

Morphological, biochemical and nutritional variations in a Mexican purslane (*Portulaca oleracea* L.) variety exposed to salt stress during the vegetative stage

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Abstract

Salt stress limits productivity of crop plants, and differential responses may be observed among genotypes. Herein we analyzed the effects of saline stress induced by the application of different concentrations of sodium chloride (0.00, 0.25, 0.50, 0.75, and 1.00 M NaCl) in a local Mexican variety of purslane (*Portulaca oleracea* L.) named 'Atlapulco' in vegetative stage. The NaCl concentrations were applied in the Hoagland nutrient solution used in irrigation for 14 days under greenhouse conditions, using perlite as a substrate. Analysis of variance and comparison of means were carried out with the data obtained. NaCl concentrations from 0.50 M reduced canopy coverage 36.8% and stem diameter by almost 21%, while all NaCl doses reduced the leaf area by 28.2%, on average, as compared to the control. Dry stem biomass and chlorophyll b were reduced by the saline gradient. Secondary stems and root length increased with 1.00 M by 23 and 29%, respectively. Proline concentration both in leaves and stems increased by 223.9 and 138%, respectively, when applying 1.00 M NaCl, compared to the control. Applying 0.75 and 1.00 M NaCl reduced N concentrations by 47 and 28.8% in leaf tissues, respectively, compared to the control. The concentrations of P and K in leaves, and K in roots also decreased with the saline treatments, while those of Ca and Mg were not affected in any of the analyzed tissues. The highest concentrations of Na in leaves were observed in doses 0.50 and 0.75 M NaCl, surpassing the control by 67.5 and 73.1%, respectively. The findings reported herein are very useful to propose programs for the recovery of saline soils in the region and design environmental policies aimed at mitigating the effects of climate change on food production.

Keywords: abiotic stress; halophytes; Portulacaceae; salinity; stress response

Received: 29 Sep 2023. Received in revised form: 15 Apr 2024. Accepted: 30 Apr 2024. Published online: 13 May 2024.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

Introduction

Salinity is one of the main abiotic stress factors that affects most plant species on Earth, as it alters their growth and development and the whole life cycle (Liang *et al.*, 2018). The first effect experienced by a plant exposed to toxic salt levels is the osmotic upset (Horie *et al.*, 2011); the excess sodium in the cells causes ionic toxicity, with a concomitant imbalance of the osmolyte concentration. Such imbalance induces oxidative stress and other physiological and biochemical alterations that ultimately may inhibit vital processes such as germination, growth, flowering, and fruiting (Munns *et al.*, 2006; Liang *et al.*, 2014).

The phenotypical responses of individual plants to the saline stimulus may result from genetic and molecular changes inside a population, which leads to a local adaptation (Brady *et al.*, 2005; Busoms *et al.*, 2015). Additionally, the adaptive response can be reinforced according to environmental conditions and be transferred from one generation to the next as a parent or phenotypical plasticity response (Germain and Gilbert, 2014) which is a mechanism expressed individually-modularly at the morphological level and responds to changes and differences in environmental conditions (De Kroon *et al.*, 2005). In the search for plant genotypes that resist the onslaught of climate change, the *Portulaca* genus has gained importance due to its ability to tolerate heat, dehydration, and salinity stress conditions (Jin *et al.*, 2016), with a special capacity for salt hyper-accumulation (Silva *et al.*, 2023). Consequently, the *Portulaca* genus can be considered as a good biological model to study the mechanisms activated by plants in saline environments (Borsari *et al.*, 2018; Silva *et al.*, 2023).

As a halophyte species, purslane (*Portulaca oleracea* L.) has the ability to counteract the effects of saline stress by increasing the activity of antioxidant enzymes such as ascorbate peroxidase, catalase, and glutathione reductase in the leaves and raising the proline levels (Yazici *et al.*, 2007). Additionally, in the presence of salts in the growth medium, this species increases the synthesis of bioactive compounds such as phenols, flavonoids, and carotenoids (Alam *et al.*, 2015). Under conditions of salinity stress, purslane exhibits alterations in the mineral composition and antagonism between Ca^{2+} and K^+ , while the levels of Na^+ and Mg^{2+} can increase (Teixeira and Carvalho, 2009). When the electrical conductivity of the nutrient solution increases from 2.5 to 12.5 dS m^{-1} , purslane can reduce root elongation and stem length (Franco *et al.*, 2011). As the saline gradient increases to 150 and 200 mM NaCl, it is possible to observe increases in the concentrations of chlorophyll a and b, in addition to a significant increase in the concentrations of proline and sugars, while lipids and proteins decrease (Rahdari *et al.*, 2012). Also in purslane seedlings, high levels of water stress induced by polyethylene glycol PEG and saline stress cause the decrease of K^+ , Ca^{2+} , Mg^{2+} , Fe^{2+} , and Mn^{2+} concentrations, and, given the low availability of water in the medium, mobility of cations decreases (Rahdari and Hosseini, 2012). Interestingly, this species predominantly displays C4 metabolism, which may change to CAM metabolism under drought stress. It is either considered a polymorphic species or a complex of subspecies, due to its numerous morphological variations (Ferrari *et al.*, 2020).

Since *P. oleracea* has high genetic variability, stress responses also vary from one cultivar to another. In a study on the effect of NaCl and Ca^{2+} deficiency, Kong *et al.* (2014) tested two cultivars and observed that one of them was more susceptible to damage than the other, which exhibited more attenuated symptoms. This indicates that the genome of *P. oleracea* allows it to adapt to a large number of environmental variables (Sdouga *et al.*, 2019), and therefore multivariate studies are currently being carried out in order to elucidate mechanisms of action in the interaction of variables at the metabolomic, proteomic, and transcriptomic levels.

Purslane is a species native to India and the Middle East, while its distribution is cosmopolitan. Since ancient times, in Mexico this species has had edible and medicinal use (Brumfiel, 2009; Mclung de Tapia *et al.*, 2014; Vázquez-Alonso *et al.*, 2014). As a food, this species shows high content of fatty acids and antioxidants (Lim and Quah, 2007; Yang *et al.*, 2009; Sarmiento-Franco *et al.*, 2016; Zaman *et al.*, 2019), which can be modified in the presence of high levels of salts, and those modifications may vary between genotypes. In the

hydrological basin of Lake Texcoco in Mexico (25.60 NL; 100.26 WL; 2240 m altitude), which covers an extension of 2,000 km², numerous varieties of purslane are sown, which have been selected by local producers over the years. This basin has saline soils, to which the varieties of purslane that are currently cultivated have adapted. This study had the objective of evaluating the effect of different concentrations of sodium chloride (NaCl) on the morphological, biochemical, and nutritional indicators of the var. 'Atlapulco', a local variety of purslane (*Portulaca oleracea* L.) widely sown around Lake Xochimilco, Xochimilco, Mexico City, during its vegetative stage. Lake Xochimilco is part of the hydrological basin of Lake Texcoco, Mexico.

Materials and Methods

Plant material

The seeds of the local purslane (*Portulaca oleracea* L.) 'Atlapulco' variety were obtained from a market located in the area of Lake Xochimilco (19.17 NL; 98.54 WL; 2241 m altitude) in the mayoralty of Xochimilco in Mexico City, Mexico. The seeds were sown in germination trays, using as a substrate a mixture 1:1 (v:v) of peat (Premier Horticulture Ltée, Quebec, Canada) and perlite (Agrolita®, Minerales Expandidos, S. A. de C. V., Tlalnepantla, State of Mexico, Mexico). When seedlings reached 27-day-old, they were transplanted to 1 L plastic pots, using perlite as substrate for the application of treatments. Each pot contained a single purslane seedling.

Experimental conditions

The study was carried out in a tunnel-type greenhouse with a zenith window, located in Montecillo, municipality of Texcoco, State of Mexico (20.17 NL; 98.36 WL; 2240 m altitude). During the experimental phase, the mean temperature was 28 °C, with a mean relative humidity of 60%. The duration of the photoperiod was 12 h with a mean luminous intensity of 565 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Treatment design and experimental design

We evaluated the following sodium chloride concentrations: 0.0, 0.25, 0.50, 0.75, and 1.00 M NaCl. These treatments were added to the Hoagland nutrient solution [Ca(NO₃)₂ 4H₂O 2.0 mM, KNO₃ 2.0 mM, NH₄NO₃ 0.5 mM, MgSO₄ 7 H₂O 0.5 mM, KH₂PO₄ 0.25 mM, Fe-EDTA 40 μM , H₃BO₃ 25 μM , MnCl₂ 4H₂O 2.0 μM , ZnSO₄ 7H₂O 2.0 μM , CuSO₄ 5H₂O 0.5 μM , KCl 50 μM , (NH₄)₅Mo₇O₂₄ 4H₂O 0.075 μM , and CoCl₂ 6H₂O 0.15 μM] with pH adjusted to 6, which was used for seedling irrigation. Since the plants were in the vegetative stage, the Hoagland nutrient solution was applied at 50% of its original strength.

The treatments were applied during 14 days, so the measurement of the variables and harvest were made when the plants reached 41-day-old.

Each treatment had eight replicates, which were distributed in a completely randomized design. The experimental unit was a 1 L capacity pot with a single purslane plant, with perlite as substrate.

Evaluated variables

Morphological variables

In this study, we evaluated the 13 growth variables described below, as indicated by Rahdari *et al.* (2012).

Canopy coverage: it refers to the proportion of the land occupied by the perpendicular projection of the aerial parts of the individual of the considered species. It was measured by visual estimation.

Leaf area: it is the capacity of the vegetation cover to intercept photosynthetically active radiation. This was estimated with a portable area meter (LI-COR-3000A; Lincoln, NE, USA).

Main stem diameter: It was determined from its base at the substrate using a digital vernier caliper (Truper, CALDI-6MP, Shanghai, China).

Total plant length: plant height was measured from the base near the substrate to the tip of the last emerged leaf, it was measured using a graduated plastic ruler.

Secondary stems: considered as secondary stems were those that originate from the subnode or first aerial nodes.

Fresh root, stem, and leaf biomass: they were determined using an analytical scale (Adventurer Ohaus Pro AV213C; Parsippany, NJ, USA).

Dry root, stem, and leaf biomass: they were evaluated after drying the plant samples for 48 h at 70 °C. To do this, the plant samples were placed in paper bags in a forced air, drying stove (Riossa HCF-125, Monterrey, Mexico) and weighed in the analytical scale mentioned above.

Root length: it was measured from the internode at the substrate level to the distal part of the furthest root, using a graduated ruler.

Root diameter: it was measured at the internode at the substrate level with the digital vernier caliper described above.

Biochemical and nutrient variables

Proline concentration. This variable was determined in leaves and stems using the method described by Bates *et al.* (1973) by colorimetric principle based on the formation of the proline-ninhydrin complex. The samples were read in a spectrophotometer (JENWAY, 6715 UV/Vis, Multi-cell changer; Staffordshire, UK) at a wavelength of 520 nm. The absorbance values obtained were compared against a standard proline curve.

Concentration of total soluble sugars. The total soluble sugars analysis was performed on leaves and stems from the maceration of fresh tissue and extraction based on the method described by Bailey (1958). Fifty mL of 80% ethanol were added to one gram of plant tissue (previously stored at -80 °C). Subsequently, the flask was placed on a boiling plate until a quantity of less than 20 mL was obtained, which was allowed to cool and then filtered, then volumetric to 20 mL with 80% ethanol and left refrigerated at -20 °C for 24 h. One mL of the solution was taken and evaporated; it was subsequently diluted in 20 mL of distilled water. For the quantification, 1 mL of the sample was taken, 2 mL of distilled water and 6 mL of anthrone solution in sulfuric acid were added, they were placed in a hot water bath for 3 min and then the reading was taken. Similarly, the preparation of a glucose solution for the standard curve was done. At the end of the methodology, samples and glucose were read with an absorbance of 620 nm in the JENWAY spectrophotometer indicated above.

Concentration of chlorophylls a, b, and total. The determination of chlorophylls in leaves was done using a triple ethanol extraction according to Harborne (1973). A total of 20 mg of plant material was weighed and placed in reaction tubes for ethanol extractions. The ethanol extractions were carried out incubating samples in a hot water bath for 20 min at 80 °C; adding 500 µL of 80% ethanol, 300 µL of 70% ethanol, and 500 µL of 50% ethanol, respectively. Phase separation was carried out by centrifugation (14,000 rpm, 5 min, 4 °C). From the three combined supernatants (results of the triple ethanol extraction), 325 mL was taken and placed in new 1.5 mL reaction tubes. Subsequently, 850 mL of 98% ethanol was added. The samples were read at 645 and 665 nm in the JENWAY spectrophotometer described above. The calculations were made using the following formulas:

$$\text{Chlorophyll a } (\mu\text{g mg}^{-1} \text{ fresh weight}) = (5.46 \times \text{Abs}_{665}) - (2.16 \times \text{Abs}_{645})$$

$$\text{Chlorophyll b } (\mu\text{g mg}^{-1} \text{ fresh weight}) = (9.67 \times \text{Abs}_{645}) - (3.04 \times \text{Abs}_{665})$$

Total chlorophyll was estimated by adding the obtained concentrations of chlorophyll a and chlorophyll b.

Macronutrient (N, P, K, Ca, and Mg) and Na⁺ concentration. It was evaluated in leaves and roots. To do this, 0.5 g of dry and ground plant material was digested with a mixture of H₂SO₄:HClO₄ (2:1, v:v) and 1 mL H₂O₂ at 30% at 350 °C. From the resulting extract, a 10 mL aliquot was taken for the determination of N with the Semimicro-Kjeldahl method described by Bremner (1965). The concentrations of P, K, Ca, Mg, and Na were determined by direct reading of the digests in an inductively coupled plasma optical emission spectrometry equipment (Agilent, ICP-Optical Emission Spectrometer, 725-ES, Santa Barbara, CA, USA).

Statistical analysis

With the results obtained, an analysis of variance and Tukey's comparison of means test ($\alpha=0.05$), were carried out using the SAS software (SAS, 2011).

Results*Effects of NaCl on morphological variables*

Canopy coverage and leaf area showed an inverse relationship with the concentration of NaCl in the nutrient solution. The 0.50, 0.75, and 1.00 M NaCl doses reduced coverage by 35.4, 41.8 and 33.3%, respectively, compared to the control (Figure 1a). All the NaCl doses evaluated significantly reduced the leaf area, by 28.2% on average, compared to the control (Figure 1b).

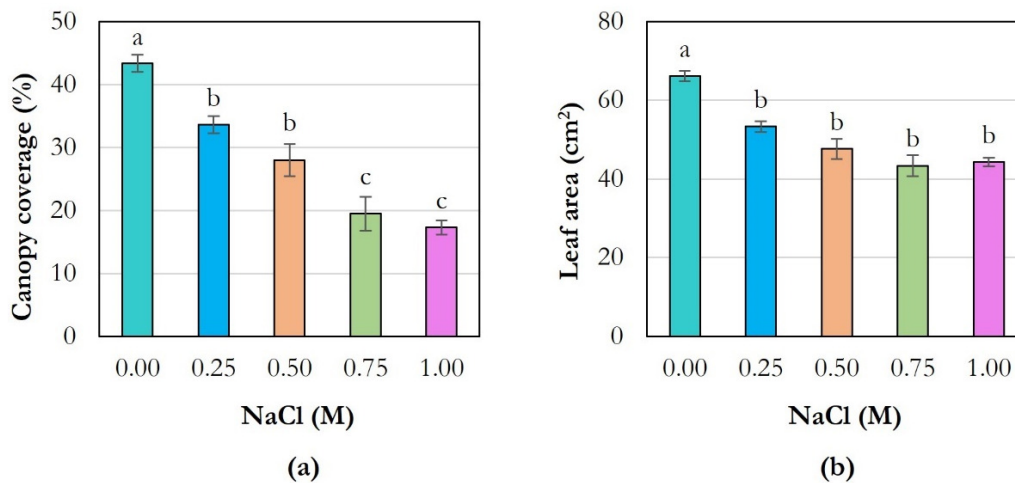


Figure 1. Canopy coverage (a) and leaf area (b) of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' treated with different NaCl concentrations in the nutrient solution during the vegetative stage. Means \pm SD in each subfigure with different letters indicate significant statistical differences (Tukey, $P \leq 0.05$)

The main stem diameter was reduced by 20.9% on average, by applying 0.50, 0.75, and 1.00 M NaCl, compared to the control. The number of secondary stems and root length had a negative relationship with the NaCl doses. It is worth mentioning that doses 0.75 and 1.00 M NaCl increased the number of secondary stems by 23.1 and 35.4%, respectively, compared to the control. Meanwhile, the 1.00 M concentration increased root length by 29%. The evaluated treatments did not affect total plant length or root diameter (Table 1).

Table 1. Morphological parameters of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' treated with different NaCl concentrations in the nutrient solution during the vegetative stage

NaCl (M)	Main stem diameter (mm)	Total plant length (cm)	Number of secondary stem	Root length (cm)	Root diameter (mm)
0.00	4.78 \pm 0.61 a	18.45 \pm 1.33 a	10.83 \pm 1.32 c	4.21 \pm 0.55 b	2.74 \pm 0.38 a
0.25	4.16 \pm 0.51 ab	18.71 \pm 1.60 a	13.16 \pm 1.47 ab	4.53 \pm 0.41 ab	2.83 \pm 0.37 a
0.50	3.77 \pm 0.18 b	17.06 \pm 0.98 a	12.33 \pm 1.36 bc	4.50 \pm 0.45 ab	2.56 \pm 0.41 a
0.75	3.76 \pm 0.14 b	17.75 \pm 0.73 a	13.33 \pm 1.33 ab	4.88 \pm 0.84 ab	2.43 \pm 0.44 a
1.00	3.82 \pm 0.19 b	18.80 \pm 0.55 a	14.66 \pm 0.816 a	5.43 \pm 0.59 a	2.21 \pm 0.23 a

Means \pm SD in each column with different letters indicate significant statistical differences (Tukey, $P \leq 0.05$)

With regard to fresh biomass weights, it is observed that the root was the only organ that was not affected by the saline gradient. The stem was the most affected organ since all the evaluated NaCl concentrations

significantly reduced the weight of its fresh biomass (Figure 2a). Stems of treated plants with doses from 0.25 M showed significant reductions in the weight of fresh biomass with respect to the control. The exception was the treatment with 0.50 M NaCl, where the fresh biomass weight of leaves was statistically similar to the control.

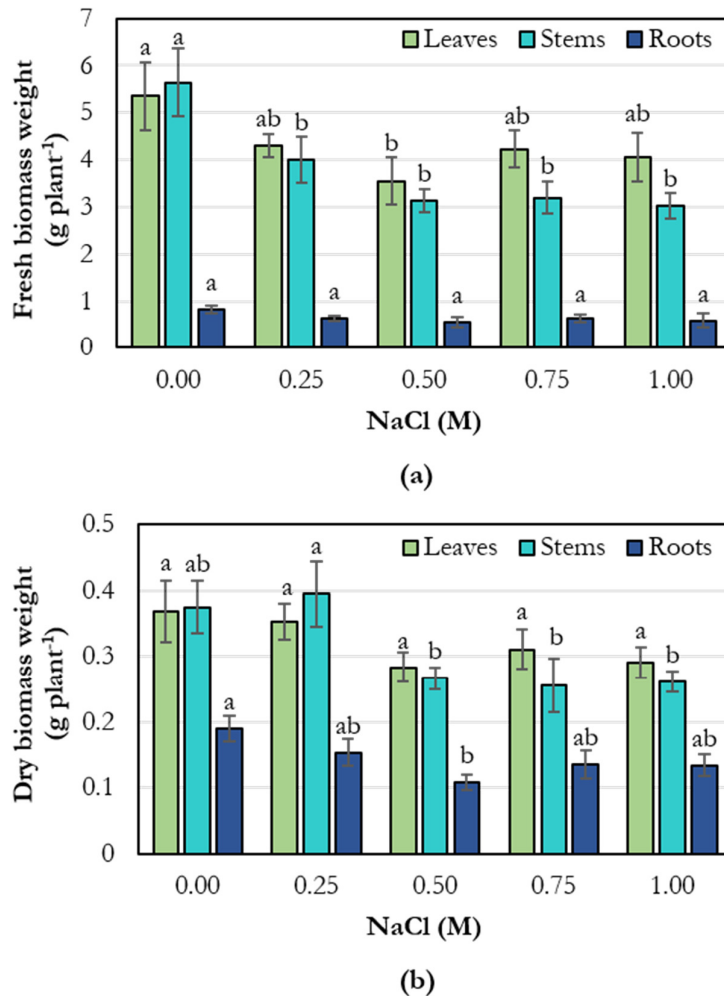


Figure 2. Fresh (a) and dry (b) biomass by organs of purslane (*Portulaca oleracea* L.) var. ‘Atlapulco’ treated with different NaCl concentrations in the nutrient solution during the vegetative stage. Means \pm SD in each subfigure and organ with different letters indicate significant statistical differences (Tukey, $P \leq 0.05$)

As for dry biomass, the treatments did not affect this variable in leaves. In stems, all treatments were similar to the control, although 0.50 M caused a statistically lower mean than 0.25 M. In roots, almost all treatments were similar to the control, with the exception of 0.50 M NaCl, which produced a mean almost twice as low as the control (Figure 2b).

Effects of NaCl on biochemical variables

When increasing the concentration of NaCl, the concentration of proline was increased both in leaves and in stems. In leaves, these same treatments increased the concentration of this amino acid by 100.2, 122.7, 176.3, and 223.9%, compared to the control (Figure 3). In stems, treatments with 0.25, 0.50, 0.75, and 1.00 M NaCl increased the concentration of proline by 94.8, 98.3, 133.4, and 138.1%, with respect to the control.

The concentrations of total soluble sugars in stems and leaves were not significantly affected by the saline treatments (Figure 3b).

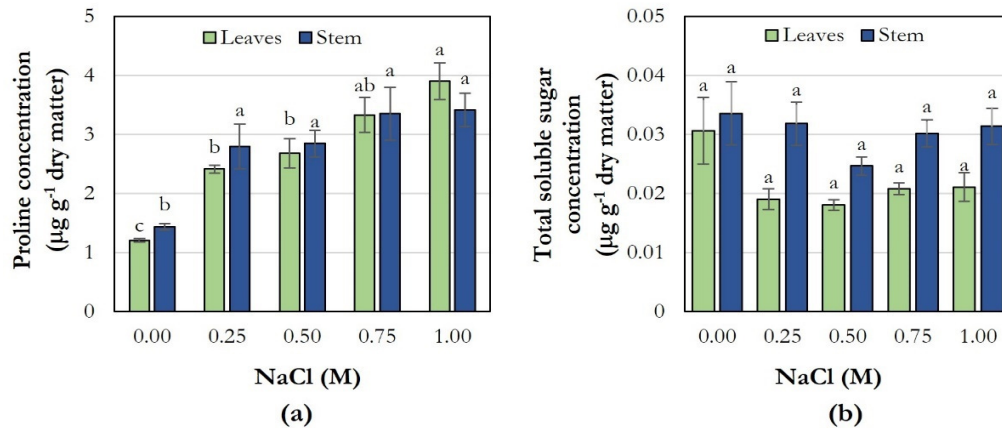


Figure 3. Proline concentration (a) and total soluble sugars (b) in stems and leaves of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' treated with different concentrations of NaCl in the nutrient solution during the vegetative stage

Means \pm SD in each organ by subfigure with different letters indicate significant statistical differences (Tukey, $P \leq 0.05$)

Leaf concentrations of chlorophyll a and total chlorophyll were not affected by the saline gradient evaluated, while the concentration of chlorophyll b was greater in the control as compared to the rest of the treatments tested (Table 2).

Table 2. Leaf concentration of chlorophylls a, b, and total in leaves of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' treated with different NaCl concentrations in the nutrient solution during the vegetative stage

NaCl (M)	Chlorophyll a	Chlorophyll b	Total chlorophyll
	(mg g ⁻¹ fresh weight)		
0.00	0.952 \pm 0.037 a	1.075 \pm 0.263 a	1.588 \pm 0.388 a
0.25	0.947 \pm 0.085 a	0.192 \pm 0.002 b	1.139 \pm 0.087 a
0.50	0.951 \pm 0.067 a	0.202 \pm 0.011 b	1.153 \pm 0.056 a
0.75	0.948 \pm 0.016 a	0.185 \pm 0.001 b	1.032 \pm 0.114 a
1.00	1.063 \pm 0.033 a	0.310 \pm 0.006 b	1.292 \pm 0.079 a

Means \pm SD in each column with different letters indicate significant statistical differences (Tukey, $P \leq 0.05$)

Effects of NaCl on nutrient concentrations

In leaf tissues, doses of 0.75 and 1.00 M NaCl significantly reduced leaf N concentration by 47 and 28.8%, respectively, compared to the control (Figure 4a). The 0.75 M NaCl dose significantly reduced the P concentration compared to 0.50 and 1.00 M NaCl, and although a 21.4% reduction was also observed compared to the control, this difference was not significant (Figure 4b). The concentration of K was only lower than the control by 30.4%, with the 0.25 M NaCl treatment (Figure 4c). The concentration of Ca in leaves was not affected by the treatments evaluated (Figure 4d). The dose of 0.75 M NaCl reduced the Mg concentration by 51%, compared to the control (Figure 4e), although this response was not related to the saline gradient. The highest Na averages were observed in plants exposed to 0.50 and 0.75 M NaCl, surpassing the control by 67.5 and 73.1%, respectively (Figure 4f).

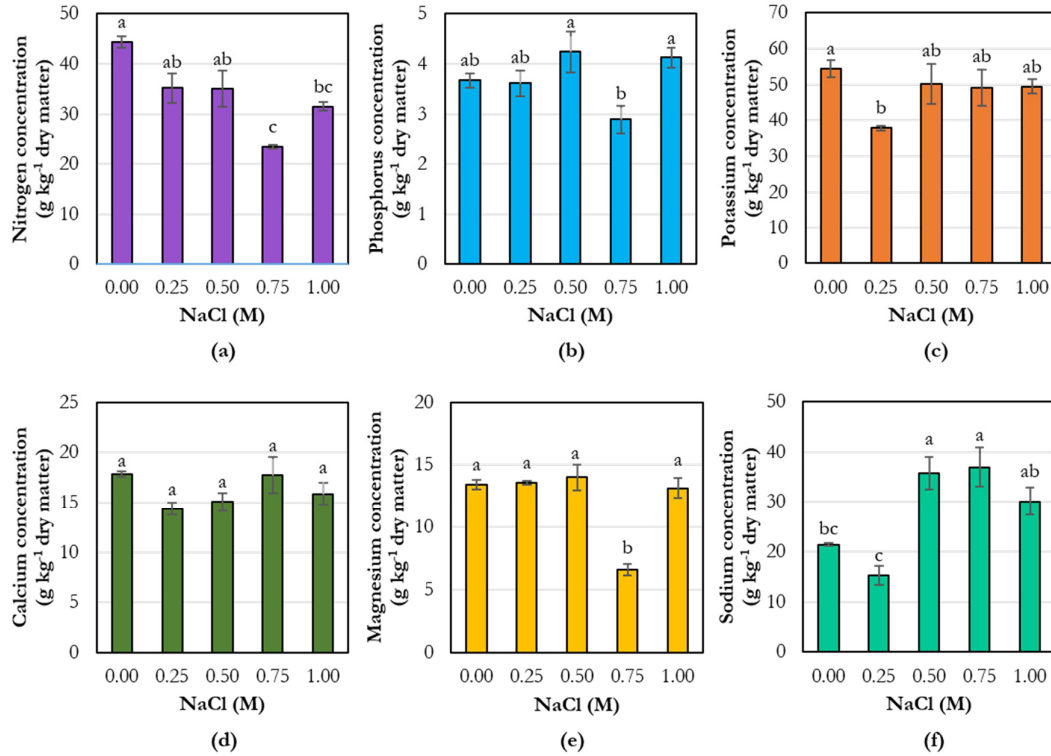


Figure 4. Concentration of N, P, K, Ca, Mg, and Na in leaves of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' treated with different concentrations of NaCl in the nutrient solution during the vegetative stage
Means \pm SD in each subfigure with different letters indicate significant statistical differences (Tukey, $P \leq 0.05$)

In roots, the N concentration was not affected by the treatments (Figure 5a). This result was also observed in the concentrations of P, Ca, and Mg in roots (Figures 5b, 5d, and 5e). The K concentration in roots was significantly reduced with the doses 0.50, 0.75, and 1.00 M NaCl by 44, 55.2, and 70.4%, respectively, compared to the control (Figure 5c). On the other hand, the concentration of Na was directly related to the dose of Na in the nutrient solution, with the highest Na concentration observed with 1.00 M NaCl (Figure 5f).

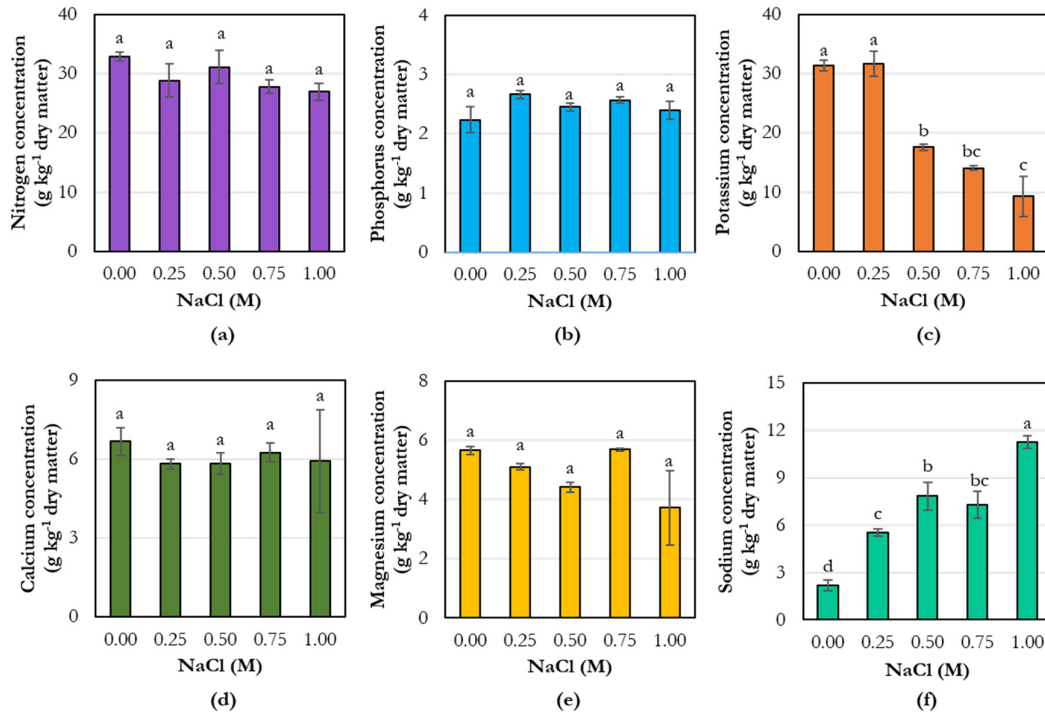


Figure 5. Concentration of N, P, K, Ca, Mg, and Na in roots of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' treated with different concentrations of NaCl in the nutrient solution during the vegetative stage
Means \pm SD in each subfigure with different letters indicate significant statistical differences (Tukey, $P < 0.05$)

Discussion

This study represents an effort to integrate morphological, biochemical, and nutritional variables that can explain the behavior of a local variety of the halophyte *Portulaca oleracea* L. selected in saline lacustrine soils in Lake Texcoco, Mexico. The analysis indicates that although some variables are negatively affected by salinity, this local genotype has developed adaptive strategies that allow it to thrive and produce good crops in the salinity conditions that derive from the saline soils of this region of Mexico, where the species has been produced extensively since ancient times.

The canopy cover and leaf area were severely affected by the doses of NaCl added to the nutrient solution (Figure 1). Salt stress increases osmotic pressure within the cell, which causes sodium accumulation to toxic levels as observed in the leaves in this study (Figure 4f), causing an ionic imbalance. In response to salt stress signals, plants activate adaptive mechanisms such as the regulation of ionic homeostasis and antioxidant processes, among others (Zhao *et al.*, 2021). In stomatal guard cells, these alterations cause the synthesis of abscisic acid and stomatal closure, which reduces the CO₂ assimilation rate (Chen *et al.*, 2022). Consequently, plants exposed to saline stress decrease leaf emission and leaf area, with direct influence on canopy coverage. In 25 accessions of *P. oleracea*, saline stress decreased plant height, number of leaves and flowers, as well as accumulated dry matter, regardless of the level of susceptibility to salinity of these genotypes (Alam *et al.*, 2014).

In our study, it was observed that the values of the main stem diameter were significantly reduced with doses equal to or greater than 0.50 M NaCl, compared to the control (Table 1). This decrease in stem diameter might be associated with the reduction in turgor potential (Díaz-López *et al.*, 2012) caused by saline stress. In

species such as tomato (*Solanum lycopersicum* L.), it has been established that there is a relationship between stem diameter with sap flow, turgor, and water potential (De Swaef and Steppe, 2010).

Contrary to what was observed in canopy coverage, leaf area, and main stem diameter (Figure 1 and Table 1), the number of secondary stems per plant was greater in the NaCl treatments compared to the control (Table 1). Furthermore, we an increase in root length caused by salinity (Table 1), which represents a relevant trait, given that this is the organ that is in direct contact with the salts (Shabala and Bose, 2015) and shows high plasticity to adapt to the environment, in particular to salt stress (González-Orenga *et al.*, 2020). In the halophyte *Suaeda salsa*, the salt stress level of 1.2‰ increased the length of lateral roots, which positively impacted the absorption of water and nutrients under stress conditions (Wang *et al.*, 2021).

Regarding fresh biomass, only the stems and leaves showed a significant reduction compared to the control from the doses of 0.25 and 0.50 M NaCl, respectively (Figure 2a). The effects recorded in the fresh leaf biomass were not related to the dry biomass of this organ since salinity did not affect this last variable (Figure 2b). Although the water content in the leaves of the control exceeded that of the leaves of plants treated with some dose of NaCl on average by 25%, the weight of dry biomass of leaves of control plants was only greater than that of those treated with NaCl by 0.84%. Some shoot growth parameters such as canopy cover (Figure 1a), leaf area (Figure 1b), and fresh biomass of leaves and stems (Figure 2a) were reduced in saline concentrations, probably due to reduced C fixation. All those adjustments turn can cause changes in the distribution of dry biomass between organs to modify the balance of photosynthesis and respiration (Flowers and Colmer, 2008). The allocation of biomass is dependent on the availability of resources and an optimal partition between organs is based on the flexibility in the exchange of biomass between the plant organs, which constitutes the balanced growth hypothesis (Bebre *et al.*, 2022).

Various species increase proline synthesis when subjected to osmotic stress, including four species of *Passiflora* (Hurtado *et al.*, 2017), the halophyte *Salvadora persica* (Parida *et al.*, 2016), and *P. oleracea* (Yazici *et al.*, 2007; Kafi and Rahimi, 2011; Rahadari *et al.*, 2012). This response was also observed in this study, where salinity significantly increased the proline concentration in leaves and stems (Figure 4a). Although normally the increase in the level of proline is associated with cellular biochemical stability as an effector of salt stress by functioning as an osmoprotective metabolite (Hasewaga and Bressan, 2000), this mechanism can also serve as an indicator of resistance to water and salt stress (Mansur and Ali, 2017). On the other hand, exogenous applications of low levels of proline help the stabilization of membrane proteins, scavenging ROS and thus reducing cellular damage (Gill and Tuteja, 2010; Slama *et al.*, 2015).

Salinity tolerance in halophytes appears to depend largely on their ability to compartmentalize toxic ions in the vacuole and accumulate compatible solutes in the cytosol (Gil *et al.*, 2011). With the exception of proline, however, in our study no significant effects of the treatments were observed with respect to sugar concentrations in stems and leaves (Figure 4b). These results are contrary to what was reported by Rahadari *et al.* (2012) who found that *P. oleracea* exposed to 50, 100, 150, and 200 mM NaCl significantly increased the concentration of total soluble sugars in leaves. These differences between the studies can be attributed to the different genotypes used (i.e., Iranian variety *vs.* Mexican variety), and to the experimental conditions of the studies (i.e., one week *vs.* 14 days exposure to NaCl; 100% *vs.* 50% Hoagland solution, etc.).

Under our experimental conditions, no significant effects of the treatments on the concentration of chlorophyll a and total chlorophyll were observed. Similarly, Jin *et al.* (2016) recorded that salinity caused a slight and non-significant decrease in chlorophyll levels in *P. oleracea*. The concentration of chlorophyll b in the control surpassed the rest by an average of 79.3% (Table 2). This coincides with what was reported by Shin *et al.* (2021), that chlorophyll b is more sensitive to salinity and drought than chlorophyll a. Contrarily, Kafi and Rahimi (2011) and Rahadari *et al.* (2012) reported an increase in chlorophyll concentrations with salt stress in *P. oleracea*. Additionally, in this same species, drought stress decreased chlorophyll content; while rehydration increased it gradually (Jin *et al.*, 2015).

Salinity significantly decreases nutrient absorption (Elkelish *et al.*, 2019). However, the effects of salinity on NO_3^- uptake vary considerably between species and between experimental conditions (Ullrich, 2002). In this study, NaCl application reduced N concentrations in leaves (Figure 4a). Likewise, reductions in leaf N concentration in *Salvadora persica* leaves exposed to 250, 500, and 750 mM NaCl were reported by Parida *et al.*, 2016. Nitrogen metabolism is affected by the increase in salt concentration in a large number of species (Uddin *et al.*, 2012). The Cl^- anion is antagonistic to NO_3^- , which negatively interferes with nitrogen nutrition, given that as Cl^- competes with NO_3^- , N assimilation is reduced and thus the growth, development, and yield of the crop. On the other hand, Cl^- facilitates the use of NO_3^- as long as they are in an optimal ratio (Hu and Schmidhalter, 2005; Rosales *et al.*, 2020).

In leaves, the significant increase in Na concentration stands out with doses of 0.50 and 0.75 M NaCl (35.77 and 36.97 mg Na kg^{-1} of dry matter, respectively; Figure 4f). In another study with purslane treated with NaCl, Na concentrations were higher than those obtained here: with doses of 120 and 240 mM NaCl, leaf Na concentrations of 72.3 and 97.3 g kg^{-1} dry matter were recorded (Kafi and Rahimi, 2011). On the contrary, in our experimental conditions the control had a leaf Na concentration of 21.36 g kg^{-1} dry matter, while in the study by Kafi and Rahimi (2011) 11.3 g Na kg^{-1} dry matter was recorded.

In this research, no antagonistic effects of Na^+ and K^+ were observed in leaves (Wakeel, 2013), since the leaf K concentration (Figure 4c) was not affected by the saline treatments. On the contrary, in roots, a decrease in the concentration of K is observed as the concentrations of Na increased in the nutrient solution (Figure 5c) (Figure 5f). In roots of this same species, similar results have been reported when plants are exposed to concentrations higher than 150 mM NaCl, due to a competitive effect between Na^+ and K^+ by K^+ transporters in root tissues (Sdouga *et al.*, 2019).

In leaves and roots there were no effects of NaCl doses on foliar Ca concentration (Figures 4d and 5d). This result is important, since Ca has a fundamental role in salinity tolerance given its participation in cell signaling and therefore in responses to abiotic stress (Lamers *et al.*, 2020). Similarly, the concentrations of P and Mg were not affected in leaves or roots by the saline treatments (Figures 4b, 4e, 5b, and 5e). These results show the importance of the Na^+ ion in *P. oleracea*, given that it is a species in which the C_4 and CAM photosynthetic metabolisms are integrated. Both types of CO_2 fixation metabolisms occur in the same cells and the metabolites generated in the CAM metabolism are directly incorporated into the C_4 cycle (Moreno-Villena *et al.*, 2022), which represents an adaptive advantage of this halophyte, and may partially explain, the stimulating results of NaCl application in some variables in this species.

This work provides new evidence that demonstrates that *Portulaca oleraceae* L. var. 'Atlapulco' has developed adaptive responses to restrictive environments, such as hypersaline environments. Specifically, this species can alternate between C_4 and CAM metabolism, depending on environmental conditions, which gives it superior phenotypic plasticity compared to other species (Ferrari *et al.*, 2022).

Conclusions

This study provides evidence of some adaptive strategies of purslane (*Portulaca oleracea* L.) var. 'Atlapulco' to saline stress, based on the measurement of morphological, biochemical, and nutritional variables. In this genotype of purslane, selected in the saline soil conditions of Lake Xochimilco, Mexico, the application of NaCl promoted a greater number of stems, root diameter and length, as well as Na concentrations in leaves and stems, while the plant length, fresh root biomass, dry leaf biomass, concentration of total sugars, chlorophyll a, total chlorophyll, concentrations of Ca and Mg in leaves and roots, and of N and P in roots, were not affected by the NaCl treatments. On the contrary, the saline treatments negatively affected the variables canopy cover, leaf area, main stem diameter, fresh biomass of leaves and stems, dry biomass of stems and roots, chlorophyll b, and concentrations of N, P, and K in leaves, and K in roots. It is concluded that the analyzed

genotype can grow under the tested conditions, and that although some variables are negatively affected, others are stimulated or show no effect by the treatments, which demonstrates the plasticity of this variety to restrictive saline environments.

Authors' Contributions

Conceptualization L.I.T.-T.; Formal analysis: B.K.G.-O.; Funding acquisition: L.I.T.-T. and F.C.G.-M.; Investigation: B.K.G.-O.; Methodology: B.K.G.-O. and L.M.R.-P.; Project administration: L.I.T.-T.; Resources: L.I.T.-T. and F.C.G.-M.; Software: B.K.G.-O.; Supervision: L.M.R.-P. and J.A.E.-E.; Validation: Y.L.F.-P.; Writing - original draft: B.K.G.-O.; Writing - review and editing: L.I.T.-T. and F.C.G.-M. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Acknowledgements

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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