller et al., 2010). Altering the zoning of *R. mangle*, which should migrate inland (toward the basin) to be able to establish itself again (Alongi, 2015), will have to compete for resources with the species *L. racemosa* and *A. germinans*, affecting the structure of the forest. In the case of the Smith Channel, which is an inland forest, the rise in sea level will increase the interstitial salinity of the soil, turning this forest into a fringe oligohaline environment. The population of *R. mangle* will collapse due to the low adaptability of functional traits to the abrupt increase in salinity, eliminating the species from the forest and perhaps the species *L. racemosa*, turning the forest into a subtidal system.

In another scenario, with the increase in the planet's temperature, migration of mangrove species to higher latitudes will first be generated (Alongi, 2015). This would not be an effective measure on the island of San Andrés because their highest altitude is 86 m above sea level (Gavio et al., 2010; Gamboa et al., 2012), which indicates that both forests would disappear. However, the increase in temperature increases evapotranspiration, increasing interstitial salinity levels in both forests, generating a total collapse of the *R. mangle* species in the Smith Channel and a population reduction in the Old Point, in both cases affecting structure and zoning. In the future scenarios established, the loss of both mangrove forests is inevitable. This would lead to the loss of the ecosystem services of these forests, such as coastal protection, food, sediment stabilization, sequestration or export of carbon, production of raw materials, improvement in water quality, faunal habitat, and tourism (FAO, 2007; Spalding, 2010; Alongi, 2011; Sandilyan and Kathiresan, 2012; Russi et al., 2013), directly affecting the human communities of the island.

Because of the response of both populations to the change in the salinity gradient, it is necessary to consider the origin, functional traits, and tolerance or susceptibility of *R. mangle* individuals used in ecological restoration or rehabilitation processes to increase the probability of survival in these processes.

5. Conclusions

The functional traits evaluated in each of the groups showed that the individuals of *R. mangle*, depending on their origin (oligohaline or euhaline), present modifications that allow them to adapt or be susceptible to changes in soil salinity. *R. mangle* individuals originating in

euhaline environments (Old Point) can establish quickly and maintain a higher percentage of survival in the face of abrupt changes in salinity, while individuals of oligohaline origin (Smith Channel) present functional traits susceptible to an increase in salinity, which reduces its survival percentage and affects its dispersal capacity. Among the functional traits evaluated, those most affected by the saline gradient involve water storage and transport and photosynthetic tissues because salinity generates changes in the efficient use of water and alterations in the photosynthetic rate, conditioning the growth and survival of the species.

The functional traits of the *R. mangle* species and its tolerance to salinity changes are crucial in the face of possible climate change scenarios since the permanence or disappearance of the species in the future will depend on them.

Since the responses to salinity were determined at the morphoanatomic level, it is necessary that future research evaluates the genetic differences at the population level to determine whether genetic factors are involved in the tolerance and susceptibility of these populations.

Finally, due to the importance of the response of *R. mangle* populations to changes in interstitial salinity, their success or failure depending on the origin and how these changes can generate a broad or limited ecological niche, we consider that these results should be considered in rehabilitation, restoration, and reforestation programs of forests of this species to generate a representative increase in the success of the recovered populations.

Declarations

Author contribution statement

Alejandra Robles Sánchez: Conceived and designed the experiments; Performed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

José Ernesto Mancera Pineda: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Xavier Marquín Casas: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Jairo Humberto Medina Calderón: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Funding statement

This work was supported by Departamento Administrativo de Ciencia, Tecnología e Innovación - COLCIENCIAS (FP44842-567-2015) and Corporation Center of Excellence in Marine Sciences – CEMarin (14-01, 2019).

Data availability statement

Data will be made available on request.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

Acknowledgements

The authors express our gratitude and appreciation to Universidad Nacional de Colombia - Bogota and Caribbean headquarters for the use of laboratories and equipment; to the San Andrés Botanical Garden, for the

company of the staff in the field work, the use of laboratories and equipment.

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