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Source: Tropical Conservation Science, 11(1)

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/1940082918805188>

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# Mangrove Productivity and Phenology in Relation to Hydroperiod and Physical–Chemistry Properties of Water and Sediment in Biosphere Reserve, Centla Wetland, Mexico

Tropical Conservation Science  
Volume 11: 1–14  
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DOI: 10.1177/1940082918805188  
journals.sagepub.com/home/trc  


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## Abstract

Mangrove is the dominant vegetation in the estuaries, river deltas, and coastal lagoons of tropical and subtropical regions. A number of factors affect the structure and productivity of mangrove forests, including hydrology, soil salinity, and soil type. In this study, litter production in the Centla Wetland Biosphere Reserve in Tabasco, Mexico, was evaluated as a function of the physical–chemical properties of water and sediments. The study cycle was from June 2015 to June 2016. Litterfall was measured, and water samples were collected at the surface, interstitial, and subterranean level to estimate the physical–chemical parameters. Sediment samples were also collected to determine the texture, pH, organic matter, bulk density, and moisture content. The mangrove was composed of *Rhizophora mangle* (L.), *Laguncularia racemosa* (L.) Gaertn, and *Avicennia germinans* (L.) Stearn. The pH was presented in a range of 5.3 to 7.4, and spatially, the texture of sediment varied significantly, with high values of sand in Playa ( $73.7\% \pm 3.4\%$ ) and high content of clay ( $57.2\% \pm 1.4\%$ ) and organic matter ( $41\% \pm 2\%$  average) in mangrove riverine type. The highest salinity of interstitial water was encountered at Beach ( $29 \pm 3.0$  PSU) and of groundwater ( $36.4 \pm 1.5$  PSU). Overall, the average estimated litter fall was  $10.45 \text{ ton} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ . These results indicate that the litter production is related to the response of the mangrove to the variation of the environmental conditions of each site (substrate texture, hydroperiod, soil moisture, water salinity, water redox potential, and soil organic matter).

## Keywords

mangrove, litter, hydroperiod, redox, salinity, phenology

## Introduction

Mangrove is the dominant vegetation in estuaries, river deltas, bays, and coastal lagoons in tropical and subtropical regions around the world (Basáñez-Muñoz, Olmedo, & Rojas-Mencio, 2006; Tomlinson, 1986; Twilley, 1985). Mangroves increase in structural complexity and productivity, as size progresses from the dwarf to the riverine type (Arreola-Lizárraga, Flores-Verdugo, & Ortega-Rubio, 2004; Lugo & Snedaker, 1974). The location of the mangrove in relation to the topography and coastal geomorphology is an important descriptor in the classification of mangrove forests (Twilley, 1998). The physical–chemical characterization of mangroves is one means of evaluating the response of mangroves to existing environmental conditions and of generating further data to support mangrove

conservation (Camargo & Coutinho, 2012). Specifically, in mangroves, species composition and growth are directly affected by the physical composition of soils and by the proportions of clay, silt, and sand in

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Received 11 July 2018; Revised 13 September 2018; Accepted 13 September 2018

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soils, which determine the permeability and the hydraulic conductivity of water and also influence soil salinity and water content (Kathiresan & Bingham, 2001). The conditions imposed by the hydroperiod are also important for the structure and functioning of mangrove ecosystems, as these conditions are responsible for the unique physical and chemical conditions of mangroves and affect numerous factors such as soil anaerobiosis, organic matter accumulation, species richness, and species composition as well as primary productivity (Flores-Verdugo, Agraz-Hernández, & Benítez-Pardo, 2007). Consequently, mangroves produce large amounts of organic matter in the form of leaves, wood or branches, flowers, and fruits that are later incorporated to surrounding environments via tides and streams (Flores-Verdugo, González-Farías, Zamorano, & Ramírez, 1992; Twilley & Day, 1999). This litter constitutes an important source of nutrients supporting marine and terrestrial food chains (Holguín, Vazquez, & Bashan, 2001). This study focuses on the primary productivity of mangroves as measured by litter production, related to environmental factors such as rainfall, hydroperiod, and physical chemistry of water and mangrove sediments.

Considering the absence of studies on the primary productivity and litter production of mangroves as well as the relationship between litter production and environmental factors in Centla Wetlands, Biosphere Reserve (CWBR), the aim of this study was to estimate the leaf litter production of three mangrove species as a function of the physical and chemical characteristics of water (surface, interstitial, and groundwater) and sediments in CWBR. The following three hypotheses were formulated: (i) Increased litter production will be associated with rainfall and the low salinity of interstitial water; (ii) the greatest production of reproductive parts (flowers and fruits) in mangroves will occur during the rainy season and will be related to the presence of flooding; finally, (iii) organic matter content in mangrove soils will have a positive correlation with the type of silt and clay sediment, with litter production and the maximum flooding as inputs of organic matter of exogenous origin.

## Methods

### Study Area

The CWBR is considered a wetland of international importance by the Ramsar Convention (Barba, Rangel, & Ramos, 2006; Diario Oficial de la Federación, 1992; RAMSAR, 1995). Located in the state of Tabasco, Mexico, the CWBR occupies 302 706 ha (17°57'–18°39'N and 92°06'–92°45'W; Barba, Valadez, Pinkus, & Flores, 2015; Bautista-Jiménez, García-Muñiz, Pérez-Alejandro, & Romero-Gil, 2000)

and is under the influence of the largest rivers in Mexico (Grijalva and Usumacinta). These rivers have a combined drainage basin that corresponds with 28% of the surface water in Mexico (Mendoza-Carranza, Hoeninghaus, García, & Romero-Rodríguez, 2010). The weather is warm humid with an average annual rainfall of 1 573 mm and an average annual temperature of 26.6°C (National Water Commission, 2000). The dry season lasts from February to May and the rainy season from June to January, although rainfall is highest from October to November (Corella et al., 2001). The main mangrove species in CWBR are *Rhizophora mangle* (L.), *Laguncularia racemosa* (L.) Gaertn, and *Avicennia germinans* (L.) Stearn (Corella et al., 2001; Thom, 1967).

### Field Study

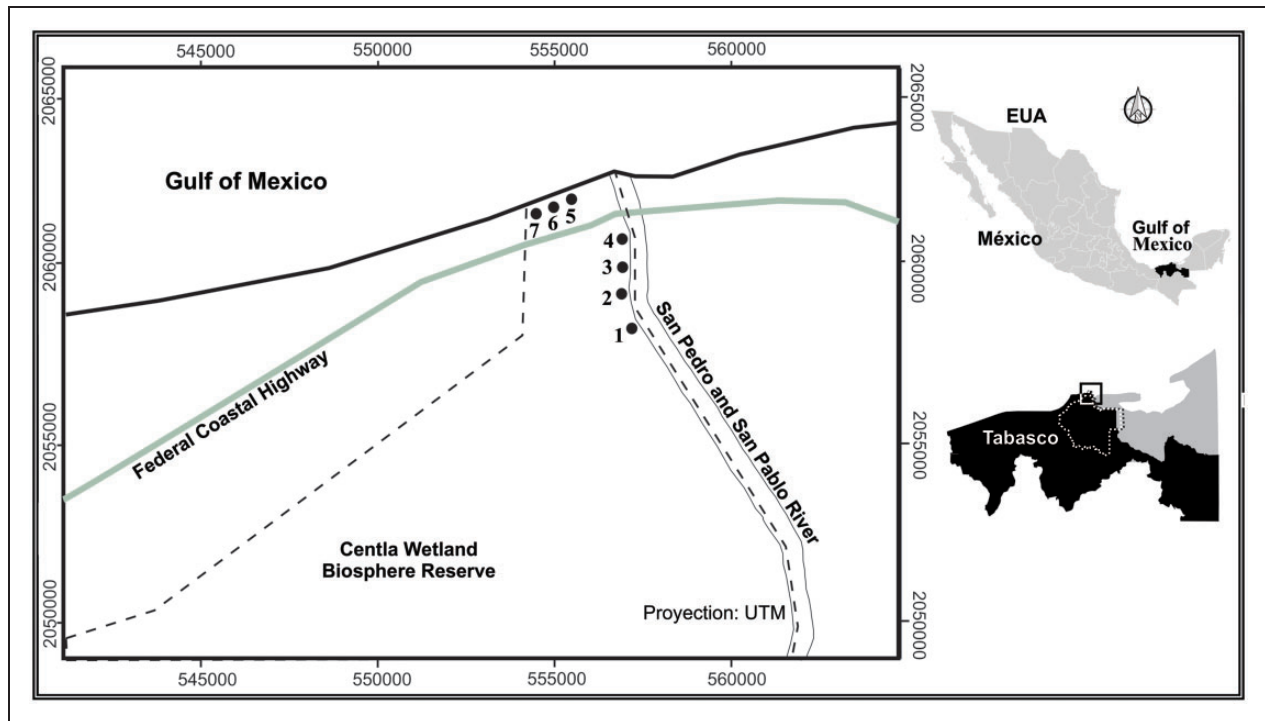
Seven sites inside the CWBR were selected. The first four sites were located 35 m from the San Pedro and San Pablo (riverine sites) river and were separated by 800 m: (1) San Juan, (2) Perico, (3) Huarache, and (4) Puente. The remaining three sites were located 200 m from the coastline (Beach sites) and were by separated 300 m (Figure 1): (5) Beach 1, (6) Beach 2, and (7) Beach 3. The rainfall data were obtained from a meteorological station of the National Water Commission (National Water Commission-National Meteorological Service-Weather Station, 2017) situated in Frontera, Tabasco (18°24'N–92°38'W).

### Forest Structure of Mangroves

The structural attributes of mangroves were evaluated from May 23 to May 29, 2015 in a quadrant of 20 × 20 m at each site. The design and method were based on Valdéz (2002). The abundance, height, and width of all adult tree species with a diameter at breast height  $\geq 2.5$  cm were recorded according to Corella et al. (2001).

### Litterfall

Mangrove litter was collected monthly by five circular litter traps (52 cm diameter) that were installed at random under the canopy (Moreno-Casasola & Warner, 2009) at each site (35 traps in total). Leaves, flowers, fruits, stipules, and wood or branches were separated per mangrove species, dried at 70°C over a 24-h period, and subsequently weighed with analytical scales (0.001 g precision). Litter production was expressed in monthly ( $\text{g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ) and annual ( $\text{ton}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ) values. The identification of mangrove species was performed according to Agraz-Hernández, Noriega-Trejo, López-Portillo, Flores-Verdugo, and Jiménez-Zacarias (2006) and of additional vegetation associated with mangroves according to Novelo (2006).



**Figure 1.** Study area, Centla Wetland Biosphere Reserve (CWBR), Gulf of Mexico. Discontinuous line presents CWBR limits. Sites: (1) San Juan, (2) Perico, (3) Huarache, (4) Puente, (5) Beach 1, (6) Beach 2, and (7) Beach 3. EUA = United States of America; UTM = Universal Transverse Mercator.

### Chemical–Physical Variables of Sediment

Sediment samples were collected monthly (91 samples) at a soil depth of 20 cm using a cylindrical soil sampler ( $0.0033 \text{ m}^{-2}$ ). Texture (Klute, 1986), pH, organic matter (Walkley & Black, 1934), bulk density, and soil moisture were determined using the methodology established by Moreno-Casasola and Warner (2009). The soil moisture was defined as a percentage based on the capacity of soil to store water; a percentage equal to 100% indicates that 1 g of soil stores 1 g of water (Infante, 2011).

### Chemical–Physical Variables of Water

Two piezometers were installed in each site according to the method proposed by Peralta, Infante, and Moreno-Casasola (2009). The first one was used to obtain interstitial water samples (at a depth of 0.5 m) and the second one to obtain groundwater samples (at a depth of 1.5 m). The piezometers were constructed with polyvinyl chloride tubes of 1 inch in diameter; in 20 cm of the end of the buried tube were made alternate slots every 2 cm and covered with  $250 \mu\text{m}$  mesh immobilized by plastic fasteners. The surface water was collected from the water column (top of the column) during the months of flooding. The salinity (PSU), redox potential (ORP; mV), temperature ( $^{\circ}\text{C}$ ), and pH of water samples were measured with a Hanna HI9828 multiparameter.

The piezometers also allowed the flood pattern to be measured monthly at each site.

### Data Analysis

The normality of the distribution of the data was analyzed by Kolmogorov–Smirnov test, and the homogeneity of the variance of the data was assessed using Levene’s test. Data sets without normality were transformed by the natural logarithm. The differences between groups of data were determined by one-way analysis of variance followed by Tukey’s post hoc honest significant difference tests. The Kruskal–Wallis nonparametric multiple comparison test was applied when normality was not fulfilled. The level of significance was set at 5% (Steel & Torrie, 1996). Pearson correlations ( $r$ ) were used to determine the correlations between total litter and the physical–chemical components of water and sediment. To identify whether a higher rate of abscission and dispersion of reproductive structures (flowers and fruits) occurred during the rainy season and the greatest flood period, a Pearson correlation analysis ( $r$ ) was carried out to evaluate the relation of the flowers and fruits with rainfall and the hydroperiod. All analyses were performed in the IBM SPSS Statistics V. 20 software.

## Results

### Chemical–Physical Variables of Sediment

Spatially, the texture of sediment varied significantly. The highest sand content ( $F=65$ ,  $p < .05$ ,  $N=91$ ) was recorded at the Beach sites (1, 2, and 3;  $73.7\% \pm 3.4\%$ ). The highest silt content ( $F=40$ ,  $p < .05$ ,  $N=91$ ) was found at Puente ( $37.3\% \pm 2.1\%$ ) and the lowest at Beach (site 2;  $8.4\% \pm 1.0\%$ ); meanwhile, the highest clay content ( $F=51$ ,  $p < .05$ ,  $N=91$ ) was found at San Juan ( $57.2\% \pm 1.4\%$ ; Figure 2). The bulk density of soil was high at the Beach sites (1, 2, and 3;  $1.3 \pm 0.1 \text{ g}\cdot\text{cm}^{-3}$ ); lower values were obtained at the riverine sites of Perico, Huarache, and Puente ( $0.5 \pm 0.04 \text{ g}\cdot\text{cm}^{-3}$ ; Figure 2). The organic matter content of sediment was high at the riverine sites of Perico, Huarache, and Puente ( $41\% \pm 2\%$  average), yet lower at the Beach sites ( $8\% \pm 1\%$  average). The lowest pH value was recorded at Perico (5.3) and the highest at Beach 3 (7.4; Figure 2). The texture parameters, apparent soil density, soil organic matter, and pH did not show significant temporal differences ( $p > .05$ ).

The hydroperiod did present significant temporal differences ( $F=3.6$ ,  $p < .05$ ,  $N=91$ ). In the riverine sites, the lowest water level was found in August ( $-68.2 \text{ cm}$  in average), and floods (surface water) occurred from October 2015 to June 2016. At the Beach sites, the minimum flood pattern was found in October, wherein the water level decreased to below  $-150 \text{ cm}$  according to the piezometer. The highest water level was recorded in November ( $+51.5 \text{ cm}$  on average). The hydroperiod was positively correlated with the moisture content ( $r = .7$ ) of interstitial sediment and with organic matter ( $r = .55$ ). Soil moisture content did not vary significantly ( $F=0.6$ ,  $p = .8$ ,  $N=91$ ), yet higher moisture was found in Huarache ( $226.3\%$ ; Figure 3). The sand content was negatively correlated with silt and clay texture and organic matter. Finally, organic matter content was positively correlated with silt substrates and negatively correlated with bulk density (Table 3).

### Chemical–Physical Variables of Water

The surface water of sites did not differ significantly in salinity ( $F=0.3$ ,  $p = .8$ ,  $N=91$ ), which ranged from  $2.9 \pm 1.3 \text{ PSU}$  (San Juan) to  $9.5 \pm 4.1 \text{ PSU}$  (Puente). The highest salinity of interstitial and groundwater was documented at Beach (Site 1;  $29 \pm 1.4$  and Site 2;  $36.4 \pm 1.5 \text{ PSU}$ , respectively). The lowest surface ORP was recorded at Perico site ( $-60.5 \pm 39 \text{ mV}$  on average). The pH ranged from  $7.5 \pm 0.1$  to  $7.8 \pm 0.2$  without significant differences ( $F=0.4$ ,  $p = .86$ ,  $N=91$ ). The temperature ranged from  $25.3^\circ\text{C} \pm 0.9^\circ\text{C}$  to  $26.1^\circ\text{C} \pm 0.8^\circ\text{C}$  without significant differences ( $F=0.1$ ,  $p = .9$ ,  $N=91$ ).

The maximum salinity of water was recorded in June 2016 for surface water ( $30.4 \pm 2.4 \text{ PSU}$ ), interstitial water ( $33.3 \pm 1.2 \text{ PSU}$ ), and groundwater ( $33.3 \pm 2.4 \text{ PSU}$ ). The highest temperature of surface water was also recorded in June ( $29^\circ\text{C} \pm 0.6^\circ\text{C}$ ), interstitial and groundwater were recorded in September ( $30.5^\circ\text{C} \pm 0.5$  and  $32^\circ\text{C} \pm 0.8^\circ\text{C}$ , respectively). The pH of surface, interstitial, and groundwater ranged from  $6.5 \pm 0.3$  to  $8 \pm 0.2$  during the study cycle (Table 1).

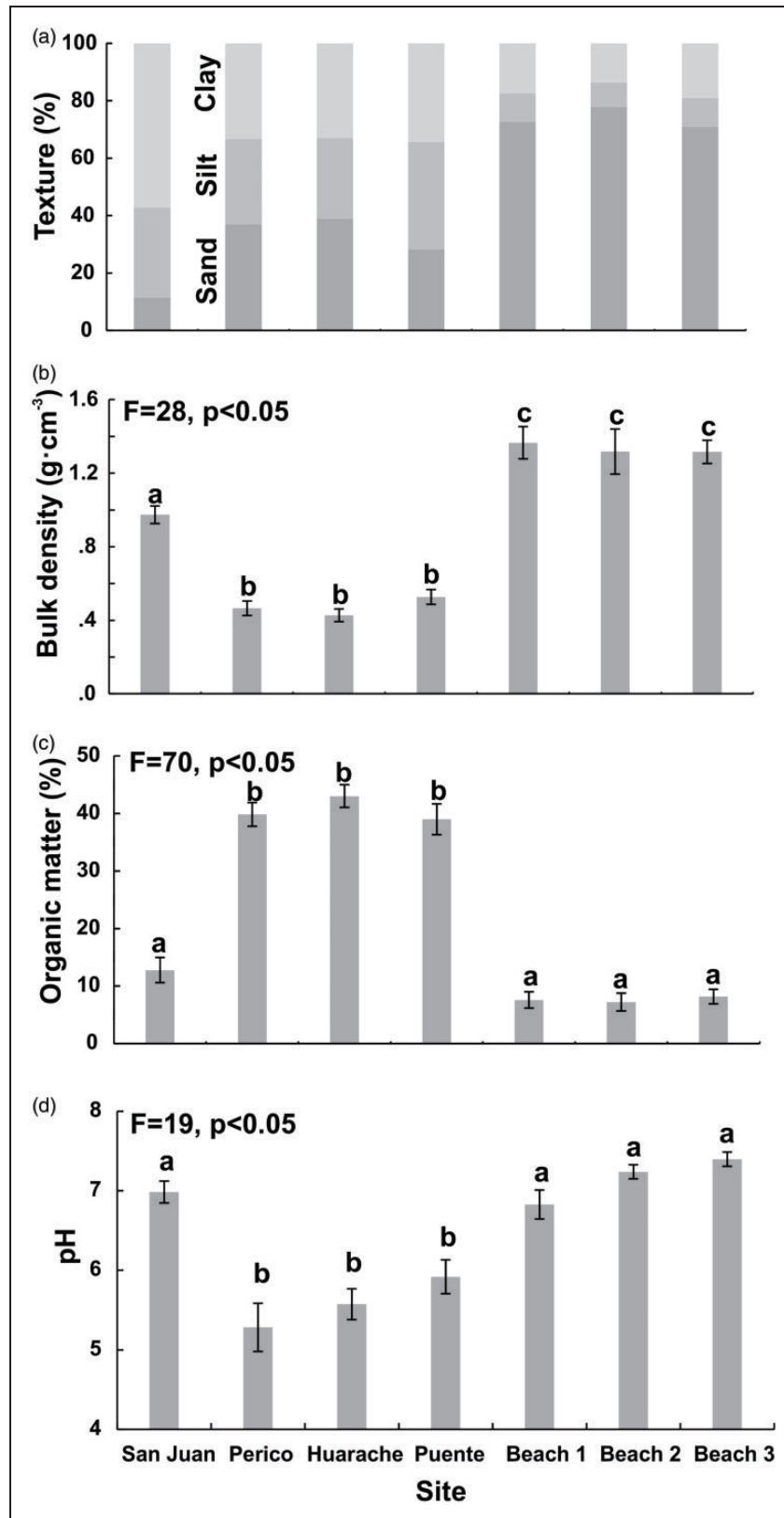
### Forest Structure of Mangroves

The mangroves were composed of *R. mangle*, *A. germinans*, and *L. racemosa* at the riverine sites, while *A. germinans* and *L. racemosa* were found at the Beach sites. The tree density was  $3\,400 \text{ trees}\cdot\text{ha}^{-1}$  in San Juan;  $1\,141 \text{ trees}\cdot\text{ha}^{-1}$  in Perico, Huarache, and Puente; and  $2\,583 \text{ trees}\cdot\text{ha}^{-1}$  at the Beach sites (1, 2, and 3). The average tree height was  $17.6 \pm 1.2 \text{ m}$  in San Juan;  $21.3 \pm 1.4 \text{ m}$  in Perico, Huarache, and Puente; and  $15.3 \pm 1.15 \text{ m}$  at the Beach sites (1, 2, and 3).

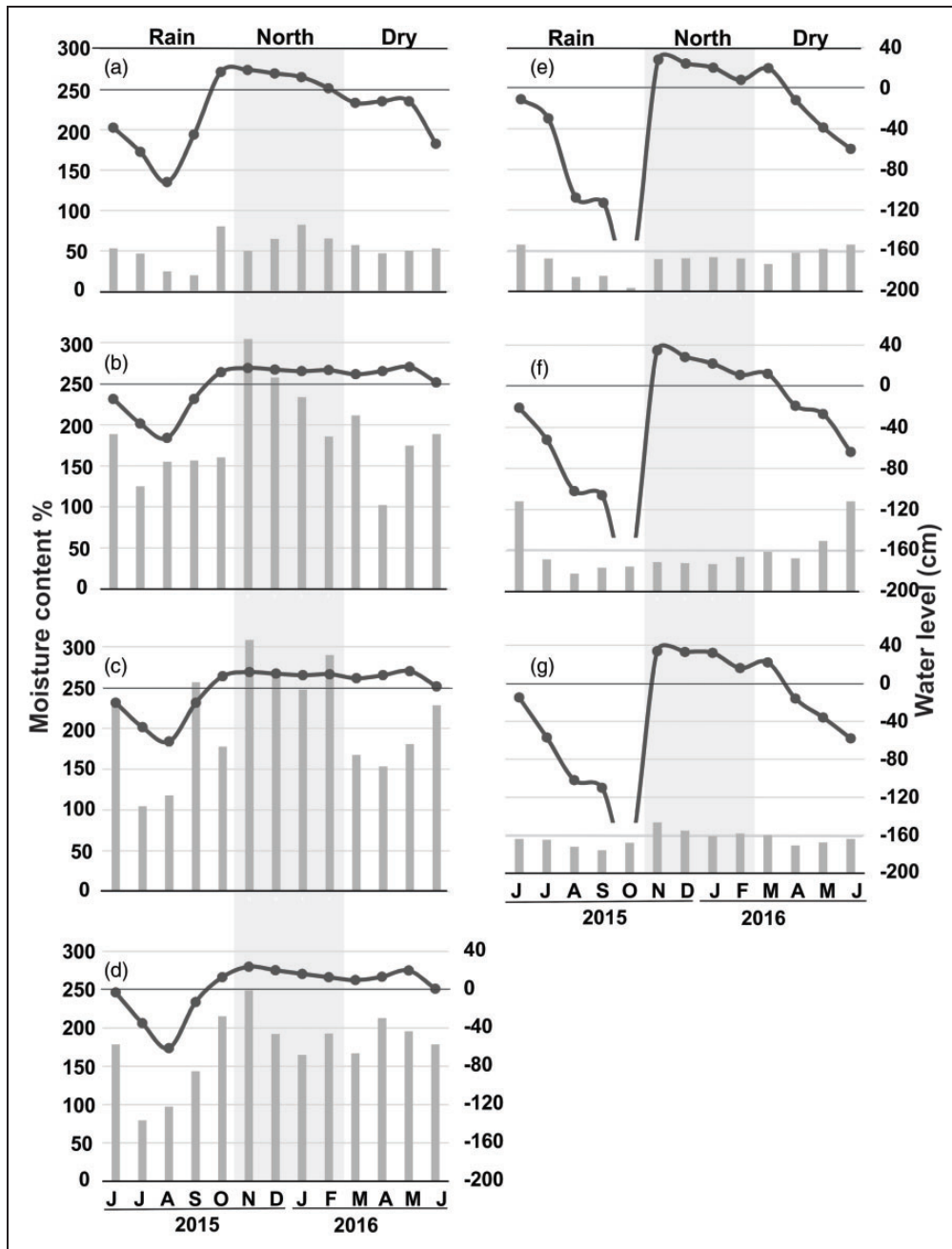
### Temporal and Spatial Variation of Litter

The estimated average litterfall was  $10.45 \text{ ton}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ . The sites showed significant differences in litter production ( $F=2.2$ ,  $p = .04$ ,  $N=91$ ) as a result of the high litter production at Huarache ( $105 \pm 10 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ) in comparison to the low litter production at Beach (site 2;  $61 \pm 7.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ). In Huarache, 71% of litter production corresponded to leaves ( $75.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; Figure 4). Overall, leaves had the highest contribution to the litter composition at all sites and represented 70% of litter on average, followed by wood or branches (17%). Stipules were recorded in the riverine sites ( $1.4 \pm 0.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$  average) with the presence of *R. mangle* (Table 2). Total litter production and the leaf proportion of litter were negatively correlated with the pH of sediments and interstitial water and were positively correlated with organic matter content. The salinity and ORP of interstitial water were negatively correlated with total litter production and the leaf proportion of litter and positively correlated with fruit production (Table 3). A litter component analysis revealed that the ORP of interstitial water was positively correlated with the leaf production of *A. germinans* ( $r = .82$ ) and negatively correlated with the leaf production of *L. racemosa* and *R. mangle* ( $r = -0.573$  and  $-0.987$ , respectively).

Three peaks in litter production occurred in June 2015 ( $112 \pm 14 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), November 2015 ( $122 \pm 9.1 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), and June 2016 ( $128 \pm 15.9 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), whereas the lowest production occurred in March ( $28 \pm 2.4 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ). Total litter was positively correlated with rainfall ( $r = .63$ ).



**Figure 2.** Physical chemical in sediment. (a) texture, (b) bulk density, (c) organic matter, and (D) pH ( $\pm$ SE = standard error). Letters show significant differences between sites (Tukey  $p < .05$ ).



**Figure 3.** Moisture content and hydroperiod at each site. (a) San Juan, (b) Perico, (c) Huarache, (d) Puente, (e) Beach 1, (f) Beach 2, and (g) Beach 3.

during the study period (Figure 5). The average litter production was similar during the rainy season (32.7%), the northerly wind season (33.6%), and the dry season (33.7%; Figure 5). Leaves had the highest contribution to litter and showed maximum production in June 2016 ( $107 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ); wood or branches had the highest production in January ( $21.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ) and February 2016 ( $31 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; Figure 5). The litter of the San

Juan site was associated with freshwater plants, including climbing plants (lianas) such as *Clytostoma binatum* (Thunb.) Sandwith, *Dalbergia tabascana* Pittier, and *Machaerium falciforme* Rudd and an arboreal species (*Haematoxylum campechianum* L.); these freshwater plants had a total contribution of  $4.5 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$  and demonstrated the highest production from March to June 2016 (59.2% of total production) in the absence of flooding.

**Table 1.** Physicochemical Parameters of Water During the Study Cycle in Centla Wetlands, Biosphere Reserve, Tabasco.

	J	J	A	S	O	N	D	J	F	M	A	M	J	F	P
<b>Surface</b>															
Sal	1.9 ± 0.4 a	3 ± 0.3 a	2.3 ± 0.3 a	1.3 ± 0.4 a	3 ± 0.6 a	2.7 ± 0.4 a	18.5 ± 3.7 b	20.7 ± 3.7 b	30.4 ± 2.4 b	23 < .05					
T (°C)	26.5 ± 0.2 a	26.5 ± 0.2 a	25.5 ± 0.1 b	24.5 ± 0.1 b	21.5 ± 0.2 c	26.9 ± 0.3 ad	27 ± 0.2 d	27.4 ± 0.2 d	29 ± 0.6 e	79 < .05					
pH	7.4 ± 0.1 a	7.5 ± 0.1 a	7.8 ± 0.1 b	8 ± 0.2 b	8 ± 0.1 b	7.8 ± 0.1 b	7.6 ± 0.1 b	7.6 ± 0.2 b	6.5 ± 0.3 c	8.6 < .05					
<b>Interstitial</b>															
Sal	16 ± 1.8 b	18 ± 3.9 ab	22.9 ± 3.3 a	19.2 ± 2.5 a	15.6 ± 2.1 ab	16.3 ± 1.6 ab	19.4 ± 2.2 ab	22.9 ± 1.9 a	26.4 ± 1.9 a	33.3 ± 1.2 c	3.3 .001				
T (°C)	29.5 ± 0.2 a	29.5 ± 0.2 a	27.1 ± 0.2 b	26 ± 0.1 c	24.8 ± 0.2 d	22 ± 0.1 e	26.5 ± 0.2 b	27 ± 0.2 b	27.4 ± 0.4 b	28.2 ± 0.2 f	84 < .05				
pH	7.4 ± 0.1 a	7.1 ± 0.2 a	6.4 ± 0.2 b	6.6 ± 0.1 b	6.8 ± 0.1 b	6.7 ± 0.1 b	6.7 ± 0.1 b	6.8 ± 0.1 b	6.8 ± 0.1 b	6.4 ± 0.1 bc	5.5 < .05				
<b>Subterranean</b>															
Sal	32.7 ± 1.8	29.6 ± 1.7	28.7 ± 3.4	25.6 ± 1.4	27 ± 1.2	29.2 ± 2.5	27.9 ± 2.7	25.9 ± 2.7	30.7 ± 1.8	33.3 ± 1.6	30.2 ± 0.9	29.9 ± 2.1	33.3 ± 2.4	1.4 .1	
T (°C)	28.3 ± 0.3 a	29.4 ± 0.6 ab	30.6 ± 0.8 bc	32 ± 0.8 cd	27.2 ± 0.1 e	27.2 ± 0.2 e	26.3 ± 0.1 f	25.4 ± 0.1 g	22.4 ± 0.2 h	26.4 ± 0.2 f	26.8 ± 0.1 f	27.2 ± 0.3 e	28.7 ± 0.7 ab	29 < .05	
pH	7.4 ± 0.1 a	7.3 ± 0.1 a	7.4 ± 0.2 a	7.2 ± 0.2 ab	7.3 ± 0.1 a	7.3 ± 0.1 a	7.3 ± 0.1 a	7.3 ± 0.1 a	7.1 ± 0.1 ab	6.9 ± 0.1 b	7 ± 0.1 b	7 ± 0.1 b	6.9 ± 0.1 b	2.1 .02	

Note. Letters indicate significant differences between months. Sal = salinity; T = temperature; F = Tukey test; (p < .05); ±SE = standard error.

## Reproductive Phenology of Mangroves

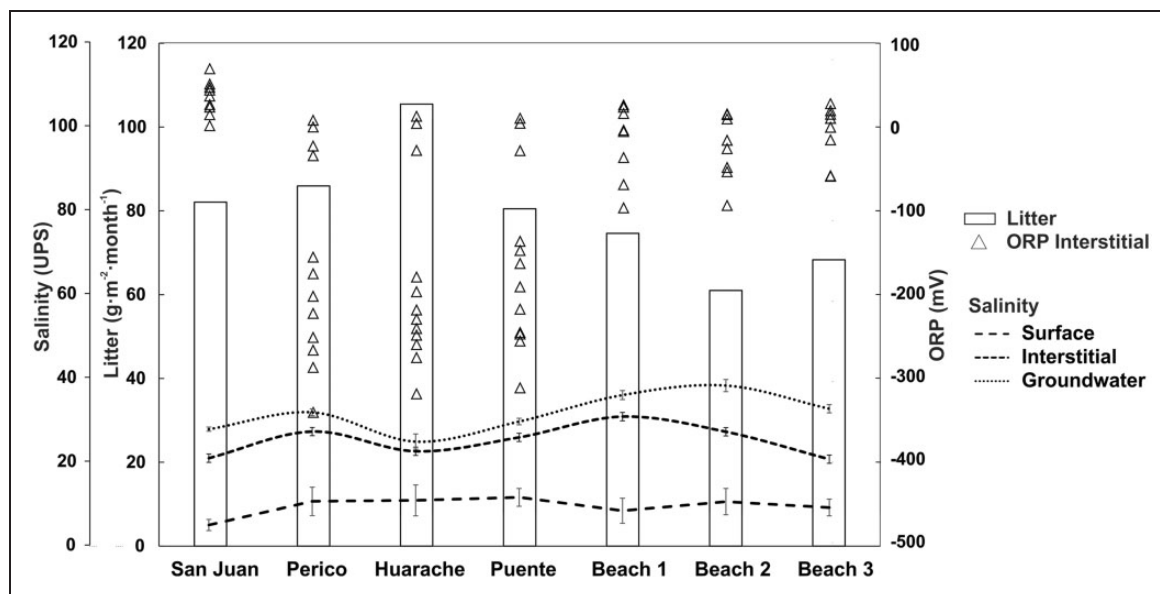
Flower production was the highest in Huarache ( $6.2 \pm 1.5 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 85% *L. racemosa*) and San Juan ( $5.8 \pm 1.1 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 70% *L. racemosa*); the lowest flower production was recorded at Beach (site 3;  $2.6 \pm 0.7 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 100% *A. germinans*; Table 2). *R. mangle* flowers were produced throughout the sampling cycle, while *A. germinans* and *L. racemosa* flowers were absent from January to May. The months of greatest flower production were June 2015 ( $17.3 \pm 2.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 51% *R. mangle* flowers), July 2016 ( $14.3 \pm 2.2 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 59% *L. racemosa* flowers), and June 2016 ( $18.2 \pm 4.7 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 81% *R. mangle* flowers; Figure 5). *L. racemosa* had the highest flower production in June 2015 ( $8.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), October 2015 ( $4.0 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), and June 2016 ( $14.8 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), while *A. germinans* had the highest flower production in June 2015 ( $8.2 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ) and July 2015 ( $8.5 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ). Flower production had a positive temporal correlation with salinity ( $r = .53$ ) and a negative temporal correlation with the ORP ( $r = -.79$ ) of interstitial water.

The highest production of fruits was recorded at Beach (Site 1;  $10.5 \pm 3.7 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 96% *A. germinans* and Site 2;  $7.7 \pm 2.4 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ; 88% *A. germinans*, Table 2). Seasonally, the highest fruit production occurred in the months of November ( $24.3 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ) and December ( $14.9 \text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ), which corresponded with 62% of fruit production over the entire study period (Figure 5). The highest fruit production at the Beach sites occurred in November and December (84% of total fruits production) in the presence of flooding; these Beach sites produced twice as many fruits (66%) in these 2 months compared with the riverine sites (34%).

## Discussion

The composition, density, and height of plant species varied across the monitored sites. San Juan was located farthest from the marine zone (located 5.1 km perpendicular to the coastline) in a transition zone where halophyte species are mixed with brackish or freshwater species (Jiménez, 1985). This ecotone results from the existence of a salinity and flood gradient that undergoes seasonal fluctuations in rainfall intensity, river flow, and tidal amplitude (Brinson, Brinson, & Lugo, 1974). Thom (1967) and Dawes (1986) state that salinity is a competitive limiting factor for freshwater plants yet is not the only determinant of zonation in mangroves that are drained by rivers and experience abundant rainfall; the nature of the substrate and the tides are the main parameters that determine zonation. In this study, the greatest structural homogeneity and the greatest tree heights and





**Figure 4.** Leaf litter, interstitial ORP and salinity in water (surface, interstitial, and subterranean) at each site ( $\pm SE$  = standard error). ORP = redox potential; UPS = Salinity Practice Units.

**Table 2.** Litterfall Component ( $\text{g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ) in Monitoring Sites in Centla Wetlands, Biosphere Reserve, Tabasco.

	San Juan	Perico	Huarache	Puente	Beach 1	Beach 2	Beach 3	F	p	Kruskal-Wallis
Leaves	53.2 $\pm$ 5.9	60.9 $\pm$ 8.1	75.3 $\pm$ 10.4	57.2 $\pm$ 10.7	39.1 $\pm$ 4.5	45.4 $\pm$ 4.4	60.1 $\pm$ 10.1	2.1	.06	
Wood or branches	12.5 $\pm$ 2.9	16.9 $\pm$ 3.1	20.9 $\pm$ 4.6	12.5 $\pm$ 2.8	8.2 $\pm$ 2.4	9.8 $\pm$ 2.3	17.3 $\pm$ 3.2	2.2	.07	
Fruit	6.1 $\pm$ 2.4 a	0.8 $\pm$ 0.3 b	1.5 $\pm$ 0.8 b	2.4 $\pm$ 1.3 b	10.5 $\pm$ 3.7 a	7.7 $\pm$ 2.4 a	1.8 $\pm$ 1 b			0.7
Flower	5.8 $\pm$ 1.1 a	5.3 $\pm$ 1.4 a	6.2 $\pm$ 1.5 a	2.4 $\pm$ 0.6 b	2.7 $\pm$ 0.7 b	5.4 $\pm$ 1.1 a	2.6 $\pm$ 0.7 b	0.65	.7	
Stipules	1.8 $\pm$ 0.3 a	1.7 $\pm$ 0.2 a	0.8 $\pm$ 0.2 b	1.4 $\pm$ 0.3 a				8.3	.001	
Total	79.4 $\pm$ 12.6	85.6 $\pm$ 13.1	104.7 $\pm$ 17.5	75.9 $\pm$ 15.7	60.5 $\pm$ 11.3	68.3 $\pm$ 10.2	81.8 $\pm$ 15			

Note. Letters indicate significant differences between sites (Tukey or Multiple Comparison Test nonparametric Kruskal Wallis,  $p < .05$ ).  $\pm SE$  = standard error.

covers were found in the Perico, Huarache, and Puente sites. These results are similar to those reported by Corella et al. (2001) and can be attributed to the contribution of sediment with a high organic matter content from the river. Also, these results are supported by those obtained by Lugo and Cintrón (1975) and Cintrón and Schaeffer-Novelli (1984) in other riparian mangroves. Meanwhile, the smallest trees heights were recorded in the Beach sites; also, greater tree densities and lower cover were encountered in areas of subsidence near the coast, this environment allows the spread of mangrove to Beach areas (Psuty, 1965; Thom, 1967).

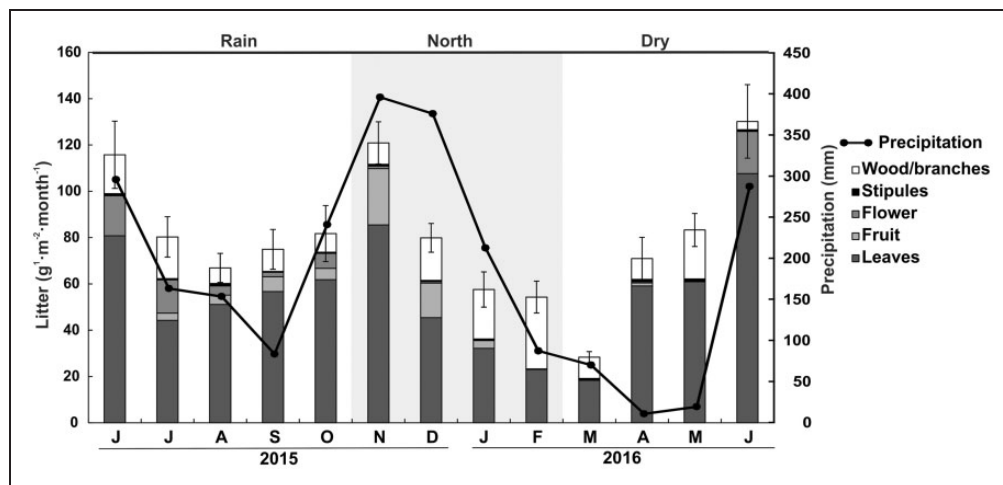
The proposed hypothesis (i) that higher litter production would be found during the months of higher rainfall when interstitial water is less saline was confirmed. Litter production showed a negative correlation with the salinity level of interstitial water and a

positive correlation with monthly rainfall. Several studies have claimed that higher litter production is related to higher rainfall (Arreola-Lizárraga et al., 2004; Day, Conner, Ley-Lou, & Navarro, 1987; Infante-Mata, Moreno-Casasola, & Madero-Vega, 2012; Zaldívar-Jiménez, Herrera-Silveira, Coronado-Molina, & Alonzo-Parra, 2004). Torres, Infante-Mata, Sánchez, Espinoza-Tenorio, and Barba (2017), for example, reported a high correlation between litter production and rainfall in the Mecoacán Lagoon ( $r = .81$ ). Meanwhile, the highly negative correlation between salinity and the total litter production or leaf proportion of litter indicates that decreasing interstitial salinity induces higher litter production. High soil salinity creates stressful conditions for mangroves and consequently leads to lower litter fall (Twilley, Lugo, & Patterson-Zucca, 1986). Similarly, Day et al.

**Table 3.** Pearson Spatial Correlation for Leaf Litter With Physical–Chemical in Water and Sediment in Centla Wetlands, Biosphere Reserve.

	Sediment							Interstitial water				Litter					
	Sand	Silt	Clay	pH	MO	BD	M	pH	T (°C)	Sal	ORP	Litter	Leaves	Flower	Fruit	Stipules	Wood
Sand	1																
Silt	-.934	1															
Clay	-.925	.762	1														
pH		-.630		1													
MO	-.665	.711		-.955	1												
BD	.641	-.805		.931	-.980	1											
M		.639		-.943	.993	-.963	1										
pH				.894	-.793		-.823	1									
T (°C)									1								
Sal										1							
ORP				.889	-.935	.851	-.957	.840	-.756		1						
Litter				-.776	.790			-.694		-.545	-.677	1					
Leaves				-.595	.738			-.517		-.614	-.665	.761	1				
Flower									.530	-.790				1			
Fruit				.585	-.723	.720				.632	-.594	-.877			1		
Stipules				-.724	.756									.675		1	
Wood						.613	.648					.675	.961		-.866		1

Note. Correlations with  $p > .05$  were removed from the table ( $p < .05$ ). MO = organic matter; BD = bulk density; T (°C) = temperature; Sal = salinity; ORP = redox potential; M = moisture.



**Figure 5.** Component litter production and precipitation in CWBR, México (Tukey test,  $p < .05$ ;  $\pm SE$  = standard error).

(1996) reported a highly negative relation ( $r^2 = -.77$ ) between leaf litter and interstitial water salinity in the Terminos lagoon. Agraz-Hernández, García-Zaragoza, Iriarte-Vivar, Flores-Verdugo, and Moreno-Casasola (2011) also encountered a highly negative correlation between litter production and salinity at a soil depth of 50 cm (interstitial) in the La Mancha Lagoon, Veracruz.

The ORP of interstitial water was negatively correlated with total litter production and the leaf proportion of litter. The component analysis revealed that ORP of interstitial water was positively correlated with the proportion of *A. germinans* leaves yet negatively correlated with the proportion of *L. racemosa* and *R. mangle* leaves; this indicates that less reducing conditions stimulate the production of *A. germinans* leaves and inhibit

the production of *L. racemosa* and *R. mangle* leaves. Torres et al. (2017) also identified similar correlations in the Mecoacán Lagoon. In this study, a similar trend was identified for the fruit component of litter; oxidative conditions were positively correlated with fruit production of *A. germinans* ( $r = .56$ ) and negatively correlated with fruit production of *R. mangle* ( $r = -0.4$ ). Several research studies have suggested that species of the *Avicennia* genus maintain the root zone of soil more oxidized in comparison to *Rhizophora* species (Nickerson & Thibodeau, 1985; Thibodeau & Nickerson, 1986; Alongi, 2009); this is likely due to the higher ratio of oxygen released by *Avicennia* roots in comparison to *Rhizophora* roots (Balk, Keuskamp, & Laanbroek, 2016). Reducing soil conditions are an important factor in wetlands, as such conditions can influence plant survival, growth, and productivity and can negatively affect the photosynthetic rates of some species (Pezeshki & DeLaune, 2012).

Several works have studied mangrove productivity (litter) in the Gulf of Mexico and have recorded results similar to those of this study in the CWBR. Rico-Gray (1979) reported litter fall values of  $1\,025\text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$  in the La Mancha Lagoon, Veracruz. In another study, Díaz-Mena (1988) recorded a litter fall  $931\text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$  in Grande Lagoon, Veracruz, where leaves represented the main component (71.5%) of litter, similar to this study. Bolio (2001) also found that 71% of litter was composed of leaves in the El Sábalo CWBR estuary and that leaves made the highest contribution toward total litter in the months of highest rainfall.

Low productivity values were reported by Day et al. (1996) at the edge of a mangrove in the Terminos Lagoon ( $793\text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$ ). Meanwhile, Barreiro-Güemes (1999) reported an annual average litter production of  $661\text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$  in the Pom-Atasta estuarine system, Campeche. Torres et al. (2017) reported a litter production of  $515\text{ g}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$  in the Laguna Mecoacán, where litter production was highly correlated with rainfall. Flores-Verdugo, Day, and Briseño-Dueñas (1987) found that litter production was not necessarily correlated with the structure of the mangrove forests; regions with high seasonal rainfall, high freshwater inflow, and large nutrient load tended to produce greater litter fall. Throughout the sampling cycle, the riverine sites had the highest productivity, except during the months of November and December. In these latter 2 months, the Beach sites attained the highest productivity as a result of the abscission of *A. germinans* fruits in response to the beginning of the flood period.

The hypothesis (ii) that a greater production of reproductive parts (flowers and fruits) would be found in mangroves during the rainy season was rejected. The greatest flower production occurred in the months of

June and July in the absence of flooding and the greatest fruit production in November and December during the highest flood levels. This confirms the marked seasonal synchronization and adaptation of flowering and fruiting seasons with respect to rainfall and the hydroperiod (Sharma, Kamruzzaman, Rafiqul, Analuddin, & Hagihara 2011; Shunula & Whittick, 1999; Stela & Salomao, 2009). Mangroves of the CWBR were similar to those of the Mecoacán Lagoon (Torres et al., 2017), where flower production was highest in the months without flooding (from June to August) and was also positively correlated with salinity. This indicates an adaptation response: Fruits are released during the period of greatest flooding and lowest salinity (November and December). Fruits and propagules then disperse via the surface hydrodynamics and flotation patterns of mangroves and are trapped or rooted to the soil by existing roots (Rabinowitz, 1978). A similar pattern was identified by Agraz-Hernández et al. (2011) in Terminos Lagoon.

The hypothesis (iii) that soil organic matter content would be positively correlated with sediment type, silt or clay proportion, litter production, and maximum flooding was confirmed. The mangroves of this study area receive a high input of organic matter of exogenous origin. A higher organic matter content was identified in sites with silt substrates and with high litter production (Perico, Huarache and Puente), and organic matter content was correlated with the hydroperiod. The Beach sites had a higher sand content, higher bulk density, lower organic matter retention, and lower soil moisture in contrast with the riverine sites (Perico, Huarache, and Puente), which had a higher percentage of silt or clay, retained more organic matter, and had greater moisture content, as also documented by De-Boer (2000) and Torres, Infante-Mata, Sánchez, Espinoza-Tenorio, and Barba (2018). Bjorn and McClaugherty (2008) found that soils with higher clay content can store more organic matter than sandy soils; these authors claimed that texture is the most important physical property of soil. Texture influences water and nutrient dynamics because of its influence on soil porosity and permeability. Notably, the San Juan site presented a high percentage of silt or clay, low organic matter, and low moisture; these characteristics can be attributed to the higher microtopography of this site in comparison to the other riverine sites.

Rainfall runoff in the study area flows from south to north. In this area, several higher sections of land (up to 28 cm in height) correspond with the federal highway 180 (see Figure 1) and lead to the retention of water in the freshwater swamps located at the southern interior of the highway. Thus, these freshwater swamps only have a scarce contribution to the hydrodynamics of the mangroves at this site (Cruz, 2001). This retention of water is

also evident in the division of vegetation on both sides of the highway. Hydrophytes or freshwater swamps are distributed along the southern interior of the highway, while the coastal mangrove fringe is distributed along the northern side of the highway (Cruz, 2001). In this study, the water level of the Beach sites decreased to less than  $-150$  cm in October (dry period) and experienced a delay of more than 1 month in reaching the surface water conditions of the riverine sites. Once again, this low water flow can be attributed to the presence of federal highway 180, which limits water flow toward the mangrove areas. However, the Beach sites have apparently adapted to the modification of the hydrological regime, as the mangrove trees of these sites release fruits during the flooding months (November–December). The mangrove trees of the riverine sites release the most fruits from September to December. The ORP levels also demonstrated the oxidative conditions of the Beach sites; these conditions can be attributed to the high sand content and the low water retention (moisture) of these sites as a consequence of the modified hydrological flow.

Finally, these results indicate that the litter production is related to the response of the mangrove to the variation of the environmental conditions of each site (sediment texture, hydroperiod, moisture content, salinity, ORP, and organic matter). Litter production is associated with fluctuations in the flood pattern (hydroperiod) and rainfall; these fluctuations directly affect salinity and ORP levels and result in spatial and temporal increases or decreases in litter production. The modification of the hydrological regime following the construction of the federal highway has also directly affected the phenology of the mangroves along the northern coastal side of the highway. Civil engineering modifications to the federal highway should be carried out to improve the local hydrological cycle, and permanent monitoring plots should be established to continuously measure litter production. The estimation of standing and belowground (roots) biomass and litter production is important for achieving a better understanding of primary productivity, nutrient dynamics, and the main sources of in situ energy in mangroves.

## Implications for Conservation

A number of factors affect the structure and productivity of mangrove forests, including hydrology, soil salinity, and soil type (Lugo, Brown, & Brinson, 1988). In this sense, the information of this study on primary productivity (litter) in relation to environmental conditions allows us to identify the relationship of the highest litter production in the months of high rainfall, higher level of flooding, sites with high content of clay, and low salinity; these relationships indicate that the hydrological regime and the substrate properties interact and influence the

productivity and distribution of mangrove species (Thom, 1967).

In addition, the results show that the mangrove in CWBR responds to changes in hydrology with high correlation with leaf litter production and fruit abscission delay at sites where surface water flow is obstructed by the federal highway 180. Pool, Snedaker, and Lugo (1977) reported that the lack of surface water runoff (in terms of fresh water and nutrients) determines the limited development of mangroves (Jiménez, 1985). The implications of the conservation of the mangroves is based on an adequate planning of the different constructions related to anthropogenic activities, to avoid changes in the hydrology of the coastal wetlands that affect the primary productivity and even at risk the survival of the mangrove forests.

## Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

## Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: This work was supported by Consejo Nacional de Ciencia y Tecnología, Mexico (269540) and the National Commission for Natural Protected Areas. Additional support was provided by the Network for the Knowledge of Coastal Resources in Southeastern Mexico (RECORECOS). Jony R. Torres was a recipient of a PhD fellowship from Consejo Nacional de Ciencia y Tecnología, Mexico (377996).

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