SEMINA
Ciências Agrárias

ARTICLES / ARTIGOS

DOI: 10.5433/1679-0359.2023v44n1p217

Hydrogen peroxide in the mitigation of salt stress in bell pepper

Peróxido de hidrogênio na mitigação do estresse salino em pimentão

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Highlights

Salt stress reduces the synthesis of photosynthetic pigments in plants.
Water salinity drastically affects gas exchange.
Hydrogen peroxide minimizes the deleterious effects of salinity.

Abstract

Bell pepper is a vegetable of great socioeconomic importance in the Brazilian market. However, in the semi-arid region of northeast Brazil, its cultivation is limited by the high concentrations of salts in water sources. On this basis, this study was developed to determine the effect of foliar application of hydrogen peroxide in mitigating salt stress by evaluating gas exchange, photosynthetic pigments, and growth in 'All Big' bell pepper plants. The experiment was conducted in greenhouse conditions in Campina Grande - PB, Brazil. Treatments were distributed in a randomized block design with a 5 × 5 factorial arrangement corresponding to five levels of irrigation-water electrical conductivity (ECw: 0.8, 1.2, 2.0, 2.6, and 3.2 dS m^{-1}) and five concentrations of hydrogen peroxide (H_2O_2: 0, 15, 30, 45, and 60 μM), with three replicates and one plant per plot. Foliar application of hydrogen peroxide at the concentration of 15 μM attenuated

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Received: May 19, 2022 Approved: Feb. 28, 2023

the effects of salt stress in 'All Big' bell pepper plants irrigated with saline water at ECw of up to 1.4 dS m^{-1}. Hydrogen peroxide at a concentration of 15 μM associated with water salinity of 0.8 dS m^{-1} increased stomatal conductance, CO_2 assimilation rate, instantaneous carboxylation efficiency, and the growth of the bell pepper plants. Application of hydrogen peroxide at concentrations greater than 15 μM intensified the deleterious effects of salt stress in 'All big' bell pepper at 90 days after sowing.

Key words: Acclimatization. *Capsicum annuum* L. Salinity.

Resumo

O pimentão é uma hortícola de grande importância socioeconômica no mercado brasileiro. Contudo, no semiárido do Nordeste brasileiro seu cultivo é limitado devido a ocorrência de fontes hídricas com elevadas concentrações de sais. Deste modo, objetivou-se com o presente estudo, avaliar o efeito da aplicação foliar de peróxido de hidrogênio na mitigação do estresse salino nas trocas gasosas, nos pigmentos fotossintéticos e no crescimento das plantas de pimentão 'All Big'. O experimento foi conduzido em condições de casa de vegetação, em Campina Grande-PB. Os tratamentos foram distribuídos no delineamento de blocos casualizados, em esquema fatorial 5 × 5, correspondendo a cinco níveis de condutividade elétrica da água de irrigação – CEa (0,8; 1,2; 2,0; 2,6 e 3,2 dS m^{-1}) e cinco concentrações de peróxido de hidrogênio – H_2O_2 (0, 15, 30, 45 e 60 μM), com três repetições e uma planta por parcela. A aplicação foliar de peróxido de hidrogênio na concentração de 15 μM atenuou os efeitos do estresse salino em plantas de pimentão 'All Big' irrigadas com águas salinas em CEa de até 1,4 dS m^{-1}. O peróxido de hidrogênio na concentração de 15 μM associado à salinidade da água de 0,8 dS m^{-1} proporcionou aumento na condutância estomática, na taxa de assimilação de CO_2, na eficiência instantânea de carboxilação e no crescimento das plantas de pimentão. Aplicação de peróxido de hidrogênio em concentrações maiores que 15 μM, intensificou os efeitos deletérios do estresse salino em pimentão 'All big', aos 90 dias após o semeio.

Palavras-chave: Aclimatação. *Capsicum annuum* L. Salinidade.

Introduction

Bell pepper (*Capsicum annuum* L.) is a non-climacteric plant of the family Solanaceae. Existing cultivars are found in different shapes, sizes, and colors, according to the stage of maturity (Lahbib et al., 2017). It is a vegetable of great socioeconomic importance in Brazil, where it is among the ten most important vegetables. Bell pepper is also the third most cultivated solanaceous plant, only behind tomatoes and potatoes (Lopes et al., 2018), although its cultivation is classified as between 'moderately sensitive' to 'sensitive' to salinity and water stress conditions (Penella et al., 2015).

Water is notably one of the main natural resources required for food production. However, due to the qualitative and quantitative scarcity of water resources a common occurrence in the semi-arid region of northeast Brazil, the use of saline water in irrigation has become inevitable to ensure agricultural production (Lima et al., 2018; R. C. P. da Silva et al., 2020; Pinheiro et al., 2022). Nonetheless, high salt concentrations change the physiology of plants, limiting their growth and development (Souza et al., 2016; Santos et al., 2016). The effects of salinity are attributed to osmotic (restriction in water and nutrient absorption) and ionic (toxicity of specific ions) activity, besides secondary effects such as oxidative stress (Soares et al., 2018; E. M. da Silva et al., 2018; Roque et al., 2022). High concentrations of salts reduce the osmotic potential of the soil and induce the plant to close its stomata to avoid losing water to the atmosphere, which limits transpiration and the photosynthetic rate (Bezerra et al., 2018; Andrade et al., 2019).

Excess salts in the soil can lead to changes in the quantum efficiency of photosystem II and in nutritional balance that culminate in decreased plant development, regardless of the nature of these salts (Lima et al., 2020). Some strategies are employed to enable the use of these waters, e.g., exogenous application of hydrogen peroxide (H2O2), a reactive oxygen species (Andrade et al., 2019, 2022). The application of H_2O_2 at low concentrations allows plants to acclimatize to salt stress through metabolic changes responsible for inducing tolerance to stress, thus enabling the use of waters with higher salt concentrations (Veloso et al., 2022).

Research has been done to determine the effects of foliar application of H_2O_2 on the acclimatization of crops to salt stress in various crops, e.g. passion fruit (Andrade et al., 2022), tomato (Nazir et al., 2021), and in Italian zucchini (Dantas et al., 2022). These studies found that the H_2O_2 concentrations of 20, 0.1, and 20 μM, respectively, alleviated the deleterious effects of salt stress on photochemical and photosynthetic efficiency, in addition to altering the chloroplast ultrastructure and the stomatal behavior of the plants. In this context, the present study was developed to investigate the effect of hydrogen peroxide application in mitigating salt stress by evaluating gas exchange, photosynthetic pigments, and growth in 'All Big' bell pepper plants.

Material and Methods

The experiment was carried out between March and June 2022, in a greenhouse belonging to the Academic Unit of Agricultural Engineering at the Federal University of Campina Grande (UAEA/UFCG), in Campina Grande - PB, Brazil (07º13'51'' S, 35º52'54'' W, 550 m average altitude). Figure 1 shows the temperature (maximum and minimum) and average relative humidity data at the experiment site.

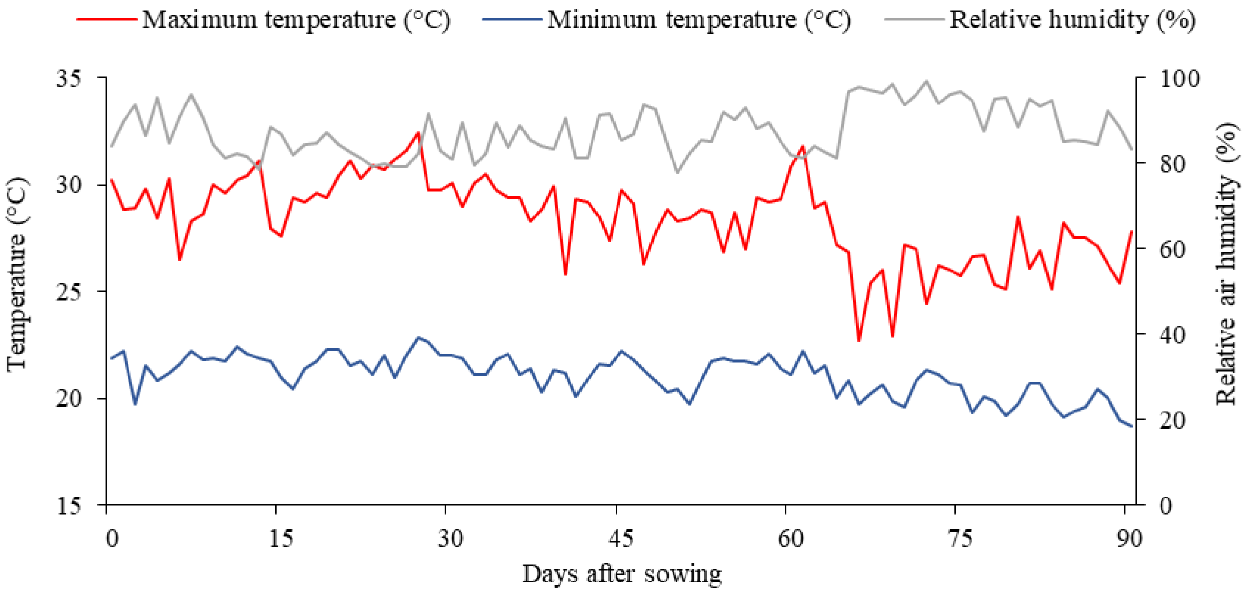

Figure 1. Maximum and minimum temperatures and mean relative humidity recorded inside the greenhouse during the experimental period.

Treatments consisted of a combination of five levels of irrigation-water electrical conductivity (ECw: 0.8, 1.4, 2.0, 2.6, 3.2 dS m-1) and five concentrations of hydrogen peroxide (H_2O_2: 0, 15, 30, 45, and 60 μM), in a 5 × 5 factorial arrangement distributed in a randomized block design with three replicates and one plant per plot. The ECw levels were based on the study developed by Veloso et al. (2021) with 'All Big' pepper (*Capsicum annuum* L.). The H_2O_2 concentrations used in this study were adapted from the work carried out with Italian zucchini cv. Caserta (Dantas et al., 2022).

Plastic pots with a capacity of 10 L, adapted as drainage lysimeters, were used. Each lysimeter was perforated at the base, to allow drainage, and attached to a 4-mm-diameter transparent drain. The end of the drain inside the lysimeter was lined with non-woven geotextile fabric (Bidim OP 30) to avoid obstruction of the soil material. Below each drain was a plastic bottle for collecting drained water and estimating water consumption.

The lysimeters were filled with a layer of 0.3 kg of gravel, followed by 9 kg of a eutric Regosol (Psamments) with sandy loam texture collected at a depth of 0-30 cm from the rural area of the municipality of Lagoa Seca - PB, Brazil. The chemical and physical attributes of the soil (Table 1) were determined according to the methodology proposed by Teixeira et al. (2017).

For sowing, three seeds were distributed equidistantly in each lysimeter, at a depth of 2 cm. After seedling emergence, thinning was performed in two steps, when the plants had two and three pairs of definitive leaves, respectively, leaving the most vigorous plant per container in the last thinning (30 days after sowing - DAS).

Table 1
Chemical and physical attributes of the soil used in the experiment, before the implementation of the treatments

Chemical characteristics									
pH (H_2O) (1:2.5)	OM dag kg^{-1}	P (mg kg^{-1})	K^+	Na^+	Ca^{2+}	Mg^{2+}	$Al^{3+} + H^+$	ESP (%)	ECse (dS m^{-1})
			.... (cmolc kg^{-1})						
6.12	1.36	6.80	0.22	0.16	2.60	3.66	1.93	1.87	1.0
Physical-water characteristics									
Particle size fraction (g kg^{-1})			Texture class	Moisture (kPa)		AW	Total porosity %	AD	PD
Sand	Silt	Clay		33.42*	1519.5** dag kg^{-1}	....		(kg dm^{-3})	
760.9	164.5	74.6	SL	13.07	5.26	7.81	41.79	1.56	2.68

OM = organic matter, Walkley-Black wet digestion; Ca^{2+} and Mg^{2+} extracted with 1 M KCl at pH 7.0; Na^+ and K^+ extracted with 1 M NH_4OAc at pH 7.0; Al^{3+} and H^+ extracted with 0.5 M CaOAc at pH 7.0; ESP = exchangeable sodium percentage; ECse = electrical conductivity of the saturation extract; SL = sandy loam; AW = available water; AD = apparent density; PD = particle density; * = field capacity; ** = wilting point.

The hydrogen peroxide concentrations were obtained by diluting H_2O_2 in deionized water. Before sowing, the seeds were pre-treated with hydrogen peroxide for a period of 24 h. The seeds were immersed in the H_2O_2 solutions (0, 15, 30, 45, and 60 μM) for 24 h. After this period, the seeds were sown in the plastic pots. Subsequently, the same concentrations of H_2O_2 were applied foliarly.

The saline waters used for cultivation were obtained by adding sodium chloride (NaCl), calcium chloride ($CaCl_2.2H_2O$), and magnesium chloride ($MgCl_2.6H_2O$) salts prepared in water from the local supply system (ECw = 0.38 dS m^{-1}), at the equivalent ratio of 7:2:1, respectively. This is the proportion of Na^+, Ca^{2+}, and Mg^{2+} commonly found in water used for irrigation in the semi-arid region of northeastern Brazil (Medeiros, 1992). In the preparation of the irrigation water, we considered the ratio between ECw and the salt concentration (Richards, 1954) according to Eq. 1:

$$Q \approx 10 \times ECw \quad (1),$$

where Q = sum of cations (mmolc L^{-1}); and ECw = electrical conductivity after deducting the ECw of the municipal water supply system (dS m^{-1}).

Irrigation was performed daily at 17h00, by applying the volume corresponding to that obtained by the water balance to each lysimeter. The volume of water to be applied to the plants was determined by Eq. 2:

$$IV = \frac{(Vp - Vd)}{(1 - LF)} \quad (2),$$

where IV = volume of water to be used in the following irrigation event (mL); Vp = volume applied in the previous irrigation event (mL); Vd = drained volume (mL); and LF = adopted leaching fraction of 0.10.

Nitrogen, phosphorus, and potassium fertilization was carried out based on the recommendation by Novais et al. (1991) for pot-grown plants. A total of 100 mg N kg^{-1}, 150 mg K_2O kg^{-1}, and 300 mg P_2O_5 kg^{-1} of soil were applied. Urea (CH_4N_2O, 45% N) and monoammonium phosphate (MAP; $NH_4H_2PO_4$, 12% N, and 61% P_2O_5) were used as the nitrogen source, whereas potassium chloride (KCl, 60% K_2O) was used as the potassium source and MAP as the phosphorus the source. The NPK fertilization was split into eight applications, via fertigation, performed every two weeks from 45 DAS. A dose of 1.0 g L^{-1} of the commercial product Dripsol® was applied foliarly to meet the need for micronutrients, every fortnight, from 35 DAS until the end of cultivation. The product contained Mg (1.1%), Zn (4, 2%), B (0.85%), Fe (3.4%), Mn (3.2%), Cu (0.5%), and Mo (0.05%) and was applied on the adaxial and abaxial faces using a backpack sprayer (Jacto XP, Jacto) with a capacity of 12 L, working pressure (maximum) of 88 psi (6 bar), and JD 12P nozzle. Phytosanitary treatments were carried out whenever necessary, using the products recommended for the crop.

Hydrogen peroxide applications (DAS) were performed via foliar spraying, between 17h00 and 18h00. The first application took place 72 h before the beginning of the application of the different ECw levels (33 DAS), and the subsequent ones were performed at 12-day intervals. Hydrogen peroxide applications were interrupted after the appearance of the fruits (80 DAS, totaling four applications of H_2O_2). The average total volume applied per plant was 80 mL. Applications were carried out manually, with a sprayer, so as to completely wet the leaves (abaxial and adaxial faces). During H_2O_2 spraying, a plastic canvas structure was used to prevent the product from drifting over to neighboring plants.

At 90 DAS, the relative water content (RWC), electrolyte leakage percentage (%EL), chlorophyll a (Cl *a*), chlorophyll *b* (Cl *b*), and total chlorophyll (Cl *t*) contents, and carotenoid contents were evaluated. In the same period, leaf gas exchange was determined by measuring stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}), transpiration (*E*, mmol H_2O m^{-2} s^{-1}), CO_2 assimilation rate (*A*, μmol CO_2 m^{-2} s^{-1}), intracellular CO_2 concentration (*Ci*, μmol CO_2 m^{-2} s^{-1}), instantaneous water use efficiency (*iWUE*, i.e. *A/E*, [(μmol CO_2 m^{-2} s^{-1}) (mol H_2O m^{-2} s^{-1})$^{-1}$]), and instantaneous carboxylation efficiency (*iCE*, i.e. *A/Ci*, [(μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 m^{-2} s^{-1})$^{-1}$]); and the growth variables of plant height (PH), stem diameter (SD), number of leaves (NL), and leaf area (LA).

To calculate RWC, two leaves were removed from the middle third of the main branch to obtain five discs (12-mm diameter) from each leaf. Soon after collection, the leaf discs were weighed, thus avoiding moisture loss, to determine their fresh weight (FW). Then, these samples were placed in a beaker, immersed in 50 mL of distilled water, and left to sit for 24 h. After this period, the excess water in the leaf discs was removed with a paper towel and the turgid weight (TW) of the samples was determined. Next, the samples were oven-dried at a temperature of 65 ± 3 ºC until constant weight to determine their dry weight (DW). The relative water content was calculated according to the methodology described by Lima et al. (2015), using Eq. 3:

$$\mathrm{RWC} = \left(\frac{\mathrm{FW - DW}}{\mathrm{TW - DW}}\right) \times 100 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots(3),$$

where RWC = relative water content (%); FW = leaf fresh weight (g); TW = turgid weight (g); and DW = dry weight (g).

Electrolyte leakage (%EL) in the leaf blade was determined using a copper perforator to obtain five leaf discs with an individual area of 1.54 cm^2, per experimental unit. These were washed and placed in an Erlenmeyer® flask containing 50 mL of distilled water. After being closed with aluminum foil, the flasks were kept at a temperature of 25 °C for 90 min, after which time the initial electrical conductivity of the medium (Xi) was measured using a bench conductivity meter (MB11, MS Techonopon®). Then, the flasks were subjected to a temperature of 90 °C, for 90 min, in a drying oven (SL100/336, SOLAB®), and after their contents were cooled, the final electrical conductivity (Xf) was measured. Electrolyte leakage in the leaf blade was expressed as the percentage of initial electrical conductivity relative to the electrical conductivity after treatment for 90 min at 90º C, in accordance with the methodology proposed by Scotti-Campos et al. (2013), considering Eq. 4:

$$\%\,\mathrm{EL} = \frac{\mathrm{Xi}}{\mathrm{Xf}} \times 100 \text{ ....(4),}$$

where % EL = electrolyte leakage percentage; Xi = initial electrical conductivity; and Xf = final electrical conductivity.

Photosynthetic pigments chlorophyll *a*, chlorophyll *b*, total chlorophyll, and carotenoids were quantified as per Arnon (1949), whereby plant extracts were made from disc samples of the blade of the third mature leaf from the apex. In each sample, 7.0 mL of 80% acetone A.R. were used. These samples were stored for 48 h in an opaque container, to prevent the passage of light, under refrigerated conditions. From these extracts, the concentrations of chlorophyll and carotenoids in the solutions were determined using a spectrophotometer at the absorbance wavelengths (ABS) of 470, 647, and 663, as shown in Eq. 5, 6, 7, and 8:

$$\mathrm{Chl}\ a = (12.25 \times \mathrm{ABS663}) - (2.79 \times \mathrm{ABS647})\text{...(5)}$$

$$\mathrm{Chl}\ b = (21.5 \times \mathrm{ABS647}) - (5.10 \times \mathrm{ABS647}) \text{ .....(6)}$$

$$\mathrm{Chl}\ t = (7.15 \times \mathrm{ABS663}) + (18.71 \times \mathrm{ABS647})\text{....(7)}$$

$$\mathrm{Car} = \frac{|(1000 \times \mathrm{ABS470}) - (1.82 \times \mathrm{Chl}\ a) - (85.02 \times \mathrm{Chl}\ b)|}{198} \text{ ....(8),}$$

where Chl *a* = chlorophyll *a*; Chl *b* = chlorophyll *b*; Chl *t* = total chlorophyll; and Car = carotenoids.

Leaf gas exchanges were evaluated from 07h00 to 09h00, using a portable photosynthesis meter (LCPro+, ADC Bio Scientific Ltd.) with irradiation of 1200 μmol photons m^{-2} s^{-1} and airflow of 200 mL min^{-1}, at the ambient CO$_2$ level. Measurements were performed on the third leaf counted from the apex.

Plant height (cm) was measured as the distance from the neck of the plant to the insertion of the apical meristem. Stem diameter (mm) was measured at 2 cm from the neck of the plant. The number of leaves was obtained by counting fully expanded leaves with a minimum length of 3 cm. Finally, leaf area (cm²) was obtained according to Rezende et al. (2002), using Eq. 9:

$$Y = 0.5979X \text{ ....(9),}$$

where Y = leaf area, in cm^2; and X = area corresponding to the product of leaf length by width, in cm^2.

The multivariate structure of the results was evaluated by principal component analysis (PCA), by summarizing the amount of relevant information contained in the original data set into fewer dimensionsproduced by the linear combination of the original variables generated by the eigenvalues ($\lambda > 1.0$) in the correlation matrix, which explain percentages greater than 10% of the total variance (Govaerts et al., 2007).

After reducing the dimensions, the original data of the variables of each component were subjected to multivariate analysis of variance (MANOVA) by the Hotelling (1947) test at 0.05 probability for the H_2O_2 concentrations and ECw levels as well as for the interaction between them.

Variables with a correlation coefficient greater than or equal to 0.6 were kept in the principal components (PC1 and PC2) (Hair et al., 2009), whereas those with a correlation coefficient lower than 0.6 were analyzed using univariate analysis at the probability level of 0.05. In the case of significance, linear and quadratic regression was performed. Statistica software v.7.0 (Statsoft, 2004) was employed for statistical analysis.

Results and Discussion

The multidimensional space of the original variables was reduced to two principal components (PC1 and PC2) with eigenvalues greater than $\lambda > 1.0$, following Kaiser (1960). There was a significant interaction effect between hydrogen peroxide (H_2O_2) concentrations and water electrical conductivity (ECw) levels for the PC1 and PC2 (Table 2). Combined, the eigenvalues and the percentage of variation explained by each component (Table 2) represented 84.9% of the total variation, with PC1 explaining 72.67% of the variance and containing the variables of *Ci, gs, E, A, iCE,* PH, SD, NL, LA, Chl *a*, and Cl *t.* Principal component 2, in turn, represented 12.23% of the remaining variance, consisting only of Chl *b.*

Figure 2 illustrates the two-dimensional projections of the effects of treatments and variables in PC1 and PC2. In the first principal component (PC1), a process was identified that was possibly characterized by the interaction effect between ECw levels and H_2O_2 concentrations, with correlation coefficients between *Ci, gs, E, A, iCE,* PH, SD, NL, LA, Chl *a*, and Cl *t* being greater than 0.60.

In PC1, we observe that the bell pepper plants cultivated under the ECw of 0.8 dS m^{-1} and subjected to the H_2O_2 concentration of 15 μM (S1H2) (Table 2) stood out among the treatments, exhibiting the highest values of *gs* (0.330 mol H_2O m^{-2} s^{-1}), A (33.11 μmol CO_2 m^{-2} s^{-1}), *iCE* (0.321 [(μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 m^{-2} s^{-1})$^{-1}$], PH (59.00 cm), SD (10.78 mm), NL (82 leaves), LA (2025.2 cm²), Chl *a* (643.6 μg mL^{-1}), and Chl *t* (1059.8 μg mL^{-1}).

From treatment S1H1 (ECw of 0.8 dS m^{-1} and 0 μM H_2O_2) to S1H2, *gs, A, iCE,* PH, SD, NL, LA, Chl *a*, and Chl *t* increased by 11.86, 11.52, 12.63, 10.36, 8.01, 12.33, 18.14, 56.06, and 47.7%, respectively, indicating a beneficial effect of the application of hydrogen peroxide at a concentration of 15 μM.

It is important to stress that the plants subjected to treatment S2H2 also showed a beneficial effect of foliar application of 15 μM of H_2O_2 when irrigated with ECw of 1.4 dS m^{-1}. From treatment S2H1 to S2H2, *gs, A, iCE,* PH, SD, NL, LA, Chl *a*, and Cl *t* increased by 3.5, 6.37, 2.87, 10.35, 8.0, 11.42, 18.13, 30.09, and 68.37%, respectively.

Table 2

Eigenvalues, percentage of total explained variance in multivariate analysis of variance (MANOVA), and correlations (r) between original variables and principal components

	Principal component	
	PC1	PC2
Eigenvalues (λ)	8.72	1.47
Percentage of total variance (S^2%)	72.67	12.23
Hotelling's test (T^2) for water electrical conductivity (ECw)	0.01	0.01
Hotelling's test (T^2) for hydrogen peroxide (H_2O_2)	0.01	0.01
Hotelling's test (T^2) for the interaction (ECw × H_2O_2)	0.01	0.02

PC	Correlation coefficient											
	Ci	*gs*	*E*	*A*	*iCE*	PH	SD	NL	LA	Chl *a*	Chl *b*	Chl *t*
PC1	0.78	-0.90	-0.86	-0.92	-0.90	-0.96	-0.94	-0.95	-0.86	-0.76	-0.58	-0.75
PC2	0.22	-0.14	-0.22	-0.21	-0.22	-0.03	-0.18	-0.07	-0.18	0.51	0.70	0.66
	Mean value											
	Ci	*gs*	*E*	*A*	*iCE*	PH	SD	NL	LA	Chl *a*	Chl *b*	Chl *t*
S1H1	104	0.295	5.40	29.69	0.285	53.46	9.98	73	1714.2	412.4	305.1	717.5
S1H2	103	0.330	4.84	33.11	0.321	59.00	10.78	82	2025.2	643.6	416.2	1059.8
S1H3	111	0.283	4.01	31.47	0.283	54.55	9.19	75	1500.9	563.0	383.1	946.1
S1H4	116	0.277	3.41	27.34	0.236	51.71	8.80	71	1386.5	570.7	244.7	815.4
S1H5	119	0.276	3.37	24.29	0.204	48.78	8.44	69	1305.6	348.0	199.1	547.2
S2H1	121	0.281	4.41	29.67	0.245	51.86	9.78	70	1645.7	448.1	119.5	567.6
S2H2	125	0.291	3.97	31.56	0.252	57.23	10.56	78	1944.1	623.3	332.4	955.7
S2H3	134	0.271	4.01	28.84	0.216	52.91	9.01	72	1440.9	551.4	276.4	827.8
S2H4	141	0.225	3.09	23.54	0.167	50.16	8.62	68	1331.0	469.4	338.6	808.0
S2H5	141	0.211	2.81	22.58	0.160	47.32	8.27	66	1253.3	329.5	183.1	512.6
S3H1	141	0.275	4.37	27.71	0.197	50.30	9.29	68	1579.8	340.4	307.0	647.4
S3H2	142	0.285	3.75	29.08	0.204	55.51	10.04	75	1866.4	399.4	185.1	584.5
S3H3	145	0.266	3.52	28.16	0.194	51.33	8.56	69	1383.3	400.9	316.4	717.3
S3H4	145	0.221	3.04	22.22	0.153	48.65	8.19	66	1277.8	503.1	329.2	832.3

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continuation...

S3H5	156	0.207	2.70	21.51	0.138	45.90	7.86	64	1203.2	434.1	155.9	590.0
S4H1	133	0.270	3.67	24.96	0.187	48.79	9.01	65	1516.6	462.3	373.1	835.5
S4H2	134	0.279	3.15	26.84	0.200	53.85	9.74	72	1791.7	478.5	367.4	845.8
S4H3	124	0.260	3.02	28.77	0.231	49.79	8.30	66	1327.9	399.5	199.0	598.4
S4H4	108	0.216	2.61	25.24	0.233	47.19	7.94	63	1226.6	295.6	213.1	508.7
S4H5	168	0.203	2.52	21.44	0.128	44.52	7.62	61	1155.1	350.2	201.8	552.1
S5H1	149	0.264	3.21	21.99	0.147	47.33	8.47	62	1456.0	393.1	233.5	626.7
S5H2	145	0.274	3.03	23.53	0.162	52.23	9.15	69	1720.1	365.0	144.6	509.6
S5H3	171	0.255	2.58	18.88	0.111	48.29	7.80	63	1274.8	462.5	322.8	785.3
S5H4	162	0.212	2.32	16.55	0.102	45.78	7.47	61	1177.6	375.2	221.9	597.1
S5H5	207	0.199	2.28	15.18	0.073	43.18	7.16	59	1108.9	247.2	156.5	403.7

S1 = 0.8 dS m^{-1}; S2 = 1.4 dS m^{-1}; S3 = 2.0 dS m^{-1}; S4 = 2.6 dS m^{-1}; S5 = 3.2 dS m^{-1}; H1 = 0 μM; H2 = 15 μM; H3 = 30 μM; H4 = 45 μM; H5 = 60 μM; *Ci* = intracellular CO_2 concentration (μmol CO_2 m^{-2} s^{-1}); *gs* = stomatal conductance (mol H_2O m^{-2} s^{-1}); *E* = transpiration (mmol H_2O m^{-2} s^{-1}); *A* = CO_2 assimilation rate (μmol CO_2 m^{-2} s^{-1}); *iCE* = instantaneous carboxylation efficiency [(μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 m^{-2} s^{-1})$^{-1}$]; PH = plant height (cm); SD = stem diameter (mm); NL = number of leaves; LA = leaf area (cm^2); Chl *a* = chlorophyll a (μg mL^{-1}); Chl *b* = chlorophyll *b* (μg mL^{-1}); Chl *t* = total chlorophyll (μg mL^{-1}).

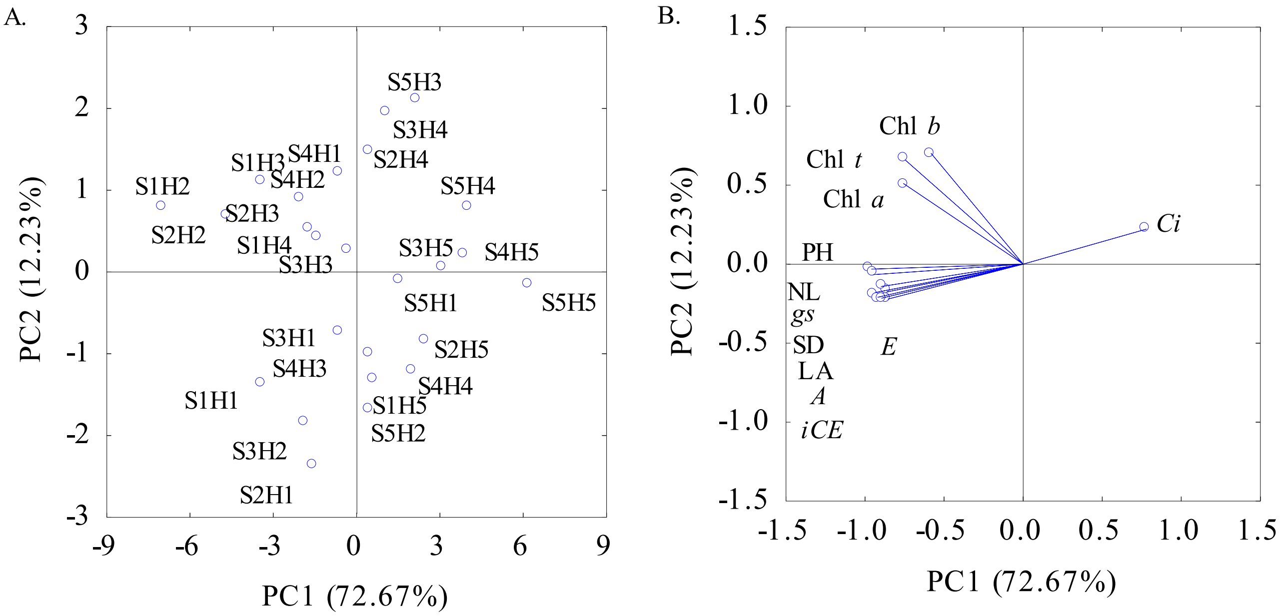

Figure 2. Two-dimensional projection of principal component scores for the factors of irrigation-water electrical conductivity (S) and hydrogen peroxide concentrations (H) (A) and variables analyzed (B) in the two principal components (PC1 and PC2).
Ci = intracellular CO_2 concentration; *gs* = stomatal conductance; E = transpiration; *A* = CO_2 assimilation rate; *iCE* = instantaneous carboxylation efficiency; PH = plant height; SD = stem diameter; NL = number of leaves; LA = leaf area; Chl *a* = chlorophyll *a*; Chl *b* = chlorophyll *b*; Chl *t* = total chlorophyll.

Ramos et al. (2022) worked with the passion fruit crop (*Passiflora edulis* Sims) under ECw ranging from 0.6 to 3.0 dS m^{-1} and foliar application of H_2O_2 and also found beneficial effects on growth and photosynthetic pigments when the plants received the H_2O_2 concentration of 15 μM. Dantas et al. (2022) studied Italian zucchini (*Cucurbita pepo* L.) under ECw ranging from 2.1 to 6.6 and exogenous application of H_2O_2 at 20 μM and described similar findings for growth rates and gas exchange. These authors attributed these results to the action of hydrogen peroxide as a signaling molecule that regulates several metabolic pathways, including responses to salt stress.

When applied at adequate concentrations, H_2O_2 can activate the antioxidant enzymatic defense mechanism (catalase and peroxidase) in plants, reducing the negative effect of reactive oxygen species (ROS) (Kilic & Kahraman, 2016), as confirmed in the present study. The beneficial effects of exogenous application of H_2O_2 in plants under salt stress may also be related to the activation of the defense system of antioxidant enzymes such as superoxide dismutase, catalase, guaiacol peroxidase, and ascorbate peroxidase, which act by reducing the deleterious effects of salinity (Carvalho et al., 2011).

Regardless of the H_2O_2 concentration, the intracellular CO_2 concentration (*Ci*) in the mesophyll cells increased and transpiration rate (*E*) decreased as the ECw level was raised, demonstrating the negative effects of salinity on the bell pepper plants. The reduction in *E* is directly related to partial stomatal closure, since less opening of the stomata will cause transpiration to decrease, restricting the loss of water from the leaf to the atmosphere in the form of steam and thus reducing the plant's dehydration (Lima et al., 2017; S. S. da Silva et al., 2019) a condition that would explain the accumulation of CO_2 in the mesophyll.

In principal component 2 (PC2), the bell pepper plants cultivated under the ECw of 0.8 dS m^{-1} and subjected to foliar application with H_2O_2 at the concentration of 15 μM (S1H2) obtained the highest Chl *b* value (416.2 μg mL^{-1}), corresponding to a 36.41% increase compared with those cultivated with the lowest ECw level (0.8 dS m^{-1}) and without application of H_2O_2 (S1H1) (Table 2).

Hydrogen peroxide is a ROS which, when applied at low concentrations, helps in the process of acclimatization to salt stress by inducing metabolic changes responsible for increasing tolerance to stress, thus enabling the use of waters with higher salt concentrations (Andrade et al., 2019, 2022; A. A. R. da Silva et al., 2022).

The hydrogen peroxide used in seed pretreatment, as performed in this study, provides moderate stress, resulting in accumulation of latent signals in different parts of the plant. However, in a more severe stress condition, the stored signals contribute to molecular adjustments, constituting a remarkable tolerance mechanism (Savvides et al., 2016).

Relative water content (RWC), electrolyte leakage (%EL), instantaneous water use efficiency (*iWUE*), and carotenoid contents showed a correlation coefficient lower than 0.6. For this reason, they were removed from multivariate analysis and instead analyzed by univariate analysis. According to the summary of analysis of variance (Table 3), the interaction between ECw levels and the H_2O_2 concentrations did not significantly affect ($p > 0.05$) these variables; however, when the factors were analyzed in isolation, the ECw levels significantly affected ($p \leq 0.01$) RWC, %EL, and *iWUE*, whereas the of H_2O_2 concentrations affected %EL and *iWUE.*

The RWC of the bell pepper plants (Figure 3A) decreased linearly, by 9.23%, per unit increase in ECw, that is, when subjected to the lowest electrical conductivity level (0.8 dS m^{-1}), the plants showed a 24.08% higher RWC than those cultivated under the ECw of 3.2 dS m^{-1}. The reduction in leaf blade water content reflects the osmotic action whereby high salt concentrations restrict water and nutrient absorption by plants (Morais et al., 2018; S. S. da Silva et al., 2021).

Table 1
Chemical and physical attributes of the soil used in the experiment, before the implementation of the treatments

Source of variation	DF	Mean square			
		RWC	% EL	*iWUE*	Car
Salinity level (SL)		1051.29**	35.91**	84.66**	0.24^{ns}
Linear regression	1	4197.19**	99.52**	327.97**	-
Quadratic regression	1	2.49^{ns}	25.91^{ns}	7.54^{ns}	-
Hydrogen peroxide (H_2O_2)	4	6.93^{ns}	114.81**	7.36**	0.64^{ns}
Linear regression	1	-	264.64*	23.99*	-
Quadratic regression	1	-	94.94**	0.15**	-
Interaction (SL × H_2O_2)	16	16.29^{ns}	1.49^{ns}	2.51^{ns}	1.56^{ns}
Blocks	2	10.28^{ns}	14.06^{ns}	5.19^{ns}	17.38^{ns}
Residual	48	15.21	5.13	1.57	0.11
CV (%)		5.01	7.01	16.27	12.82

ns, *, ** = not significant and significant at $p \leq 0.05$ and $p \leq 0.01$, respectively. CV = coefficient of variation.

Electrolyte leakage in the leaf blades of the bell pepper plants rose with ECw (Figure 3B), increasing by 5.42% with each unit increase in conductivity. From the ECw level of 0.8 to 3.2 dS m^{-1}, %EL increased by 12.48%. As regards the effects of H_2O_2 concentrations, they reduced electrolyte leakage up to the concentration of 15 μM, after which %EL started to increase (Figure 3C). The increase in %EL in plants subjected to hydrogen peroxide concentrations greater than 15 μM may occur because, at high concentrations, H_2O_2 can intensify the deleterious effects of salt stress, causing alterations in plant metabolism by restricting photosynthetic processes. Under salt stress conditions, photosynthetic processes can be affected directly by stomatal restriction, reduced transpiration, and the consequently reduced CO_2 uptake; or, indirectly, by the imbalance between the production and removal of ROS during the photosynthetic process, causing oxidative stress (Carvalho et al., 2011; R. C. P. da Silva et al., 2020).

Under salinity, plants are affected by osmotic and ionic stresses, which reduce RWC and increase electrolyte leakage through the plasma membrane (Rady et al., 2018; Venâncio et al., 2022). The present results corroborate this assertion, as there was a significant reduction in the RWC and an increase in the %EL in response to the increase in irrigation-water electrical conductivity.

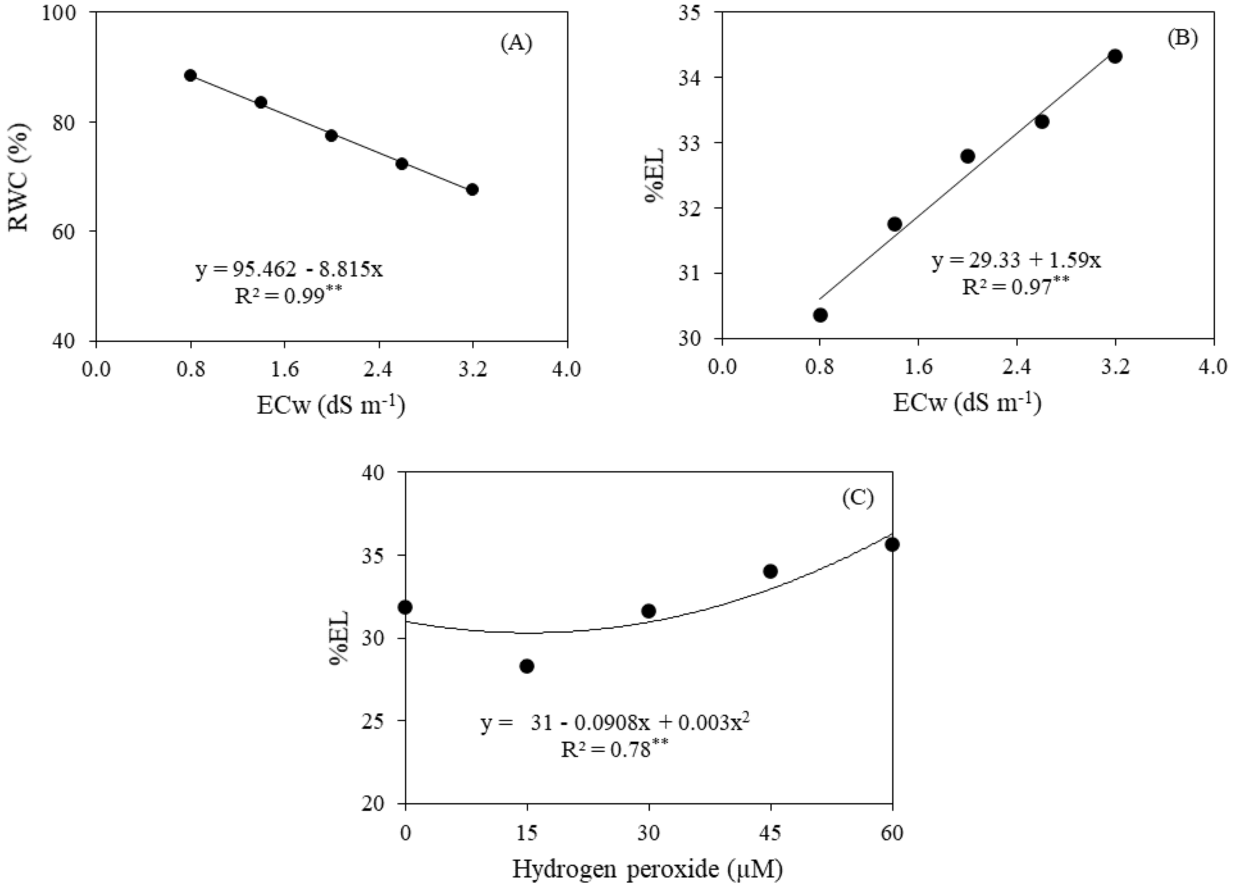

Figure 3. Relative water content (RWC, A) and electrolyte leakage (%EL, B) as a function of irrigation water electrical conductivity (ECw) and electrolyte leakage as a function of hydrogen peroxide (C) concentrations at 90 days after sowing.
**, significant at $p \leq 0.01$.

Instantaneous water use efficiency by the bell pepper plants decreased linearly, by 19.5%, with each unit increase in ECw (Figure 4). In relative terms, plants subjected to the ECw of 3.2 dS m^{-1} had a 5.91 [(μmol CO_2 m^{-2} s^{-1}) (mol H_2O m^{-2} s^{-1})$^{-1}$] lower *iWUE* than those that received water with the lowest salinity level (0.8 dS m^{-1}). According to Sá et al. (2019), plants attempt to overcome osmotic stress and reduce the uptake of toxic ions by reducing stomatal conductance and transpiration, thereby increasing water use efficiency and the relative water content of their leaves. Nevertheless, this mechanism was not sufficient to increase the water use efficiency of bell pepper under saline conditions. Veloso et al. (2021) obtained similar results in a study with the bell pepper crop under water salinity (ECw ranging from 0.8 to 3.2 dS m^{-1}), where increasing ECw levels reduced *iWUE.* As explained by the authors, this reduction is related to the fact that bell pepper is moderately sensitive to salinity and thus unable to increase its water utilization, having its efficiency reduced under salinity conditions.

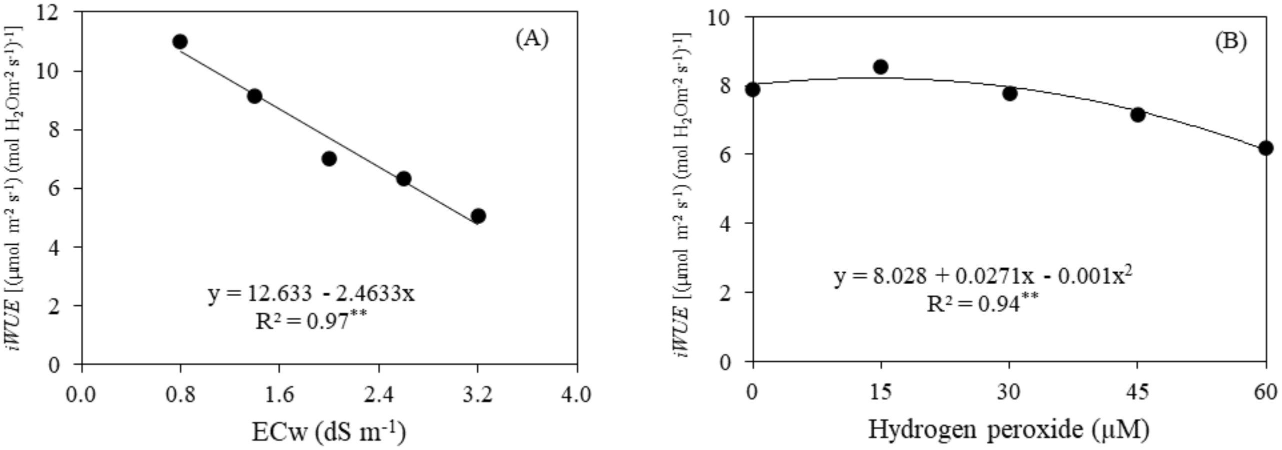

Figure 4. Instantaneous water use efficiency (*iWUE*) as a function of irrigation-water electrical conductivity (ECw, A) and as a function of hydrogen peroxide concentrations (B), at 90 days after sowing.
**, significant at $p \leq 0.01$.

Hydrogen peroxide concentrations also affected the plants' *iWUE* (Figure 4B). The application of 13.55 μM of H_2O_2 provided the maximum estimated *iWUE* value of 8.21 [(μmol CO_2 m^{-2} s^{-1}) (mol H_2O m^{-2} s^{-1})$^{-1}$], decreasing from this concentration and to a minimum value of 6.05, under foliar application of 60 μM of H_2O_2. This demonstrates the efficiency of H_2O_2 in attenuating the damage caused by salinity on the analyzed variables. The stress-signaling function performed by hydrogen peroxide is assumed to be able to trigger the activation of plant antioxidant enzymes to mitigate oxidative damage (Dito & Gadallah, 2019).

Conclusions

The application of hydrogen peroxide at the concentration of 15 μM attenuates the deleterious effects of salt stress in 'All Big' bell pepper plants irrigated with saline water with ECw of up to 1.4 dS m^{-1}. When associated with water salinity of 0.8 dS m^{-1}, hydrogen peroxide at a concentration of 15 μM increases stomatal conductance, CO_2 assimilation rate, instantaneous carboxylation efficiency, and growth in pepper plants. The application of hydrogen peroxide at concentrations greater than 15 μM intensifies the deleterious effects of salt stress on 'All big' bell pepper at 90 days after sowing.

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