GERMINATION AND GROWTH OF MONTEZUMA CYPRESS (*Taxodium mucronatum* Ten.) FROM THE NAZAS RIVER TO EXPERIMENTAL SALINITY TREATMENTS

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SUMMARY

The Chihuahuan Desert harbors populations of Taxodium mucronatum *adapted to arid and saline conditions, so that a better understanding of its life history constraints may inform wetland management planning if climates become hotter and drier in the future. Furthermore, this species has a high cultural value in the Nazas River region in Mexico, where nursery facilities often utilize water from brackish or slightly brackish phreatic mantles. This study tested the seed germination and seedling growth responses of* T. mucronatum *from the arid lower watershed of the Nazas River to water salinity levels of 0.4 and 9g·l^{-1} under controlled environmental conditions. Seeds germinated similarly in all salinity levels, but elevated salinity levels reduced the height, biomass and leaf number of seedlings. Notably, there was no mortality in these salinity treatments, which suggests that* T. mucronatum *from this region has adaptations for tolerating salinity stress.*

Introduction

Future climates in Mexico and elsewhere are projected to be warmer with increased frequencies of drought and flood events (Pavia *et al*., 2009). Desert regions such as the Chihuahuan Desert are at increasing risk of soil salinization (CONAGUA, 2018). There is a need for the identification of ecophysiological traits in foundational plant species adapted to these arid drought-prone environments, since these have a key role on the climax communities in a long-term. It is important to note that natural occurring salinity can reduce both the regeneration and primary productivity of foundational tree species (Fischer and Turner, 1978; Denny *et al*., 2008; Munns and Tester, 2008). Another challenge is that reforestation efforts involve tree propagation by seed, which take place in facilities that very often use pumped water from phreatic mantles, which may contain dissolved salts, as is the case in the Nazas River region (Job *et al*., 1998; Serrato-Sánchez *et al*., 2002; Santamaría-César *et al*., 2004; Azpilcueta-Pérez *et al*., 2017). According to CONAGUA (2018), in the Central Northern Watersheds group (where Nazas river basin is located within) in Northern-Central Mexico, 6% of groundwater sources are classified as brackish and 15% slightly brackish.

Taxodium mucronatum Ten. 1853 is the 'national tree' of Mexico and it is a species of great cultural significance and conservation interest (CONAFOR, 2020). Therefore, it is necessary to better understand tree establishment traits for this species, such as germination and growth rate, in order to ascertain if the Nazas River populations are well adapted to saline conditions, because salinity is naturally elevated in this region (McMillan, 1974; Zhou *et al*., 2010; CONAGUA, 2020). If so, the populations from the Nazas River region might be useful in restoration, particularly if future environments there and elsewhere become hotter, drier or more saline. Seed germination studies can benefit the development of conservation strategies, particularly by providing information on species survival strategies, seed dispersal and dormancy/germination, particularly when these develop under salinity conditions (Middleton, 2009; Baskin and Baskin, 2014). In particular, a population of *T. mucronatum* from the Nazas River has a characteristic terpenoid profile likely related to aridity adaptations that other populations of *Taxodium* from North and Central America do not possess (Adams *et al*., 2012). Also, *T. mucronatum* and *T. distichum* respond differently to photoperiod and soil alkalinity (McMillan, 1974). Distinct

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GERMINACIÓN Y CRECIMIENTO DE CIPRÉS DE MOCTEZUMA (*Taxodium Mucronatum* Ten.) DEL RÍO NAZAS BAJO TRATAMIENTOS EXPERIMENTALES DE SALINIDAD

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RESUMEN

El Desierto Chihuahuense aloja poblaciones de Taxodium mucronatum *con adaptaciones a condiciones áridas y salinas, por lo que una mejor comprensión de las limitaciones de su ciclo vital puede servir como información para planes de manejo en humedales, si las condiciones climáticas se vuelven más cálidas y secas en el futuro. Además, esta especie tiene un alto valor cultural en la región del Río Nazas en México, donde los viveros a menudo utilizan agua proveniente de mantos freáticos salobres o ligeramente salobres. Este estudio evaluó las respuestas de germinación de semillas y crecimiento de plántulas de* T. mucronatum *provenientes de la cuenca baja árida del río Nazas bajo niveles de salinidad del agua de 0,4 y 9g·l*$^{-1}$ *en condiciones ambientales controladas. Las semillas germinaron de manera similar en todos los niveles de salinidad, pero los niveles elevados de salinidad redujeron la altura, biomasa y número de hojas de las plántulas. En particular, no hubo mortalidad en estos tratamientos de salinidad, lo que sugiere que* T. mucronatum *de esta región tiene adaptaciones para tolerar el estrés por salinidad.*

GERMINAÇÃO E CRESCIMENTO DO CIPRESTE DE MONTEZUMA (*Taxodium mucronatum* Ten.) DO RIO NAZAS SOB TRATAMENTOS EXPERIMENTAIS DE SALINIDADE

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RESUMO

O Deserto de Chihuahua abriga populações de Taxodium mucronatum *com adaptações a condições áridas e salinas, portanto, uma melhor compreensão das limitações de seu ciclo de vida pode servir de informação para planos de manejo em zonas úmidas, caso as condições climáticas se tornem mais quentes e secas. Além disso, esta espécie tem alto valor cultural na região de Río Nazas, no México, onde os viveiros costumam usar água de lençóis freáticos salobra ou levemente salobra. Este estudo avaliou as respostas de germinação de sementes e crescimento de plântulas de* T. mucronatum *da bacia árida do baixo rio Nazas sob níveis de salinidade da água de 0,4 e 9g·l*$^{-1}$ *em condições ambientais controladas. As sementes germinaram de forma semelhante em todos os níveis de salinidade, mas níveis elevados de salinidade reduziram a altura das mudas, a biomassa e o número de folhas. Em particular, não houve mortalidade nesses tratamentos de salinidade, sugerindo que* T. mucronatum *dessa região possui adaptações para tolerar o estresse salino.*

population-level responses of *T. mucronatum* to drought and salinity are possible because ancient trees in the Nazas watershed have survived drought conditions over thousands of years (Stahle *et al*., 2016).

Salinization in both water and soil cause stress on various species and age classes of freshwater *Taxodium* (Stiller, 2009; Herbert *et al*., 2015; Middleton and Souter, 2016). Taxodium distichum seeds from brackish sources germinate and grow best in water salt concentrations below 6g·l^{-1} (Allen *et al*., 1994; Krauss *et al*., 1998), but the response of *T. mucronatum* is less well known. *Taxodium* hybrids with higher levels of salt and flooding tolerance can be developed asexually for the purpose of propagating resistant trees that can be used for restoration projects in areas where saline water is present (Creech *et al*., 2011; Yu *et al*., 2016).

Adult trees of *T. distichum* are reported more tolerant to higher salinity levels than younger age classes when subjected to experimental salt concentrations of 4-6g·l^{-1} (Allen *et al*., 1994; Krauss *et al*., 1998). Increasing salinity stress on *T. distichum* causes a reduction in biomass, especially of leaves (Allen *et al*., 1997). In a greenhouse study, *T. distichum* survived periods of salt stress below 10g·l^{-1}, and recovered normal metabolism when subjected to freshwater flushing (Allen *et al*., 1997). *Taxodium mucronatum* trees are more salt tolerant than *T. distichum* (Zhou *et al*., 2010), which could be related to both soil and water levels present within these species' native ranges (McMillan, 1974; Denny *et al*., 2008). Because data on germination and early establishment of *T. mucronatum* under water salinity stress are limited, the aim of this work was to evaluate the germination and establishment of *T. mucronatum* seeds along a water salinity gradient (fresh, moderate and high). We suspected that these arid zone populations would tolerate moderate and high salinity levels. In particular, the tested hypothesis was that germination, seedling height, as well as leaf and root biomass would decrease as salinity levels rise. The results of this study could aid efforts to identify salt resistant *T. mucronatum* seedlings that are better suited to soil and water salinity stress.

Materials and methods

Habitat description

The distribution range of *T. mucronatum* includes freshwater floodplains in Guatemala, USA and Mexico, as shown in Figure 1 (CONAFOR, 2020). This study examined a population from the lower Nazas Watershed (Durango) at the natural protected area State Park Fernandez Canyon, this basin is one of the most arid zones within the range of *T. mucronatum*. where this species is dominant among other trees like willows (*Salix nigra*) and poplars (*Populus tremoloides*). However, the riparian forest only represents 7% of the protected area, surrounded by desert shrub vegetation. Moreover, soil salinization is

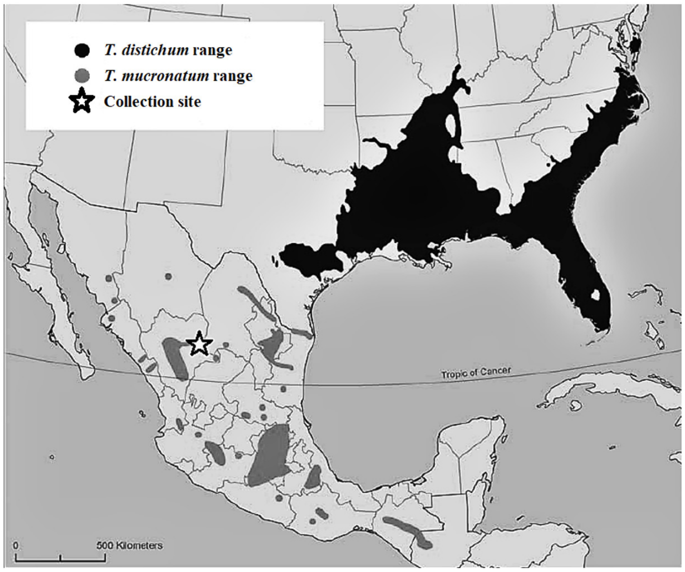

Figure 1. Natural distribution of baldcypress (*T. distichum*) and Montezuma baldcypress (*T. mucronatum*) (based on Stahle *et al*., 2005). Collection site is depicted with a star.

prevalent throughout this region, particularly in the lower parts of the watersheds in the Northern Central Mexico region, where Nazas River is found (CONAGUA, 2018; 2020).

Plant material

Mature seeds from one population were collected from *T. mucronatum* trees during March-April of 2018 along natural floodplains in the riparian forest within public use areas at Cañón de Fernández State Park in Lerdo, Durango, selecting mature cones from both standing branches and on the ground. Afterwards, cones were carefully examined for parasites or signs of damage. The seeds were stored dry for two months in brown paper bags at room temperature in the botanical laboratory of the Biological Sciences Faculty, University Juarez of the State of Durango (following methods of Aclorn and Kurtz Jr. 1959; Krauss *et al*., 1998). Seeds were shipped for experimental study to the U.S. Geological Survey, Wetland and Aquatic Research Center (WARC) facilities, Lafayette, LA, USA under USDA Permit P37-18-01318-USDA.

Experimental design

For a growth chamber study, experimental units consisted of a black plastic pot 15 cm in diameter and 10 cm in height, with 10 seeds per pot sewn at a depth equivalent to the width of the seed (0.75 cm). A total of 45 pots was grouped into three sets of 15 assigned to one of three salinity treatments: 0.4 and $9g\cdot l^{-1}$ (fresh, moderate and high). In order to recreate the salinity levels of the local water supply in the collection site from Mexico, Forty Fathoms Marine Mix® (Marine Enterprises, Baltimore, MD) was used (Cl^- 51%, Na^+ 30%, Mg^{2+} 4%, Ca^{2+} 1% and K^+ 1%, micronutrients/trace elements 13%) to obtain water salinity levels of 0. 4 and $9g\cdot l^{-1}$ of salinity (CONAGUA, 2020). The substrate was a 50% mix of sand/commercial peat moss (Pezeshki, 1990), moistened with distilled water in a tank filled, marked (at 5cm of height), and maintained at the experimental salinity level. There were three tanks (7.5cm of height, 3cm of width and 45cm of length), which acted as randomized blocks containing 15 experimental units, corresponded to each of the three salinity treatments (a total of 45 experimental units was used). Each treatment was set into a corresponding growth chamber (Percival® model E-36L2) housed at the U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA USA. All growth chambers were set at a constant temperature of 25°C, 60% relative humidity and 14h/10h light/dark conditions in moist soil (as in McMillan, 1974) on November, 2018. Individual seedling height and leaf count were recorded at days 30, 60 and 120 after the first emergence of the seedlings (Liu *et al*., 2009). At day 120, as the maximum carrying capacity of the experimental units was met when the growth was inhibited by overcrowding in the same experimental unit (Herms and Mattson, 1992), plants from all treatments were harvested, their main root lengths measured, and secondary (adventitious) roots counted. Harvested plants were dried at 70ºC for a 10-day period and weighed.

Statistical analyses

Mean germination per pot (at day 30) for each treatment was compared via one-way ANOVA to assess differences ($p<0.05$). Mean height and leaf number were analyzed using repeated measures ANOVA to observe differences ($p<0.05$) among salinity treatments over time (30, 60 and 120 days) (Zhou *et al*., 2010; Lei y Middleton, 2018). Total biomass measurements (Day 120) were analyzed using a one-way ANOVA to assess differences ($p<0.05$) among salinity treatments. A *post hoc* means comparison using a Tukey test was used to compare variable and treatment differences (JMP SAS, 2019).

Results

Germination in relation to salinity

Seed germination percentage did not differ among treatments, at day 30 control 0.4 and $9g\cdot l^{-1}$; (fresh, medium and high salinity): 18± 0.07%, 18.67± 0.08% and 18± 0.07%, respectively).

Development of seedlings and salinity

Even though seedlings in all salinity treatments were similar in height throughout the experiment ($p> 0.05$) (Figure 2a, Table I), seedlings from the high salinity treatment displayed fewer leaves than moderate and freshwater treatments at day 30 and 120 (Figure 2b, Table I); also, there was a trend towards reduced height at high salinity more pronounced at day 120. On day 120, the mean root length and adventitious root number were similar among treatments ($p> 0.05$; Figure 2c and 2d). Total biomass of seedlings in high salinity was less than the fresh treatment, while the medium salinity treatment did not differ from either the fresh or high salinity treatment (Figure 3 and Table I).

Discussion

The identification of foundational species with increased tolerance for drought and salinization may be important in future wetland conservation and management to support resilient floodplain forests. Our study tested the germination and early growth of *T. mucronatum* from the Nazas River subjected to experimental salinity, and supported the Adams *et al*. (2012) finding that Taxodium from this region is phenotypically unique. Our study determined that the seeds and seedlings of a population of *Taxodium mucronatum* from the gallery forest of the lower Nazas river basin in northern Mexico are adapted to salinity stress of 4 and $9g\cdot l^{-1}$ salinity, which suggests that this species is more tolerant than *T. distichum* to salinity, as reported in previous experimental salinity stress studies (Allen *et al*., 1997; Krauss *et al*., 1998). As well, *Taxodium* trees are important from the perspective of conservation, management and restoration in riparian forest communities, as these can provide ecosystem services for thousands of years (Stahle *et al*., 2016).

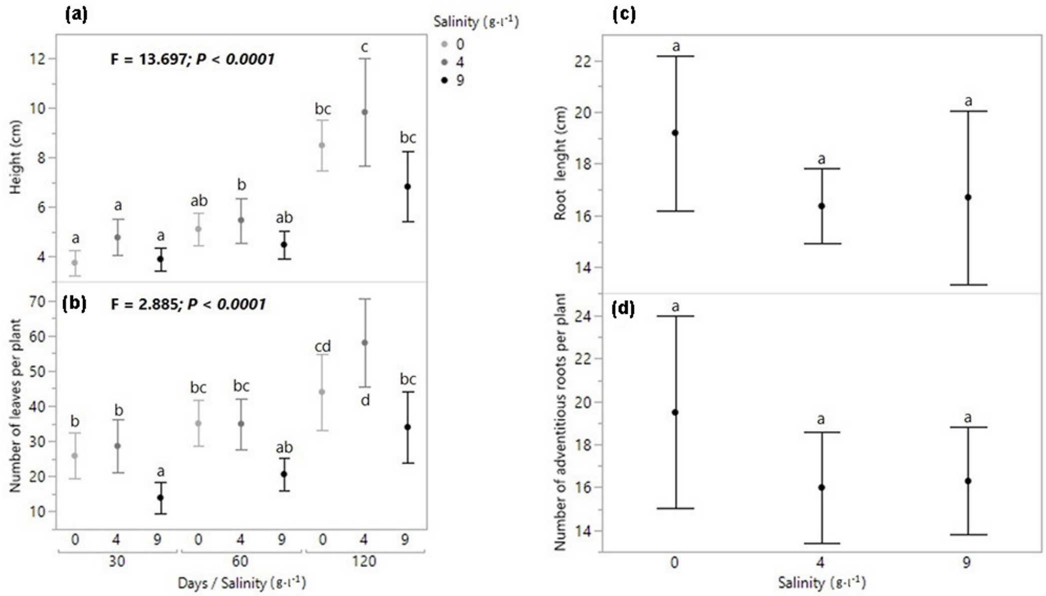

Figure 2. Means and confidence intervals of height in cm (a), number of leaves per plant (b) after 30, 60 and 120 days; and main root length (c) and number of adventitious roots per plant (d) at Day 120, as affected by salinity treatments. Similar letters indicate lack of statistical difference between means using a Tukey test.

TABLE I
ANALYSIS OF VARIANCE OF VARIABLES INCLUDING MEAN ± SE. FOR *Taxodium mucronatum* FROM THE LOWER NAZAS RIVER SUBJECTED TO VARIOUS EXPERIMENTAL SALINITY LEVELS (0.4 AND 9g·l^{-1}; FRESH, MEDIUM AND HIGH, RESPECTIVELY)

Variable	Source	df	*F*	*p*	Mean (± SE)
Germination per pot (%)	Salinity	2	0.01	0.9904	18.22± 0.43
Height (cm) per plant	Salinity × Time	8	13.697	<0.0001***	5.94± 1.52
Leaf count per plant	Salinity × Time	8	2.885	<0.0001***	33.2± 7.85
Main root length (cm) per plant	Salinity	2	1.24	0.3067	17.42± 3.89
Number of adventitious roots per plant	Salinity	2	1.63	0.2139	17.26± 4.77
Dry weight (g) per plant	Salinity	2	5.14	0.0129*	0.12± 0.07

Significant mean contrasts are designated as: * p< 0.05, ** p< 0.01, and *** p< 0.001.

Following our hypothesis, *T. mucronatum* germinated similarly in all salinity levels tested in this experiment (~18%); in contrast, *T. distichum* has greatly reduced seed germination in moderate to high salinity levels (i.e., >6g·l^{-1} with less than 10% seed germination vs. 26.3% at 0g·l^{-1}) (Krauss *et al*., 1998). Other studies for *T. mucronatum* from Queretaro and Texas populations resulted in germination ranging from ~20% to 70% (Enríquez-Peña *et al*., 2004) and 27% to ~40% (Fierro-Cabo and Plamann, 2021) respectively. In contrast to our hypothesis, *T. mucronatum* seedlings had reduced levels of performance in higher levels of salinity with respect to leaf count and biomass (compared to treatments of moderate salinity and control, respectively); such trend has also been reported for *T. distichum* seedlings subjected to salinity concentrations of 0, 2, 4, 6 and 8g·l^{-1} (Allen *et al*., 1994). Yet, 100% of the seedlings in our study survived in all salinity levels suggesting that individuals from the Nazas River populations can tolerate salinity, as reported for different families of *T. distichum*. On one hand, there was a 100% survival rate for seedlings under experimental salinity concentration of 10g·l^{-1} for three months (Conner, 1994). On the other hand, *T. distichum* under experimental salt concentrations of 4g·l^{-1} caused 'moderate' decreases in survival and at 8g·l^{-1} survival decreased as low as 42% (Allen *et al*., 1996). Since the patterns for germination (Enríquez-Peña *et al*., 2004; Fierro-Cabo and Plamann, 2021) growth and survival (Allen *et al*., 1994; Conner, 1994; Allen *et al*., 1996) of Taxodium can vary among populations, there is a need for more experimentation on the salinity effects over *T. mucronatum* development at different biological stages.

Physiological mechanisms undoubtedly underlie the ability of *T. mucronatum* to tolerate salinity e.g. *T. mucronatum* can excrete salts from its leaf tissue (Zhou *et al*., 2010). Taxodium distichum photosynthesis rate and chlorophyll level were reduced as salinity levels increased, which was related to an excessive ion concentration of ions (Na$^+$, Ca^{+2}, Mg^{+2}, K$^+$) in leaf tissue (Pezeshki *et al*., 1988). Another example of the distinctiveness of *T. mucronatum* from the Nazas River compared to other *T. mucronatum* populations and *T. distichum* is the presence of an outstanding terpenoid profile (Adams *et al*., 2012). The Nazas River seedlings tested in this study had 100% survival in the high salinity treatment; meanwhile, in other studies, *T. distichum* mortality was 27% and 100% after two months of exposure to salt concentrations of 8g·l^{-1} and 10g·l^{-1} respectively (Allen *et al*., 1994; Conner, 1994). In this study, *Taxodium mucronatum* was tallest in freshwater (Figure 2a). Similarly, *T. distichum* seedlings were tallest in freshwater (Krauss *et al*., 1999). Flooding reduced the height of *T. distichum* seedlings under water salinity concentrations above 4g·l^{-1} by 56% (Pezeshki, 1990). Meanwhile, leaf biomass of *T. distichum* was higher in freshwater than those in salinity levels above 4g·l^{-1} (Allen *et al*., 1997; Krauss *et al*., 1999; Zhou *et al*., 2010). Similar to Pezeshki *et al*. (1988), the root biomass was not necessarily affected by salinity increase in the plant tissue; instead, the main differences for *T. mucronatum* development under water salinity were found in the leaves. Overall, both *T. distichum* and *T. mucronatum* seedlings had lower total biomass when subjected to salinities above 4g·l^{-1} (Allen *et al*., 1994).

In floodplains of desert regions such as the lower Nazas River in Mexico, salinization and drought episodes are likely to increase by 2050 and 2080 (López-Santos y Martínez-Santiago, 2015). *Taxodium*

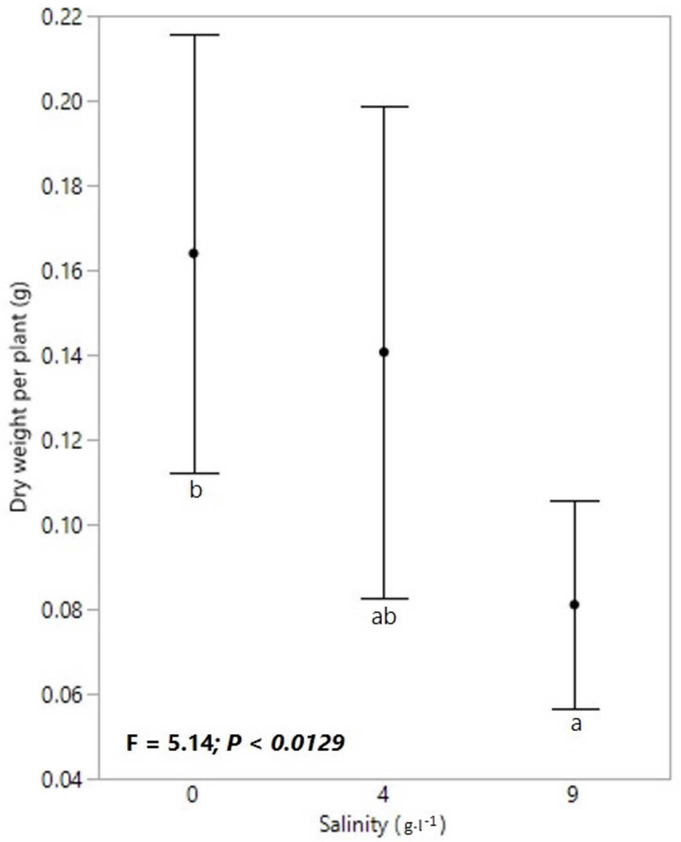

Figure 3. Means and confidence intervals of dry weight (g) at day 120. Different letters indicate statistical differences of means using a Tukey test.

mucronatum is a critical foundation species with a probable high tolerance to salinity stress, in drying floodplains, which might make the species more desirable than others for ecosystem management and restoration. High quality riparian forests comprised of native species enhance the ecosystem services provided by wetlands with respect to water quality, biotic support, soil protection, recreational value and carbon storage (Middleton and Souter, 2016). Thus, it is important to evaluate salinity tolerance thresholds of *T. mucronatum* not only in the study region, but also in different ecosystems and provinces of Mexico, in which salinity is likely to prevail and intensify in the future.

Conclusions

Early life history stages of *T. mucronatum* from gallery forests of the lower Nazas basin in Mexico displayed adaptations to salinity regarding germination, survival and growth. Because there is a growing salinization problem in certain riparian forests, it is important to better understand the salinity tolerance of the early regeneration stages of this species to assess its potential utility for future restoration and management. Better knowledge of the traits of *T. mucronatum* to stress conditions is important for the mitigation and adaptation of floodplain wetlands to climate and land-use change in arid lands.

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