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MARLENILDO FERREIRA MELO

EFFECT OF SALICYLIC AND JASMONIC ACID ON CHERRY TOMATO GROWTH, PHYSIOLOGY, AND FRUIT QUALITY UNDER SALINE STRESS

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Tese apresentada ao Doutorado em Fitotecnia do Programa de Pós-Graduação em Fitotecnia da Universidade Federal Rural do Semi-Árido como requisito para obtenção do título de Doutor em Fitotecnia.

Linha de Pesquisa: Melhoramento Genético e Tecnologia em Sementes e Pós-Colheita

Orientadora: Patrícia Lígia Dantas de Morais, Profa. Dra.

Coorientador: Hozano de Souza Lemos Neto, Prof. Dr.

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Aos meus pais e minha reca de irmãos e sobrinhos, as pessoas mais importantes da minha vida.

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RESUMO

MELO, Marlenildo Ferreira. **Efeito do ácido salicílico e jasmônico no crescimento, fisiologia e qualidade do fruto de tomate cereja sob estresse salino.** 2022. 73p. Thesis (Doctorate in Agronomy: Phytotechnics) – Universidade Federal Rural do Semi-Árido (UFERSA), Mossoró-RN, 2022.

O uso de salmoura de osmose reversa é uma alternativa para lidar com a escassez de água no semiárido. Portanto, um experimento foi conduzido para avaliar a aplicação foliar de ácido salicílico (SA) e ácido jasmônico (JA) como mitigantes do estresse salino em tomate cereja (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) cultivado em solução nutritiva não salina (2,16 dS m^{-1}), moderadamente salina (4,50 dS m^{-1}) e severamente salina (9,00 dS m^{-1}) preparada com salmoura de osmose reversa diluída. 500 μM de SA e 50 μM de JA foram pulverizados isoladamente ou em combinação nas folhas, e água destilada como controle. Os resultados mostraram que a salinidade, moderada e severa, reduziu o crescimento das plantas devido à diminuição das trocas gasosas, aumento do acúmulo de Na^+ e redução de K^+ e Ca^{2+} nos tecidos das plantas, e aumento da peroxidação lipídica e extravasamento de eletrólitos, o que, consequentemente, reduziu a produtividade de frutos. Por outro lado, o estresse salino melhorou o sabor e a qualidade dos frutos, aumentando o teor de sólidos solúveis, acidez titulável e açúcares. A pulverização foliar com SA e JA mitigou os danos causados pelo estresse salino, reduzindo o teor de Na^+ nos tecidos, mantendo a integridade das membranas celulares e as trocas gasosas. Além disso, o tratamento com fitorreguladores aumentou a acidez, teor de vitamina C, conteúdo de licopeno, intensificou a coloração da casca e melhorou o sabor dos frutos. Concluindo, a adição de salmoura à solução nutritiva reduz o crescimento e a produtividade do tomate cereja, mas melhora a qualidade dos frutos. O SA e o JA exógenos aliviam a toxicidade da salinidade, porém sem manter o crescimento das plantas e a produtividade de frutos.

Palavras-chave: qualidade de fruto, salmoura de osmose reversa, estresse salino, *Solanum lycopersicum* L. var. *cerasiforme*.

ABSTRACT

MELO, Marlenildo Ferreira. **Effect of salicylic and jasmonic acid on cherry tomato growth, physiology, and fruit quality under saline stress.** 2022. 73p. Thesis (Doctorate in Agronomy: Phytotechnics) – Universidade Federal Rural do Semi-Árido (UFERSA), Mossoró-RN, 2022.

Using reverse osmose wastewater is an alternative to cope with water scarcity in the semiarid. Thus, an experiment was conducted to evaluate exogenous salicylic acid (SA) and jasmonic acid (JA) as mitigants of salt stress on cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) under non-saline (2.16 dS m^{-1}), moderate saline (4.50 dS m^{-1}) and severe saline (9.00 dS m^{-1}) nutrient solution prepared with diluted reverse osmosis brine. Single and combined 500 μM SA and 50 μM JA were sprayed on leaves, and distilled water was sprayed as control. Results showed that moderate and severe salinity reduced plant growth due to reduced gas exchange, increased accumulation of Na^+ and reduced K^+ and Ca^{2+} in plant tissues, and increased lipid peroxidation and cell electrolyte leakage, which consequently reduced fruit productivity. On the other hand, salt stress improved fruit flavor and quality by enhancing the content of soluble solids, titratable acidity, and sugars. Foliar spray of SA and JA mitigated damages caused by salt stress by reducing Na^+ content, maintaining membrane integrity, and gas exchange. Also, the treatment with growth regulators enhanced fruit acidity, vitamin C content, lycopene, skin color, and flavor. In conclusion, adding brine to the nutrient solution reduce cherry tomato growth and productivity, but improve fruit quality. Exogenous SA and JA alleviate salt toxicity but without maintaining plant growth and productivity.

Keywords: fruit quality, reverse osmosis brine, salt stress, *Solanum lycopersicum* L. var. *cerasiforme*.

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SUMMARY

CHAPTER I

1 GENERAL INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is the second most important vegetable in the world after potato (*S. tuberosum* L.). It belongs to the Solanaceae family with more than 3,000 species, including potato, pepper, bell pepper, and eggplant (KNAPP; PERALTA, 2016). Its fruits have a high concentration of health-promoting compounds, such as pectins, vitamins, phenolic compounds, flavonoids, and carotenoids, being the main source of lycopene and β-carotene for the human diet, which confer its high antioxidant activity. Thus, tomato is highly appreciated, being consumed fresh or processed as juices, puree, pasta sauces, powder, ketchup, soup, and canned fruits (KUMAR et al., 2021; QUINET et al., 2019). Adapted to a wide variety of climates, tomato is produced in all regions of the world. In Brazil, 3.75 million tons of tomatoes were produced, of which 13.5% were from the Northeast region IBGE (2020). Several tomato varieties are produced in Brazil, intended for fresh consumption and processing, with fruits weighing from 5 g, like cherry tomatoes, to 500 g, as salad tomatoes EMBRAPA (2019).

One of the main problems for tomato production in Northeastern Brazil is water scarcity. Water available for irrigation in the semiarid is collected underground through wells. However, groundwater is saline with an electrical conductivity (EC) that reaches up to 7 dS m^{-1}, thus needing to be desalinated before use (SILVA; SHARQAWY, 2020). In the Brazilian semiarid, reverse osmosis systems are used to remove salts from groundwater, supplying potable water for human consumption and irrigation. In addition, hypersaline water of up to 10 dS m^{-1} EC is released in the process and usually disposed directly into the environment Oliveira et al. (2020). Such brine is unsuitable for irrigation of tomatoes since the crop tolerates EC of water up to 1.5 dS m^{-1}. A previous study on cherry tomato (*S. lycopersicum* L. var. *cerasiforme* cv. Samambaia) cultivated hydroponically using diluted reverse osmosis brine showed it tolerated EC of the nutrient solution up to 3.5 dS m^{-1} without yield losses. Above this EC, plants suffer from salt stress negatively affecting their growth and productivity (GOMES et al., 2011).

A high concentration of salts in saline water increases the osmotic potential at the root zone, thus reducing water uptake by the plants and causing water stress. Plants close stomata as an immediate response to salt stress, thus limiting CO_2 fixation and reducing photosynthesis (HUANG et al., 2016). Subsequently, salinity reduces photosynthesis due to non-stomatal limitations, by reducing chlorophyll content and electron transport in chloroplasts, and

consequently decreasing the photosynthetic apparatus efficiency Mimouni et al. (2016). Also, a high concentration of sodium (Na^+) and chloride (Cl^-) ions in saline water compete for root uptake with essential ions, such as potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}), accumulating in plant tissues causing nutrient imbalance and toxicity Albaladejo et al. (2017 e Assaha et al. (2017). Salinity also induces oxidative stress that occurs due to the production of reactive oxygen species (ROS), such as superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($^{\bullet}OH$), which in excess, are reactive and toxic to cells, causing an imbalance in their redox state. These ROS oxidize biomolecules such as proteins, chlorophylls, and nucleic acids, inhibit enzymatic activities, and cause lipid peroxidation thus degrading cell membranes and causing electrolyte leakage (MIR et al., 2018; STEVENS et al., 2006).

Although reduce plant growth and productivity, salinity improves tomato fruit quality by both concentrating and increasing the content of soluble solids, organic acids, total soluble sugars, and reducing sugars, thus improving fruit taste (SAITO; MATSUKURA, 2015; ZHANG et al., 2016). Also, salt stress improves fruit antioxidant activity by enhancing the content of carotenoids, flavonoids, and vitamins (EL-MOGY et al., 2018; ISLAM et al., 2018).

Therefore, using reverse osmosis brine in tomato cultivation can be promising to deal with water scarcity in the semiarid, in addition to avoiding the improper disposal of this wastewater and avoiding environmental contamination. Diluted in potable water, reverse osmosis brine has been used to irrigate tomatoes (COSME et al., (2011), besides other crops such as melon (DIAS et al., 2010), arugula (SILVA et al., 2011), and lettuce (SARMENTO et al., 2014), saving 20 to 80% freshwater in cultivation.

Studies have shown that the exogenous application of plant growth regulators, such as salicylic acid (SA) and jasmonic acid (JA), facilitates the acclimatization of tomato plants to saline stress (MIMOUNI et al., 2016; NAEEM et al., 2020). Besides inducing the plant defense mechanisms against pests and pathogen attacks, SA and JA act mediating plant defense responses to salt stress, such as increasing the synthesis of antioxidant enzymes that scavenge ROS and inducing osmotic adjustment. The same benefits were observed in other crop species such as maize (MIR et al., 2018), soybean (GHASSEMI-GOLEZANI et al., 2018), and canola (FARHANGI-ABRIZ et al., 2019).

Thus, this work aimed to evaluate exogenous SA and JA as mitigants of salt stress on cherry tomato grown in saline nutrient solution produced with reverse osmosis brine.

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CHAPTER II

ACTION OF BIOTIC ELICITORS ON CHERRY TOMATO UNDER SALINE STRESS: PHYSIOLOGICAL AND BIOCHEMICAL VARIABLES

HIGHLIGHTS

Cherry tomato was grown in nutrient solution with reverse osmosis brine.

Cherry tomato exhibit different adaptation mechanisms under severe salinity than under moderate salinity.

Severe salinity affects fruit quantity rather than fruit size.

Exogenous salicylic and jasmonic acid alleviate salt toxicity in cherry tomato.

ABSTRACT

Using reverse osmose wastewater is an alternative to cope with water scarcity in the semiarid. Due to the high concentration of salts in brine, strategies have been developed to improve salinity tolerance. Thus, an experiment was carried out to investigate the protective role of salicylic acid (SA) and jasmonic acid (JA) in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) under non-saline (2.16 dS m^{-1}), moderate saline (4.50 dS m^{-1}) and severe saline (9.00 dS m^{-1}) nutrient solutions prepared with diluted reverse osmosis brine. 500 µM SA and 50 µM JA were sprayed, single or combined (SA+JA), exogenously on leaves, and water was sprayed as control. Results showed that moderate and severe salinity reduced plant growth and productivity due to accumulation of Na^+ and reduced K^+ and Ca^{2+} in plant tissues, increased lipid peroxidation and cell electrolyte leakage, and reduced photosynthetic pigment content. Foliar spray of SA and JA mitigated damages caused by salt stress by reducing Na^+ content and maintaining membrane integrity, although it did not influence plant growth and productivity. In conclusion, adding brine to the nutrient solution reduce cherry tomato growth and productivity, and exogenous SA and JA alleviate salt toxicity.

Keywords: reverse osmosis brine, salt stress, *Solanum lycopersicum* L. var. *cerasiforme*, water reuse.

1 INTRODUCTION

In Brazilian semiarid, surface water availability is scarce because of irregular and low rainfall (350-700 mm). Thus, water is mostly collected underground through wells. However, this groundwater has a high concentration of salts with electrical conductivity (EC) from 3.69 to 7.00 dS m^{-1}, thus needing to be desalinated before use (Silva and Sharqawy, 2020). Reverse osmosis desalination systems are used to remove salts providing potable water for human consumption and irrigation. In addition, a brine with EC that reaches 10 dS m^{-1} is produced and discharged directly into rivers, lakes, and the ocean leading to environmental contamination (Oliveira et al., 2020).

Reverse osmosis-brine diluted in potable water has been used for irrigation of several crops species as melon (*Cucumis melo* L.) (Dias et al., 2010), arugula (*Eruca sativa* Mill) (Silva et al., 2011), tomato (*Solanum lycopersicum* L.) (Cosme et al., 2011), and lettuce (*Lactuca sativa* L.) (Sarmento et al., 2014) saving 20 to 80% freshwater in cultivation. However, adding brine to freshwater raises water salinity and may cause salt stress on plants, leading to increased sodium (Na) concentration in plant tissues, nutrient imbalance, osmotic stress, membrane degradation due to lipid peroxidation, accumulation of reactive oxygen species, adversely affecting plant physiology, growth, and development (El-Mogy et al., 2018; Naeem et al., 2020).

Most crops tolerate water salinity with EC up to 1.5 dS m^{-1}, however, cherry tomato grown hydroponically can tolerate up to 3.5 dS m^{-1} without significant productivity losses. Above this conductivity, a 10.9% productivity loss occurs per EC unit increase (Gomes et al., 2011). Exogenous application of plant growth regulators can mitigate the deleterious effects of salinity on plants (Farhangi-Abriz and Ghassemi-Golezani, 2018; Naeem et al., 2020).

Salicylic (SA) and jasmonic (JA) acid are plant hormones that play key roles in systemic acquired resistance (SAR) to pathogens, and in response to abiotic stress such as salinity (Mimouni et al., 2016). Foliar application of SA and JA in salt-stressed plants improved resistance against salinity in various crop species such as canola (*Brassica napus* L.) (Farhangi-Abriz et al., 2019), maize (*Zea mays* L.) (Mir et al., 2018), soybean (*Glycine max* (L.) Merrill) (Ghassemi-Golezani et al., 2018), and tomato (Mimouni et al., 2016; Naeem et al., 2020). The ameliorative effects of exogenous SA and JA on plant physiology, growth, and development resulted in inhibited Na uptake, improved antioxidant system reducing the content of reactive oxygen species (ROS), decreased lipid peroxidation, and improved osmotic adjustment due to

increased proline and glycine betaine contents (Farhangi-Abriz and Ghassemi-Golezani, 2018; Naeem et al., 2020; Torre-González et al., 2018).

Reusing reverse osmosis brine from the desalination process for irrigation is an alternative to deal with water scarcity in the semiarid, in addition, to avoiding the direct disposal of brine into the environment. Thus, we aimed to evaluate exogenous SA and JA as mitigants of salt stress on cherry tomato cultivated in saline nutrient solution produced with reverse osmosis brine.

2 MATERIAL AND METHODS

2.1 Plant material and growth conditions

Cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants were cultivated hydroponically under greenhouse conditions in nutrient solutions prepared with diluted reverse osmosis brine. The greenhouse (6.4 m wide, 18 m long, and 3.0 m ceiling height) where the experiment was carried out was located at Federal Rural University of Semiarid (UFERSA), Mossoró, Rio Grande do Norte, Brazil. It was covered with low-density polyethylene film (150 μm thick) with an anti-ultraviolet additive and the sides were covered with 50% shading mesh.

Initially, cherry tomato seeds were sown in polyethylene trays filled with coconut (*Cocos nucifera* L.) fiber and organic compost at 1:2 (v:v). The coconut fiber acquired from Amafibra (Nogueira, SP, Brazil) had electrical conductivity (EC) of 1.4 mS cm^{-1}, water retention capacity of 507 mL L^{-1}, 95% porosity, and 150 kg m^{-3} density. The organic compost acquired from Nibrafértil (Mossoró, RN, Brazil) had 1.0% nitrogen, 50% humidity, 15% organic carbon, 6.0 pH, 18:1 C: N ratio, and 80 $mmol_c$ dm^{-3} cation exchange capacity.

After 24 days from sowing, the tomato seedlings were transplanted to perforated plastic bags (4.0 L capacity) filled with coconut fiber over a layer of gravel covered by a piece of fabric to facilitate water drainage. The pots were spaced 0.5 m by 1.0 m apart. Plants were grown for 82 days after transplanting (DAT) and temperature and air relative humidity inside the greenhouse were monitored daily using a portable thermo-hygrometer, and climatic data were obtained from the weather station at UFERSA, and data are shown in (**Fig. 1**).

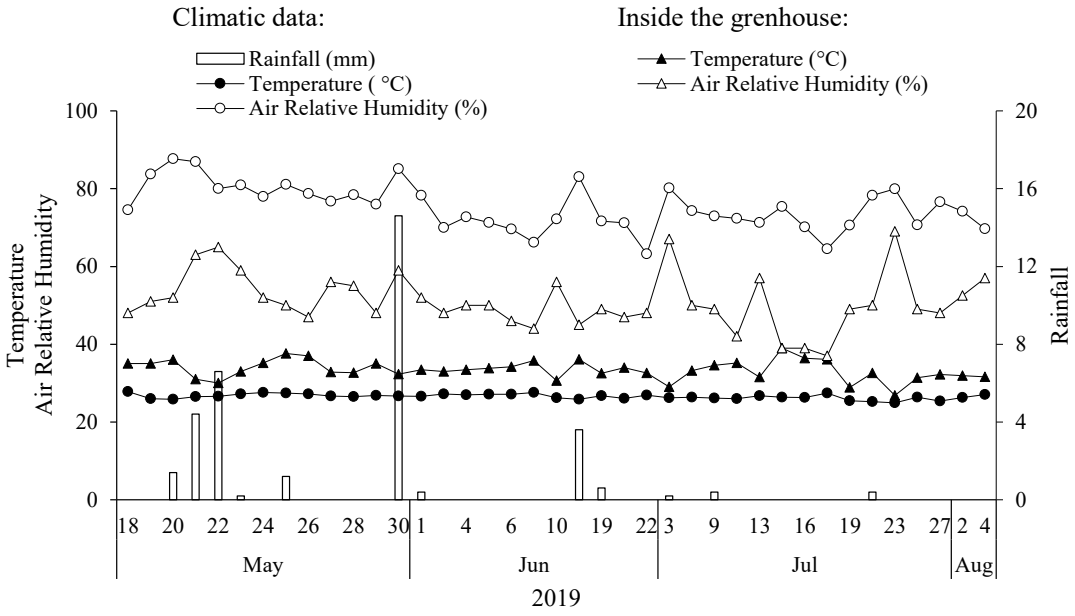

Fig. 1. Climatic data during the experiment. Average temperature, air relative humidity, and rainfall in Mossoró city, RN, Brazil, and temperature and air relative humidity (from 7 to 11 a.m.) inside the greenhouse.

From 14 DAT, axillary branches were removed as they sprouted. From 17 DAT, the plants were trained in a trellis system in which the plant branches were tied on three strings of wire stretched at 0.4, 1.0, and 1.8 m height on wooden poles. Also, plants were sprayed with Connect® (10% Imidacloprid + 1.25% β-Cyfluthrin, Bayer, Belford Roxo, RJ, Brazil) at 14, 26, 33, 41, and 54 DAT to control whitefly (*Bemisia tabaci*).

2.2 Nutrient solution

Until the 12th DAT, all plants were grown in a non-saline nutrient solution that had 2.16 dS m^{-1} electrical conductivity (EC). This nutrient solution was prepared by diluting chemical fertilizers directly in supply water that had 0.65 dS m^{-1} EC. From the 12th day, one-third of the plants were grown in moderate saline nutrient solution (4.50 dS m^{-1} EC), and one-third in severe saline nutrient solution (9.00 dS m^{-1} EC). These saline nutrient solutions were prepared by initially diluting reverse osmosis brine in supply water in the proportion of 20% and 80%, respectively, to adjust their electrical conductivities to 4.50 and 9.00 dS m^{-1} after adding the fertilizers.

The brine was obtained from a desalination process by a reverse osmosis system located in Mossoró (5°01'47.3" S, 37°19'29.5" W, 28 m above the sea level, Rio Grande do Norte state, Brazil). The chemical characteristics of the brine and supply water are shown in **Table 1**.

Table 1. Chemical characteristics of supply water and reverse osmosis brine used in the nutrient solution.

Characteristic	Unit	Supply water	Brine
pH		7.60	7.20
Electrical conductivity	dS m^{-1}	0.65	10.68
K^+	$mmol_c$ L^{-1}	0.26	0.70
Na^+	$mmol_c$ L^{-1}	3.76	45.46
Ca^{2+}	$mmol_c$ L^{-1}	0.80	36.50
Mg^{2+}	$mmol_c$ L^{-1}	1.00	21.20
Cl^-	$mmol_c$ L^{-1}	2.60	81.00
CO_3^{2-}	$mmol_c$ L^{-1}	0.30	0.20
HCO_3^{2-}	$mmol_c$ L^{-1}	2.50	4.90
Sodium adsorption ratio	$mmol_c$ L^{-1}	4.0	8.5
Cations	$mmol_c$ L^{-1}	5.8	103.9
Anions	$mmol_c$ L^{-1}	5.4	86.1
Hardness	mg L^{-1}	90	2885

The fertilizers used were potassium nitrate (KNO_3: 13% N, 44% K_2O), calcium nitrate ($Ca(NO_3)_2$: 15% N, 19% Ca), monoammonium phosphate ($NH_4H_2PO_4$: 11% N, 50% P_2O_5), magnesium sulfate ($MgSO_4.7H_2O$: 9% Mg, 12% S), and potassium chloride (KCl: 60% K_2O, 47% Cl) at the concentrations of 2.0, 50.0, 12.5, 20.0, and 30.0 g L^{-1}, respectively, to obtain a 25% ionic strength of the nutrient solution proposed by (Moraes and Furlani, 1999). Then, the concentration was doubled to 50% ionic strength from the 7th DAT. Also, a mix of micronutrients (Rexolin BRA, Yara Tera, Yara Brasil Fertilizantes S.A., Porto Alegre, RS, Brazil), containing 11.6% K_2O, 1.28% S, 2.1% B, 0.36% Cu, 2.66% Fe, 2.48% Mn, 0.036% Mo, and 3.38% Zn, was added at the concentrations of 3.0 and 6.0 g L^{-1} to the solutions of 25 and 50% ionic strength, respectively.

We reduced the concentration of the nutrient solution to 25% and 50% ionic strength due to the higher concentration of minerals in the brine and because hydroponically grown plants conserve water and nutrients (Rosa-Rodríguez et al., 2020). The EC and pH of the nutrient solutions were monitored daily using a portable pH meter (PH-700, Instrutherm, São Paulo, SP, Brazil) and conductivity meter (CD-860, Instrutherm, São Paulo, SP, Brazil), respectively. When necessary, pH was adjusted to 6.0 by adding hydrochloric acid (HCl). An open hydroponic system was used, and the nutrient solution was manually delivered to the plants until the substrate was drained, to maintain adequate runoff to keep nutrient balance in the root zone.

2.3 Salicylic acid and jasmonic acid application

At 12 DAT, the same day the saline solutions were applied, plants were sprayed with 500 µM of salicylic acid (SA), 50 µM of jasmonic acid (JA), or both (SA+JA) to evaluate them as mitigants of the deleterious effects of salt stress on plants. SA was applied at 12, 20, 32, and 40 DAT, which corresponded to applications at the vegetative, flowering, and fruiting developmental stages. In turn, JA was sprayed at 13 and 24 DAT at the vegetative and flowering developmental stages. In addition, plants were sprayed with distilled water as control (C) treatment. The plant growth regulator and control solutions were sprayed throughout the plant using a hand spray bottle. Salicylic acid P.A. ACS (138.12 g mol^{-1}, 99.0%) was obtained from Dinâmica Química Contemporânea Ltda. (Indaiatuba, SP, Brazil), and jasmonic acid (210.27 g mol^{-1}, ≥ 95.0%) was obtained from Sigma-Aldrich Brasil Ltda. (São Paulo, SP, Brazil).

2.4 Experimental design

The experimental design was completely randomized in a double factorial scheme (3 × 4), with the electrical conductivities of the nutrient solution (2.16, 4.50, and 9.00 dS m^{-1}) and growth regulators treatments (C, SA, JA, SA+JA) as the source of variation. Four replicates were used, and the experimental plot corresponded to two plants randomly spaced over the greenhouse.

2.5 Chlorophyll content evaluation

Chlorophyll (Chl) *a* and *b* content were evaluated at 45 DAT on three fully expanded leaves at the middle third of the plant canopy using a chlorophyll meter (CFL1030 ClorofiLOG, Falker, Porto Alegre, RS, Brazil), and values expressed as Chlorophyll Falker Index (CFI). Then, Chl *a*+*b* and Chl *a*/*b* were calculated.

2.6 Electrolyte leakage

Electrolyte leakage (EL) was measured as an indicator of cell membrane permeability of leaves from imposed stress. Ten leaf discs (10 mm in diameter) from fully expanded leaves were placed in plastic vials filled with 30 mL of distilled water and kept in darkness for 24 h at room temperature. The electrical conductivity (EC1) of the bathing solution was measured at the end of the incubation period. Then, the same vials were heated in a water bath at 95ºC for 20 min and then cooled to room temperature (25 °C) and the electrical conductivity (EC2) was

again measured. Electrolyte leakage was calculated as [(EC1/EC2) × 100] according to (Shi et al., 2006), and values were expressed as a percentage.

2.7 Protein extraction and superoxide dismutase (SOD) activity

Initially, for the enzyme extraction, 0.3 g of leaf were ground into a fine powder in liquid nitrogen in a mortar and then homogenized with 20% polyvinylpolypyrrolidone (PVPP) and 1 mL potassium phosphate buffer (pH 7.5) containing 1 mM EDTA and 3 mM dithiothreitol (DTT). The homogenate was centrifuged at 4 °C for 30 min at 10,000 rpm. The resulting supernatant was used to determine protein content according to (Bradford, 1976) and stored at -80 °C for the determination of the enzymatic activity.

Superoxide dismutase (SOD) activity was assayed by measuring the ability to inhibit the photochemical reduction of nitroblue tetrazolium (NBT), thus avoiding the formation of the formazan chromophore, following the method of (Giannopolitis and Ries, 1977), with minor modifications. The reaction solution (3 mL) was composed by 85 mM phosphate buffer (pH 7.8), 75 μM NBT, 5 μM riboflavin, 13 mM methionine, 0.1 mM EDTA, and 50 μL enzymatic extract. The solution was transferred to glass tubes and irradiated with white light (15 W fluorescent lamp) for 5 min. After the exposure time, the solution was analyzed in a spectrophotometer at 560 nm. One activity unit was defined as the amount of enzyme that inhibits 50% of formazan formation per gram of protein, with results expressed as U g protein^{-1}.

2.8 Lipid peroxidation and hydrogen peroxide content

Lipid peroxidation (LP) was estimated by measuring the concentration of malondialdehyde (MDA) following the method of (Heath and Packer, 1968). 0.2 g leaf was macerated in a mortar with 2 mL of 0.1% trichloroacetic acid (TCA) and 20% PVPP. The homogenate was centrifuged at 20 °C for 5 min and used to determine MDA and hydrogen peroxide (H_2O_2) concentrations. 1 mL of 0.5% thiobarbituric acid (TBA) in 20% TCA was added to 1 mL of the supernatant and the mixture was heated in a water bath at 95 °C for 30 min then quickly cooled on ice. After centrifugation at 10,000 rpm for 10 min, the absorbance of the supernatant was measured at 535 nm and corrected for nonspecific turbidity by subtracting the absorbance at 600 nm. The amount of MDA was calculated by using an extinction coefficient of 155 mM^{-1} cm^{-1} and expressed as nmol g^{-1} fresh weight (FW).

Hydrogen peroxide concentration was measured spectrophotometrically at 390 nm after reaction with potassium iodide (KI) according to (Agrawal et al., 2004), and results were expressed as mmol g^{-1} FW. The reaction mixture consisted of 0.2 mL of the supernatant, 0.8 mL KI, and 0.2 mL potassium phosphate buffer 100 mM (pH 7.5) in darkness for 1 h on ice. The blank probe consisted of 0.1% TCA in the absence of leaf extract.

2.9 Plant growth

At 82 DAT, stem diameter (SD, mm) was measured using a digital caliper (0,01 mm), and plant height (PH, cm) was measured using a graduated ruler. Then the plants were removed from the pots and separated into leaves, stems, and roots, and the number of leaves (NL) of each plant was counted. Then, each plant organ was packed separately in paper bags, and leaf, stem, and root fresh matter (LFM, SFM, and RFM respectively) were measured on a semi-analytical scale and expressed as g $plant^{-1}$. Afterward, the plant material was dried in a forced circulation oven at 65±1 °C for 72 h to measure leaf, stem, and root dry matter (LDM, SDM, and RDM respectively) as g $plant^{-1}$. Also, total (leaves + stem + roots) fresh (TFM) and dry matter (TDM) were recorded.

2.10 Mineral nutrient content

The dried plant material was ground in a Wiley mill to determine K^+, Na^+, Ca^{2+}, and Mg^{2+} concentrations in the leaves, stems, and roots according to Tedesco (1997) and expressed as g kg^{-1}. Also, total (leaves + stem + roots) nutrient content was determined as g kg^{-1}.

2.11 Plant productivity

Fruits were harvested at the red ripening stage and then transported to Physiology and Postharvest Laboratory at UFERSA to evaluate yield. The number of fruits per plant (NF) and yield (Y) as g $plant^{-1}$ were determined by counting and weighing fruits on a semi-analytical scale. Then, marketable yield (MY, t ha^{-1}) was estimated considering 20,000 plants per hectare, since the plants were spaced 0.5 m × 1.0 m in the greenhouse. Then, a sample of ten fruits of each treatment was taken to measure fruit mass (FM, g) on a semi-analytical scale (±0.01 g).

2.12 Statistical analyzes

Data were tested for normality and homoscedasticity by the Shapiro-Wilk and Bartlett test, respectively. Then, data were submitted to two-way analysis of variance by the F test, and

means were grouped by Tukey's test. Also, a Principal Component Analysis was performed to overview data variation. All statistical analyses were considered significant at $p \leq 0.05$ and performed in R software (R Core Team, 2020).

3 RESULTS

3.1 Mineral nutrient content

Salinity altered the mineral nutrient content in the cherry tomato tissues, and exogenous SA and JA affected K^+/Na^+ (**Table 2**).

Table 2. Analysis of variance for mineral nutrient content in the different organs of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions and sprayed with 500 μM salicylic acid and 50 μM jasmonic acid alone or in combination.

Organ	SV	DF	MS				
			Na^+	K^+	K^+/Na^+	Ca^{2+}	Mg^{2+}
Root	EC_{ns}	2	57.92^{***}	65.76^{**}	4.01^{***}	3324.20^{***}	14.64^{***}
	PGR	3	9.57^{ns}	7.67^{ns}	0.01^{ns}	375.27^{ns}	1.38^{ns}
	EC_{ns} × PGR	6	8.25^{ns}	11.76^{ns}	0.14^{*}	493.12^{ns}	2.11^{ns}
	Error	36	6.37	10.33	0.04	352.58	1.45
	CV (%)		30.38	34.44	17.25	36.38	19.30
Stem	EC_{ns}	2	185.82^{***}	145.60^{**}	105.33^{***}	159.60^{ns}	55.12^{***}
	PGR	3	14.29^{ns}	13.06^{ns}	1.21^{ns}	196.50^{ns}	8.25^{ns}
	EC_{ns} × PGR	6	22.93^{*}	6.75^{ns}	1.47^{ns}	174.85^{ns}	11.85^{ns}
	Error	36	8.79^{ns}	18.44	0.85	107.99	5.38
	CV (%)		34.39	13.41	19.80	49.33	32.81
Leaf	EC_{ns}	2	327.81^{***}	1359.50^{***}	53.93^{***}	2608.50^{ns}	33.29^{ns}
	PGR	3	36.53^{ns}	26.93^{ns}	0.62^{ns}	1540.00^{ns}	23.97^{ns}
	EC_{ns} × PGR	6	17.82^{ns}	35.67^{ns}	0.19^{ns}	1033.50^{ns}	12.66^{ns}
	Error	36	16.79	47.73	0.96	1437.33	19.95
	CV (%)		28.32	19.46	32.87	30.11	20.85
Total	EC_{ns}	2	1533.35^{***}	3109.55^{***}	39.78^{***}	8386.50^{*}	206.70^{**}
	PGR	3	79.70^{ns}	50.50^{ns}	0.18^{ns}	3772.00^{ns}	18.56^{ns}
	EC_{ns} × PGR	6	77.12^{ns}	87.30^{ns}	0.14^{ns}	956.50^{ns}	7.24^{ns}
	Error	36	48.82	81.23	0.50	1879.28	26.19
	CV (%)		22.25	11.73	24.76	21.83	17.74

SV source of variation, *DF* degrees of freedom, *MS* mean square, EC_{ns} electrical conductivity of the nutrient solution, *PGR* plant growth regulator, *CV* coefficient of variation. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns: non-significant.

Plants grown in both saline nutrient solutions (4.50 and 9.00 dS m^{-1}) accumulated 84.2% more Na^+ than non-salinized plants (2.16 dS m^{-1}). In contrast, plants grown under moderate (4.50 dS

m^{-1}) and severe (9.00 dS m^{-1}) saline solutions accumulated less K^+ (17.5% and 30.6%, respectively) compared to non-salinized plants, resulting in lower K^+/Na^+ (-58.1%) ratio in tissues (

Table 3). Moreover, plants under severe salinity accumulated 19% less Ca^{2+} than plants non-salinized and under moderate salinity. In contrast, Mg^{2+} content was 23.1% and 11.3% higher in tissues of plants grown under moderate and severe salinity, respectively, compared to non-salinized plants (**Table 3**).

Table 3. Mineral nutrient content (g kg^{-1}) in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions.

EC_{ns} (dS m^{-1})	Na^+	K^+	K^+/Na^+	Ca^{2+}	Mg^{2+}
2.16	20.11±2.15 b	90.98±5.78 a	4.68±0.48 a	210.36±16.59 a	31.15±2.18 b
4.50	37.53±4.20 a	76.52±3.70 b	2.13±0.23 b	213.22±15.68 a	38.34±2.06 a
9.00	36.56±3.00 a	63.11±3.06 c	1.79±0.14 b	172.21±26.94 b	34.68±2.53 ab

EC_{ns} electrical conductivity of the nutrient solution. Values are mean ± SE (*n* = 4). Different letters in column indicate significant difference (Tukey's test, P <0.05).

Regarding mineral nutrient content in the different plant organs, Na^+ content significantly increased in leaves (+90.6%), stems (+125,6%), and roots (+50.7%) of plants grown in both moderate and severe saline solutions compared to plants grown in non-saline solution (**Fig. 2A**). On the other hand, K^+ accumulation was reduced in leaves (-25.4%) and stems (-7.7%) of plants under moderate salinity and reduced in leaves (-40.1%), stems ($^{-1}$7.2%), and roots (-34.1%) of plants grown under severe salinity (**Fig. 2B**). Due to reduced K^+ and increased Na^+ accumulation in tissues, K^+/Na^+ declined in leaves, stems, and roots of salinized tomato plants (**Fig. 2E**). Moreover, Ca^{2+} content decreased in roots (-26.9%), while Mg^{2+} increased in stem (+69.0%) and roots (+35.3%) in plants grown under moderate and severe salinity (**Fig. 2C-D**).

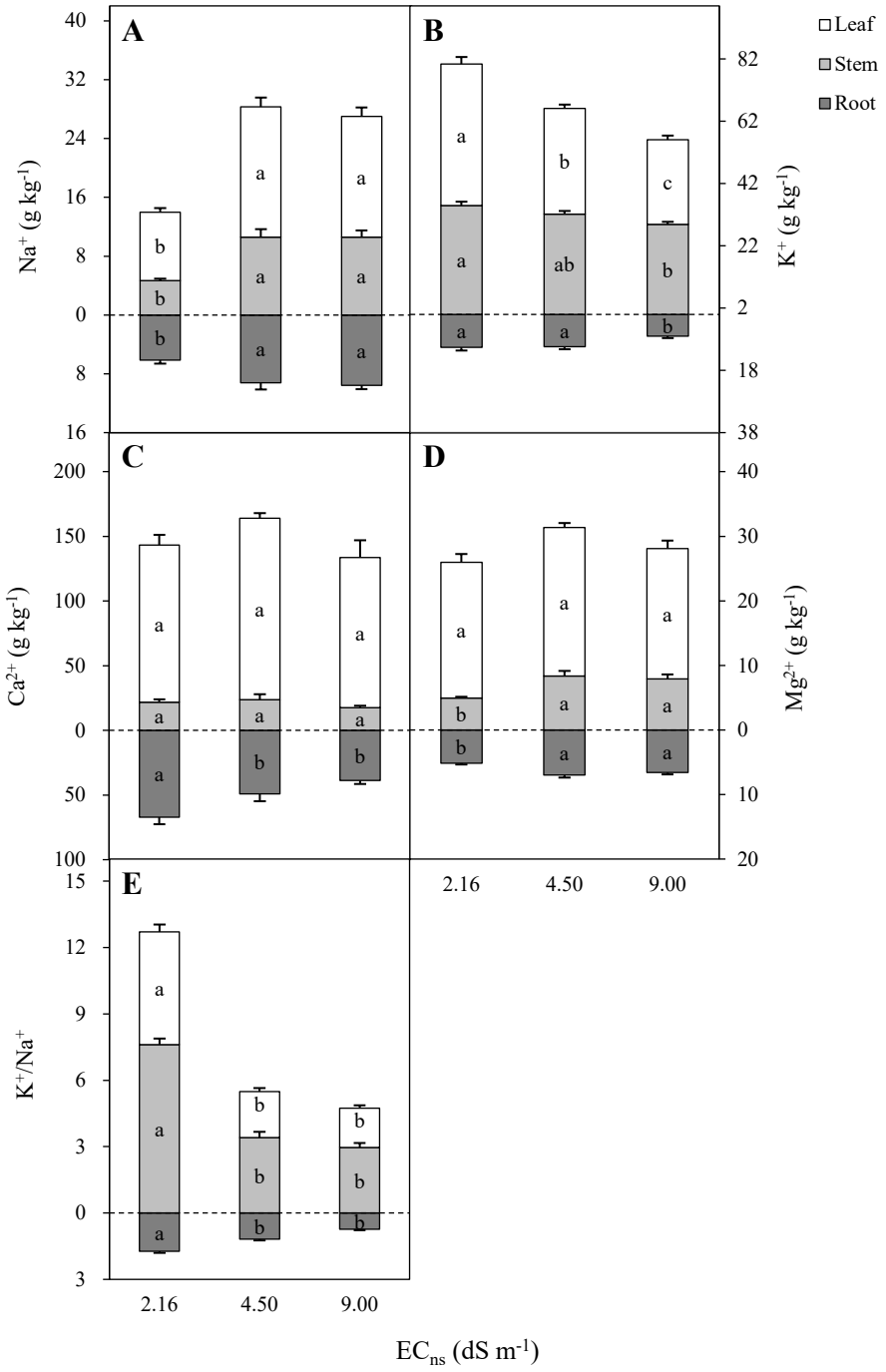

Fig. 2 Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} content in leaves, stem, and roots of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) grown in different nutrient solutions. *EC_{ns}* electrical conductivity of the nutrient solution. For each plant organ, different letters indicate significant difference (Tukey's test, $P < 0.05$).

Foliar spray of JA alone significantly reduced Na^{+} accumulation in the stem of plants grown in 4.50 dS m^{-1} compared to non-treated plants (**Fig. 3A**). A slightly decreased was also observed in plants treated with combined SA and JA (SA+JA). In plants grown in 9.00 dS m^{-1},

JA sprayed alone or combined with SA significantly increased Na^+ content in stems, and decreased K^+/Na^+ in roots (**Fig. 3B**).

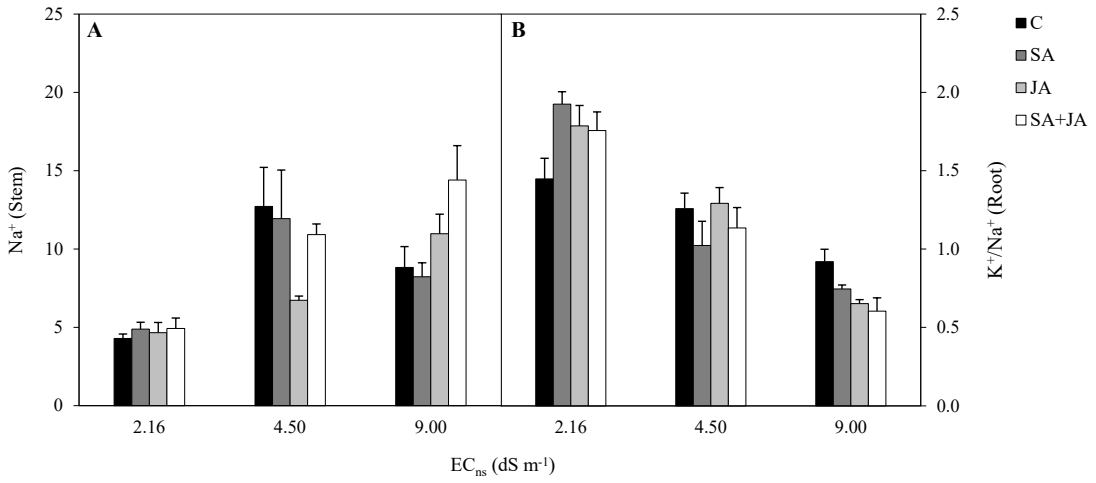

Fig. 3 Na^+ in stem and K^+/Na^+ ratio in roots of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) grown in different nutrient solutions and sprayed with 500 µM salicylic acid (SA) and 50 µM jasmonic acid (JA) alone or in combination (SA+JA), and water as control (C). *EC_{ns}* electrical conductivity of the nutrient solution.

3.2 Chlorophyll content

Chl content was significantly affected by salinity, but not by phytoregulator treatment (**Table 4**).

Table 4. Analysis of variance for chlorophyll content and physiological attributes in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions and sprayed with 500 μM salicylic acid and 50 μM jasmonic acid alone or in combination.

SV	DF	MS			
		Chl *a*	Chl *b*	Chl *a*+*b*	Chl *a*/*b*
EC_{ns}	2	13.27^{*}	10.82^{*}	47.47^{**}	0.31^{*}
PGR	3	1.32^{ns}	0.72^{ns}	3.71^{ns}	0.03^{ns}
EC_{ns} × PGR	6	3.88^{ns}	3.66^{ns}	14.24^{ns}	0.15^{ns}
Error	84	3.38	2.26	9.65	0.10
CV (%)		6.14	14.24	7.67	10.73
		LP	H_2O_2	SOD	EL
EC_{ns}	2	3.47^{**}	0.29^{ns}	6178.00^{ns}	5391.57^{***}
PGR	3	1.03^{ns}	0.09^{ns}	4739.00^{ns}	66.24^{ns}
EC_{ns} × PGR	6	0.48^{ns}	0.19^{ns}	4885.00^{ns}	161.81^{*}
Error	36	0.41	0.19	3145.00	52.10
CV (%)		15.39	32.96	35.25	9.82

SV source of variation, *DF* degrees of freedom, *MS* mean square, *EC_{ns}* electrical conductivity of the nutrient solution, *PGR* plant growth regulator, *CV* coefficient of variation. *Chl a* chlorophyll a, *Chl b* chlorophyll b, *LP* lipid peroxidation, *H_2O_2* hydrogen peroxide, *SOD* superoxide dismutase enzyme activity, *EL* electrolyte leakage. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns: non-significant.

Chl *a* and *b* significantly reduced with increasing EC_{ns}, which thus increased Chl *a*/*b*. Also, plants cultivated under severity salinity showed higher chlorophyll content than plants cultivated under moderate salinity (**Table 5**).

Table 5. Chlorophyll (Chl) content in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions.

EC_{ns} (dS m^{-1})	Chl *a*	Chl *b*	Chl *a*+*b*	Chl *a*/*b*
2.16	30.60±0.64 a	11.13±0.54 a	41.74±1.08 a	2.78±0.10 b
4.50	29.33±0.71 b	9.97±0.56 b	39.30±1.22 b	2.98±0.10 a
9.00	29.94±0.57 ab	10.58±0.52 ab	40.52±1.00 ab	2.87±0.12 ab

EC_{ns} electrical conductivity of the nutrient solution. Chlorophyll (Chl) content was expressed as Chlorophyll Falker Index (CFI, CFL1030 ClorofiLOG, Falker, Porto Alegre, RS, Brazil). Values are mean ± SE (n = 8). Different letters in column indicate significant difference (Tukey's test, $P < 0.05$).

3.3 Lipid peroxidation, electrolyte leakage, and SOD activity

Salinity significantly affected lipid peroxidation (LP) and electrolyte leakage (EL), while exogenous SA and JA did not affect these variables (**Table 4**). LP decreased with increasing

salinity and was higher in plants under moderate than under severe salt stress conditions, indicating LP was reduced under salt stress conditions (**Table 6**).

Table 6. Lipid peroxidation (LP), hydrogen peroxide (H_2O_2) content and superoxide dismutase (SOD) activity in leaves of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions.

EC_{ns} (dS m^{-1})	LP (nmol MDA g^{-1} FW)	H_2O_2 (mmol g^{-1} FW)	SOD (U g^{-1} protein)
2.16	4.63±0.31 a	1.20±0.24 a	137.87±23.76 a
4.50	3.70±0.29 b	1.29±0.19 a	162.77±25.44 a
9.00	4.18±0.31 ab	1.46±0.18 a	176.65±28.27 a

EC_{ns} electrical conductivity of the nutrient solution, *MDA* malondialdehyde, *FW* fresh weight. Values are mean ± SE (*n* = 4). Different letters in column indicate significant difference (Tukey's test, P <0.05).

EL increased with increasing salinity. Foliar spray of SA and JA, alone or in combination (SA+JA), did not significantly affect EL in non-salinized tomato plants and under moderate salinity. However, SA and JA treatment, alone or combined, reduced the ion leakage in plants under severe salinity, indicating that these phytoregulators aid in maintaining the membrane integrity under severe salt stress conditions (**Fig. 4**).

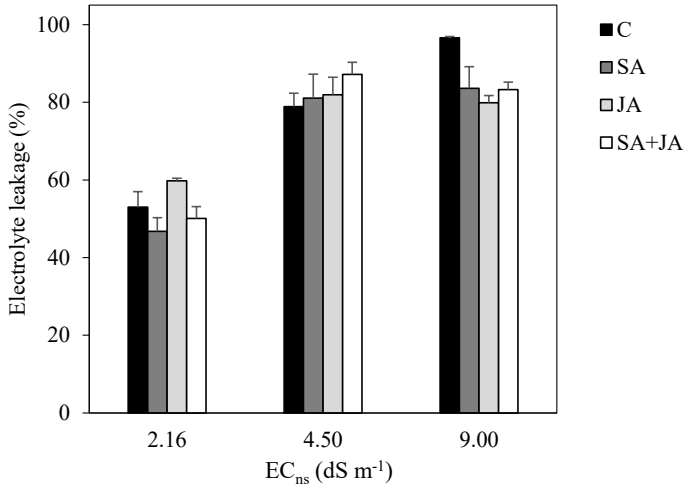

Fig. 4 Electrolyte leakage in leaves of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) grown in different nutrient solutions and sprayed with 500 μM salicylic acid (SA) and 50 μM jasmonic acid (JA) alone or in combination (SA+JA), and water as control (C). *EC_{ns}* electrical conductivity of the nutrient solution.

H_2O_2 content and SOD activity were not significantly affected by salinity and phytoregulator treatment (**Table 4**, **Table 6**).

3.4 Plant growth

The saline nutrient solution significantly affected cherry tomato growth and exogenous SA and JA did not influence plant growth variables (**Table 7**).

Table 7. Analysis of variance for growth parameters in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions and sprayed with 500 μM salicylic acid and 50 μM jasmonic acid alone or in combination.

SV	DF	MS		DF	MS		
		SD	PH		NL	TFM	TDM
EC_{ns}	2	53.33^{***}	8719.50^{***}	2	13307.27^{***}	3678654.00^{***}	64030.01^{***}
PGR	3	2.01^{ns}	123.33^{ns}	3	1452.11^{ns}	19885.37^{ns}	448.12^{ns}
EC_{ns} × PGR	6	0.33^{ns}	462.67^{ns}	6	1215.13^{ns}	30392.14^{ns}	1257.63^{ns}
Error	96	1.89	259.16	36	1231.47	54591.6	1446.42
CV (%)		10.37	16.02		42.71	18.28	18.96
SV	DF	MS					
		LFM	SFM	RFM	LDM	SDM	RDM
EC_{ns}	2	746070.38^{***}	158849.22^{***}	457671.44^{***}	7353.21^{***}	4313.65^{***}	10608.92^{***}
PGR	3	1834.77^{ns}	2857.73^{ns}	6646.69^{ns}	44.83^{ns}	69.84^{ns}	142.1^{ns}
EC_{ns} × PGR	6	3822.76^{ns}	4314.44^{ns}	7790.89^{ns}	103.27^{ns}	146.36^{ns}	247.19^{ns}
Error	36	5835.95	4547.55	26078.28	95.03	141.58	561.33
CV (%)		12.63	25.77	39.2	12.26	21.61	35.91

SV source of variation, *DF* degrees of freedom, *MS* mean square, EC_{ns} electrical conductivity of the nutrient solution, *PGR* plant growth regulator, *CV* coefficient of variation. *SD* stem diameter, *PH* plant height, *NL* number of leaves, *TFM* total fresh matter, *TDM* total dry matter, *LFM* leaf fresh matter, *SFM* stem fresh matter, *RFM* root fresh matter, *LDM* leaf dry matter, *SDM* stem dry matter, *RDM* root dry matter. $^{***}P < 0.001$, ns: non-significant.

Stem diameter and plant height were reduced respectively by 10.5% and 11.1% in plants grown in moderate saline solution, and by 16.5% and 26.9% in plants grown in severe saline solution as compared to plants grown in non-saline solution (**Table 8**).

Table 8. Growth of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions.

EC_{ns} (dS m^{-1})	SD (mm)	PH (cm)	NL	TFM (g $plant^{-1}$)	TDM (g $plant^{-1}$)
2.16	14.57±0.28 a	115.05±2.41 a	113.13±10.38 a	1783.47±80.14 a	269.98±13.43 a
4.50	13.04±0.20 b	102.25±3.38 b	77.31±7.43 b	1222.21±41.65 b	185.5±6.30 b
9.00	12.17±0.19 c	84.09±2.23 c	56.06±8.39 b	829.42±32.24 c	146.18±5.83 c

EC_{ns} electrical conductivity of the nutrient solution, *SD* stem diameter, *PH* plant height, *NL* number of leaves, *TFM* total fresh matter, *TDM* total dry matter. Values are mean ± SE (*n* = 36 for SD and NL; *n* = 16 for NL, TFM and TDM). Different letters in column indicate significant difference (Tukey's test, $P < 0.05$).

Also, the number of leaves was reduced by 31.7% under both moderate and severe salinity. Consequently, total fresh and dry matter were reduced respectively by 31.5% and 31.3% in plants grown in moderate saline solution, and by 53.5% and 45.9% in plants grown in severe saline solution, as compared to non-salinized plants (**Table 8**).

Regarding the different plant organs, plants grown under moderate salinity reduced fresh matter in leaves (-24.4%), stems (-32.1%) and roots (-40.7%), and even more, reduced in leaves (-53.0%) and stems (-54.0%) under severe salinity (**Fig. 5**). Furthermore, leaf, stem, and root dry matter decreased by 23.4%, 31.1%, and 39.9%, respectively, in plants grown under moderate salinity. However, no additional dry matter reduction occurred in plants grown under severe salinity compared to plants under moderate salinity (**Fig. 5**).

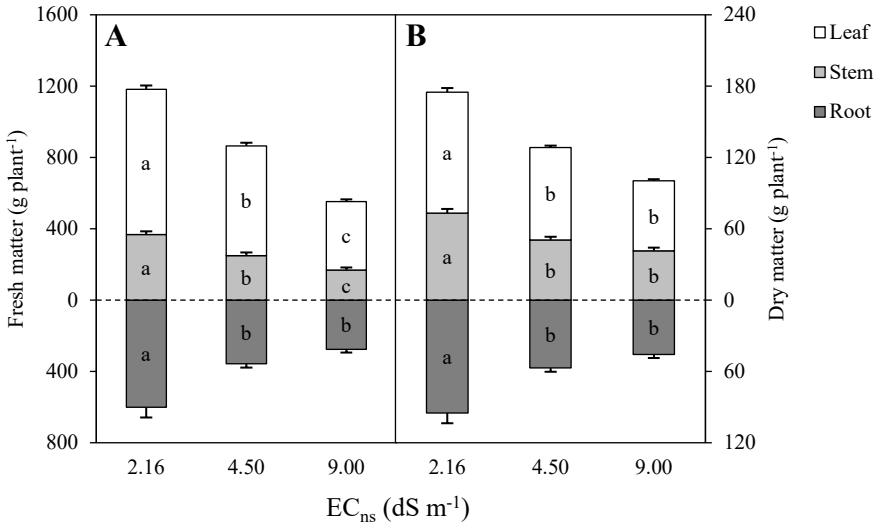

Fig. 5 Fresh and dry matter partitioning in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) grown in different nutrient solutions. *EC_{ns}* electrical conductivity of the nutrient solution. For each plant organ, different letters indicate significant difference (Tukey's test, P <0.05).

3.5 Fruit productivity

Productivity declined due to salinity, and phytoregulator treatment did not counteract the negative effects of salinity on fruit yield (**Table 9**).

Table 9. Analysis of variance for fruit mass and yield of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions.

SV	DF	MS			
		FM	NF	Y	MY
EC_{ns}	2	13.68***	32054.00***	1609909.00***	643.77***
PGR	3	0.48ns	142.00ns	10661.00ns	4.26ns
EC_{ns} × PGR	6	0.38ns	270.33ns	6922.33ns	2.77ns
Error	36	0.57	922.28	14250.58	5.70
CV (%)		15.28	28.83	22.41	22.41

SV source of variation, *DF* degrees of freedom, *MS* mean square, *EC_{ns}* electrical conductivity of the nutrient solution, *PGR* plant growth regulator. *FM* fruit mass, *NF* number of fruits per plant, *Y* yield, *MY* marketable yield. ***P <0.001, ns: non-significant.

The plants grown in the non-saline solution produced fruits with a 5.99 g average weight, and a total of 153.72 fruits per plant, which corresponded to productivity of 890.31 g plant^{-1}. Considering 20,000 plants per hectare, the marketable yield was estimated as 17.81 t ha^{-1} (**Table**

10). Under moderate salinity, fruit mass and the number of fruits per plant declined 26.0% and 37.6%, respectively, which consequently reduced yield by 52.6%. Under severe salinity, although fruit mass did not reduce significantly as compared to plants under moderate salinity, the number of fruits per plant further decreased by 57.3%, and productivity declined by 67.9% (**Table 10**).

Table 10. Yield of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions.

EC_{ns} (dS m^{-1})	FM (g)	NF	Y (g $plant^{-1}$)	MY (t ha^{-1})
2.16	5.99±0.23 a	153.72±10.62 a	890.31±40.07 a	17.81±0.80 a
4.50	4.43±0.19 b	95.94±4.86 b	422.37±24.97 b	8.45±0.50 b
9.00	4.36±0.12 b	65.63±3.13 c	285.35±14.65 c	5.71±0.29 c

EC_{ns} electrical conductivity of the nutrient solution, *FM* fruit mass, *NF* number of fruits per plant, *Y* yield, MY marketable yield (20,000 plants per ha). Values are mean ± SE (*n* = 4). Different letters in column indicate significant difference (Tukey's test, P <0.05).

3.6 Principal Component Analysis

The first two principal components explained 58.2% of the total dataset inertia and the best qualitative variable to illustrate the distance between the individuals on this plane was ECns (**Fig. 6**). Non-salinized tomato plants showed higher values for growth parameters such as NL, SD, TFM, TDM, Y, and MY, being positioned on the right side of the loading plot (**Fig. 6**). On the other hand, with increasing salinity (4.50 and 9.00 dS m^{-1} EC_{ns}), plant growth reduced while Na^+, K^+, and H_2O_2 contents and cell electrolyte leakage increased (**Fig. 6A**), and individuals were positioned left side of the loading plot (**Fig. 6B**). Furthermore, increased Na^+ and H_2O_2 contents were positively correlated with electrolyte leakage and negatively correlated with plant growth and productivity, demonstrating the toxic effects of Na_+ accumulation in plant tissues. For each factor, eigenvalues above 1.0 were considered significant.

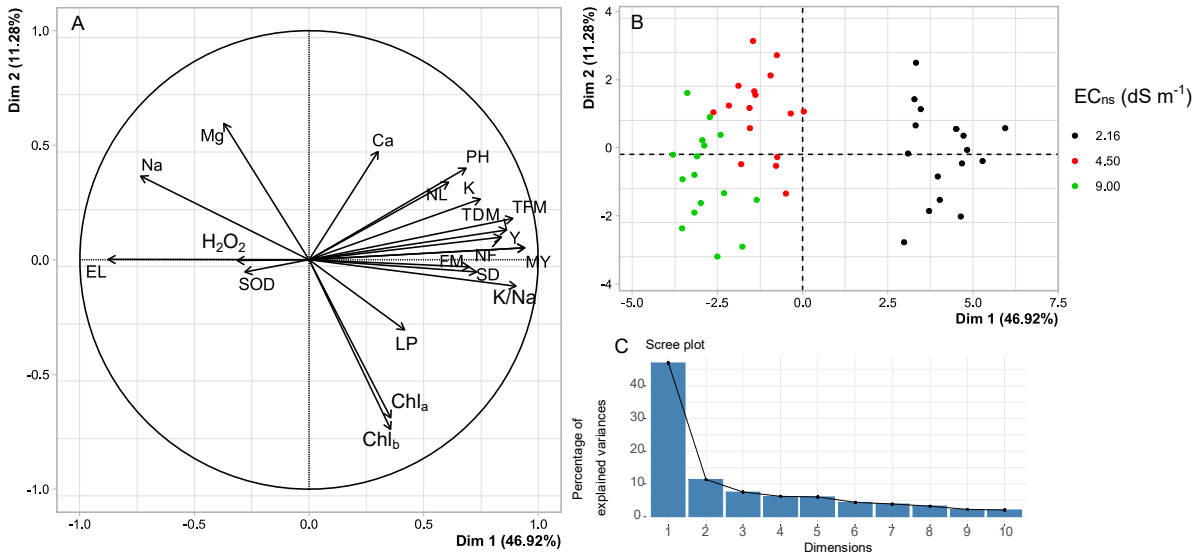

Fig. 6 PCA score (A), loading (B), and scree plot (C) for mineral nutrient content, chlorophyll content, and physiological and growth parameters, and productivity of cherry tomato plants (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) grown in different nutrient solutions. *Na*, *K*, *Ca*, *Mg*, *K/Na*: total sodium, potassium, calcium, and magnesium content, and potassium/sodium ratio, respectively; *Chla* chlorophyll a, *Chlb* chlorophyll b, *EL* electrolyte leakage, *LP* lipid peroxidation, *H_2O_2* hydrogen peroxide, *SOD* superoxide dismutase enzyme activity, *SD* stem diameter, *NL* number of leaves, *PH* plant height, *TFM* total fresh matter, *TDM* total dry matter, *FM* fruit mass, *NF* number of fruits per plant, *Y* yield, *MY* marketable yield.

4 DISCUSSION

We studied the effect of a nutrient solution added with brine from the reverse osmosis system on the physiology, growth, and productivity of cherry tomato and the use of salicylic and jasmonic acid as mitigants of salt stress on plants. The high Na^+ and Cl^- concentration in the nutrient solution affected mineral nutrient uptake (**Table 3**). Excess Na+ in the saline nutrient solution competes for root uptake with essential ions, such as K^+, Ca^{2+}, and Mg^{2+}, and enters the root cells, where accumulate and can be transported to stems and leaves. It has been shown the expression of transporter genes induced by salinity increases the Na^+ transport from root to shoot (Albaladejo et al., 2017). Also, the difference in protein and gene expression associated

with membrane ion transporters explains the varying salt tolerance among cultivars (Assaha et al., 2017).

Due to its similar physicochemical properties, Na^+ adversely affects K^+ uptake specifically competing with high-affinity potassium transporters (HKTs) and nonselective cation channels (NSCCs) (Assaha et al., 2017; Willey, 2016). Also, Na^+ causes membrane depolarization which difficult for K^+ uptake by inward-rectifying channels (KIRs) and increases K^+ leakage from the cell by activating potassium outward-rectifying channels (KORs) (Wakeel, 2013). Consequently, the salinized plants showed increased Na^+ and reduced K^+ and Ca^{2+} concentrations in roots, stems, and leaves, which thus reduced the cell K^+/Na^+ ratio (**Fig. 2**, **Fig. 3**), in addition to higher cell ion leakage (**Fig. 4**). JA treatment alone was effective in reducing Na^+ content in stems, which significantly increased the K^+/Na^+ ratio. Also, both SA and JA, alone or combined, reduced leaf cell electrolyte leakage under severe salinity. Foliar spray of SA and JA was reported to stimulate H^+-ATPase activity of tonoplast in root cells that pump H^+ into vacuoles, providing adequate protons for Na^+/H^+ antiporters to include Na^+ into the vacuoles enhancing salt resistance (Ghassemi-Golezani and Farhangi-Abriz, 2018).

In constrat, Mg^{2+} increased in stem and root due to salinity (**Table 1**). A high Mg^{2+} concentration in the saline solution, supplied by brine addition, may result in a significant decrease in K^+ and Ca^{2+} uptake, increased Mg content in plant tissues, and an imbalanced ratio of Ca to Mg, adversely affecting physiological and biochemical processes, such as membrane stability and permeability due to Ca displacement by Mg (Dehghani et al., 2021). However, increased Mg^{2+} concentration in stems and roots under salinity maintains Mg content in leaves by phloem translocation and increases Chl concentration. Salinity reduced Chl content, but plants under severe salinity had higher Chl content than those under moderate salinity (**Table 5**) because of reduced leaf growth, which concentrates Chl per leaf unit area.

Furthermore, Na^+ accumulation increased in plants grown under 4.50 dS m^{-1} as compared to plants under 2.16 dS m^{-1}, and no further Na^+ increased in plants under 9.00 dS m^{-1}. This suggests plants exhibited mechanisms to counteract Na^+ accumulation under severe salt stress. Because Na^+ is toxic, plants compartmentalize it inside vacuoles, thereby moving it away from the cytosol and proteins, being an effective mechanism to avoid the toxic effects of Na^+ in the cytosol (Maathuis, 2014). But such accumulation induces osmotic stress, which may culminate in cytosol dehydration, protein degradation, and eventually cell death. Therefore, cells accumulate compatible osmolytes as proline, that unlike Na^+ ions do not affect chemical reactions and perform the osmotic adjustment necessary to balance the osmotic pressure caused by Na^+ accumulation inside vacuoles (Manan et al., 2016).

In addition to affecting mineral nutrient balance, increased Na^+ concentration in tissues causes osmotic stress and increases the synthesis of reactive oxygen species, such as hydrogen peroxide, those damage molecules including chlorophyll and proteins (Manan et al., 2016). Chl and protein degradation due to salinity vary significantly among tomato cultivars (Furdi et al., 2013). Exogenous JA and SA were reported to enhance chlorophyll content in salt-stressed tomato plants, inducing the synthesis of antioxidant enzymes such as catalase, superoxide dismutase, ascorbate peroxidase, and catalase that scavenge ROS counteracting the negative effect of salt stress (Manan et al., 2016; Mimouni et al., 2016). Here, JA and SA treatment did not counteract the negative effect of salt stress on chlorophyll content, which suggests this treatment effectiveness is dependent on cultivar and phytoregulator concentration. Also, it has been shown that Chl and protein degradation due to salinity vary significantly among tomato cultivars (Furdi et al., 2013).

Also, increased ROS due to salt stress damage cell membranes increasing lipid peroxidation and electrolyte leakage, as we observed in the present study (**Fig. 4**). However, H_2O_2 concentration and SOD activity did not vary between salt-stressed and non-stressed plants in this study, which suggests that the tomato plants scavenged ROS through other metabolic pathways and may explain why SA and JA treatment was not effective in enhancing the plant antioxidant system.

Salinity significantly reduced plant growth, as a result of reduced water uptake, nutrient imbalance, membrane degradation, decreased Chl content, and photosynthesis (El-Mogy et al., 2018). Salinized tomato plants exhibited reduced height, stem diameter, and number of leaves, and therefore decreased fresh and dry matter accumulation (**Table 8**, **Fig. 5**). Optimal cell hydration and K^+/Na^+ ratio are vital to activate enzymatic reactions in the cytoplasm necessary for the maintenance of plant growth (Assaha et al., 2017). Fresh matter accumulation was reduced under moderate salt stress, and further reduced under severe salinity. However, dry matter accumulation did not further reduce under severe salt stress conditions. It suggests that tomato plants reduced cell water retention and exhibited mechanisms to counteract the negative effects of salinity on plant growth, by accumulating osmolytes to maintain cell turgidity and performing the osmotic adjustment (Mimouni et al., 2016). Therefore, plants under severe salt stress maintained their biomass accumulation despite lower water retention.

Salinity limited water uptake due to increased osmotic pressure at the root zone, leading to the closing of stomata, reducing cell water potential and elongation. Also, nutrient imbalance and accumulation of toxic ions, Na^+ and Cl^-, degrading proteins and photosynthetic pigments

then declining photosynthesis. As a result, plant height, stem diameter, and number of leaves were reduced, which consequently decreased root, stem, and leaf fresh and dry matter.

Also, reduced photosynthesis under salt stress conditions affected plant growth and therefore reduced fruit productivity by reducing fruit mass and size. As a result, fruit productivity declined with increasing salinity. Salinity negatively affects tomato yield due to reduced fruit mass and size and number of fruits per plant. The number of fruits per plant was reduced because salt stress suppressed flower and fruit production in addition to inducing flower dropping (Parvin et al., 2015).

5 CONCLUSIONS

Adding reverse osmosis brine to the nutrient solution reduces cherry tomato growth and productivity.

Salt stress decreases K^+ and Ca^{2+} while increasing Na^+ and Mg^{2+} accumulation in plant tissues, reducing chlorophyll content, and increasing cell electrolyte leakage.

Foliar spray of salicylic acid and jasmonic acid on salt-stressed tomato plants reduces Na^+ content in plant tissues and cell electrolyte leakage, thus alleviating salt toxicity.

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7 CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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CHAPTER III

FOLIAR SPRAY OF SALICYLIC AND JASMONIC ACID AFFECTS GAS EXCHANGE AND FRUIT QUALITY OF CHERRY TOMATO UNDER SALINE STRESS

ABSTRACT

Saline groundwater is generally the main source of water for human consumption and irrigation in the Brazilian semiarid, needing to be desalinated before use. Using reverse osmosis brine from the desalination process for irrigation is an alternative to deal with water scarcity in the region, in addition to avoiding its direct disposal into the environment. In this sense, cherry tomato plants (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) were grown hydroponically in nutrient solutions of 2.16, 4.50 and 9.00 dS m^{-1} prepared with brine diluted in potable water and sprayed with 500 mM salicylic acid (SA) and 50 mM jasmonic acid (SA), alone or in combination, as salt stress attenuators, and water as control. Gas exchange and fruit quality in light red and red ripening stages were evaluated. Results showed that salinity negatively affected plant photosynthesis and gas exchange and reduced fruit mass and size. On the other hand, salt stress improved fruit flavor and quality by enhancing soluble solids content, acidity, and sugars. Exogenous SA and JA alone alleviated damages caused by moderate salt stress (4.50 dS m^{-1}) on gas exchange, but not when sprayed combined. Application combined was advantageous under severe salinity (9.00 dS m^{-1}). Also, although phytoregulator treatment did not counteract the negative effect of salt stress on fruit mass and size, it enhanced fruit acidity, vitamin C content, lycopene, color, and flavor. In conclusion, although saline solution reduced fruit mass and size, it improved fruit quality. Foliar spray of SA and JA alleviated damages caused by salt stress on plant gas exchange and improved fruit quality.

Keywords: fruit quality, reverse osmosis brine, salt stress, *Solanum lycopersicum* L. var. *cerasiforme*, water reuse

1 INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is the second most important vegetable after potato (*S. tuberosum* L.), with 186.8 million tons of fruit produced on 5.05 million ha worldwide [1].

Consumed fresh or processed as canned tomatoes, puree, juices, ketchup, pasta sauces, and dried powders, tomatoes are rich in health-promoting macromolecules such as proteins, pectins, vitamins, phenolic compounds, flavonoids, and carotenoids. These bioactive compounds possess antioxidant, anticancer, and antimicrobial activities, important for treating cardiovascular ailments and neurological disorders [2–4].

Although with high economic potential and nutritional value, tomato production is impaired in regions with a shortage of quality water, such as in the semiarid. Due to the scarcity of surface water, in the Brazilian semiarid groundwater becomes the main source of water for human consumption and irrigation. However, these groundwaters are usually saline and non-potable, reaching up to 6.80 dS m^{-1} [5], requiring prior treatment before use [6]. Thus, desalination systems are used to remove salts by reverse osmosis, but about half of the water becomes hypersaline, with an even higher concentration of salts, exceeding 10 dS m^{-1} EC [7]. In Northeastern Brazil where this process is carried out, this brine is disposed directly into the soil, lake, rivers, and the sea, causing soil salinization and environmental contamination [8,9].

Strategies have been developed to use reverse osmosis brine in agriculture, but due to the high concentration of salts, the wastewater is harmful to plant growth and development. Depending on time and intensity, salinity limits water uptake and induces stomatal closure, negatively affecting gas exchange and photosynthesis [10]. Also, salt stress disrupts mineral supply, inducing the accumulation of toxic ions in tissues and causing nutrient imbalance, stimulating the synthesis of reactive oxygen species that destroy membranes and disrupt chemical reactions, consequently reducing tomato growth and productivity.

Although negatively affects plant growth and development, salt stress improves fruit quality by enhancing the soluble solids content, total soluble sugars, and reducing sugars, thus improving fruit taste and flavor. Furthermore, salinity increase the content of bioactive compounds such as carotenoids, flavonoids, and vitamins, increasing the antioxidant activity and color intensity [11–13].

Therefore, growing tomatoes with reverse osmosis brine contributes to reducing the direct disposal of these wastewaters into the environment. Due to the high concentration of salts, the wastewater can be diluted in potable water thereby reducing the water demand for the cultivation [14]. Tomato can tolerate soil salinity of up to 2.5 dS m^{-1} and irrigation water salinity of up to 1.7 dS m^{-1} without productivity losses, above the average tolerance of most cultivated plants (1.5 dS m^{-1}) [15]. In addition, tomato grown hydroponically can tolerate salinity up to 3.5 dS m^{-1} [14]. Such characteristics are important for the cultivation of tomatoes in regions with a shortage of quality water, such as in semiarid regions.

Moreover, the exogenous application of plant growth regulators such as salicylic acid (SA) and jasmonate (JA) has contributed to acclimatizing tomato plants to saline environments by mediating growth, development, nutrient balance, osmotic adjustment, and antioxidant enzyme synthesis, in addition to improving fruit quality [16–19]. These growth regulators improved the performance of various plant species under salinity conditions, such as cucumber [20], soybean [21], and wheat [22]. Thus, this work aimed to evaluate gas exchange and fruit quality of cherry tomatoes cultivated hydroponically in saline nutrient solution produced with reverse osmosis brine and sprayed with SA and JA.

2 MATERIAL AND METHODS

2.1 Plant material and growth conditions

Cherry tomato (*Solanum lycopersicum* L. var *cerasiforme* cv. Samambaia) seeds were sown in polyethylene trays filled with coconut (*Cocos nucifera* L.) fiber and organic compost at 1:2 (v:v) and irrigated daily. The coconut fiber was obtained from Amafibra (Nogueira, SP, Brazil) and had 1.4 mS cm^{-1} electrical conductivity, 507 ml L^{-1} water retention capacity, 95% porosity, and 150 kg m^{-3} density. The organic compost was obtained from Nibrafértil (Mossoró, RN, Brazil) and had 1.0% nitrogen, 50% humidity, 15% organic carbon, 6.0 pH, 18:1 C: N ratio, and 80 $mmol_c$ dm^{-3} cation exchange capacity. After 24 days from sowing, the tomato seedlings were transplanted to perforated plastic bags (4.0 L capacity) filled with coconut fiber over a layer of gravel covered by a piece of fabric to facilitate water drainage.

The pots were spaced 0.50 m × 1.0 m in a greenhouse at Federal Rural University of Semiarid (UFERSA), Mossoró, Rio Grande do Norte, Brazil. The greenhouse was 6.4 m wide, 18 m long, and 3.0 m ceiling height, and covered with an LDPE film (150 μm thick) with an anti-ultraviolet additive and sides covered with mesh 50% shade. The plants were grown for 82 days in the greenhouse. Temperature and air relative humidity inside the greenhouse were monitored daily using a portable thermos-hygrometer, and climatic data were obtained from the weather station at UFERSA, and data are shown in **Figure 1**.

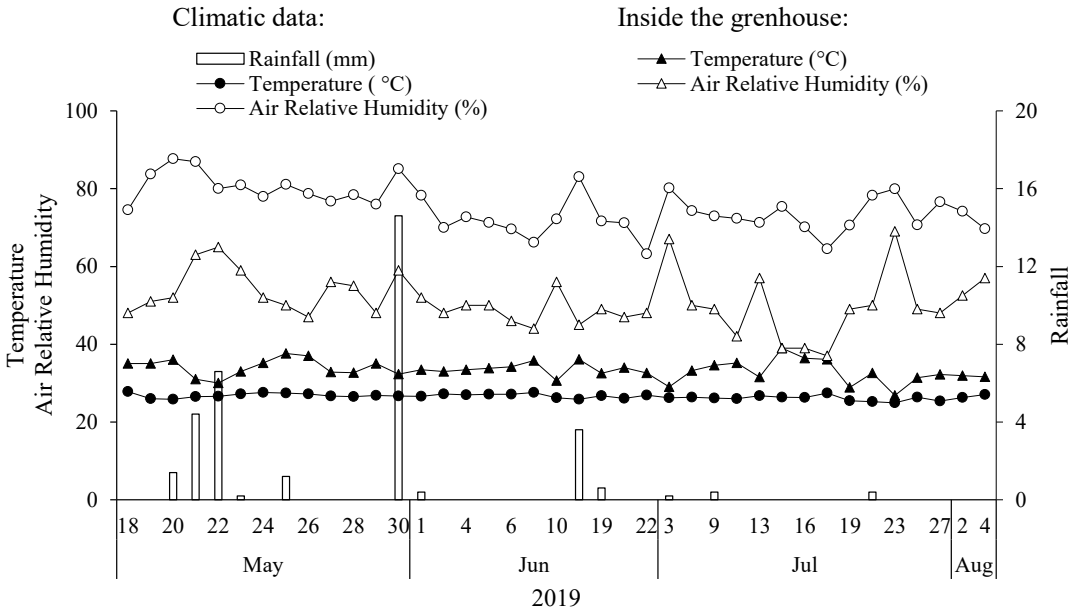

Figure 1. Climatic data during the experiment. Average temperature, air relative humidity, and rainfall in Mossoró city, RN, Brazil, and temperature and air relative humidity (from 7 to 11 a.m.) inside the greenhouse.

2.2 Nutrient solutions

Plants were cultivated hydroponically in a nutrient solution prepared with diluted reverse osmosis wastewater. Until the 12th day after transplanting (DAT), all plants were grown in a non-saline nutrient solution of 2.16 dS m^{-1} electrical conductivity (EC_{ns}). This nutrient solution was prepared by diluting the chemical fertilizers directly in the supply water, which had 0.65 dS m^{-1} EC. From the 12th DAT, one-third of the plants were grown in moderate (4.50 dS m^{-1}) and one-third in severe (9.00 dS m^{-1}) saline nutrient solutions. These solutions were prepared by initially diluting brine from reverse osmosis in supply water in the proportion of 20% and 80%, respectively, to adjust their electrical conductivities to 4.50 and 9.00 dS m^{-1} after adding the fertilizers. The brine was obtained from a desalination process by a reverse osmosis system located in Mossoró (5°01'47.3" S, 37°19'29.5" W, 28 m above the sea level, Rio Grande do Norte state, Brazil). The chemical characteristics of brine and supply water are shown in **Table 1**.

Table 1. Chemical composition of supply water and reverse osmosis brine used in the nutrient solution.

Characteristic	Unit	Supply water	Brine
pH		7.60	7.20
Electrical conductivity	dS m^{-1}	0.65	10.68
K^+	$mmol_c$ L^{-1}	0.26	0.70
Na^+	$mmol_c$ L^{-1}	3.76	45.46
Ca^{2+}	$mmol_c$ L^{-1}	0.80	36.50
Mg^{2+}	$mmol_c$ L^{-1}	1.00	21.20
Cl^-	$mmol_c$ L^{-1}	2.60	81.00
CO_3^{2-}	$mmol_c$ L^{-1}	0.30	0.20
HCO_3^{2-}	$mmol_c$ L^{-1}	2.50	4.90
Sodium adsorption ratio	$mmol_c$ L^{-1}	4.0	8.5
Cations	$mmol_c$ L^{-1}	5.8	103.9
Anions	$mmol_c$ L^{-1}	5.4	86.1
Hardness	mg L^{-1}	90	2885

The fertilizers used were potassium nitrate (KNO_3: 13% N, 44% K_2O), calcium nitrate ($Ca(NO_3)_2$: 15% N, 19% Ca), monoammonium phosphate ($NH_4H_2PO_4$: 11% N, 50% P_2O_5), magnesium sulfate ($MgSO_4.7H_2O$: 9% Mg, 12% S), and potassium chloride (KCl: 60% K_2O, 47% Cl) at the concentrations of 2.0, 50.0, 12.5, 20.0, and 30.0 g L^{-1}, respectively, to obtain a 25% ionic strength of the nutrient solution proposed by [23]. Then, the concentration was doubled to 50% ionic strength from the 7th day after transplanting. Also, a mix of micronutrients (Rexolin BRA, Yara Tera, Yara Brasil Fertilizantes S.A., Porto Alegre, RS, Brazil), containing 11.6% K_2O, 1.28% S, 2.1% B, 0.36% Cu, 2.66% Fe, 2.48% Mn, 0.036% Mo, and 3.38% Zn, was added at the concentrations of 3.0 and 6.0 g L^{-1} to the solutions of 25 and 50% ionic strength, respectively. We reduced the concentration of the nutrient solution to 25% and 50% ionic strength due to the higher concentration of minerals in the brine and because hydroponically grown plants conserve water and nutrients [24].

The EC and pH of the nutrient solutions were monitored daily using a portable pH meter (PH-1700, Instrutherm, São Paulo, SP, Brazil) and conductivity meter (CD-860, Instrutherm, São Paulo, SP, Brazil), respectively. When necessary, pH was adjusted to 6.0 by adding hydrochloric acid (HCl). The nutrient solutions were applied to plants manually until the substrate was saturated.

2.3 SA and JA treatment

On the same day the saline solutions were applied, plants were sprayed with salicylic acid (SA), jasmonic acid (JA), or both SA and JA at the concentrations of 500 µM and 50 µM,

respectively, to test these phytoregulators as mitigants of the deleterious effect of salt stress on plant gas exchange and fruit quality. SA was applied at 12, 20, 32, and 40 days after transplanting (DAT), and JA was applied at 13 and 24 DAT, which corresponded to applications at the vegetative, flowering, and fruiting stages. In addition, plants were sprayed with distilled water as control. The plant growth regulators and water were sprayed throughout the plant using a hand spray bottle. Salicylic acid P.A. ACS (138.12 g mol^{-1}, 99.0%) was obtained from Dinâmica Química Contemporânea Ltda. (Indaiatuba, SP, Brazil), and jasmonic acid (210.27 g mol^{-1}, ≥ 95.0%) was obtained from Sigma-Aldrich Brasil Ltda. (São Paulo, SP, Brazil).

From the 14 DAT, axillary branches were removed as they sprouted. From 17 DAT all plants were trained in a trellis system constructed with strings of wire stretched at 0.4, 1.0, and 1.8 m on wooden poles. Also, plants were sprayed with Connect® (10% Imidacloprid + 1.25% beta-Cyfluthrin, Bayer, Belford Roxo, RJ, Brazil) at 14, 26, 33, 41, and 54 days after transplanting to control whitefly (*Bemisia tabaci*).

2.4 Experimental design

The experimental design was completely randomized in a double factorial scheme (3 × 4). The factors corresponded to the electrical conductivity of the nutrient solution (2.16, 4.50, and 9.00 dS m^{-1}) and phytoregulator treatment (Control, SA, JA, SA+JA). Four replicates were used, and the experimental plot corresponded to two plants randomly spaced over the greenhouse.

2.5 Gas exchange and chlorophyll *a* fluorescence analysis

At 55 DAT, plants were analyzed for gas exchange using an infrared gas analyzer (IRGA, Li-Cor, model LI-6400XT). Net assimilation rate of CO_2 (A, μmol m^{-2} s^{-1}), stomatal conductance (gs, mol m^{-2} s^{-1}), transpiration rate (E, mmol m^{-2} s^{-1}), and internal concentration of CO_2 (Ci, μmol mol^{-1}) were measured on healthy and fully expanded leaves located in the middle portion of the plant canopy. Then, instantaneous water use efficiency ($WUE = A/E$), intrinsic water use efficiency ($iWUE = A/gs$), and instantaneous carboxylation efficiency ($ICE = A/Ci$) were calculated. A leaf chamber (6 cm^2) coupled with a natural irradiance sensor was used, with air humidity between 50 and 60%, airflow of 300 μmol s^{-1}, and atmospheric CO_2 concentration of 400 μmol mol^{-1}. Analyzes were carried out between 11 and 12 a.m. on a sunny day without cloudiness.

Also, chlorophyll *a* fluorescence parameters were measured using a fluorimeter (LI-6400-40 LCF, LI-COR) coupled to IRGA. Leaves were subjected to a saturating flash of actinic irradiation (approximately 2,500 µmol photons m^{-2} s^{-1}) and a pulse of far-red light to determine initial fluorescence (F_0), maximum fluorescence (F_m), variable fluorescence (F_v), F_v/F_m, and electron transport rate (*ETR*). The measurements were performed on three healthy and fully expanded leaves located in the middle third of the plants.

2.6 Postharvest quality evaluation

Fruits were harvested at the light red and red ripening stages, then transported to Physiology and Postharvest Laboratory at UFERSA to evaluate their physicochemical traits separately. A sample of ten fruits in both light red and red ripening stage of each treatment was taken to measure fruit mass (FM, g) on a semi-analytical scale (±0.01 g) and longitudinal (LD) and transversal (TD) diameter (cm) using a digital caliper (±0.01 cm). Subsequently, fruit skin color was measured with a colorimeter (model CR-400, Konica Minolta, Tokyo, Japan) on ten fruits per treatment using the CIELab color parameters: lightness (L*) and chromaticity coordinates (a* and b*). Then, fruit firmness (Firm) was measured on ten fruits using a texture analyzer (TA.XTExpress, Stable Micro Systems, Vienna, United Kingdom) equipped with a 5 mm diameter flat probe, which was inserted to a 5 mm distance at a test velocity of 2 mm s^{-1}, and 5 g trigger force, and values were expressed as N.

Afterward, the fruits were processed in a kitchen blender to determine vitamin C by titration with Tillman's solution (2,6-dichlorophenol-indophenol), according to the methodology proposed by [25] and the results were expressed as mg ascorbic acid (AsA) 100 g^{-1} FW. Then, soluble solids content (SSC), titratable acidity (TA), and pulp pH was determined according to [26]. SSC content was measured directly on the puree using a digital refractometer (model PR101, Atago Palette Co. Ltd., Tokyo, Japan). TA was determined by titration with 0.1 M NaOH of 1.0 g puree diluted in 50 mL distilled water using 1.0% phenolphthalein as a color indicator, and values were expressed as g citric acid 100 g^{-1} fresh weight (FW). The pH of the puree was determined using a pH meter (Model mPA-210 Tecnal, Piracicaba, SP, Brazil). Also, from the soluble solids and titratable acidity values, maturation index (SSC/TA) and taste index {[SSC/(20 + TA)]+TA} were calculated using the equations proposed by [27,28].

Furthermore, a sample of the puree was packed in plastic pots and stored in a freezer (-20 °C) for further evaluation of total soluble sugars (TSS), reducing sugars (RS), lycopene, and β-carotene. Total soluble sugars and reducing sugars content were determined by the anthrone

and dinitrosalicylic acid reagent methods as described by [29] and [30], respectively, and values were expressed as g 100 g^{-1} FW. Lycopene and β-carotene were determined spectrophotometrically by extracting the pigment with acetone-hexane (4:6) at once, then measuring the optical density of the supernatant at 663 nm, 645 nm, 505 nm, and 453 nm at the same time, and estimating the contents (as mg 100 mL^{-1} pulp) using the equations proposed by [31].

Furthermore, total extractable polyphenols content was determined spectrophotometrically using the Folin Ciocalteau phenol reagent according to [32]. Total antioxidant activity (TAA) was assayed by capturing the free radicals DPPH (1,1-diphenyl-2-picryl-hydrazyl) and ABTS (2,2'-azino-*bis*(3-ethylbenzothiazoline-6-sulfonic acid) following the methods adapted by [33] and [34], respectively.

2.7 Statistical analyses

Data were tested for normality and homoscedasticity by the Shapiro-Wilk and Levene test, respectively. Then, gas exchange variables and fruit traits were submitted to two-way analysis of variance by the F test, with EC_{ns} and phytoregulator treatments as sources of variation, and means were grouped by Tukey's test. Fruits in the light red and red ripening stage were evaluated separately. Also, a Principal Component Analysis was performed with fruit traits on both red and light red ripening stages to overview data variation. All statistical tests were considered significant at $p \leq 0.05$ and performed in R software [35].

3 RESULTS

3.1 Gas exchange and chlorophyll *a* fluorescence

A significant interaction ($p < 0.001$) between the electrical conductivity of the nutrient solution and phytoregulator treatment was observed for all the gas exchange variables (**Table 2**).

Table 2. Analysis of variance for gas exchange variables on cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in different nutrient solutions and sprayed with salicylic acid (SA) and jasmonic acid (JA).

SV	DF	MS						
		A	*E*	*gs*	*Ci*	*A/E*	*A/gs*	*A/Ci*
EC_{ns}	2	10.8871***	1.1178***	0.0024***	1514.0208***	0.6264***	714.350***	0.0004***
PGR	3	16.3972***	0.8673***	0.0056***	2728.8542***	0.9026***	945.233***	0.0006***
EC_{ns} × PGR	6	90.1619***	6.4745***	0.0234***	435.4375***	0.3530***	312.183***	0.0022***
Error	36	0.0964	0.0238	0.0001	73.5764	0.0253	29.908	0.0000
CV (%)		2.86	4.5	7.91	4.02	5.06	7.01	6.54

SV source of variation, *DF* degrees of freedom, *MS* mean square, EC_{ns} electrical conductivity of the nutrient solution, *PGR* plant growth regulator, *CV* coefficient of variation. ***: Significant at $p \leq 0.001$ according to the F test. *Ci* internal concentration of CO_2, *E* transpiration rate, *gs* stomatal conductance, *A* net assimilation rate of CO_2, *A*/*E* instantaneous water use efficiency, *A*/*gs* intrinsic water use efficiency, and *A*/*Ci* instantaneous carboxylation efficiency.

In plants grown in the non-saline solution (2.16 dS m^{-1}), phytoregulator treatment significantly reduced *A, E*, and *gs*, which consequently reduced *A*/*E* and *A*/*Ci*. Such a reduction was greater in plants treated with SA or JA single (**Figure 2**). On the other hand, *Ci* slightly increased in treated plants. When grown in the nutrient solution of 4.50 dS m^{-1}, non-treated plants significantly reduced *A* (-61.1%), *E* (-54.9%) and *gs* (-66.2%). Exogenous SA or JA single improved these gas exchange variables, but not when these growth regulators were sprayed combined (SA+JA). In plants grown in the nutrient solution of 9.00 dS m^{-1}, phytoregulator treatment significantly reduced *A*, *E,* and *gs*, similarly to plants in the nutrient solution of 2.16 dS m^{-1} (**Figure 2**). Therefore, SA and JA applied single improves gas exchange under moderate salt stress, but not under severe stress conditions.

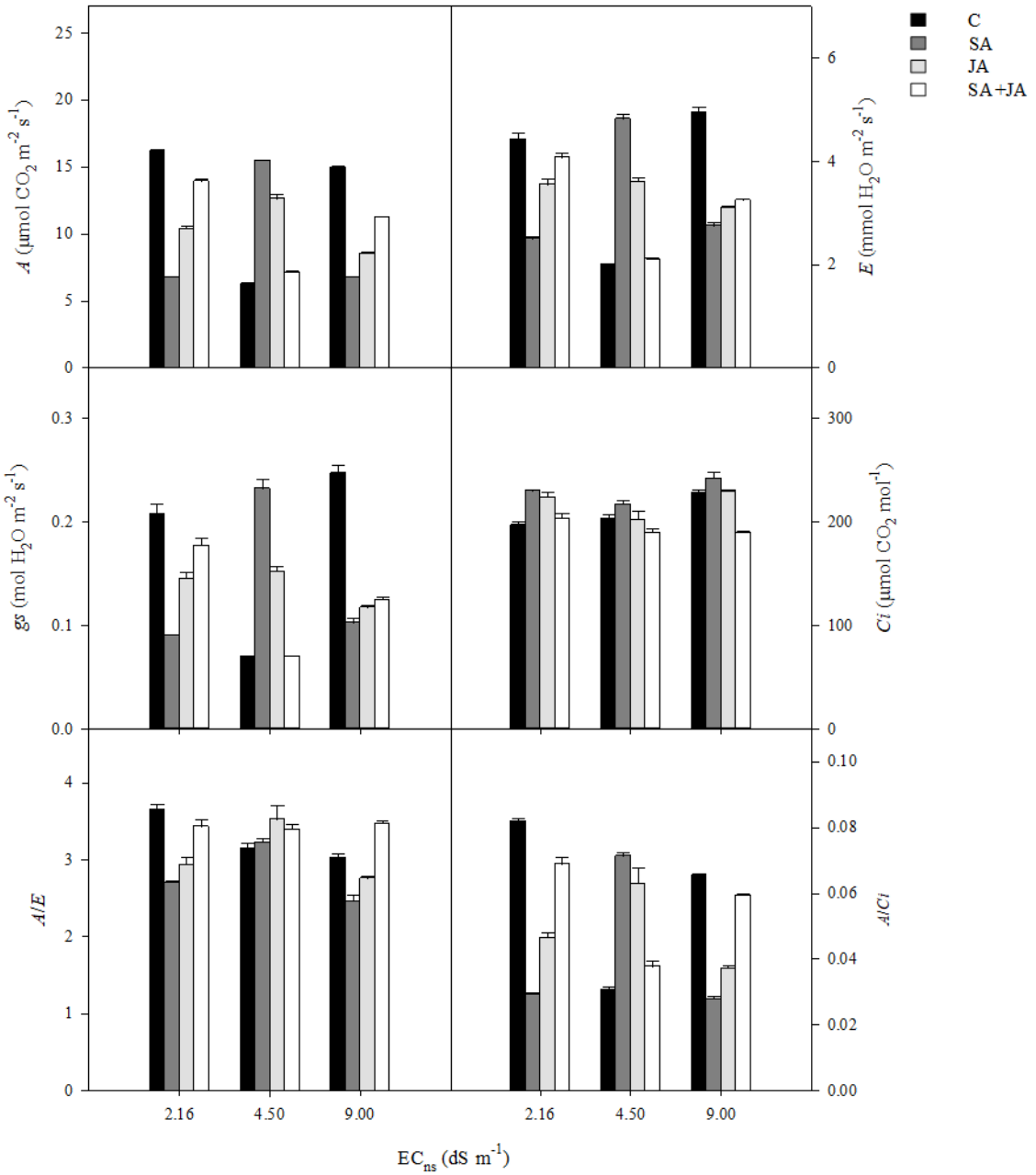

Figure 2. Gas exchange on cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) plants grown in saline nutrient solution and sprayed with 500 µM salicylic acid (SA) and 50 µM jasmonic acid (JA) single or combined (SA+JA) and water as control (C). Values are mean ± SE (n = 4). A net assimilation rate of CO_2, gs stomatal conductance, E transpiration rate, Ci internal concentration of CO_2, A/E instantaneous water use efficiency, and

A/*Ci* instantaneous carboxylation efficiency. EC_{ns} electrical conductivity of the nutrient solution.

Regarding chlorophyll *a* fluorescence, there was a significant interaction (p = 0.0484) between factors for maximum fluorescence (F_m). SA and JA sprayed combined (SA+JA) increased F_m in plants grown in 2.16 dS m^{-1} (2625.75±145.74) and decreased in plants under 4.50 dS m^{-1} (2286.25±48.11), and 9.00 dS m^{-1} (2467.00±54.52). In the other plants, F_m was 2442.64. However, the other fluorescence parameters (F_0 = 660.73±9.12, F_m = 2446.90±25.60, F_v = 1786.17±21.50, F_v/F_m = 0.73±0.003, *ETR* = 65.99±2.88) were not affected by salinity and phytoregulator treatment. Furthermore, F_v/F_m ratio was less than 0.80 in all plants, indicating no damage to photosystem II.

3.2 Physicochemical traits

Salinity significantly affected the physicochemical traits of fruits in both light red and red ripening stages, and exogenous SA and JA application influenced some fruit traits (**Table 3**)

Table 3. Analysis of variance for physicochemical traits of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) fruits, in light red and red ripening stages, grown in different nutrient solutions and sprayed with salicylic acid (SA) and jasmonic acid (JA).

Light red stage							
SV	DF	MS					
		FM	LD	TD	L	a	b
EC_{ns}	2	21.210^{**}	0.415^{**}	0.622^{**}	36.430^{*}	11.980^{ns}	1.900^{ns}
PGR	3	1.788^{ns}	0.034^{ns}	0.061^{ns}	3.930^{ns}	19.360^{ns}	68.570^{*}
EC_{ns} × PGR	6	1.376^{ns}	0.018^{ns}	0.011^{ns}	5.210^{ns}	19.550^{ns}	49.160^{*}
Error	36	3.099	0.065	0.092^{ns}	7.340	17.960^{ns}	18.950
CV (%)		36.33	12.76	16.58	6.36	15.28	13.75
		Firm	SSC	TA	pH	MI	TI
EC_{ns}	2	1.992^{ns}	2.278^{***}	0.029^{ns}	0.009^{ns}	0.852^{ns}	0.040^{**}
GR	3	0.862^{ns}	0.193^{ns}	0.013^{ns}	0.022^{ns}	0.117^{ns}	0.010^{ns}
EC_{ns} × PGR	6	0.446^{ns}	0.082^{ns}	0.014^{ns}	0.020^{ns}	0.286^{ns}	0.010^{ns}
Error	36	1.183	0.193	0.011	0.024	0.388	0.007
CV (%)		10.65	8.00	9.33	4.20	12.62	6.10
		TSS	RS	VitC	β-carot	Lyco	
EC_{ns}	2	0.007^{ns}	0.006^{ns}	28.410^{ns}	0.001^{ns}	0.005^{ns}	
PGR	3	0.000^{ns}	0.002^{ns}	0.870^{ns}	0.001^{ns}	0.007^{**}	
EC_{ns} × PGR	6	0.002^{ns}	0.003^{ns}	16.400^{ns}	0.001^{ns}	0.009^{**}	
Error	36	0.004	0.002	31.930	0.001	0.002	
CV (%)		18.52	18.94	18.77	30.27	36.22	
Red stage							
SV	DF	MS					
		FM	LD	TD	L	a	b
EC_{ns}	2	54.560^{***}	0.387^{***}	0.734^{***}	11.452^{ns}	41.750^{*}	18.014^{ns}
PGR	3	3.860^{ns}	0.044^{ns}	0.061^{ns}	0.282^{ns}	2.610^{ns}	3.179^{ns}
EC_{ns} × PGR	6	4.010^{ns}	0.041^{ns}	0.090^{ns}	3.495^{ns}	13.030^{ns}	15.878^{ns}
Error	36	4.290	0.032	0.048	5.532	10.320	8.454
CV (%)		31.66	7.98	10.55	7.07	8.70	13.18
		Firm	SSC	TA	pH	MI	TI
EC_{ns}	2	3.431^{*}	9.767^{***}	0.137^{***}	0.008^{ns}	1.132^{*}	0.172^{***}
PGR	3	0.968^{ns}	0.494^{ns}	0.000^{ns}	0.002^{ns}	0.500^{ns}	0.001^{ns}
EC_{ns} × PGR	6	1.515^{ns}	0.388^{ns}	0.015^{*}	0.004^{ns}	0.192^{ns}	0.013^{*}
Error	36	1.004	0.341	0.006	0.004	0.289	0.005
CV (%)		10.32	9.15	7.30	1.79	8.94	5.13
		TSS	RS	VitC	β-carot	Lyco	
EC_{ns}	2	0.053^{***}	0.046^{***}	9.320^{ns}	0.0003^{ns}	0.008^{ns}	
PGR	3	0.007^{ns}	0.005^{*}	141.060^{*}	0.0003^{ns}	0.028^{ns}	
EC_{ns} × PGR	6	0.006^{ns}	0.004^{*}	24.240^{ns}	0.0006^{ns}	0.062^{***}	
Error	36	0.004	0.002	41.360	0.0008	0.013	
CV (%)		18.25	11.85	22.22	22.52	21.26	

SV source of variation, *DF* degrees of freedom, *MS* mean square, EC_{ns} electrical conductivity of the nutrient solution, *PGR* plant growth regulator, *CV* coefficient of variation. *, **, ***: Significant at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively, according to the F test; ns: non-significant. *FM* fruit mass, *LD* longitudinal diameter, *TD* transverse diameter, *L a b* skin color coordinates, *Firm* firmness, *SSC* soluble solids content, *TA* titratable acidity,

pH pulp pH, *MI* maturation index (*SSC*/*TA*), *TI* taste index {[*SSC*/(20 + *TA*)]+*TA*}, *TSS* total soluble sugars, *RS* reducing sugars, *VitC* vitamin C, *β-carot* β-carotene, *Lyco* lycopene.

Without brine (2.65 dS m^{-1}), fruit mass, longitudinal diameter, and transversal diameter were 6.13 g, 2.19 cm, and 2.05 cm in the light red stage, and 8.65 g, 2.42 cm, and 2.32 cm in the red stage. Plants grown in the nutrient solution with brine significantly reduced fruit mass and size but reduced equally under moderate and severe salt stress. On both 4.50 dS m^{-1} and 9.00 dS m^{-1} EC_{ns}, fruit mass, longitudinal diameter, and transversal diameter reduced respectively by 31.5%, 12.7%, and 16.7% in fruits in the light red stage, and by 36.6%, 11.2%, and 15.9% in fruits in red stage. Exogenous SA and JA, single or in combination, did not affect fruit mass and size (**Table 4**).

Table 4. Physicochemical traits of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) fruits, in light red and red ripening stages, grown in different nutrient solutions and sprayed with salicylic acid (SA) and jasmonic acid (JA).

Trait		**Light red stage**			**Red stage**		
		2.16	4.50	9.00	2.16	4.50	9.00
FM	C	5.63±0.60^{aA}	3.65±1.05^{aB}	3.88±0.75^{aB}	10.48±1.92^{aA}	6.21±0.56^{aB}	5.34±0.62^{aB}
	SA	5.77±0.67^{aA}	3.77±0.84^{aB}	4.51±0.54^{aB}	7.99±1.17^{aA}	4.93±0.94^{aB}	6.00±0.77^{aB}
	JA	6.22±0.56^{aA}	3.84±0.60^{aB}	5.64±0.97^{aB}	7.83±1.04^{aA}	4.97±0.45^{aB}	5.28±0.46^{aB}
	SA+JA	6.93±1.59^{aA}	4.41±1.21^{aB}	3.92±0.46^{aB}	8.30±1.12^{aA}	6.90±1.60^{aB}	4.27±0.58^{aB}
LD	C	2.06±0.12^{aA}	1.86±0.19^{aB}	1.92±0.09^{aB}	2.57±0.11^{aA}	2.25±0.07^{aB}	2.17±0.07^{aB}
	SA	2.14±0.10^{aA}	1.91±0.11^{aB}	1.88±0.15^{aB}	2.35±0.14^{aA}	2.04±0.11^{aB}	2.21±0.08^{aB}
	JA	2.30±0.19^{aA}	1.90±0.07^{aB}	2.00±0.12^{aB}	2.34±0.10^{aA}	2.07±0.06^{aB}	2.20±0.09^{aB}
	SA+JA	2.27±0.08^{aA}	1.94±0.16^{aB}	1.87±0.07^{aB}	2.43±0.03^{aA}	2.26±0.10^{aB}	2.03±0.09^{aB}
TD	C	1.93±0.09^{aA}	1.61±0.19^{aB}	1.66±0.11^{aB}	2.58±0.15^{aA}	2.03±0.08^{aB}	1.93±0.11^{aB}
	SA	2.06±0.13^{aA}	1.74±0.18^{aB}	1.73±0.15^{aB}	2.23±0.10^{aA}	1.84±0.12^{aB}	2.11±0.09^{aB}
	JA	2.12±0.18^{aA}	1.77±0.10^{aB}	1.83±0.14^{aB}	2.22±0.04^{aA}	1.90±0.07^{aB}	1.96±0.07^{aB}
	SA+JA	2.10±0.22^{aA}	1.75±0.20^{aB}	1.62±0.05^{aB}	2.26±0.14^{aA}	2.07±0.15^{aB}	1.77±0.12^{aB}
Firm	C	9.70±0.43^{aA}	9.73±0.77^{aA}	10.56±0.61^{aA}	9.55±0.29^{aB}	10.52±0.48^{aAB}	10.22±0.62^{aA}
	SA	9.50±0.46^{aA}	10.50±0.35^{aA}	10.29±0.47^{aA}	9.10±0.51^{aB}	9.13±0.42^{aAB}	10.00±0.53^{aA}
	JA	10.67±0.47^{aA}	10.25±0.75^{aA}	10.89±0.59^{aA}	9.62±0.47^{aB}	9.00±0.81^{aAB}	10.49±0.59^{aA}
	SA+JA	9.79±0.33^{aA}	10.02±0.67^{aA}	10.68±0.38^{aA}	8.59±0.43^{aB}	10.49±0.32^{aAB}	9.81±0.32^{aA}
L	C	42.04±0.82^{aB}	42.93±1.43^{aA}	44.01±1.90^{aA}	31.94±0.15^{aA}	34.12±0.89^{aA}	33.96±1.66^{aA}
	SA	39.45±0.78^{aB}	45.27±1.88^{aA}	43.62±1.04^{aA}	33.52±1.50^{aA}	32.17±1.40^{aA}	34.62±1.42^{aA}
	JA	40.60±1.32^{aB}	42.37±1.29^{aA}	42.34±1.42^{aA}	31.57±0.86^{aA}	34.21±1.60^{aA}	33.75±0.93^{aA}
	SA+JA	41.43±0.86^{aB}	43.13±0.85^{aA}	44.25±1.90^{aA}	32.43±1.21^{aA}	33.02±0.30^{aA}	33.85±1.05^{aA}
a	C	26.92±2.93^{aA}	24.36±1.34^{aA}	27.98±2.45^{aA}	33.70±0.91^{aB}	36.57±0.80^{aAB}	39.01±2.62^{aA}
	SA	30.72±1.70^{aA}	27.94±1.74^{aA}	29.72±2.12^{aA}	38.56±2.61^{aB}	35.05±0.49^{aAB}	38.97±2.29^{aA}
	JA	25.99±2.01^{aA}	29.93±0.23^{aA}	26.26±3.01^{aA}	34.13±0.68^{aB}	37.83±1.49^{aAB}	39.04±1.72^{aA}
	SA+JA	30.40±2.18^{aA}	24.96±1.18^{aA}	27.64±2.79^{aA}	35.14±1.53^{aB}	37.70±1.30^{aAB}	37.40±0.81^{aA}
b	C	31.65±0.89^{aA}	27.91±2.85^{bA}	35.13±3.09^{aA}	20.81±1.62^{aA}	20.79±0.17^{aA}	23.43±2.41^{aA}
	SA	32.56±0.22^{aA}	37.34±3.08^{aA}	35.30±2.61^{aA}	22.03±0.30^{aA}	19.01±1.16^{aA}	23.90±2.20^{aA}
	JA	29.41±0.66^{aA}	32.80±1.49^{abA}	27.12±2.42^{aA}	19.91±0.75^{aA}	25.20±2.02^{aA}	23.13±1.42^{aA}
	SA+JA	33.81±1.47^{aA}	29.43±1.20^{abA}	27.51±3.16^{aA}	21.26±1.06^{aA}	23.14±0.37^{aA}	22.03±1.65^{aA}

Continuation…

Trait		Light red stage			Red stage		
		2.16	4.50	9.00	2.16	4.50	9.00
SSC	C	4.99±0.24^{aB}	5.73±0.08^{aA}	5.95±0.38^{aA}	5.39±0.23^{aB}	6.15±0.12^{aA}	6.93±0.25^{aA}
	SA	4.99±0.10^{aB}	5.55±0.28^{aA}	5.43±0.17^{aA}	5.20±0.29^{aB}	7.03±0.37^{aA}	6.75±0.23^{aA}
	JA	5.11±0.23^{aB}	5.74±0.27^{aA}	5.55±0.00^{aA}	5.64±0.24^{aB}	6.56±0.30^{aA}	7.04±0.14^{aA}
	SA+JA	5.13±0.30^{aB}	5.76±0.11^{aA}	5.95±0.19^{aA}	5.88±0.54^{aB}	6.55±0.25^{aA}	7.50±0.32^{aA}
TA	C	1.07±0.00^{aA}	1.11±0.06^{aA}	1.22±0.06^{aA}	0.93±0.04^{aB}	1.08±0.06^{aA}	1.17±0.02^{aA}
	SA	1.03±0.06^{aA}	1.11±0.08^{aA}	1.08±0.05^{aA}	0.92±0.02^{aB}	1.18±0.02^{aA}	1.09±0.04^{aA}
	JA	1.11±0.03^{aA}	1.25±0.06^{aA}	1.09±0.02^{aA}	1.01±0.03^{aA}	1.09±0.06^{aA}	1.08±0.04^{aA}
	SA+JA	1.12±0.04^{aA}	1.19±0.00^{aA}	1.09±0.08^{aA}	0.96±0.03^{aB}	1.04±0.04^{aB}	1.18±0.04^{aA}
pH	C	3.67±0.02^{aA}	3.66±0.02^{aA}	3.65±0.01^{aA}	3.72±0.01^{aA}	3.68±0.03^{aA}	3.65±0.03^{aA}
	SA	3.83±0.16^{aA}	3.81±0.17^{aA}	3.61±0.01^{aA}	3.69±0.03^{aA}	3.77±0.07^{aA}	3.65±0.03^{aA}
	JA	3.66±0.03^{aA}	3.69±0.02^{aA}	3.65±0.05^{aA}	3.73±0.02^{aA}	3.69±0.02^{aA}	3.69±0.03^{aA}
	SA+JA	3.66±0.00^{aA}	3.64±0.02^{aA}	3.73±0.11^{aA}	3.73±0.03^{aA}	3.72±0.03^{aA}	3.71±0.02^{aA}
MI	C	4.74±0.17^{aA}	5.20±0.33^{aA}	4.94±0.46^{aA}	5.82±0.36^{aB}	5.75±0.22^{aAB}	5.90±0.24^{aA}
	SA	4.89±0.35^{aA}	5.14±0.59^{aA}	5.03±0.23^{aA}	5.39±0.03^{aB}	5.99±0.39^{aAB}	6.19±0.14^{aA}
	JA	4.62±0.13^{aA}	4.59±0.06^{aA}	5.16±0.12^{aA}	5.64±0.33^{aB}	6.06±0.28^{aAB}	6.59±0.28^{aA}
	SA+JA	4.58±0.23^{aA}	4.79±0.04^{aA}	5.55±0.45^{aA}	6.08±0.35^{aB}	6.30±0.16^{aAB}	6.38±0.23^{aA}
TI	C	1.29±0.02^{aB}	1.38±0.05^{aA}	1.46±0.04^{aAB}	1.22±0.03^{aB}	1.37±0.05^{aA}	1.47±0.02^{aA}
	SA	1.28±0.04^{aB}	1.37±0.05^{aA}	1.34±0.04^{aAB}	1.20±0.03^{aB}	1.48±0.01^{aA}	1.40±0.04^{aA}
	JA	1.34±0.04^{aB}	1.48±0.06^{aA}	1.35±0.01^{aAB}	1.29±0.02^{aA}	1.39±0.05^{aA}	1.40±0.03^{aA}
	SA+JA	1.35±0.04^{aB}	1.43±0.00^{aA}	1.37±0.07^{aAB}	1.27±0.05^{aB}	1.36±0.04^{aB}	1.50±0.04^{aA}
TSS	C	0.36±0.02^{aA}	0.34±0.04^{aA}	0.37±0.02^{aA}	0.28±0.02^{aB}	0.31±0.03^{aA}	0.35±0.03^{aA}
	SA	0.31±0.05^{aA}	0.36±0.04^{aA}	0.35±0.03^{aA}	0.27±0.06^{aB}	0.41±0.00^{aA}	0.30±0.05^{aA}
	JA	0.33±0.03^{aA}	0.36±0.03^{aA}	0.36±0.01^{aA}	0.24±0.03^{aB}	0.38±0.01^{aA}	0.36±0.03^{aA}
	SA+JA	0.31±0.03^{aA}	0.36±0.03^{aA}	0.39±0.03^{aA}	0.29±0.03^{aB}	0.40±0.02^{aA}	0.43±0.01^{aA}
RS	C	0.25±0.02^{aA}	0.26±0.02^{aA}	0.27±0.04^{aA}	0.30±0.00^{aA}	0.36±0.01^{aA}	0.33±0.02^{bA}
	SA	0.25±0.04^{aA}	0.28±0.01^{aA}	0.27±0.02^{aA}	0.26±0.02^{abB}	0.38±0.03^{aA}	0.35±0.01^{abA}
	JA	0.23±0.03^{aA}	0.23±0.03^{aA}	0.24±0.01^{aA}	0.23±0.03^{bB}	0.32±0.02^{aA}	0.38±0.02^{abA}
	SA+JA	0.19±0.01^{aA}	0.23±0.02^{aA}	0.31±0.02^{aA}	0.29±0.01^{abB}	0.37±0.03^{aA}	0.42±0.00^{aA}
VitC	C	26.16±1.09^{aA}	33.56±0.38^{aA}	30.69±4.20^{aA}	28.93±1.93^{abA}	24.92±2.44^{abA}	28.94±2.31^{abA}
	SA	29.25±4.59^{aA}	29.76±1.65^{aA}	30.57±2.94^{aA}	24.65±0.09^{bA}	24.94±2.04^{bA}	25.20±4.17^{bA}
	JA	30.53±3.08^{aA}	29.03±2.73^{aA}	31.88±4.53^{aA}	29.28±0.21^{abA}	32.84±5.15^{abA}	28.97±4.37^{abA}
	SA+JA	28.41±0.21^{aA}	31.84±2.45^{aA}	29.68±0.91^{aA}	35.09±3.50^{aA}	34.34±3.75^{aA}	29.15±3.95^{aA}

Continuation…

Trait		Light red stage			Red stage		
		2.16	4.50	9.00	2.16	4.50	9.00
β-carot	C	0.06±0.01^{aA}	0.09±0.02^{aA}	0.06±0.01^{aA}	0.11±0.01^{aA}	0.12±0.02^{aA}	0.14±0.02^{aA}
	SA	0.06±0.01^{aA}	0.09±0.01^{aA}	0.08±0.01^{aA}	0.13±0.02^{aA}	0.12±0.02^{aA}	0.14±0.02^{aA}
	JA	0.08±0.01^{aA}	0.08±0.02^{aA}	0.08±0.01^{aA}	0.14±0.02^{aA}	0.11±0.01^{aA}	0.11±0.00^{aA}
	SA+JA	0.08±0.01^{aA}	0.08±0.01^{aA}	0.10±0.01^{aA}	0.13±0.01^{aA}	0.13±0.01^{aA}	0.13±0.01^{aA}
Lyco	C	0.09±0.01^{aA}	0.08±0.00^{bA}	0.09±0.00^{bA}	0.35±0.05^{cB}	0.59±0.09^{aA}	0.43±0.02^{aAB}
	SA	0.09±0.02^{aB}	0.21±0.04^{aA}	0.10±0.01^{bB}	0.40±0.01^{bcB}	0.61±0.03^{aA}	0.64±0.09^{aA}
	JA	0.10±0.01^{aA}	0.11±0.02^{bA}	0.09±0.01^{bA}	0.68±0.06^{aA}	0.45±0.03^{aB}	0.52±0.04^{aAB}
	SA+JA	0.10±0.01^{aB}	0.11±0.02^{bB}	0.21±0.04^{aA}	0.59±0.08^{abA}	0.50±0.03^{aA}	0.60±0.08^{aA}

FM fruit mass (g), *LD* longitudinal diameter (cm), *TD* transverse diameter (cm), *Firm* firmness (N), *L a b* skin color coordinates, *SSC* soluble solids content (°Brix), *TA* titratable acidity (g citric acid g^{-1} fresh weight), *pH* pulp pH, *MI* maturation index (*SSC*/*TA*), *TI* taste index {[*SSC*/(20 + *TA*)]+*TA*}, *TSS* total soluble sugars (g 100 g^{-1} fresh weight), *RS* reducing sugars (g 100 g^{-1} fresh weight), *VitC* vitamin C (mg ascorbic acid 100 g^{-1} fresh weight), *β-carot* β-carotene (mg 100 mL^{-1} pulp), *Lyco* lycopene (mg 100 mL^{-1} pulp). *C* water as control, *SA* 500 µM salicylic acid, *JA* 50 µM jasmonic acid, *SA + JA* 500 µM salicylic acid and 50 µM jasmonic acid combined. Electrical conductivity of the nutrient solution (EC_{ns}): 2.16, 4.50, and 9.00 dS m^{-1}. Values are mean ± SE (n = 4). For each variable on each ripening stage, means followed by the same letter, lowercase in column and uppercase in row, are not significantly different (Tukey's test, $p \leq 0.05$).

Salinity also influenced fruit skin color (**Table 3**). In light red fruits, luminosity (L) increased while chromaticity coordinates (a and b) values did not change under both 4.50 dS m^{-1} and 9.00 ds m^{-1} EC_{ns}. On the other hand, in red fruits, L and b were not affected while a increased with increasing salinity. L indicates black to white variation, b blueish to yellowish, and a greenish to reddish. Thus, light red fruits became brighter, while red fruits intensified the red color due to salinity. Furthermore, exogenous phytoregulator, especially SA applied single, enhanced yellowish (b) in light red fruits. In red fruits, SA and JA treatment did not affect fruit skin color (**Table 4**).

The firmness of light red fruits was not affected by salinity (**Table 3**), but it slightly increased in red fruits by 6.2% and 10.0% in the nutrient solution of 4.50 and 9.00 dS m^{-1}, respectively (**Table 4)**. SA and JA did not affect fruit firmness (**Table 3**). Pulp pH did not change in fruits in both ripening stages. Titratable acidity (TA), total soluble sugars (TSS), and reducing sugars (RS) of light red fruits did not change due to salinity and hormone treatment (**Table 3**). On the other hand, TA and TSS of red fruits significantly increased due to salinity in treated and non-treated plants, while RS enhanced only in fruits of treated plants. Soluble solids content increased on average by 12.9% in light red fruits and 23.3% in red fruits due to salinity, both in treated and non-treated plants. Because of increased sugar content and SSC, maturation index and taste index were increased by salinity, indicating that imposed stress on plants improved fruit quality. And phytoregulator treatment improved fruit quality by increasing sugar content (**Table 4**).

Furthermore, salinity did not affect vitamin C content in fruits in both ripening stages (**Table 3**). On the other hand, exogenous SA and JA did not increase the vitamin C content in light red fruits but enhanced in red fruits when the hormones were applied combined (SA+JA). Regarding carotenoid content (**Table 3**), β-carotene did not change due to salinity and phytoregulator treatment. Differently, lycopene in light red fruits increased due to salinity in plants treated with SA single or SA+JA. In red fruits, SA applied single increased while JA single decreased lycopene content.

Salinity and phytoregulator treatment affected total antioxidant activity (TAA) and total extractable polyphenols (TEP) content (**Table 5**).

Table 5. Analysis of variance for total extractable polyphenols (TEP) content and total antioxidant activity (DPPH and ABTS) in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) fruits, in light red and red ripening stages, grown in different nutrient solutions and sprayed with salicylic acid (SA) and jasmonic acid (JA).

Light red stage				
SV	DF	MS		
		TEP	DPPH	ABTS
EC_{ns}	2	406.000 ^{ns}	6362275 ^{ns}	0.320 ^{ns}
PGR	3	171.100 ^{ns}	3108719 ^{ns}	0.120 ^{ns}
EC_{ns} × PGR	6	53.900 ^{ns}	6937280 ^{ns}	0.856 *
Error	24	363.5	6358291	0.315
CV (%)		25.33	12.69	14.30
Red stage				
SV	DF	MS		
		TEP	DPPH	ABTS
EC_{ns}	2	43.510 ^{ns}	114296889 ^{ns}	0.081 ^{ns}
PGR	3	53.930 *	39943893 ^{ns}	0.829 ^{ns}
EC_{ns} × PGR	6	15.430 ^{ns}	33290825 ^{ns}	0.492 ^{ns}
Error	24	14.55	77063872	0.417
CV (%)		9.93	20.00	36.77

SV source of variation, *DF* degrees of freedom, *MS* mean square, EC_{ns} electrical conductivity of the nutrient solution, *PGR* plant growth regulator, *CV* coefficient of variation.

*: Significant at $p \leq 0.05$ according to the F test; ns: non-significant.

Total extractable polyphenols (TEP) content did not change in light red fruits of both treated and non-treated plants. In red fruits, TEP was not affected by salinity but increased in fruits when SA or JA was applied single (**Table 6**).

Table 6. Total extractable polyphenols (TEP) content and total antioxidant activity by DPPH and ABTS in cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) fruits, in light red and red ripening stages, grown in different nutrient solutions and sprayed with salicylic acid (SA) and jasmonic acid (JA).

Trait		**Light red stage**			**Red stage**		
		2.65	4.50	9.00	2.65	4.50	9.00
TEP	C	59.55±0.28 ^{aA}	81.47±13.07 ^{aA}	71.08±2.71 ^{aA}	36.19±1.60 ^{bA}	40.01±1.54 ^{bA}	33.62±2.62 ^{bA}
	SA	78.60±6.54 ^{aA}	84.88±10.40 ^{aA}	79.42±13.95 ^{aA}	40.17±0.82 ^{aA}	42.63±0.73 ^{aA}	41.91±1.93 ^{aA}
	JA	66.21±2.56 ^{aA}	88.09±25.40 ^{aA}	70.42±1.65 ^{aA}	37.39±1.86 ^{abA}	39.47±0.69 ^{abA}	40.61±0.96 ^{abA}
	SA+JA	66.93±1.71 ^{aA}	73.08±8.71 ^{aA}	71.03±6.43 ^{aA}	31.84±2.98 ^{bA}	38.60±2.98 ^{bA}	38.65±4.34 ^{bA}
ABTS	C	3.28±0.07 ^{bA}	4.33±0.18 ^{aA}	4.31±0.36 ^{aA}	1.86±0.01 ^{aA}	2.34±0.63 ^{aA}	1.37±0.16 ^{aA}
	SA	3.76±0.29 ^{abA}	4.09±0.37 ^{aA}	3.84±0.18 ^{aA}	1.98±0.28 ^{aA}	1.71±0.48 ^{aA}	2.47±0.14 ^{aA}
	JA	3.28±0.31 ^{bA}	4.27±0.58 ^{aA}	3.80±0.28 ^{aA}	1.42±0.39 ^{aA}	1.67±0.25 ^{aA}	1.52±0.48 ^{aA}
	SA+JA	4.70±0.53 ^{aA}	3.63±0.09 ^{aA}	3.84±0.20 ^{aA}	1.17±0.30 ^{aA}	1.69±0.38 ^{aA}	1.52±0.32 ^{aA}
DPPH	C	19820.63±58.11 ^{aA}	17860.32±990.31 ^{aA}	18088.39±852.00 ^{aA}	56248.37±137.59 ^{aA}	41780.21±880.34 ^{aA}	41557.63±4444.57 ^{aA}
	SA	19480.71±1836.77 ^{aA}	19856.15±1620.92 ^{aA}	18519.13±1367.80 ^{aA}	40693.66±1264.63 ^{aA}	40828.24±2631.44 ^{aA}	41481.61±7452.81 ^{aA}
	JA	21230.85±1750.17 ^{aA}	20602.78±797.06 ^{aA}	19486.40±967.24 ^{aA}	48911.13±3128.41 ^{aA}	38230.37±7029.70 ^{aA}	44646.67±2077.14 ^{aA}
	SA+JA	19142.79±1722.15 ^{aA}	21429.81±203.62 ^{aA}	20338.49±1281.19 ^{aA}	49550.64±2737.33 ^{aA}	46655.15±10205.12 ^{aA}	41745.91±4104.15 ^{aA}

TEP Total extractable polyphenols (mg 100 g^{-1} fresh weight), DPPH (g fresh weight g^{-1} DPPH), ABTS (mM Trolox g^{-1} fresh weight). *C* water as control, *SA* 500 μM salicylic acid, *JA* 50 μM jasmonic acid, *SA* + *JA* 500 μM salicylic acid and 50 μM jasmonic acid combined. Electrical conductivity of the nutrient solution (EC_{ns}): 2.16, 4.50, and 9.00 dS m^{-1}. Values are mean ± SE (n = 3). For each variable on each ripening stage, means followed by the same letter, lowercase in column and uppercase in row, are not significantly different (Tukey's test, $p \leq 0.05$).

TAA by DPPH of fruits on both light red and red ripening stages was not affected by salinity and hormone treatment (**Table 5**). On the other hand, SA sprayed single or combined with JA (SA+JA) enhanced the TAA by ABTS of light red fruits from non-salt stressed plants. In salt-stressed plants, the growth regulators did not influence the TAA of light red fruits. Salinity and growth regulators did not affect the TAA of red fruit (**Table 6**).

3.3 Principal Component Analysis

Tomato fruits were separated on each side of the loading plot according to their ripening stage (**Figure 3**). On the left side, fruits on the light red stage have higher L* and b* values, polyphenols content, and antioxidant activity than red ripe fruits. However, on the right side, fruits on the red stage share higher weight, diameter, lycopene, and β-carotene. Furthermore, the fruits were separated according to salinity by the second dimension. Lower down are the fruits from non-stressed plants (2.16 dS m^{-1}), which are larger and heavier. As salinity increases (4.50 and 9.00 dS m^{-1}), they were positioned higher up, sharing higher soluble solids content and sugars, and therefore better maturation and taste index. The first two principal components explained 58.36% of the dataset inertia, and eigenvalues greater than 1.0 were considered significant for each factor (**Figure 3**).

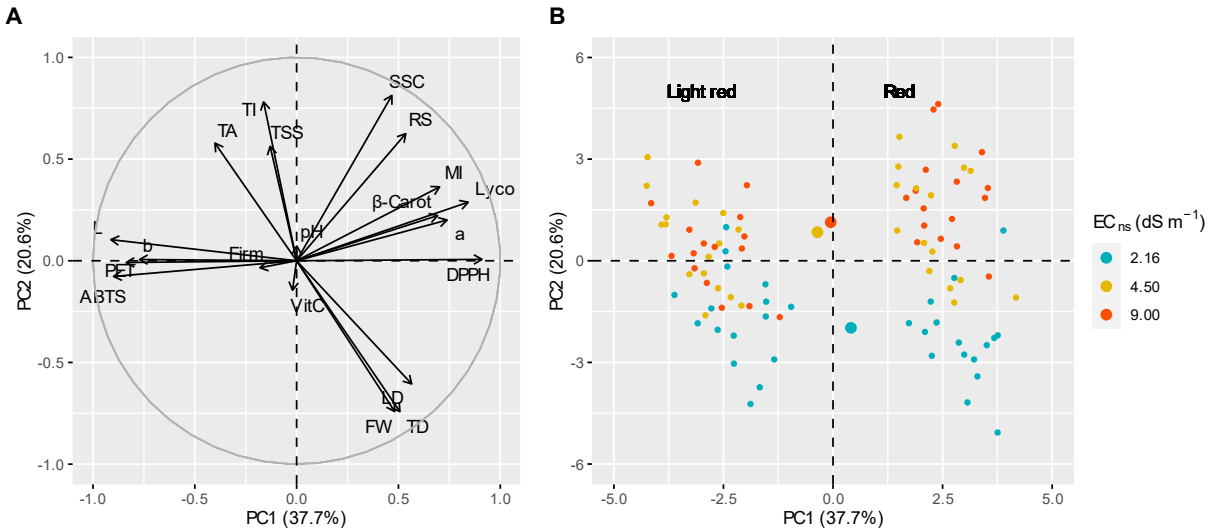

Figure 3. PCA of cherry tomato (*Solanum lycopersicum* L. var. *cerasiforme* cv. Samambaia) fruit traits on light red and red ripening stages. Plants were grown in nutrient solutions of 2.16, 4.50, and 9.00 dS m^{-1} electrical conductivity, which were prepared with respectively 0, 20, and 80% reverse osmosis brine diluted in potable water. Then plants were sprayed with 500 µM salicylic acid (SA) and 50 µM jasmonic acid (JA) single or in combination (SA+JA), and with water as control (C). *FM* fruit mass, *LD* longitudinal diameter, *TD* transversal diameter, *L a b* skin color coordinates, *Firm* firmness, *SSC* soluble solids content, *TA* titratable acidity, *pH* pulp pH, *MI* maturation index, *TI* taste index, *TSS* total soluble sugars, *RS* reducing sugars, *VitC* vitamin C, *β-carot* β-carotene, *Lyco* lycopene, *DDPH* and *ABTS* total antioxidant activity, *TEP* total extractable polyphenols content.

4 DISCUSSION

Reverse osmosis brine diluted in potable water was used to hydroponically cultivate cherry tomato. Then we studied the plant response to moderate (4.50 dS m^{-1}) and severe (9.00 dS m^{-1}) salinity and the protective role of exogenous SA and JA against salt toxicity. Tomato can open and close their stomata in response to changing environmental conditions. Under no stress conditions, K^+ accumulates into the guard cells inducing water diffusion into the cells through osmosis, increasing cell turgor, and opening the stomata allowing for gas exchange. Then CO_2 from the air diffuses into the leaf chamber while water diffuses out to the air, creating tension along the xylem, through which water moves from root to shoot, supporting plant transpiration and photosynthesis [36]. On the other hand, under stress conditions, such as salinity, plants reduce water uptake and photosynthesis, and close stomata to maintain cell turgor. The

tomato plants grown in the nutrient solution of 4.50 dS m^{-1} significantly reduced *A*, *E*, and *gs* because the excessive salt concentration in the saline nutrient solution containing brine may increase the osmotic potential while reducing water potential at the root zone, decreasing root water uptake through osmotic effects subsequently inducing water stress [37]. In this sense, the literature points out that as a response to imposed saline stress, plants release abscisic acid (ABA) that binds to receptors proteins in the plasma membrane and cytosol of the guard cells inducing Ca^{2+} accumulation outside the cell and K^{+} and organic ions efflux, and hence leading to water exit to the cell by diffusion, making cell plasmolyzed, and closing the stomata [38,39]. Consequently, salinized tomato plants reduced transpiration and photosynthetic rate under moderate salinity (4.50 dS m^{-1}).

When treated with SA or JA single, plants grown in the nutrient of 4.50 dS m^{-1} maintained higher *A*, *E*, and *gs* as compared to non-treated plants. It has been shown that SA and JA act by inhibiting the action of ABA, thus keeping the stomata open [40]. In addition, these growth regulators increase the synthesis and activity of antioxidant enzymes that protect the photosynthetic apparatus by scavenging reactive oxygen species (ROS) arising during stress [41]. However, such a response was not observed in plants treated with SA and JA combined (SA+JA), which maintained similar gas exchange rates to non-treated plants, suggesting no synergism between these phytoregulators.

Furthermore, reduced gas exchange was observed in plants under moderate salinity (4.50 dS m^{-1}), but not in plants under severe salt stress conditions (9.00 dS m^{-1}). Non-treated plants grown in the nutrient solution of 9.00 dS m^{-1} showed similar gas exchange to plants in the nutrient solution of 2.16 dS m^{-1}. Studies have shown that a decreased sensitivity of response to ABA was identified in tomato at a specific EC, approximately 9.6 dS m^{-1}, which may characterize a transition of many stress adaptations responses mediated by ABA, including stomatal closure, activation of genes involved in osmotic adjustment, ion compartmentation, regulation of shoot versus root growth and modifications of root hydraulic conductivity properties [42]. It may explain why plants grown in the nutrient solution of 9.00 dS m^{-1} EC showed different stress adaptative responses from plants grown in 4.50 dS m^{-1} EC.

Due to excessive salt concentration at the root zone, plants suffer from uptaking water and nutrients because of reduced water potential and nutrient imbalance. Stomatal closure and reduced photosynthesis in salt-stressed tomato plants contributed to reducing fruit growth, which may consequently diminish productivity, as previous studies reported [43,44]. Reduced fruit mass and size might be due to the adverse effects of salinity on cell expansion and low water influx [19].

Moreover, excessive concentration of Na^+ and Cl^- in the nutrient solutions containing brine (4.50 and 9.00 dS m^{-1}) lower mineral uptake during fruit development, reducing fruit growth. K^+, Ca^{2+}, and Mg^{2+} can compete with Na^+ for root uptake, since these ions share some influx sites at the root cells, such as directly through the plasma membrane, aquaporins, and non-selective cation channels [39]. Within the cell, Na^+ is toxic as it causes nutrient imbalance and osmotic stress and alters protein conformation, especially enzymes, disrupting chemical reactions. The most visible symptom is yellowing, then browning of leaves due to leaf senescence and death, mainly in older leaves that had a long time to accumulate Na^+ and suffer from toxic effects [45].

Therefore, plants may deal with excessive Na^+ within the cell by compartmentalizing it inside vacuoles and performing osmotic adjustment by accumulating compatible osmolytes in the cytosol as well as preventing Na^+ movement through tissues [46]. However, this requires energy expenditure that is diverted from primary growth, that is, plant growth and fruit set and development. Consequently, fruit growth and size were reduced in salinized tomato plants. Also, energy is expended to synthesize antioxidants to protect cell membrane and molecules from the toxic effects of Na^+, and osmolyte compounds to perform the osmotic adjustment. Exogenous SA and JA may contribute to enhancing the synthesis of these compounds and antioxidants [47].

Although salinity reduced fruit growth and productivity, it improved fruit quality by enhancing the content of soluble compounds, total soluble sugars, reducing sugars, organic acids, and lycopene (**Table 3**). The same results were found in various tomato cultivars under saline culture [11–13]. And high soluble solids content in red fruits was higher because it was subjected to a longer period of salinity stress [48]. Consequently, the maturation and taste index of fruits from salinized plants was higher than from non-salinized plants.

The increase in the soluble solids content of fruits from salt-stressed plants was due to limited root water uptake imposed by salinity resulting in reduced water transport to fruits, concentrating sugars, and other soluble compounds [37]. Reduced water content in the fruit increased the soluble solids content by concentrating sugars, organic acids, and other soluble substances. However, it has been shown that molecular and genetic responses to salinity are also involved in the development of fruit tomatoes, metabolically altering fruit components such as sugars, amino acids, organic acids, and carotenoids, contributing to increasing the content of soluble compounds [49]. Such substances may contribute to increasing osmotic potential in fruit cells allowing for osmotic adjustment to support fruit growth under osmotic stress in addition to increasing fruit taste and quality.

Acidity also affects fruit flavor by interacting with sugars, and the expression of genes involved in acid metabolism is upregulated by both moderate and severe salt stress conditions [49]. The accumulation of organic acids in the fruit under salinity counterbalances excessive cations to maintain fruit pH [49]. It may explain why fruits from salinized plants increased acidity but did not change pulp pH.

SA and JA treatment enhanced the content of antioxidants in fruits, such as vitamin C, lycopene, and β-carotene, contributing to increasing total antioxidant activity. Vitamin C content was not affected by salinity, but the foliar spray of SA and JA combined increased vitamin C content in fruit in the red ripening stage. Other studies have found the application of these growth regulators alone or in combination increased vitamin C content on tomato fruits [50], but the mechanisms remain unclear. Salt stress may affect the metabolism of carotenoids in tomato fruits since many of these compounds are powerful antioxidants and can dissipate the excess absorbed energy caused by stressful conditions [51]. Also, an increase in lycopene contributed to enhancing the fruit skin color since this carotenoid is responsible for the tomato red color in both skin and pulp [4].

The firmness of light red ripe fruits was not affected by salinity or hormone treatment. However, red ripe fruits enhanced firmness with increasing salinity. Studies have shown that free N-glycan processing enzymes, such as a-mannosidase and b-D-N-acetylhexosaminidase, are commonly presented in tomato fruit cell walls and accumulate during ripening contributing to fruit softening [52]. Salt stress during fruit ripening decreases the N-glycosylation level of these two enzymes [53], thus explaining the enhancement of tomato fruit firmness under salt stress. On the other hand, the increase in fruit firmness under salinity conditions was attributed to the thickening of hypodermal cell layers rather than to changes and cell wall composition [54]. Increasing fruit firmness is important to prolong shelf life, in addition, to reducing susceptibility to pathogens [55].

In general, fruits in the light red ripening stage have greater antioxidant activity than red fruits. As ripen, fruits increase in weight and size, soften, and accumulate sugars, soluble solids, and carotenoids, improving flavor and quality [2]. Salinity reduced fruit mass and size while increasing sugar content and soluble solids, but equally in both ripening stages (). Although growing cherry tomato in saline solution reduced fruit growth and productivity, it improved the fruit physicochemical traits. These traits enhance the fruit nutritional value and taste, important quality parameters for the fresh and processing tomato market [43].

In conclusion, SA and JA applied alone alleviate damages caused by moderate salt stress on plant gas exchange, but not when applied in combination. Combined application is

advantageous under severe salinity. Growing cherry tomato in saline nutrient solution decreases fruit mass and size but improves quality. Salinity increases the content of soluble solids, sugars, acids, and carotenoids in cherry tomato, and exogenous SA and JA increase vitamin C content, lycopene, and flavor. Although salinity improves fruit quality, it may not compensate for the productivity loss.

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6 CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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