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# Physiological and biochemical indicators of *Physalis angulata* L. plants submitted under salinity

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**Abstract**

Saline environments may limit the growth and yield of agricultural crops, mainly in arid and semiarid regions, causing negative impacts to the plant physiology. Therefore, the objective of this work was to evaluate the growth and physiological and biochemical indicators of *Physalis angulata* L. plants grown in hydroponic nutrient solutions with different salinities. The experiment was conducted in a greenhouse in a floating hydroponic system, using a completely randomized design. The treatments consisted of five levels of electrical conductivity (EC) of the nutrient solution ($EC_0$ = 0.00 – Control; $EC_1$ = 1.80; $EC_2$ = 3.60; $EC_3$ = 5.40; and $EC_4$ = 7.2 dS $m^{-1}$). Plant gas exchanges, water relations, total chlorophyll contents, organic solute accumulation, and growth parameters were evaluated at 35 days after the application of the treatments. The salinity of the nutrient solution had significant effect on the variables analyzed, denoting adaptation of the plants up to the EC of 2.10 dS $m^{-1}$. Decreases in photosynthetic rates at the highest salinity levels affected the plant growth, causing pronounced decreases. The *P. angulata* plants showed osmotic adjustment after the induction of a severe salt stress at 35 days after sowing; they accumulated organic solutes that increased leaf turgidity, even at lower salinity levels, maintaining the plant water status.

**Keywords:** salt stress, osmoregulation, gas exchange

## Introduction

Saline environments cause one of the main abiotic stresses that decrease the yield of several crops and negatively affect the metabolism of plants in semiarid regions (Oliveira et al., 2019). Increases in concentration of salts in the water and soil are undesirable (Maciel et al., 2012), since excess salt may cause ionic toxicity to plants, mainly by $Na^+$ and $Cl^-$ ions, and nutritional imbalance, caused by limitations in the capacity of plants to absorb and transport nutrients to their aerial part (Lima et al., 2019).

Plants developed adaptive mechanisms to support salt stress and maintain their water status, by reducing the number of leaves, controlling the stomata opening, and decreasing transpiration and water losses (Flowers, 2004; Dias & Blanco, 2010). The osmotic adjustment is a mechanism that decreases the water potential to ensure the maintenance of cell turgidity (Silveira et al., 2009). Decreases in water potential is related to accumulation of organic solutes, mainly soluble sugars and amino acids (Souza et al., 2011), which contribute to the maintenance of physiological processes, although at low levels of activity (Verslues & Bray, 2004).

Some crops have tolerance to high salinity levels, such as melon (Araujo et al., 2016), cucumber (Ventura et al., 2019), and passion fruit (Moura et al., 2016), which varies according to the plant species, cultivars, and accessions within a same species (Fageria et al., 2010; Sá et al., 2016). Thus, the search for resistant native species is essential to maintain crops. One of these species is *Physalis angulata* L. which is a strategic horticultural plant, known as camapú or joá-de-capote in Brazil (Lorenzi & Matos, 2008), that presents small fruits and can be grown throughout the year by using low technology (Vargas-Ponce et al., 2016); their fruits are used for human consumption and their organs are used in popular


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medicine (Rengifo & Vargas, 2013; Zamora-Tavares et al., 2015).

The medicinal potential of *P. angulata* is due to its phytochemical composition, which includes alkaloids, flavonoids, and different steroids, mainly physalins (Sisley et al., 2017). Meira et al. (2013) reported anti-*Trypanosoma cruzi* activity of physalins B and F. In addition, Lima et al. (2014) observed antinociceptive activity of physalins from *P. angulata*.

Some studies on high-salinity environments have evaluated the growth of *Physalis peruviana* (Rezende et al., 2018) and *P. angulata* (Souza et al., 2007) plants, however, the physiological and biochemical mechanisms involved in the tolerance and susceptibility to high salinity levels are still not fully understood. Therefore, the objective of this work was to evaluate the growth and physiological and biochemical indicators of *P. angulata* L. plants grown in hydroponic nutrient solutions with different salinities.

**Material and Methods**

The experiment was conducted in a greenhouse at the Horto Florestal Experimental Unit of the State University of Feira de Santana (UEFS), Feira de Santana, BA, Brazil (12°16'00"S, 38°58'00"W, and 258 meters of altitude), from September to December 2019; the growth, biochemical, and physiological evaluations were carried out in laboratory.

The seedlings were produced from seeds collected in the Semiarid region of the state of Bahia, Brazil (Freitas, 2004) and multiplied by a research group. The seeds were sown at 2 cm depth in disposable cups filled with a mixture of commercial substrate and sand (1:1) and irrigated daily by a sprinkler system in the greenhouse.

When seedlings reached two pairs of true leaves, they were transplanted to a floating hydroponic system; the plants were arranged individually in 6-dm³ pots spaced 0.8 m between rows and 0.2 m between plants, partially immersed in the nutrient solution, supported by an expanded polyethylene structure placed directly on the nutrient solution surface.

Each unit (pot) had an independent oxygenation system for the nutrient solution, based on a compressor with a timer programed for an oxygenation of 20 minutes every four hours. The nutrient solution used (Sarruge, 1975) contained the following macronutrients (mg $L^{-1}$): 210 of N, 31 of P, 234 of K, 200 of Ca, 48 of Mg, 64 of S; and micronutrients (µg $L^{-1}$): 500 of B, 39 of Cu, 722 of Cl, 5000 of Fe, 502 of Mn, 12 of Mo, and 98 of Zn.

The nutrient solutions were diluted in 6 dm³ of distilled water in the pots, using half of the concentrations suggested by Sarruge (1975), and after 10 days (period of adaptation to the hydroponic system), the complete solution was used and the treatments were applied. The treatments consisted of five levels of electrical conductivity (EC) of the nutrient solution ($EC_0$ = 0.00 – Control; $EC_1$ = 1.80; $EC_2$ = 3.60; $EC_3$ = 5.40; and $EC_4$ = 7.2 dS $m^{-1}$), resulted from the addition of different amounts of NaCl to the solution, following the curve developed with dilutions from 0.1 to 4.4 g of NaCl per 1 dm³ of water, adding 0.1 g per reading, totaling 44 concentrations (Aquino et al., 2017).

The nutrient solution was evaluated daily for measure of pH, using a portable pHmeter (Ak90, ASKO), to maintain it within the range of 5.5 to 6.5; and for measure of EC, using a portable conductivity meter (AK51 V4, ASKO). The nutrient solution was completely exchanged every time the EC decreased 20% from the initial EC. A solution with 5% *Azadirachta indica* extract (Neemmax®, 0.12% *A. indica* oil; Insentimax, Jardinopolis, Brazil) was applied three times to all plants after transplanting, at 8-day intervals, for prevention and control of pests.

The temperature conditions and relative air humidity in the greenhouse were monitored daily with a digital thermo-hygrometer installed at the same height of the plants' canopy (Figure 1).

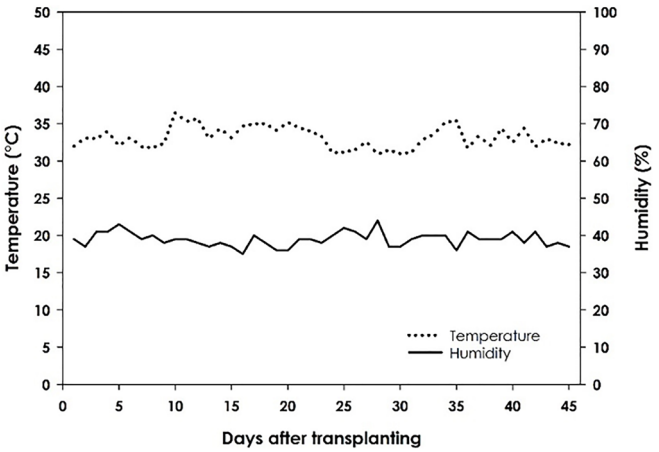


**Figure 1.** Air temperature and relative humidity throughout the experiment period.

The analyses were carried out at 35 days after application of the treatments, with a crop cycle of 45 days in the hydroponic system. The leaf water potential was determined at 4:00 a.m., using a Scholander pressure chamber (PMS1000; PMS Instrument, Corvallis, USA) and leaves collected from the middle third of the plants. The leaf succulence (g $cm^{-2}$) was determined as proposed by Mantovani (1999), through the formula: *(fresh phytomass – dry phytomass) / leaf area*.

Biochemical analyses were carried out using

a gross extract obtained by maceration of 1 g of fresh leaves in a mortar with 15 mL of buffer phosphate 0.1 M, at pH 7.0. The homogenized solution was filtered and centrifuged at 12,000 g for 15 minutes and the supernatant was collected and analyzed for determination of the following parameters: total soluble sugar contents, by the anthrone method (Yemm & Willis, 1954); reducing sugar contents, by the dinitro salicylic acid method (Miller, 1959); total free amino acid contents, by the ninhydrin method (Yemm & Cocking, 1955); and total soluble proteins, by the Bradford method (Bradford, 1976). Saccharose content was measured by the difference between total soluble sugar and reducing sugar contents.

The gas exchanges were assessed using an infra-red gas analyzer (IRGA CIRAS-3, PPSystems, Amesbury, USA). The results were read from 08:30 a.m. to 10:00 a.m. on fully developed leaves, consisting of three readings of 60 seconds per plant. The parameters obtained were: photosynthetic rate, (μmol $CO_2$ $m^{-2}$ $s^{-1}$), transpiration rate (mmol $H_2O$ $m^{-2}$ $s^{-1}$), internal $CO_2$ concentration (μmol $mol^{-1}$), stomatal conductance (mmol $H_2O$ $m^{-2}$ $m^{-1}$), leaf temperature (°C), and water use efficiency (mmol $CO_2$ $mol^{-1}$ $H_2O$).

Dimethyl sulfoxide was used to extract the chlorophyll, using leaf discs of known area from the middle third of the plants. These discs were immersed in tubes containing dimethyl sulfoxide and wrapped in foil sheets to keep them in the dark for 24 hours. The absorbance was measured in a double-beam spectrophotometer (FEMTO 800XI), and total chlorophyll contents were calculated according to the methodology proposed by Wellburn (1994), by summing the chlorophyll *a* and chlorophyll *b*.

Plant height (cm) and stem diameter (mm) were measured using, respectively, a ruler and a digital caliper with precision of 0.01. The plants were collected, separated into root, stem, leaves, and fruits, and evaluated for number of fruits and leaf area, which was measured using a leaf area meter (Li-Cor, model Li-3100C).

The plant parts were placed in paper bags and taken to a forced air circulation oven at 60 °C to determine their dry weights. The dry weight data were used to calculate the salt tolerance. The EC data (dS $m^{-1}$) of the saline treatments were compared to those of the Control (Fageria et al., 2010; Moura et al., 2016), according to the equation: *salt tolerance (%) = (total dry weight of the saline treatment / total dry weight of the Control treatment) × 100*, which determined the salt tolerance in the plants (≥ 100% = tolerant; 50% to 99% = moderately tolerant; ≥ 50% = susceptible).

A completely randomized experimental design with 12 replications was used, considering each pot as an experimental unit. The data were subjected to the Shapiro-Wilk normality test and Bartlett homogeneity test. Then, they were subjected to analysis of variance (ANOVA) and, when the means were significant, they were analyzed through regression analysis. All procedures were carried out in the R program (R development core team, 2019).

**Results and Discussion**

The salt stress simulated by NaCl affected the water relations and accumulation of organic solutes in *Physalis angulata* plants (Figure 2). Plants of all saline treatments presented lower leaf water potentials than those of the Control (EC = 0.0 dS $m^{-1}$) (Figure 2A). The more negative leaf water potentials were found for the electrical conductivities (EC) of 5.4 dS $m^{-1}$ (-1.05 MPa) and 7.2 dS $m^{-1}$ (-1.21 MPa). The leaf water potentials and organic solutes showed that the plants maintained their hydration, although at lower levels, through mechanisms that avoid water loss, even when they were subjected to the highest salinity level. This was shown by the data of water potential, stomatal conductance, and transpiration; moreover, the results showed higher organic solute accumulation in leaf tissues in this treatment.

According to Benzarti et al. (2014), species that present tolerance to salt prevent salt deleterious effects by decreasing the osmotic potential, which decreases the leaf water potential and increases water flow inside the plant; this responses of plants to maintain their water status require the maintenance of their physiological processes, as found in the present work. Similar results were found by Coelho et al. (2013) for *Vigna* sp. and by Silva et al. (2016) for *Cocos nucifera*, who reported that high-salinity treatments decreased the leaf water potential.

The leaf succulence of the *P. angulata* plants increased linearly as the salinity of the nutrient solution was increased (Figure 2B); plants under EC of 7.2 dS $m^{-1}$ showed leaf succulence 24.05% (0.0144 g $H_2O$ $cm^{-2}$) higher than Control plants. This indicates a possible osmotic adjustment of the plants (Martínez et al., 2004), which regulates salt contents in the leaves (Trindade et al., 2006). Lima et al. (2019) found similar results for cotton plants in a high-salinity environment.

The contents of leaf total soluble sugars and saccharose increased as the salinity of the nutrient solution was increased (Figure 2C and 2D). The lowest values were found for Control plants, followed by plants under EC of 1.8 and 3.6 dS $m^{-1}$. Some plant species under

salt stress conditions produce and accumulate organic solutes inside their cells as a strategy for their survival (Silva et al., 2017). Plants under EC of 7.2 dS $m^{-1}$ had higher soluble sugars and saccharose contents, probably due to osmoregulation, since their water status was maintained. These organic solute accumulations assist in maintaining a water potential gradient in the plant, thus favoring absorption and transport of water, directing it to the shoot, even when the plant is subjected to a high salinity level (Bosco et al., 2009).

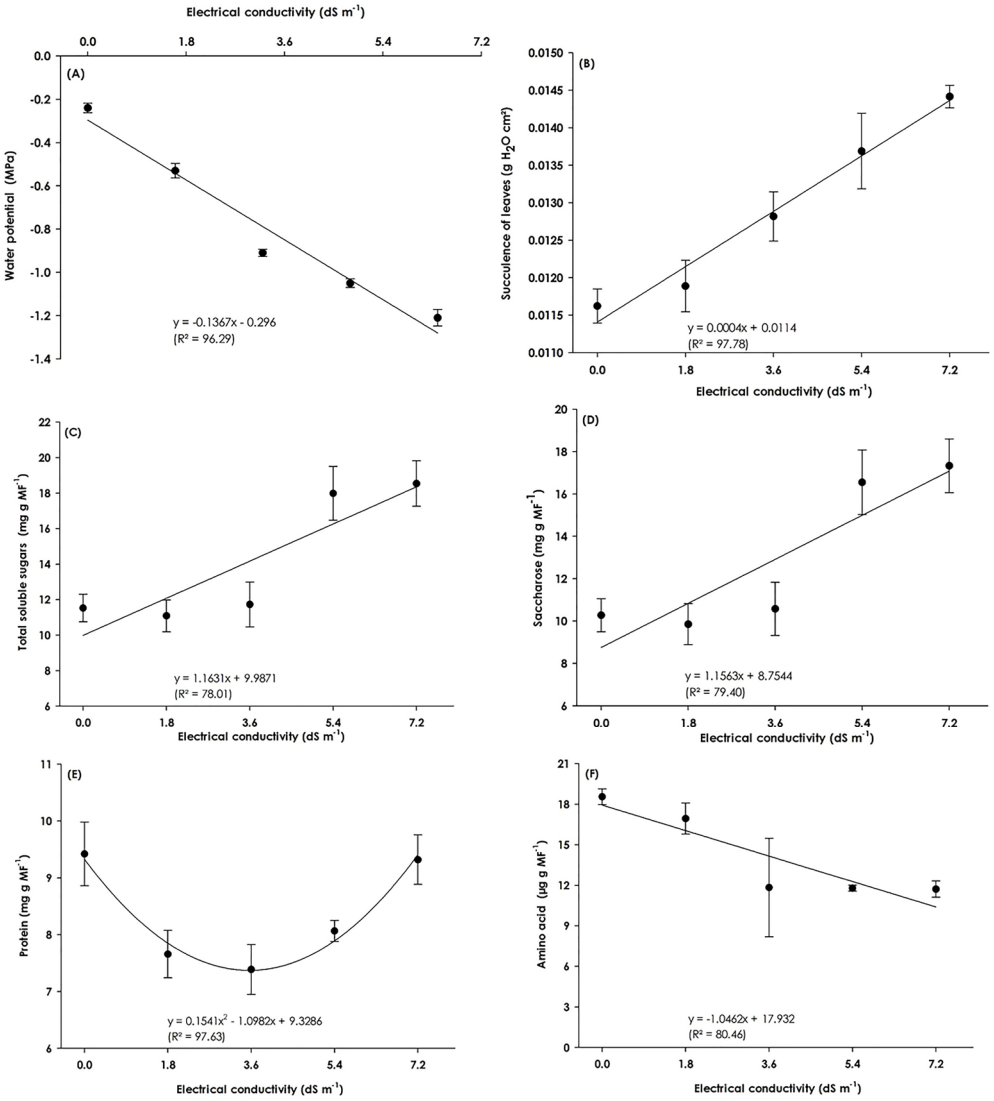


**Figure 2.** Water relations and organic solutes in leaves of *Physalis angulata* plants under salt stress: water potential (A), succulence (B), total soluble sugars (C), saccharose (D), protein (E) and amino acid (F).

The leaf soluble protein contents in plants under EC of up to 3.56 dS $m^{-1}$ (20.99%) were lower than those of Control plants; however, protein contents increased up to the highest salinity level (7.2 dS $m^{-1}$) and were close to those of Control plants, presenting a decrease of only 1.06% (Figure 2E).

Despite the increase in proteolysis in plants under EC of 1.8 and 3.6 dS $m^{-1}$, the protein concentration in plants of the treatment with EC of 7.2 dS $m^{-1}$ was high probably because of increases in synthesis of proteins caused by salt stress (Forsyth & Shewry, 2002). The synthesis of proteins tends to increase when plants are grown under high salinity levels (Pedranzani et al., 2003) because some proteins contribute to plant tolerance to salt stress (Mohammadkhani & Heidari, 2008).

The proteolytic degradation of proteins up to the EC of 3.56 dS $m^{-1}$ increased total free amino acid contents, which decreased at EC of 7.2 dS $m^{-1}$. Despite total free amino acid contents presented no significant differences, they presented a trend of low values for plants under the highest salinity levels (Figure 2F).

The photosynthetic rates were lower in plants under EC above 2.12 dS $m^{-1}$ (Figure 3A), which were 20.63% (11.62 µmol $CO_2$ $m^{-2}$ $s^{-1}$) lower in plants under 7.2 dS $m^{-1}$ when compared to Control plants (14.64 µmol $CO_2$ $m^{-2}$ $s^{-1}$). However, the photosynthetic rate of plants under

EC of 2.12 dS $m^{-1}$ was 6.34% (15.58 µmol $CO_2$ $m^{-2}$ $s^{-1}$) higher than that of Control plants. Stomatal conductance was significantly affected by the saline treatments (Figures 3B); plants grown under salt stress presented higher stomatal conductance under the estimated EC of 2.0 dS $m^{-1}$ (331.32 mmol $H_2O$ $m^{-2}$ $s^{-1}$). However, plants under EC of 7.2 dS $m^{-1}$ had 45.33% lower stomatal conductance than Control plants. The toxicity of sodium ($Na^+$) and chloride ($Cl^-$) ions decreases the growth and development of plants (Modesto et al., 2019) due to negative effects on their photosynthetic rate, stomatal opening, transpiration, and water use efficiency, causing pronounced decreases in photosynthesis (Acosta-Motos et al., 2017).

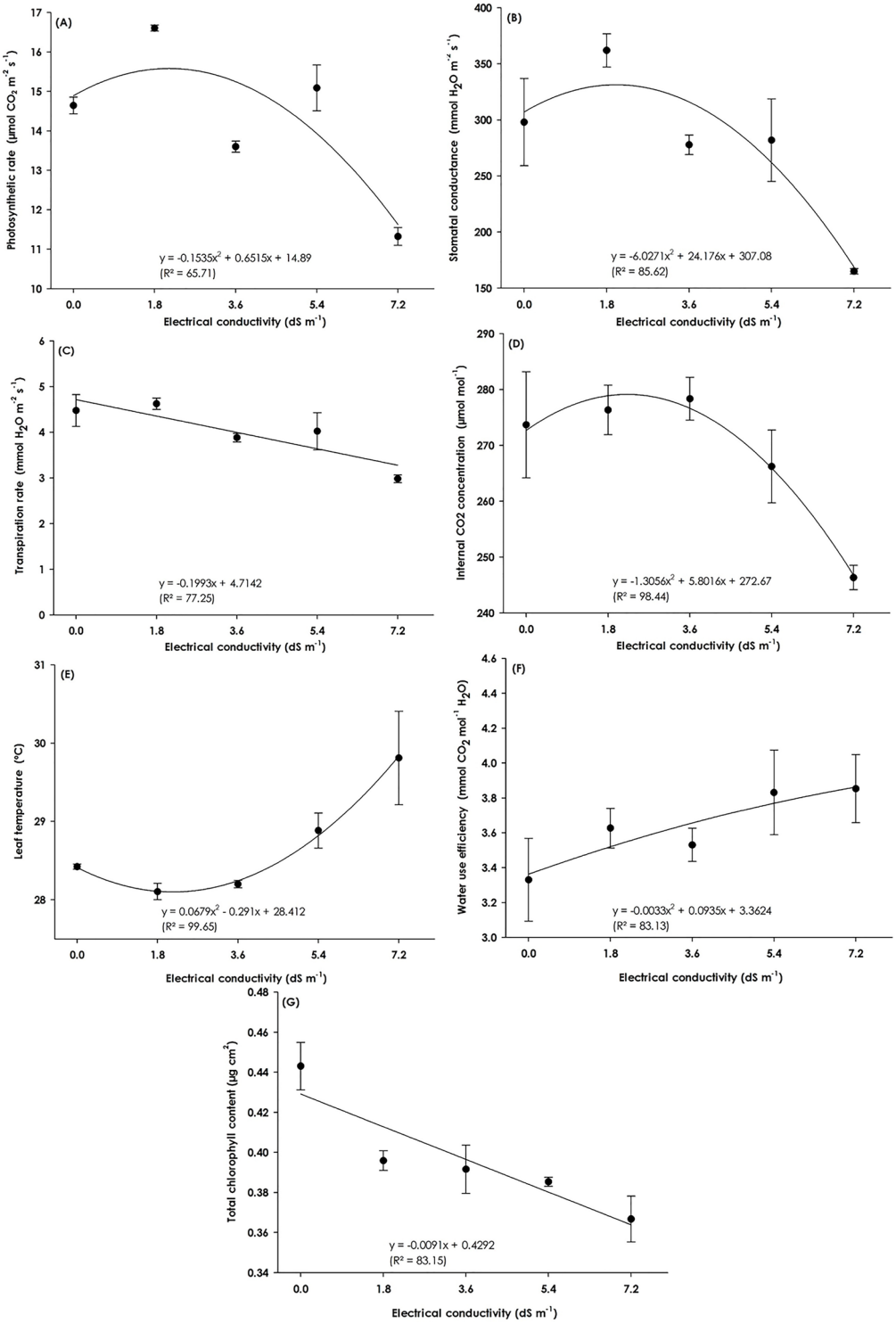


**Figure 3.** Gas exchange and chlorophyll content in leaves of *Physalis angulata* plants under salt stress: photosynthetic rate (A), stomatal conductance (B) transpiration rate (C), internal $CO_2$ concentration (D), leaf temperature (E), water use efficiency (F) and total chlorophyll content (G).

According to Dias et al. (2018), the salinity of the irrigation water decreased the gas exchange of *Sesamum indicum* plants. According to Leite et al. (2017), salt stress hinders the plant's capacity to absorb water, thus, the plant limits its stomatal opening to reduce water loss. Decreases in photosynthesis in plants under salt stress are related to stomatal closure, which occurs under high EC (5.4 and 7.2 dS $m^{-1}$), and due to limitations in $CO_2$ flow to the carboxylation site (Bosco et al., 2009).

The transpiration rates were up to 33.33% lower than that of Control plants (Figure 3C), which may be related to the stomatal closure. According to Lima et al. (2010), the transpiration demand is determined by the stomatal dynamics, which controls the loss of water to the environment as vapor.

Internal $CO_2$ concentration in plants under EC of 2.2 dS $m^{-1}$ was higher than that of Control plants; however, it was 9.50% lower in plants under EC of 7.2 dS $m^{-1}$ (Figure 3D). Internal $CO_2$ concentration is commonly related to the stomatal dynamics, since stomatal closure hinders $CO_2$ influx and, consequently, decreases its concentration in the substomatal chamber (Silva et al., 2011; Prazeres et al., 2015). Thus, stomatal closure is the most important physiological mechanism for plants under salt stress (Sousa et al., 2014; Brito et al., 2016). Decreases in stomatal conductance and photosynthetic efficiency caused by high salinity levels had been found for melon (Morais et al., 2018) and cassava (Cruz et al., 2017) crops.

The leaf temperature of plants under EC of 7.2 dS $m^{-1}$ increased by 1.39 °C (Figure 3E); however, it decreased up to the EC of 2.14 dS $m^{-1}$ when compared to Control plants. Increases in leaf temperature in *P. angulata* plants can be related to their transpiration, which is the main leaf temperature regulator mechanism; this is due to the stomatal closure and a subsequent decrease of transpiration, which increases leaf temperature (Machado et al., 2005). Despite the water use efficiency of plants under the highest salinity levels were 8.18% (EC of 1.8) and 13.58 (EC 7.2 dS $m^{-1}$) higher than that of Control plants (Figure 3F), no statistical differences were found.

Total chlorophyll content in plants under salt stress decreased, mainly in plants under EC of 7.2 dS $m^{-1}$, which showed 0.36 µg $cm^2$ (Figure 3G). This decrease may represent a plant defense mechanism, which decreases the capture of light for a lower electron flow in the electron transport chain, decreasing the production of reactive oxygen species (Brosché et al., 2010). Decreases in chlorophyll contents in plants under high salinity levels had also been reported for other species (Aras & Esitken, 2019; Rezende et al., 2018; Silva et al., 2016).

The height of plants under high salinity levels decreased. Plants under EC of 7.2 dS $m^{-1}$ had 21.09% lower height than Control plants. However, the height of plants under EC of 1.8 dS $m^{-1}$ were higher than that of Control plants (Figure 4A), since the photosynthetic rates also increased under this EC.

This benefic effect can also be due to the $Na^+$ concentration, since this ion may substitute potassium in some functions in the plants (Marschner, 2011), such as osmoregulation, nutrient absorption, and stomatal opening and closure (Korndorfer, 2006). However, the plant growth was negatively affected by the other salt concentrations, since the use of high salinity levels decreases the osmotic potential of the nutrient solution and the water absorption and possibly causes toxicity by $Na^+$ and $Cl^-$ ions (Coelho et al., 2013).

The salinity levels showed a linear decrease in leaf area of *P. angulata* plants; plants under EC of 7.2 dS $m^{-1}$ had 59.64% lower leaf area than Control plants (Figure 4B). Decrease in leaf area is one of the first responses of plants to salt stress, since leaf abscission minimizes the transpiration surface and favors the maintenance of the water potential in the plant (Dantas et al., 2003). However, this adaptive mechanism tends to reduce the plant's capacity to produce photoassimilates, limiting plant growth and yield, as shown by the results of the present study.

The shoot, root, and total dry weights showed similar dynamics, remaining high up to the EC of 3.6 dS $m^{-1}$ (Figure 4C and 4D), presenting 7.75% higher total dry weight under EC of 1.86 dS $m^{-1}$ when compared to Control plants. Gas exchange also had similar dynamics (Figure 3), indicating the tolerance of *P. angulata* to this adverse condition.

The increase in salinity levels showed pronounced decreases in total phytomass accumulation in *P. angulata* plants. The lowest mean of total phytomass accumulation (13.49 g) was found for plants under EC of 7.2 dS $m^{-1}$, which was 61.81% lower than that of Control plants (Figure 4E). This decrease was due to nutritional and physiological imbalances caused by the high salinity levels, which affect the conversion of carbon accumulated by plants and, consequently, decrease the plant phytomass (Taiz et al., 2017). Similar results had been found in several studies with other crops, such as cassava (Cruz et al., 2017), peanut (Sá et al., 2020), and rocket (Dias et al., 2019).

*P. angulata* plants were classified as tolerant to effects of high salinity levels of the water (nutrient solution) up to the EC of 1.8 dS $m^{-1}$; moderately tolerant up to 5.4

dS $m^{-1}$; and susceptible to EC of 7.2 dS $m^{-1}$, considering the analysis of the tolerance of these plants to salt stress based on plant dry weight (Figure 4F), according to Fageria et al. (2010) and Moura et al. (2016). According to Ayers & Westcot (1999), moderately tolerant plants tend to grow and develop in salinity levels between 0.77 and 3.0 dS $m^{-1}$; however, the present study showed that *P. angulata* plants present moderate tolerance to higher EC levels.

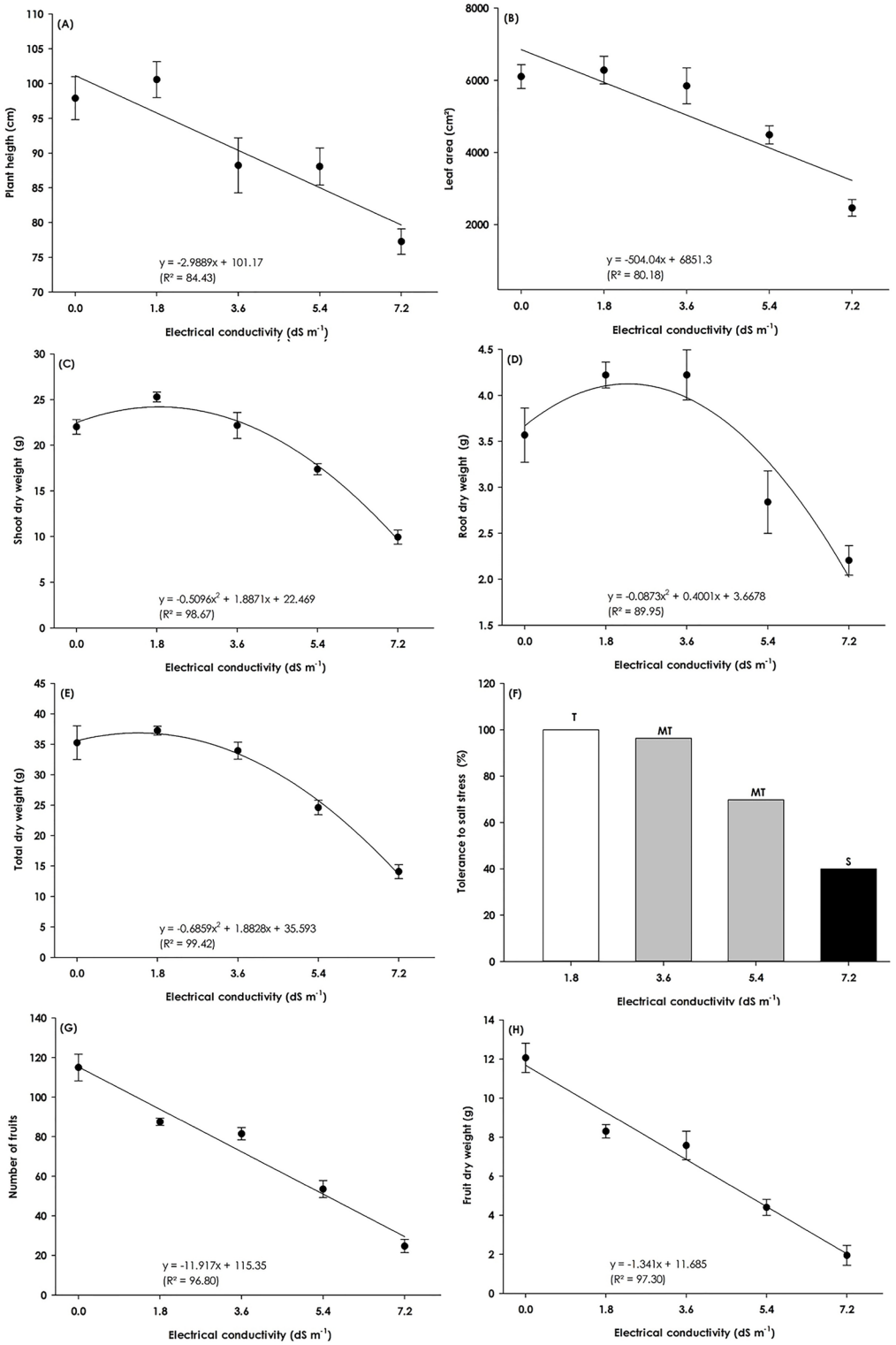


**Figure 4.** Growth and tolerance to salt stress of *P. angulata* plants under salt stress: plant height (A), leaf area (B), shoot dry weight (C), root dry weight (D), total dry weight (E), tolerance to salt stress (T = tolerant, MT = moderately tolerant, S = susceptible) (F), number of fruits (G) and fruit dry weight (H).

Despite the decreases in water potential and increases in accumulation of organic solutes, the osmoregulation in plants occurred only for the maintenance of the water status and survival of the plants, since the number of fruits and fruit dry weight of plants under the highest EC (5.4 and 7.2 dS $m^{-1}$) were significantly lower than those of Control plants. Therefore, the fruit production is compromised when *P. angulata* plants are subjected to nutrient solutions with high salt concentrations. Similar results were found for *Morinda citrifolia* plants (noni) (Souto et al., 2015) and *Lycopersicon esculentum* plants (cherry tomato) (Guedes et al., 2015).

**Conclusions**

The use of nutrient solutions with high salinity levels decreases the photosynthetic rate, stomatal conductance, transpiration rates, and internal $CO_2$ concentration in *Physalis angulata* plants. In addition, it increases sugars and saccharose contents in the plants, which present efficient osmoregulation up to the salinity level equivalent to an electrical conductivity of 5.4 dS $m^{-1}$, maintaining the plant water status.

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**References**

Acosta-Motos, J.R., Ortuño, M.F., Bernal-Vicente, A., Diaz-Vivancos, P., Sanchez-Blanco, M.J., Hernandez, J.A. 2017. Plant Responses to Salt Stress: Adaptive Mechanisms. *Agronomy* 7: 1-38.

Aquino, J.P.A., Bezerra, A.A.C., Alcântara Neto, F.A., Lima, C.J.G.S., Sousa, R.R. 2017. Morphophysiological responses of cowpea genotypes to irrigation water salinity. *Revista Caatinga* 30: 1001-1008.

Aras, S., Esitken, A. 2019. Responses of Apple Plants to Salinity Stress. Yüzüncü Yıl University. *Journal of Agricultural Science* 29: 253-257.

Araujo, E.B.G., Sá, F.V.S., Oliveira, F.A., Souto, L.S., Paiva, E.P., Silva, M.K.N., Mesquita, E.F., Brito, M.E.B. 2016. Crescimento inicial e tolerância de cultivares de meloeiro à salinidade. *Revista Ambiente e Água* 11: 462-471.

Ayers, R.S., Westcot, D.W. 1999. *A qualidade da água na agricultura*. 2. ed. UFPB, Campina Grande, Brazil. 153 p.

Benzarti, M., Rejeb, K.B., Messedi, D., Mna, A.B., Hessini, K., Ksontini, M., Abdelly, C., Debez, A. 2014. Effect of high salinity on *Atriplex portulacoides*: Growth, leaf water relations and solute accumulation in relation with osmotic adjustment. *South African Journal of Botany* 95: 70-77.

Bosco, M.R.O., Oliveira, A.B., Hernandez, F.F.F., Lacerda, C.F. 2009. Efeito do NaCl sobre o crescimento, fotossíntese e relações hídricas de plantas de berinjela. *Revista Ceres* 56: 296-302.

Bradford, M.M. 1976. A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry* 72: 248-254.

Brito, M.E.B., Sá, F.V.S., Soares Filho, W.S., Silva, L.A., Fernandes, P.D. 2016. Gas exchange and fluorescence of citrus rootstocks varieties under saline stress. *Revista Brasileira de Fruticultura* 38: 1-8.

Brosché, M., Overmyer, K., Wrzaczek, M., Kangasjarvi, J. 2010. Stress Signaling III: Reactive Oxygen Species (ROS). In: Pareek, A., Sopory, S.K., Bohnert, H., Govindjee (eds.) *Abiotic Stress Adaptation in Plants: Phisiological, Molecular and Genomic Foundation*. Springer, Dordrecht, Holanda. p. 91-102.

Coelho, J.B.M., Barros, M.F., Neto, E.B., Correa, M.M. 2013. Comportamento hídrico e crescimento do feijão *Vigna* cultivado em solos salinizados. *Revista Brasileira de Engenharia Agrícola e Ambiental* 17: 379-385.

Cruz, J.L., Filho, M.A.C., Coelho, E.F., Santos, A.A. 2017. Salinity reduces carbon assimilation and the harvest index of cassava plants (*Manihot esculenta* Crantz). *Acta Scientiarum Agronomy* 39: 545-555.

Silva, E.C.A., Lucena, P.G.C., Nascimento, R.M., Santos, C.A., Araújo, R.P.S., Nogueira, R.J. M.C. 2017. Mecanismos bioquímicos em *Moringa oleifera* Lam. para tolerância à salinidade. *Acta Iguazu* 6: 54-71.

Dantas, J.P., Ferreira, M.M.M., Marinho, F.J.L., Amorim Nunes, M.S., Queiroz, M.F., Santos, T.A. 2003. Efeito do estresse salino sobre a germinação e produção de sementes de caupi. *Revista Agropecuária Técnica* 24: 119-130.

Dias, A.S., Lima, G.S., Gheyi, H.T., Nobre, R.G., Fernandes, P.D., Silva, F.A. 2018. Trocas gasosas e eficiência fotoquímica do gergelim sob estresse salino e adubação com nitrato-amônio. *Irriga* 23: 220-234.

Dias, M.S., Reis, L.S., Santos, R.H.S., Almeida, C.A.C., Paes, R.A., Albuquerque, A.W., Silva, F.A. 2019. Crescimento de plantas de rúcula em substratos e níveis de salinidade da água de Irrigação. *Colloquium Agrariae* 15: 22-30.

Dias, N.S., Blanco, F.F. 2010. Efeitos dos sais no solo e na planta. In: Gheyi, H.R., Dias, N.S., Lacerda, C.F. *Manejo da salinidade na agricultura: estudos básicos e aplicados*. INCT sal, Fortaleza, Brazil. p. 129-141.

Fageria, N.K., Soares Filho W.S., Gheyi, H.R. 2010. Melhoramento genético vegetal e seleção de cultivares tolerantes à salinidade. In: Gheyi, H.R, Dias, N.S, Lacerda, C.F. *Manejo da salinidade na agricultura: estudos básicos e aplicados*. INCT Sal, Fortaleza, Brazil. p. 205-216.

Flowers, T.J. 2004. Improving crop salt tolerance. *Journal of Experimental Botany* 55: 307-319.

Forsyth, J.L, Shewry, P.R. 2002. Characterization of the major proteins of tubers of yam bean (*Pachyrhizus ahipa*). *Journal of agricultural and Food Chemistry* 50:1939-1944.

Freitas, T.A. 2004. Influência do substrato e da luminosidade na germinação, crescimento e caracterização físico-química do fruto de camapú (*Physalis angulata* L.) (M.Sc. Thesis) – State University of Feira de Santana, Feira de Santana, Brasil.

Guedes, R.A.A., Oliveira, F.A., Alves, R.C., Medeiros, A.S., Gomes, L.P., Costa, L.P. 2015. Estratégias de irrigação com água salina no tomateiro cereja em ambiente protegido. *Revista Brasileira de Engenharia Agrícola e Ambiental* 19: 913-919.

Korndorfer, G.H. 2006. Elementos benéficos. In: Fernandes, M.S. *Nutrição mineral de plantas*. Sociedade Brasileira de Ciência do Solo, Viçosa, Brazil. p. 355-374.

Leite, J.V.Q., Fernandes, P.D., Oliveira, W.J., Souza, E.R., Santos, D.P., Santos, C.S. 2017. Efeito do estresse salino e da composição iônica da água de irrigação sobre variáveis morfofisiológicas do feijão-caupi. *Revista Brasileira de Agricultura Irrigada* 11: 1825-1833.

Lima, M.A., Bezerra, M.A., Gomes Filho, E., Pinto, C.M., Enéas Filho, J. 2010. Trocas gasosas em folhas de sol e sombreadas de cajueiro anão em diferentes regimes hídricos. *Revista Ciência Agronômica* 41: 654-663.

Lima, M.S., Evangelista, A.F., Santos, G.G.L., Ribeiro, I.M., Tomassini, T.C.B., Soares, M.B.P., Villarreal, C.F. 2014. Antinociceptive Properties of Physalins from *Physalis angulata*. *Journal of Natural Products* 77: 2397-2403.

Lima, G.S., Dias, A.D., Soares, L.A., Gheyi, R.G.N., Silva, A.A.R. 2019. Eficiência fotoquímica, partição de fotoassimilados e produção do algodoeiro sob estresse salino e adubação nitrogenada. *Revista de Ciências Agrárias* 42: 214-225.

Lorenzi, H., Matos, F.J.A. 2008. *Plantas medicinais no Brasil: nativas e exóticas cultivadas.* Instituto Plantarum, Nova Odessa, Brazil. 576 p.

Machado, E.C., Schmidt, P.T., Medina, C.L., Ribeiro, R.V. 2005. Respostas da fotossíntese de três espécies de citros a fatores ambientais. *Pesquisa Agropecuária Brasileira* 40: 1161-1170.

Maciel, K.S., Lopes, J.C., Mauri, J. 2012. Germinação de sementes e vigor de plântulas de brócolis submetidas ao estresse salino com NaCl. *Nucleus* 9: 221-228.

Mantovani, A. 1999. A method to improve leaf succulence quantification. *Brazilian Archives of Biology and Technology* 42: 9-14.

Marschner, P. 2011. *Marschner's Mineral nutrition of higher Plants*. Academic Press, Amsterdam, Netherlands. 672 p.

Martínez, J.P., Lutts, S., Schanck, A., Bajji, M., Kinet, J.M. 2004. Is osmotic adjustment required for water stress resistance in the Mediterranean shrub *Atriplex halimus* L. *Journal of Plant Physiology* 161: 1041-1051.

Meira, C.S., Guimarães, E.T., Bastos, T.M., Moreira, D.R.M., Tomassini, T.C.B., Ribeiro, I.M., Ribeiro-dos-Santos, R., Soares, M.B.P. 2013. Physalins B and F, seco-steroids isolated from *Physalis angulata* L., strongly inhibit proliferation, ultrastructure and in fectivity of *Trypanosoma cruzi*. *Parasitology* 140: 1811-1821.

Miller, G.L. 1959. Use of dinitrosalicylic acid reagent for determination of reducing sugar. *Analytical Biochemistry* 31: 426-428.

Modesto, F.J.N., Santos, M.A.C.M., Soares, T.M., Santos, E.P.M. 2019. Crescimento, Produção e Consumo Hídrico do Quiabeiro Submetido à Salinidade em Condições Hidropônicas. *Irriga* 24: 86-97.

Mohammadkhani, N., Heidari, R. 2008. Effects of Drought Stress on Soluble Proteins in two Maize Varieties. *Turk Journal Biology* 32: 23-30.

Morais, P.L.D., Dias, N.S., Oliveira, A.M., Sousa Neto, O.N., Sarmento, J.D.A., Silva, M. I. 2018. Effects of Nutrient Solution Salinity on The physiological performance of Melon Cultivated in Coconut fiber**.** *Revista Caatinga* 31: 713-718.

Moura, R.S., Gheyi, H.R., Coelho Filho, M.A., Jesus, O.N., Sá, F.V.S., Lima, L.K. 2016. Tolerance of passion fruit species under salt stress. *International Journal of Current Research* 8: 37689-37695.

Oliveira, C.E.S., Steiner, F., Zuffo, A.M., Zoz, T., Alves, C.Z., Aguiar, V.C.B. 2019. Seed priming improves the germination and growth rate of melon seedlings under saline stress. *Ciência Rural* 49: 01-07.

Pedranzani, H., Racagni, G., Alemano, S., Miersch, O., Ramírez, I., Pena-Cortés, H., Taleisnik, E., Machado-Domenech, E., Abdala, G. 2003. Salt tolerant tomato plants show increased levels of jasmonic acid. *Plant Growth Regulation* 41: 149-158.

Prazeres, S.S., Lacerda, C.F., Barbosa, F.E.L., Amorim, A.V., Araujo, I.C.S., Cavalcante, L.F. 2015. Crescimento e trocas gasosas de plantas de feijão-caupi sob irrigação salina e doses de potássio. *Revista Agro@mbiente On-line* 9: 111-118.

R Development Core Team. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing. 2019. https://www.R-project.org/ <Access on 10 Jan. 2020>

Rengifo, E., Vargas, G. 2013. *Physalis angulata* L. (Bolsa Mullaca): a review of its traditional uses, chemistry and pharmacology. *Boletín Latinoamericano y del Caribe de Plantas Medicinales y Aromáticas* 12: 31-445.

Rezende, R.A.L.S., Rodrigues, F.A., Soares, J.D.R., Silveira, H.R.O., Pasqual, M., Dias, G.M.G. 2018. Salt stress and exogenous silicon influence physiological and anatomical features of in vitro-grown cape gooseberry. *Ciência Rural* 48: 01-09.

Sá, F.V.S., Paiva, E.P., Mesquita, E.F., Bertino, A.M.P., Barbosa, M.A., Souto, L.S. 2016. Tolerance of castor bean cultivars under salt stress. *Revista Brasileira de Engenharia Agrícola e Ambiental* 20: 557-563.

Sá, F.V.S., Santos, M.G., Júnior, A.P.B., Albuquerque, J.R.T., Souza, A.R.E., Pinheiro, R.M.P. 2020. Tolerance of peanut (*Arachis hypogea*) genotypes to salt stress in the initial phase. *Revista Brasileira de Engenharia Agrícola e Ambiental* 24: 37-43.

Sarruge, J.R. 1975. Soluções nutritivas. *Summna Phytopathologica* 1: 231-233.

Silva, E.N., Ribeiro, R.V., Ferreira-Silva, S.L., Viégas, R.A., Silveira, J.A.G. 2011. Salt stress induced damages on the photosynthesis of physic nut young plants. *Scientia Agricola* 68: 62-68.

Silva, A.R.A., Bezerra, F.M.L., Lacerda, C.F., Sousa, C.H., Chagas, K.L. 2016. Pigmentos fotossintéticos e potencial hídrico foliar em plantas jovens de coqueiro sob estresses hídrico e salino. *Revista Agro@mbiente On-line* 10: 317-325.

Silveira, J.A.G., Araújo, S.A.M., Lima, J.P.M.S., Viégas, R.A. 2009. Roots and leaves display contrasting osmotic adjustment mechanisms in response to NaCl salinity in *Atriplex numularia*. *Environmental and Experimental Botany* 66: 01-08.

Sisley, G.M.M., Horna, F.Y.M., Isern, F.R., Aranda-Ventura, J., Vallejo, J.V. 2017. Actividaed inmunoestimulante del extracto acuoso liofilizado de la planta entera de *Physalis angulata* L. em ratas albinas cepa Holtzman. *Revista Peruana de Medicina Integrativa* 2: 38-46.

Souto, A.G.L., Cavalcante, L.F., Diniz, B.L.M.T., Mesquita, F.O., Nascimento, J.A.M., Lima Neto, A.J. 2015. Água salina e biofertilizante bovino na produção de frutos e alocação de biomassa em noni (*Morinda citrifolia* L.). *Revista Brasileira de Plantas Medicinais* 17: 340-349.

Sousa, G.G., Viana, T.V.A., Lacerda, C.F., Azevedo, B.M., Silva, G.L., Costa, F.R.B. 2014. Estresse salino em plantas de feijão-caupi em solo com fertilizantes orgânicos. *Revista Agro@mbiente On-line* 8: 359-367.

Souza, R.P., Machado, E.C., Silveira, J.A.G., Ribeiro, R.V. 2011. Fotossíntese e acúmulo de solutos em feijoeiro caupi submetido à salinidade. *Pesquisa agropecuária brasileira* 46: 586-592.

Souza, N.K., Alcântara-Júnior, J.P., Amorim, S.M.C. 2007. Efeito do estresse salino sobre a produção de fitomassa em *Physalis angulata* L. (Solanaceae). *Revista Acadêmica Curitiba* 5: 379-384.

Taiz, L., Zeiger, E., Moller, I.M., Murphy, A. 2017. *Fisiologia e Desenvolvimento Vegetal*. Artmed, Porto Alegre, Brazil. 858 p.

Trindade, A.R., Lacerda, C.F., Gomes Filho, E., Prisco, J.T., Bezerra, M.A. 2006. Influência do acúmulo e distribuição de íons sobre a aclimatação de plantas de sorgo e feijão-de-corda, ao estresse salino. *Revista Brasileira de Engenharia Agrícola e Ambiental* 10: 804-810.

Vargas-Ponce, O., Martínez, J.S., Tavares, M.P.Z., Mares, L.E.V. 2016. Traditional management of a small-scale crop of *Physalis angulata* in Western Mexico. *Genetic Resources and Crop Evolution* 63: 1383-1395.

Verslues, P.E., Bray, E.A. 2004. LWR1 and LWR2 are required for osmoregulation and osmotic adjustment in *Arabidopsis thaliana*. *Plant Physiology* 136: 2831-2842.

Ventura, K.M., Alves, D.A.S, Filho, H.G., Román, R.M.S. 2019. Tolerância de híbridos de pepino à níveis de salinidade em ambiente protegido. *Revista Brasileira de Agricultura Irrigada* 13: 3783-3791.

Wellburn, A.R. 1994. The spectral determination of chlorophyll a and b, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *Journal of Plant Physiology* 144: 307-313.

Yemm, E.W., Coccking, E.C. 1955. The determination of amino acid with ninhydrin. *Analyst* 80: 209-213.

Yemm, E.W., Willis, A.J. 1954. The estimation of carbohydrates in plant extracts by anthrone. *The Biochemical Journal* 57: 508-514.

Zamora-Tavares, M.P., Vargas-Ponce, O., Sánchez-Martinez, J., Cabrera-Toledo, D. 2015. Diversity and genetic structure of the husk tomato (*Physalis philadelphica* Lam.) in Western Mexico. *Genetic Resources and Crop Evolution* 62:141-162.

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