Effect of water level and salinity on the growth of *Annona glabra* L. seedlings

Edgar Abel Sánchez-García · Hugo López-Rosas · Vinicio J. Sosa · Roberto Lindig-Cisneros · Patricia Moreno-Casasola

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Abstract  During the last century the mean sea level has been increasing at a rate of 0.2–0.4 mm·year⁻¹, and that rate is expected to accelerate during this century. Coastal wetland ecosystems are sensitive to the potential changes and impacts resulting from a rise in sea level. In the coastal region of the Gulf of Mexico, freshwater swamps are wetlands located further inland than mangroves, and while influenced by the tides, maintain freshwater conditions. Due to their location, the rise in sea level could increase the levels of flooding and salinity in these ecosystems. The objective of this study was to evaluate, under greenhouse conditions, the effect of nine flood and salinity treatments on the survival, growth, and increase in the biomass of *Annona glabra* (pond apple) seedlings (average height: 18.6±1.61 cm). The treatments combined two factors: water level (Saturation, Flood, Flood-Drought) and salinity (0, 5 and 15‰). Seedling survival was greater under freshwater conditions. Increases in height and diameter, and leaf and biomass gain, were more significant under saturation and freshwater conditions. Based on our results, we conclude increased flood levels and salinity will negatively affect the natural establishment of *A. glabra* seedlings in freshwater swamps under a scenario of rising sea level.

Keywords  Coastal zone · Flooding · Sea level rise · Swamps · Wetlands

Introduction

Coastal wetlands are transition zones between the terrestrial environment and the marine environment (An and Verhoeven 2019), which makes these ecosystems sensitive to changes in sea level rise and their potential impacts, since their location is closely linked to the sea (Nicholls et al. 1999). Sea level is not rising...
uniformly in all of the world’s regions (Nicholls and Cazenave 2010). For example, there is evidence that mean sea level in the Gulf of Mexico has risen faster than the global trend in the last 60 years (IPCC 2007), with satellite records suggesting an increase in average elevation of $3.3 \pm 0.4$ mm year$^{-1}$ since 1992 (Parris et al. 2012). Therefore, the wetlands in the coastal region of the Gulf of Mexico are more vulnerable to the possible effects of rising sea levels (Day et al. 2008; Ortiz-Pérez and Méndez-Linares 1999; Yáñez-Arancibia et al. 2010). Coupled with changing sea levels, increasing temperature and changes in precipitation patterns due to climate change could exacerbate the threats and pressure on coastal wetlands in the future (Junk et al. 2013). Changes to the precipitation regime will affect surface hydrology, modifying runoff and groundwater inflow to wetlands (Junk et al. 2013; Nielsen and Brock 2009). The arrival of less freshwater from the continent to coastal wetlands is expected to increase salinity levels, which would cause changes in the vegetation and a decrease in soil quality (Herbert et al. 2015; Xian et al. 2019). In addition, the damage to and loss of wetlands would be greater particularly for those located at the deltas of large rivers, where soil subsidence is already occurring and where the development of economic activities will prevent the migration of these ecosystems towards the interior (Mitsch and Gosselink 2015), which is referred to as “coastal squeeze” (Doody 2013). Due to the high degree of vulnerability of coastal wetlands to climate change and anthropogenic pressures, there is an urgent need to better understand the risks these ecosystems face.

In the Gulf of Mexico region, the highest subsidence rates occur in the Mississippi River Delta Plain (Parris et al. 2012). The swamps in this plain and in the Atlantic Ocean coast of the United States of America are dominated by Taxodium distichum (L.) Rich. and Nyssa aquatica L. (Mitsch and Gosselink 2015). These wetlands have been subject to environmental pressures such as increased flooding and salinity (Conner and Inabinette 2005; Hoeppner and Rose 2011; Middleton 2009). The seedlings of both species have been found to be resistant to flooding, but are sensitive to the combined effect of increased flooding and salinity (Allen et al. 1994; Conner et al. 1997; Pezeshki et al. 1989). López-Rosas et al. (2021) describe an increase of saltwater in oligohaline swamps and marshes from south of the Gulf of Mexico, resulting in the replacement of oligohaline species with mangrove species. These results indicate that an increase in salinity in these freshwater ecosystems will affect seedling survival and growth. In Mexico, the coastal wetlands of the Gulf of Mexico receive freshwater from the Sierra Madre Oriental range (Sánchez-Higueredo et al. 2020; Yetter 2004), freshwater from extensive dune system coastal waters (Yetter 2004) and seawater from tides and coastal lagoons. Therefore, in coastal wetlands the mixture between the freshwater and seawater creates a flood and salinity gradient that results in the establishment of various types of wetlands (Infante-Mata 2011; Lara-Lara et al. 2008; López-Rosas et al. 2021). In this region, there are mosaics of coastal wetlands, with mangroves being exposed to the highest salinity (15–25 parts per thousand), because they are in contact with the sea. Further inland, there are freshwater swamps (salinity: 1–2 parts per thousand) and marshes, such as “popales” and “tulares” (salinity: 1–3 parts per thousand) that contribute to reducing the speed of water currents leading to a high deposition of sediments (Infante-Mata 2011; Moreno-Casasola et al. 2020).

The freshwater swamps of the Gulf of Mexico in the state of Veracruz are dominated by the money tree, Pachira aquatica Aubl. (Malvaceae) and the pond apple, Annona glabra L. (Annonaceae) (Infante-Mata et al. 2011; Moreno-Casasola and Infante-Mata 2016), the former being more widely dispersed. A. glabra is distributed from the southern United States of America (Florida), to tropical South America and the Caribbean (Niembro-Rocas et al. 2010). In Australia and west Africa it was introduced and is considered invasive (Setter et al. 2004; Shanungu 2009). The fruit production of A. glabra is synchronized with the rainy season when the flood level increases and water disperses the seeds (Infante-Mata and Moreno-Casasola 2005). This species has been reported in areas where the water table rises slowly, and flood remains for several weeks, or months (Infante-Mata 2011). The A. glabra’s seeds can float for up to 90 days and germinate wherever an appropriate site when the water level decreases; furthermore, under these saturated soil conditions, there is a greater probability of seedling establishment success (Infante-Mata et al. 2019; Infante-Mata and Moreno-Casasola 2005; Sánchez-García 2020).
Among the freshwater coastal wetlands of the Gulf of Mexico region, freshwater swamps provide the most significant number of ecosystem services. These wetlands store a large amount of carbon in the soil (0.92 ± 0.12 kg C m⁻² year⁻¹), even storing 66% more than other wetlands such as marshes (Marín-Muñiz et al. 2014). In Tabasco, south of the Gulf of Mexico, Sjögersten et al. (2021) found that the C stock was 180 ± 28.3 kg C m⁻². In addition, they are critical in flood control, because their soils act as sponges, storing 556–834 L m⁻² of water (Campos et al. 2011). Freshwater swamps are also a source of wood, fuel, and food for local populations (González-Marín et al. 2016). In addition, freshwater swamps provide economic benefits equivalent to $192,993 USD/ha, greater than the estimated value for mangroves ($154,237 USD/ha; Vázquez-González et al. 2016).

Freshwater swamps dominated by *A. glabra* are distributed mainly in the vicinity of coastal lagoons and on floodplains where there is no marine influence. There, water currents are calmer, and quite shallow (Moreno-Casasola et al. 2012; Niembro Rocas et al. 2010). However, the pressure exerted by human activities has left remnants in between marshes, in small fringes bordering the mangroves, and in some protected natural areas (Infante-Mata 2011). In addition to anthropogenic factors, the increase in salinity caused by rising sea levels will exert greater pressure on these ecosystems. Although studies on germination and growth of *A. glabra* seedlings have been done (Infante-Mata et al. 2019; Infante-Mata and Moreno-Casasola 2005), there is no information on possible responses of this species to the potential increase in salinity or the combined increase of salinity and flooding. Both are fundamental factors that will affect wetlands according to projected scenarios for climate change. Therefore, it is essential to generate information for the seedling establishment stage of dominant species of freshwater swamps such as *A. glabra*. The information obtained will be used for future conservation and restoration plans for floodplains on the coastal plain of the Gulf of Mexico. The objective of this study was to experimentally evaluate the effect of nine combinations of water level and salinity conditions on the survival and growth (height and biomass) of *A. glabra* seedlings. We hypothesized that the seedlings will have a higher survival rate and better development under saturated soil conditions and no salinity.

### Methods

#### Collection site and plant material

*Annona glabra* seedlings were obtained from germinated seeds. The seeds were collected from a flooded pasture with isolated trees of *A. glabra* dominated by the exotic African grass *Echinochloa pyramidalis* (Lam.) Hitchc. & Chase, with an area of approximately 3.5 ha and located in central Veracruz (19° 33'17"N and 96° 22'43"W), close to a swamp patch dominated by this species. The flooded pasture is bordered to the north and west by a mangrove community, to the east by tropical forest and coastal dunes, and to the south by cattle pastures for raising livestock interspersed with the remnants of the disturbed marsh (Fig. 1). The mangrove hydroperiod is determined by the level of flooding of the La Mancha coastal lagoon and the subsurface freshwater flows (Yetter 2004); the latter influences the level of the water table of the flooded pasture.

In August 2019, the pond apple fruits were collected. They were taken to a greenhouse at the Centro de Investigaciones Costeras La Mancha (CICOLMA) run by the Instituto de Ecología, A.C., located 3.6 km north of the collection site. The seeds were placed in soil recollected from a marsh located in CICOLMA in polyethylene greenhouse bags 25 cm high and 15 cm in diameter for germination. At the beginning of the experiment, the seedlings had an average height of 18.6 ± 1.6 cm.

#### Experimental design

The experimental design combined two factors (water level and salinity) with three levels each:

1. **Water level:** (i) 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 seedling bag; (ii) Flooded: the water level was permanently maintained at 10 cm above soil level; (iii) 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, 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. This process was repeated
Fig. 1 Location of the study area in Veracruz, in the Gulf of Mexico, and the environmental surroundings of the La Mancha Lagoon. The lower map shows the diverse vegetation communities in the study area, including the pond apple swamp (flooded), and the flooded pasture with isolated pond apple trees (*Annona glabra*).
alternately over the duration of the experiment (18 weeks).

(2) Salinity: (i) 0 parts per thousand (%); (ii) 5%; (iii) 15‰.

Thus, the combination of the two factors resulted in the following nine treatments: (1) Saturation0‰, (2) Flooded0‰, (3) Flood-Drought0‰, (4) Saturation5‰, (5) Flooded5‰, (6) Flood-Drought5‰, (7) Saturation15‰, (8) Flooded15‰, and (9) Flood-Drought15‰.

For the experiment, five seedlings were randomly assigned to each treatment for a total of 45 seedlings. To apply the treatments, four fiberglass tubs 130 cm long × 60 cm wide × 70 cm high were used 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. For the different flood levels, PVC tubes of two heights (45 and 20 cm) were placed inside the tubs to keep the water level at 15 cm (Saturation) and −10 cm (Flooded). A polyethylene bag with a seedling was placed on top of each tube. The fourth tub had no water, and this is where the seedlings of the Flood-Drought treatments were placed during the weeks they did not have contact with the water.

The experiment lasted 18 weeks to prevent the roots of the seedlings from coming into contact with the polyethylene bag and thus influencing their growth pattern. On October 27, 2019, the experiment began with the placement of the polyethylene bags in the treatment tubs. The average temperature inside the greenhouse for the duration of the experiment was 26.8 ± 0.1 °C (data obtained with a HOBO® Onset Pendant data logger, which recorded the temperature every two hours). No environmental or management factor was detected that could affect the tubs differentially inside the greenhouse. When the experiment began, height and basal diameter were measured for each of the 45 seedlings, and the number of leaves were counted. The seedlings were monitored and measured every two weeks: height, diameter and leaf count, and percent seedling survival. On March 1, 2020, the experiment ended. All seedlings were harvested and separated into roots, stems, and leaves, which were oven-dried at 70 °C for 72 h. Afterward, the structures were weighed to obtain their biomass. Throughout the experiment, when a seedling died, it was removed from the tub, its height and diameter measured, its leaves counted, and its structures separated and dried to obtain its biomass.

Data analyses

The effect of the different treatments on the growth (change in height) of the seedlings was evaluated through the fitting of a Linear Mixed Model (LMM), a suitable approach to analyze experimental designs where there are factors of both, fixed and random effects (Bolker 2015; Pinheiro and Bates 2000). In our model, height or diameter (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, 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. The syntax in R code was:

```R
Model ← lme(Height ~ Salinity × Water_level × Time, random = ~ Time|Plant/Salinity/Water_level, na.action = na.omit, weight = varPower(form = ~ Time).
```

Finally, because the variance of the response variable increased with time (a very common case in growth curves), a power variance function was specified in the model to weight monotonic heteroscedasticity.

To evaluate the effect of treatments on the number of leaves gained or lost by each seedling, as well as the root, stem, and leaf biomass of each plant at the end of the experiment or its death, a nested analysis of variance (ANOVA) was carried on (water level was nested on salinity); thus, the interaction (multiplicative effect) between water level and salinity was not possible to be evaluated. The loss or gain of leaves was obtained by subtracting the final number of leaves from the initial number for each seedling. Before carrying out the analysis, the values of the root, stem, and leaf biomass were log-transformed to meet the residuals’ Normal distribution assumption of the test. In all cases, a Tukey HSD test was carried out to detect differences between treatments when the analysis detected a significant effect of any factor. All analyses were run in R software, version 3.6.1.
with the MASS, nlme, lattice and emmeans libraries (Team R Core 2019).

**Results**

**Survival**

A 100% survival rate was recorded for the seedlings exposed to 0‰ salinity. However, some seedlings died in all treatments exposed to 5 and 15‰. All the seedlings died when exposed to the Flood-Drought15‰ treatment (Table 1).

**Height and number of leaves**

Overall, the growth of seedlings throughout the experiment was greater in the treatment under conditions of Saturation and low salinity (0 and 5‰; Figs. 2, 3). The growth of seedlings and their final height were affected by salinity independently of water level (Table 2); the mean height of the 0‰ treatment was significantly different from the 15‰ treatment ($P=0.03$, 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). The interactions of each factor with the covariable time were statistically significant, indicating at least one line not parallel to the others. This was the slope of the Saturation 0‰ treatment which is the steepest and different from all others (Fig. 3). The seedling in the Saturation0‰ treatment grew the most ($27.6 \pm 7.37$ cm), while the seedlings in the Flood-Drought15‰ treatment, grew the least. Even negative values were observed ($-0.5 \pm 0$ cm), in addition to the death of all individuals subjected to this treatment six weeks after starting the experiment (Fig. 2). For water level, seedling growth was greater under the Saturation condition and was lowest in the Flood-Drought treatments, although the difference was not significant ($P$’s > 0.05). Seedlings under the treatments with 0‰ salinity (fresh water) had the greatest growth, while the seedlings subjected to the 15‰ salinity treatments grew the least. These results were very similar to growth in diameter (Fig. S1).

The gain (or loss) in the number of leaves in A. glabra seedlings was affected by salinity only (Table 3). The seedlings under the Saturation0‰ treatment had a gain of $10.2 \pm 1.15$ leaves, which was significantly higher with respect to the seedlings in the other treatments. On the other hand, seedlings lost leaves under conditions Saturation, Flooded and Flooded-Drought combined with salinities 5 and 15‰. Specifically under the treatment Flooded15‰ this loss ($-11 \pm 2.62$ leaves) was significantly greater than that of the other treatments (Fig. 4).

**Biomass**

The final biomass of three structures of the seedlings (roots, stems, leaves) was lower in the treatment with the highest salinity (Fig. 5). However, the biomass of the root and stem was only affected by salinity (Table 4). The lowest value for seedling root biomass was recorded for the Flood-Drought15‰ treatment. In contrast, the highest biomass values of the roots of the seedlings were recorded for the treatment Saturation0‰. The only significant difference was between

### Table 1

| Treatment               | Number of seedlings at the beginning | Number of seedlings at the end | Survival (%) |
|-------------------------|--------------------------------------|--------------------------------|--------------|
| Saturation0‰           | 5                                    | 5                              | 100          |
| Flooded0‰              | 5                                    | 5                              | 100          |
| Flood-Drought0‰        | 5                                    | 5                              | 100          |
| Saturation5‰           | 5                                    | 2                              | 40           |
| Flooded5‰              | 5                                    | 3                              | 60           |
| Flood-Drought5‰        | 5                                    | 3                              | 60           |
| Saturation15‰          | 5                                    | 3                              | 60           |
| Flooded15‰             | 5                                    | 2                              | 40           |
| Flood-Drought15‰       | 5                                    | 0                              | 0            |
the 0‰ and 15‰ salinity levels ($P = 0.0042$, Tukey test; Fig. 5a).

The seedlings subjected to the Flood-Drought 15‰ treatment had the lowest amount of biomass in the stem, compared to the seedlings in the other treatments. The Saturation 0‰ treatment had the highest stem biomass (Fig. 5b). There was a significant difference only between the 15‰ salinity levels ($P = 0.036$, Tukey test). The water level and salinity had no effect on the biomass of the leaves of the surviving seedlings (Table 4, Fig. 5c).

**Discussion**

Our results show that salinity affected the growth of *A. glabra* seedlings, consistent with the hypothesis of a more significant biomass gain and number of leaves, and greater growth in height under saturated soil conditions and without salinity. Also, seedlings performed better under saturated soil conditions. However, differences with the other flooding levels were not statistically significant, perhaps due to a high variance of data and a small number of replicates. These results coincide with those of various authors who have evaluated biomass gain and growth in height and diameter in seedlings of dominant tree species from swamps in the southeastern United States such as *Fraxinus pennsylvanica* Marshall, *Nyssa aquatica*, *Nyssa sylvatica* Marshall, *Quercus michauxii* Nutt., *Quercus nigra* L., *Quercus nuttallii* E.J. Palmer and *Sapium sebiferum* (L.) Dum. Cours. In these species, it has been found that there is a greater gain in root and stem biomass, as well as greater increase in diameter and height when the plants are in saturated soil conditions in comparison with soil with less than five centimeters of permanent flooding (Conner 1994; Conner et al. 1998, 1997; McCarron et al. 1998; Pezeshki 1990; Pezeshki et al. 1989). Of the studies carried out in this region, only *Taxodium distichum* has shown a broad tolerance to flooding; the increase in water level does not have any

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**Fig. 2** Increase in height (cm) over time (weeks) of *A. glabra* seedlings under different water level treatments and salinity. Regression lines fitted with a linear mixed model with the plant as a random effects factor. Same symbols belong to the same seedling (plant replicate).
**Fig. 3** Mean increase in height ± 1 SE of *A. glabra* seedlings under different treatments over the 18 weeks of the experiment. Saturation0‰ = Sat0‰, Flooded0‰ = Fl0‰, Flood-Drought0‰ = Fl-Dr0‰, Saturation5‰ = Sat5‰, Flooded5‰ = Fl5‰, Flood-Drought5‰ = Fl-Dr5‰, Saturation15‰ = Sat15‰, Flooded15‰ = Fl15‰, and Flood-Drought15‰ = Fl-Dr15‰.

**Table 2** Summary of the effect of different salinity and water level treatments on *A. glabra* seedlings growth (change in height) over time, as yielded by a linear mixed model. Significant effects are shown in bold.

| Source of variation | Numerator degrees of freedom | Denominator degrees of freedom | F       | P       |
|---------------------|------------------------------|--------------------------------|---------|---------|
| **Fixed effects**   |                              |                                |         |         |
| Intercept           | 1                            | 260                            | 0.3518  | 0.5536  |
| Salinity            | 2                            | 36                             | 5.6462  | **0.0074** |
| Water level         | 2                            | 36                             | 1.7150  | 0.1943  |
| Time                | 1                            | 260                            | 27.8563 | **< 0.0001** |
| Salinity × water level | 4                          | 36                             | 14256   | 0.2453  |
| Salinity × time     | 2                            | 260                            | 4.7219  | **0.0097** |
| Water level × time  | 2                            | 260                            | 9.9987  | **0.0001** |
| Salinity × water level × time | 4  | 260          | 0.9558  | 0.4323  |

*P* is the probability that the effect of a factor or covariable is null.

**Table 3** Nested analysis of variance of the final number of leaves on *A. glabra* seedlings under different water level and salinity treatments. Significant effects are shown in bold.

| Factor                               | Degrees of freedom | Sum of squares | Mean squares | F       | P       |
|--------------------------------------|--------------------|----------------|--------------|---------|---------|
| Salinity                             | 2                  | 1405.0         | 702.5        | 16.634  | **< 0.001** |
| Water level nested in salinity       | 6                  | 366.5          | 61.1         | 1.446   | 0.224   |
| Residuals                            | 36                 | 1520.4         | 42.2         |         |         |
significant effect on seedling height (Pezeshki 1990). In coastal wetlands of southeastern Australia, it was also observed that *Melaleuca ericifolia* Sm. grew taller and gained more biomass in wet or saturated soil treatments compared to seedlings that remained totally submerged (Salter et al. 2007). In addition, it has been documented that growth in flooded soil reduces the height of *Calophyllum brasiliense* Cambess. seedlings, a dominant species of freshwater swamps of the Amazon region in Brazil, compared to moist soil treatments; likewise, flooding also significantly reduced its root and stem biomass (Oliveira and Joly 2010). In Mexico, the dominant species of flooded forests on the coast of the Gulf of Mexico, such as *Pachira aquatica* and *A. glabra*, gain more root biomass in saturated soils than in flooded soils (Infante-Mata et al. 2019), which coincides with the results we obtained. The reduction in root biomass may result from cell death due to the lower availability of oxygen associated with flood conditions.

As expected, salinity negatively affected survival, biomass gain, leaf gain, and height and diameter growth (we found similar results for diameter and height, Fig. S1) in *A. glabra* seedlings. Various studies have been carried out to evaluate the response of biomass gain and growth in height or diameter to the increase in salinity of swamp tree species that are distributed in the southeastern United States such as *Cephalanthus occidentalis* L., *Fraxinus pennsylvanica*, *Nyssa aquatica*, *Nyssa sylvatica*, *Quercus lyrata* Walter, *Quercus michauxii*, *Quercus nigra*, *Quercus nuttallii*, *Sapium sebiferum* and *Taxodium distichum* (Allen et al. 1994; Conner 1994; Conner et al. 1998, 1997; McCarron et al. 1998; Pezeshki 1990; Pezeshki et al. 1989), in the Caribbean such as *Pterocarpus officinalis* Jacq. (Bompy et al. 2015; Rivera-Ocasio et al. 2007), and in southeastern Australian wetlands such as *Melaleuca ericifolia* (Salter et al. 2007) and *Eucalyptus tereticornis* Sm. (Grieger et al. 2019). In these studies, it was observed that the seedlings biomass, height, and diameter were greater in the treatments with no or low salinity compared to the high salinity treatments.

Salinity is a limiting environmental factor for the establishment of wetland plant species. It causes physiological drought by producing a water deficit that reduces the osmotic potential of the soil (Salter et al. 2007). This represents an ecological and evolutionary barrier that prevents the germination and establishment of numerous freshwater wetland species.
Fig. 5 Final mean biomass (dry weight) ± 1 SE for the roots (a), stem (b) and leaves (c) for A. glabra seedlings under the different water level and salinity treatments. Shared letters indicate no difference between salinity treatments. No significant differences were found among water level treatments.
species (Wieski et al. 2010). Salinity occurs in coastal wetlands when marine water enters (Flores-Verdugo et al. 2007). In tropical or subtropical areas, the species categorized as mangroves have adaptations to survive in saline soils (Cronk and Fennesy 2001). The freshwater swamps on the coastal plain of the state of Veracruz are located inland of the mangrove zone, where the sea’s influence is minimal, so the species that make up these wetlands do not have any adaptations to withstand increases in salinity. Our results showed survival, height increases, and leaf and biomass gain diminished as salinity increased. However, despite the stress imposed by salinity, the seedlings under the Flooded15‰ and Saturation15‰ treatments slightly increase in height and diameter (we found similar results between diameter and height, Fig. S1), and a slight gain in biomass. This may be because the seedlings in this study came from a population that is very close to a mangrove area where salinity increases periodically during the rainy and the cold-fronts season (called locally “nortes”), as occurs in T. distichum, where the seedlings from brackish populations grow more (height and biomass) than do those from freshwater populations (Allen et al. 1997, 1994; Conner and Inabinette 2005). In Veracruz, freshwater swamps with saline influence have lower species richness, leading to the dominance of a few salinity-tolerant species and even mixing with mangrove species (Infante-Mata et al. 2011).

Although wetland plant species have various adaptations that allow them to tolerate flooding and changes in soil chemistry (Mitsch and Gosselink 2015; Pezeshki 2001), most of the seedlings of these species do not grow or their growth is slower under flood conditions, because the low oxygen level of these environments is too stressful for them (Cronk and Fennesy 2001). This may indicate that these species can tolerate rather than require high levels of flooding to establish successfully (Infante-Mata et al. 2019). Annona glabra establishes in depressions or areas with languard water flow, where it is not subjected to notable changes in flood level. Sexual reproduction and the establishment of pond apple are synchronized with the rainy and dry seasons, and the seedlings establish when the flood level drops and the soils remain humid (Infante-Mata et al. 2019; Infante-Mata and Moreno-Casasola 2005). Therefore, the higher growth under water-saturated soil conditions seems to reflect 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 swamps on the floodplains of Veracruz will increase the pressure on the species that inhabit them. Our results suggest that an increase in sea level could strongly impact the establishment of A. glabra seedlings. However, P. aquatica (the dominant species in the other type of swamp) can survive a wide range of salinity (0.02–18‰), so its germination and establishment can occur close to mangroves, and occur under a scenario of rising sea level (Infante-Mata et al. 2014). Increased levels of flooding and salinity could alter the floristic composition of freshwater swamps to more tolerant species.
(i.e., *Pachira aquatica*) against less tolerant species (i.e., *Ficus* spp., *Pouteria* sp., *Salix humboldtiana* Willd., *Inga vera* Willd.), including *A. glabra*, frequent in areas subject to shorter and intermittent flood periods (Moreno-Casasola and Infante-Mata 2010). This could also alter the functional ecology of these ecosystems. As with *A. glabra*, some tree species on the Gulf of Mexico coast in the United States of America cannot tolerate high levels of salinity (Duberstein et al. 2020). The consequences of rising sea levels could deteriorate or disappear the freshwater swamps on the coastal plain of the Gulf of Mexico.

Despite the potentially dire consequences to freshwater swamps, with the exception of our studies, there has been no work to evaluate tolerance during the seedling establishment of dominant species of tropical freshwater swamps in the face of flood conditions and increased salinity that are expected with changes in sea level in the Gulf of Mexico. It is important to mention that this study was experimental and carried out under greenhouse conditions. Thus, it serves as an important reference for the analysis and understanding of the seedling’s response of this species in the field. It is necessary to continue field and greenhouse studies in the long and medium-term to determine the possible impact of rising sea levels on the regeneration of freshwater swamps. This would make it possible to propose ecological restoration strategies. The results obtained in this study for *A. glabra*, and those mentioned for species of freshwater swamps in other regions, show that most of these species will be negatively impacted by increased flooding and salinity. This negative effects makes this type of wetland particularly vulnerable to climate change, highlighting the importance of extensive research, legislation and restoration efforts.

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**Author contributions** EASG, HLR, PMC, and RLC: Conceived the idea and designed the experiment. EASG: Carried out the greenhouse work and the performed data collection. EASG and VJS: Performed the analyses. EASG: Wrote the first version of the manuscript. All authors contributed to the discussion, review, and approval of the final manuscript.

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**Data availability** The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Consent for publication** All authors consent for the manuscript to be published.

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