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Salicylic acid attenuates the harmful effects of salt stress on basil[1]

Ácido salicílico atenua os efeitos nocivos do estresse salino em manjericão

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HIGHLIGHTS:

High levels of salt stress limit the development of basil.
High levels of salt stress limit the gas exchange and chlorophyll of basil.
The use of salicylic acid may be a strategy to mitigate the harmful effects of salt stress on basil.

ABSTRACT: The salinity of irrigation water and soil create considerable challenges in agriculture, as they harm the physiological processes and growth of plants. The exogenous application of antioxidant compounds, such as salicylic acid, can reduce the damage caused by salt stress. Thus, this study aimed to evaluate the attenuation of salt stress induced by salicylic acid in *Ocimum basilicum* "Cinnamon". The experiment was performed in randomized blocks with five irrigation water salinity levels (0.5, 1.3, 3.25, 5.2 and 6.0 dS m^{-1}) and five salicylic acid concentrations (0, 0.29, 1.0, 1.71 and 2.0 mM), with five repetitions and two plants per plot. Growth, gas exchange, and chlorophyll indices and fluorescence were evaluated 30 days after the salt treatment was applied. An increase in the salinity of irrigation water decreased the plant height, stem diameter, number of leaves, stomatal conductance, instantaneous water use efficiency, and initial fluorescence of basil "Cinnamon". Salicylic acid was revealed to attenuate the harmful effects of irrigation water salinity on gas exchange, total chlorophyll, and initial and maximum fluorescence of basil plants.

Key words: *Ocimum basilicum*, salinity, gas exchange, photosynthesis

RESUMO: A salinidade da água de irrigação e do solo é um dos grandes desafios da agricultura, pois prejudica os processos fisiológicos e o crescimento das plantas. A aplicação exógena de compostos antioxidantes, como o ácido salicílico, pode reduzir os danos causados pelo estresse salino nas plantas. Assim, o presente estudo teve como objetivo avaliar a ação atenuante do ácido salicílico sobre o estresse salino em *Ocimum basilicum* cv. Cinnamon. O experimento foi conduzido em blocos casualizados com cinco níveis de salinidade da água de irrigação (0,5; 1,3; 3,25; 5,2 e 6,0 dS m^{-1}) e cinco concentrações de ácido salicílico (0; 0,29; 1,0; 1,71 e 2,0 mM), com cinco repetições e duas plantas por parcela. O crescimento, as trocas gasosas, os índices de clorofila e a fluorescência da clorofila foram avaliados 30 dias após a aplicação do estresse salino. O aumento da salinidade da água de irrigação diminui a altura da planta, diâmetro do caule, número de folhas, condutância estomática, eficiência instantânea do uso da água e fluorescência inicial do manjericão cv. Cinnamon. A aplicação de ácido salicílico atenua os efeitos nocivos da salinidade da água de irrigação nas trocas gasosas, clorofila total e fluorescência inicial e máxima de plantas de manjericão.

Palavras-chave: *Ocimum basilicum*, salinidade, trocas gasosas, fotossíntese

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Introduction

The salinization of soil and irrigation water represents a challenge for agriculture, as it compromises agricultural production. It is estimated that by 2050, approximately 50% of the world's agriculturally productive area will show negative effects related to salinization (Shrivasta & Kumar, 2015). In Brazil, the most affected region is the northeast, which has a semi-arid climate and evaporation rates that exceed those of precipitation. In addition, the introduction of low-quality irrigation water contributes to the process of soil salinization (Hannachi & van Labeke, 2018).

High concentrations of sodium and potassium can damage photosynthetic processes by restricting stomatal opening and CO_2 assimilation, and enhancing the production of reactive oxygen species (ROS) concomitant with the degradation of chlorophyll reactions (Silveira et al., 2010). To alleviate the harmful effects of salt stress, tolerance inducers have been considered, such as the exogenous application of salicylic acid (SA). SA is a phenolic compound that plays an important role in maintaining resistance to stress, such as by the production of osmolytes and secondary metabolites (Khan et al., 2015). The mitigation of salt stress by salicylic acid has been observed in *Vigna angularis* (Ahanger et al., 2020), *Triticum aestivum* (Azeem et al., 2018), *Egletes viscosa* (Batista et al., 2019), and *Ocimum basilicum* (Silva et al., 2018a; Silva et al., 2018b; Kahveci et al., 2021). SA application has been shown to alleviate the harmful effects of salt stress on medicinal aromatic plants, such as basil.

Basil (*Ocimum basilicum* L. – Lamiaceae) is a medicinal aromatic plant originating from the tropical and subtropical climates of Asia, Africa, and the Americas. This species is economically important because of its medicinal, aromatic, and flavor characteristics, both *in natura* and processed, as well as the potential for the extraction and production of the essential oil from its leaves, which has attracted the interest of both manufacturers and researchers (Mohammadzadeh et al., 2013). Thus, this study aimed to evaluate the attenuation of salt stress induced by salicylic acid in *Ocimum basilicum* "Cinnamon".

Material and Methods

The experiment was carried out in a greenhouse at the Center for Agricultural Sciences, Universidade Federal da Paraíba, Areia, Paraíba, Brazil (6°58'1.45" S, 35º42'48.90" W, 575 m.a.s.l.). The experimental design was in randomized blocks, with five electrical conductivities of irrigation water (ECw – 0.5, 1.3, 3.25, 5.2, and 6.0 dS m^{-1}) and five concentrations of salicylic acid (SA – 0, 0.29, 1.0, 1.71, and 2.0 mM), with five repetitions and two plants per plot. Nine combinations were generated using the central composite design.

The seeds of *Ocimum basilicum* "Cinnamon" were placed in 162-cell polyethylene trays filled with soil and commercial organic compost (1:1, volume basis). Seedlings were transplanted 25 days after sowing (DAS) into pots with previously moistened soil to field capacity. The experimental units consisted of 5.0 dm^3 polyethylene pots filled with soil and 100 g of poultry manure per pot. A sample of the substrate was collected and following chemical attributes were determined: pH (H_2O): 6.9; P (mg dm^{-3}): 11.71; K^+ (mg dm^{-3}): 873.43; Na^+ (cmol dm^{-3}): 0.24; $H^+ + Al^{+3}$ ($cmol_c$ dm^{-3}): 1.6; Al^{+3} ($cmol_c$ dm^{-3}): 0; Ca^{+2} ($cmol_c$ dm^{-3}): 4.65; Mg^{+2} ($cmol_c$ dm^{-3}): 0.39; SB ($cmol_c$ dm^{-3}): 7.52; CEC ($cmol_c$ dm^{-3}): 9.12; V (%): 82.45; and OM (g dm^{-3}): 22.73. The soil used was Alfisol (Soil Taxonomy, United States, 2014) which had a sandy loam texture, with the following physical characteristics: sand (g kg^{-1}): 756.9; silt (g kg^{-1}): 59.1; clay (g kg^{-1}): 184.0; apparent density (kg dm^{-3}): 1.38; particle density (kg dm^{-3}): 2.67; total porosity (%): 48; field capacity (g kg^{-1}): 78; and permanent wilting point (g kg^{-1}): 43. No further fertilization was performed.

The irrigation depths were determined by a drainage lysimeter, using four plants that were subjected to 0.5 dS m^{-1} ECw and 0 mM SA, and irrigated until drainage. The volume of water applied was reduced by the proportion drained, and the resultant amount was used for the remaining plants. Saline water was prepared by adding NaCl, $CaCl_2.2H_2O$, and $MgCl_2.6H_2O$ salts, in the equivalent ratio of 7:2:1, respectively, to water (0.5 dS m^{-1}), based on the relationship between ECw and salt concentration. Salicylic acid was prepared in 30% ethyl alcohol with 0.05% Tween 80 as a surfactant to improve absorption by the plants. The control consisted of distilled water and Tween 80. The plants were wetted thoroughly by weekly spraying (approximately 10 mL per plant) with the solutions described above for 21 days. Plants were subjected to salt stress and salicylic acid application 30 days after sowing. Weeds and pests (mainly caterpillars) were manually controlled by picking.

Growth, gas exchange, and chlorophyll indices and fluorescence were evaluated 30 days after beginning saline water irrigation (DAI). Plant height was assessed with a graduated ruler, stem diameter with a caliper, and the number of leaves was evaluated manually. Gas exchange measurements were performed using an infrared gas analyzer (LI-COR®-model LI-6400XT, Nebraska, USA), and measurements were taken between 09:00 and 10:00. The CO_2 assimilation rate (A – μmol CO_2 m^{-2} s^{-1}), stomatal conductance (gs – mol H_2O m^{-2} s^{-1}), internal carbon concentration (Ci – μmol CO_2 mol air^{-1}), transpiration (E – mmol H_2O m^{-2} s^{-1}), vapor pressure deficit (VPD – $VPD_{leaf-air}$), instantaneous water use efficiency (WUE – A/E), intrinsic water use efficiency (iWUE – A/E), and intrinsic carboxylation efficiency (iCE – A/Ci) were determined.

The indices for chlorophyll a, b, and total chlorophyll, as well as the a/b ratio were measured non-destructively using a portable electronic chlorophyll meter (ClorofiLOG®, model CFL 1030, Porto Alegre, RS, Brazil), and the values were dimensioned with the Falker chlorophyll index (FCI). A modulated fluorometer (Model OS-30p, Sciences Inc., Hudson, USA) was used to assess the chlorophyll fluorescence. Tweezers were placed on the leaves for 30 min before the readings to adapt the leaves to the dark. The initial fluorescence (F_0), maximum fluorescence (F_m), variable fluorescence ($F_v = F_m - F_0$), and photosystem II quantum yield (F_v/F_m) were determined.

Data were subjected to the normality (Shapiro-Wilk) and homogeneity of variance tests (Bartlett) as well as regression analysis, and when the interaction between the factors was significant, response surface graphs were created, with the equations generated by the rsm (Lenth, 2009) and GA packages (Scrucca, 2013). An analysis of canonical variables and confidence ellipses ($p \leq 0.01$) was performed to study the interrelationship between variables and factors using the candisc package (Friendly & Fox, 2021). The statistical program R (R Core Team, 2021) was used to perform the statistical analyses.

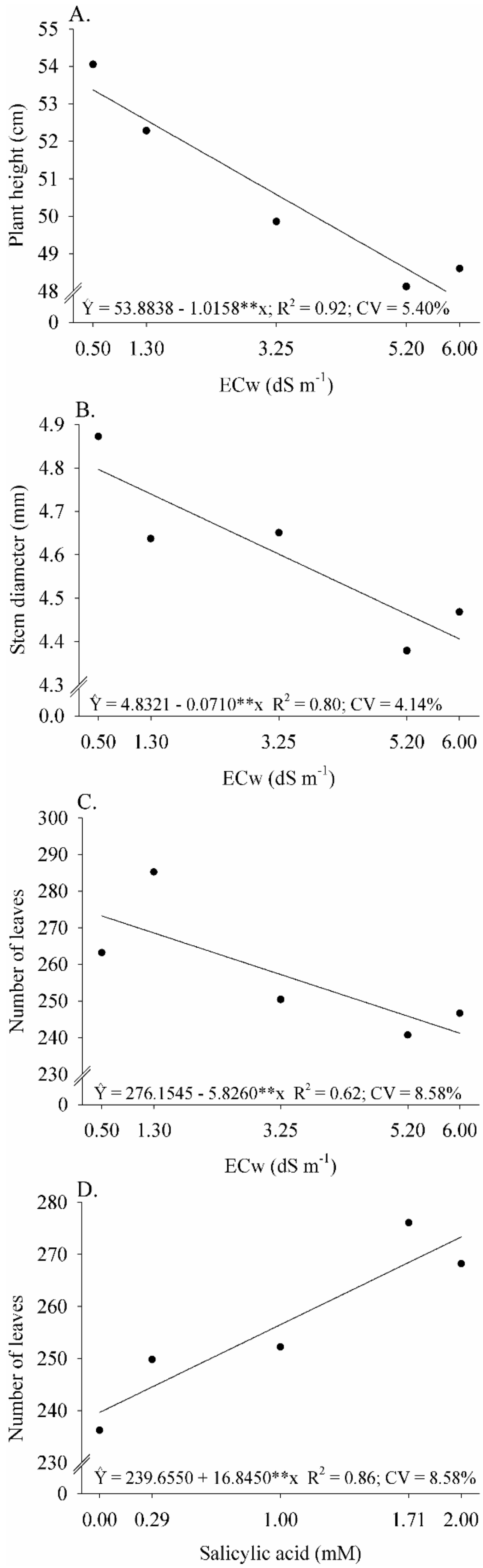
Results and Discussion

Plant height, stem diameter, and the number of leaves decreased by 1.89, 1.47 and 2.11%, respectively, with a unitary increase in ECw. The number of leaves increased by 7.03% with a unitary addition of salicylic acid (Figure 1).

The negative effect on the growth of basil plants by the increased salinity was likely due to the excessive absorption of ions such as Na^+ and Cl^-, changes in the nutritional imbalance and mineral nutrient metabolism, or oxidative stress due to the physiological imbalance between oxidants and antioxidants (Isayenkov & Maathuis, 2019). Plants under stress can slow their growth to conserve energy and reduce the risk of damage.

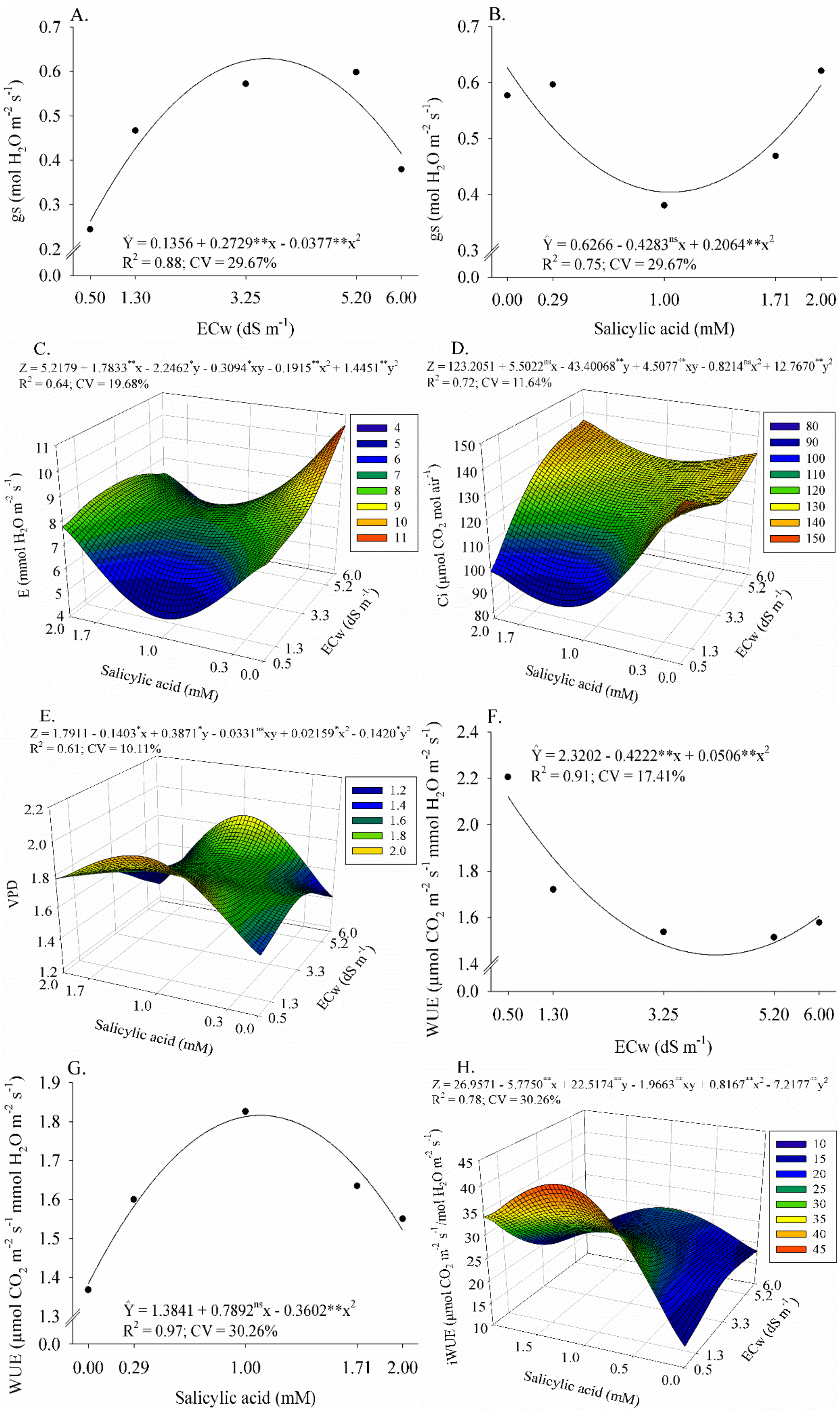
The growth reduction could also be related to the increase in reactive oxygen species that cause various physiological and biochemical disturbances in plants. The increased number of leaves after the application of salicylic acid can be attributed to the action of that compound on proteins and enzymes involved in cell growth (Miura & Tada, 2014). Salicylic acid application attenuated the harmful effects of salt stress on basil "Cinnamon" (Silva et al., 2018a), and "Genovese" (Mousa et al., 2020), as well as tomato (*Solanum lycopersicum* – Souri & Tohidloo, 2019), rice (*Oryza sativa* – Kim et al., 2018), and pepper (*Capsicum annuum* – Kaya et al., 2020).

Stomatal conductance (0.63 mol H_2O m^{-2} s^{-1}) was greatest with the ECw of 3.62 dS m^{-1}, and decreased at higher ECw values (Figure 2A). Application >1.0 mM of salicylic acid increased gs (Figure 2B). The harmful effects of salinity (up to ECw of 3.73 dS m^{-1}) on the CO_2 assimilation rate were reduced with the application of 0.0015 mM of salicylic acid. Salinity up to an ECw of 4.66 dS m^{-1} restricted the effects on transpiration, which were mitigated with the application of 0.0026 mM of salicylic acid (Figure 2C). The highest concentration of internal carbon (144.75 μmol CO_2 mol air^{-1}) was observed in the ECw of 5.98 dS m^{-1} and with the application of 1.99 mM of salicylic acid (Figure 2D). The greatest vapor pressure deficit (1.97 $VPD_{leaf\text{-}air}$) was observed at an ECw of 0.50 dS m^{-1} and with 1.31 mM of salicylic acid (Figure 2E). The variables A ($Z = 9.4084 + 1.7388^{**}x + 0.3592^{ns}y - 0.3026^{ns}xy + 0.2333^{*}x^2 + 0.2599^{ns}y^2$; $R^2 = 0.59$; CV = 12.62%) and iCE ($Z = 0.0779 - 0.0084^{ns}x + 0.0403^{*}y - 0.0403^{*}xy - 0.0010^{ns}x^2 - 0.0082^{*}y^2$; $R^2 = 0.59$; CV = 15.97%) had interactions between the factors, but with an R^2 of less than 60%. Therefore, the graphs of these variables were not presented.



** Significant at $p \leq 0.01$ by the F test

Figure 1. Plant height (A), stem diameter (B), number of leaves (C) of *Ocimum basilicum* "Cinnamon" under salt stress (ECw) and number of leaves (D) under salicylic acid application



ns, ** - Not significant, significant at ≤ 0.01 by the F test, respectively

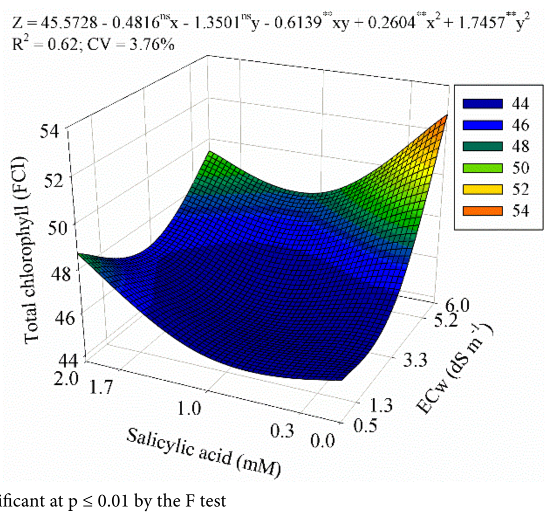
Figure 2. Stomatal conductance (gs - A and B), transpiration (E - C), internal carbon (Ci - D), vapor pressure deficit (VPD - E), instantaneous water use efficiency (WUE - F and G), and intrinsic water use efficiency (iWUE - H) of *Ocimum basilicum* “Cinnamon” under salt stress (ECw) and/or salicylic acid

The lowest instantaneous water use efficiency (1.44 μmol CO_2 m^{-2} s^{-1} $mmol^{-1}$ H_2O m^{-2} s^{-1}) was observed with the ECw of 4.17 dS m^{-1} (Figure 2F) and the highest (1.82 μmol CO_2 m^{-2} s^{-1} $mmol^{-1}$ H_2O m^{-2} s^{-1}) with the application of 1.10 mM of salicylic acid (Figure 2G). The highest intrinsic water use efficiency (40.19 μmol CO_2 m^{-2} s^{-1} mol^{-1} H_2O m^{-2} s^{-1}) occurred with an ECw of 0.52 dS m^{-1} and 1.48 mM of salicylic acid (Figure 2H) and the highest intrinsic carboxylation efficiency (0.123 μmol CO_2 m^{-2} s^{-1} μmol^{-1} CO_2 mol air^{-1}) was observed with an ECw of 0.52 dS m^{-1} and 1.98 mM of salicylic acid.

Stomatal regulation is among the first protective responses of plants, and its function is to establish communication between the leaf mesophyll and the atmosphere to regulate water efflux and CO_2 inflow (Hlaváĉová et al., 2018). The attenuation of the harmful effects of salinity on gas exchange by salicylic acid is related to the induction of plant tolerance through antioxidant activity, stomatal opening regulation, and carbohydrate metabolism, especially that of non-reducing sugars, which can act in osmotic regulation (Silva et al., 2020). Furthermore, this behavior may be related to the action of salicylic acid in strengthening stress resistance and improving antioxidant function and glycine betaine accumulation, resulting in protection of photosynthesis processes (Ahanger et al., 2020).

Thus, the beneficial effects of salicylic acid on gas exchange in plants subjected to salt stress may be related to its ability to improve enzymatic and photosynthetic responses, in addition to inducing changes in carbohydrate metabolism, thereby acting as an osmoregulator and osmoprotector against salt stress (Batista et al., 2019; Silva et al., 2020). These results are similar to those found with soursop plants (*Annona muricata* L.) by Silva et al. (2020).

The harmful effects of salinity (up to ECw of 5.99 dS m^{-1}) on chlorophyll a were attenuated with the application of 0.0108 mM of salicylic acid, and up to an ECw of 5.98 dS m^{-1}, chlorophyll b was mitigated with the application of 0.003 mM. The effects on total chlorophyll were reduced with 0.006 mM of salicylic acid (Figure 3). Salinity exerted restrictions up to ECw of 0.68 dS m^{-1} for the chlorophyll a/b ratio, which decreased with the application of 0.57 mM of salicylic acid. Chlorophyll a



** Significant at p ≤ 0.01 by the F test

Figure 3. Total chlorophyll of *Ocimum basilicum* "Cinnamon" under salt stress (ECw) and salicylic acid

($Z = 33.0406 - 0.3700^{ns}x - 0.5505^{ns}y - 0.3019^{*}xy + 0.1533^{**}x^2 + 0.8001^{*}y^2$; $R^2 = 0.54$; CV = 3.01%), b ($Z = 12.5321 - 0.1115^{ns}x - 0.7995^{ns}y - 0.3120^{**}xy + 0.1071^{*}x^2 + 0.9456^{**}y^2$; $R^2 = 0.52$; CV = 6.80%), and the a/b ratio ($Z = 2.6427 - 0.0091^{ns}x + 0.1165^{ns}y + 0.0357^{*}xy - 0.0084^{ns}x^2 - 0.1225^{*}y^2$; $R^2 = 0.49$; CV = 3.76%) had interactions between the factors, but had R^2 values less than 60%. Therefore, the graphs of these variables are not displayed.

The harmful effects of salinity on chlorophyll were reduced by the application of salicylic acid due to the action of this phytohormone in transcription regulation and gene translation that affects pigment synthesis, leading to an increase in the chlorophyll index, even in plants under salt stress (Kittipornkul et al., 2020). Similar results were observed with *Silybum marianum* through ROS elimination (Ghassemi-Golezani et al., 2016).

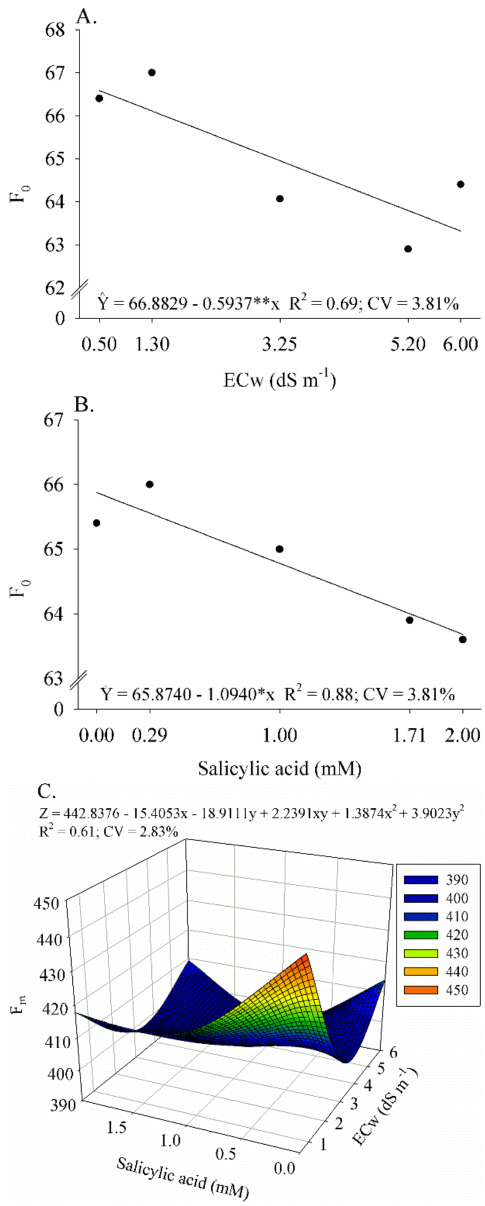
The initial fluorescence decreased by 0.89% with a unitary increase in ECw (Figure 4A) and 1.66% with a unitary increase in salicylic acid (Figure 4B). The highest maximum fluorescence (434.99) occurred with an ECw of 0.51 dS m^{-1} and 0.017 mM of salicylic acid (Figure 4C), while the variable fluorescence was greatest (365.78) with ECw of 0.51 dS m^{-1} and 0.0006 mM of salicylic acid. The variable F_v ($Z = 372.3253 - 13.1591^{**}x - 16.8238^{*}y + 1.8418^{ns}xy + 1.2119^{*}x^2 + 3.9751^{ns}y^2$; $R^2 = 0.53$; CV = 2.99%) presented interactions between the factors, but had an R^2 of less than 60%; therefore, it was decided not to display the graph of this variable.

The increase in chlorophyll fluorescence of plants under stress is related to the constant reduction in the rate of energy capture by the photosystem II (PSII) centers and by the physical separation of the light-gathering complex from the PSII nucleus (Lotfi et al., 2020). Thus, the beneficial effects of salicylic acid on chlorophyll fluorescence may be related to its action on chlorophyll biosynthesis and nitrate mobilization in the tissue, which stimulates Rubisco activity, favoring the transfer of electrons to the reaction centers (Nazar et al., 2011).

An analysis of canonical variables and confidence ellipses was performed to assess the interrelationships between variables and factors (Figure 5). Plant height (PH) and stem diameter (SD) had a strong relationship with the ECw of 0.5 dS m^{-1} and 1.0 mM of salicylic acid, while the number of leaves (NL) had a greater relationship with the ECw of 1.3 dS m^{-1} and 1.0 mM of salicylic acid (Figure 5A).

The intrinsic carboxylation efficiency (iCE) was related to the ECw of 1.3 dS m^{-1} and 1.7 mM of salicylic acid (Figure 5B). Transpiration (E) and CO_2 assimilation rate (A) had a strong relationship with the ECw of 5.2 dS m^{-1} and 0.29 mM of salicylic acid, and stomatal conductance (gs) had a greater relationship with the ECw of 3.2 dS m^{-1} and 2 mM salicylic acid (Figure 5B). The variables VPD, WUE, and iWUE were associated with the ECw of 0.5 dS m^{-1} and 1 mM of salicylic acid (Figure 5B).

The internal carbon (Ci) was strongly connected with the ECw of 5.2 dS m^{-1} and 1.71 mM of salicylic acid (Figure 5B), while the chlorophyll a and b indices were more aligned with the ECw of 5.2 dS m^{-1} and 0.29 mM of salicylic acid (Figure 5C). In general, the photosynthetic pigments were positively correlated with salicylic acid. The F_0 and F_m had a greater



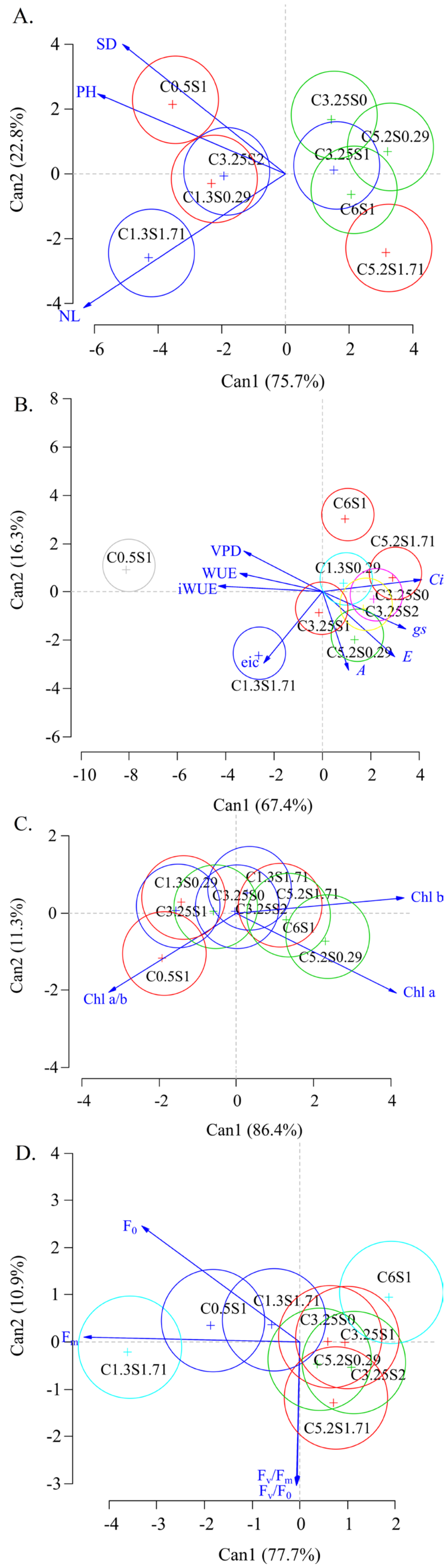
ns, *, ** - Not significant, significant at $p \leq 0.05$, and at $p \leq 0.01$ by F test, respectively

Figure 4. Initial fluorescence (F_0 – A and B) and maximum fluorescence (F_m – C) of *Ocimum basilicum* "Cinnamon" under salt stress (ECw) and/or salicylic acid

relationship with ECw values of 0.5 and 1.3 dS m^{-1} and 1.0 and 1.71 mM of salicylic acid, respectively, and the variables F_v/F_m and F_v/F_0 were correlated with the ECw of 5.2 dS m^{-1} and 1.71 mM salicylic acid (Figure 5D).

The attenuating effects of salicylic acid under salt stress may be related to the action of this phytohormone as a plant signaling molecule and growth regulator that exhibits several regulatory responses and induces specific reactions to salt stress that consequently favor growth and plant development (Azeem et al., 2018).

The application of salicylic acid mitigated the harmful effects of salt stress on basil plants (Kahveci et al., 2021). Under conditions of salt stress, this phytohormone acts by protecting and regulating several physiological processes, respiratory enzymes, and gene expression and is considered a signaling molecule that acts with the defense mechanisms of plants under stressful conditions (Sharma et al., 2017; Silva et al., 2018b).



** - Significant at $p \leq 0.01$ by the F test

Figure 5. Analysis of canonical variables and confidence ellipses between growth variables (A), gas exchange (B), chlorophyll indices (C), and chlorophyll fluorescence (D) of *Ocimum basilicum* "Cinnamon" under salt stress (C) and salicylic acid (S)

Conclusions

1. An increase in the salinity of irrigation water decreases the plant height, stem diameter, number of leaves, stomatal conductance, instantaneous water use efficiency, and initial fluorescence of basil "Cinnamon".

2. The application of salicylic acid attenuates the harmful effects of irrigation water salinity on gas exchange, total chlorophyll, and initial and maximum fluorescence of basil plants.

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