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Carbon Store Dynamics in the Structure of Mangrove in the Southern Pacific of Mexico

Dinámica de almacenamiento de carbono en la estructura de manglar en el Pacífico Sur de México

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Resumen

Mangroves are recognized as the wetlands with the most significant capacity to store carbon, this ability to store carbon is due to their high productivity and the low rates of organic matter decomposition. The study area is one of the Intensive Carbon Monitoring Sites (SMIC, initials in Spanish) in Mexico. In the southern coast of the Mexican Pacific, in the La Encrucijada Biosphere Reserve (REBIEN). The SMIC has an extension of 1x1 km. In this area there are eight conglomerates. Each conglomerate contains four circular-shaped secondary units of 400 m2. The inventory includes trees ≥ 2.5 cm of DBH (Diameter at breast height). Tree species, DBH, height, canopy diameter, the basal area and tree density. Tree biomass was quantified, and the carbon store was determined using the biomass-to-carbon conversion factor of 0.48. The carbon in standing dead trees was estimated using the methodology of Kauffman et al. (2012). The environmental parameters quantified: interstitial salinity, pH, temperature and flood level. Results R. mangle is the dominant species, conglomerate 2 presented the highest tree density and conglomerate 4 the lowest. Conglomerates 8 and 4 had the highest averages for DBH, basal area, height, and crown area, in contrast, the conglomerates 1, 5, and 2, had the lowest averages. In the study area, the fall of trees was the factor that most affected the aboveground (aerial) carbon content, which increased 6.91 and 3% respectively during the second and third year of monitoring. Natural mortality increased and affected mostly young trees 2.5 to 10 cm tall. Wood extraction remained constant during the three years of study. During the three years of study, conglomerate 6 presented the highest biomass averages with 210.4 Mgha-1 and carbon stores of 101.0 MgCha-1; in contrast, conglomerate 5 registered the lowest average with 124.9 Mgha-1 and 60.0 MgCha-1. R. mangle presents the biggest store of carbon with 60.4 MgCha-1. This mangrove system registered an increase in natural mortality during the study period, which could be the result of the massive amounts of sediment the river has been carrying after the passage of Hurricane "Stan" in 2005.

Palabras clave: store carbon, inventory, conglomerates, natural mortality, hurricanes.

Introduction

Coastal wetlands are important in global carbon dynamics, due to their high capacity to store carbon, now known as blue carbon (Bridgham et al., 2006). Mangroves are recognized as the wetlands with the most significant capacity to store carbon, which exceeds two to three times the amounts stored by terrestrial systems (Donato et al., 2011; Adame et al., 2013). This ability to store carbon is due to their high productivity and the low rates of organic matter decomposition, which tends to occur under total or partial flooding conditions (Adame et al., 2015).

Mangroves store considerable amounts of carbon, mainly in the soil, product of the accumulation and burial of sediments, and the constant production of organic matter (Donato et al., 2011). In principle, the degradation of organic remains is associated not only with the reduction of carbon sequestration but also with the release into the atmosphere of large amounts of CO2 and of methane (CH4) as a product of respiration during the decomposition of organic matter in anoxic soils (Kauffman et al., 2012). Consequently, the conservation of these forests as carbon stores is critical.

The La Encrucijada Biosphere Reserve (REBIEN) extends along a portion of the South Pacific coast of Mexico. It includes an estimated 29,522 hectares of mangroves (Valderrama et al., 2017), and Mexico's most noteworthy mangrove forests thrive in this locality, with trees up to 38 m tall (Tovilla et al., 2007). The dominant physiognomic type in the Biosphere Reserve is the riparian forest, dominated by Red Mangrove (Rhizophora mangle). This species occupies extensive areas as a result of the presence of fresh water derived from abundant rainfall and six rivers that drain into the area's coastal lagoons, estuaries, or directly to the sea. The influence of tides, waves, and tropical storms throughout the year is minimal (Adame et al., 2015).

Despite their grandeur, the mangroves present signs of deterioration caused by the expansion of the agricultural frontier, poaching, logging, forest fires, siltation, and hydrological modifications (Tovilla et al., 2007b; Adame et al., 2015). These factors have pushed their degradation, causing the loss of significant mangrove areas in many sectors.

Studies have been performed in this area to determine carbon dynamics, focusing on the influence of geomorphology and the water gradient (upper, intermediate, and lower estuary) on the volume of the carbon reservoir in mangroves, marshes, and swamps. Comparisons were then performed between other mangrove regions of Mexico (Adame et al., 2015; Herrera et al., 2016). The objective of this study is to quantify over a three-year period the dynamics of structurally stored carbon in a mangrove forest in the REBIEN.

Methods

Study area

The study area is one of the Intensive Carbon Monitoring Sites (SMIC, for its initials in Spanish) in Mexico. Bordering the southern coast of the Mexican Pacific, in the core zone of the La Encrucijada Biosphere Reserve (REBIEN), in the state of Chiapas, the study site is located between 15° 10'30" and 15° 12' 15" Latitude North and 92° 50'40" and 92° 49' 20" Longitude West (Figure 1). The reserve has an extension of 144,868 ha (INE, 1999). The REBIEN is subject to a warm sub-humid climate with abundant rains in summer, and the average annual rainfall is 1567 mm, with an average annual temperature of 28.2ºC (Adame et al., 2015).

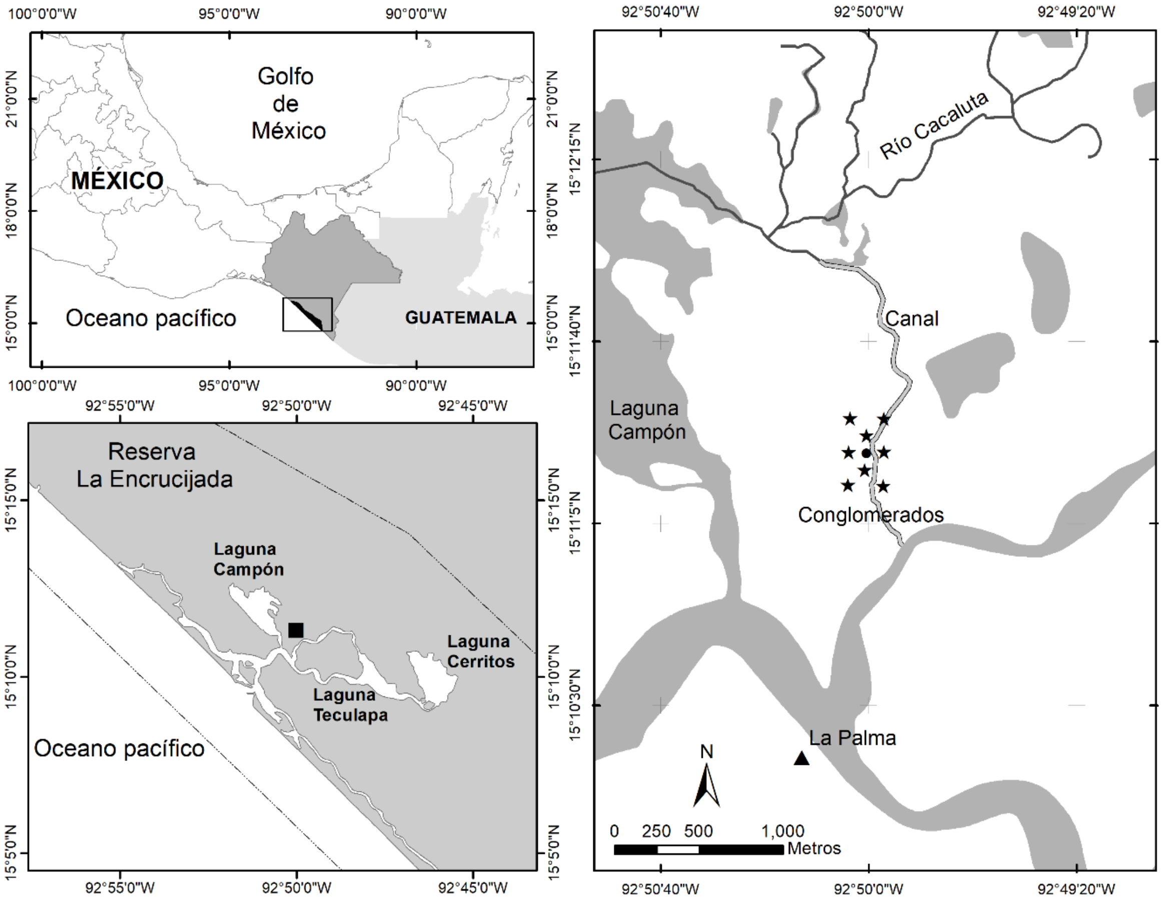

Figure 1. *Location of the Study Area*

Establishment of the conglomerates

The SMIC La Encrucijada has an extension of 1x1 km. In the center of this area is an Eddy-Covariance tower, and around it, there are eight conglomerates or primary sampling units. Each conglomerate contains four circular-shaped secondary units of 400 m2, arrayed in the form of an inverted "Y" oriented towards the North (Conafor 2012; Red Mex-SMIC 2015). This type of plot allows extrapolating estimates obtained from information collected in the field to other regions in the country with similar characteristics (Red Mex-SMIC 2015; Tovilla et al., 2015).

Method

The inventory includes trees ≥ 2.5 cm of DBH (Diameter at breast height). Tree species, DBH, height, canopy diameter, and tree density were identified (Tovilla et al., 2018). The basal area was estimated using the formula of Torres and Magaña (2001); the crown area was estimated according to the criteria of Jiménez et al. (2002) and Rodríguez et al. (2008). The classification of forest types present in the area follows the structural characteristics proposed by Lugo and Snedaker (1974).

Tree biomass was quantified using the equations proposed by Fromard et al. (1998), and the carbon store was determined using the biomass-to-carbon conversion factor of 0.48 (Kauffman et al., 2012). The similarity of the study area with the particular climatic characteristics at the Equator –and its nearby mangrove growth zones– determined the choice of these equations.

TB = 0.1282 × DR 2.6 Rhizophora mangle

TB = 0.140 × DBH 2.4 Avicennia germinans

TB =0.1023 × DBH 2.5 Laguncularia racemosa

TB: Total biomass (Kg), DR: Diameter above the last root (cm), DBH: Diameter at breast height (cm).

The carbon in standing dead trees was estimated using the methodology of Kauffman et al. (2012), which consists of classifying trees into three categories: category 1 – standing dead trees without leaves; category 2 – dead trees without secondary branches, and category 3 – dead trees without primary and secondary branches. Category (1) carbon corresponds to total dry biomass minus 2.8 % of foliar biomass; category (2) carbon equals total dry biomass minus 2.8 % of foliar biomass and 18.7 % of secondary branches. Finally, category (3) carbon corresponds to 76 % of total dry biomass (Kauffman et al. 2012).

The environmental parameters quantified include interstitial salinity, pH, temperature, flood level, and distance of each site to the tidal channel. They were measured using a HANNA®multi-parameter meter and a Garmin GPSMAP 64s GPS.

Data analysis

Data were analyzed using normality tests (Anderson and Darling, 1954). Data were subject to a logarithmic transformation where the assumptions of normality and homoscedasticity did not hold. A two-factor analysis of variance (ANOVA) allowed determining the possible significant differences between DBH, height, crown area, biomass, and carbon by species and conglomerate. "Time" is one of the factors, and "Species and Conglomerate" the second. Subsequently, a Tukey multiple comparisons test with a significance level of 95% was applied. Further analyzes consisted of a Spearman correlation test –as the data presented an asymmetric distribution– and an analysis of variance and covariance to determine if there is a relationship between physicochemical parameters and tree biomass. The analyses mentioned above used the R 3.5.1 software (R Core Team, 2018).

Results

In the SMIC of the REBIEN, 72% of the mangrove forest classifies as a riverine mangrove type, 25% are border type mangroves, and 3% are basin type mangroves. The dominant species in all conglomerates is *R. mangle*: conglomerate 2 presented the highest tree density and conglomerate 4 the lowest. Conglomerates 8 and 4 had the highest averages for DBH, basal area, height, and crown area; in contrast, the conglomerates 1, 5, and 2, had the lowest averages (Table 1). Considering possible increases in the parameters evaluated during the study period, the DBH did not change significantly ($p < 0.05$); both height and crown area showed significant increases, however only until the third year of study (Table 2).

Table 1

Structural characteristics for eight conglomerates in the SMIC La Encrucijada (Average ± standard deviation for DBH, height, and crown area) C: Conglomerate, *Rm*: *R. mangle, Ag: A. germinans, Lr: L. racemosa.*

C	Association	Density (Ind ha^{-1})	DBH (cm)	Basal Area (m^2 ha^{-1})	Height (m)	Crown area (m^2)
1	Rm / Lr / Ag	2025	7.8 ± 6.4	16.60	11.8 ± 7.2	9.9 ± 13.9
2	Rm / Ag / Lr	3013	7.9 ± 5.8	20.35	10.8 ± 5.6	8.9 ± 14.8
3	Rm / Ag / Lr	1950	9.5 ± 7.0	19.38	14.1 ± 7.6	10.8 ± 13.1
4	Rm / Ag / Lr	1313	11.8 ± 4.9	20.22	17.6 ± 5.8	13.4 ± 9.8

C	Association	Density (Ind ha^{-1})	DBH (cm)	Basal Area (m^{2} ha^{-1})	Height (m)	Crown area (m^{2})
5	Rm / Lr / Ag	2613	8.5 ± 4.6	14.01	12.6 ± 4.8	5.6 ± 5.1
6	Rm / Lr / Ag	2138	8.5 ± 7.2	20.38	11.7 ± 7.0	10.2 ± 16.1
7	Rm / Ag / Lr	2013	8.0 ± 7.7	18.16	11.6 ± 7.0	11.4 ± 25.4
8	Rm / Ag / Lr	1763	11.9 ± 6.2	21.38	17.5 ± 8.1	12.1 ± 12.1

Table 2
Comparison of structural parameters (average ± standard deviation) of the conglomerates (C) in the SMIC during the period 2016-2018
[Different letters indicate significant differences (*fide* Tukey test; P <0.05)]

C	DBH (cm)			Height (m)			Crown area (m^{2})		
	2016	**2017**	**2018**	**2016^{b}**	**2017^{ab}**	**2018^{a}**	**2016^{b}**	**2017^{ab}**	**2018^{a}**
1	6.6 ± 5.5	7.3 ± 6.0	7.8 ± 6.4	9.2 ± 5.4	11.2 ± 6.7	11.8 ± 7.2	5.9 ± 9.6	8.0 ± 12.9	9.9± 13.9
2	7.0 ± 5.4	7.1 ± 5.5	7.9 ± 5.8	9.3 ± 4.7	9.8 ± 5.1	10.8 ± 5.6	8.3 ± 12.5	7.3 ± 8.6	8.9 ± 14.8
3	6.7 ± 5.7	7.8 ± 6.5	9.5 ± 7.0	9.9 ± 6.4	11.6 ± 6.9	14.1 ± 7.6	5.0 ± 8.8	7.0 ± 9.0	10.8 ± 13.1
4	10.0 ± 5.5	11.7 ± 5.7	11.8 ± 4.9	13.6 ± 5.3	15.8 ± 5.2	17.6 ± 5.8	8.4 ± 7.2	10.4 ± 7.8	13.4 ± 9.8
5	6.9 ± 3.9	7.3 ± 4.1	8.5 ± 4.6	10.1 ± 4.2	10.2 ± 4.3	12.6 ± 4.8	4.5 ± 4.1	6.1 ± 5.5	5.6 ± 5.1
6	7.6 ± 7.0	8.3 ± 7.1	8.5 ± 7.2	10.1 ± 6.1	10.1 ± 5.8	11.7 ± 7.0	8.6 ± 12.9	11.7 ± 18.2	10.2 ± 16.1
7	7.1 ± 6.8	7.4 ± 7.1	8.0 ± 7.7	10.2 ± 6.0	10.8 ± 6.6	11.6 ± 7.0	8.0 ± 15.3	11.2 ± 20.2	11.4 ± 25.4
8	9.3 ± 6.1	10.6 ± 6.8	11.9 ± 6.2	13.3 ± 7.6	13.6 ± 7.8	17.5 ± 8.1	6.7 ± 7.9	8.3 ± 8.0	12.1 ± 12.1

The mangrove forest is affected by several disturbance factors, among them the natural mortality that starts with trees still standing; however, even in this condition, they continue to provide aerial biomass. Subsequently, standing dead trees fall to the ground, and when disintegrated, they become part of the carbon stored in the ground. The extraction of trees for firewood or timber is another factor that affects mangrove forests, and the removal of trees reduces the forest biomass.

In the study area, the fall of trees was the factor that most affected the aboveground (aerial) carbon content, which increased 6.91 and 3% respectively during the second and third year of monitoring. Natural mortality increased and affected mostly young trees 2.5 to 10 cm tall. Wood extraction remained constant during the three years of study (Fig. 2).

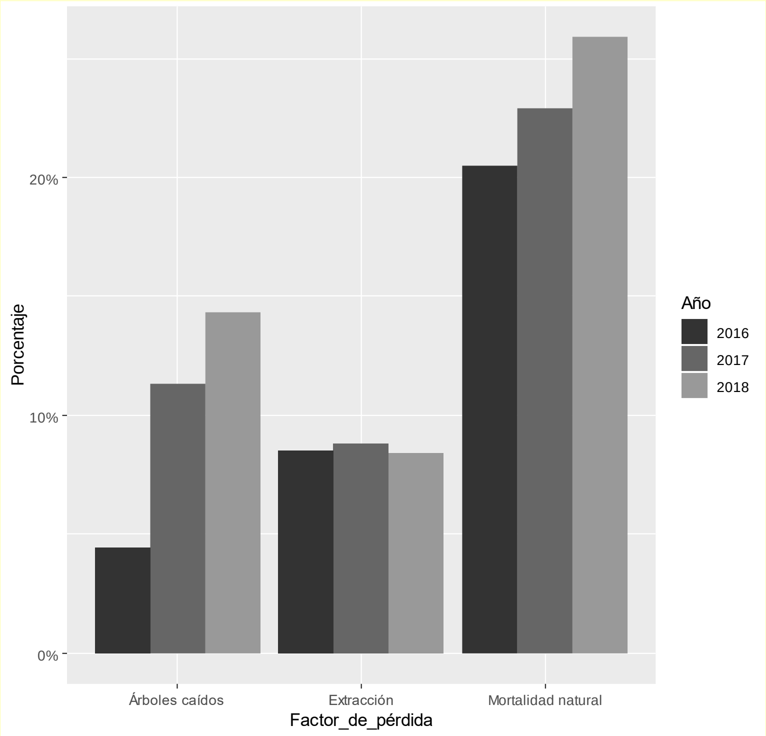

Figure 2. *Percentage of tree loss due to extraction, natural mortality, and tree fall registered in the SMIC La Encrucijada in the period 2016-2018.*

Conglomerates 5 and 4 were the most affected by natural mortality, and conglomerates 5 and 6 by tree extraction and fall, with the highest number of trees removed per loss factor. This volume of loss could be due to a more considerable number of older trees that reduce light penetration into the lower strata, causing the death of a higher percentage of young trees. On the other hand, conglomerates 2 and 7 had the lowest densities of old trees, so they become open forests that allow higher survival of young trees and are, therefore, the least affected by the disturbance factors.

In almost all the conglomerates, there were increases in dead standing and fallen trees; however, the extraction of wood (stumps) for the three species remained constant throughout the study (Table 3).

By species, *R. mangle* presented the highest loss of trees due to the three perturbation factors under consideration, mainly because it is the dominant species with the most significant number of individuals, followed by *L. racemosa* and *A. germinans.* This last species was the least affected by the above factors, which could be attributed to its high range of tolerance against extreme salinity and low nutrient content (Agraz-Hernández, 2016). Regarding the changes in affected population numbers, all three species showed increases in standing and fallen dead trees throughout the study period (Table 4).

Table 3
Comparison of the total number of dead standing trees, stumps, and dead fallen trees by conglomerate (C) in the SMIC La Encrucijada during the period 2016-2018

C	Dead standing			Tree stump			Dead fallen		
	2016	2017	2018	2016	2017	2018	2016	2017	2018
1	103	157	215	38	43	45	29	36	57
2	47	61	105	2	3	2	6	15	25
3	114	172	223	28	31	31	12	50	82
4	248	232	270	85	86	81	43	101	107
5	301	248	223	102	102	98	28	175	225
6	94	97	100	137	144	141	60	109	125
7	38	63	90	11	12	13	12	11	24
8	92	141	130	29	30	31	34	82	107

Table 4.
Comparison of the total number of trees per species cataloged as dead standing, dead fallen, and stump in the SMIC during the 2016-2018 period

Specie	Dead standing			Tree stump			Dead fallen		
	2016	2017	2018	2016	2017	2018	2016	2017	2018
A. germinans	160	212	225	90	100	98	37	83	114
L. racemosa	280	235	236	152	149	147	55	124	153
R. mangle	597	724	895	190	202	197	132	372	485

During the study period, the mangrove forest showed slight increases in both biomass and carbon storage. In 2017 the carbon concentration increased 1.5 MgCha^{-1} and in 2018 it increased to 5.4 MgCha^{-1}. At the conglomerate level, there were no significant increases in biomass and carbon content at the beginning of the study; it was not until the third year when conglomerates 1, 2, 5, 6, and 7 presented significant increases (p <0.001). During the three years of study, conglomerate 6 presented the highest biomass averages with 210.4 Mgha^{-1} and carbon stores of 101.0 MgCha^{-1}; in contrast, conglomerate 5 registered the lowest average with 124.9 Mgha^{-1} and 60.0 MgCha^{-1} (Table 5.)

Table 5
Biomass and carbon (average ± standard deviation) in the aerial component by (C) conglomerate registered in the SMIC in the period 2016-2018. Different letters indicate significant differences (*fide* Tukey test; P <0.05)

C	**Biomass (Mg ha)$^{-1}$ (p <0.001)**			**Carbon (Mg C ha)$^{-1}$ (p <0.001)**		
	2016^{b}	**2017^{b}**	**2018^{a}**	**2016^{b}**	**2017^{b}**	**2018^{a}**
1^{e}	136.6 ± 42.7	149. ± 38.2	156.3 ±38.4	65.6 ±20.5	71.5 ±18.3.	75.0 ±18.4
2^{cd}	165.4 ± 29.1	171.2 ± 33.7	179.2 ±41.7	79.4 ±13.9	82.2 ±16.2	86.0 ±20.0
3^{cd}	162.4 ± 55.3	177.5 ±54.6	185.6 ±62.4	78.0 ±26.5	85.2 ±26.2	89.1 ±29.9
4^{d}	156.6 ±10.4	163.6 ±9.3	178.1 ±9.1	75.2 ±5.0	78.4 ±4.4	85.5 ±4.3
5^{f}	132.5 ±19.7	118.1 ±14.7	124.1 ±22.0	63.6 ±9.5	56.7 ±7.1	59.6 ±10.5
6^{a}	211.4 ±78.7	208.4 ±79.7	211.4 ±79.9	101.5 ±37.8	100.0 ±38.3	101.5 ±38.4
7^{bc}	181.0 ±59.8	181.4 ±68.5	194.8 ±63.5	86.9 ±28.7	87.1 ±32.9	93.5 ±30.5
8^{b}	189.5 ±32.3	190.4 ±25.3	196.1 ±28.0	90.9 ±15.5	91.4 ±12.1	94.1 ±13.4
Average	166.9	169.9	178.2	80.1	81.6	87.0

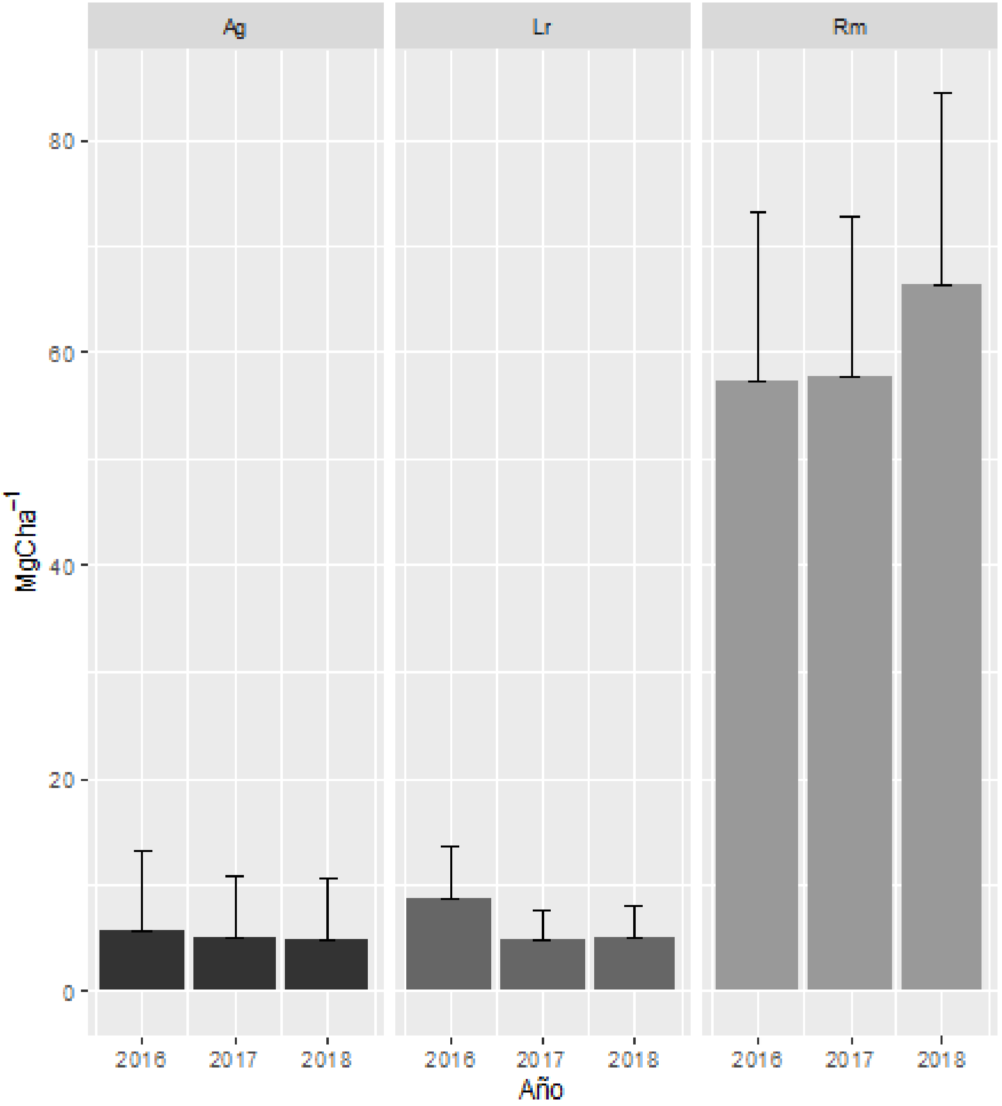

Figure 3. *Carbon storage by species in the SMIC during the study period 2016-2018.*

The structural parameters DBH, height, basal area, and crown area show a high correlation with forest biomass, which means that the increase in these parameters influences the production of tree biomass. Concerning the relationship between parameters, the four attributes present a high correlation between them in all directions. It seems likely that the increase in one variable is a function of the increase in the other, i.e., the increase in the basal area depends on the increase in DBH, and the increase in the crown area could depend on the height and the basal area (Figure 4).

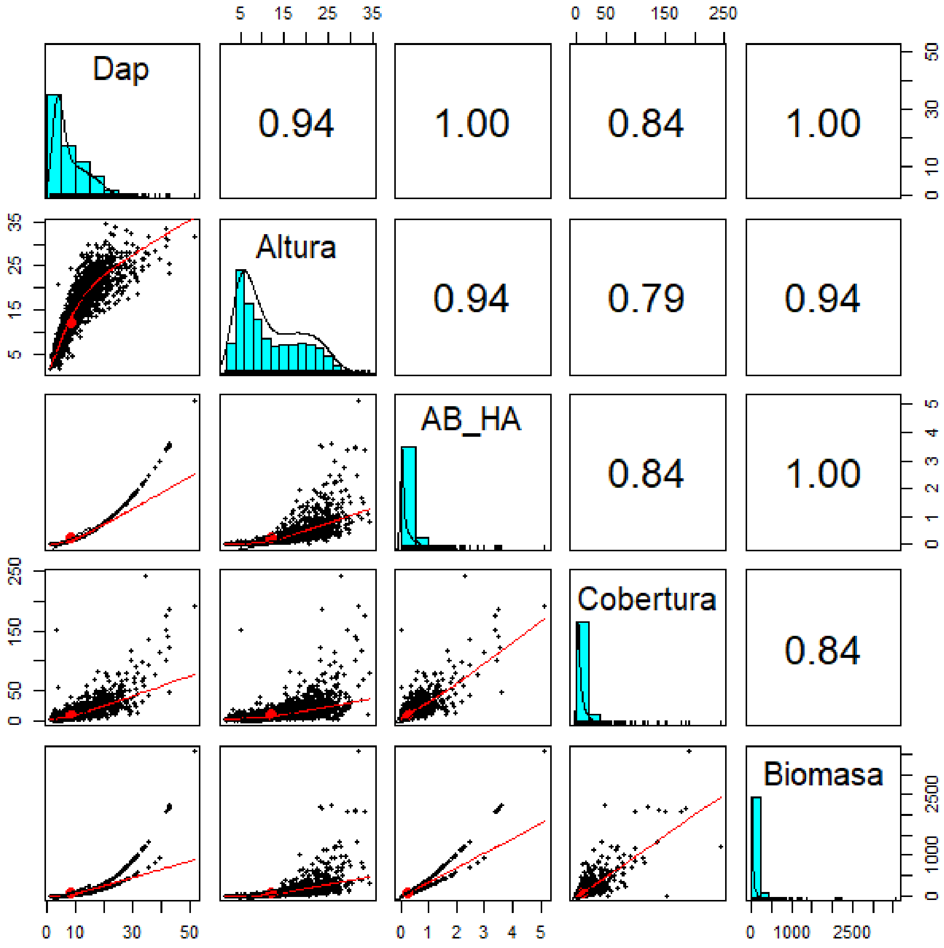

Figure 4. *Relationship of the variables DBH, height, basal area (BA), and crown area with tree biomass*.

The environmental variables salinity, temperature, and distance to the canal present a linear relationship with tree biomass. Salinity (p <0.01) and the distance to the channel (p 0.001) show a negative relationship; that is, as the salinity and the distance to the channel increases, the biomass decreases. The fact that salinity increases as mangrove development moves away from the channel or body of water, and trees invest more energy in salt regulation and less energy in biomass production, can explain this decrease in biomass production (Manrow, 2011; Agraz-Hernandez, 2016). The temperature (p <0.05) presents a positive correlation: the higher the temperature, the more abundant the biomass. The Box-Cox transformation of the data (Figure 5) determines the need to interpret graphs in a reverse manner.

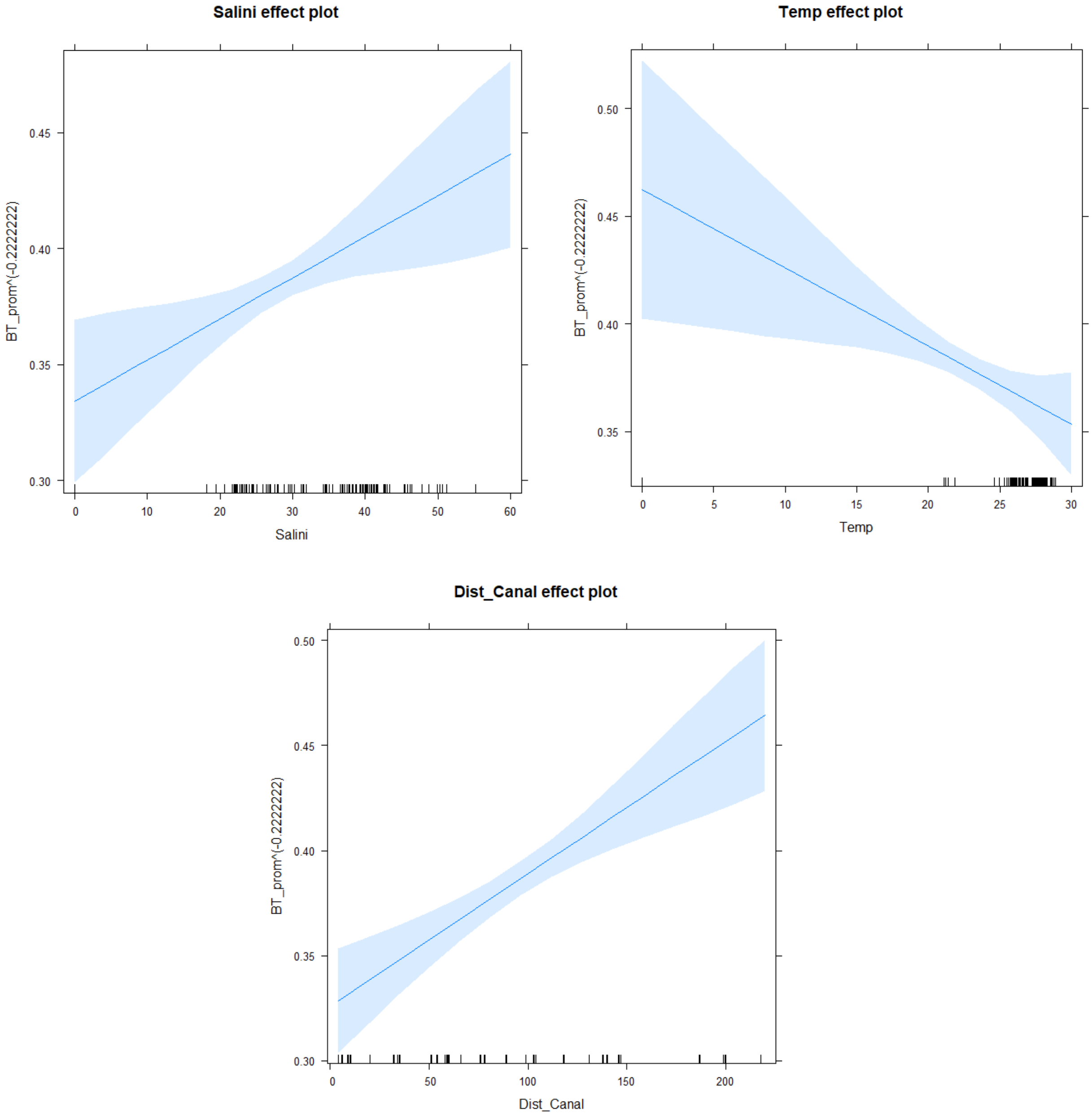

Figure 5. *Relationship of the environmental parameters salinity, temperature, and distance to the canal with forest biomass.*

Discussion

Its geomorphological characteristics, prevailing precipitation patterns, and the influence of the six rivers that drain into the core zone of the reserve are the basis of the dominance of riparian forests in the Biosphere Reserve (INEGI, 2010). They consistently provide water to the lagoon systems and estuaries;

furthermore, tidal influence, waves, and storms are infrequent. Due to the circumstances mentioned above, R. mangle is the most abundant species, distributed along both sides of the estuary in flooded areas with low interstitial salinity. The direct input of the Cacaluta River that drains into the study area 2.3 km upstream favors these conditions. This freshwater is distributed to most of the conglomerates through the channel passing through the center of the study area (Tovilla et al., 2018).

The structure of the site shows high variability. Conglomerates 4 and 8 presented higher structural averages, with the presence of many mature trees, while in conglomerates 3, 6, and 7, there are intermediate tree structures and some old trees. On the contrary, conglomerates 1, 2, and 5 were dominated by young trees, with less structural development.

This mangrove system registered an increase in natural mortality during the study period, which could be the result of the massive amounts of sediment the river has been carrying, a result in turn of the rectification and channeling works carried out after the passage of Hurricane Stan through the coast of Chiapas in 2005. Those works caused the silting of lagoons, estuaries, and mangroves during the past 13 years throughout the core area of the REBIEN (Gálvez 2017).

Probably the excessive sedimentation of the Campón lagoon may be causing the reduction of water renewal rates, of nutrient supply, and the accumulation of litter and substances derived from leaf decomposition in the substrate, as it previously happened in Juluápan lagoon, Colima, Mexico (Von Prahl, 1990; Ayerdis, 1996). Depending on the duration of flood conditions, water stagnation affects the processes of mangrove root gas exchange, causing the death of trees (Jiménez and Gonzalez, 1992).

The conglomerates most affected by perturbation factors also possess some unique features that could account for their vulnerability. Clusters 4 and 5 are the farthest from the canal, at 146 and 187 m. The low freshwater input –particularly during the dry season– could be the cause of the death of numerous trees due to the increase in interstitial salinity. Clusters 2 and 7 are close to the canal, at 59 and 66 m, respectively. The high freshwater supply that regulates the salinity of the substrate can be responsible for their low mortality. The high rate of tree falls in conglomerate 6 could be attributed to its localization as it is the first conglomerate from north to south and is, therefore, the first to receive the impact of wind.

Rhizophora mangle was the species most affected by natural mortality due to its higher density and number of individuals, while A. germinans was the least affected. However, considering the relative mortality of each species, L. racemosa is the most affected, and A. germinans is the least affected. The highest mortality in R. mangle and L. racemosa may be due to their limited tolerance to increased salinity during the dry season (Agraz-Hernández et al., 2011).

The dynamics of carbon stores are affected by high tree mortality: there was no significant storage increase during the study period. The last registry of 87 MgC ha-1 was lower than the reported carbon content for other areas of the REBIEN with 215 MgCha-1 (Adame et al., 2015), and to those at Pantanos de Centla, Mexico, with 100.1 MgCha-1 (Kauffman et al., 2016). Nevertheless, it was slightly larger than the store reported for the tall mangroves of the Sian Ka'an Biosphere Reserve, Mexico, with 77.064 MgCha-1 (Adame et al., 2013). Aerial carbon stores registered in other countries, such as the Can Gio forest park, Vietnam, with 214.7 MgCha-1 (Viet Dung et al., 2016), as well as in Semarang, Indonesia, with 118.03 MgCha-1 (Martuti et al., 2017), are larger than the stores found in the study area. On the other hand, the aerial stores reported for the Protection Forest Kien Vang, Vietnam, of 69 MgCha-1 (Nam et al., 2016), are less than the stores found during this study, as are also the values registered in the Sundarbans, Bangladesh, with 76.83 MgCha-1 (Kamruzzaman et al., 2018).

The carbon content in the conglomerates starts showing significant increases ($p < 0.001$) until the third year of study, probably associated with an increase in the recruitment of seedlings from 35 to 89 Indha-1. There was even an increase in tree width. Conglomerates 6, 8, and 7 present the oldest and thickest trees and also the most significant carbon stores. By contrast, juvenile trees dominate conglomerates 5 and 1 and present the lowest basal area and lowest carbon reserve. These data indicate that the development of woodland determines a potential increase in carbon storage, as stated by Camacho et al. (2011).

When considering carbon storage in these three species, R. mangle presents the biggest store of carbon with 60.4 MgCha-1, like amounts reported for this species in the Sian Ka´an reserve, Mexico, with 69.6 MgCha-1 (Adame et al., 2013). The opposite is the case for A. germinans, which presented the smallest store with 5.2 MgCha-1, less than the carbon store for the same species reported in French Guiana with 86.4 MgCha-1 and a density of 788 Indha-1 (Fromard, 1998). In the study area, R. mangle had the higher carbon content produced by a higher density of 1578 Ind ha-1, while A. germinans and L. racemosa had low densities, with only 362 and 163 Ind ha -1.

The decrease in mangrove stand density is always associated with an increase in tree thickness, a determinant factor for carbon storage in mangrove forests. In the case of A. germinans and L. racemosa, due to their low density, these species have a low carbon reservoir. In the case of A. germinans, in addition to a low density, the species invests most of its available energy in the process of salt regulation, a physiological process that is reflected in a reduced structural development and, therefore, less capacity for carbon storage (Agraz-Hernández et al., 2011). According to Manrow (2011), wood density can also influence carbon storage in mangroves. As in this study, R. mangle presented the most significant carbon store due to high tree density, thickening of trunks, and more dense wood (0.81-1.05 g cm3). A. germinans, due to lower repopulation values, both less dense wood (0.67-0.90) and structural thickening, also had the lowest carbon content (Chave et al., 2009; Zanne et al., 2009).

As to what concerns the carbon dynamics of the three species registered at the site, A. germinans y L. racemosa saw a decrease in the carbon store during the study period. However, R. mangle presented an increase de 8.7 MgCha-1 during the last year of field research. The reduction of carbon in the first two species is explained by the increase in tree fall, which grew 8.2% and 13.4% respectively during the second and third years of study. The thickening of trees and the recruitment of new individuals (57 Indha-1) are considered responsible for the increase in carbon store in R. mangle.

The increase or reduction of biomass and carbon manifests itself in the structural characteristics of the forest; structural variables such as DBH, basal area, height, and crown area show high correlation (1.00, 1.00, 0.94, and 0.85, respectively) with the aerial biomass. Similar correlations also exist in mangroves in Quanzhou Bay, China (Fu and Wu, 2011). This pattern arises from the growth of trees that manifests itself in the increase of forest mensuration features; it is associated with an increase in tree biomass, as suggested by Camacho et al., (2011), given that biomass and carbon storage increase depending on the growth rate and age of the trees. In this study, the growth of trees contributed to an increase in the carbon store in the third year of study.

Environmental parameters also influence biomass production of the forest. The presence of freshwater regulates the salinity of the site; this characteristic is considered a determining factor in the structural development of the community, the productivity and zoning of the mangrove species, particularly in the drier areas, where high salinities limit forest growth and development (Lugo and Snedaker, 1974; Pool et al., 1977; Cintrón et al., 1978; Castañeda-Moya et al., 2006; Castañeda-Moya et al., 2013). In this study, the average interstitial salinity of the site was 33.9 PSU, and, like the distance to the canal, it has a negative correlation with biomass, which indicates that as the distance to the canal and the interstitial salinity increases, tree development becomes limited. Several authors also found similar conditions in various tropical mangrove regions (Corella et al 2004; López-Portillo and Ezcurra, 1989; Agraz-Hernández et al., 2011; Mitra et al., 2011; Adame et al., 2013; Dominguez-Cadena et al., 2016). This response takes place because the sites farthest from the canal maintain higher salinity levels and lower nutrient content, so the trees show less structural development and have a lower capacity for carbon storage (Jiménez and Sauter, 1991).

The substrate temperature also influences biomass production. In this study, temperature shows a positive correlation with biomass, i.e., the higher the temperature of the substrate, the greater the production of biomass. The average temperature at the site was 26.7 ºC, higher than 24 ºC, which is the temperature at which microorganisms become active, and organic matter starts to decompose (Montenegro and Malagon, 1990; Buol et al., 1991). Soil temperature influences biomass production because it plays an essential role in the vital processes of the radical zone, such as root growth, nutrient and water absorption, and microbial transformation of soil organic substances, which are determinant factors for tree growth (Fischer et al., 1977).

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