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Ecophysiological Response of *Rhizophora mangle* to the Variation in Hydrochemistry during Five Years along the Coast of Campeche, México

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Abstract: We evaluated the phenological response and litterfall production of *Rhizophora mangle* to changes in pore water chemistry over a five-year period (from 2009 to 2014 and 2010 to 2016) along the coast of Campeche, México. Severe drought conditions were recorded in 2009 with a Standardized Precipitation Index (SPI) of −1.5 and again in 2015 with a SPI of −1.16). A precipitation deficit of 22.1% was recorded between 2009 and 2016 ranging from 9.5% in Laguna de Terminos in the south to 64.4% in Los Petenes Biosphere Reserve in the north. Precipitation varied significantly per year ($p < 0.001$), seasonally ($p < 0.001$), and between years and seasons ($p < 0.001$). An interaction was observed in the salinity ($p < 0.05$), redox potential ($p < 0.001$), and precipitation ($p < 0.001$) of the Laguna de Terminos, Rio Champoton, and Los Petenes Biosphere Reserve regions. Significant differences were found between the years in the leaf and propagule production ($p < 0.001$), and between seasons in production of leaves, flowers, and propagules ($p < 0.001$). The determining factor in the production of flowers during both the rainy and dry seasons was the salinity, and the determining factors for the production of propagules were the redox potential and salinity. The results of this study suggest a low phenotypic plasticity in *R. mangle.*

Keywords: total litterfall; drought; mangrove; salinity; potential redox; standardized index of precipitation

1. Introduction

Seasonal and annual variation in climate affect the temporal and spatial patterns of precipitation and temperature, on both local and global scales, of many coastal regions around the world [1]. Climate change is considered to be a threat to individuals, species, and ecosystems, because it affects their structure and functioning, as well as the interactions of ecosystems, such as biological, geochemical, and hydrological systems. Climate change also affects the welfare of human society [2–4].

Drexler et al. [5] demonstrated that short-term climatic disturbances, such as El Niño/South Oscillation (ENSO) and the Pacific Decadal Oscillation (DPO) influence important coastal processes.

Disrupting the normal intensity, frequency, and duration of precipitation, storms and hurricanes, droughts, hails, and frosts. With repeated drought cycles, these disturbances can potentially affect the structure and function of mangrove forests and upstream ecosystems [6,7]. This situation was observed in 2008 when the cold phase of ENSO, called LA NIÑA, was recorded, and the warm phase of this phenomenon, called EL NIÑO, then occurred in 2009. Thus, rapid environmental changes have prompted increased interest in understanding current and future threats to biodiversity and their consequences for ecosystem health and services [8]. Growing evidence is demonstrating that climate change has altered the phenological synchrony of various organisms, but the underlying mechanisms are unclear, particularly in plants [9,10]. Other authors have indicated that the phenological patterns are closely related to climate [11]. As such, climate change is expected to affect growth patterns in the phenological stage and during the flowering and fruiting of plants, including mangroves. Wang'ondu et al. [12] reported that the plasticity of the reproductive phenology of *Rhizophora mucronata* and *Sonneratia alba* in Kenya is related to certain variations in the climate and environment.

Plants respond to imbalances caused by environmental variations, offsetting this plasticity through mechanisms that change the biochemical capacity for assimilation of resources, such as changes in biomass and the rate of tissue loss. This adaptation allows plants to grow in a broad range of levels of reserves. However, the plasticity or the suitability of the species to its environment is limited, and substantial changes in the balance of resources can cause changes in the composition of the species, with a greater impact on the phenology of the plants [10,13]. Consequently, studying phenology is an excellent tool for examining climate change [14,15]. Conversely, resistance is the capacity to withstand change, which is the ability to not be perturbed or affected by a climate extreme; resilience is the capacity to recover after perturbation, i.e., the ability to recover after being affected by a climate extreme [16,17]. Changes in rainfall, hydroperiod, and the physicochemical properties of pore water and sediments as consequences of climatic variations affect the functioning and modify the structures of mangrove communities such as photosynthesis, biomass, composition, richness, and productivity [5,18–21].

The distribution of Mexican mangroves varies along the coast of México. The extensive continental platform and high rainfall in the Gulf of Mexico promote the development of vast coastal wetlands. This is particularly obvious in the Yucatan Peninsula, which has the most extensive mangrove coverage in the state of Campeche [22,23]. However, climate variation in the state of Campeche may alter the periods of reduction or an excess of fresh water, generating a combination of extreme conditions, including salinization of soils, sustained waterlogging, and decreases in oxygen and pH [24]. From 2006 to 2010, significant changes in the chemical conditions of the pore water and the production of total litterfall and hypocotyls occurred as a result of the variations in the seasonal precipitation in monospecific forests of *Rhizophora mangle* L., located in Laguna de Terminos, Campeche, México [18]. The mangrove forests located along the coast of Campeche exhibited drought conditions in 2009 compared to in 2010. During this period, seasonal changes in rainfall were also apparent [25]. There is a study which reported on the annual reduction in rainfall in the Maya region of México (which included the states of Quintana Roo, Campeche, Chiapas, Tabasco, and Yucatan), Belize, Guatemala, Honduras, and El Salvador during the 21st century [26]. These authors predicted a decrease in rainfall between 10% and 22% during the rainy season, and 48% during the dry season. This severe change in the regime of rainfall in 2009 caused a hydrologic change along the coast of Campeche, in the south–southwest region. As a result, salinity increased and the redox potential in the pore water decreased. Laguna de Terminos and the Rio Champoton showed anoxic conditions, whereas the Los Petenes Biosphere Reserve showed hypoxic conditions, which were considered remarkably marginal conditions [25]. The hydrological variations that occurred in 2009 also caused significant changes in the physiological indicators studied in populations of mangroves along the coast of Campeche.

The objective of this study was to evaluate the variations in the hydrochemical characteristics of the pore water, including salinity and the redox potential, and precipitation and its effects in seven *R. mangle* (L.) dominated mangrove forests along the coast of Campeche during 2009, 2010, 2014, 2015, and 2016. We asked the following questions: (1) How does the precipitation vary, on a yearly and seasonal basis, along the coast of Campeche, during the study period? (2) Are there significant differences among years and seasons in the variation of the salinity and the redox potential of the groundwater? (3) What are the responses to this variation in terms of the productivity (total litterfall) and the reproductive phenology (flower and hypocotyl production) with the environmental factors in the different *R. mangle* forests between the three areas? (4) Is *R. mangle* resilient to seasonal and yearly variations in salinity and redox potential?

2. Materials and Methods

2.1. Study Area

The state of Campeche is located in Southern México, with 523 km of coastline along the Gulf of México. Campeche has a tropical savanna climate, classified as Aw by the Köppen–Geiger system, with heavy rain falling during summer from June to October. Precipitation increases from the northwest (600 mm/year) to the southeast (1400 mm/year) [27,28]. Campeche has the largest Mexican coast mangrove coverage, at 25.9%, and the best-preserved forests, with a total area of 197,620 ha, and is considered as part of the most critical coastal ecosystem in Mesoamerica [29,30]. Along the Campeche coast, the largest mangrove forest is located in the northern area in Laguna de Terminos with a total area of 107,262 ha and is best preserved in the southern area in the Los Petenes Biosphere Reserve with 73,776 ha. The species that dominates in the north is *R. mangle*, and *A. germinans* in the south. In this study, we only analysed *R. mangle* in seven mangrove forests, distributed in three main areas: Laguna de Terminos (LT; Atasta, Estero Pargo, Sabancuy, and Xibuja), Rio Champoton (RC; Champoton), and Los Petenes Biosphere Reserve (PBR; Rio Verde and Peten Neyac) (Figure 1).

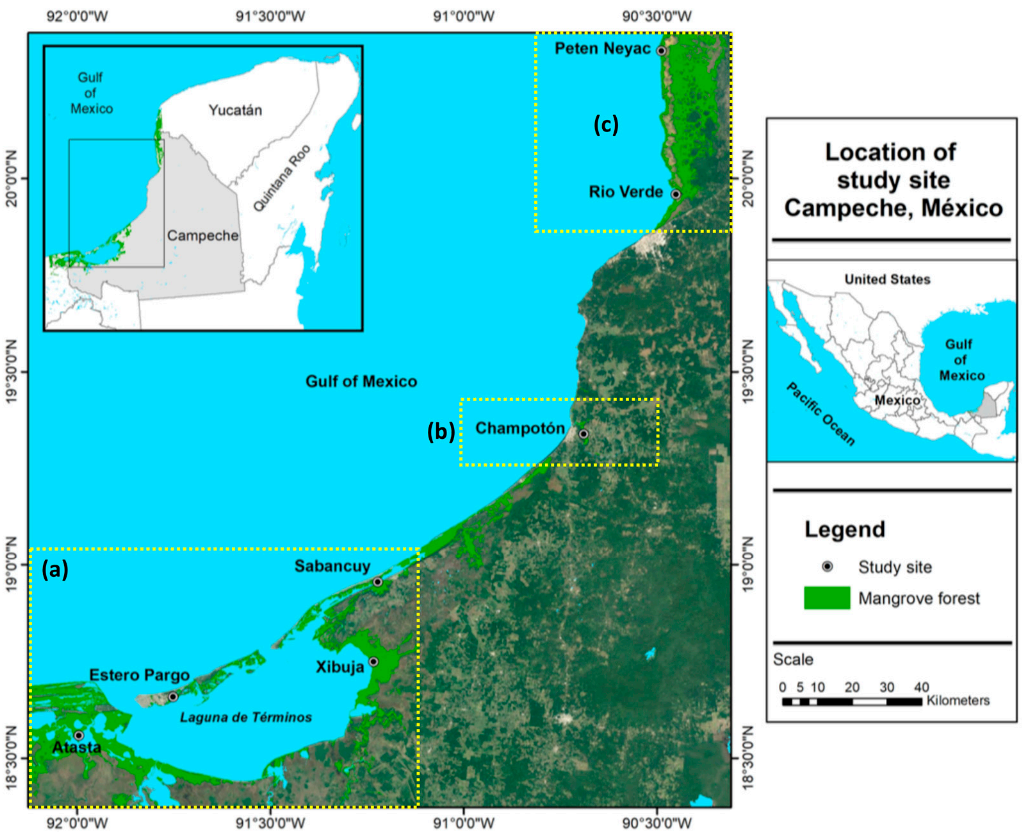

Figure 1. Map of the seven study mangrove forests bordering the coast of Campeche, México. (**a**) Laguna de Terminos, (**b**) Rio Champoton, and (**c**) Los Petenes Biosphere Reserve.

2.2. Analysis of Drought

The standardized precipitation index (SPI) assessed the deficit or excess of precipitation in 2009, 2010, 2014, 2015, and 2016 based on the criteria provided by Mckee et al. [31] (Table 1). The SPI evaluates the deficit or excess precipitation for a site during a given period, from one month up to four years [32,33]. SPI values most commonly fall in the range of −2 to +2. The values correspond to different categories of drought [24]. To calculate the SPI, we used the Climate Computing Project (CLICOM) of the Comision Nacional del Agua (CONAGUA) [34]. This database collected the daily precipitation accumulated data from 48 stations (meteorological number stations 4001–4088) in the state, for the period of 1920 to 2016. The SPI was calculated based on the analysis of both annual and seasonal (dry season is February–April and the rainy season is May–October) data [18].

Table 1. Standardized precipitation index (SPI) categories, based on the criteria provided by McKee et al. (1993).

Category	SPI
Extreme wet	≥2.00
Severe wet	1.50–1.99
Moderate wet	1.00–1.49
Humidity	0.50–0.99
Normal prone to wet	0.00–0.49
Normal prone to dry	−0.49 to 0.00
Drought	−0.99 to −0.49
Moderate Drought	−1.49 to −1.00
Severe Drought	−1.99 to −1.50
Extreme Drought	≤−2.00

2.3. Pore Water Salinity and Redox Potential

Each month, we measured the pore water salinity and redox potential in the seven mangrove forests up to the forest border edge during a five-year period. The pore water is defined as the water that flows between the particles of the sediment. The redox potential measures the activity of the electrons of the chemicals found in the ground water, and it is related to the oxygen dissolved in water [35]. We installed three PVC tube collectors, 10.16 cm in diameter and 1.5 m in length, at a depth of 0.50 m from the sediment surface in each mangrove forest. The most substantial amount of tree root biomass is usually located at this depth [19,20]. The tubes were installed transversally to the coastline. The first tube was placed at the edge of the shoreline and the third was placed inside the mangrove forest. These 1 cm tube holes were drilled to a depth of 30 cm [36]. Water samples were collected after the tubes were drained and the water was stabilized. The redox potential was measured using a HACH HQ40d Portable Multi Meter. The HQd meter used an oxide reduction potential probe (ORP-Redox), which was not filled with gel. The ORP-Redox solution used intervals of ±1200 mV. The salinity was determined with refractometers ATAGO, Inc., with a measurement range of from 0 to 100 Practical Salinity Units (PSU) [20].

2.4. Litterfall Production

Litterfall production was evaluated each month, measured by dry weight of the total litterfall and its components for *R. mangle*, and collected during a five-year period (2009, 2010, 2014, 2015, and 2016). In each forest, 14 litterfall baskets that were 0.25 m^2, with 0.1 mm mesh, and 30 ± 5 cm deep, were installed [20]. Seven baskets were placed in each 10 × 10 m plot, across the two plots per study site. Baskets were suspended under the tree canopy using nylon threads tied to each corner of the basket and above the highest tide level. The collected material was dried at 65 °C in a convection oven until a constant weight was obtained [20,37]. The dry material was separated into leaves, flowers, propagules, branches, stipules, and miscellaneous. We calculated productivity as the total litterfall dry weight and as the proportion of each type of litterfall dried weight fractioned per square meter per day and per year. Baskets were installed in February 2009, so January data does not exist for this year.

2.5. Statistical Analysis

The pore water physicochemical parameters and phenological characteristics between and among sites, years (2009, 2010, 2014, 2015 and 2016), and seasons (dry and rainy) were tested using factorial ANOVA. Subsequently, Fisher's Least Significant Difference test (LSD) was applied post hoc to determine significant differences among the means using an $\alpha = 0.05$ level of significance. The normality was analyzed using the Shapiro–Wilk test with an $\alpha = 0.05$ significance level; data did not show a normal distribution were transformed [38]. We applied the Pearson correlation coefficient to correlate the precipitation with the years, salinity, redox potential, forest structure, and litterfall. Finally, a simple regression analysis was used to evaluate the dependence of the total litterfall and the phenological characteristics on precipitation, salinity, and the redox potential. All statistical analyses were performed using STATISTICA V.12 (StatSoft, Inc., Palo Alto, CA, USA, 1984–2014).

3. Results

3.1. Analysis of Drought

Along the coast of Campeche, the precipitation was heterogeneous between 1960 and 2016 (Figure 2). Severe droughts were registered from 1960 to 1970, 1981, 1982, 1990, and 1998. However, the most intense drought occurred from 1960 to 1965 in LT and in 1982 for PBR. In contrast, the precipitation surpassed the reference average in 1975, 1980, 1992, and 1997 (Figure 2). From 1960 to 1999, the extreme drought presented every six years, while for the period from 2000 to 2016, droughts were more frequent, between 3 to 4 years apart, but were classified as severe to moderate droughts.

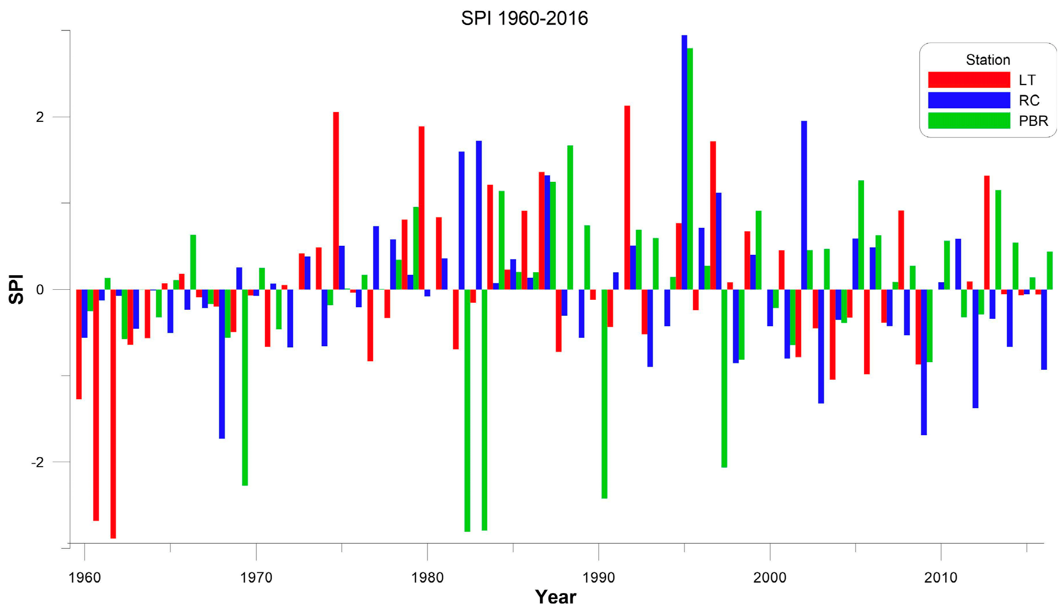

Figure 2. Standardized Precipitation Index (SPI) for the period of 1929 to 2016. SPI was calculated based on the annual precipitation data for 48 stations along the coast of Campeche.

Severe drought conditions were registered in 2009 (SPI = −1.5) and moderate drought in 2015 (SPI = −1.16), whereas 2010 and 2014 were wet with SPI values of 0.56 and 0.54, respectively. In 2009, the SPI was negative in all seasons, and particularly during the rainy season (−1.34) (Figure 3). A precipitation deficit of 22.1% was registered between 2009 and 2016, increasing from 9.5% in LT in the south to 64.4% in PBR in the north. The precipitation significantly differed between years (F = 6.76,

$p < 0.05$), seasons ($F = 216.05$, $p < 0.001$), and the year–season interaction ($F = 11.82$, $p < 0.05$) (Table 2, Figure 3). Conversely, the most severe drought was registered in the southern area (LT; SPI = −0.80 in Atasta and −0.65 in Sabancuy). Precipitation significantly differed between LT, RC, and PBR ($p < 0.05$; Table 3). Factorial ANOVA showed that the precipitation varied significantly between areas (LT vs. RC vs. PBR) ($F = 13.12$, $p < 0.001$), years ($F = 6.90$, $p < 0.001$), seasons ($F = 171.79$, $p < 0.001$), and between years and seasons ($F = 10.36$, $p < 0.001$) (Table 3).

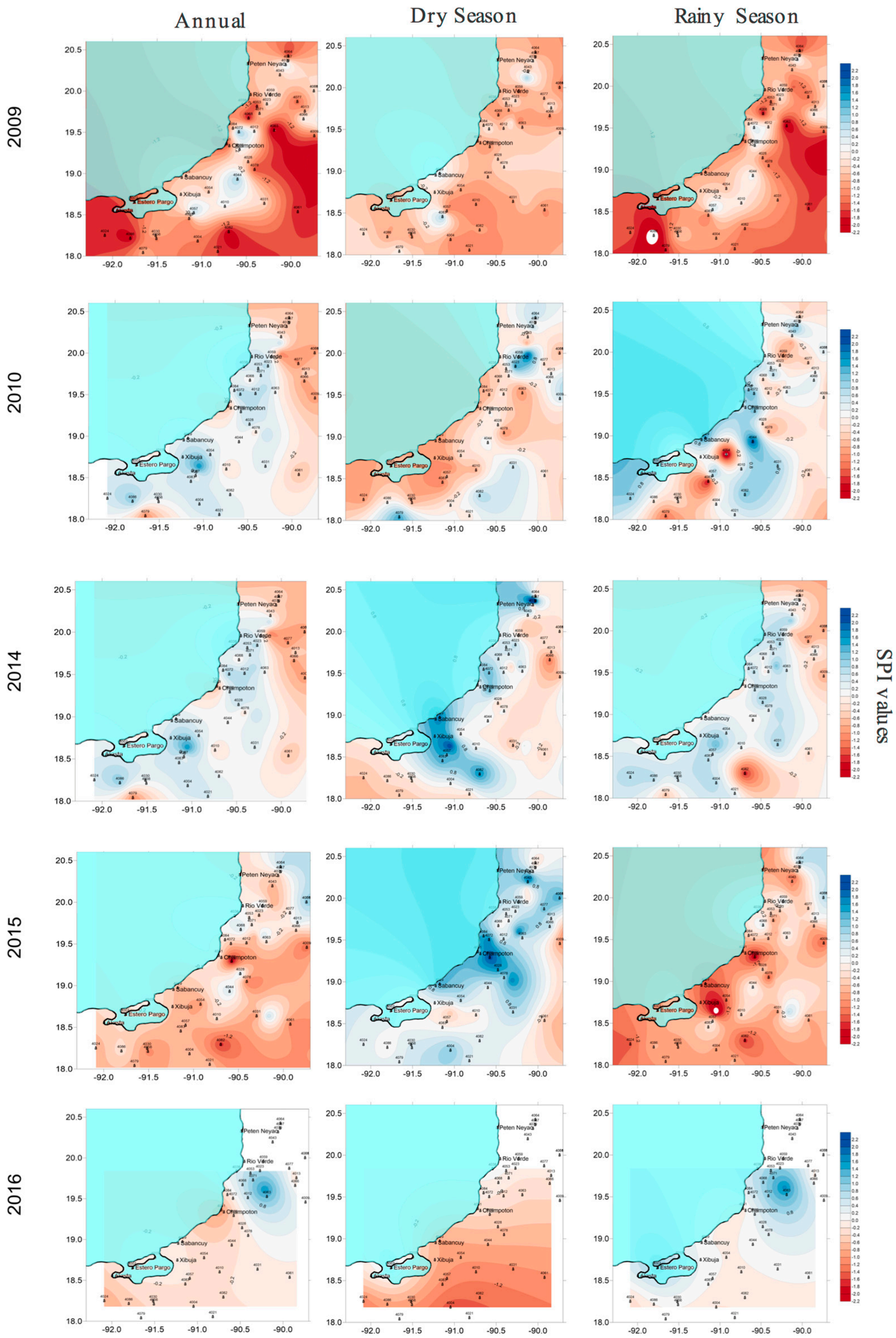

Figure 3. Standardized precipitation index (SPI) along the coast of Campeche, México.

Table 2. Factorial ANOVA (three-factor) for (**A**) sites, (**B**) years, and (**C**) seasons for salinity, redox potential, and precipitation in seven mangrove forests along the coast of Campeche (2009–2010 and 2014–2016).

Factor	Variables (Value F)			
	df	Salinity	Redox Potential	Precipitation
A: Sites	6	261.28 **	12.40 **	4.24 **
B: Year	4	10.59 **	265.43 **	6.76 **
C: Season	1	5.55 *	3.71 *	216.05 **
A × B	24	4.33 **	4.47 **	0.55
A × C	6	7.03 **	3.22 *	0.27
B × C	4	11.41 **	24.45 **	11.82 **
A × B × C	24	4.88 **	2.24 **	1.21
Error	377			

p-value: * $p < 0.05$, ** $p < 0.001$.

Table 3. Factorial ANOVA (three-factor) (**A**) sites, (**B**) year, and (**C**) seasons for salinity and precipitation between the three areas (Laguna de Terminos, Rio Champoton, and Los Petenes Biosphere Reserve) along the coast of Campeche (2009–2010, 2014–2016).

Factor	Variables (Value F)			
	df	Salinity	Redox Potential	Precipitation
A: Sites	2	79.74 **	6.23 *	13.12 **
B: Year	4	4.62 *	145.38 **	6.90 **
C: Season	1	3.26 *	1.67	171.79 **
A × B	8	0.85	6.08 **	1.68
A × C	2	4.22 *	3.00 *	0.80
B × C	2	2.29 *	21.30 **	10.36 **
A × B × C	8	1.57 *	3.8 **	3.61 **
Error	343			

p-value: * $p < 0.05$, ** $p < 0.001$.

3.2. Pore Water Salinity and Redox Potential

The highest salinity and reduced pore water concentration values were recorded in 2009 at 41.5 ± 13.9 PSU and –245.6 ± 95.6 mV, respectively, which correspond to mesohaline–hypersaline conditions. For 2010, the average salinity was slightly lower, and the oxic condition was higher (37.3 ± 16.9 PSU and −117 ± 84 mV, respectively). From 2014 to 2016, salinity increased by 3.9 ± 1.6 PSU, meaning that the hypoxic condition changed to an anoxic condition at −317.1 ± 86.3 mV. Similar to precipitation, the salinity and redox potential significantly varied between ecosystems (F = 79.74, $p < 0.001$; 6.23 $p < 0.05$), years (F = 4.62, $p < 0.05$; 145.38, $p < 0.001$), and seasons (F = 3.26, $p < 0.05$; F = 1.67, $p < 0.001$; Table 2). Salinity and precipitation showed an inverse correlation in 2009 (r = −0.270, $p < 0.05$) and 2015 (r = −0.316, $p < 0.001$). Salinity and redox potential were significantly different among years (F = 10.59 and F = 265.43, $p < 0.001$) and the year–season interaction (F = 11.41, F = 24.45, $p < 0.001$) (Table 2). In addition, salinity was significantly different between 2010 and 2014 and between 2015 and 2016 ($p < 0.05$; Table 4, Figure 5).

Table 4. Comparison of the Fisher's Least Significant Difference post hoc tests conducted for the nested ANOVA on potential redox, salinity, and precipitation in terms of area and year. LT: Laguna Terminos; RC: Rio Champoton; RBP: Los Petenes Biosphere Reserve.

Areas	LSD (Least Significant Difference)		
	Redox Potential	Salinity	Precipitation
LT–RC	−11.9135	−19.7876 *	−41.2691 *
RC–RBP	12.7994	−25.0285 *	−5.438
RBP–LT	24.7128 *	−5.24087 *	35.8311 *
Years			
2009–2010	89.6869 *	−2.97143 *	−37.9746 *
2009–2014	248.949 *	−2.13294 *	−7.95345
2009–2015	211.541 *	−5.27381 *	−31.6606 *
2009–2016	174.552 *	−5.91964	23.7823
2010–2014	159.262 *	0.838492	30.0212 *
2010–2015	121.854 *	−2.30238 *	6.31405
2010–2016	84.8649 *	−2.94821 *	61.7569 *
2014–2015	−37.4079 *	−3.14087 *	−23.7071 *
2014–2016	−74.3968 *	−3.78671 *	31.7357 *
2015–2016	−36.9889 *	−0.645833	55.4429 *

p-value: * $p < 0.05$.

In 2009, the southern (LT) and northern (PBR) areas showed the highest salinities at 43.7 ± 7.0 PSU and 48.6 ± 6.0 PSU, respectively. A mesohaline condition, at 22 ± 5 PSU, was recorded for RC. Conversely, PBR showed anoxic conditions at −307.4 ± 31.2 mV, whereas RC and LT were hypoxic at −252.2 ± 110.3 mV and −214.1 ± 97.2 mV, respectively (Figure 5). PBR showed the most severe conditions, being both hypersaline and anoxic in both the rainy season (47.0 ± 7.0 PSU and −310.3 ± 33.9 mV) and the dry season (49.1 ± 3.0 PSU and −269.4 ± 24.2 mV). However, for LT, hypersalinity was registered only during the rainy season (44.5 ± 13.76 PSU) with hypoxic–anoxic conditions (−222.2 ± 69.7 mV). For RC, the conditions were mesohaline and anoxic for both seasons (Figure 5). An inverse correlation was detected between the salinity and redox potential in the three mangrove areas ($r = -0.40$, $p < 0.05$) in the same year.

During 2010, oxic and mesohaline conditions were recorded in both seasons in the three areas (Figure 5). From 2014 to 2016, PBR reported similar severe conditions compared to those in 2009, and hypersalinity and anoxic conditions were registered in both seasons at 49.8 ± 5.4 PSU and −329.5 ± 29.9 mV, respectively. For LT, the salinity (41.5 ± 1.8 PSU) was higher and it was more anoxic (−332.7 ± 30.1 mV) than RC (26.0 ± 3.3 PSU, −323.7 ± 36.3 mV). The year–ecosystem interaction showed significant differences in salinity ($p < 0.05$; and redox potential ($p < 0.05$) (Table 3).

Despite the changes in salinity and redox potential between 2014 and 2016 in both seasons, the mesohaline condition remained stable in the three areas. In general, significant differences in salinity and redox potential were detected among sites ($F = 79.74$, $p < 0.001$; $F = 6.23$, $p < 0.05$) and among years ($F = 4.62$, $p < 0.05$; $F = 145.38$, $p < 0.001$, Table 2). The most extreme and stressful conditions (>50 PSU and anoxic) for *R. mangle* were found in Atasta, which is located in the southwest (LT), with a recorded SPI of −0.80 during 2014 to 2016 (Figure 5).

3.3. Reproductive Phenology Based on Litterfall

The highest litterfall production was registered in 2010 at 992.4 ± 450.4 $g \cdot m^{-2} \cdot year^{-1}$ and in 2014 at 999.7 ± 450.4 $g \cdot m^{-2} \cdot year^{-1}$, whereas the lowest production was in 2016 at 823.9 ± 30 $g \cdot m^{-2} \cdot year^{-1}$ (Figure 4). Litterfall production in 2016 decreased 20.4% during the dry season and 15.1% during the rainy season. Mangroves from Sabancuy in LT and Peten Neyac in PBR showed the highest litterfall decreases at 29.4% and 46.3%, respectively. Leaf production was significantly different between years ($F = 5.85$, $p < 0.0001$, Table 5).

Table 5. Factorial ANOVA (three factors) (**A**) sites, (**B**) years, and (**C**) seasons for salinity for the litterfall components of *Rhizophora mangle* along the coast of Campeche (2009–2010 and 2014–2016).

Factor	Variables (Value F)				
	df	**Leaves**	**Propagules**	**Flowers**	**Total Litterfall**
A: Site	6	29.60 **	4.56 **	23.93 **	9.90 **
B: Year	4	5.00 **	5.11 **	1.09	5.85 ***
C: Season	1	40.00 **	53.74 **	50.15 **	105.79 **
A × B	24	6.30 **	2.08 **	5.16 **	1.24
A × C	6	2.60 **	3.85 **	2.01	1.05
B × C	4	3.90 **	4.39 **	2.53 *	12.32 **
A × B × C	24	0.72	1.75 *	1.66 *	0.90
Error	420				

Sites: Atasta, Estero Pargo, Sabancuy, and Xibuja; Rio Champoton; Rio Verde and Peten Neyac. *p*-value: * $p < 0.05$, ** $p < 0.001$, *** $p < 0.0001$.

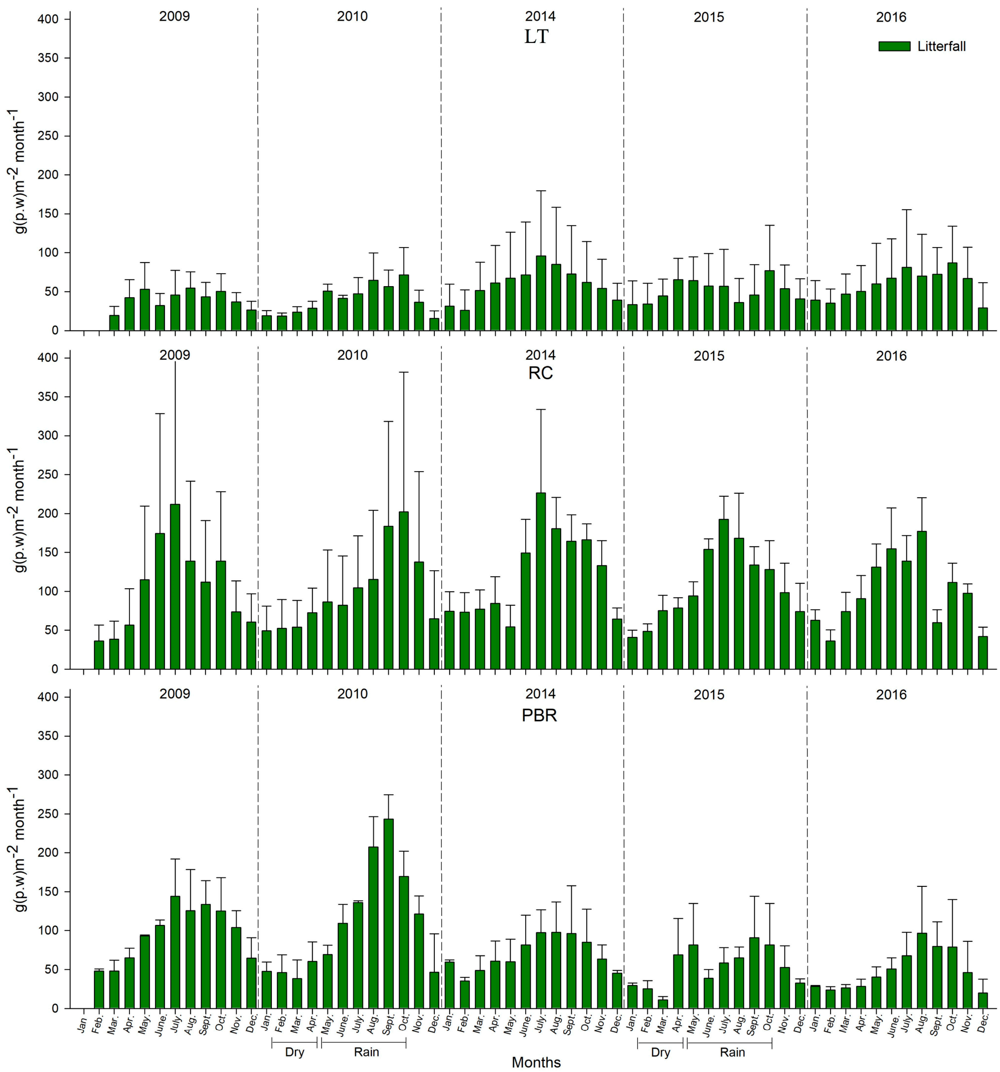

Figure 4. Total litterfall production in seven mangrove forests along the coast of Campeche, México from 2009 to 2010 and 2014 to 2016. The southern region includes Laguna de Terminos, and the northern region includes Rio Champoton and the Los Petenes Biosphere Reserve.

Leaf and propagule production were significantly different among years and seasons ($p < 0.001$), while flower production was only significantly different among seasons ($p < 0.001$) (Figure 5). Interactions between years and seasons were significant for leaf ($p < 0.001$), propagule ($p < 0.001$), and flower ($p < 0.05$) production (Figure 5). During the rainy season, leaf, propagule, and flower production in all three areas were higher than during the dry season (Figure 5). Notably, PBR showed the highest production in 2010, while RC did so during 2014. Production was similar each year for LT. From 2014 to 2016 in PBR, 39%, 83%, and 63% lower production of leaves, flowers, and propagules, respectively, were recorded (Figure 5). For the same period, RC registered only a 25% lower production.

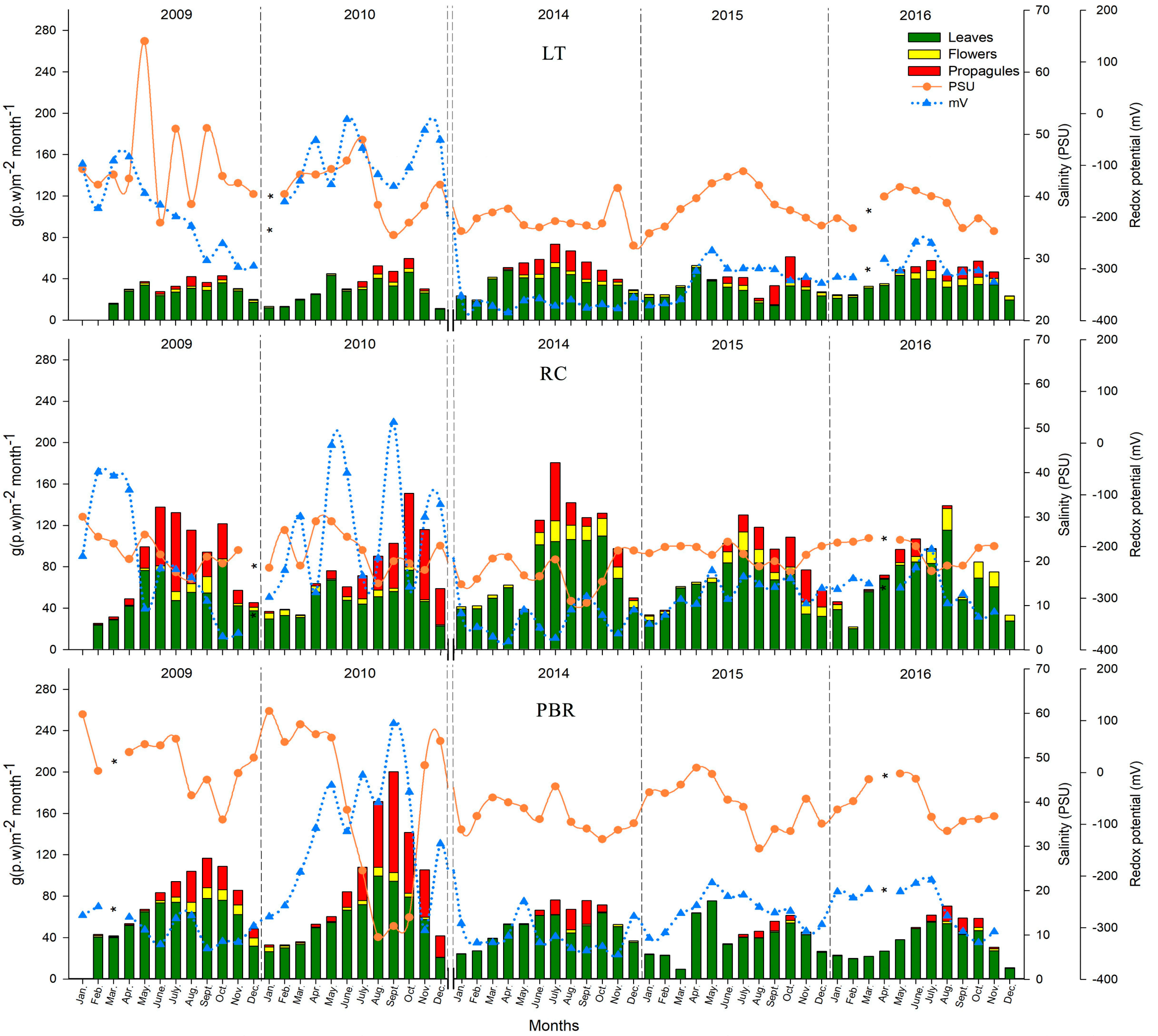

Figure 5. Reproductive phenology based on litterfall in seven mangrove forests along the coast of Campeche, México from 2009 to 2010 and 2014 to 2016. The southern region includes Laguna de Terminos, and the northern region includes Rio Champoton and the Los Petenes Biosphere Reserve.

We registered significant differences between leaf, propagule, and flower production among areas ($F = 34.88$; $F = 53.74$; $F = 9.01$; $F = 7.40$, $p < 0.001$), years ($F = 3.91$; $F = 7.51$, $p < 0.001$; $F = 3.73$, $p < 0.05$), and seasons ($F = 32.39$; $F = 69.05$; $F = 29.23$, $p < 0.001$). Additionally, interactions between years and seasons were significant for propagule ($F = 6.23$, $p < 0.001$) and flower ($F = 2.41$, $p < 0.05$) production (Table 6), which was validated by the significant differences between the production of leaves and propagules of LT vs. RC and PBR ($p < 0.05$, Table 7). In PBR, leaf production decreased 32.3% from 2014 to 2016 during the rainy season, and 49% from 2010 to 2016 during the dry season (Figure 5). Conversely, production increased by 69% during the rainy season in RC.

Propagule production decreased during the rainy season in RC, to 65% and 75% of the production in PBR from 2014 to 2016 (Figure 5). Significant differences were detected between the leaf and propagule production in LT and PBR vs. RC ($p < 0.05$, Table 7). Leaf production was significantly different between 2015 and 2016 vs. 2014 and a similar pattern was observed for the propagule production ($p < 0.05$) (Table 7).

Table 6. Factorial ANOVA (three-factor) per area (**A**), year (**B**), and season (**C**), concerning the production of the litterfall component of *Rhizophora mangle* along the coast of Campeche.

Factor	Variables (value F)				
	df	**Leaves**	**Propagules**	**Flowers**	**Total Litterfall**
A: Area	2	34.88 **	9.01 **	7.40 **	7.85 **
B: Year	4	3.91 **	7.51 **	3.73 *	5.57 **
C: Season	1	32.39 **	69.05 **	29.23 **	95.11 **
A × B	8	2.83 *	4.12 **	2.42 *	1.16
A × C	2	3.90 *	7.54 **	1.40	1.84
B × C	4	1.72	6.23 **	2.41 *	8.98 **
A × B × C	8	0.51	3.39 **	1.86	0.93
Total	355				

Areas: Laguna de Términos, Rio Champotón, and Los Petenes Biosphere Reserve. Year: 2009–2010 and 2014–2016. Season: Dry and Rainy. p-value: * $p < 0.05$, ** $p < 0.001$.

Table 7. Summary of Fisher's Least Significant Difference post hoc tests conducted for the factorial ANOVA on litterfall production and components comparing the areas and years. Bold values are significantly different ($p < 0.05$).

Areas	*Rhizophora mangle*			Total Litterfall
	Leaves	**Flowers**	**Propagules**	
LT–RC	**0.803154**	**0.0611683**	**0.25965**	**0.858922**
RC–RBP	0.210777	**0.0584981**	0.109847	1.06168
PBR–LT	**−0.592377**	−0.00267021	**−0.149803**	0.202761
Years				
2009–2010	−0.0781107	−0.0056902	−0.106271	−0.341993
2009–2014	−0.0219248	0.00934916	0.0483087	0.226141
2009–2015	**0.209839**	0.0154209	0.134122	**0.569957**
2009–2016	**0.282486**	0.0211747	**0.204706**	**0.882393**
2010–2014	0.0561859	0.0150394	**0.15458**	**0.568133**
2010–2015	**0.287949**	0.0211111	**0.240393**	**0.91195**
2010–2016	**0.360597**	0.026865	**0.310977**	**1.22439**
2014–2015	**0.231763**	0.0060717	0.085813	0.343816
2014–2016	**0.304411**	0.0118255	**0.156397**	**0.656253**
2015–2016	0.0726473	0.0057538	0.0705844	0.312436

Areas: Laguna de Terminos (LT), Rio Champoton (RC), and Los Petenes Biosphere Reserve (PBR).

3.4. Prediction Models for Litterfall and Phenology

Salinity was significantly correlated to leaf production in LT during the 2015 dry season ($R^2 = 0.91$, $p < 0.0001$) and 2016 ($R^2 = 0.92$, $p < 0.0001$) (Table 8). In RC, the pore water salinity and redox potential were significantly correlated with propagule production ($R^2 = 0.91$, $p < 0.02$) (Table 8). In RBP, leaf production was significantly correlated with salinity ($R^2 = 0.71$, $p < 0.001$) (Table 8).

Table 8. Linear and multiple regression analysis of pore water physicochemical parameters, precipitation, and phenological characteristics in three mangrove forests of *Rhizophora mangle* along the coast of Campeche.

Year	Season	Equation	R^2	p
		Laguna de Términos (LT)		
2010	Dry	$Y_1 = 4.392 - 0.04649 \cdot X_1$	0.50	0.01
2014	Dry	$Y_2 = 0.1884 - 0.003630 \cdot X_1$	0.62	0.001
2015	Rainy	$Y_2 = 0.3603 - 0.006350 \cdot X_1$	0.53	0.001
	Dry	$Y_2 = 0.2785 - 0.005424 \cdot X_1$	0.91	0.0001
2016	Dry	$Y_2 = 0.2686 - 0.004976 \cdot X_1$	0.92	0.0001
		Rio Champoton (RC)		
2010	Rainy	$Y_3 = -0.40344 - 0.0170378 \cdot X_2 - 0.172673 \cdot X_1$	0.91	0.022
		Los Petenes Biosphere Reserve (PBR)		
2014	Dry	$Y_4 = 7.202 - 0.1131 \cdot X_1$	0.71	0.001

Significance level $p < 0.05$. Y_1 = litterfall production ($g \cdot m^{-2}día^{-1}$), Y_2 = flower production ($g \cdot m^{-2}día^{-1}$), Y_3 = propagule production ($g \cdot m^{-2}día^{-1}$), Y_4 = leaf production ($g \cdot m^{-2}día^{-1}$), X_1 = salinity (PSU), and X_2 = redox potential (mV).

4. Discussion

The severe drought conditions registered in 2009 (SPI = −1.50) and 2015 (SPI = −1.16) were caused by a precipitation deficit. The northern area (PBR and RC) registered the most severe drought with 64.4% less precipitation compared to 2010, which was the wettest year. Since the 1950s in Mexico, the second most extreme drought year was 2009 [39]. In contrast, 2010 was the wettest year. In addition, 2011 and 2012 showed severe drought conditions in the Mexican territory. Consequently, 64 of the 174 natural protected areas in Mexico were at risk due to extreme drought [40–43]. These results may be related to the impacts of ENSO and DPO, climatic phenomena that disrupt the normal intensity, frequency, and duration of storms and hurricanes, droughts, hail, and frosts [44]. These events affect biodiversity, the ecosystem services, and the general wellbeing of human society [3]. Mangrove communities are particularly vulnerable to changes in precipitation because the hydroperiod and the physicochemical conditions of the soil and pore water are directly modified by the climatic variables [5,36]. A small change in the precipitation dynamics could cause a response in the entire biota, including the composition species richness, and the productivity of mangroves [45]. According to Field [10], changes in precipitation may cause differences in the distribution and the area covered by mangrove ecosystems, affecting the unusually diverse regeneration processes of these ecosystems. Pore water salinity gradients caused by precipitation changes, the inundation regime, and the microtopography, among other hydroperiod factors, may act as regulating determinants of physiologic processes in mangrove communities, such as tree photosynthesis and growth [21].

Along the coast of Campeche, the salinity and redox potential of the pore water were heterogeneous. Salinity increased during the drought years in 2009 and 2015, creating mesohaline–hypersaline and hypoxic to anoxic conditions. In contrast, during the wet years of 2010 and 2014, oxic conditions were registered. During the drought in 2009 and 2015, salinity and precipitation had an inverse correlation with each other, whereas salinity and the redox potential among the sites showed an inverse relationship only during 2009. Similarly, Saravanakumar et al. [46] reported a high inverse correlation between oxygen in the pore water and salinity and temperature in mangroves along the Indian coast. When precipitation decreases, the entry of fresh surface water and interstitial water also decrease, and soil salinity increases, altering the average salinity between the seasons [47]. By reducing the input of fresh water in wetlands, the dissolved oxygen decreases in the pore water and increases their demand for bacterial respiration processes and the degradation of the organic matter, among other biogeochemical processes [48]. Variations in the dissolved oxygen concentrations in the pore water depend on the salinity concentration and temperature, establishing an inverse correlation between these parameters [46,49].

During the rainy seasons of 2014 to 2016, all three mangrove areas (LT, RC, and PBR), demonstrated mesohaline conditions. However, PBR in the north showed the highest salinity (52.93 ± 7.1 PSU) and anoxic conditions (−331.8 ± 32.0 mV). Meanwhile, in LT in the south, a shift in the seasons from 2014 to 2016 was detected, with the most rainfall occurring in the dry season and drought occurring during the rainy season. In LT, anoxic conditions of less than −300 mV were recorded during the 12 months of 2014, where the southwest site (Atasta), had the most stressful conditions for *R. mangle* (>50 PSU, −313.3 ± 25.2 mV) during the rainy season. Along the coast of Campeche, the periods of reduction or the excess of fresh water generated a combination of extreme conditions, including salinization of soils, sustained waterlogging, oxygen, and decreases in pH [24,50]. The southern region (LT) has many rivers compared to the northern region (PBR), where the rivers are scarce and the soils are karstic. The circulation of the water is also limited, increasing the temperature and evaporation [51]. CONAGUA [25] reported extreme drought during the first nine months of 2009, including the basins of the Palizada and Candelaria rivers, which provide water to the wetlands of LT. The effect of climate variability reduces the flow in the rivers and increases the variability of the hydrological regime which involves episodes of drought and changes in the river system [52]. CONAGUA [53] also reported severe drought in south and southeast Mexico during the period of 2014 to 2016.

In the Gulf of Mexico, climate change is impacting the increase in the surface temperature of the ocean and the rising sea level, changing the rainfall regime and the discharge pattern of fresh water, changing the frequency and intensity of tropical storms, and increasing the inland ambient temperature [54]. Méndez and Magaña [55] mentioned that Mexico is extremely vulnerable to the negative impacts of significant rainfall deficits (drought) due to its geographic location, with scarce water availability to the north and with drought more significantly impacting the south. Conversely, several studies have reported on drought scenarios in the Yucatan peninsula, with high severity indices in the central and southern areas, and severe in the northwestern region [28,56].

Litterfall Production and Phenological Reproduction

From 2009 to 2010 and 2014 to 2016, significant decreases in litterfall production were found of 14.2 ± 10.5% and 17.5 ± 9.5%, respectively. Litterfall production was significantly lowest in RBP at 29.3 ± 19.3%, which corresponds to a precipitation deficit (22.1%) and hypersaline and anoxic conditions, which are stressful for *R. mangle*. A greater impact was registered in the PBR mangroves, where leaf and propagule production decreased by 32.3% and 75%, respectively, from 2014 to 2016 during the rainy season, and 49% from 2010 to 2016 during the dry season ($p < 0.05$). However, although hypoxic–anoxic and mesohaline conditions in the pore water were registered in LT from 2014 to 2016, the litter production declined by only 1.7%, the leaf production was unchanged, and the flowering and production of propagules recovered in 2015 to 2016, in comparison to 2009–2010. Several authors indicated that changes in the precipitation pattern affect the productivity decline and survival of the propagules in the mangrove forests [10,57–59]. Gilman et al. [60] stated that an increase in salinity conditions can cause a severe reduction in the mangrove coverage due to the conversion of upper tidal zones into hypersaline flats. This behaviour reflects differences in the degree of tolerance to drought, saline stress, and prolonged anoxia. The mangroves in LT exhibited more adaptive plasticity than those in PBR. The mangroves of PBR are less tolerant to drought stress, increased salinity, and poorer pore water conditions, meaning that they are more dependent on surface runoff and the contribution of fresh water flow via interstitial means. These mangroves are also influenced by the tide, because the tide helps to dilute the salts throughout a large portion of the year, and by the fresh water that receives surface runoff and groundwater during the rainy season. The mangroves in PBR are also dependent on rain to contribute nutrients during leaching, mainly consisting of phosphates which are critical for the production of photosynthetic tissue.

Rhizophora mangle is especially vulnerable to a PSU value below 30 because this species neither has desalination glands, nor accumulates salts in vacuoles, and it requires oxygen availability and frequent flooding [48,61]. For this species, the elimination of salts requires a high energy investment. When pore water salinity becomes extremely high, above 90 PSU, and the redox potential becomes lower than −230 mV, individual mangrove trees suffer detrimental effects, such as the inhibition of photosynthesis and enzyme processes, and, consequently, a reduction in the carbon dioxide (CO_2) assimilation rate [21,48]. Also, the transpiration and exclusion of salts may be affected as a result of an excess of salts inside mangrove plants [61].

Along the coast of Campeche, the ecophysiological response of *R. mangle* varies according to the environmental factors, which is reflected in the differences in the salinity and redox potential between sites ($p < 0.05$), between years ($p < 0.001$), and between the seasons ($p < 0.05$). These factors are significantly correlated with the production of *R. mangle*. Drought reduces the ecological functions and services of many estuaries and mangroves, inhibiting the production of hypocotyls of *R. mangle* to exponentially increase the salinity [47,62].

Some authors estimated that the variation in the flooding period modifies the physiological process, productivity, and phenology of mangroves [18,63]. Sharma et al. [64] mentioned that the environmental factors change the ecophysiological responses, such as litterfall production, propagules, leaves, and flowers. Saenger [48] reported that the plants show an enzymatic and photosynthetic inhibition under anoxic (less than −320 mV) and hypersaline conditions. Some plants modify their morphology, physiology, and reproduction to different environmental conditions through variation in genetic expression [65,66]. Adaptive phenotypic plasticity is the ability of a particular genotype to express different phenotypes depending on variation in the environment by altering their morphology and physiology [65,67]. Mainly, the morphophysiological adaptations of the mangrove forests depend on the restrictions on the gas exchange, flood levels, temperature, electrochemical characteristics, nutrients, and salinity [18].

5. Conclusions

Significant variation in precipitation was observed in the periods of 2009 to 2010 and 2014 to 2016, associated with changes in the salinity concentration and the redox potential of the pore water, which caused stress in the litterfall production and phenology of *R. mangle* along the coast of the state of Campeche, Mexico. The forests in LT and RC showed the most significant adaptive plasticity (resilience). This behaviour reflects differences in the degree of tolerance to drought, saline stress, and prolonged anoxia. The ecophysiological response of *R. mangle* was diverse among the three mangrove areas in the state of Campeche (LT, RC, and PBR). RC had the lowest propagule production (65%) during the rainy season. An extreme impact on the forests of PBR was observed in the period of 2014 to 2016, decreasing litterfall by 29.31% and lowering flowering rates, with a more significant effect on the phenological characteristics during the rainy season in terms of the leaves and propagules (32.3% and 75%, respectively). In addition, a 49% decrease in the production of leaves was observed from 2010 to 2016 during the dry season. The survival of mangroves depends on their ability to adapt to these ecosystems given ongoing climate change and the random effects of anthropogenic activities. Finally, we concluded that the ecophysiological response of *R. mangle* is a reflection of the intense droughts that occurred in 2009–2010 and 2014–2016 [68].

The salinity was the determining factor in the production of flowers during the rainy and dry seasons, and precipitation was the determining factor in the production of propagules during the rainy season. Likewise, for the generation of leaves, salinity and redox potential were the determining factors. The results of this study suggest a low phenotypic plasticity of *R. mangle*.

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