Tolerance and Recovery Capacity of Tropical Native Tree Species to Water and Saline Stress: An Experimental Approach for Wetland Rehabilitation

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INTRODUCTION

The accelerated urban expansion in coastal areas in combination with the effects of climate change promotes excessive loss of green infrastructure, including urban wetlands (Faulkner 2004). Coastal estuarine wetland structure and composition is mainly determined by their microclimate, hydrological dynamics, tidal influence, and edaphic composition (Lambs et al. 2015). All of these factors determine the physiological success or response capacity of wetland plant species and are identified as abiotic determinants (Lambers et al. 2008; Chaipin III et al. 2002; Figure 1).

Climate change models for the Caribbean region predict an accelerated sea level rise, frequent drought periods and changes in the intensity, frequency, and distribution of the precipitation events (Lambs et al. 2015; Cardona-Olarte et al. 2013; Erwin 2009; PRCCC 2013). Abiotic determinants are and will continue to change in the region. These changes could result in a greater reduction in coastal wetlands and thus, the loss of important ecological services such as flood control, climate regulation, pollutant retention, pest control, carbon sequestration, among others (Mitsh and Gosselink 2000; Farber et al. 2006; Zedler and Kercher 2005). Studies from estuarine coastal wetlands in the Caribbean and Puerto Rico have recorded frequent and prolonged periods of drought and significant increases in soil and groundwater salinity as a result of the expansion of the marine intrusion and sea level rise (Rivera-De Jesús 2019; Lambs et al. 2015; Colón-Rivera et al. 2014; Bompy et al. 2014; Flower and Imbert 2006). Soil and groundwater salinity is mainly caused by the increase in concentration of ions, especially Na^+ and Cl^-, which promotes reductions in freshwater availability. This condition results in water and salt stress in plant species associated with these ecosystems.

Rehabilitation practices in wetlands ecosystems must consider the present and future climate changes when developing a restoration or rehabilitation project since variations in abiotic conditions will influence the tolerance and recovery potential of the species. The tolerance capacity of a species refers to the resistance that it can present, maintaining its physiological functioning within a range of environmental conditions (Lambers et al. 2008; Osmond et al. 1987). Rosenthal and Kotanen (1994) define tolerance in plant species as the ability to maintain their physiological functioning and the maintenance of their biological processes, such as growth, energy processing and reproduction, within a stressful environmental range.

In this study we want to establish the range of tolerance and recovery capacity of three species that inhabit estuarine coastal wetlands in the Caribbean region and are frequently used in rehabilitation projects: *Pterocarpus officinalis* (Jacq.), *Thespesia populnea* (L.), and *Amphitecna latifolia* (Mill.) *A. H. Gentry*). These species are used due to their adaptations to flooded conditions, while more information is needed about the range of tolerance of these species to water and saline stress. To achieve these objectives, we evaluated structural and ecophysiological parameters, and species survival rates at different saline treatments under greenhouse conditions. The knowledge provided by this study will help to make effective decisions and promote best practices in the use of these species in reforestation and rehabilitation projects in estuarine-coastal wetlands.

METHODS

Plant Species

The three studied species - *Pterocarpus officinalis*, *Amphitecna latifolia* and *Thespesia populnea* - are native species commonly used in rehabilitation and reforestation projects in estuarine coastal wetlands in the Caribbean and Puerto Rico (Figure 2).

Pterocarpus officinalis, a member of the Fabaceae family (Little et al. 1988; Little and Wadsworth 1995), is a tropical tree that can reach up to 20m height. Members of this species are easily recognized by its basal roots that form narrow plates extending from the trunk and the presence of roots nodules for bacteria nitrogen fixation (Little et al. 1988; Little and Wadsworth 1995). This species can occupy both riparian and estuarine coastal wetlands, with the capacity to tolerate prolonged flooding and saline conditions (Eusse and Aide 1999). Its ability to tolerate levels of salinity has been attributed to its capacity to accumulate Na in the leaf rachis and to maintain high K/Na ratios in the leaf blades (Medina et al. 2007). Nevertheless, additional information is necessary to better understand its tolerance to changes in salinity conditions and to determine how these conditions may affect the ecophysiological fitness of this species.

Amphitecna latifolia is another tropical tree species (Family Bignoniaceae) that can reach 10m height

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with relatively large leaves and round seeds between 7cm to 10cm in diameter. While it can occupy fresh water flooded areas (Gilman and Watson 1993), there is limited information about its salt tolerance although it has been reported as a halophyte in Mexico and Florida, (Meerow et al. 2001; Flores-Olvera et al. 2016). Its specific range of tolerance to salinity and water stress are unknown.

Thespesia populnea is a tropical tree (Family Malvaceae) that commonly occupy coastal areas, with a wide distribution that includes inland and riparian wetlands. It is an evergreen tree with a height between 6m to 10m. Individuals of this species can grow on flooded and saline-influenced lands (Feng-ying et al. 2011). Despite its frequency in coastal areas particularly in sand dunes, few studies have evaluated the ecophysiological performance of adult trees under saline conditions (Miah 2013). Nonetheless, a recent study found that *T. populnea* seedlings can survive and maintain high rates of photosynthesis and stomatal conductance even at 90% seawater (De Sedas et al. 2019). Thus, more information is needed about the tolerance and ecophysiological mechanisms used by the species to cope with changing salinity conditions in both juveniles young and adult individuals.

Greenhouse Experiments

To determine the range of tolerance of these species to water and salt stress, we first collected seeds from adult individuals planted in field conditions, and then germinated them under greenhouse conditions. The individuals were left to grow until they reached an approximate age of 2 to 3 years - the juvenile stage. The experiments were performed using multiple flow hydroponic systems, where four individuals of each species were planted (Figure 3). Each system was supplied with a stable concentration of nutrients, but salt concentration was varied in the order of 5ppt,

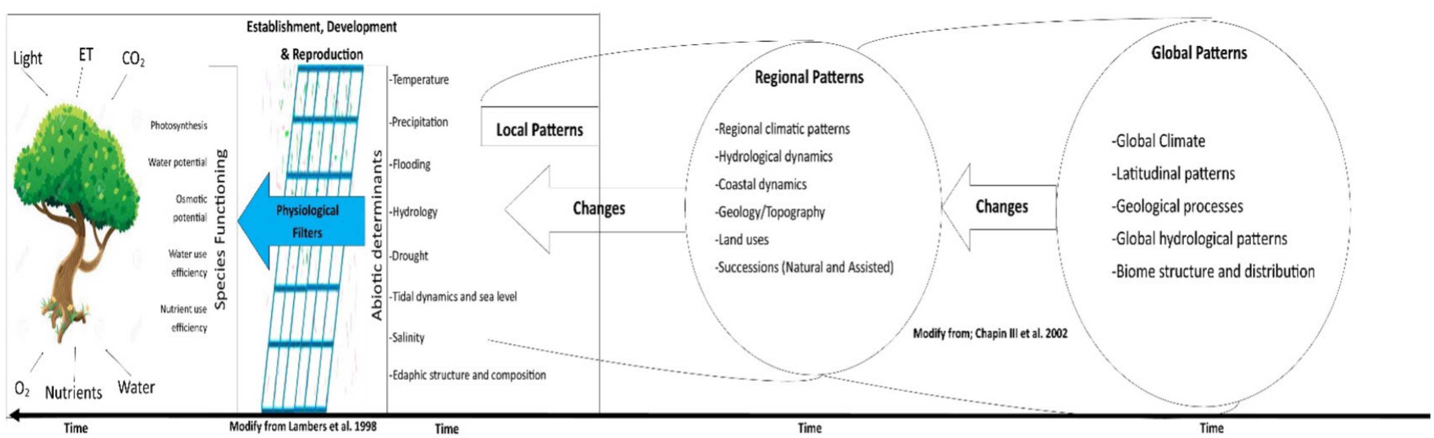

Figure 1. Conceptual model that expose how the survival of a plant species is related to physiological filters associated to local abiotic determinants. Physiological filters are influenced by regional and global changes that may occur in a temporal scale. (Modified model from Chapin III et al. 2002 and Lambers et al. 2008)

Figure 2. Study species: A) *Pterocarpus officinalis*, B) *Amphitecna latifolia,* and C) *Thespesia populnea.* (Photos by Wilmer Rivera-A & C,and Herbario-Universidad de Panamá-B)

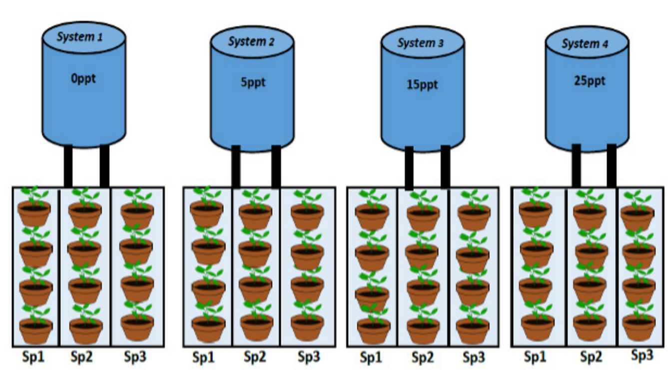

Figure 3. Experimental multiple flow systems, salinity treatments and distribution of the individuals by species type.

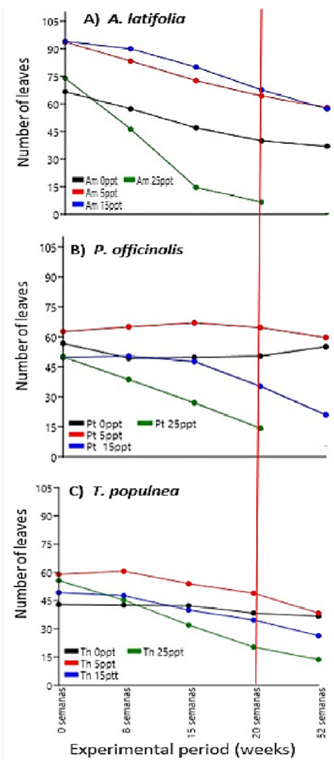

Figure 4. Temporal variation in the number of leaves in all the study species as a function of experimental treatments: 0ppt (dark line), 5ppt (red line), 15ppt (blue line) and 25ppt (green line). Each point represents the total number of leaves counted per species for each period and per treatment. The red vertical line identifies the recovery period from week 20 to week 52.

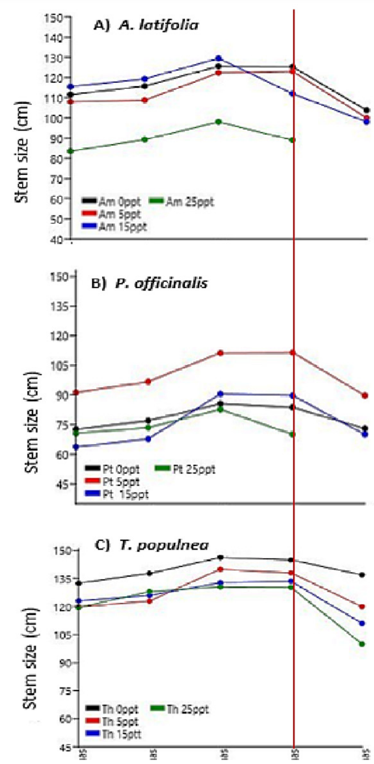

Figure 5. Temporal variation in stem size (A, B, and C) in all the study species as a function of experimental treatments: 0ppt (dark line), 5ppt (red line), 15ppt (blue line) and 25ppt (green line). Each point represents the average stem size per species for each period and per treatment. The red vertical line identifies the recovery period from week 20 to week 52.

15ppt and 25ppt (Figure 3). These salt concentrations were established based on data collected during field conditions in wetlands where these species are used for reforestation purposes (Rivera-De Jesús 2019). A control group (0ppt) was maintained for each of the species to establish comparisons with the experimental groups, in terms of structural and ecophysiological parameters and survival rates. The experiments were performed for 5 months, and at the end of the eighth, fifteen and twenty weeks, structural measurements were made in terms of number of developed leaves and stem height(cm)., We also counted the number of dead individuals during the experiment to establish survival rates for each species.

In terms of ecophysiological parameters we evaluated the net carbon assimilation (A) in µmol CO2 m^{-2} s^{-1}, the stomatal conductance (*gs*) in µmol m^{-2} s^{-1} and the long-term water use efficiency (WUE) through the isotopic signal of $\delta^{13}C$. The net carbon assimilation and the stomatal conductance were determined using a portable gas exchange system, CIRAS-3-Photosynthesis System. High values of net carbon assimilation (A) indicate a greater degree of stomatal opening at the foliar level, while high values of stomatal conductance (*gs*) indicate a high rate of net carbon assimilation by the plant. Long-term (WUE) can be determined by the concentration of the ^{13}C isotope in leaf tissues. Medina and Francisco (1997); Lin and Sternberg (1992) and Farquhar et al. (1989) demonstrated that tolerant species, to avoid the effects of water and saline stress, increase and maintain a stable WUE, which is positively correlated with an increase in the concentration of carbon 13 isotope ($\delta^{13}C$) in leaf tissues. After five months of experiment, in the surviving plants, we removed the experimental salinity treatments with continuous flows of fresh water to evaluate the recuperation capacity of these species. The recovery period lasted until week 52 from the final week of the experiment (week 20). In the recovery period we evaluated the same structural parameters (number of leaves and stem height) and the same ecophysiological parameters (A, *gs* and WUE) to compare with the experimental period.

Statistical Analysis

To determine differences between salinity treatments and between experimental periods on structural changes and ecophysiological parameters we did an analysis of variance for each species. To establish the range of tolerance of the species to salinity and hydric stress, we compared the A, *gs* and WUE between experimental periods. We compared the mean differences in the number of leaves, stem height and survival rates for each species. To establish the recovery capacity of the species to water and saline stress we compared the same structural and ecophysiological parameters

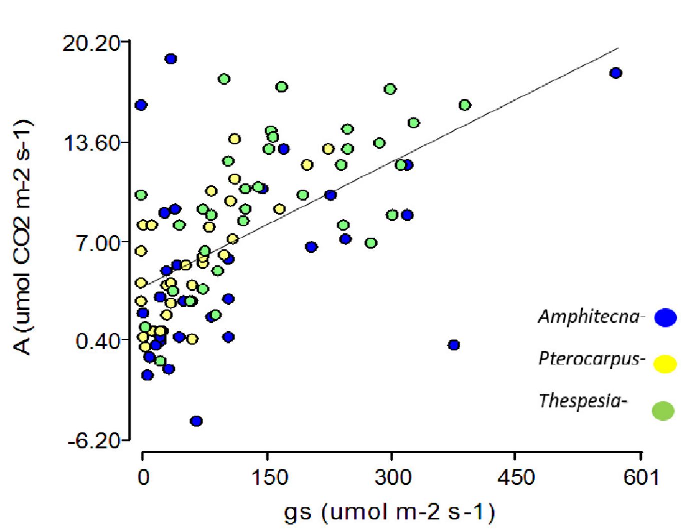

Figure 6. Relationship between stomatal conductance (A) and net carbon assimilation (gs) (n = 97, R2 = 0.55), p <0.001 according to the statistical regression model Mallows's Cp. The points in the dispersion represent values of gs and A among the study species in all the evaluated periods in which the measurements were made.

between the final period of experiment and the recovery period. We used the Tukey-Kramer post-hoc test with a significance level of $p \leq 0.05$. Statistical analyzes and figures were developed using Info-Stat and Past 4v.

RESULTS AND DISCUSSION

Structural Variations: Leaves and Stem

There were differences in the structural variables from individuals of each species in the different saline treatment and in the time in which these treatments were sustained. The temporal variation in the number of leaves resulted in considerable reductions when the salinity levels and the exposure time increased for all species (Figure 4). In control groups, all the species showed the highest number of leaves, which indicates that the saline condition impacts important plant structures such as leaf tissue (Figure 4-dark lines). Wright and Cornejo (1990) demonstrated that in the face of low water availability, many species present a high loss in their leaf tissue to avoid the effects of water limitation, the excessive loss of water by transpiration and the limitation in biomass production under these stressful conditions**.** In comparison with the other two species, *A. latifolia* showed a considerable reduction in the total number of leaves in all saline treatments: 5ppt- (91 to 75) ; 15ppt- (91 to 76) ; 15ppt- (75 to 3) (Figure 4). The greatest loss occurred at 25ppt, with an abrupt fall in the number of leaves from the eighth week of experiment to a substantial removal of the leaf tissue towards the final period of the experiment (week 20). Among all species *A. latifolia* showed

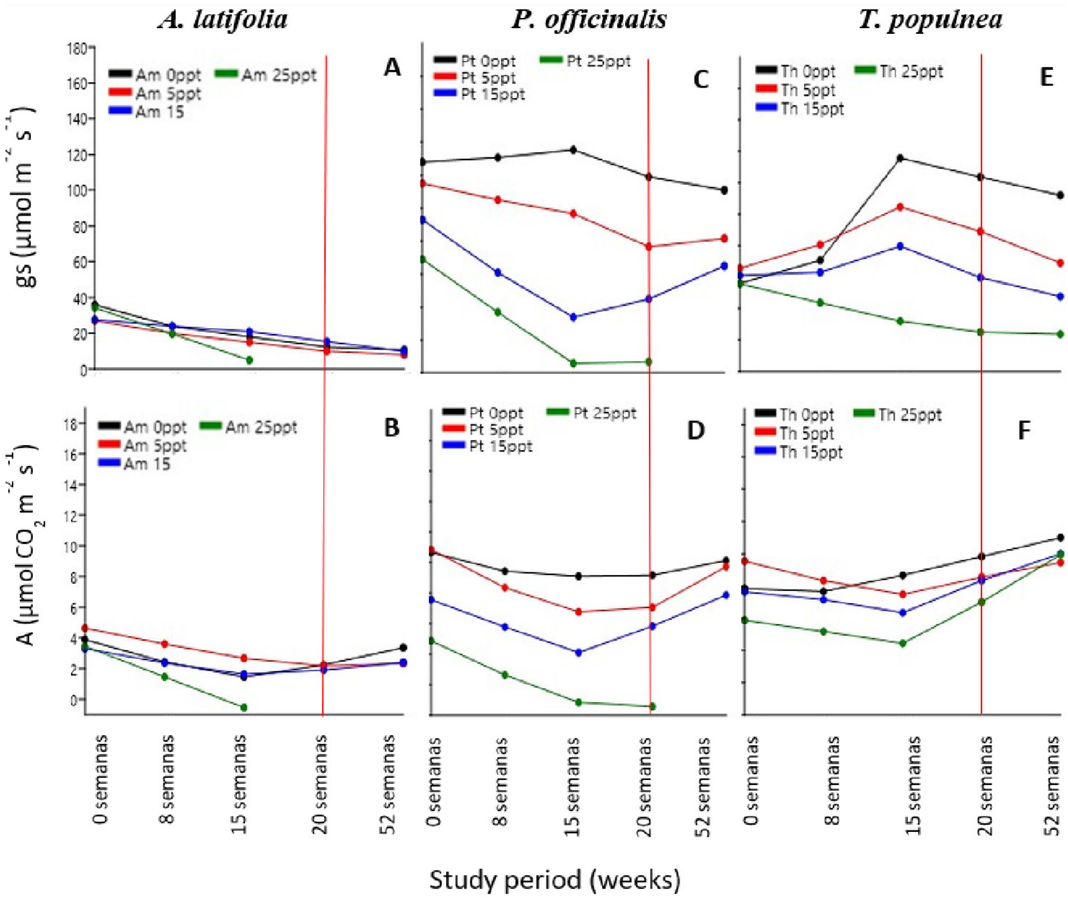

Figure 7. Temporal variation of stomatal conductance (gs) (graphs A, C and E) and net carbon assimilation (A) (graphs B, D and F) in all study species as a function of the experimental treatments: 0ppt (dark line), 5ppt (red line), 15ppt (blue line) and 25ppt (green line). Each point represents the average obtained in (gs) and (A) by species type and experimental salinity treatments. The red vertical line identifies the recovery period from week 20 to week 52.

the lowest tolerance to water and salt stress. Both *P. officinalis* and *T. populnea* maintained a more stable number of leaves in the treatments ranging from 0ppt to 5ppt and showed less pronounced losses compared to *A. latifolia* in the high salinity treatments at 15ppt and 25ppt (Figure 4B and 4C - blue and green lines). The reduction in number of leaves become more evident from week 15, particularly in *P. officinalis* compared to *T. populnea*. In *Thespesia* the presence of leaves was observed in all experimental treatments, including the extreme salinity treatment (i.e., 25ppt) and also during the recovery period (Figure 4C).

All of the species showed continuous growth in stem size at all experimental treatments during the first weeks, but there was a reduction at week 20 (Figure 5). *A. latifolia* showed an earlier reduction in stem size on week 15 in the 15ppt and 25ppt treatments (Figure 5A - blue and green lines). The hydric and salt stress were more pronounced in this species and produced a high impact in the stem size compared to the other species. During the recovery period, the effects that these saline treatments exerted in *Amphitecna*, in terms of number of leaves and stem height, prevented a recovery, suggesting that its recuperation capacity is limited.

Ecophysiological Response to Water and Saline Stress

Stomatal conductance (*gs*) and net carbon assimilation (A) were different on each species at the experimental treat-

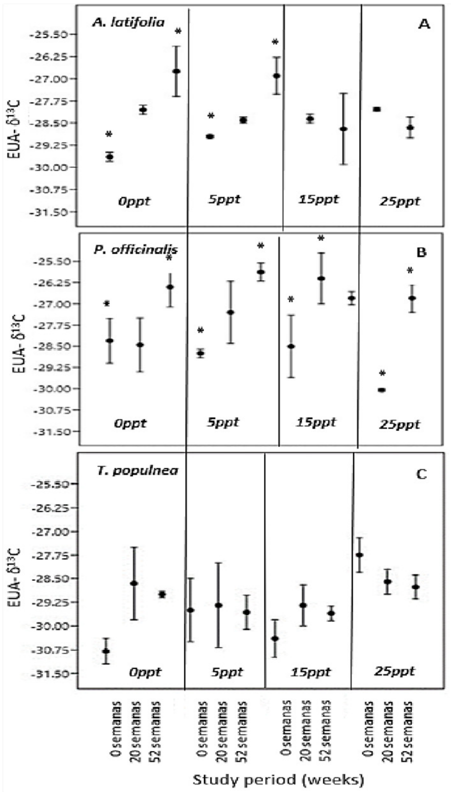

Figure 8. WUE comparisons between the beginning of the experimental period (week 0), the end of the experimental period (week 20) and the recovery period (week 52), by means of the isotopic signal of 13C, by species type and treatments. The (*) represent significant difference in (WUE- 13C) between periods, according to the Tukey-Kramer test, $p < 0.05$.

ments. The values showed a direct proportional relationship between stomatal conductance and the net carbon assimilation in all the species (Figure 6; n = 97, $R^2 = 0.55$, p <0.001). This significant relation indicates that high values in stomatal conductance are positively related to elevated net carbon assimilation, product of a greater stomatal opening. Through the experimental treatments we found reductions in both *gs* and A in all species as the saline and hydric stress increased, particularly in the experimental treatments of 15ppt and 25ppt (Figure 7). The values that we found in *gs* and A showed a greater tolerance and recovery capacity to water and saline stress in *T. populnea,* followed by *P. officinalis* and a greater vulnerability in *A. latifolia.* In the most tolerant species, high values of *gs* and A were observed, including at the highest salinity treatments of 15ppt and 25ppt (Figures 7C to 7F). These values were maintained throughout the entire experimental period and showed a recovery, mainly in the net carbon assimilation during the recuperation period towards week 52 (Figures 7C to 7F). This implies that *T. populnea* and *P. officinalis* have a greater ecophysiological tolerance and a greater recovery capacity to water and salt stress by maintaining their photosynthetic structures (leaves), a greater degree of stomatal opening (*gs*) and a high net carbon assimilation (A). It is important to highlight that during its recovery period, *T. populnea* showed carbon assimilation rates equals to the initial values when the experimental period was started (Figure 7E and 7F). In this species, values of (A) rised significantly, relative to the other species, in the order of 8 to 12 μmol CO2 m^{-2} s^{-1}, during the recovery period.

In terms of water use efficiency (WUE), through the isotopic signal of $\delta^{13}C$, *T. populnea* presented the lower and more consistent WUE at all experimental treatments compared to the other species including the recovery phase (mean = -30 to -28; Figure 8C). All species showed an increase in WUE due to water and saline stress, but *P. officinalis* and *A. latifolia* showed a significant increase in WUE from the initial to the final period of the experimental weeks and even in the recovery phase, mainly in the extreme salinity treatments at 15ppt and 25ppt (Figure 8A, mean = -28.5 and Figure 8B, mean = -26). The increase in WUE reflected in *P. officinalis* and *A. latifolia* demonstrated the high sensitivity of these species to the increase in water and salt stress and to the persistence of these conditions. The increase in WUE explains the reductions in *gs* and A, which is related to a low tolerance and recovery capacity to water and saline conditions. In *T. populnea,* the low WUE, relative to the other species, reflected the highest tolerance to salinity and water stress of the species, which is directly related to high values in *gs* and A throughout all the treatments including the recovery period (Figure 8C). The WUE observed in *Thespesia* and its relationship with *gs* explains the greater net carbon assimilation (A) reflected in this species, including at the highest salinity treatments and during the recovery phase, and therefore explains the structural stability and survival rates reflected by the experiment. The consistency in WUE, *gs*, and A in *T. populnea* shows its greater ecophysiological tolerance to water and salt stress and its greater recovery capacity to these conditions.

Survival and Salinity Range of Tolerance

The mortality showed by all species tells us about the specific range of tolerance that they show to different salinity levels. Mortality in our species increased considerably from the week 15 of the experiment to between 50% to 70%, mainly in the saline treatments at 15ppt and 25ppt. *A. latifolia* and *P. officinalis* experienced the lowest survival rates (0%), particularly in the highest salinity treatment at 25ppt (Figure 9).*A. latifolia* showed the earliest mortality, at 8th week of experiment, also in the lowest saline treatment at 5ppt.. The lowest survival rate demonstrated its high sensitivity to water and saline stress relative to the other species. Rivera-Ocasio and others (2007) found that species with a lower tolerance to water and salt stress experienced higher mortality associated with physiological problems due to the toxic effect of salinity. In our study *T. populnea* had the survival rates (Figure 9). At the extreme salinity treatments, the total mortality in this species did not exceed 50%, therefore, it is the only species that had live individuals at the end of all the experimental treatments (Figure 9). The highest survival rates reflected in this species can be explained by its ecophysiological properties. Such trends are consistent with experimental studies evaluating net carbon assimilation rates (A) and stomatal conductance (*gs*), where an increase in water deficit reduced both parameters significantly, leading to increased mortality (Angelopoulos et al. 1996).

CONCLUSION

Increased water and salt stress affects plant structure and ecophysiological response as well as survival rates of *P. officinalis*, *T. populnea* and *A. latifolia.* The limitation in freshwater availability due to an increase in salinity promotes differentiated effects in terms of A, *gs* and WUE. Compared to the other species, *T. populnea* showed better structural and ecophysiological responses. The survival rate observed in this species, even under extreme conditions, is the product of its ability to preserve its stomatal opening and maintain its net carbon assimilation, avoiding the effects of water and saline stress. The maintenance in the net carbon assimilation (A) allows this species to constantly generate biomass for its survival and structural development (Miah 2013; Atkinson et al. 2000, 1999). Species tolerant to water deficit not only show a better stomatal opening under a low water availability, but also a high carbon assimilation, which is reflected in the production of biomass, structural development and survival of the plant within an extreme environmental condition (Maréchaux et al. 2015). In *A. latifolia* the stomatal closure experienced by this species limited the entry of CO_2, affecting the rate of photosynthesis and forcing the plant to use the carbon that has already been synthesized into organic compounds to maintain its basic cellular functions (respiration) (Pezeshki et al. 1996). When a plant is in a physiological respiration, it implies that the net photosynthesis rate is limited, reflecting A values equal to 0 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ or less, as was the case of *A. latifolia*. In terms of the recovery capacity to water and saline stress, both *T. populnea* and *P. officinalis* demonstrated the highest ecophysiological recovery as shown by their net carbon assimilation, maintaining their stomatal opening, and their survival, even during the recovery phase. However, we do not know for how long these more tolerant species could persist under these water and saline conditions. Considering the survival rates, we found that the range of tolerance to saline conditions varied between the species. *T. populnea* exhibited the highest range of tolerance to salinity from 0ppt to 25ppt (Figure 9). In the case of *P. officinalis* we established a tolerance range from 0ppt to 15ppt and for *A. latifolia* a lesser range from 0ppt to 5ppt (Figure 9). The optimal tolerance range for all the species generally occurs between 0ppt to 5ppt, extending up to 15ppt in the case of *T. populnea* (Figure 9).

Addressing changes in environmental conditions experienced in wetland ecosystems associated with climate change and their impacts on biodiversity are challenges that any rehabilitation and reforestation effort must consider. This work can be used to identify species that exhibit a great environmental plasticity as well as those with a high vulnerability to environmental stressors. For conservation and management purposes vulnerable species could then be relocated to areas with optimal conditions for their development and allows the identification of habitat conditions that will likely promote the successful establishment of these species. Rehabilitation practices should consider the response capacity of species (including ecotypes) and focus on selecting tolerant individuals with a greater environmental plasticity. Wetlands experience changes in their abiotic conditions as a result of climate change and anthropogenic impacts. Consequently, our experimental approach and similar studies can be used to help improve rehabilitation practices in these dynamic ecosystems.

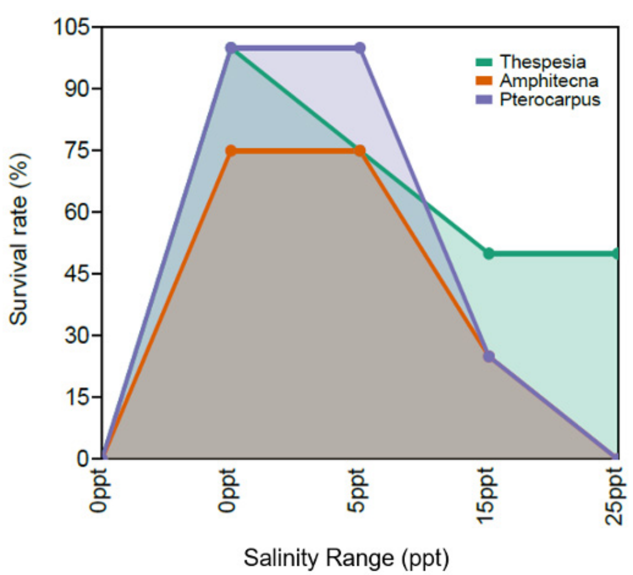

Figure 9. Survival rates and salinity range of tolerance in all study species. Purple line represents *Pterocarpus officina*lis, orange line *Amphitecna latifolia* and green line *Thespesia populnea*.

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