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Physiological changes of bell pepper grown under nutrient solutions prepared with brackish water and H_2O_2 concentrations

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Abstract

Adopting strategies to mitigate the negative effects of salt excess in irrigation water is essential to maintain production systems, especially in semi-arid regions. From this perspective, this study aimed to evaluate the gas exchange and photosynthetic pigments of hydroponic bell pepper grown under different water combinations (brackish water and rainwater) and foliar application of hydrogen peroxide (H_2O_2). The study was conducted in a protected environment at the Agricultural Engineering Academic Unit of the Federal University of Campina Grande, Brazil. The experiment was set up in a completely randomized design with 12 treatments and a 4 x 3 factorial arrangement with five replications, each consisting of four brackish water and rainwater combinations (10%/90%; 20%/80%; 30%/70%;40%/60%) and three H_2O_2 concentrations: 0.0 (control), 7.5 µM, and 15 µM supplied via foliar application every seven days starting 42 days after sowing (DAS). The application of 15.0 µM of H_2O_2 in bell pepper plants grown with the nutrient solution containing the 30%/70% and 40%/60% combinations between brackish water and rainwater increased photosynthesis 24 days after sowing and increased stress 61 days after sowing. After 61 DAS, the highest *gs* and *E* values of bell pepper grown with the nutrient solution at the electrical conductivity of 2.72 dS m^{-1} (10%/90%) were obtained by applying 15.0 µM of H_2O_2. The contents of chlorophyll "a", "b", total chlorophyll, and carotenoids of bell pepper plants showed deleterious effects caused by the salinity of the nutrient solution, mitigated by the exogenous application of 15 µM hydrogen peroxide.

Keywords: *Capsicum annuum* L., hydrogen peroxide, photosynthesis, salt stress

Introduction

The growing food demand due to the increasing worldwide population has promoted significant challenges to agriculture, which faces a serious problem with the shortage of water resources in both quantitative and qualitative aspects. This problem is aggravated in arid and semi-arid regions, such as the Northeast region of Brazil. According to Genhua & Raul (2010) and Alados et al. (2011), the water available in that region shows salinity levels ranging from 0.1 to 5.0 dS m^{-1}. However, rational and proper water management could eventually allow using those water sources.

In this scenario, several studies (Paulus et al., 2010; Paulus et al., 2012; Cavalcante et al., 2019) have been conducted aiming to investigate mechanisms to allow using brackish water in agricultural production, not only to optimize the available water resources, which are limited, but also as a means of environmental preservation, especially in hydroponic systems. According to Guimarães et al. (2017), tolerance to salinity in plants grown in hydroponic systems is higher than in conventional planting since the matric potential is insignificant in the former, facilitating water uptake by plants.

Under stressful conditions, the gas exchange properties are negatively affected due to the lower CO_2 absorption from the atmosphere, consequently reducing photosynthesis (Bezerra et al., 2018). Furthermore, reactive oxygen species (ROS) are produced when plants are grown under high salinity levels, potentially characterizing oxidative stress. However, reactive species also play a cell signaling role under stress conditions, favoring the acclimation process, an alternative to increase plant survival under adverse conditions.

Acclimation refers to the process in which an individual is previously exposed to a given stress, favoring metabolic changes that increase its tolerance to new

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stress exposure. When the first exposure is performed with a different stress source from the second one (definitive stress), acclimation is said to have induced cross-tolerance (Neill et al., 2002). From this perspective, Andrade (2013) stressed that H_2O_2 is the most appropriate molecule for acclimation purposes due to its long half-life, high stability, and ability to diffuse through cell membranes freely.

The treatment with low H_2O_2 concentrations has stood out in plant acclimation to salt stress. According to Silva et al. (2019), foliar H_2O_2 application at the concentrations of 25 and 50 μM mitigates the deleterious effects of salt stress on stomatal conductance and CO_2 assimilation in soursop.

Bell pepper (*Capsicum annuum*) stands out among the vegetable crops grown in Brazil. This crop is cultivated in virtually the entire national territory, and 87% of the national bell pepper production in 2017 was concentrated in the states of São Paulo, Minas Gerais, Ceará, Rio de Janeiro, Espírito Santo, and Pernambuco (Cepea, 2017). However, bell pepper cultivation in the semi-arid region of northeastern Brazil is performed by smallholder farmers using water sources inappropriate for agricultural use due to salt excess, requiring technologies to minimize the negative effects of irrigation water salinity on the production of crops with such social and economic importance (Cosme et al., 2011).

From this perspective, hydroponic cultivation emerges as an alternative to optimize and facilitate the use of water resources available in the region, including high-salinity water. Allied to that, the mixture of different waters can mitigate the deleterious effect of salinity (Soares et al., 2010) and even allow using brackish water along with hydrogen peroxide (H_2O_2).

In this scenario, this study aimed to evaluate the gas exchange and photosynthetic pigments of bell pepper grown under hydroponic cultivation and different combinations of irrigation water (brackish water and rainwater) and foliar H_2O_2.

Material and Methods

The experiment was developed in a protected environment from November 2017 to March 2018 at the Agricultural Engineering Academic Unit of the Center of Technology and Natural Resources (CTRN) of the Federal University of Campina Grande (UFCG), Brazil, located at the following coordinates: 7° 12' 52" S and 35° 54' 24" W, at an elevation of 550 m.

The experimental design adopted was completely randomized and arranged in a 4 x 3 factorial with five replications and three usable plants per replicate, with treatments consisting of a mixture between brackish water (BW) and rainwater (RW), resulting in 4 combinations: C1 = 10% BW + 90% RW; C2 = 20% BW + 80% RW; C3 = 30%BW + 70%RW; C4 = 40%BW + 60%RW) and three hydrogen peroxide concentrations (H_2O_2) [0.0 (control), 7.5 μM, and 15 μM] supplied via foliar application every seven days starting 42 days after sowing (DAS) until 63 DAS (flowering stage), resulting in 12 treatments and 60 experimental units. The H_2O_2 solutions were prepared using a 1 mmol L^{-1} H_2O_2 solution based on molecular weight until reaching the desired concentrations. Dilution was performed using deionized water.

The brackish water used to prepare the nutrient solution came from the community weir of the Vitória Settlement (7°20'47.49" S and 36° 2"28.00" W), collected after six months with no rainfall evens, and having the following physicochemical characteristics (Embrapa, 2011): pH (8.24), EC (29.15 dS m^{-1}), K (0.012 g L^{-1}), Na (5.50 g L^{-1}), Ca (0.41 g L^{-1}), Mg (1.2 g L^{-1}), and SAR of 30.74 (mmol L^{-1})$^{0.5}$. In order to allow the use of brackish water, this water source (Lacerda et al., 2010) was diluted in rainwater (EC≈0) by establishing the water salinity level of 3.0 dS m^{-1}, which, after adding more rainwater following the pre-established combinations and the solubilization of fertilizers (Furlani et al., 1999), reached the electrical conductivity levels of the nutrient solution (EC_{sn}) according to Table 1.

Table 1. Electrical conductivity of the nutrient solution as a function of treatments

Combinations	EC_{sn}* (dS m^{-1})
C1= 10%BW + 90%RW	2.72
C2= 20%BW + 80%RW	3.02
C3= 30%BW + 70%RW	3.32
C4= 40%BW + 60%RW	3.62

*EC_{sn}: electrical conductivity of the nutrient solution.

The seedlings of the bell pepper cv. All Big were produced in 36-cell plastic trays by sowing two or three seeds per cell. The plants were thinned to one seedling per cell 15 DAS and irrigated daily with rainwater in the morning and the afternoon until 30 DAS. The seedlings were then transplanted to 200-mL plastic cups perforated on the sides and bottom and filled with coconut fiber 31 DAS.

The hydroponic system adopted consisted of 12 leveled PVC tubes measuring 100 mm in diameter and with elbows at their ends, in one of which a faucet was installed as a water outlet, thus ensuring a depth of 0.04 m of solution along the tube. The cups containing the seedlings were then placed in openings 60 mm wide and spaced 30 cm. These tubes were supported by a vertical wooden structure six meters long, 1.4 m wide, and 1.8 m high (Santos Júnior et al., 2016).

The nutrient solution was placed in different reservoirs according to each treatment, and initial volumes of 100 L were prepared. Then, according to the treatments, each tube received a 40 L volume of the nutrient solution, added daily and manually twice a day (8:00 a.m. and 5:00 p.m.), aiming at nutrient recirculation. Moreover, the ECsn and pHsn were monitored daily, and the water depth lost by evapotranspiration in the respective reservoirs was replaced weekly using the water mixture.

The evaluations were performed 24 and 61 DAS, corresponding to the vegetative and flowering stages. The following parameters were evaluated: stomatal conductance (gs) (mol of H_2O m^{-2} s^{-1}), transpiration (*E*) (mmol of H_2O m^{-2} s^{-1}), internal CO_2 concentration (Ci) (μmol m^{-2} s^{-1}), CO_2 assimilation rate – photosynthesis (*A*) (μmol of CO_2 m^{-2} s^{-1}), instantaneous water-use efficiency (WUE-*A*/*E*), calculated by relating the CO_2 assimilation rate with transpiration [(μmol m^{-2} s^{-1})/(mmol of H_2O m^{-2} s^{-1})], and instantaneous carboxylation efficiency (ICE-*A*/Ci) [(μmol m^{-2} s^{-1})/(μmol $m^{-2}s^{-1}$)] based on the relationship between the CO_2 assimilation rate and the internal CO_2 concentration, measured in the third leaf from the apex of the plant using an infrared gas analyzer (ACD, LCPro SD, Hoddesdon, UK) with an airflow of 300 mL min^{-1} and a light source of 1,200 μmol m^{-2} s^{-1}.

The photosynthetic pigments were analyzed 57 DAS according to the method proposed by Arnon (1949) and Lichtenthäler (1987). Chlorophyll was extracted in plastic containers containing 8 mL of 80% acetone and a leaf disk measuring 2.8 cm^2, which was kept in the dark and under refrigeration for 48 hours. Then, the contents of chlorophyll "a", "b", total chlorophyll, and carotenoids were quantified by emission spectrophotometry at 470 nm, 645 nm, and 663 nm using equations 1, 2, 3, and 4 according to Lichtenthäler (1987), where A is the absorbance at the wavelength used. The values were expressed as μm g^{-1} MF (fresh matter).

$$\text{Chlorophyll a} = (12.7 \times A663 - 2.69 \times A645) \quad \text{Eq. (1)}$$

$$\text{Chlorophyll b} = (22.9 \times A645 - 4.68 \times A663) \quad \text{Eq. (2)}$$

$$\text{Total chlorophyll} = \text{Chlorophyll a} + \text{Chlorophyll b} \quad \text{Eq. (3)}$$

$$\text{Total carotenoids} = (1000 \times A470 - 1.82\ \text{Chl a} - 85.02\ \text{Chl b})/198 \quad \text{Eq. (4)}$$

The data obtained were subjected to analysis of variance by the F-test at the $p \leq 0.05$ and $p \leq 0.01$ probability levels. If the interaction between factors or the main factors in isolation showed significance, the Tukey test was performed using the statistical software -SISVAR (Ferreira, 2014).

Results and Discussion

According to the F-test, the interaction between brackish water and rainwater combinations (C) x H_2O_2 concentrations in the experimental units had a significant effect ($p \leq 0.01$) on all physiological variables of bell pepper 24 and 61 days after sowing (DAS) (Table 2): stomatal conductance (gs) (mol of H_2O m^{-2} s^{-1}), transpiration (*E*) (mmol of H_2O m^{-2} s^{-1}), internal carbon concentration (Ci) (μmol m^{-2} s^{-1}), net photosynthesis (*A*) (μmol of CO_2 m^{-2} s^{-1}), instantaneous water-use efficiency (WUE-*A*/*E*) [(μmol m^{-2} s^{-1})/(mmol of H_2O m^{-2} s^{-1})], and instantaneous carboxylation efficiency (EIC-A/Ci) [(μmol m^{-2} s^{-1})/(μmol $m^{-2}s^{-1}$)].

Table 2. Summary of the F-test for stomatal conductance (*gs*), transpiration (*E*), internal carbon concentration (*Ci*), net photosynthesis (*A*), instantaneous water-use efficiency (WUE), and instantaneous carboxylation efficiency (ICE) of bell pepper 24 and 61 days after sowing – DAS.

Source of Variation	F-test					
24 DAS	*gs*	*E*	*Ci*	*A*	WUE	ICE
Combinations (C)	**	**	**	**	**	**
Hydrogen peroxide (H_2O_2)	ns	*	**	**	**	**
C x H_2O_2	**	**	**	**	**	**
CV (%)	8.63	4.80	8.63	7.66	9.09	10.12
61 DAS	*gs*	*E*	*Ci*	*A*	WUE	ICE
Combinations (C)	**	**	**	**	ns	**
Hydrogen peroxide (H_2O_2)	**	**	**	**	**	**
C x H_2O_2	**	**	**	**	**	**
CV (%)	16.02	9.20	6.18	11.86	12.42	12.90

(**), (*); (ns) significant at ($p \leq 0.01$) and ($p \leq 0.05$) non-significant, respectively.

According to the means comparison test, the increase of brackish water in the combination increased the EC_{sn} of the nutrient solution and promoted a general reduction in the *gs* during both evaluated periods. However, this reduction was more pronounced 61 DAS (Table 3), possibly due to the duration of plant exposure to stress.

In the evaluation performed 24 DAS, the highest *gs* was observed in the plants cultivated in the nutrient solution containing combination 1 (10%BW+90%RW) and without H_2O_2 (control), with a mean of 0.29 mol of H_2O m^{-2} s^{-1} (Table 3). When comparing the H_2O_2 concentrations within each combination, the means comparison test reveals that combination 2 (20%BW+80%RW) resulted in no significant differences in the *gs* of plants treated with 0.0 and 7.5 μM of H_2O_2. In contrast, in the plants grown under combinations 3 and 4 (30%/70% and 40%/60 % of BW/RW, respectively), the highest *gs* values were obtained by the plants that received H_2O_2 compared to the control treatment.

Table 3. Unfolding of the interaction between treatments for the stomatal conductance– *gs* (mol of H_2O m^{-2} s^{-1}) of the bell pepper cv. All Big 24 and 61 days after sowing – DAS.

H_2O_2 (μM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	24 DAS			
0.0	0.29 Aa	0.23 Bb	0.16 Bc	0.08 Cd
7.5	0.19 Cb	0.23 Ba	0.20 Aab	0.12 Bc
15.0	0.22 Ba	0.20 Aa	0.17 Bb	0.17 Ab
Mean	**0.23**	**0.22**	**0.17**	**0.12**
	61 DAS			
0.0	0.06 Bab	0.06 ABab	0.07 Ab	0.06 Ab
7.5	0.06 Ba	0.07 Aa	0.05 Bb	0.03 Bb
15.0	0.08 Aa	0.05 Bb	0.04 Bb	0.05 Ab
Mean	**0.07**	**0.06**	**0.05**	**0.05**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H_2O_2 concentrations by the Tukey test ($p \leq 0.05$).

Moreover, according to the means comparison test, H_2O_2 application at the concentration of 15.0 μM promoted a higher *gs* in the plants grown under combination 1 (10%BW + 90%RW) 61 DAS, which was 33.0% higher than the means observed in the plants that did not receive H_2O_2. It should also be noted that, in the plants grown with the solution containing combination 3 (30%AS +70%RW), the highest *gs* was observed in the plants without H_2O_2. However, under combinations 2 (20%BW + 80%RW) and 4 (40%BW + 60%RW), the plants treated with the highest H_2O_2 concentration did not differ statistically from those subjected to the control treatment.

Plant pre-exposure to moderate stresses or signaling metabolites such as H_2O_2 can result in metabolic signaling in the cell (increased metabolites and/or antioxidant enzymes), thus resulting in better physiological performance when the plant is exposed to more severe stress conditions (Forman et al., 2010). Carvalho et al. (2011) induced rice acclimation to salt stress after exogenous application of H_2O_2 and observed that the plants treated with 10 μM of H_2O_2 and then subjected to salt stress also showed higher stomatal conductance than plants exposed only to salt stress.

The transpiration (*E*) behavior of the bell pepper plants was similar to stomatal conductance in both periods (Table 4). The highest transpiration rate achieved 24 DAS was observed in control plants irrigated with combination 1. According to the test of means, the transpiration of control plants did not differ significantly ($p \leq 0.01$) from the plants acclimated with 15.0 μM of H_2O_2 using combinations 2 and 3. On the other hand, when the plants were irrigated with the nutrient solution of 3.62 dS m^{-1} (combination 4), the treatment with 7.5 and 15.0 μM of H_2O_2 resulted in transpiration values 24.91 and 48.24% higher than those observed in bell pepper plants free of hydrogen peroxide.

Table 4. Unfolding of the interaction between treatments for the transpiration – *E* (mmol of H_2O m^{-2} s^{-1}) of the bell pepper cv. All Big 24 and 61 days after sowing– DAS.

H_2O_2 (μM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	24 DAS			
0.0	3.13 Aa	2.75 Ab	2.32 Bc	1.36 Cd
7.5	2.39 Bb	2.70 Aa	2.59 Aa	1.81 Bc
15.0	2.38 Bb	2.52 Bab	2.34 Bb	2.62 Aa
Mean	2.63	2.65	2.41	1.93
	61 DAS			
0,0	0.82 Bc	1.05 Bb	1.33 Aa	1.03 Ab
7.5	0.93 Bb	1.28 Aa	0.90 Bb	0.72 Bc
15.0	1.38 Aa	1.03 Bb	1.01 Bb	0.90 Ab
Mean	**1.04**	**1.12**	**1.08**	**0.88**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H_2O_2 concentrations by the Tukey test ($p \leq 0.05$).

The *E* parameter of bell pepper 61 DAS reveals a similar trend to that observed for *gs* in the same evaluation period, in which the highest H_2O_2 concentration (15.0 μM) promoted the highest transpiration rate in plants grown under the lowest salinity level (combination 1 – 2.72 dS m^{-1}). Also, according to the test of means, the plants grown at this concentration did not differ statistically from those that did not receive H_2O_2 when grown with the 3.02 dS m^{-1} (20%/80%) and 3.62 dS m^{-1} solutions (40%BW/60%RW) (Table 4). These results imply that, with the increase in stress exposure, the effect of exogenous H_2O_2 becomes more evident, whereas, in the short term or under lower stress intensities, this concentration had no mitigating effect on stress for the studied crop.

These different responses of bell pepper to H_2O_2 could be related to the fact that this component is a reactive oxygen species capable of oxidizing membrane lipids and denaturing proteins (Silva et al., 2015) when the plant does not produce sufficient antioxidant enzymes to avoid compromising its cells. However, Mittler (2002) stresses that foliar spraying with adequate H_2O_2 concentrations works as an important intracellular signal to activate responses to stress and plant defense pathways, promoting cross-tolerance.

According to the data contained in Table 5, the means comparison test between H_2O_2 concentrations reveals that the highest internal CO_2 concentration was observed in the plants that received 15.0 μM and grown with the nutrient solution of combination 1. When analyzing combination 2, there was no significant difference between H_2O_2 concentrations, with a mean Ci of 230.76 μmol m^{-2} s^{-1}. However, in combinations 3 and 4, the Ci was reduced by 24.26% and 39.75% when comparing plants that received 15.0 μM against those that did not receive H_2O_2 (Table 5). This result suggests that exogenous hydrogen peroxide application at 15.0 μM in bell pepper plants subjected to the high salinity levels of combinations 3 and 4 (3.32 and 3.62 dS m^{-1} respectively) reduced the Ci 24 DAS, possibly by contributing to the metabolism of this element. According to Melo et al. (2017), the Ci reduction under salt stress, such as in the present study, does not imply reductions in carbon metabolization but rather stomatal restrictions given the *gs* reductions observed (Table 3).

Table 5. Unfolding of the interaction between treatments for the internal CO_2 concentration – *Ci* (μmol m^{-2} s^{-1}) of the bell pepper cv. All Big 24 and 61 days after sowing – DAS.

H_2O_2 (μM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	24 DAS			
0.0	246.00 Bb	226.15 Ab	253.72 Ab	302.83 Aa
7.5	277.50 Ba	239.40 Ab	232.80 Ab	313.25 Aa
15.0	337.44 Aa	226.74 Ab	152.85 Bc	229.34 Bb
Mean	**286.98**	**230.76**	**213.12**	**281.81**
	61 DAS			
0.0	221.68 Aa	155.25 Bb	172.69 Ab	159.32 Ab
7.5	226.75 Aa	182.24 Ab	148.51 Bc	158.50 Ac
15.0	221.50 Aa	165.36 Bb	133.75 Bc	154.94 Ab
Mean	**223.31**	**167.62**	**151.65**	**157.59**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H2O2 concentrations by the Tukey test ($p \leq 0.05$).

The increase in the salinity of the nutrient solution due to the combinations between BW and RW reduced the internal CO_2 concentration of bell pepper plants 61 DAS (Table 5). The means comparison test reveals that only the plants grown with combinations 2 (20%BW + 80%RW) and 3 (30%BW + 70%RW) showed a statistical difference ($p \leq 0.01$) between H_2O_2 concentrations. In the plants grown under combination 2, the concentration of 7.5 μM promoted the highest Ci (182.24 μmol m^{-2} s^{-1}), whereas the control treatment (0.0 μM of H_2O_2) did not differ from the highest concentration. The analysis of the Ci of plants grown with 3.32 dS m^{-1} (combination 3) reveals that the increase in the H_2O_2 concentrations from 0.0 to 15.0 μM decreased the Ci by 22.54% (Table 5).

The Ci reduction in plants subjected to pre-treatment with hydrogen peroxide means that this signaling agent favored the carbon metabolism in bell pepper plants. In the study developed by Gondim et al. (2011), the authors observed that the foliar spraying of H_2O_2 in maize plants under salt stress increased the soluble solids contents, which, according to Weidlich et al. (2010), use most of the carbon fixed during photosynthesis and provide energy for respiration and carbon skeletons for the synthesis of other molecules.

According to the means comparison test, the unfolding of the interaction between BW + RW combinations and H_2O_2 concentrations on the CO_2 assimilation rate (*A*) 24 DAS reveals that H_2O_2 supply to plants irrigated with the lowest salinity levels, referring to combinations 1 and 2 (2.72 and 3.02 dS m^{-1} respectively), promoted reductions in the *A* parameter. In contrast, in the plants grown with the nutrient solution of 3.32 (combination 3) and 3.62 dS m^{-1} (combination 4), the supply of 15.0 µM of hydrogen peroxide increased photosynthesis by 29.81% and 45.75%, respectively, in relation to the control treatment (Table 6). These results agree with the observations for the Ci in the same period (Table 5) as the carbon concentration decreased with the application of 15.0 µM of H_2O_2 under the highest salinity level, reinforcing the idea that, under stressful conditions, this concentration favored the carbon metabolism no only by increasing the synthesis of carbohydrates, as mentioned before (Gondim et al., 2011), but also by favoring the photosynthetic process. Moreover, it has also been reported that exogenous treatment with H_2O_2 increased the *A* parameter in cucumber (Sun et al., 2016) and soybean (Ishibashi et al., 2011).

Table 6. Unfolding of the interaction between treatments for the CO_2 assimilation rate - *A* (µmol of CO_2 m^{-2} s^{-1}) of the bell pepper cv. All Big 24 and 61 days after sowing – DAS.

H_2O_2 (µM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
24 DAS				
0.0	17.71 Aa	17.12 Aa	11.26 Cb	9.50 Bc
7.5	10.38 Bb	13.45 Ba	14.21 Ba	9.56 Bb
15.0	7.79 Cc	14.44 Bb	17.51 Aa	16.05 Aab
Mean	**11.96**	**15.00**	**13.84**	**12.19**
61 DAS				
0.0	6.17 Bb	8.26 Aa	8.49 Aa	6.82 Ab
7.5	6.06 Bbc	7.11 ABab	7.76 Aa	4.75 Bc
15.0	7.96 Aa	6.89 Bab	5.94 Bbc	5.38 Bc
Mean	**6.73**	**7.42**	**7.40**	**5.65**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H2O2 concentrations by the Tukey test ($p \leq 0.05$).

The means comparison test reveals that the plants that did not receive H_2O_2 had the lowest photosynthetic rate 61 DAS when grown with combination 1(10%BW + 90% RW), not differing from the concentration of 7.5 µM. With the increase in the salinity of the nutrient solution in combinations 2, 3, and 4 (3.02, 3.32, and 3.62 dS m^{-1}, respectively), the application of 15.0 µM of H_2O_2 promoted the lowest photosynthetic rates (Table 6). On the other hand, no statistical difference was observed between the concentrations of 0.0 and 7.5 µM of H_2O_2 in plants grown with the nutrient solution containing combinations 2 (EC_n = 3.02 dS m^{-1}) and 3 (EC_n = 3.32 dS m^{-1}), suggesting that, in the long term, the supply of high hydrogen peroxide concentrations could limit the photosynthetic efficiency of bell pepper plants.

The reduction in the photosynthetic rate and the higher H_2O_2 concentration in bell pepper plants under salt stress are due to the increase in foliar temperature, which is common in stressed species. According to Araújo & Deminicis (2009), this process dissociates the protein-pigment complex of the light-harvesting antenna of PSII due to the reaction between O^{2-} and hydrogen peroxide (H_2O_2), the latter from the exogenous application, causing enzyme inactivation and pigment discoloration. However, according to Gill & Tuteja (2010), these deleterious effects depend on the intensity of stress and the ability of the plant antioxidant system to degrade H_2O_2. Therefore, the *gs* reduction and the resulting *E* limitation observed in this study (Tables 3 and 4, respectively) could be responsible for this leaf temperature increase since, according to Silva et al. (2015), transpiration is the main mechanism involved in regulating leaf temperature, with the reduction in stomatal opening decreasing the foliar *E* and increasing leaf temperature as a result of the reduced latent heat dissipation.

After 24 DAS, the bell pepper plants showed increased instantaneous water-use efficiency (WUE) with the increase in the salinity of the nutrient solution resulting from the BW and RW combinations (Table 7). According to the means comparison test, when the plants grew under combination 1, H_2O_2 application at 15.0 µM promoted the lowest WUE (3.29). However, this concentration did not differ from the controls or the plants treated with 7.5 µM when both were subjected to combination 2 (EC_{sn}= 3.02 dS m^{-1}), promoting the highest instantaneous water-use efficiency (7.50) when in the presence of the solution containing combination 3, whose EC_{sn} is 3.32 dS m^{-1} (Table 7). After 61 DAS, the highest WUE was obtained with the treatment using 7.5 µM of H_2O_2 and the nutrient solution containing combination 3 (EC_{sn}= 3.32 dS m^{-1}). This H_2O_2 concentration also promoted the highest WUE in plants irrigated with combination 4 (EC_{sn} = 3.62 dS m^{-1}), not differing from the control treatment, according to the test of means.

Table 7. Unfolding of the interaction between treatments for the instantaneous water-use efficiency (WUE-*A*/*E*) of the bell pepper cv. All Big 24 and 61 days after sowing– DAS.

H_2O_2 (μM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	24 DAS			
0.0	5.66 Abc	6.24 Aab	4.86 Bc	7.04 Aa
7.5	4.35 Bb	4.99 Bab	5.50 Ba	5.30 Ca
15.0	3.29 Cc	5.74 ABb	7.50 Aa	6.12 Bb
Mean	**4.43**	**5.65**	**5.95**	**6.15**
	61 DAS			
0.0	7.53 Aab	7.89 Aa	6.40 Bb	6.61 Aab
7.5	6.51 ABb	5.56 Bb	8.84 Aa	6.58 Ab
15.0	5.73 Ba	6.71 ABa	5.93 Ba	6.10 Aa
Mean	**6.59**	**6.72**	**7.06**	**6.43**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H2O2 concentrations by the Tukey test (p ≤ 0.05).

This increase in the WUE reflects a possible bell pepper acclimation to salinity in response to H_2O_2 supply since these results represent the increases in net photosynthesis (Figure 4), resulting in greater production of organic osmolytes such as soluble sugars and proline, essential for osmotic adjustment (Sun et al., 2016). These findings suggest that H_2O_2 spraying increased stress tolerance through the synthesis and accumulation of solutes (Ishibashi et al., 2011), and this maintenance of osmotic balance was probably caused by the promotion of the activity of antioxidant enzymes (Sun et al., 2016).

With regard to the instantaneous carboxylation efficiency (ICE), the highest value was observed 24 DAS when the plants were grown with combinations 1 and 2 and H_2O_2 was not applied. However, according to the means comparison test, the application of 15.0 μM of H_2O_2 increased this variable by 60.90% and 54.15% in bell pepper plants using combinations 3 and 4 in relation to the control treatment (Table 8). When analyzing the ICE 61 DAS, the application of 15.0 μM of H_2O_2 increased the ICE by 22.52% in relation to the plants that did not receive H_2O_2 when these were grown with combination = 1(10%BW + 90%RW). However, no significant difference was observed between this concentration and 0.0 and 7.5 μM of H_2O_2 in bell pepper plants grown with the nutrient solution containing combinations 3(EC_{sn}= 3.32 dS m^{-1}) and 4(EC_n= 3.62 dS m^{-1}).

Table 8. Unfolding of the interaction between treatments for instantaneous carboxylation efficiency (ICE-*A*/*Ci*) of the bell pepper cv. All Big 24 and 61 days after sowing – DAS.

H_2O_2 (μM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	24 DAS			
0.0	0.072 Aa	0.076 Aa	0.045 Cb	0.032 Bc
7.5	0.038 Bb	0.056 Ba	0.061 Ba	0.031 Bb
15.0	0.023 Cc	0.064 Bb	0.115 Aa	0.070 Ab
Mean	**0.044**	**0.065**	**0.074**	**0.044**
	61 DAS			
0.0	0.028 Bc	0.054 Aa	0.049 Aab	0.043 Ab
7.5	0.027 Bc	0.039 Bb	0.052 Aa	0.030 Bc
15.0	0.036 Aab	0.042 Bab	0.044 Aa	0.035 ABb
Mean	**0.031**	**0.045**	**0.049**	**0.036**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H2O2 concentrations by the Tukey test (p ≤ 0.05).

The study of the instantaneous carboxylation efficiency allows identifying whether non-stomatal factors influence photosynthesis (Oliveira et al., 2016). Therefore, the increase in this variable and in the photosynthesis rate (Table 6) of plants subjected to the salt stress promoted by exogenous H_2O_2 reflects an acclimation induced by this metabolite since the increase in the ICE indicates a better use of fixed CO_2, preventing possible metabolic restrictions in the Calvin cycle of these plants, reducing the synthesis of sugars during the photosynthetic process (Freire et al., 2014), and providing a substrate for the activity of Rubisco (Silva et al., 2015).

With regard to photosynthetic pigments, there was a significant interaction between the brackish water and rainwater combinations (C) x H_2O_2 concentration in the experimental units on the contents of chlorophyll "a" (CL a), chlorophyll "b" (CL b), total chlorophyll (*Cl T*), and carotenoids (*Car*) in bell pepper according to the F-test (Table 9).

Table 9. Summary of the F-test for the contents of chlorophyll "a" (*Cl a*), chlorophyll "b" (*Cl b*), total chlorophyll (*Cl T*), and carotenoids (*Car*) of bell pepper 57 days after sowing (DAS)

Source of Variation	F-test			
	Cl a	*Cl b*	*Cl T*	*Car*
Combinations (C)	**	**	**	**
Hydrogen peroxide (H_2O_2)	**	ns	**	**
C x H_2O_2	**	**	**	**
CV (%)	4.89	5.71	4.36	3.83

(**), (*); (ns) significant at ($p \leq 0{,}01$) and ($p \leq 0{,}05$) and non-significant, respectively.

Based on the means comparison test, the increase in the combination between brackish water and rainwater increased the EC_{sn} of the nutrient solution (Table 1) and promoted an overall reduction in the content of *Cl a*, with the highest values corresponding to plants grown with the nutrient solution containing combinations 1 (10%BW+90%RW) and 2 (20%BW+80%RW) and no application of H_2O_2, resulting in 9.26 µm g^{-1} MF and 9.54 µm g^{-1} MF, respectively, (Table 10). Moreover, there was also a reduction of 8.21% in this variable when the plants were grown with the nutrient solution containing combination 4 (40%BW+60%RW) in relation to combination 1. When comparing the H_2O_2 concentrations within each combination between brackish water and rainwater, the application of 15.0 µM of H_2O_2 mitigated the deleterious effects of salinity in the nutrient solution, with an increase of 8.41% in the *Cl a* content compared to the control treatment (0.0 µM) and combination 4 (40%BW+60%RW), whose salinity was 3.62 dS m^{-1}.

Table 10. Unfolding of the interaction between treatments for the contents of chlorophyll "a" (*Cl a*) and chlorophyll "b" (*Cl b*) of the bell pepper cv. All Big 57 days after sowing – DAS.

H_2O_2 (µM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	Cl a (µm g^{-1} MF)			
0.0	9.26 Aa	9.54 Aa	9.17 Bab	8.50 Bb
7.5	8.69 ABb	9.48 Aa	7.04 Cc	9.09 ABab
15.0	8.17 Bb	9.07 Aa	9.30 Aa	9.28 Aa
Mean	**8.71**	**9.36**	**8.50**	**8.62**
	Cl b (µm g^{-1} MF)			
0.0	2.50 Aa	2.63 Ba	2.48 ABa	2.49 Aa
7.5	2.53 Ab	2.89 Aa	2.44 Bb	2.50 Ab
15.0	2.23 Bc	2.45 Bbc	2.70 Aa	2.59 Aab
Mean	**2.42**	**2.66**	**2.54**	**2.53**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H2O2 concentrations by the Tukey test ($p \leq 0.05$).

The chlorophyll "b" content (*Cl b*) of plants grown with H_2O_2 and the nutrient solution containing combinations 2 (20%BW+80%RW) and 3 (30%AS+70%RW) increased and achieved the highest values of 2.89 and 2.70 µm g^{-1} with the application of 7.5 and 15 µM of H_2O_2, respectively (Table 10). However, there was no significant difference between H_2O_2 concentrations for combination 4 (40%BW+60%RW), although there was a numerically superior value at the concentration of 15 µM (2.59 µm g^{-1} MF).

The total chlorophyll content (*Cl T*) followed the same trend observed for *Cl a* and *Cl b*, with the highest salinity levels (combinations 3 and 4) reducing the *Cl T* content (Table 11). When comparing the H_2O_2 concentrations within each combination between brackish water and rainwater, the means comparison test revelated those combinations 1 (10%BW+90%RW) and 2 (20%BW+80%RW) and the application of 15.0 µM of H_2O_2 contributed negatively to the *Cl T* content. However, for the plants grown under combinations 3 (30%BW+70%RW) and 4 (40%BW/60%RW), the highest *Cl T* values were obtained by those that received 150 µM of H_2O_2, increasing this variable by 2.91% (12.0 µm g^{-1} MF) and 7.41% (11.87 µm g^{-1} MF), respectively, compared to the control treatment (0.0 µM).

From this perspective, the highest salinity levels (combinations 3 and 4) and the application of 15 µM of H_2O_2 promoted the highest values of *Cl a* Cl *b* and *Cl T*. On the other hand, the lowest chlorophyll values observed in the plants of the control treatment (0.0 µM) can be attributed to the increase in the activity of chlorophyllase, which degrades chlorophyll, considering that salt stress induces the degradation of ß-carotene and reduces the formation of zeaxanthin, thus decreasing the carotenoids, pigments apparently involved in the protection against photoinhibition (Freire et al., 2013). Lima et al. (2017) observed a linear reduction in the contents of *Cl b* and *Cl T* in bell pepper plants by increasing the salinity of the nutrient solution at growing levels starting at 1.5 dS m^{-1}. However, Silva et al. (2019) observed that the foliar application of H_2O_2 at the concentration of 25 µM effectively mitigated the deleterious effects of water salinity on the contents *Cl a*, *Cl b*, and *Car* in soursop.

Table 11. Unfolding of the interaction between treatments for the content of total chlorophyll (*Cl T*) and carotenoids (*Car*) of the bell pepper cv. All Big 57 days after sowing – DAS.

H_2O_2 (µM)	Brackish water/rainwater combinations (%)			
	10%/90%	20%/80%	30%/70%	40%/60%
	Cl T (µm g^{-1} MF)			
0.0	11.76 Aab	12.17 ABa	11.65 Aab	10.99 Bb
7.5	11.22 Ab	12.37 Aa	9.48 Bc	11.59 ABab
15.0	10.40 Bb	11.52 Ba	12.00 Aa	11.87 Aa
Mean	**11.13**	**12.02**	**11.04**	**11.48**
	Car (µm g^{-1} MF)			
0.0	2.55 Aa	2.38 Ab	2.31 Ab	2.14 Bc
7.5	2.15 Bb	2.36 Aa	1.71 Bc	2.27 ABab
15.0	2.11 Bb	2.31 Aa	2.22 Aab	2.35 Aa
Mean	**2.27**	**2.35**	**2.08**	**2.25**

Means followed by the same lowercase letters do not differ statistically between brackish water /rainwater combinations, whereas uppercase letters do not differ between H2O2 concentrations by the Tukey test ($p \leq 0.05$).

With regard to the content of carotenoids (*Car*), the means comparison test revealed that the highest values of this variable were observed in the control treatment for combinations 1 (10%BW+90%RW), 2 (20%BW+80%RW), and 3 (30%BW+70%RW), respectively 2.55, 2.38, and 2.31 µm g^{-1} MF (Table 11). However, in combination 4 (40%BW/60%RW), the plants treated with hydrogen peroxide showed increased contents of *Car*, with 5.73% and 8.94% when comparing the respective concentrations of 7.5 and 15.0 µM against the control treatment (0.0 µM). Carotenoids can exert a photoprotective action in the photochemical apparatus, working as a defense mechanism and preventing photooxidative damage to the chlorophyll molecules (Kerbauy, 2004; Raven et al., 2007). From this perspective, the reduction in the carotenoid content could be related to its antioxidant activity, resulting in a more constant content even under increased salinity (Ziaf et al., 2009; Ashraf & Harris, 2013).

Conclusions

The application of H_2O_2 favors the acclimation of bell pepper plants to nutrient solution salinity.

After 61 DAS, the highest *gs* and *E* values in bell pepper plants grown with the nutrient solution with EC_{sn} of 2.72 dS m^{-1} (10%BW + 90%RW) are obtained by applying 15.0 µM of H_2O_2.

The bell pepper plants treated with 15.0 µM of H_2O_2 and grown with the nutrient solution containing combinations 3 (30%BW + 70%RW) and 4 (40%BW + 60%RW) showed increased photosynthesis 24 DAS. On the other hand, stress increased 64 DAS.

The highest WUE and ICE values were achieved when the bell pepper plants were grown with combination 3 (EC_{sn} = 3.32 ds m^{-1}) and received 15.0 and 7.5 µM of H_2O_2 after 24 and 61 DAS, respectively.

The contents of chlorophyll "a", "b", total chlorophyll, and carotenoids in bell pepper showed deleterious effects caused by nutrient solution salinity, mitigated by hydrogen peroxide at the concentration of 15 µM.

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