How Will Sea Level Rise Affect Coastal Wetlands on the Atlantic Coast of Mexico: Impacts and Species Responses?

Edgar Abel Sánchez-García[1,2], Patricia Moreno-Casasola[1] and Roberto Monroy Ibarra[1]

ABSTRACT

Mexico's Atlantic Coast with its mosaic of coastal wetlands is vulnerable to sea level rise. These wetlands are transition zones between the terrestrial and the marine environments. Due to their location, the rise in sea level could increase the level of flooding and salinity in these ecosystems. A synthetic model was applied to the Mexican Atlantic coast, and the La Mancha lagoon was used for local experiments with wetland species. Our objectives were: 1) identify the potentially floodable coastal wetlands in the face of a sea level rise of one and two meters, and 2) determine the percentages of germination for seven popal (freshwater marsh) species and the survival and growth of a swamp tree species, *Annona glabra* seedlings under different flood and salinity conditions. For the first objective, we developed a synthetic model using three information layers: altitude of the land (elevation), water bodies, and wetland vegetation. For the second, we carried out two experiments: 1) a laboratory germination experiment with eight treatments (2 flood levels × 4 salinity levels), and 2) greenhouse growth seedlings experiment with nine treatments (3 flood levels × 3 salinity levels). Our model identified 470,480 and 720,902 ha of wetlands potentially affected under one- and two-meter scenarios, respectively. The germination experiment results showed that most popal species germinated higher under no salinity conditions as expected. The seedling experiment recorded that survival and growth were higher under no salinity conditions. In both experiments, salinity was the most stressful factor. According to the model, the tulares and mangroves will have significant areas affected by sea level rise. In addition, freshwater wetlands will be affected in two crucial stages of their cycle life: germination and seedlings establishment.

Key words: Climate change; flood; mangroves; marsh; salinity

RESUMEN

La costa atlántica de México, con su mosaico de humedales costeros, es vulnerable al aumento del nivel del mar. Estos humedales son zonas de transición entre el medio terrestre y el marino. Debido a su ubicación, el aumento del nivel del mar podría incrementar el nivel de inundación y salinidad en estos ecosistemas. Se aplicó un modelo sintético en la costa atlántica mexicana y se utilizó la laguna de La Mancha para realizar experimentos locales con especies de humedales. Nuestros objetivos fueron: 1) identificar los humedales costeros potencialmente inundables ante un aumento del nivel del mar de uno y dos metros, y 2) determinar los porcentajes de germinación de siete especies de popales (humedales herbáceos de agua dulce) y la supervivencia y crecimiento de plántulas de Annona glabram una especie de selva inundable, bajo diferentes condiciones de inundación y salinidad. Para el primer objetivo, desarrollamos un modelo sintético utilizando tres capas de información: altitud del terreno (elevación), cuerpos de agua y vegetación de humedales. Para el segundo, llevamos a cabo dos experimentos: 1) un experimento de germinación en laboratorio con ocho tratamientos (2 niveles de inundación × 4 niveles de salinidad) y 2) un experimento en invernadero de crecimiento de plántulas con nueve tratamientos (3 niveles de inundación × 3 niveles de salinidad). Nuestro modelo identificó 470,480 y 720,902 ha de humedales potencialmente afectados en escenarios de uno y dos metros, respectivamente. Como se esperaba, los resultados del experimento de germinación mostraron que la mayoría de las especies de popales tuvieron mayor germinaron en condiciones sin salinidad. El experimento con plántulas registró que la supervivencia y el crecimiento fueron mayores en condiciones sin salinidad. En ambos experimentos, la salinidad fue el factor más estresante. De acuerdo al modelo, los tulares y manglares tendrán importantes áreas afectadas por el aumento del nivel del mar. Además, los humedales de agua dulce se verán afectados en dos etapas cruciales de su ciclo de vida: la germinación y el establecimiento de plántulas.

Palabras clave: Cambio climático; humedal herbáceo; inundación; manglares; salinidad

INTRODUCTION

Global climate change will increase the mean temperature, droughts, and tropical cyclones, alter precipitation patterns, and raise the rate of sea level changes (IPCC 2021). Sea level rise is the consequence of various processes, among them, thermal expansion of the ocean caused by warming water and melting of glaciers and polar caps which promotes the addition of water to the oceans (Cazenave and Cozannet 2014; IPCC 2014; Frederikse et al. 2020). As a result, global mean sea level has risen at a rate of ~3 ± 0.04 mm/year since 1993 (Nerem et al. 2018). On the Mexican Atlantic coast, this rate is similar to the global trend,

1 Red de Ecología Funcional, Instituto de Ecología, A.C., Carretera antigua a Coatepec 351, El Haya C. P. 91073, Xalapa, Veracruz, Mexico
2 Corresponding author contact: edgarabel.sanchez@gmail.com

between 1.8 mm/year in Alvarado, Veracruz, and up to 3.6 mm/year in Isla Mujeres, Quintana Roo (Zavala-Hidalgo et al. 2011; Ruiz-Ramírez et al. 2014).

Coastal wetlands are particularly vulnerable to changes in sea level rise because they are closely linked with it - they are transition zones between the terrestrial environment and the marine aquatic environment. According to Reed et al. (2020), there are three main mechanisms through which sea level rise causes the degradation and/or loss of coastal wetlands: 1) wetland edge erosion when adjacent to major water bodies (such as rivers and lagoons), 2) increase in salinity level leading to physiological stress (mainly in freshwater wetland species), and 3) temporal and spatial increase in flooding, which causes tolerance thresholds to be exceeded in various species. The continued rise in sea level will lead to changes in hydrology, increasing seawater intrusion, rising water levels, and salinity in coastal wetlands (Li and Pennings 2018).

It is essential to increase our knowledge of the impact of sea level rise on coastal wetlands. In this paper, we combine the information generated over several years with some results from our studies - the first results for freshwater coastal wetlands in Mexico. We have identified the potentially floodable coastal wetlands in the Mexican Atlantic coast (Sánchez-García et al. 2023). To explore with a major detail, we chose La Mancha lagoon, a coastal lagoon surrounded by mangroves and freshwater wetlands - part of La Mancha y El Llano Ramsar site on the central coast of Veracruz, in the Gulf of Mexico. In this site, we tested seed germination of various freshwater marsh species (Sánchez-García et al. 2017) and seedling establishment of a freshwater tree species (Sánchez-García et al. 2022).

MATERIALS AND METHODS

Study Area

The study area is the Mexican coast of the Gulf of Mexico and the Caribbean Sea (Figure 1A). The wetlands of the Gulf of Mexico receive freshwater from the Sierra Madre Oriental range (Sánchez-Higueredo et al. 2020), and also rainwater filtered from nearby extensive dune system coastal waters (Yetter 2004) and seawater from tides and coastal lagoons. The wetlands along the Caribbean Sea and on the Yucatan Peninsula are established on an oligotrophic karstic landscape with a highly permeable carbonate substrate and a complex subsurface hydrologic system that transports freshwater to the coast, where it mixes with seawater (Bauer-Gottwein et al. 2011), there are no rivers. Coastal wetlands are affected by the mixture of freshwater and seawater that creates a flood and salinity gradient producing a mosaic or zonation of wetland types (Lara-Lara et al. 2008; Infante-Mata et al. 2011; López-Rosas and Moreno-Casasola 2022). The mangroves are exposed to the highest salinity level (15–25 parts per thousand) because they are in contact with the sea, and the tides greatly influence the flood level. Typically, behind mangroves, "tulares" (cattail marshes) occur in areas exposed to lower salinity (2-4 parts per thousand) with less tidal influence and with the major water level from freshwater of the inland. Behind them, the "popales" (broadleaf freshwater marshes) are established - freshwater wetlands (salinity: 0–2 parts per thousand) with a high water level with little movement, leading to a high deposition of sediments. Further inland, freshwater swamps (salinity: 0–2 parts per thousand) are distributed mainly in the vicinity of coastal lagoons and on floodplains. Finally, the most landward of the coastal wetlands are palm groves dominated by freshwater flooded for shortest duration and have the shallowest depth (Moreno-Casasola and Infante-Mata 2010). Other types of wetlands are not so widely distributed. In Madre Lagoon, north of Mexico, there are areas covered by halophilic hydrophilic vegetation with very high salinities. In the Yucatan Peninsula, dwarf mangroves are found in high salinity areas, and in coastal areas where freshwater emerges from the karstic platform, petenes or hammocks are formed. This is a type of mangrove with two different communities in structure and function: in the area with the freshwater spring, trees are higher and mangrove species mix with tropical forest species. The surrounding

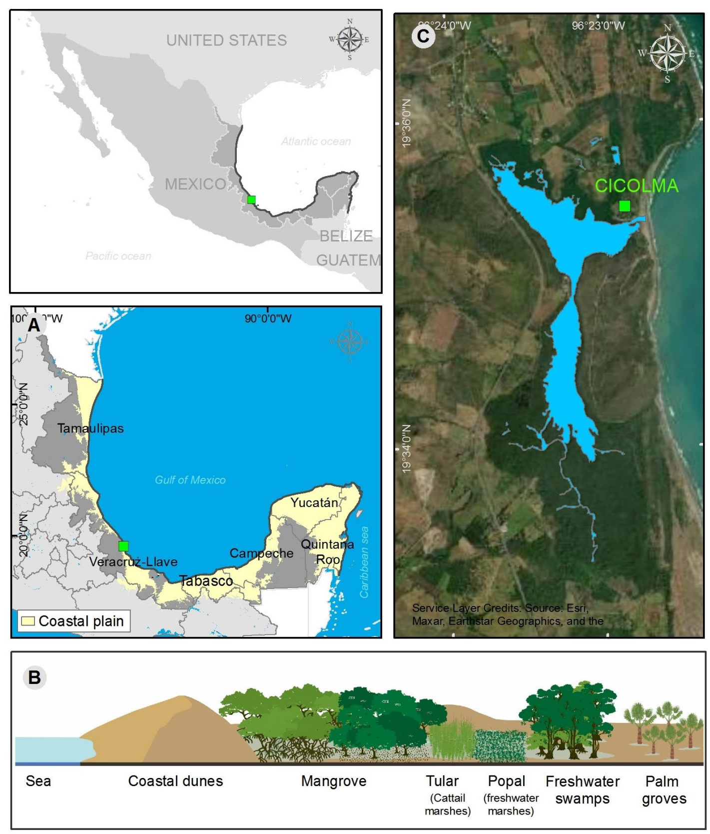

Figure 1. Location of study area and schematic showing the variety of wetland habitats in the area: A) Location of the Mexican states on the Atlantic Coast, B) The variety of contiguous coastal wetlands from the sea to inland, and C) aerial view of La Mancha lagoon, part of the La Mancha y El Llano Ramsar site 1336. Note: CICOLMA is the La Mancha Coastal Research Center (Centro de Investigaciones Costeras La Mancha; noted as green points). It is worth noting that sometimes the gradient in the schematic drawing (1B) is interrupted by changes in land use, i.e., converted into flooded pastures, interrupted by roads, etc.

mangrove is stressed by salinity, and trees are smaller, and one or two mangrove species dominated. Mexican wetlands are described by Moreno-Casasola et al. (2012).

We carried out experiments using La Mancha's wetlands as a case study. This site is located approximately 60 km north of the city of Veracruz, in the municipality of Actopan (between 19°40'33" and 19°31'49"N, and between 96°24'48" and 96° 22' 25''W; Figure 1C). The most characteristic community is the mangrove swamp dominated by *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. The freshwater swamp is dominated by *Annona glabra*, with the presence of individuals of *Salix humboldtiana* and *Pachira aquatica*. The "popal" is a broadleaved freshwater marsh community dominated by *Sagittaria lancifolia*, *Hymenocallis littoralis*, and *Pontederia sagittata*. The "tular" is cattail marsh dominated by Typha domingensis (Moreno-Casasola 2003).

Synthetic Model for Identifying Potentially Floodable Zones

To identify potentially floodable zones, we applied a bathtub inundation model with a Digital Elevation Model (DEM) based on Shuttle Radar Topography Mission (SRTM) images at 30-meter spatial resolution. Two elevation layers of one and two meters were extracted from the DEM to identify potentially floodable zones due to sea level rise. Two crucial aspects were considered to avoid overestimating the potentially floodable zones. First, all existing bodies of water within these zones were not included in the analysis because, at present, it is a floodable zone. Second, also excluded were zones that did not have a hydrographic connection with the sea since they did not have a tidal flood pathway (Li et al. 2009). All data processing and analyses were conducted using ArcMap 10.8 software (ESRI 2019).

To develop the model, we used three information layers: altitude of the land, water bodies, and wetland vegetation (Table 1). The information from "Manglares de México 2020" (Velázquez-Salazar et al. 2021) and the "Carta de Uso del Suelo y Vegetación Serie VI" (INEGI, 2017) were merged to create a new layer of wetland vegetation. It is essential to mention that the scale differs between both sources (1:50,000 and 1:250,000, respectively). Therefore, we used "Manglares de México 2020" as a base for merging both information sources.

Popal Seed Germination Experiment

Mature seeds of seven popal species were collected at La Mancha from several adult individuals of *T. domingensis, S. lancifolia, P. sagittata, Boehmeria cylindrica, Ludwigia octovalvis, Cyperus digitatus*, and *Fuirena simplex*. The experimental design combined two factors that we considered would change with sea level rise: water level and degree of water salinity. Two water levels were used: Moist (water was added to the filter paper as necessary to keep the paper moist) and Flooded (filter paper was always kept saturated ─thoroughly soaked, showing a film of water on top of the paper). Four levels of salinity were used: 0 parts per thousand (‰), 5‰, 10 ‰, and 15‰. Thus, the combination of the two factors resulted in eight treatments.

The experiment lasted four weeks. For each treatment, 25 seeds per Petri dish were sown with five replicates. The seeds were incubated in 90-mm diameter Petri dishes filled with sterilized sand as a substrate and one layer of Whatman No. 1 filter paper on top. An emerged radicle was the criterion for germination. The seed germination occurred in controlled germination chambers in the laboratory at 25 °C during 14 h of light and 20 °C during ten h of darkness. Germination was recorded every 48 hours, and germinated seeds were counted and removed from the dishes. Seed germination percentage was expressed as the mean ± S.E. One-way or two-way analysis of variance (ANOVA; $P < 0.05$) was used to compare the treatment effects (Sokal and

Table 1. Data sources for the three layers of information used in the synthetic model.

Information layer	**Source of information layer**	**Resolution / scale**	**Data source**
Altitude data	DEM from Shuttle Radar Topography Mission images	30 meters	United States Geological Survey (USGS)
Water bodies	Hydrographic vectors of the Mexican Hydrological Regions	1:250,000	Comisión Nacional del Agua (CONAGUA)
Vegetation and type of land use	Vectors of vegetation and type of land use from Manglares de México 2020	1:50,000	Comisión Nacional para el Uso y Conocimiento de la Biodiversidad (CONABIO)
Vegetation and type of land use	*Vectors of vegetation and type of land use from Carta de Uso del Suelo y Vegetación Serie VI*	1:250,000	Instituto Nacional de Geografia y Estadística (INEGI)

Figure 2. *Annona glabra* seedling experiment. A) *Annona glabra* trees, B) Polyethylene bag with *Annona glabra* seedling under Saturation (water level kept at 15 cm from soil level) and Flooded (water level kept at 10 cm above from soil level) at the beginning of experiment.

Rohlf 1995). When ANOVA detected significant effects, Tukey's test determined significant differences among the treatments. Nested ANOVAs were used to show how the germination of the species differed between water level and salinity. The proportion of germinated seeds at the end of the experiment was calculated for each species and for each Petri dish. The effect of treatments on the germination proportion by species was compared using a Nested ANOVA's and Tukey posthoc tests ($P \leq 0.05$). The salinity factor was nested within the water level factor. In order to meet the assumptions of parametric tests, the proportion of germination of all species was arcsine transformed. The species S. lancifolia presented many zero values, so no statistical analysis was made. Detailed descriptions of the methodology can be found in Sánchez-García et al. (2017). All analyses were performed with the statistic package PAST, v. 3.14 (Hammer et al. 2001).

Annona glabra *Growth Seedlings Experiment*

Annona glabra seedlings were obtained from germinated seeds. The *A. glabra* fruits were collected from trees of the surroundings of La Mancha lagoon (Figure 2A) and taken to a greenhouse at the Centro de Investigaciones Costeras La Mancha (CICOLMA) run by the INECOL. The seeds were placed in soil recollected from a popal in CICOLMA, in polyethylene greenhouse bags 25 cm high and 15 cm in diameter for growth. At the beginning of the experiment, the seedlings had an average height of 18.6 ± 1.6 cm. The experimental design combined the same two factors (water level and salinity). Three water levels were used: Saturation (all soil's spaces are filled with water; for that purpose, the water was permanently kept 15 cm below the soil surface in the plastic bag), Flooded (the water level was permanently maintained at 10 cm above soil level), and Flood-Drought (for four weeks, the water level was 10 cm above the soil's surface. After this time, the bags were removed from the water and allowed to drain until they lost the water due to evapotranspiration and gravity, and later, for the next four weeks, the plant had no contact with the water). Three level of salinity were used: 0‰, 5‰, and 15‰. Thus, the combination of the two factors resulted in nine treatments.

The experiment lasted 18 weeks. For the experiment, five seedlings were randomly assigned to each treatment. Four fiberglass tubs (130 cm long × 60 cm wide × 70 cm high) were used to apply the treatments in the greenhouse. Three tubs were filled with tap water at a constant level of 55 cm. Each of these tubs had a different salinity: 0‰, 5‰, and 15‰. Instant Ocean artificial salt (Aquarium Systems) was used to achieve salinity levels. PVC tubes of two heights (45 and 20 cm) were placed inside the tubs to obtain the different water levels. On the top for each PVC tube, we put a polyethylene bag with a seedling (Figure 2B). The seedlings were subjected a Saturation (water level kept at 15 cm below the soil surface) and Flooded conditions (water level kept at 10 cm above the soil surface). The fourth tub had no water. This is where the seedlings of the Flood-Drought treatments were placed during the weeks they did not have contact with the water. The seedlings were monitored and measured every two weeks: percent seedling survival and height. Throughout the experiment, when a seedling died, it was removed from the tub, and its height was measured. The effect of the different treatments on the seedlings' growth (change in height) was evaluated by fitting a Linear Mixed Model (LMM). In our model, height (the difference between the final and initial value for each seedling) was specified as the response variable, water level, and salinity as fixed effects factors, and plant as a random-effects factor (to control for the measurements to which they were subjected through time), and time as a continuous random-effects variable (Crawley 2013). The water level was specified as nested in salinity. Detailed methodology can be found in Sánchez-García et al. (2022). All analyses were run in R software, version 3.6.1 (Team R Core 2019).

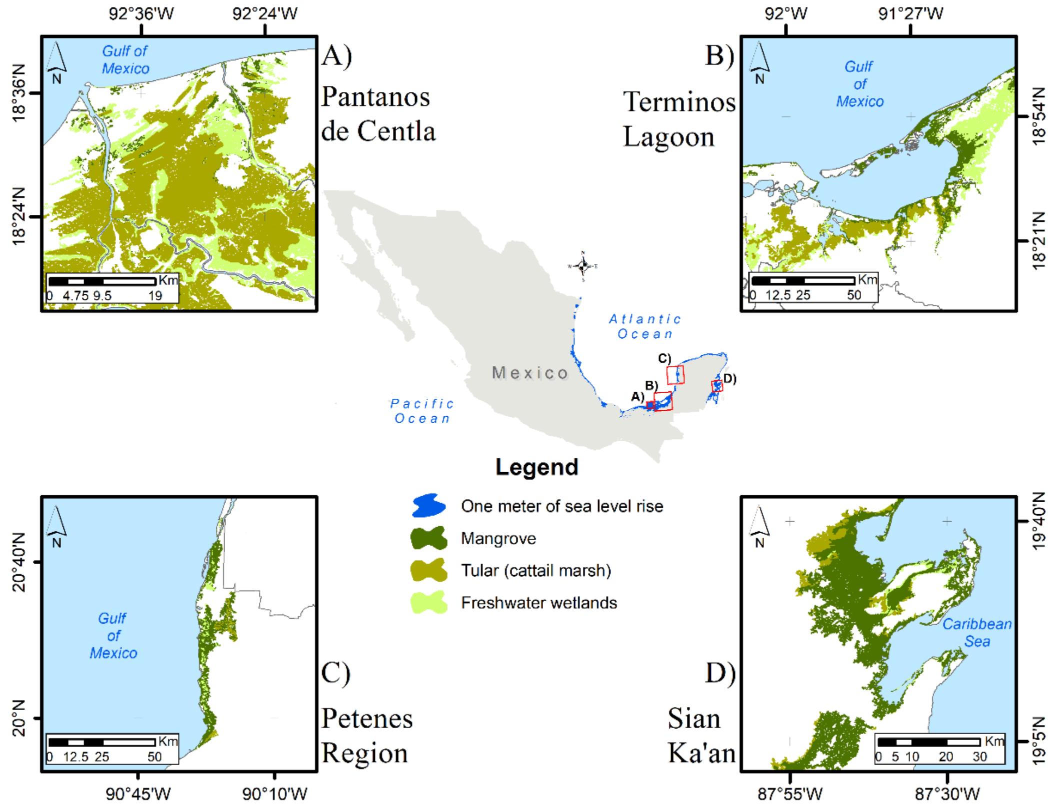

Figure 3. Four central wetland regions with major surface potentially floodable coastal wetlands under scenarios of an increase of one meter of sea elevation were detected: A) Pantanos de Centla, Tabasco; B) Terminos lagoon, Campeche C) Petenes, Campeche; D) Sian Ka'an, Quintana Roo. * Freshwater wetlands refer to all the other categories from Table 2.

RESULTS

Synthetic Model

We identified eight types of wetlands potentially affected (Table 2). Under a one-meter sea level rise scenario, a total area of 470,480 ha of potentially affected wetlands was recorded, where tulares (35.93%), mangroves (33.68%), and other types of wetlands (24.58%) would be the main types of wetlands affected. Under a two-meter increase in sea level, the potentially affected wetlands area increased to 720,902 ha. The main types of wetlands potentially affected would be the same as for the one-meter sea rise scenario: tulares (36.52%), mangroves (34.51%), and other types of wetlands (22.87%). The Grijalva-Usumacinta delta complex in Tabasco, the Terminos lagoon and the Petenes region in Campeche, the coast in Yucatan, and the bays of Sian Ka'an in Quintana Roo, were the primary areas with potentially affected wetlands by sea level rise under one and two meters scenarios (Figure 3).

Seed Germination

The salinity was the primary factor that affected the species' germination. The general pattern found in most species was lower germination due to increased salinity levels, as expected. However, we recorded salinitytolerant species, such a *C. digitatus, L. octovalvis, T. domingensis*, and the fruits of *P. sagittata* (Figure 4A). The germination percentages of these species were ≥ 18% in any treatment.

Table 2. Potentially affected wetlands under sea level rise scenarios of one and two meters. "Popal" is the common name for broadleaved freshwater marsh; "tular" is the local name for cattail marsh.

Type of wetland	Area potentially affected (ha) with one-meter sea level increase (% of the total)	Area potentially affected (ha) with two-meters sea level increase (% of the total)
Mangrove	157,755.68 (33.531)	247,263.48 (34.299)
Disturbed mangrove	728.95 (0.155)	1,508.13 (0.209)
Natural palm grove	10.84 (0.002)	33.96 (0.005)
Halophytic grassland	4,534.42 (0.964)	4,986.95 (0.689)
Petén	480.66 (0.102)	915.84 (0.127)
Popal*	19,602.91 (4.167)	32,378.09 (4.491)
Tular*	169,049.80 (35.931)	263,310.99 (36.525)
Halophilic hydrophilic vegetation	2,645.82 (0.562)	5,664.43 (0.786)
Other wetlands	115,671.41 (24.586)	164,855.68 (22.869)
TOTAL	**470,480.5**	**720,901.63**

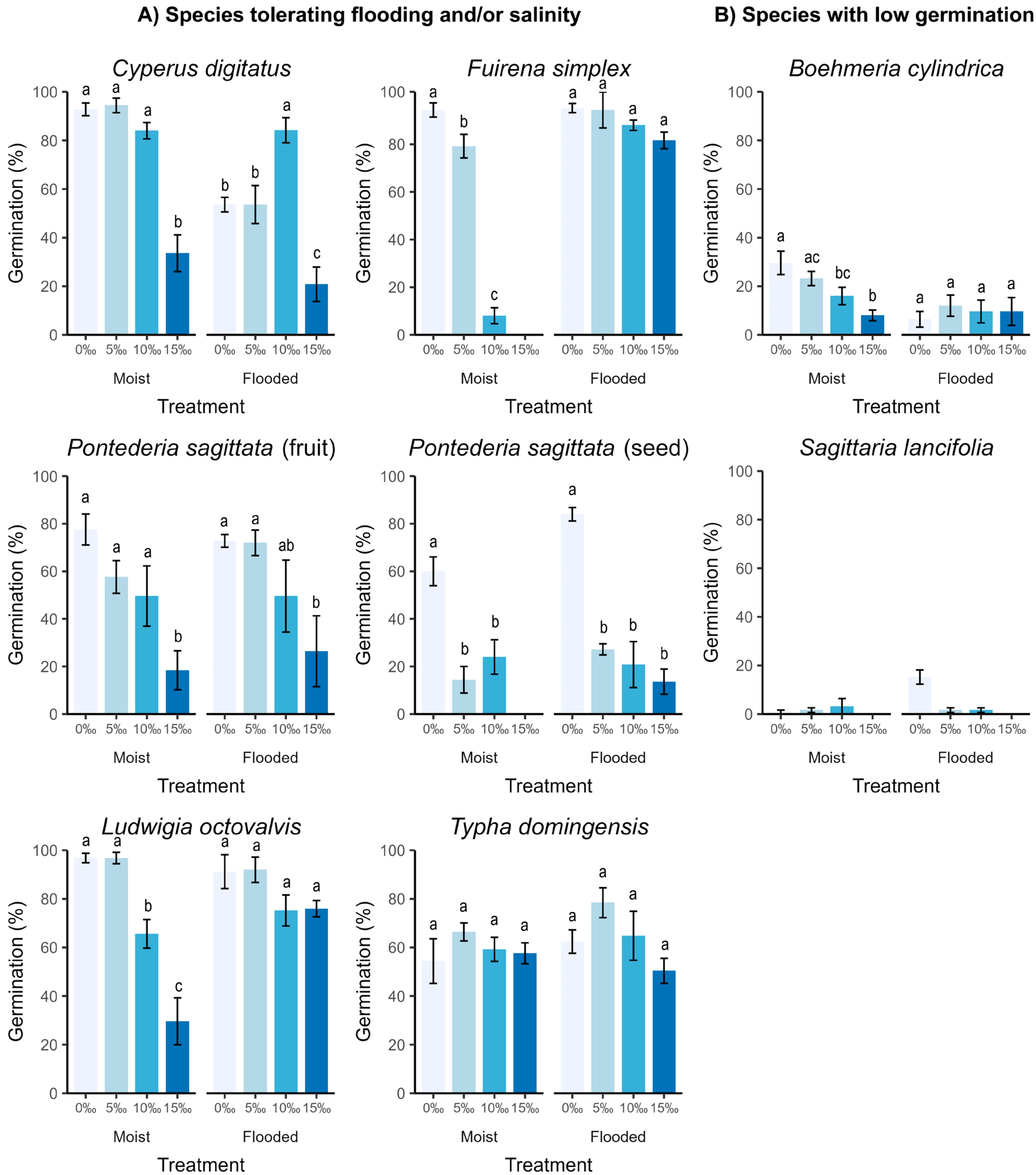

Figure 4. Final germination percentages of seven popal species under moist and flooded conditions. We group the species into two groups according to their germination response to salinity and flooding: A) column with salinity and flooding tolerant species, and B) column with low germination species Data obtained under the four salinity levels are shown, with the germination mean values (%) ± SE. Values with a different letter are significantly different at $P < 0.05$. Modified from Sánchez-García et al. (2017).

Typha domingensis was the only species that showed no significant differences in germination among the different salinity treatments, and germination remained above 50%. It is worth noting that although it did not show significant differences in germination, the higher percentages were found in the treatment Flooded 5‰.

The water level factor had less impact on the germination results. *Fuirena simplex, L. octovalvis* and the seeds of *P. sagittata* showed better germination in Flooded treatments (Figure 4A). The treatment Moist 15‰ inhibited germination for *F. simplex* and *P. sagittata* seeds. On the other hand, some species like *B. cylindrica* and *S. lancifolia*, showed lower germination in all treatments (Figure 4B). The extreme treatments of 15‰ (Moist and Flooded) completely inhibited germination for seeds of *S. lancifolia*.

Seedling Growth of Annona glabra

We recorded a 100% survival rate for the *Annona glabra* seedlings exposed to 0‰ salinity, whereas some seedlings died in all treatments exposed to 5 and 15‰. All the seedlings died when exposed to the Flood-Drought 15‰ treatment (Table 3). Overall, the growth of seedlings throughout the experiment was more significant in the treatment under conditions of Saturation and low salinity (0 and 5‰; Figure 5A,B). Seedling growth and final height were affected by salinity independent of the water level; the mean height of the 0‰ treatment (13.66 cm) was significantly different from the 15‰ treatment (2.75 cm; P = 0.03, Tukey test). However, there were no significant differences in height between the 5‰ treatment and any of the two salinity treatments (P = 0.27 for 0 vs 5‰; P = 0.35 for 5 vs 15‰, Tukey test). For water level, seedling growth was higher under the Saturation condition and lowest in the Flood-Drought treatments, although the difference was insignificant (P's > 0.05). Seedlings under the treatments with 0‰ salinity (freshwater) had the most significant growth, while the seedlings subjected to the 15‰ salinity treatments grew the least (Figure 5C).

DISCUSSION

Our study found that the wetlands with the largest surface area of potentially floodable zones are mangroves and tulares. It is vital to specify that our synthetic model is a static model, and thus does not consider coastal dynamics taking place in the future. Therefore, there is not a projection. Rather, it reflects the current portion of wetlands that could be at risk, which can be interpreted as a threat indicator.

Along the Mexican Atlantic coast's landscape, it is common to find these wetlands close to one another, although land use change has caused fragmentation and the loss of natural connectivity. This vicinity can be seen in the four wetland regions with the largest surface area vulnerable to scenarios of increased sea level rise (Figure 1B). In coastal areas, wetlands are often contiguous and form spatial gradients where flood level and salinity fluctuate (Moreno-Casasola et al. 2017; López-Rosas and Moreno-

Table 3. Number of Annona glabra seedlings at the beginning and end of the experiment and percent survival of seedlings under the different water level and salinity treatments

Treatment	**Number of seedlings at the beginning**	**Number of seedlings at the end**	**Survival (%)**
Saturation 0‰	5	5	100
Flooded 0‰	5	5	100
Flood-Drought 0‰	5	5	100
Saturation 5‰	*5*	2	40
Flooded 5‰	*5*	3	60
Flood-Drought 5‰	*5*	3	60
Saturation15 ‰	*5*	3	60
Flooded 15‰	*5*	2	40
Flood-Drought 15‰	*5*	0	0

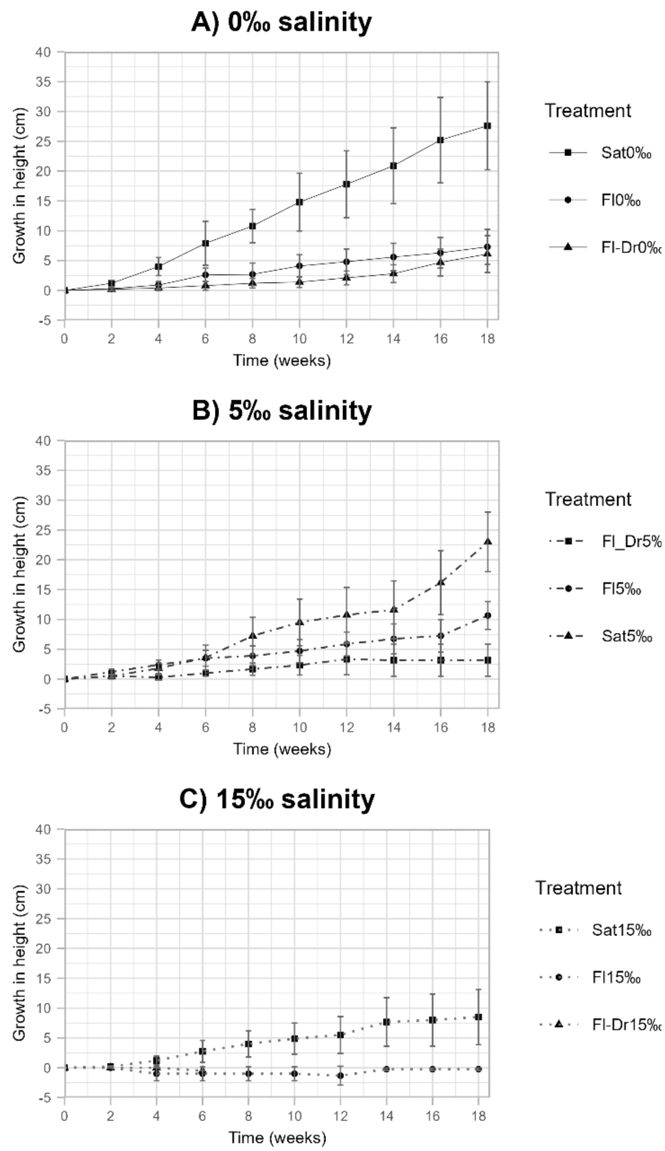

Figure 5. Mean increase in height (cm) ± SE of A. glabra seedlings under different treatments over the time: A) 0‰ salinity treatments; B) 5‰ salinity treatments; and C) 15‰ salinity treatments. Modified from Sánchez-García et al. (2022). Note: Sat = Saturation; Fl = Flooded; Fl-Dr = Flood-Drought.

Casasola 2022). The mangroves are particularly vulnerable to sea level rise due to their proximity to the sea and location in intertidal environments (McLeod and Salm 2006). The results obtained in our synthetic model indicate that 24.6 and 38.6% of the mangroves in the Mexican Atlantic could be potentially floodable zones under scenarios of sea level rise of one and two meters, respectively. This means that flooding would be permanent and could alter water level fluctuations and salinity, affecting severely these wetlands.

Given these scenarios, the wetlands responses, specifically of mangroves, could be three: 1) vertical growth, 2) lateral migration, and/or 3) degradation and loss. The plants contribute to vertical growth or accretion in two ways: indirectly by slowing water flow and turbulence, trapping and binding mineral sediment, and directly across production and accumulation of organic matter, primarily plant roots and rhizomes (Cahoon et al. 2021). Suppose the acceleration rate of sea level rise exceeds the capacity of the wetlands to maintain optimum vertical position within the tidal frame. In that case, the lateral migration is the only possible option. The mangroves could migrate inland as supratidal areas landward of the current mangrove extent become increasingly intertidal and suitable for mangrove colonization, which allows them some adaptation under rising sea levels (Friess et al. 2022). However, the migration of the mangroves would cause the displacement of tulares and other freshwater wetlands, such as popales, freshwater swamps, and palm groves. López-Rosas et al. (2021) have reported this taking place in Pantanos de Centla Biosphere Reserve. The increase in salinity caused the inland migration of mangroves; the tulares died, and *Laguncularia racemosa* (white mangrove) took its place. Nevertheless, landward rigid coastal developments and topographical barriers could prevent the migration of mangroves and wetlands in many areas, for example, in the northern Gulf of Mexico (Borchert et al. 2018), leading to potentially extensive losses in areal extent because of coastal oppression (Enwright et al. 2015). Finally, if wetlands fail to adapt through vertical growth or lateral migration, they will begin to degrade due to rising water levels and salinity. The degradation and plant mortality will cause submersion of surfaces, and the substrate will begin to break up as peat collapses (Carrasco et al. 2016; Andres et al. 2019).

CONCLUSION

We found that the increase in water level and salinity directly affected the germination of seeds of freshwater wetlands and the seedling survival of *A. glabra* from freshwater swamps. In both cases, salinity turned out to be the most stressful factor. Soil salinity is a crucial factor in the early stages of development for many coastal wetland species. Studies have shown that a prolonged period of soil salinization changes species composition, reduces species richness, and diminishes biomass in different types of wetlands (Sharpe and Baldwin 2012; Li and Pennings 2018, 2019; Buffington et al. 2020). Ongoing sea level rise alters wetland hydrology over time, resulting in increased saline water incursion into previously freshwater marshes (Li and Pennings 2018). Our results show that a combination of rises in water level and salinity will cause a decrease or even impede the germination of dominant species of popales, such as *Pontederia sagittata* and that seedling establishment of dominant species of freshwater swamps, such as *A. glabra* could be negatively affected. The *A. glabra* swamps are established in depressions of interdune lagoons and rivers or streams with slow water flow and no abrupt flood-level changes. Sexual reproduction and seedling establishment are synchronized with the rainy and dry seasons, and the seedlings establish when the flood level drops and the soils remain moist (Infante-Mata and Moreno-Casasola 2005; Infante-Mata et al. 2019). Therefore, the higher growth under water-saturated soil conditions observed in our study reflects the adaptations of *A. glabra* to the natural conditions of the environment where it has developed. The increase in water level and salinity in freshwater wetlands from the Gulf of Mexico will increase the pressure on the existing vegetation since sexual reproduction (seeds and seedlings) will be difficult for most species. Further, it has been observed that under higher salinities, plants may produce fewer reproductive structures, such as flowers or stolons (Buffington et al. 2020), which could exacerbate the regeneration issue for these wetlands. Both flooding and salinity have a more significant inhibitory effect on seedling regeneration of the species of freshwater systems than in brackish or salt wetlands, which suggests that sea level rise is likely to have more significant adverse effects on the regeneration of freshwater than salt wetlands (Middleton 2009). The outcome of the scenarios we modeled lead us to conclude that coastal wetlands along the Mexican Atlantic coast will probably be poorer in species composition, with accompanying changes in their functions and extent.

ACKNOWLEDGEMENTS

E.A.S.G. acknowledges the master and doctoral scholarship provided by the Mexican Consejo Nacional de Humanidades Ciencias y Tecnologías (723842 and 779009) and the Doctoral Program of the Instituto de Ecología, A.C. We thank the Instituto de Ecología, A.C. for financial, support, and CICOLMA for providing the space and resources needed to carry out seedling growth experiment. The authors are grateful to Kerenha Hernández for her support in the design of Figure 1B, and to Ecoguías La Mancha en Movimiento for their support during field work.

REFERENCES

Andres, K., M. Savarese, B. Bovard, and M. Parsons. 2019. Coastal wetland geomorphic and vegetative change: Effects of sea-level rise and water management on brackish marshes. *Estuaries and Coasts* 42:1308–1327. https://doi.org/10.3389/fenvs.2019.00025

Bauer-Gottwein, P., B.R.N. Gondwe, G. Charvet, L.E. Marín, M. Rebolledo-Vieyra, and G. Merediz-Alonso. 2011. Review: The Yucatán Peninsula karst aquifer, Mexico. *Hydrogeology Journal* 19:507–524. https://doi.org/10.1007/s10040-010-0699-5

Borchert, S.M., M.J. Osland, N.M. Enwright, and K.T. Griffith. 2018. Coastal wetland adaptation to sea level rise: Quantifying potential for landward migration and coastal squeeze. *Journal of Applied Ecology* 55:2876–2887. https://doi.org/10.1111/1365-2664.13169

Buffington, K.J., A.C. Goodman, C.M. Freeman, and K.M. Thorne. 2020. Testing the interactive effects of flooding and salinity on tidal marsh plant productivity. *Aquatic Botany* 164:103231. https://doi.org/10.1016/j.aquabot.2020.103231

Cahoon, D.R., K.L. McKee, and J.T. Morris. 2021. How plants influence resilience of salt marsh and mangrove wetlands to sea-level rise. *Estuaries and Coasts* 44:883–898. https://doi.org/10.1007/s12237-020-00834-w

Carrasco, A.R., O. Ferreira, and D. Roelvink. 2016. Coastal lagoons and rising sea level: A review. *Earth-Science Reviews* 154:356–368. https://doi.org/10.1016/j.earscirev.2015.11.007

Cazenave, A., and G. Le Cozannet. 2014. Sea level rise and its coastal impacts. *Earth's Future* 2:15–34. https://doi.org/10.1002/2013EF000188

Crawley, M.J. 2013. The R book. Second edition. Wiley & Sons, Chichester, United Kingdom. 1051 pp.

Enwright, N.M., K.T. Griffith, and M.J. Osland. 2015. Incorporating future change into current conservation planning: evaluating tidal saline wetland migration along the U.S. Gulf of Mexico coast under alternative sea-level rise and urbanization scenarios. *U.S. Geological Survey Data Series* 969. https://doi.org/10.3133/ds969

ESRI. 2019. ArcGIS Desktop 10.8. Environmental Systems Research Institute, Redlands, USA.

Frederikse, T., F. Landerer, L. Caron, S. Adhikari, D. Parkes, V. W. Humphrey, S. Dangendorf, P. Hogarth, L. Zanna, L. Cheng, and Y.H. Wu. 2020. The causes of sea-level rise since 1900. *Nature* 584:393–397. https://doi.org/10.1038/s41586-020-2591-3

Friess, D.A., M.F. Adame, J.B. Adams, and C.E. Lovelock. 2022. Mangrove forests under climate change in a 2°C world. *Wiley Interdisciplinary Reviews: Climate Change* 13:1–15. https://doi.org/10.1002/wcc.792

Hammer, Ø., D.A.T. Harper, and P.D. Ryan. 2001. Past: Paleontogical statistics software packge for education and data analysis. Paleontologia Electronica 4:4–9.

INEGI. 2017. Conjunto de datos vectoriales de Uso del Suelo y Vegetación Escala 1:250 000, Serie VI.

Infante-Mata, D., and P. Moreno-Casasola. 2005. Effect of in situ storage, light, and moisture on the germination of two wetland tropical trees. *Aquatic Botany* 83:206–218. https://doi.org/10.1016/j.aquabot.2005.06.009

Infante-Mata, D., P. Moreno-Casasola, C. Madero-Vega, G. Castillo-Campos, and B.G. Warner. 2011. Floristic composition and soil characteristics of tropical freshwater forested wetlands of Veracruz on the coastal plain of the Gulf of Mexico. *Forest Ecology and Management* 262:1514–1531. https://doi.org/10.1016/j.foreco.2011.06.053

Infante-Mata, D., P. Moreno-Casasola, T. Valverde, and S. Maza-Villalobos. 2019. Effects of soil flooding, sunlight and herbivory on seedlings of *Annona glabra* and *Pachira aquatica* in a tropical swamp. *Wetlands Ecology and Management* 27:539–551. https://doi.org/10.1007/s11273-019-09676-1

IPCC. 2014. Summary for policymakers. Page Climate Change 2014: synthesis report. contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland. 151 pp. https://doi.org/10.1017/CBO9781139177245.003

IPCC. 2021. Climate Change 2021: The physical science basis. Contribution of working group I to the sixth sssessment report of the Intergovernmental Panel on Climate Change. Page (V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, Y. Chen, L. Goldfarb, M. I. Gomis, J. B. R. Matthews, S. Berger, M. Huang, O. Yelekçi, R. Yu, B. Zhou, E. Lonnoy, T. K. Maycock, T. Waterfield, K. Leitzell, and N. Caud, Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 2391 pp. ttps://doi.org/10.1017/9781009157896

Lara-Lara, J.R., J.A. Arreola-Lizárraga, L.E. Calderón-Aguilera, V.F. Camacho-Ibar, G. de la Lanza-Espino, A. Escofet-Giansone, I. Espejel-Carbajal, M. Guzmán-Arroyo, L.B. Ladah, M. López-Hernández, E.A. Meling-López, P. Moreno-Casasola Barceló, H. Reyes-Bonilla, E. Ríos-Jara, and J.A. Zertuche-González. 2008. Los ecosistemas costeros, insulares y epicontinentales. In: J. Soberón, G. Halfter, and J. Llorente-Bousquets (eds). Capital natural de México. Vol. 1.: Conocimiento actual de la biodiversidad. CONABIO, México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F. 109-134 pp.

Li, F., and S.C. Pennings. 2018. Responses of tidal freshwater and brackish marsh macrophytes to pulses of saline water simulating sea level rise and reduced discharge. *Wetlands* 38:885–891. https://doi.org/10.1007/s13157-018-1037-2

Li, F., and S.C. Pennings. 2019. Response and recovery of low-salinity marsh plant communities to presses and pulses of elevated salinity. *Estuaries and Coasts* 42:708–718. https://doi.org/10.1007/s12237-018-00490-1

Li, X., R.J. Rowley, J.C. Kostelnick, D. Braaten, J. Meisel, and K. Hulbutta. 2009. GIS analysis of global impacts from sea level rise. *Photogrammetric Engineering and Remote Sensing* 75:807–818. https://doi.org/10.14358/PERS.75.7.807

López-Rosas, H., V.E. Espejel-González, and P. Moreno-Casasola. 2021. Variaciones espacio-temporales del nivel y salinidad del agua afectan la composición de especies del manglar-tular. *Ecosistemas y Recursos Agropecuarios* 8:1–21.

López-Rosas, H., and P. Moreno-Casasola. 2022. From marsh to swamps : vegetation gradient linked to estuarine hydrology. *Wetland Science & Practice* 40:26–35.

McLeod, E., and R.V Salm. 2006. Managing mangroves for resilience to climate change. IUCN, Gland, Switzerland. 64pp.

Middleton, B.A. 2009. Regeneration of coastal marsh vegetation impacted by hurricanes Katrina and Rita. Wetlands 29:54–65. https://doi.org/10.1672/08-18.1

Moreno-Casasola, P. 2003. Ficha informativa de los humedales de Ramsar. La Mancha y El Llano. 11 pp.

Moreno-Casasola, P., and D. Infante-Mata. 2010. Veracruz. Tierra de ciénagas y pantanos. Gobierno del Estado de Veracruz para la Conmemoración de la Independencia Nacional y de la Revolución Mexicana-Universidad Veracruzana., Xalapa, Veracruz. 411 pp.

Moreno-Casasola, P., D. Infante-Mata, and H. López-Rosas. 2012. Tropical freshwater swamps and marshes. In: Batzer DP, Baldwin AH (eds) Wetlands habitats of North America: ecology and conservation concerns. University of California Press, California. 267–282 pp.

Moreno-Casasola, P., M.E. Hernández, and A. Campos. 2017. Hydrology, soil carbon sequestration and water retention along a coastal wetland gradient in the Alvarado Lagoon System, Veracruz, Mexico. *Journal of Coastal Research* 77:104–115. https://doi.org/10.2112/SI77-011.1

Nerem, R.S., B.D. Beckley, J.T. Fasullo, B.D. Hamlington, D. Masters, and G.T. Mitchum. 2018. Climate-change–driven accelerated sea-level rise detected in the altimeter era. *Proceedings of the National Academy of Sciences of the United States of America* 115:2022–2025. https://doi.org/10.1073/pnas.171731211

Reed, D., Y. Wang, E. Meselhe, and E. White. 2020. Modeling wetland transitions and loss in coastal Louisiana under scenarios of future relative sea-level rise. *Geomorphology* 352:106991. https://doi.org/10.1016/j.geomorph.2019.106991

Ruiz-Ramírez, J.D., J.I. Euán-Ávila, and E. Torres-Irineo. 2014. Tendencias del nivel del mar en las costas del Caribe mexicano. *European Scientific Journal* 10:86–96.

Sánchez-García, E.A., K. Rodríguez-Medina, and P. Moreno-Casasola. 2017. Effects of soil saturation and salinity on seed germination in seven freshwater marsh species from the tropical coast of the Gulf of Mexico. *Aquatic Botany* 140:4–12. https://doi.org/10.1016/j.aquabot.2017.04.002

Sánchez-García, E.A., H. López-Rosas, V.J. Sosa, R. Lindig-Cisneros, and P. Moreno-Casasola. 2022. Effect of water level and salinity on the growth of *Annona glabra* L. seedlings. *Wetlands Ecology and Management* 30:579–593. https://doi.org/10.1007/s11273-022-09884-2

Sánchez-García, E.A., C. Yañez-Arenas, R. Lindig-Cisneros, A. Lira-Noriega, R. Monroy Ibarra, and P. Moreno-Casasola. 2023. The expected impacts of sea level on the Mexican Atlantic coast. *Science of the Total Environment* 903:1–12. https://doi.org/10.1016/j.scitotenv.2023.166317

Sánchez-Higueredo, L.E., J.A. Ramos-Leal, J. Morán-Ramírez, P. Moreno-Casasola, U. Rodríguez-Robles, and M.E. Hernández. 2020. Ecohydrogeochemical functioning of coastal freshwater herbaceous wetlands in the Protected Natural Area, Ciénaga del Fuerte (American tropics): Spatiotemporal behaviour. *Ecohydrology* 13:1–13. https://doi.org/10.1002/eco.2173

Sharpe, P.J., and A.H. Baldwin. 2012. Tidal marsh plant community response to sea-level rise: A mesocosm study. *Aquatic Botany* 101:34–40. https://doi.org/10.1016/j.aquabot.2012.03.015

Sokal, R.R., and F.J. Rohlf. 1995. Biometry. The principles and practice of statistics in biological research. 3°. W. H. Freeman and company, New York. 850 pp.

Team R Core, R.F. for S.C. 2019. R: A Language and Environment for Statistical Computing. Vienna, Austria.

Velázquez-Salazar, S. Rodríguez-Zúñiga, M.T. Alcántara-Maya, J.A.E. Villeda-Chávez, C. Valderrama-Landeros, L. Troche-Souza, B. Vázquez-Balderas, I. Pérez-Espinosa, M.I. Cruz-López, R. Ressl, D.V.G. De la Borbolla, O. Paz, V. Aguilar-Sierra, F. Hruby, and J.H. Muñoa-Coutiño. 2021. Manglares de México. Actualización y análisis de los datos 2020. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Ciudad de México. 166 pp.

Yetter, J. 2004. Hydrology and geochemistry of freshwater wetlands on the Gulf coast of Veracruz, Mexico. Masther's Thesis.University Waterloo. Ontario, Canada. 168 pp.

Zavala-Hidalgo, J.R., R. de Buen-Kalman, R. Romero-Centeno, and F. Hernández-Maguey. 2011. Tendencias del nivel del mar en la costas mexicanas. In. Botello A. V., S. Villanueva-Fragoso, J. Gutiérrez, and J. L. Rojas Galaviz, (eds). Vulnerabilidad de las zonas costeras mexicanas ante el cambio climático. SEMARNAT-INE, UNAM-ICMyL, Universidad Autónoma de Campeche. 249-268 pp.