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Scientific Article

Hydrogen peroxide in attenuating salt stress in soursop

Peróxido de hidrogênio na atenuação do estresse salino em gravioleira

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ABSTRACT - In semi-arid regions, the use of saline water for irrigation has become an increasingly frequent reality due to the qualitative and quantitative scarcity of water sources occurring most of the year. Thus, the use of hydrogen peroxide can be a strategy capable of mitigating the deleterious effects of salt stress on plants and guaranteeing the agricultural production of crops such as soursop. Thus, the objective of this study was to evaluate the effects of foliar application of hydrogen peroxide on the physiological and growth indices of soursop plants cv. Morada Nova irrigated with waters of different salinity levels. The treatments were distributed in a randomized block design, in a 4 × 4 factorial scheme, corresponding to four levels of electrical conductivity of irrigation water and four concentrations of hydrogen peroxide, with three replicates. Foliar application of hydrogen peroxide at concentrations of 12, 18 and 15 µM, respectively, attenuated the effects of salt stress on stomatal conductance, CO_2 assimilation rate and chlorophyll *a* synthesis of soursop, at 780 days after transplanting. The 30 µM hydrogen peroxide concentration intensified salt stress on gas exchange, variable fluorescence and electrolyte leakage in the leaf blade of soursop plants cv. Morada Nova, 780 days after transplanting.

Keywords: *Annona muricata* L. Salinity. Reactive oxygen species. Oxidative stress.

RESUMO - Em regiões semiáridas, a utilização de água salina para irrigação, tem se tornado uma realidade cada vez mais frequente em função da escassez qualitativa e quantitativa das fontes hídricas que ocorre na maior parte do ano. Assim, a utilização de peróxido de hidrogênio pode ser uma estratégia capaz de amenizar os efeitos deletérios do estresse salino sobre as plantas e garantir a produção agrícola de culturas, como a gravioleira. Deste modo, objetivou-se com esta pesquisa avaliar os efeitos da aplicação foliar de peróxido de hidrogênio sobre os índices fisiológicos e de crescimento de plantas de graviola cv. Morada Nova irrigadas com águas de diferentes níveis salinos. Os tratamentos foram distribuídos em um delineamento de blocos casualizados, em esquema fatorial 4 × 4, correspondendo a quatro níveis de condutividade elétrica da água de irrigação e quatro concentrações de peróxido de hidrogênio, com três repetições. A aplicação foliar de peróxido de hidrogênio nas concentrações de 12, 18 e 15µM, respectivamente, atenuaram os efeitos do estresse salino sobre a condutância estomática, a taxa de assimilação de CO_2 e a síntese de clorofila *a* de gravioleira, aos 780 dias após o transplantio. A concentração de peróxido de hidrogênio de 30 µM intensificou o estresse salino sobre as trocas gasosas, a fluorescência variável e o extravasamento de eletrólitos no limbo foliar de plantas de graviola cv. Morada Nova, aos 780 dias após o transplantio.

Palavras-chave: *Annona muricata* L. Salinidade. Espécie reativa de oxigênio. Estresse oxidativo.

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INTRODUCTION

Belonging to the Annonaceae family, soursop (*Annona muricata L.*) is a fruit tree cultivated in Brazil, mainly in the semi-arid region of the Northeast, due to the multifunctionality of its production, standing out as a good source of vitamins B and C (HASMILA; NATSIR; SOEKAMTO, 2019). It is a source of carbohydrates, minerals, antioxidant substances and important bioactive compounds, such as acetogenins, which act in the prevention of degenerative diseases (MUTAKIN et al., 2022).

Although the semi-arid region of Northeastern Brazil has edaphoclimatic conditions for soursop cultivation, but the scarcity of rainfall and the high evapotranspiration that occur in most months of the year contribute for the sources of water, whether underground (wells) and/or superficial (small and medium-sized dams and lagoons), to contain high levels of salts, limiting its use for irrigation (BRITO et al., 2020).

Excess salts in the water reduce the osmotic potential of the soil solution, affecting water availability and causing ionic effect and changes in soil physical and chemical properties (SOARES et al., 2018). In addition, excessive presence of salts in the root zone of plants can negatively affect cell membrane integrity, limiting the photosynthetic process due to the partial stomatal closure, resulting in damage to the photosynthetic apparatus and/or the enzymatic system of CO_2 fixation, regardless of the nature of the salts (VELOSO et al., 2020a).

However, salt stress effects on plants can be mitigated with the use of elicitors, such as hydrogen peroxide (H_2O_2) (CAPITULINO et al., 2022). When plants are subjected to pre-treatment with adequate concentrations of H_2O_2, they undergo changes in their metabolism, through the activation of the enzymatic and non-enzymatic antioxidant defense system, which confers greater tolerance to abiotic stresses such as salinity (VELOSO et al., 2020b).

In this context, some studies have reported that H_2O_2 application can increase tolerance to salt stress, as observed in passion fruit plants (RAMOS et al., 2022) and in soursop in the seedling formation phase (CAPITULINO et al., 2022). In view of the above, the objective of this study was to evaluate the effects of foliar application of H_2O_2 on the physiological indices and growth of soursop under irrigation with saline waters.

MATERIAL AND METHODS

The experiment was carried out between April 2020 and May 2022 in a greenhouse, located at the Academic Unit of Agricultural Engineering - UAEA of the Federal University of Campina Grande - UFCG, in Campina Grande, Paraíba, at geographic coordinates 7°15'18" South latitude, 35°52'28" West longitude and average altitude of 550 m. Temperature (maximum and minimum) and relative humidity data measured inside the greenhouse are shown in Figure 1.

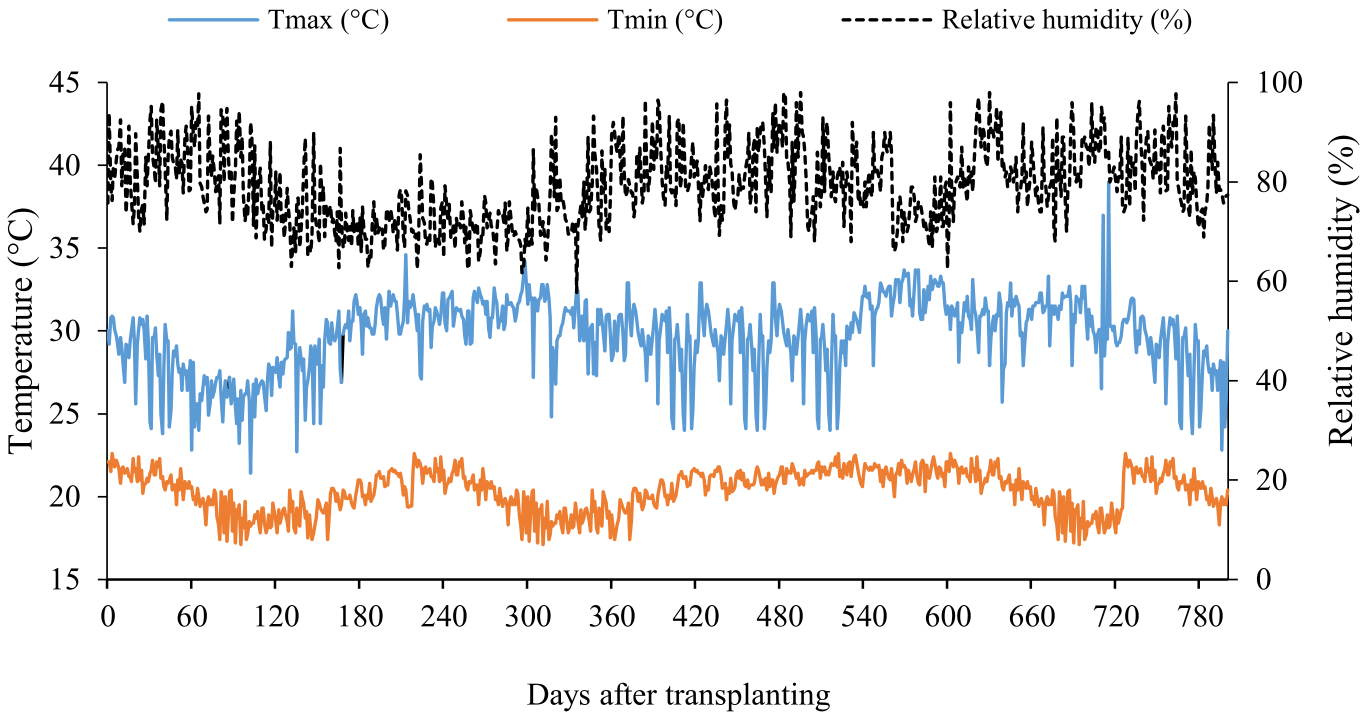


Figure 1. Air temperature (maximum and minimum) and average relative humidity in the internal area of the greenhouse during the experimental period.

The treatments consisted of four levels of electrical conductivity of irrigation water - ECw (0.8, 1.6, 2.4 and 3.2 dS m^{-1}) and four concentrations of hydrogen peroxide - H_2O_2 (0, 10, 20 and 30 μM), in a 4 × 4 factorial arrangement, distributed in randomized blocks, with three replicates. Water electrical conductivity levels were based on a previous study conducted by Silva et al. (2019a), while H_2O_2 concentrations were established based on a study conducted by Veloso et al. (2020b).

Soursop seedlings cv. Morada Nova were obtained in a commercial nursery accredited by the Registry of Seeds and Seedlings, in the District of São Gonçalo, Sousa, PB, produced in polyethylene bags with dimensions of 10 × 20 cm. The Morada Nova cultivar was chosen due to its greater use in commercial orchards in Brazil, as well as its production potential and the size of its fruits, which can weigh up to 15 kg (SÃO JOSÉ et al., 2014).

The experiment was conducted using plastic pots adapted as drainage lysimeters, with 211.5 L (depth of 0.75 m and area of 0.2115 m²) and filled with a 1.0-kg layer of crushed stone followed by 230 kg of soil classified as *Neossolo Regolítico* (Entisol) of clayey loam texture, collected at 0-30 cm depth, from the municipality of Riachão do Bacamarte, PB, Brazil, whose physicochemical characteristics (Table 1) were determined according to Teixeira et al. (2017).

Table 1. Chemical and physical characteristics of the soil (0-30 cm depth) used in the experiment, before application of the treatments.

Physical-chemical characteristics								
pH H_2O	OM	P	K^+	Na^+	Ca^{2+}	Mg^{2+}	Al^{3+}	H^+
1:2.5	g dm^{-3}	mg dm^{-3}	----------cmol$_c$ kg^{-1}----------					
6.5	8.1	79	0.24	0.51	14.9	5.4	0	0.9
---------Chemical characteristic ---------				---------Physical characteristics---------				
EC_{se}	CEC	SAR_{se}	ESP	Particle-size fraction (g kg^{-1})			Moisture (dag kg^{-1})	
dS m^{-1}	cmol$_c$ kg^{-1}	(mmol L^{-1})$^{0.5}$	%	Sand	Silt	Clay	33.42 kPa[1]	1519.5 kPa[2]
2.15	16.54	0.16	3.08	572.7	100.7	326.6	25.91	12.96

pH – Hydrogen potential, 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+}+H^+ extracted with 0.5 M CaOAc at pH 7.0; EC_{se} - Electrical conductivity of saturation extract; CEC - Cation Exchange Capacity; SAR_{se} - Sodium adsorption ratio of saturation extract; ESP - Exchangeable sodium percentage; [1,2] Referring to field capacity and permanent wilting point.

The saline waters were prepared by the addition of NaCl, $CaCl_2.2H_2O$ and $MgCl_2.6H_2O$ salts, in the equivalent ratio of 7:2:1, which prevails in the main sources of water available for irrigation in the Brazilian Northeast (MEDEIROS, 1992), following the relationship between ECw and the concentration of salts (RICHARDS, 1954), according to Equation 1:

$$Q \approx 640 \times ECw \quad (1)$$

where:
Q = Quantity of salts to be applied (mg L^{-1});
ECw = Electrical conductivity of water (dS m^{-1})

At 60 days after transplanting, irrigation with saline water began to be performed, applying water to each lysimeter according to treatment, in order to keep soil moisture close to field capacity and avoid excessive accumulation of salts in the soil. The volume to be applied was determined according to the water needs of the plants. Every day, at 5 p.m., the volume corresponding to that obtained by the water balance was manually applied to each container, according to Equation 2:

$$VI = \frac{(Va - Vd)}{(1 - LF)} \quad (2)$$

where:
VI = volume of water to be used in the next irrigation event (mL);
Va = volume applied in the previous irrigation event (mL);
Vd = volume drained (mL); and
LF = leaching fraction of 0.10, applied every 30 days.

NPK fertilization was carried out as recommended by Cavalcante et al. (2008), applying 40 g of N, 60 g of K_2O and 40 g of P_2O_5 per plant $year^{-1}$. Fertilization was split into 24 portions and applied every 15 days. Urea (45% N), potassium sulfate (50% K_2O and 17% S) and monoammonium phosphate (12% N and 54% P_2O_5) were used as sources of nitrogen, potassium and phosphorus, respectively.

Micronutrients were applied through the leaves from 60 days after transplanting and 2.5 g L^{-1} of a Dripsol® Micro solution with the following composition continued to be applied fortnightly: N (15%); P_2O_5 (15%); K_2O (15%); Ca (1%); Mg (1.4%); S (2.7%); Zn (0.5%); B (0.05%); Fe (0.5%); Mn (0.05%); Cu (0.5%); Mo (0.02%).

The different concentrations of H_2O_2 were obtained by dilution in distilled water, with subsequent calibration using a spectrophotometer at an absorbance wavelength of 240 nm. Foliar applications began 45 days after transplanting (DAT) of seedlings grown in lysimeters and were performed at 30-day intervals. To ensure that the leaves were completely wet, a knapsack sprayer with an adjustable conical 1 cm metal nozzle, service pressure of 2.07 MPa and flow rate of 1.1 L min^{-1} was used to spray the solution on the abaxial and adaxial sides of the leaves, between 5 and 6 p.m. The volume of H_2O_2 solution per plant was approximately 400 mL. In addition, to control the drift of the solution between treatments, a plastic tarpaulin curtain was placed around each plant during the application of the H_2O_2 solution.

Formative pruning was carried out when the plant reached 60 cm height, when the apical meristem was cut. From the shoots that emerged, three well-distributed and equidistant branches were selected and then pruned when they reached 40 cm in length (SILVA et al., 2020). During the experiment, the appearance of pests and diseases was monitored and, when the incidence was observed, these were eradicated with the use of pesticides.

At 780 DAT, gas exchange, chlorophyll *a* fluorescence, photosynthetic pigments, electrolyte leakage, saturation deficit in the leaf blade and relative growth rate in stem diameter of soursop cv. Morada Nova were evaluated. Gas exchange was evaluated in leaves of the middle third of the plants, using a portable infrared gas analyzer – IRGA (Infrared Gas Analyser, LCpro-SD model, from ADC BioScientific, UK). The variables analyzed were CO_2 assimilation rate - A (μmol CO_2 m^{-2} s^{-1}), transpiration - E (mmol H_2O m^{-2} s^{-1}), stomatal conductance - gs (mol H_2O m^{-2} s^{-1}) and internal CO_2 concentration - Ci (μmol CO_2 m^{-2} s^{-1}).

A/gs and A/Ci ratios were used to determine water use efficiency – $WUEi$ [(μmol CO_2 m^{-2} s^{-1}) (mmol H_2O m^{-2} s^{-1})$^{-1}$] and carboxylation efficiency – CEi [(μmol CO_2 m^{-2} s^{-1}) (μmol CO_2 m^{-2} s^{-1})$^{-1}$], respectively. The readings were taken between 7:00 and 10:00 a.m., on the third fully expanded leaf counted from the apical bud, under natural conditions of air temperature, atmospheric CO_2 concentration, using constant light of 1,200 µmol m^{-2} s^{-1}, established through the light-photosynthesis response curve (FERNANDES et al., 2021).

Chlorophyll *a* fluorescence was measured on the same leaves using a pulse-modulated fluorometer, OS5p model from Opti Science. Initial (F_0), maximum (Fm) and variable (Fv) fluorescence and quantum efficiency of photosystem II (Fv/Fm) were measured; this protocol was performed after adaptation of the leaves to the dark for a period of 30 min, between 6:00 and 9:00 am, using a clip of the device, to ensure that all primary acceptors were fully oxidized.

Contents of chlorophyll *a*, chlorophyll *b*, total chlorophyll and carotenoids were also determined at 780 DAT, according to the methodology of Arnon (1949), using 5 leaf discs obtained from the third mature leaf from the apex, immersed in 80% acetone and stored in the dark for 48 hours. The extracts obtained were subjected to spectrophotometer readings at wavelengths of 470, 647 and 663 nm. The values observed in the readings were applied in the following equations (Equations 3, 4, 5):

$$\text{Chlorophyll } a \text{ (Chl } a) = (12.21 \times ABS_{663}) - (2.81 \times ABS_{647}) \quad (3)$$

$$\text{Chlorophyll } b \text{ (Chl } b) = (20.13 \times ABS_{647}) - (5.03 \times ABS_{663}) \quad (4)$$

$$\text{Carotenoids (Car)} = [(1000 \times ABS_{470}) - (1.82 \times \text{Chl } a) - (85.02 \times \text{Chl } b)]/198 \quad (5)$$

The values obtained for the contents of chlorophyll *a*, chlorophyll *b*, total chlorophyll and carotenoids in the leaves were expressed in mg g^{-1} FM (fresh matter).

Electrolyte leakage (%EL) in the leaf blade was determined using a copper hole punch to obtain five leaf discs with area of 1.54 cm² each, per experimental unit, which were washed and placed in an Erlenmeyer flask containing 50 mL of distilled water. After being closed with aluminum foil, the Erlenmeyer flasks were stored at a temperature of 25 °C for 24 hours, and then the initial conductivity of the medium (Xi) was measured using a benchtop conductivity meter (MB11, MS Techonopon®). Then, the Erlenmeyer flasks were subjected to a temperature of 90 °C for 120 minutes in a drying oven (SL100/336, SOLAB®) and, after their contents cooled down, the final conductivity (Xf) was measured. Electrolyte leakage was expressed as the percentage of initial electrical conductivity relative to electrical conductivity after treatment for 90 minutes at 90 ºC, according to the methodology described by Scotti-Campos et al. (2013), as shown in Equation 6:

$$\%EL = \frac{Xi}{Xf} \text{ x } 100 \quad (6)$$

where:
%EL = electrolyte leakage (%);
Xi = initial conductivity of the medium;
Xf = final conductivity.

To determine the water saturation deficit (WSD), two leaves were collected from the middle third of the main branch and four 12-mm-diameter discs were obtained from each leaf. Immediately after collection, the discs were weighed, avoiding moisture loss, and fresh mass (FM) was obtained; then, these samples were placed in beaker, immersed in 50 mL of distilled water, and kept at rest for 24 hours. After this period, excess water was removed from the resting discs using paper towels and the turgid mass (TM) of the samples was obtained. These samples were then dried in an oven at a temperature of ≈ 65 ± 3 ºC until reaching constant weight to obtain the dry mass (DM). WSD was determined according to Lima et al. (2015), using Equation 7:

$$WSD = \frac{TM - FM}{TM - DM} \text{ x } 10 \quad (7)$$

where:
WSD = water saturation deficit (%);
FM = leaf fresh mass (g);
TM = leaf turgid mass (g);
DM = leaf dry mass (g).

Soursop growth was evaluated based on stem diameter (SD) and on the relative growth rates of stem diameter (RGRsd) following the methodology of Benincasa (2003), according to Equation 8:

$$RGRsd = \frac{(\ln A2 - \ln A1)}{(t2 - t1)} \quad (8)$$

where:
RGRsd = Relative growth rate of stem diameter (mm day^{-1}),
A_2 = stem diameter at 780 DAT;
A_1 = stem diameter at 210 DAT;
$t_2 - t_1$ = time difference between assessments; and
ln = natural logarithm.

The collected data were subjected to the distribution normality test (Shapiro-Wilk test). Then, analysis of variance was performed at 0.05 probability level and, in cases of significance of individual factors, regression analysis was performed, using the statistical program SISVAR-ESAL (FERREIRA, 2019). In case of significance of the interaction between factors, SigmaPlot v.12.5 software was used to construct the response surfaces.

RESULTS AND DISCUSSION

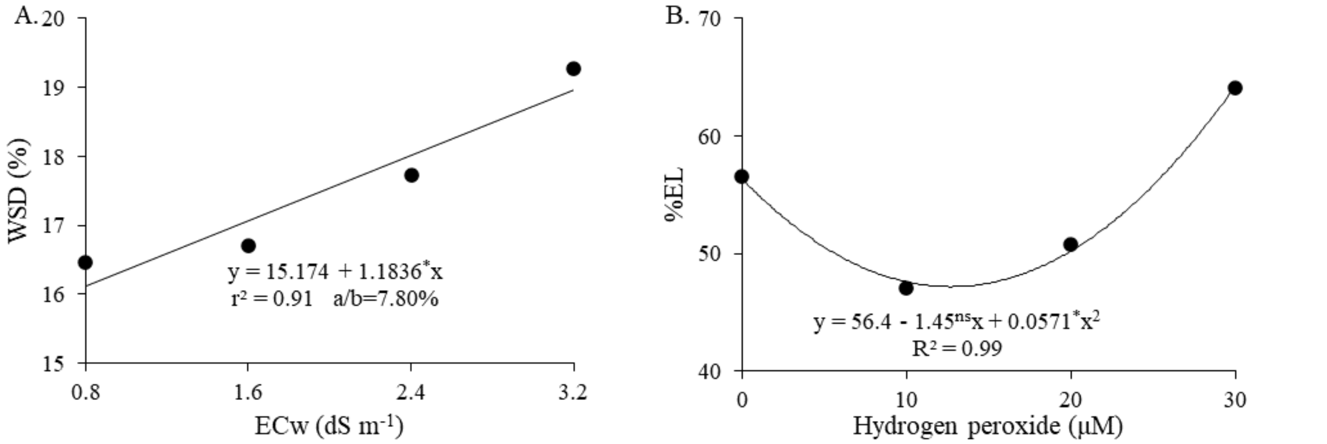
There were significant effects (Table 2) of the interaction between water salinity levels and H_2O_2 concentrations on the internal CO_2 concentration (*Ci*) CO_2 assimilation rate (*A*), transpiration (*E*) and instantaneous water use efficiency (*WUEi*) of soursop plants. The water salinity levels alone influenced the water saturation deficit. On the other hand, H_2O_2 concentrations alone influenced electrolyte leakage (%EL), stomatal conductance (*gs*) and instantaneous carboxylation efficiency (CEi).

Table 2. Summary of the analysis of variance for water saturation deficit (WSD), electrolyte leakage (%EL), stomatal conductance (*gs*), internal CO_2 concentration (*Ci*), CO_2 assimilation rate (*A*), transpiration (*E*), instantaneous water use efficiency (*WUEi*) and instantaneous carboxylation efficiency (CEi) of soursop plants cv. Morada Nova irrigated with saline water and subjected to foliar application of hydrogen peroxide at 780 days after transplanting.

Source of variation	DF	Mean Squares							
		WSD	%EL	*gs*	*Ci*	*A*	*E*	*WUEi*	CEi
Salinity level (SL)	4	27721.1^{*}	1142.7^{ns}	0.001669^{ns}	102476.1^{ns}	2.2700^{ns}	0.3615^{ns}	9.4981^{ns}	0.00001^{ns}
Linear regression	1	*	-	-	-	-	-	-	-
Quadratic regression	1	-	-	-	-	-	-	-	-
Hydrogen peroxide (H_2O_2)	4	9085.01^{ns}	934.59^{**}	0.000793^{*}	12203.1^{ns}	3.7700^{ns}	0.7204^{ns}	2.3299^{ns}	0.000010^{**}
Linear regression	1	-	-	-	-	-	-	-	-
Quadratic regression	1	-	*	**	-	-	-	-	**
Interaction (H_2O_2 × SL)	16	14039.55^{ns}	1103.2^{ns}	0.000473^{ns}	46429.0^{*}	0.1342^{**}	0.2583^{*}	1.2202^{*}	0.000082^{ns}
Blocks	3	540.58^{ns}	127.06^{ns}	0.000055^{ns}	130.13^{ns}	0.0193^{ns}	0.0126^{ns}	0.0051^{ns}	0.000002^{ns}
Residual	30	1836.82	28.82	0.000048	1607.28	0.03670	0.02780	0.02012	0.000007
CV (%)		1.77	0.90	15.27	2.75	5.64	13.07	4.81	6.91

ns, * and ** respectively not significant, significant at $p \le 0.05$ and $p \le 0.01$. DF- Degree of freedom. CV: Coefficient of variation.

Water saturation deficit in the leaf blade increased linearly (Figure 2A) by 7.80% per unit increase in ECw. Soursop plants irrigated with water of highest salinity (3.2 dS m^{-1}) showed an increase of 17.61% (2.84) compared to those irrigated under ECw of 0.8 dS m^{-1}. Increase in WSD is a consequence of the lower relative water content due to the restriction in the absorption of water and nutrients imposed by salt stress. On the other hand, soursop plants subjected to H_2O_2 concentration of 13 µM (Figure 2B) obtained lower % EL (47.19%), with an increase in electrolyte leakage of soursop plants from this concentration. This increase in %EL of plants grown under H_2O_2 concentration of 30 µM may be related to the fact that H_2O_2 is the most stable reactive oxygen species in cells and, at high concentrations, can spread rapidly across the subcellular membrane, resulting in oxidative damage to the membrane (FAROUK; AMIRA, 2018). Veloso et al. (2020b) also observed that foliar application of H_2O_2 (0 and 20 µM) to soursop (*Anonna muricata* L.) plants irrigated with saline waters (ECw ranging from 1.6 to 4.0 dS m^{-1}) reduced electrolyte leakage at 150 days after transplanting.

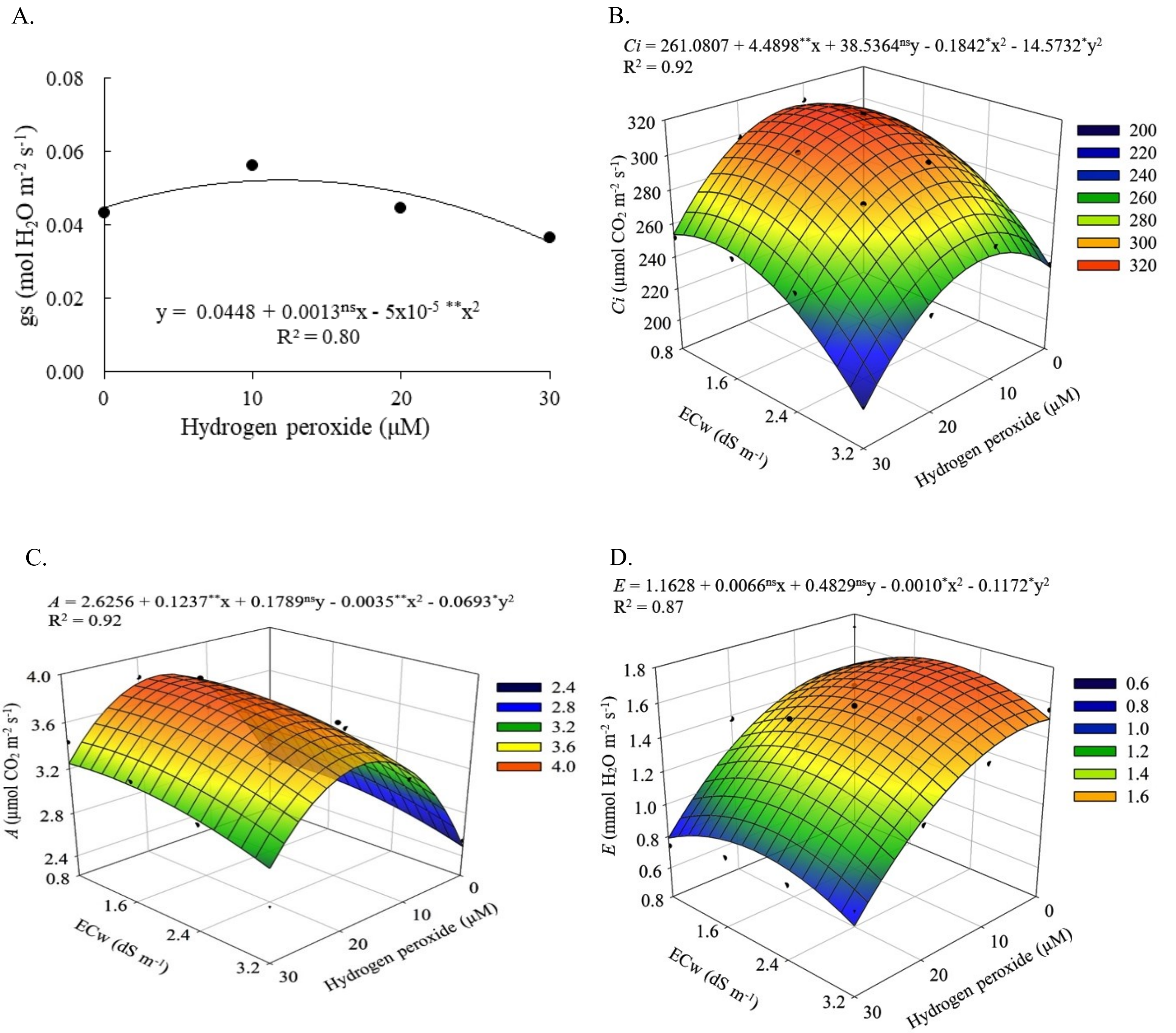


ns, * respectively not significant, significant at $p \le 0.05$.

Figure 2. Water saturation deficit – WSD (A) of soursop plants as a function of irrigation water salinity – ECw and electrolyte leakage – %EL (B) as a function of hydrogen peroxide concentrations, at 780 days after transplanting.

H_2O_2 concentrations significantly influenced the stomatal conductance (Figure 3A) of soursop plants, whose maximum estimated value (0.05325 mol H_2O m^{-2} s^{-1}) was obtained under foliar application of H_2O_2 at 13 µM. On the other hand, the lowest value (0.03880 mol H_2O m^{-2} s^{-1}) was observed in soursop plants cultivated under foliar application of H_2O_2 at 30 µM. For the internal CO_2 concentration (Figure 3B), irrigation with 1.32 dS m^{-1} water associated with foliar application of H_2O_2 at 12.19 µM promoted the highest estimated value (313.916 µmol CO_2 m^{-2} s^{-1}), being limited by the ECw of 3.2 dS m^{-1} and the highest concentrations of H_2O_2 (30 µM), with reduction of 109.74 µmol CO_2 m^{-2} s^{-1} (34.96%). The reductions in *Ci* with the increase of ECw in soursop plants treated with H_2O_2 concentrations above 12 µM probably occurred due to the lower CO_2 diffusion in the substomatal chamber, as a consequence of stomatal closure.

Stomatal closure can be considered a strategy to reduce water losses to the atmosphere and, consequently, maintain the turgidity of guard cells, directly affecting the formation of carbohydrates in photosynthesis and production (LIMA et al., 2020). The beneficial effect of H_2O_2 at low concentrations was also observed by Silva et al. (2019a), who evaluated the gas exchange and photosynthetic pigments of soursop cv. Morada Nova irrigated with saline water (ECw ranging from 0.7 to 3.0 dS m^{-1}) and subjected to the application of H_2O_2 (H_2O_2 ranging from 0 to 100 μM) by seed soaking and foliar spraying and observed that the H_2O_2 concentration of 25 μM mitigated the deleterious effects of salt stress on stomatal conductance and CO_2 assimilation rate at 120 days after sowing. However, it is important to emphasize that the application of H_2O_2 at inadequate concentrations can cause oxidative stress and, consequently, damage the cell membrane and other cellular structures, compromising the photosynthetic efficiency of the plant.



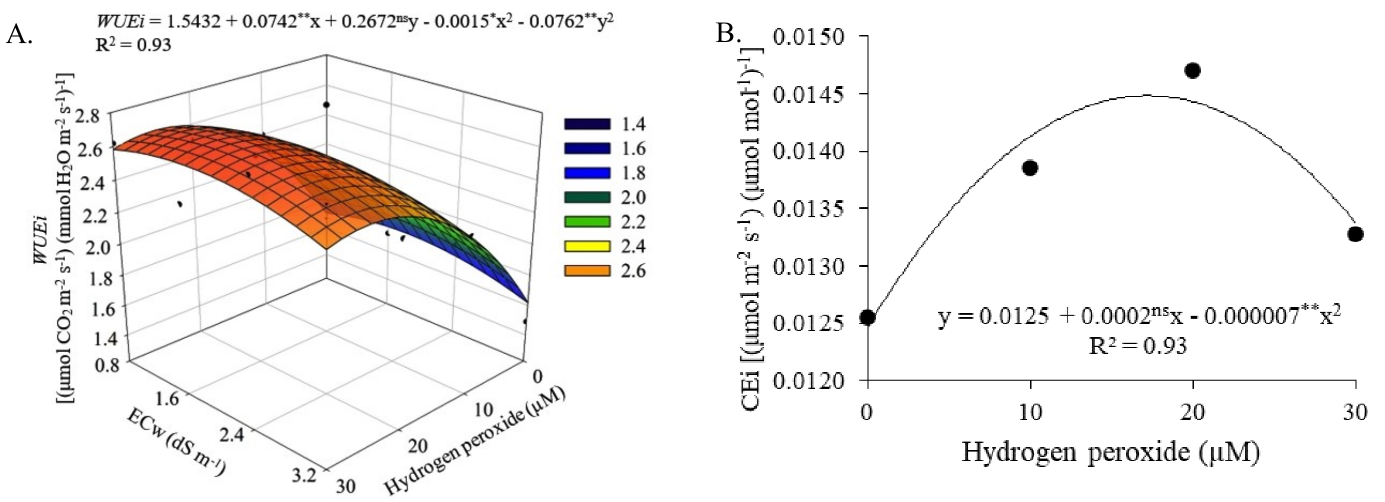
ns, * and ** respectively not significant, significant at $p \leq 0.05$ and $p \leq 0.01$. X and Y correspond to the concentrations of hydrogen peroxide and ECw, respectively.

Figure 3. Stomatal conductance – gs (A) of soursop plants cv. Morada Nova, as a function of the concentrations of hydrogen peroxide – H_2O_2, and internal CO_2 concentration – Ci (B), CO_2 assimilation rate – A (C) and transpiration – E (D) as a function of the interaction between ECw levels and peroxide concentrations, at 780 days after transplanting.

As observed for *Ci*, foliar application of H_2O_2 concentrations increased the CO_2 assimilation rate (Figure 3C) and transpiration (Figure 3D), with the highest values of 3.83 μmol CO_2 m^{-2} s^{-1} and 1.6404 mmol H_2O m^{-2} s^{-1} obtained in the treatments with ECw of 1.6 dS m^{-1} and H_2O_2 concentration of 18 μM for *A* and 11 μM for *E*. The lowest *A* value (2.49 μmol CO_2 m^{-2} s^{-1}) was observed in plants that did not receive H_2O_2 associated with ECw of 3.2 dS m^{-1}. On the other hand, the lowest *E* value was found when the plants were subjected to a H_2O_2 concentration of 30 μM associated with ECw of 0.8 dS m^{-1}, which was 0.6754 mol H_2O m^{-2} s^{-1}. Reduction in transpiration rate is directly linked to the decrease in *gs*, because with less opening of the stomata there will be a decline in transpiration, restricting the loss of water from the leaf to the atmosphere in the form of vapor, thus reducing the transpiration rate of the plant (LIMA et al., 2017).

Capitulino et al. (2022), in a study evaluating the gas exchange and growth of soursop seedlings under salt stress (ECw ranging from 0.6 to 3.0 dS m^{-1}) and application of H_2O_2 (0 and 20 μM), found that the application of H_2O_2 at concentration of 20 μM attenuated the deleterious effects of irrigation water salinity on gas exchange at 85 days after sowing.

Figure 4A shows that the highest value for instantaneous water use efficiency – *WUEi* (2.69 [(μmol CO_2 m^{-2} s^{-1}) (mmol H_2O m^{-2} s^{-1})$^{-1}$])$^{-1}$]) was obtained in plants irrigated using water with ECw of 1.75 dS m^{-1} and under H_2O_2 concentration of 25 μM. On the other hand, irrigation with water of 3.2 dS m^{-1} in the absence of H_2O_2 application led to the minimum estimated value for *WUEi* (1.62 [(μmol CO_2 m^{-2} s^{-1}) (mmol H_2O m^{-2} s^{-1})$^{-1}$]). With the increase in the concentration of salts in water and/or soil, plants have greater difficulty absorbing water and nutrients. Consequently, to prevent excessive water loss, they close their stomata, restricting the entry of CO_2 into the substomatal chamber, compromising instantaneous carboxylation and water use efficiency (SILVA et al., 2019b).



^{ns}, * and ** respectively not significant, significant at p≤0.05 and p≤0.01. X and Y correspond to the concentrations of hydrogen peroxide and ECw, respectively.

Figure 4. Instantaneous water use efficiency - *WUEi* (A) of soursop cv. Morada Nova, as a function of the interaction between the salinity levels of the irrigation water - ECw and the concentrations of hydrogen peroxide - H_2O_2 and instantaneous carboxylation efficiency - CEi (B) as a function of the concentrations of hydrogen peroxide - H_2O_2, at 780 days after transplanting.

Foliar application of H_2O_2 increased the instantaneous carboxylation efficiency - CEi of soursop plants at 780 DAT (Figure 4B), with the highest value (0.01435 [(μmol CO_2 m^{-2} s^{-1}) (μmol]) observed in plants subjected to H_2O_2 application of 17 μM. It was also observed that the lowest CEi value was obtained when the plants were cultivated in the absence of H_2O_2 application (0.01246 [(μmol CO_2 m^{-2} s^{-1}) (mmol H_2O m^{-2} s^{-1})$^{-1}$]). Thus, pretreatment of plants with H_2O_2 may cause a metabolic signaling in the cell, inducing the antioxidant defense system and/or the increase of a metabolite, minimizing the negative effects caused by salinity, which may favor the physiological performance of plants exposed to subsequent conditions of more severe stress (PANHWAR; KEERIO; ROBERT, 2017). Silva et al. (2021), when evaluating the effect of exogenous application of H_2O_2 on emergence, growth and gas exchange of yellow passion fruit subjected to salt stress, observed that the H_2O_2 concentration of 10 μM induces the acclimatization of passion fruit plants to salt stress, mitigating the deleterious effects of salinity on CO_2 assimilation rate and instantaneous carboxylation efficiency.

There was a significant effect of the interaction between water salinity levels and H_2O_2 concentrations on the variable fluorescence, chlorophyll *b* and carotenoids of soursop plants (Table 3). The salinity levels of irrigation water significantly influenced the initial and maximum fluorescence, the quantum efficiency of photosystem II and the total chlorophyll contents of soursop. H_2O_2 concentrations, as individual factor, did not influence the initial fluorescence, chlorophyll *a* and total chlorophyll.

Table 3. Summary of the analysis of variance for initial fluorescence (F_0), maximum fluorescence (Fm), variable fluorescence (Fv), quantum efficiency of photosystem II (Fv/Fm), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), total chlorophyll (Chl *t*) and carotenoids (Car) of soursop cv. Morada Nova irrigated with saline water and subjected to foliar application of hydrogen peroxide at 780 days after transplanting.

Source of variation	DF	Mean Squares							
		F_0	Fm	Fv	Fv/Fm	Chl *a*	Chl *b*	Chl *t*	Car
Salinity level (SL)	4	1566.33^{*}	1599^{*}	5260.24^{ns}	0.000281^{**}	2134.12^{ns}	4578.92^{ns}	10508^{**}	305.69^{ns}
Linear regression	1	*	-	-	**	-	-	*	-
Quadratic regression	1	-	*	-	-	-	-	-	-
Hydrogen peroxide (H_2O_2)	4	146.22^{**}	3095^{ns}	536.276^{ns}	0.000053^{ns}	9288.86^{ns}	6518.91^{ns}	30042^{**}	2199.7^{ns}
Linear regression	1	-	-	-	-	-	-	**	-
Quadratic regression	1	**	-	-	-	-	-	-	-
Interaction (H_2O_2 × SL)	16	1179.67^{ns}	1014^{ns}	19408.2^{*}	0.000110^{ns}	1963.26^{*}	2193.02^{**}	4167.0^{ns}	417.88^{*}
Blocks	3	36.88^{ns}	622^{ns}	616.91^{ns}	0.000054^{ns}	73.5520^{ns}	32.275^{ns}	1.551^{ns}	1.537^{ns}
Residual	30	64.091	399.7	627.78	0.000164	60.597	39.615	87.439	5.666
CV (%)		1.47	0.91	1.54	1.70	15.27	12.06	5.08	6.23

^{ns}, * and ** respectively not significant, significant at $p \leq 0.05$ and $p \leq 0.01$. DF - Degrees of freedom. CV: Coefficient of variation.

Irrigation with saline water linearly increased the initial fluorescence of soursop plants (Figure 5A), by 1.97% per unit increment in ECw, i.e., plants grown under water salinity of 3.2 dS m^{-1} reduced their F_0 by 4.65% (557.059) compared to those under irrigation with the lowest salinity level (0.8 dS m^{-1}) (532.265). F_0 expresses the loss of photochemical energy released by the chlorophyll *a* molecules of the photosystem antenna, so the F_0 value may increase when the reaction centers of photosystem II are compromised or the transfer of excitation energy from the antenna to the reaction centers is impaired, i.e., when there is a reduction in the electron transport capacity (CINTRA et al., 2020), which may have occurred in the present study, as the water electrical conductivity levels increased.

It was also observed that the highest value of F_0 (Figure 5B) was obtained in soursop plants subjected to the application of 21 µM of H_2O_2 (547.631), while the lowest value was observed in the absence of H_2O_2 application (0 µM) (539.5). As already mentioned, an increase in F_0 is indicative of damage to the reaction center of photosystem II or reduction in the ability to transfer energy from the excitation of the light-harvesting system to the reaction center of PSII (FAROUK; AMIRA, 2018), so the increase of F_0 in soursop cv. Morada Nova is probably related to the high H_2O_2 concentration used and/or the time of exposure of the plants, since H_2O_2 is a more stable reactive oxygen species in cells and, at high concentrations, can spread rapidly through the subcellular membrane, resulting in oxidative damage to the membrane cell.

For maximum fluorescence (Figure 5C), the highest estimated value was observed in plants subjected to irrigation with ECw of 1.9 dS m^{-1} (2233.107). From this ECw level, there was a reduction, and the lowest Fm was obtained in plants cultivated under ECw of 3.2 dS m^{-1} (2158.599). Andrade et al. (2022), when evaluating the physiology of passion fruit under salt stress (ECw ranging from 0.7 to 2.8 dS m^{-1}), also found that the increase in salt stress inhibited the photochemical activity of photosystem II, observed by the reduction of maximum fluorescence at 205 days after transplanting (DAT).

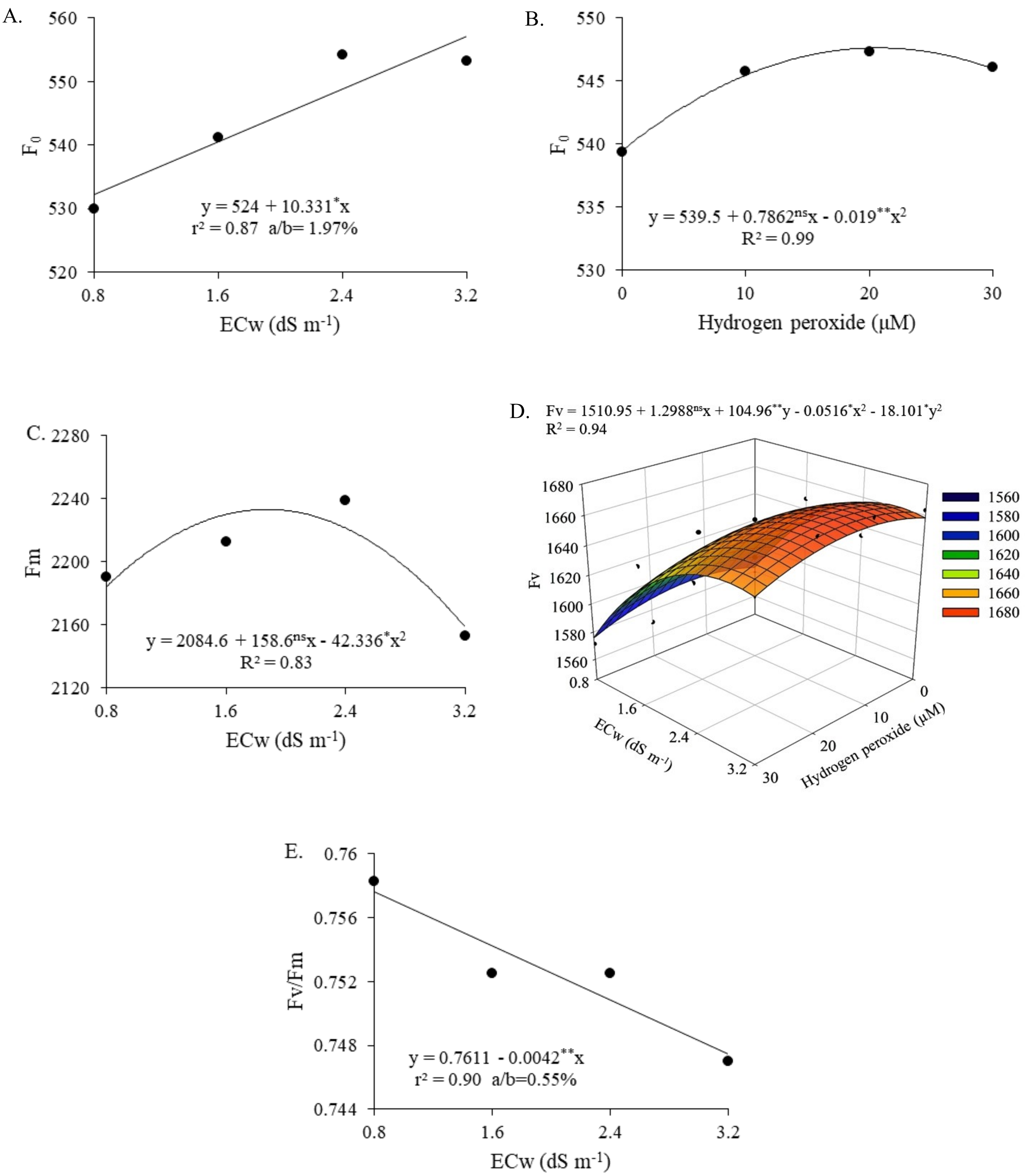
Soursop plants irrigated with ECw of 2.9 dS m^{-1} and subjected to H_2O_2 concentration of 13 µM (Figure 5D) stood out with the highest Fv value (1671.27). The lowest Fv value (1575.86) was obtained in plants irrigated with ECw of 0.8 dS m^{-1} and subjected to a H_2O_2 concentration of 30 µM. At high concentrations, H_2O_2 can cause changes in plant metabolism, mainly as a consequence of oxidative stress, limiting photosynthetic activities; however, when applied at low concentrations, it can induce the action of antioxidant enzymes, reducing the deleterious effects of salt stress (CATTIVELLI et al., 2008).

Veloso et al. (2020a), when evaluating the photosynthetic pigment contents and photochemical efficiency of soursop plants under irrigation with saline water (ECw ranging from 0.6 to 3.0 dS m^{-1}) and different methods of H_2O_2 application (0 and 20 µM), found that the application of 20 µM of H_2O_2 via seed imbibition resulted in increments in maximum and variable fluorescence.

Water salinity linearly reduced the quantum efficiency of photosystem II (Fv/Fm) (Figure 5E), by 0.55% per unit increment in ECw. When comparing the Fv/Fm of plants grown under 3.2 dS m^{-1} to the values of those grown under water salinity of 0.8 dS m^{-1}, a decrease of 1.35% was observed.

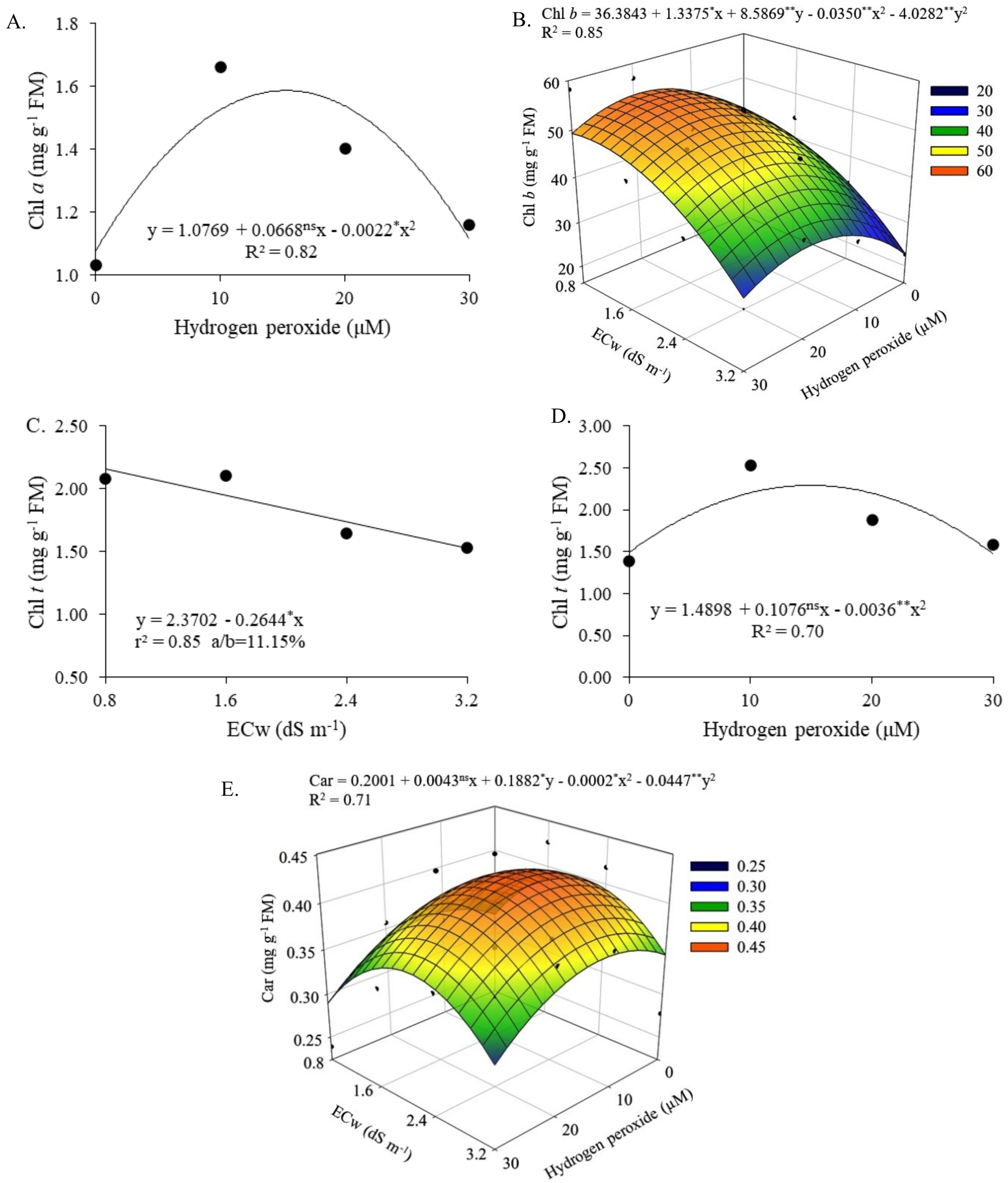
Foliar application of H_2O_2 promoted a quadratic effect on the contents of chlorophyll *a* (Figure 6A), with a maximum value of 1.5839 mg g^{-1} FM obtained in plants subjected to H_2O_2 concentration of 15 µM, while the minimum value was observed in the absence of H_2O_2 application (1.0769 mg g^{-1} FM). At low concentrations, H_2O_2 can stimulate antioxidant enzyme activity, promoting less pigment degradation and increase in photosynthetic activity, which results in greater plant growth and development (VELOSO et al., 2022).

In a study evaluating the effect of the application of H_2O_2 (0, 15, 30 and 45 µM) to mitigate salt stress (ECw from 0.6 to 3.0 dS m^{-1}) on the growth of sour passion fruit (*Passiflora edulis* Sims) at 240 days after transplanting, Ramos et al. (2022) also found a beneficial effect of the application of 15 µM of H_2O_2 on the contents of photosynthetic pigments.



ns, *, ** not significant, significant at $p \leq 0.05$ and $p \leq 0.01$ by the F test, respectively. X and Y correspond to the concentrations of hydrogen peroxide and ECw, respectively.

Figure 5. Initial fluorescence – F_0 (A), maximum fluorescence – Fm (C) and quantum efficiency of photosystem II – Fm/Fv (E) of soursop plants cv. Morada Nova, as a function of irrigation water salinity – ECw, initial fluorescence – F_0 (B) as a function of concentrations of hydrogen peroxide - H_2O_2, and variable fluorescence – Fv (D) as a function of the interaction between irrigation water salinity levels – ECw and H_2O_2 concentrations, at 780 days after transplanting.



ns, *, ** not significant, significant at $p \leq 0.05$ and $p \leq 0.01$ by the F test, respectively. X and Y correspond to the concentrations of hydrogen peroxide and ECw, respectively.

Figure 6. Chlorophyll *a* – Chl *a* (A) and total chlorophyll – Chl *t* (D) of soursop plants cv. Morada Nova, as a function of the concentrations of hydrogen peroxide, total chlorophyll – Chl *t* (C) as a function of irrigation water salinity – ECw, and chlorophyll *b* – Chl *b* (B) and carotenoids – Car (E) as a function of the interaction between the salinity levels of irrigation water – ECw and concentrations of hydrogen peroxide at 780 days after transplanting.

Foliar application of 17 μM of H_2O_2 increased the chlorophyll *b* contents of soursop cv. Morada Nova (Figure 6B), irrigated with water of 1.1 dS m^{-1} (0.5217 mg g^{-1} FM). In the absence of H_2O_2 (0 μM) and subjected to the highest salinity level (3.2 dS m^{-1}), soursop plants obtained the lowest value of Chl *b* (0.2236 mg g^{-1} FM). This was possibly due to the multiple physiological functions performed by H_2O_2 in the plant, such as the ability to increase chlorophyll biosynthesis, since the use of signaling agents in plants, such as H_2O_2, can promote metabolic alteration in the cell and activation of antioxidant enzymes such as superoxide dismutase, catalase, guaiacol peroxidase and ascorbate peroxidase, resulting in a decrease in oxidative stress (RAMOS et al., 2022).

The increase in the electrical conductivity of irrigation water reduced the synthesis of total chlorophyll (Figure 6C), which decreased by 11.15% per unit increase in ECw. When comparing the Chl *t* contents of plants irrigated with water of 3.2 dS m^{-1} with the values of those cultivated under water salinity of 0.8 dS m^{-1}, a reduction of 41.63% (0.635 mg g^{-1} FM) was observed. Decrease in chlorophyll contents is usually accompanied by the inactivation of photochemical reactions, especially those mediated by photosystem II (PSII) in plants under salt stress (ZHAO et al., 2019). Irrigation with saline water (ECw from 0.6 to 3.0 dS m^{-1}) also reduced the contents of chlorophyll *a* and total chlorophyll of sour passion fruit cv. BRS Rubi do Cerrado, at 240 days after transplanting (RAMOS et al., 2022).

As observed for chlorophyll *a* synthesis, soursop plants obtained the highest total chlorophyll content (Figure 6D) when subjected to a H_2O_2 concentration of 15 μM (2.293 mg g^{-1} FM). On the other hand, the lowest Chl *t* value was obtained at H_2O_2 concentration of 30 μM (1.4779 mg g^{-1} FM). At low concentrations, H_2O_2 helps plants acclimatize to the deleterious effects of salt stress, due to metabolic changes that are responsible for increasing their tolerance to stress, thus enabling the use of waters with higher concentrations of salts (ANDRADE et al., 2019).

The carotenoid contents of soursop plants cv. Morada Nova were significantly affected by the interaction between ECw and H_2O_2 concentrations (Figure 6E). Plants cultivated under ECw of 2.1 dS m^{-1} obtained the maximum estimated value of 0.4213 mg g^{-1} FM under foliar application of 12 μM of H_2O_2. On the other hand, plants grown in water with ECw of 0.8 dS m^{-1} and that received the highest concentration of H_2O_2 (30 μM) had the lowest value of Car (0.2711 mg g^{-1} FM). Thus, it is suggested that, for the carotenoid content, H_2O_2 at concentration of 12 μM may act as an abiotic stress-signaling molecule, through the action of enzymatic and non-enzymatic components, promoting an increase in carotenoid content, induced by the production of β-carotenes, which are integrated components of thylakoids, involved in the absorption and transfer of light to chlorophyll (SILVA et al., 2017).

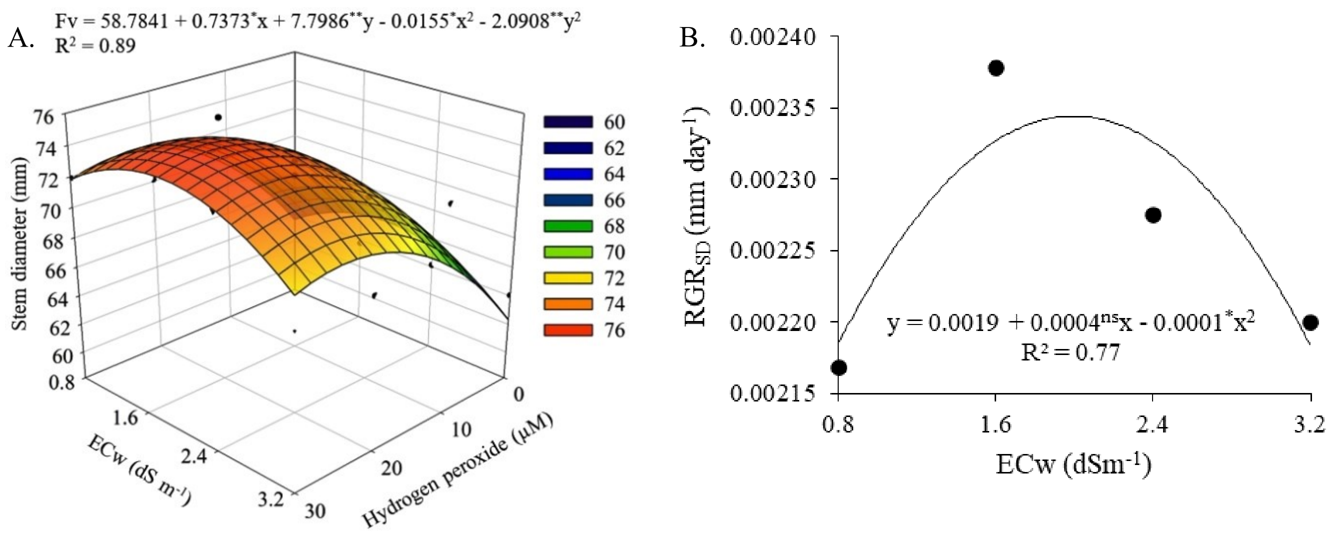
There was a significant effect of the interaction between water salinity levels and H_2O_2 concentrations on stem diameter (SD) (Table 4). Water salinity levels significantly affected the relative growth rate of stem diameter (RGRsd). H_2O_2 concentrations alone did not influence any of the variables analyzed.

Table 4. Summary of the analysis of variance for stem diameter (SD) and relative growth rate of stem diameter (RGRsd) of soursop plants cv. Morada Nova irrigated with saline water and subjected to foliar application of hydrogen peroxide at 780 days after transplanting.

Source of Variation	Mean Squares		
	DF	SD	RGRsd
Salinity levels (SL)	4	60541.0^{ns}	0.00069^{*}
Linear regression	1	-	-
Quadratic regression	1	-	*
Hydrogen peroxide (H_2O_2)	4	6027.86^{ns}	0.00008^{ns}
Linear regression	1	-	-
Quadratic regression	1	-	-
Interaction (SL x H_2O_2)	16	23588.34^{**}	0.00011^{ns}
Blocks	3	2680.89^{ns}	0.000365^{ns}
Residual	30	587.18	0.000103
CV (%)		3.07	1.35

^{ns}, * and ** respectively not significant, significant at p≤0.05 and p≤0.01. DF - Degrees of freedom. CV: Coefficient of variation.

The stem diameter (Figure 7A) of soursop plants was favored by the foliar application of H_2O_2 at an estimated concentration of 24 μM and ECw of 1.86 dS m^{-1}. On the other hand, the lowest SD was obtained in the absence of H_2O_2 (0 μM) and when the plants were irrigated with the highest ECw (3.2 dS m^{-1}). The higher estimated value of SD in plants subjected to H_2O_2 concentration of 24 μM may be associated with the ability of the H_2O_2 molecule to stimulate plant growth, promoting cell division and elongation (ORABI; DAWOOD; SALMAM, 2015). Veloso et al. (2022), when studying the growth of soursop seedlings under salt stress (ECw from 0.7 to 3.7 dS m^{-1}) and foliar application of H_2O_2 (0, 25, 50 and 75 μM), also observed that the application of H_2O_2 favored growth in stem diameter and plant height.



ns, *, ** non-significant, significant at p≤0.05 and at p ≤ 0.01 by the F test, respectively. X and Y correspond to the concentrations of hydrogen peroxide and ECw, respectively.

Figure 7. Stem diameter – SD (A) of soursop plants cv. Morada Nova as a function of the interaction between the salinity levels of irrigation water – ECw and concentrations of hydrogen peroxide – H_2O_2 and the relative growth rate of stem diameter – RGRsd (B) as a function of the concentrations of hydrogen peroxide, at 780 days after transplanting.

Regarding the relative growth rate of stem diameter (RGRsd), the maximum estimated value (0.00230 mm day^{-1}) was obtained in plants irrigated with ECw of 2.0 dS m^{-1} (Figure 7B). From this salinity level, there was a reduction and RGRsd reached 0.002156 mm day^{-1} at ECw of 3.2 dS m^{-1}. The reduction in RGRsd may have occurred due to the decrease in the osmotic potential of the soil solution caused by the excess of soluble salts in the root zone, which limits the absorption of water by the roots, causing the plant to reduce stomatal opening, as a mechanism to reduce water loss, which leads to the reduction of cell turgor and, consequently, to reductions in cell expansion and plant growth (LIMA et al., 2020), which may have occurred in this study, causing reductions in the RGRsd of soursop plants.

CONCLUSIONS

Foliar application of hydrogen peroxide at concentrations ranging from 11 to 13 µM attenuates the effects of salt stress up to ECw of 1.6 dS m^{-1} on the stomatal conductance and CO_2 assimilation rate of soursop cv. Morada Nova, respectively.

Hydrogen peroxide concentration of 30 µM intensifies salt stress effects on gas exchange, variable fluorescence and electrolyte leakage in the leaf blade of soursop cv. Morada Nova, at 780 days after transplantation.

Foliar application of hydrogen peroxide at concentrations of up to 15 µM stimulates the biosynthesis of chlorophyll *a* and total chlorophyll and increases the instantaneous carboxylation efficiency and, at concentration of 11 µM, alleviates the effect of water salinity up to 2.1 dS m^{-1} on the carotenoid contents of soursop plants cv. Morada Nova.

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