

Effect of Water Level and Salinity on the Growth of *Annona Glabra* L. Seedlings

Edgar Abel Sánchez-García

INECOL: Instituto de Ecología <https://orcid.org/0000-0003-4241-0342>

Hugo López-Rosas

El Colegio de Veracruz

Vinicio J. Sosa

INECOL: Instituto de Ecología

Roberto Lindig-Cisneros

UNAM IIES: Universidad Nacional Autónoma de México Instituto de Investigaciones en Ecosistemas y Sustentabilidad

Patricia Moreno-Casasola (✉ patricia.moreno@inecol.mx)

INECOL: Instituto de Ecología

Research Article

Keywords: coastal zone, flooding, sea level rise, swamps, wetlands

Posted Date: July 22nd, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-734846/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

During the last century the mean sea level has been increasing at a rate of 0.2 to 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 of 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. The treatments combined two factors: water level (saturation, flood, flood-drought) and salinity (0, 5 and 15 ‰). Germinated seedlings were used (average height: 18.6 ± 1.61 cm). Seedling survival was greater under freshwater conditions. Increase in height and diameter, as well as leaf and biomass gain, were greater under saturation and freshwater conditions. Based on our results, we conclude that under a scenario of rising sea level, increased flood levels and salinity will negatively affect the natural establishment of *Annona glabra* seedlings in freshwater swamps.

Introduction

Globally, sea levels rose between 0.1 and 0.2 m during the last century, and this rise is expected to accelerate during this century, though the magnitude is still unknown (Nicholls and Cazenave 2010). According to different scenarios, a mean global increase in sea level of 0.2-2.0 m as a consequence of climate change is estimated for the year 2100 (Parris et al. 2012). 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). These ecosystems could experience changes in their composition and structure, in addition to suffering losses in area in various locations of the planet (Nicholls 2004).

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 ± 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 (Ortíz-Pérez and Méndez-Linares 1999; Day et al. 2008; 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, which will cause a decrease in the level and timing of flooding (Nielsen and Brock 2009; Junk et al. 2013). The arrival of less water from the continent to freshwater coastal wetlands is expected to increase salinity and flood levels, which would be reflected in 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). Changes in topography are also a concern and together, these factors are referred to as “coastal squeeze” (Nicholls 2004). Due to the high degree of vulnerability of coastal wetlands to climate change, as well as the anthropogenic pressures these wetlands face, there is an urgent need to better understand the risks these ecosystems face.

In the Gulf of Mexico region, the highest subsidence rates are occurring in the Mississippi River Delta Plain (Parris et al. 2012). The swamps that are located on this plain and on the coast of the Atlantic Ocean 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 et al. 1997). Various studies have been carried out to evaluate the response of these species during the seedling establishment and growth stages to the increase in these environmental variables. The seedlings of both species have been found to be resistant to flooding, but are sensitive to stress caused by the combination of increased flooding and salinity (Pezeshki et al. 1989; Allen et al. 1994; Conner et al. 1997). The results indicate that an increase in salinity in these freshwater ecosystems will generate adverse effects for the physiological processes that control seedling survival and growth. In Mexico, the coastal wetlands of the Gulf of Mexico region receive freshwater that flows from the mountains of the Sierra Madre Oriental range (Yetter 2004; Sánchez-Higuero et al. 2020), freshwater from extensive dune system coastal waters (Yetter 2004) and seawater from tides and coastal lagoons. This creates a flood and salinity gradient that results in the establishment of various types of wetlands throughout the coastal zone (Lara-Lara et al. 2008; Infante-Mata 2011). In this region, there are mosaics of coastal wetlands, with mangroves being the wetlands with the highest levels of salinity (15-25 parts per thousand), because they are in contact with the sea. Further inland (where the marine influence is less), there are freshwater swamps (salinity: 1-3 parts per thousand). Finally, going deeper inland, there are marshes such as “popales” and “tulares” (marshes with salinity: 2-3 parts per thousand) and these 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 coastal zone on the Gulf of Mexico in the state of Veracruz are dominated by two species: the “apompo” or “zapote reventador”, *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. *Annona glabra* is distributed from the southern United States of America (Florida), to South America, the Caribbean and West Africa. In Australia it was introduced and is considered invasive (Setter et al. 2004). 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). The presence of this species has been reported in areas where the water table rises slowly and remains flooded for several weeks, sometimes months (Infante-Mata 2011), with no currents. These seeds can float for up to 90 days and germinate when the water level decreases; furthermore, under these saturated soil conditions there is a greater probability of seedling

establishment success (Infante-Mata and Moreno-Casasola 2005; Infante-Mata et al. 2019; Sánchez-García 2020).

Among the freshwater coastal wetlands of the Gulf of Mexico region, freshwater swamps provide the greatest number of ecosystem services. These wetlands store a large amount of carbon in the soil ($0.92 \pm 0.12 \text{ kgC m}^{-2} \text{ yr}^{-1}$), even storing 66% more than other wetlands such as marshes (Marín-Muñiz et al. 2014). In addition, they are very important in flood control, because their soils act as sponges, absorbing a large amount of water during the rainy season; freshwater swamp soils can store 556 to 834 L m^{-2} (Campos et al. 2011). Freshwater swamps are also a source of resources such as wood, fuel, and food for local populations (González-Marín et al. 2016). In a study carried out by Vázquez-González et al. (2016) to quantify the ecosystem services provided by coastal wetlands in the central region of the Gulf of Mexico, it was estimated that the freshwater swamps is the type of wetland that in economic terms provides the greatest benefits with an approximate value of \$192,993 USD/ha/2007. According to this study, the economic value provided by freshwater swamps is even greater than that provided by mangroves.

The freshwater swamps dominated by *A. glabra* are distributed along the edges of water currents with little movement, and mainly in the vicinity of coastal lagoons and on floodplains where there is no marine influence (Niembro Rocas et al. 2010; Moreno-Casasola et al. 2012). However, the pressure exerted by human activities has led to a decrease in their cover, leaving only some remnants in the middle of marshes, in small areas that border 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. In the state of Veracruz Infante-Mata and Moreno-Casasola (2005) and Infante-Mata et al. (2019) studied the germination and growth of *A. glabra* seedlings in their natural environment, evaluating the germination of seeds under different levels of humidity and light, and the effect of these two factors together with herbivory on the survival and the establishment of seedlings in their natural environment. However, 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 important 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. Therefore, the objective of this study was to experimentally evaluate the effect of nine treatments under different flood and salinity conditions on the survival and growth (height, diameter and biomass) of *A. glabra* seedlings. Our hypothesis is that the seedlings will have a higher survival rate and better development under lower stress conditions, that is, under saturated soil conditions and without exposure salinity.

Methods

Collection site and plant material

Annona glabra seeds were collected from a flooded pasture dominated by the exotic African grass *Echinochloa pyramidalis* (Lam.) Hitchc. & Ch, 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 low deciduous forest and coastal dunes and to the south pastures cultivated for raising livestock interspersed with the remnants of herbaceous wetlands (Figure 1). The mangrove hydroperiod is determined by the level of flooding of the La Mancha coastal lagoon and by 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, where the seeds were extracted. For germination, the seeds were placed in polyethylene bags 25 cm high and 15 cm in diameter, filled with soil from a marsh located in CICOLMA. At the beginning of the experiment, the seedlings had an average height of 18.63 ± 1.61 cm.

Experimental design

The experimental design combined two factors (water level and salinity), with three levels each, resulting in nine treatments (Table 1).

1. Water level: i) Saturation: the water was permanently kept 15 cm below the level of the soil's surface in the seedling bag; ii) Flooding: the water was permanently maintained at a level of 10 cm above the soil's level; iii) Flood-Drought: alternately, every four weeks the water level to which the seedling was exposed was changed. For four weeks the water was 10 cm above the soil's surface and for the next four the plant had no contact with the water. These changes were made over the duration of the experiment (18 weeks).
2. Salinity: i) Water with a salinity of 0 parts per thousand (‰); ii) Water with a salinity of 5 ‰; iii) Water with a salinity of 15 ‰.

For the experiment, five seedlings were randomly assigned to each treatment, for a total of 45 seedlings. To apply the treatments, inside the greenhouse four fiberglass tubs 130 cm long x 60 cm wide x 70 cm high were used. Three tubs were filled with tap water at a constant level of 55 cm. Each of these three tubs had a different salinity level: 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 different heights (45 and 20 cm) were placed inside the three tubs to manipulate the water level to which the seedlings were subjected (15 cm below the soil surface and 10 cm above the soil surface respectively). A polyethylene bag with a seedling was placed on top of each tube. The water levels were kept constant throughout the experiment. The fourth tub had no water, and this is where the seedlings of the Flood-Drought treatments were placed during the weeks that 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. On October 27, 2019, the experiment began with the

placement of the polyethylene bags with seedlings in the treatment tubs. The average temperature inside the greenhouse for the duration of the experiment was 26.8 ± 0.07 °C (data obtained with a Hobo® Onset Pendant data logger, which recorded temperature every two hours). When the experiment began, height and basal diameter *sensu strictu* 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 the seedlings were harvested, and separated into three structures: root, stem and leaves, which were dried in an oven at 70 °C for 72 hours. Afterwards, 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 were measured, the leaves were counted, and later its structures were separated and dried to obtain their biomass.

Data analysis

The effect of the different treatments on the change in height and diameter of the seedlings was evaluated with an analysis of covariance (ANCOVA), where the categorical explanatory variables were water level and salinity and the continuous explanatory variable (covariate) was time. The change in height and diameter was obtained by subtracting the final value from the initial value for each seedling. The evaluation of the final number of leaves was carried out on the amount of leaves gained or lost by each seedling using a bifactorial analysis of variance (ANOVA) with interaction. The loss or gain of leaves was obtained by subtracting the final number of leaves from the initial number for each seedling. When the analysis detected significant differences, a Tukey test was used to determine differences between treatments.

Root, stem and leaf biomass were also evaluated through a bifactorial ANOVA with interaction. Before carrying out the analysis, the root, stem and leaf biomass values for the seedlings were log-transformed to meet the assumptions of the model. A Tukey test was carried out to detect differences between treatments when the analysis detected a significant effect of any of them. Root, stem and leaf biomass were recorded at the end of the experiment, but for the seedlings that died before the end of the experiment, their final biomass was obtained when their death was detected. All analyses were run in R software, version 3.6.1 (Team R Core 2019).

Results

Survival

A 100% survival was recorded for the seedlings that were under all the three treatments with 0 ‰ salinity (Sat0‰, Flo0‰ and Flo-Dro0‰). However, in all treatments under conditions of 5 and 15 ‰ salinity the death of some seedlings was observed. The only treatment in which the death of all the seedlings was recorded was Flood-Drought at 15 ‰ (Table 2).

Height, diameter and number of leaves

The growth of seedlings and their final height was affected by water level, salinity and time, as well as by the interactions between water level and time, salinity and time, and water level and salinity (Table 3). For water level, seedling growth was greater under the Saturation condition and was lowest in the Flood-Drought treatments. In addition, the increase in salinity decreased growth, so that the 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. The growth of the seedlings over the course of the experiment was greater in the treatments under conditions of Saturation and low salinity (0 and 5 ‰), and this became evident in the eighth week (Figure 2). The seedlings in the Saturation 0 ‰ treatment grew the most (27.6 ± 7.37 cm), while the seedlings in the Flood-Drought 15 ‰ treatment, grew the least, and even negative values were observed (-0.5 ± 0 cm), in addition to the death of all individuals subjected to this treatment six weeks after starting the experiment (Figure 2).

Similarly, the increase in the diameter of the seedlings was affected by water level, salinity and time, and by the interaction of the two factors and the covariate (Table 4). A greater increase in diameter was recorded in seedlings subjected to Saturation treatments, and smaller increases in diameter in Flood-Drought treatments. Salinity also negatively affected the diameter increase, since the greatest increase occurred in seedlings under treatments with 0 ‰ salinity, and the smallest increase in those under 15 ‰ salinity. Over the 18 weeks of the experiment, the increase in diameter in the seedlings was greater in the treatments under conditions of Saturation and low salinity (0 and 5 ‰), and this was more notable from the eighth week onwards (Figure 3). The interaction between the three factors affected the increase in diameter, with the seedlings subjected to the 0 ‰ Saturation treatment exhibiting the greatest increase in diameter (7.02 ± 1.31 mm), while those in the 15 ‰ Flood-Drought treatment did not grow, and the death of all seedlings subjected to this treatment was recorded six weeks after starting the experiment (Figure 3).

The gain (or loss) in the number of leaves in *A. glabra* seedlings was affected by both water level and salinity, and by the interaction of these two factors (Table 5). For the seedlings subjected to salinity treatments of 0 ‰ and under Saturation conditions, leaf gain was recorded (Saturation 0 ‰, Flood 0 ‰, Flood-Drought 0 ‰, Saturation 5 ‰ and Saturation 15 ‰; Figure 4). The seedlings under the 0 ‰ Saturation treatment had a gain of 10.2 ± 1.15 leaves, which was significantly higher with respect to the seedlings in the other treatments. On the other hand, under the Flood 5 ‰, Flood-Drought 5 ‰, Flood 15 ‰ and Flood-Drought 15 ‰ treatments, the seedlings lost leaves. In the seedlings under the 15 ‰ Flood treatment, this loss (16.5 ± 2.04) was significantly greater than that of the other treatments with (Figure 4).

Biomass

The increase in the biomass of the three structures of the seedlings (roots, stems, leaves) was lower in the treatment with the highest salinity. The final biomass of the root was only affected by salinity (Table 6). The lowest value for seedling root biomass was recorded for the Flood-Drought 15 ‰ treatment. In

contrast, the highest values of biomass of the roots of the seedlings were recorded for the treatments Saturation 0 ‰ and Saturation 5 ‰, (Figure 5a). These differences were statistically significant.

Seedling stem biomass was affected both by salinity and by water level, albeit marginally (Table 5). The seedlings subjected to the Flood-Drought 15 ‰ treatment had significantly 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 (Figure 5b). The water level, salinity and the interaction of these two factors had no effect on the biomass of the leaves of the surviving seedlings (Figure 5c).

Discussion

Our results show that water level affected the growth of *A. glabra* seedlings, consistent with the hypothesis of a greater biomass gain and number of leaves, as well as greater growth in height and diameter under saturated soil conditions and without salinity. 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., where it has been found that there is a greater gain in root and stem biomass, as well as greater growth in diameter and height when the plants are in saturated soil conditions in comparison with soil with less than five centimeters of permanent flooding (Pezeshki et al. 1989; Pezeshki 1990; Conner 1994; Conner et al. 1997, 1998; McCarron et al. 1998). Of the studies carried out in this region, only *Taxodium distichum* has shown a broad tolerance to flooding, with the increase in water level not having any 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, which is 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, it has been reported that the dominant species of flooded forests that are distributed on the coast of the Gulf of Mexico, such as *Pachira aquatica* and *Annona glabra*, gain more root biomass in saturated soils compared to 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.

Although wetland plant species have various adaptations that allow them to tolerate the stress caused by flooding and changes in soil chemistry (Pezeshki 2001; Mitsch and Gosselink 2015), 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 Fennessy 2001). This may indicate that these species are able to tolerate rather than require high levels of flooding to establish successfully (Infante-Mata et al. 2019). *Annona glabra* establishes in depressions or areas with very slow

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 and Moreno-Casasola 2005; Infante-Mata et al. 2019). Therefore, the higher growth under saturated soil conditions seems to reflect the adaptations of *A. glabra* to the natural conditions of the environment where it has developed.

As expected, salinity also negatively affected survival, biomass gain, leaf gain, and height and diameter growth 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 sebiferu* and *Taxodium distichum* (Pezeshki et al. 1989; Pezeshki 1990; Allen et al. 1994; Conner 1994; Conner et al. 1997, 1998; McCarron et al. 1998) , in the Caribbean such as *Pterocarpus officinalis* Jacq. (Rivera-Ocasio et al. 2007; Bompoy et al. 2015), 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 biomass, height and diameter of the seedlings 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, because 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 (Wieski et al. 2010). Salinity occurs in coastal wetlands when there is the entry of marine water (Flores-Verdugo et al. 2007). In tropical or subtropical areas, the species categorized as mangroves are those that have adaptations to survive in saline soils (Cronk and Fennessy 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. As observed in our results, survival, increases in height and diameter, and leaf and biomass gain decreased as salinity increased. However, despite the stress imposed by saline conditions, the seedlings under the FI15‰ and Sat15‰ treatments had a slight increase in height and diameter, and a slight gain in biomass. This may be due to the fact that the seedlings in this study came from a population that is very close to a mangrove area where salinity increases periodically during the rainy season, as occurs in the species *T. distichum*, where the seedlings from brackish populations grow more (height and biomass) than do those from freshwater populations (Allen et al. 1994, 1997). In Veracruz, freshwater swamps with saline influence have lower species richness, and this leads to the dominance of a few salinity-tolerant species and even mixing with mangrove species (Infante-Mata 2011).

The combined increase of water and salinity levels in freshwater swamps on the floodplains of Veracruz will increase the pressure on the species that inhabit them. *A. glabra* seedlings were sensitive to the increase in both factors, so an increase in sea level could have a strong impact on seedling establishment in this species. However, it has been observed that the species *P. aquatica* (the dominant species in the

other type of swamp) can survive a wide range of salinity (0.02-18 ‰) and is able to germinate in a saline solution of up to 9.2 ‰, which indicates that its germination and seedling establishment can occur in areas close to mangroves or in coexistence with them, or could 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, favoring the species that have a greater tolerance to these environmental factors (i.e., *Pachira aquatica*) and could damage less tolerant species (i.e., *Ficus* spp., *Pouteria* sp., *Salix humboldtiana* Willd., *Inga vera* Willd.), and even *A. glabra* that develop in areas with 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 are glycophytes and are unable to tolerate high levels of salinity (Pezeshki et al. 1990). The consequences of rising sea levels could cause the deterioration or even the disappearance of freshwater swamps on the coastal plain of the Gulf of Mexico.

Despite the potentially dire consequences to freshwater swamps, with the exception of our study, 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, nor have scenarios been evaluated for this region of the Gulf of Mexico. It is important to mention that this study was experimental and carried out under greenhouse conditions, and thus serves as an important reference for the analysis and understanding of the response of the seedlings 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 the rise in sea level on the regeneration of freshwater swamps. This would make it possible to propose ecological restoration strategies. Additionally, this type of information is important for developing models of the response of key ecological processes in the establishment of dominant species of freshwater swamps such as pollination, seed dispersal, productivity, germination and the establishment of seedlings. The results obtained in this study for *A. glabra*, as well as 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, which makes this type of wetland particularly vulnerable to climate change, highlighting the importance of extensive research, legislation and restoration efforts.

Declarations

Acknowledgements

This study was funded by the Consejo Nacional de Ciencia y Tecnología (scholarship no. 723842 granted to the first author), DIADA SA de CV and the Instituto de Ecología A.C. (INECOL). We also thank the Centro de Investigaciones Costeras La Mancha for providing the space and resources needed to carry out the study. We thank Máximo Azua, Boni Azua and Luis Miguel Rodríguez for their support in the field and in setting up the experiment, and Roberto Monroy for his support in preparing the map. Patricia Moreno-Casasola translated the manuscript from the original in Spanish. Bianca Delfosse edited the final version.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Contributions

EASG, HLR, PMC, and RLC conceived the idea and designed the experiment. EASG carried out the greenhouse work and the performed data collection. 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.

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.

Funding sources

This study was funded by the Consejo Nacional de Ciencia y Tecnología (scholarship no. 723842 granted to the first author), DIADA SA de CV and the Instituto de Ecología A.C. (INECOL). We also thank the Centro de Investigaciones Costeras La Mancha for providing the space and resources needed to carry out the study.

References

1. Allen JA, Chamber JL, Pezeshki SR (1997) Effect of salinity on Baldcypress seedlings: Physiological responses and their relation to salinity tolerance. *Wetlands* 17:310–320. <https://doi.org/10.1007/BF03161419>
2. Allen JA, Chambers JL, McKinney D (1994) Intraspecific variation in the response of *Taxodium distichum* seedlings to salinity. *For Ecol Manage* 70:203–214. [https://doi.org/10.1016/0378-1127\(94\)90087-6](https://doi.org/10.1016/0378-1127(94)90087-6)
3. An S, Verhoeven JTA (2019) Wetland functions and ecosystem services: implications for wetland restoration and wise use. In: An S, Verhoeven JTA (eds) *Wetlands: Ecosystem services, restoration and wise use*. Springer, pp 1–10. https://doi.org/10.1007/978-3-030-14861-4_1
4. Bompuy F, Imbert D, Dulormne M (2015) Impact patterns of soil salinity variations on the survival rate, growth performances, and physiology of *Pterocarpus officinalis* seedlings. *Trees* 29:119–128. <https://doi.org/10.1007/s00468-014-1096-9>

5. Campos A, Hernández ME, Moreno-Casasola P, et al (2011) Soil water retention and carbon pools in tropical forested wetlands and marshes of the Gulf of Mexico. *Hydrol Sci J* 56:1388–1406. <https://doi.org/10.1080/02626667.2011.629786>
6. Conner WH (1994) The effect of salinity and waterlogging on growth and survival of Baldcypress and Chinese tallow seedlings. *J Coast Res* 10:1045–1049.
7. Conner WH, McLeod KW, McCarron JK (1997) Flooding and salinity effects on growth and survival of four common forested wetland species. *Wetl Ecol Manag* 5:99–109. <https://doi.org/10.1023/A:1008251127131>
8. Conner WH, McLeod KW, McCarron JK (1998) Survival and growth of seedlings of four bottomland oak species in response to increases in flooding and salinity. *For Sci* 44:618–624. <https://doi.org/10.1093/forestscience/44.4.618>
9. Cronk JK, Fennesy MS (2001) *Wetland plants. Biology and ecology*. Lewis Publishers
10. Day JW, Christian RR, Boesch DM, et al (2008) Consequences of climate change on the ecogeomorphology of coastal wetlands. *Estuaries and Coasts* 31:477–491. <https://doi.org/10.1007/s12237-008-9047-6>
11. Flores-Verdugo F, Moreno-Casasola P, Agraz-Hernández CL, et al (2007) La topografía y el hidroperíodo: dos factores que condicionan la restauración de los humedales costeros. *Boletín la Soc Botánica México* 80:33–47. <https://doi.org/10.17129/botsoci.1755>
12. González-Marín RM, Lazos-Ruiz AE, Escamilla-Pérez BE, et al (2016) El aprovisionamiento. In: Moreno-Casasola P (ed) *Servicios ecosistémicos de las selvas y bosques costeros de Veracruz*. Inecol A.C., ITTO, Conafor, INECC, Xalapa, Veracruz, pp 160–184
13. Grieger R, Capon S, Hadwen W (2019) Resilience of coastal freshwater wetland vegetation of subtropical Australia to rising sea levels and altered hydrology. *Reg Environ Chang* 19:279–292. <https://doi.org/10.1007/s10113-018-1399-2>
14. Herbert ER, Boon P, Burgin AJ, et al (2015) A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. *Ecosphere* 6:1–43. <https://doi.org/10.1890/ES14-00534.1>
15. Infante-Mata D (2011) *Estructura y dinámica de las selvas inundables de la planicie costera central del Golfo de México*. Instituto de Ecología, A.C. PhD thesis. Instituto de Ecología, A.C. Xalapa, México. 179 pp
16. Infante-Mata D, Moreno-Casasola P (2005) Effect of in situ storage, light, and moisture on the germination of two wetland tropical trees. *Aquat Bot* 83:206–218. <https://doi.org/10.1016/j.aquabot.2005.06.009>
17. Infante-Mata D, Moreno-Casasola P, Madero-Vega C, et al (2011) Floristic composition and soil characteristics of tropical freshwater forested wetlands of Veracruz on the coastal plain of the Gulf of Mexico. *For Ecol Manage* 262:1514–1531. <https://doi.org/10.1016/j.foreco.2011.06.053>
18. Infante-Mata D, Moreno-Casasola P, Madero-Vega C (2014) ¿*Pachira aquatica*, un indicador del límite del manglar? *Rev Mex Biodivers* 85:143–160. <https://doi.org/10.7550/rmb.32656>

19. Infante-Mata D, Moreno-Casasola P, Valverde T, Maza-Villalobos S (2019) Effects of soil flooding, sunlight and herbivory on seedlings of *Annona glabra* and *Pachira aquatica* in a tropical swamp. *Wetl Ecol Manag* 27:539–551. <https://doi.org/10.1007/s11273-019-09676-1>
20. IPCC (2007) Synthesis report. Contribution of working groups I, II and III to the fourth assessment report of the Intergovernmental Panel on Climate change. Geneva, Switzerland
21. Junk WJ, An S, Finlayson CM, et al (2013) Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquat Sci* 75:151–167. <https://doi.org/10.1007/s00027-012-0278-z>
22. Lara-Lara JR, Arreola-Lizárraga JA, Calderón-Aguilera LE, et al (2008) Los ecosistemas costeros, insulares y epicontinentales. In: Capital natural de México. Vol. 1.: Conocimiento actual de la biodiversidad. CONABIO, México. pp 109–134
23. Marín-Muñiz JL, Hernández ME, Moreno-Casasola P (2014) Comparing soil carbon sequestration in coastal freshwater wetlands with various geomorphic features and plant communities in Veracruz, Mexico. *Plant Soil* 378:189–203. <https://doi.org/10.1007/s11104-013-2011-7>
24. McCarron JK, McLeod KW, Conner WH (1998) Flood and salinity stress of wetland woody species, buttonbush (*Cephalanthus occidentalis*) and swamp tupelo (*Nyssa sylvatica* var. *biflora*). *Wetlands* 18:165–175. <https://doi.org/10.1007/BF03161653>
25. Mitsch WJ, Gosselink JG (2015) *Wetlands*, Fifth Edit. Wiley
26. Moreno-Casasola P, Aguirre-Franco L, Campos-Cascaredo A, et al (2020) Humedales costeros de agua dulce y bases para su gobernanza. In: Rivera-Arriaga E, Azuz-Adeath I, Cervantes-Rosas OD, et al. (eds) *Gobernanza y Manejo de las Costas y Mares ante la Incertidumbre. Una Guía para Tomadores de Decisiones*. Universidad Autónoma de Campeche, RICOMAR, pp 617–648
27. Moreno-Casasola P, Infante-Mata D (2016) Conociendo los manglares, las selvas inundables y humedales herbáceos. Instituto de Ecología, A.C., ITTO, CONAFOR, Xalapa, Veracruz
28. Moreno-Casasola P, Infante-Mata D (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
29. Moreno-Casasola P, Infante-Mata D, López-Rosas H (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, pp 267–282. <https://doi.org/10.1525/9780520951419-021>
30. Nicholls RJ (2004) Coastal flooding and wetland loss in the 21st century: Changes under the SRES climate and socio-economic scenarios. *Glob Environ Chang* 14:69–86. <https://doi.org/10.1016/j.gloenvcha.2003.10.007>
31. Nicholls RJ, Cazenave A (2010) Sea-level rise and its impact on coastal zones. *Science* 328:1517–1520. <https://doi.org/10.1126/science.1185782>
32. Nicholls RJ, Hoozemans FMJ, Marchand M (1999) Increasing flood risk and wetland losses due to global sea-level rise: Regional and global analyses. *Glob Environ Chang* 9:S69–S87.

[https://doi.org/10.1016/S0959-3780\(99\)00019-9](https://doi.org/10.1016/S0959-3780(99)00019-9)

33. Nielsen DL, Brock MA (2009) Modified water regime and salinity as a consequence of climate change: prospects for wetlands of Southern Australia. *Clim Change* 95:523–533.
<https://doi.org/10.1007/s10584-009-9564-8>
34. Niembro Rocas A, Vázquez Torres M, Sánchez Sánchez O (2010) Árboles de Veracruz: 100 especies para la reforestación estratégica. Gobierno del Estado de Veracruz, Secretaría de Educación del Estado de Veracruz, Comisión del Estado de Veracruz de Ignacio de la Llave para la conmemoración de la Independencia Nacional y la Revolución, Centro de Investigaciones Tropicales., Xalapa, Veracruz
35. Oliveira VC, Joly CA (2010) Flooding tolerance of *Calophyllum brasiliense* Camb. (Clusiaceae): morphological, physiological and growth responses. *Trees* 24:185–193.
<https://doi.org/10.1007/s00468-009-0392-2>
36. Ortiz-Pérez MA, Méndez-Linares AP (1999) Escenarios de vulnerabilidad por ascenso del nivel del mar en la costa mexicana del Golfo de México y el Mar Caribe. *Investig Geográficas* 68–81
37. Parris A, Bromirski P, Burkett V, et al (2012) Global sea level rise scenarios for the US National Climate Assessment
38. Pezeshki SR (1990) A comparative study of the response of *Taxodium distichum* and *Nyssa aquatica* seedlings to soil anaerobiosis and salinity. *For Ecol Manage* 33/34:531–541.
[https://doi.org/10.1016/0378-1127\(90\)90216-X](https://doi.org/10.1016/0378-1127(90)90216-X)
39. Pezeshki SR (2001) Wetland plant responses to soil flooding. *Environ Exp Bot* 46:299–312.
[https://doi.org/10.1016/S0098-8472\(01\)00107-1](https://doi.org/10.1016/S0098-8472(01)00107-1)
40. Pezeshki SR, Delaune RD, Patrick WH (1990) Flooding and saltwater intrusion: Potential effects on survival and productivity of wetland forests along the U.S. Gulf Coast. *For Ecol Manage* 33–34:287–301. [https://doi.org/10.1016/0378-1127\(90\)90199-L](https://doi.org/10.1016/0378-1127(90)90199-L)
41. Pezeshki SR, Patrick WH, DeLaune RD, Moser ED (1989) Effects of waterlogging and salinity interaction on *Nyssa aquatica* seedlings. *For Ecol Manage* 27:41–51. [https://doi.org/10.1016/0378-1127\(89\)90081-9](https://doi.org/10.1016/0378-1127(89)90081-9)
42. Rivera-Ocasio E, Aide TM, Rios-López N (2007) The effects of salinity on the dynamics of a *Pterocarpus officinalis* forest stand in Puerto Rico. *J Trop Ecol* 23:559–568.
<https://doi.org/10.1017/S0266467407004361>
43. Salter J, Morris K, Bailey PCE, Boon PI (2007) Interactive effects of salinity and water depth on the growth of *Melaleuca ericifolia* Sm. (Swamp paperbark) seedlings. *Aquat Bot* 86:213–222.
<https://doi.org/10.1016/j.aquabot.2006.10.002>
44. Sánchez-García EA (2020) Germinación y crecimiento de *Annona glabra* L. bajo condiciones experimentales como base para la restauración de un humedal arbóreo en la zona costera del centro de Veracruz. Instituto de Ecología, A.C. Master's thesis. Instituto de Ecología, A.C. Xalapa, México. 100 pp

45. Sánchez-Higueredo LE, Ramos-Leal JA, Morán-Ramírez J, et al (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>
46. Setter SD, Setter MJ, Campbell SD (2004) Longevity of pond apple (*Annona glabra* L.) seed and implications for management. *Foutteent Aust Weeds Conf* 551–554
47. Team R Core RF for SC (2019) R: A Language and Environment for Statistical Computing
48. Vázquez-González C, Moreno-Casasola P, Espejel I, et al (2016) Valor económico de los ecosistemas. In: Moreno-Casasola P (ed) *Servicios ecosistémicos de las selvas y bosques costeros de Veracruz*. Inecol A.C., ITTO, Conafor, INECC, Xalapa, Veracruz, pp 186–203
49. Wieski K, Guo H, Craft CB, Pennings SC (2010) Ecosystem functions of tidal fresh, brackish, and salt marshes on the Georgia coast. *Estuaries and Coasts* 33:161–169. <https://doi.org/10.1007/s12237-009-9230-4>
50. Xian X, Pang M, Zhang J, et al (2019) Assessing the effect of potential water and salt intrusion on coastal wetland soil quality: simulation study. *J Soils Sediments* 19:2251–2264.
<https://doi.org/10.1007/s11368-018-02225-y>
51. Yáñez-Arancibia A, Day JW, Willey RR, Day RH (2010) Los manglares frente al Cambio Climático ¿Tropicalización global del Golfo de México? In: Yáñez-Arancibia A (ed) *Impactos del Cambio Climático sobre la zona costera, 1°*. Secretaría de Medio Ambiente y Recursos Naturales, Instituto Nacional de Ecología, Instituto de Ecología, AC., Texas Sea Grant Program, México, p 180
52. Yetter J (2004) Hydrology and geochemistry of freshwater wetlands on the Gulf coast of Veracruz, Mexico. University Waterloo. Master's Thesis. University Waterloo. Ontario, Canada. 168 pp

Tables

Table 1 Treatments applied to the seedlings during the experiment. The nine treatments were the result of the combinations of three levels of the water level and salinity factors

Salinity	Water level		
	Saturation	Flood	Flood-Drought
0 ‰	Saturation 0 ‰ (Sat0‰)	Flood 0 ‰ (FI0‰)	Flood-Drought 0 ‰ (FI-Dr0‰)
5 ‰	Saturation 5 ‰ (Sat5‰)	Flood 5 ‰ (FI5‰)	Flood-Drought 5 ‰ (FI-Dr5‰)
15 ‰	Saturation 15‰ (Sat15‰)	Flood 15‰ (FI5‰)	Flood-Drought 15‰ (FI-Dr15‰)

Table 2 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 ‰ (Sat0‰)	5	5	100
Flood 0 ‰ (Flo0‰)	5	5	100
Flood-Drought 0 ‰ (Flo-Dro0‰)	5	5	100
Saturation 5 ‰ (Sat5‰)	5	2	40
Flood 5 ‰ (Flo5‰)	5	3	60
Flood-Drought 5 ‰ (Flo-Dro5‰)	5	3	60
Saturation 15 ‰ (Sat15‰)	5	3	60
Flood 15 ‰ (Flo15‰)	5	2	40
Flood-Drought 15 ‰ (Flo-Dro15‰)	5	0	0

Table 3 Covariance analysis of the growth (height) of *Annona glabra* seedlings under different salinity and water level treatments over time. *P* is the probability that the effect of a factor or covariable is null

Factor	Degrees of freedom	Sum of squares	Mean squares	<i>F</i>	<i>P</i>
Salinity	2	1218.0	609.0	25.09	<0.001
Water level	2	3692.1	1846.1	76.08	<0.001
Time	1	3830.3	3830.3	157.85	<0.001
Salinity x water level	4	1145.6	286.4	11.8	<0.001
Salinity x time	2	417.4	208.7	8.6	<0.001
Water level x time	2	2230.8	1115.4	45.96	<0.001
Salinity x water level x time	4	199.1	49.8	2.05	0.0868

Table 4 Covariance analysis of the increase in the diameter of *Annona glabra* seedlings under different levels of salinity and water levels over time and their interactions. *P* is the probability that the effect of a factor or covariable is null

Factor	Degrees of freedom	Sum of squares	Mean squares	<i>F</i>	<i>P</i>
Salinity	2	64.88	32.44	36.82	<0.001
Water level	2	162.16	81.08	92.02	<0.001
Time	1	308.41	308.41	350.04	<0.001
Salinity x water level	4	50.77	12.69	14.4	<0.001
Salinity x time	2	30.32	15.16	17.21	<0.001
Water level x time	2	140.41	70.2	79.68	<0.001
Salinity x water level x time	4	11.79	2.94	3.34	0.01048

Table 5 Covariance analysis of the number of leaves on *Annona glabra* seedlings under different salinity and water levels over time, and their interactions. *P* is the probability that the effect of a factor or covariable is null

Factor	Degrees of freedom	Sum of squares	Mean squares	<i>F</i>	<i>P</i>
Salinity	2	3213.1	1606.57	62.19	<0.001
Water level	2	2436.4	1218.21	47.16	<0.001
Salinity: water level	4	347.8	86.96	3.36	0.0101

Table 6 Analysis of variance in the biomass of the roots, stems and leaves of *Annona glabra* seedlings under different levels of salinity and water, and their interaction

Source of variation	Degrees of freedom	Sum of squares	Mean squares	<i>F</i>	<i>P</i>
<i>Roots</i>					
Salinity	2	25.27	12.63	6.13	0.005
Water level	2	12.07	6.03	2.93	0.066
Salinity x water level	4	4.65	1.16	0.56	0.689
<i>Stem</i>					
Salinity	2	13.41	6.7	3.33	0.046
Water level	2	14.09	7.04	3.5	0.040
Salinity x water level	4	2.45	0.61	0.3	0.872
<i>Leaves</i>					
Salinity	2	3.63	1.81	1.33	0.289
Water level	2	3.66	1.83	1.35	0.285
Salinity x water level	4	3.77	1.88	1.39	0.276

Figures

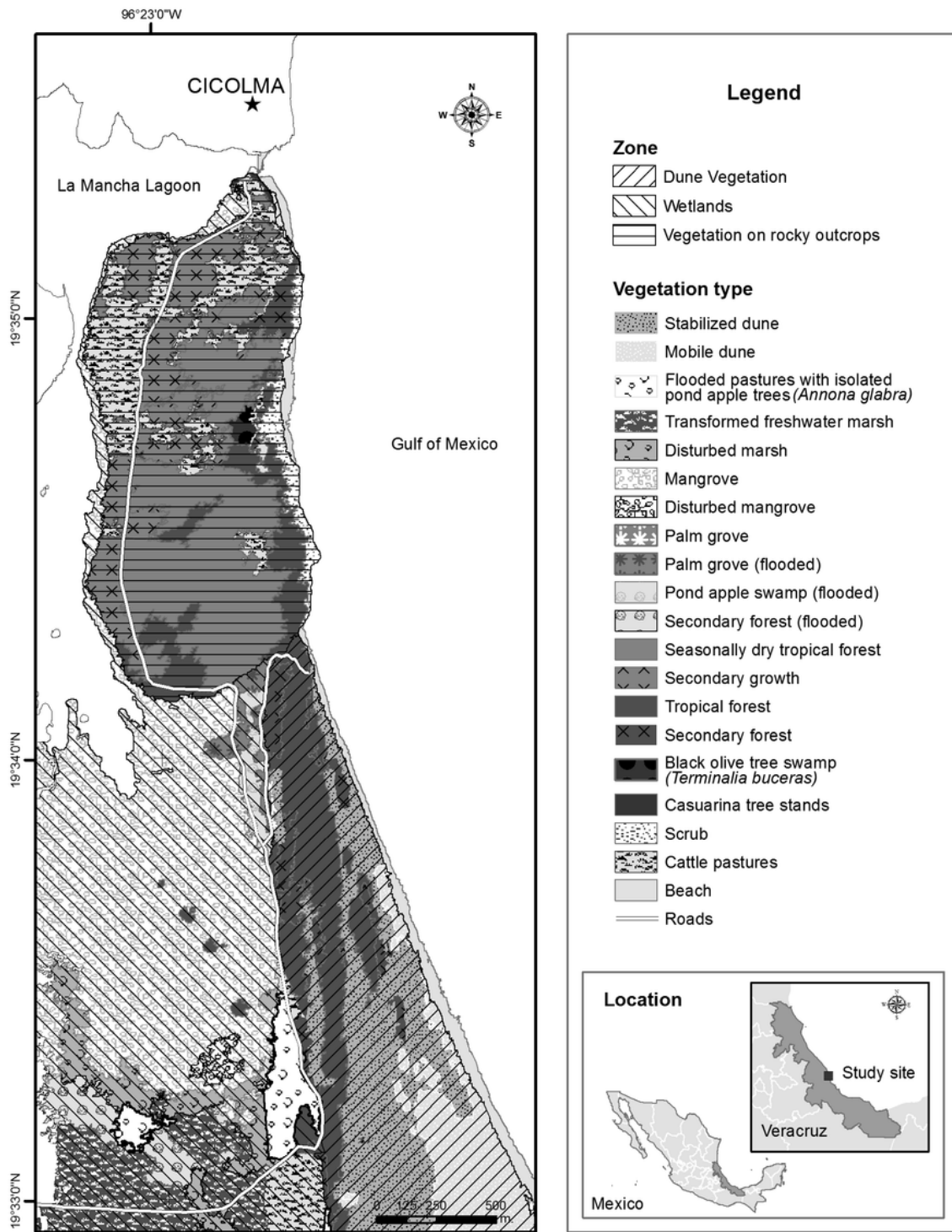


Figure 1

Location of the pond apple swamp (flooded), where seeds were collected (freshwater marsh with isolated pond apple trees (*Annona glabra*))

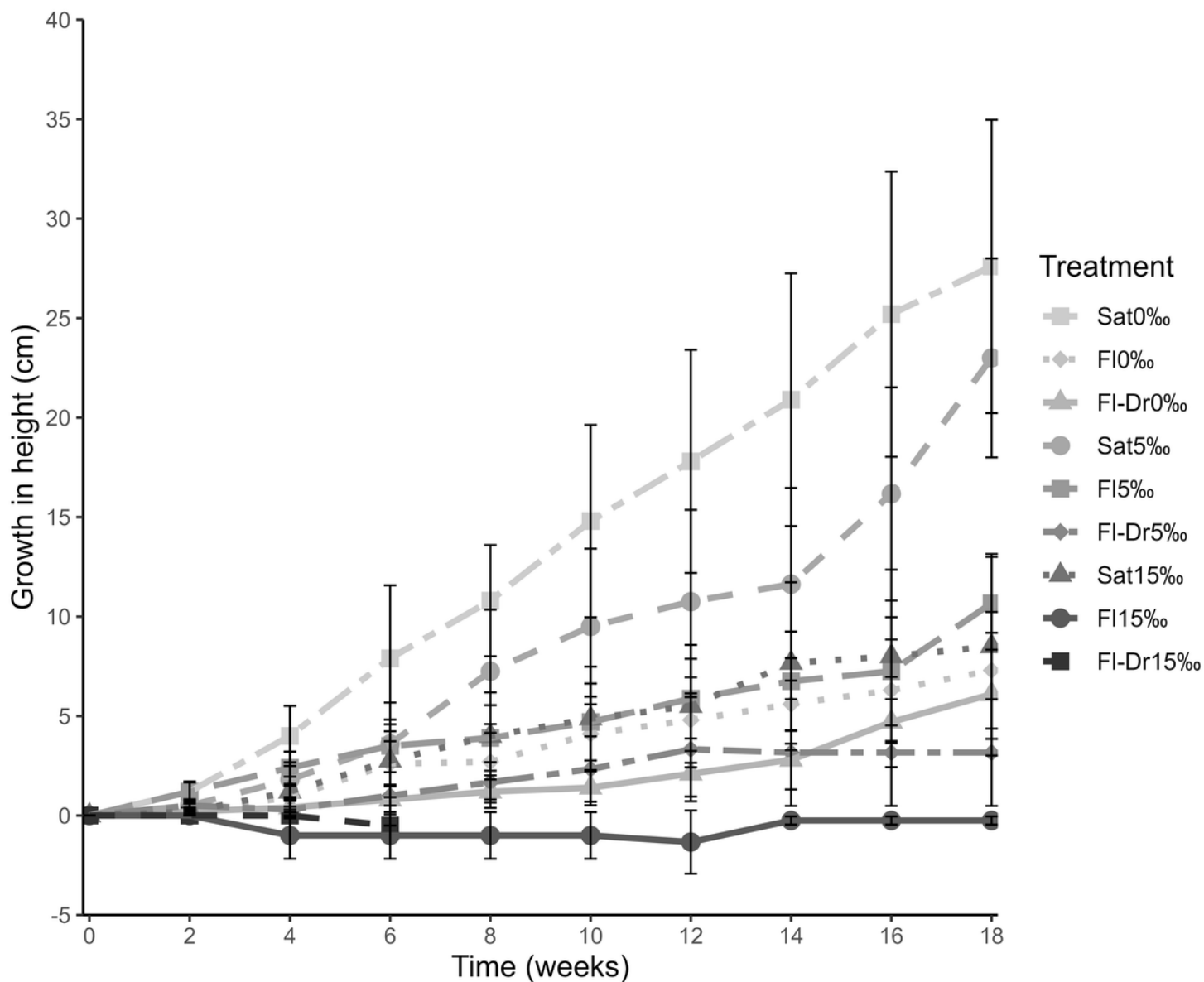


Figure 2

Mean increase in height $\pm$ standard error of *Annona glabra* seedlings under different treatments over the 18 weeks of the experiment. Saturation with 0 ‰ = Sat0‰, Flood with 0 ‰ = FI0‰, Flood-Drought with 0 ‰ = FI-Dr0‰, Saturation with 5 ‰ = Sat5‰, Flood with 5 ‰ = FI5‰, Flood-Drought 5 ‰ = FI-Dr5‰, Saturation with 15 ‰ = Sat15‰, Flood 15 ‰ = FI15‰, and Flood-Drought 15 ‰ = FI-Dr15‰. Trend lines are drawn to better distinguish among treatments. They are not the fitted curves

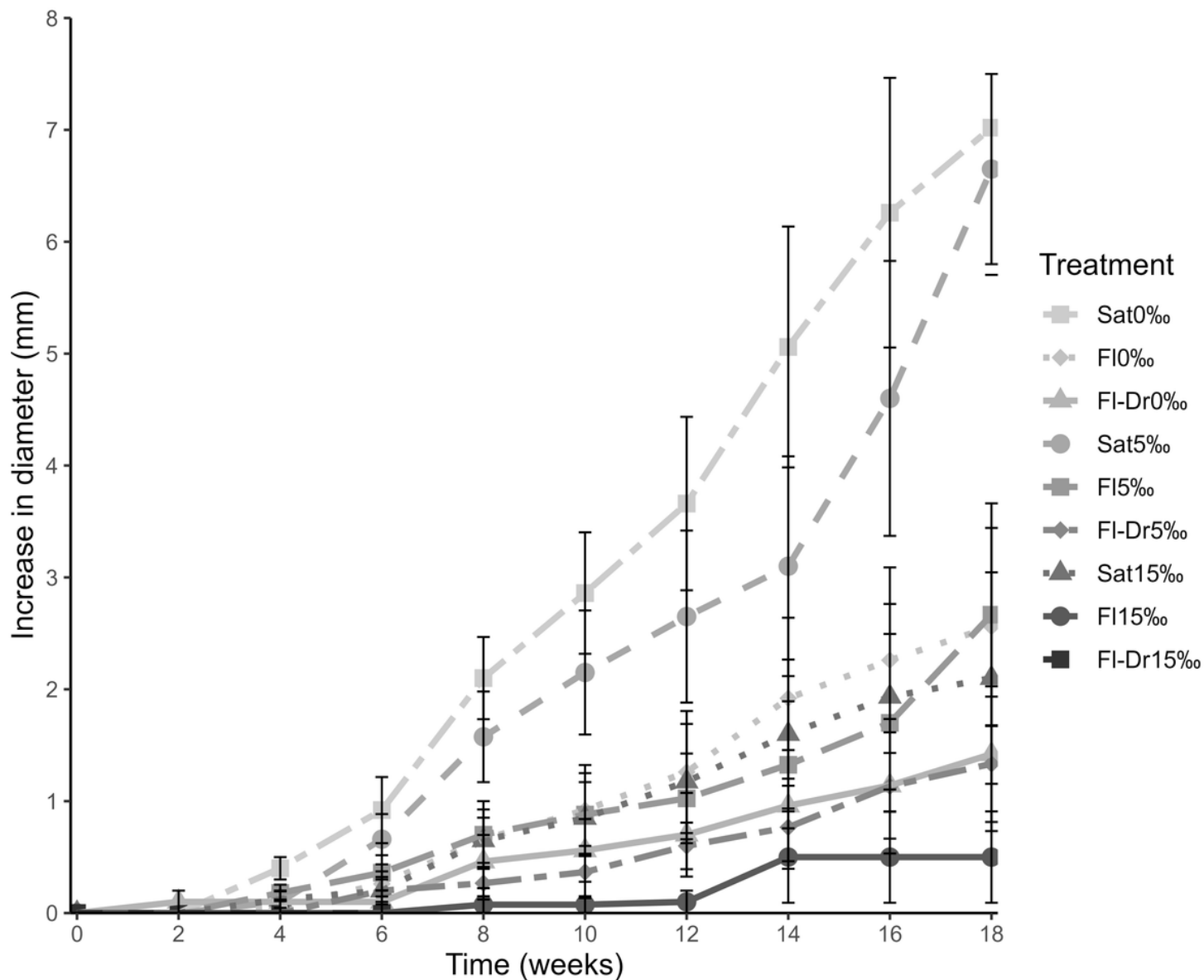


Figure 3

Mean increase in diameter $\pm$ standard error for *Annona glabra* seedlings under different treatments over the 18 weeks of the experiment. Saturation with 0 ‰ = Sat0, Flood with 0 ‰ = Flo0‰, Flood-Drought with 0 ‰ = Flo-Dro0‰, Saturation with 5 ‰ = Sat5‰, Flood with 5 ‰ = Flo5‰, Flood-Drought 5 ‰ = Flo-Dro5‰, Saturation with 15 ‰ = Sat15‰, Flood 15 ‰ = Flo15‰, and Flood-Drought 15 ‰ = Flo-Dro15‰. Trend lines are drawn to better distinguish among treatments. They are not the fitted curves

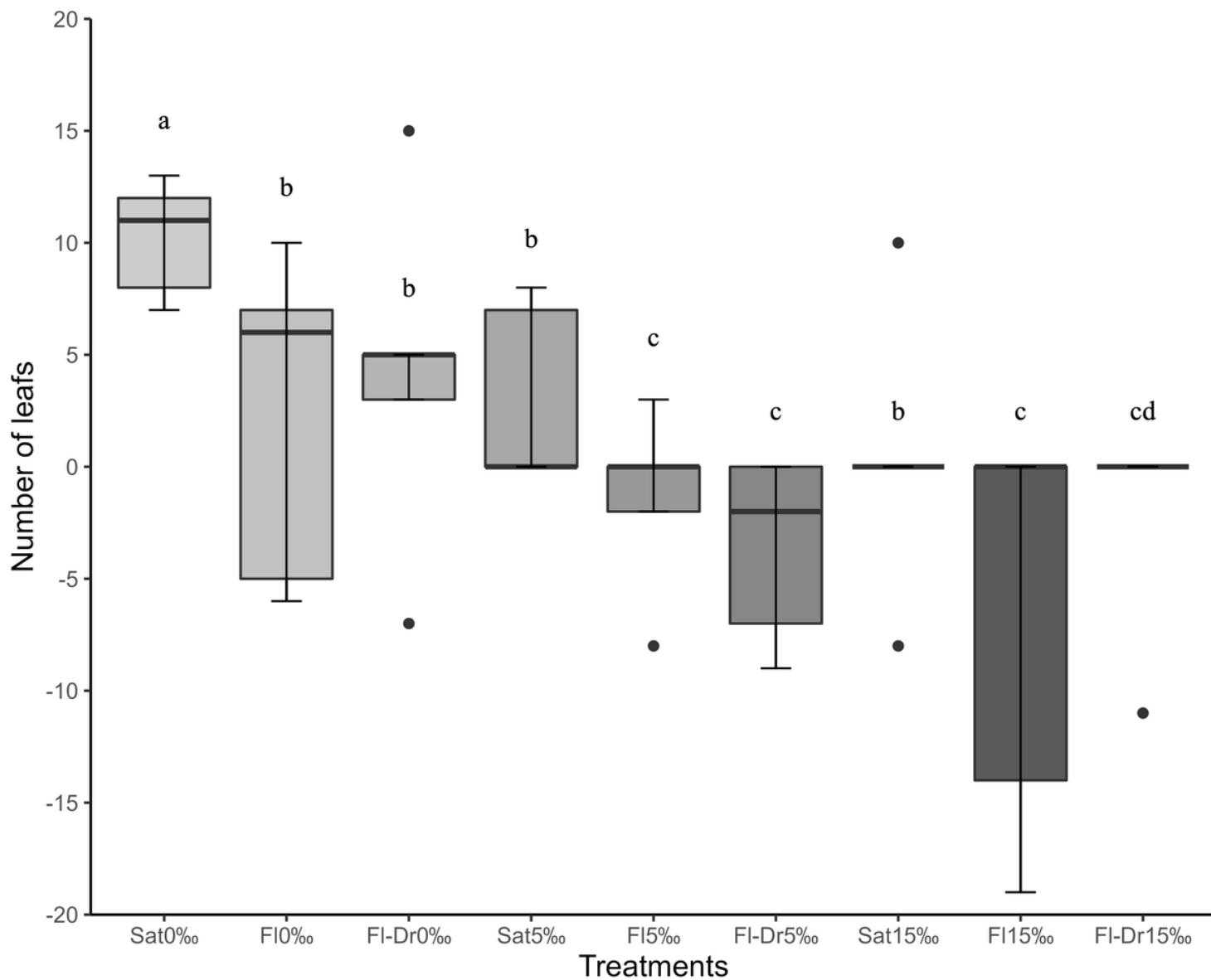


Figure 4

Mean gain or loss in the number of leaves $\pm$ standard error of *Annona glabra* seedlings under different treatments after 18 weeks of the experiment. Values with a different letter are significantly different ($P < 0.05$). Saturation with 0 ‰ = Sat0‰, Flood with 0 ‰ = FI0‰, Flood-Drought with 0 ‰ = FI-Dr0‰, Saturation with 5 ‰ = Sat5‰, Flood with 5 ‰ = FI5‰, Flood-Drought 5 ‰ = FI-Dr5‰, Saturation with 15 ‰ = Sat15‰, Flood 15 ‰ = FI15‰, and Flood-Drought 15 ‰ = FI-Dr15‰

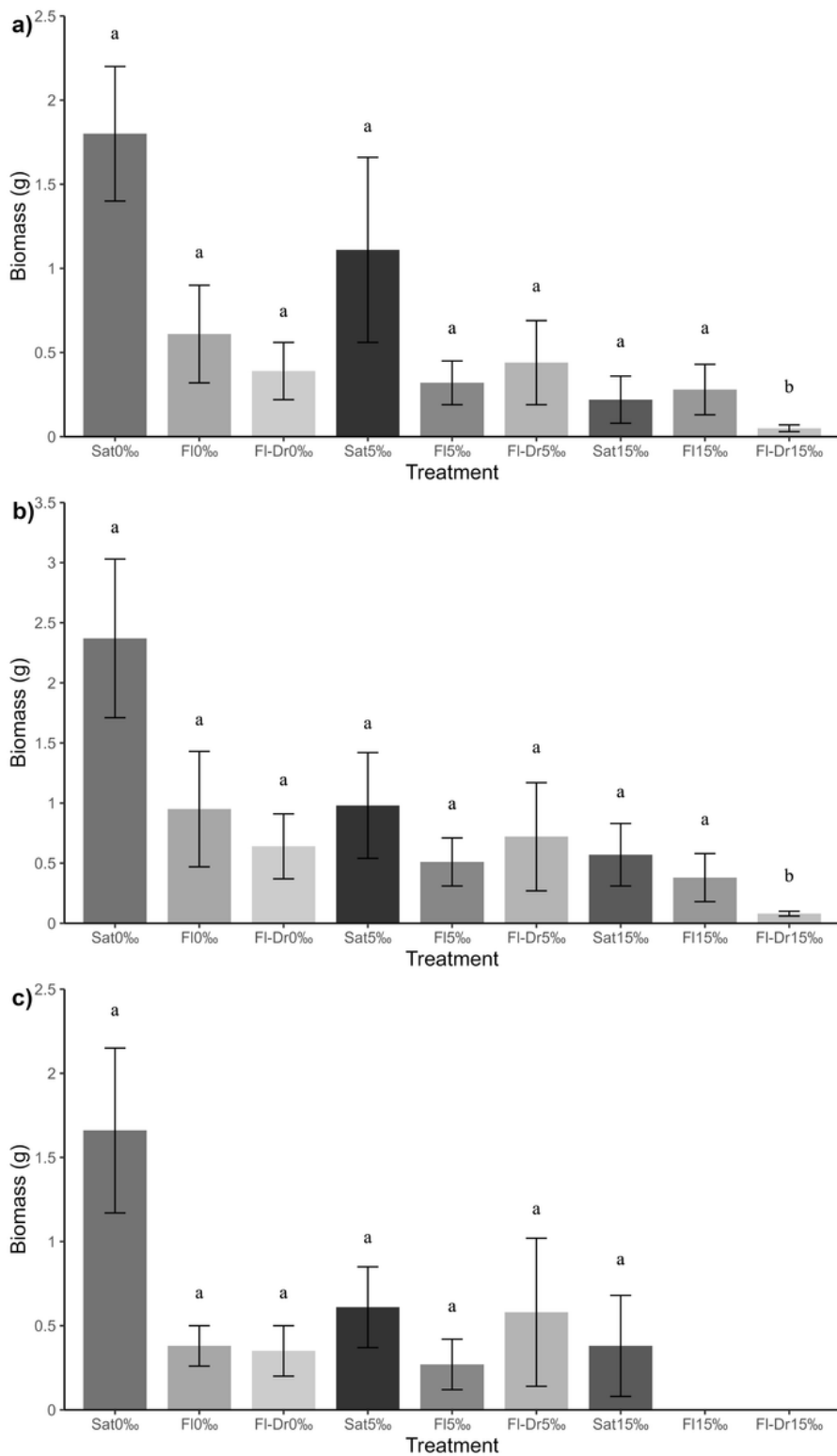


Figure 5

Final mean biomass (dry weight) for the roots (a), stem (b) and leaves (c) $\pm$ standard error for *Annona glabra* seedlings under the different levels of water level and salinity