

Physiology and production components of cotton plants under salt stress and salicylic acid application

Fisiologia e componentes de produção do algodoeiro sob estresse salino e aplicação de ácido salicílico

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Highlights

Salt stress decreases stomatal conductance and photosynthesis in cotton.

The salicylic acid concentration of 0.8 mM increases cottonseed weight.

Cotton cv. BRS Jade is sensitive to water salinity from 0.3 dS m⁻¹.

Abstract

The use of saline waters in irrigated agriculture has become a reality in several regions of the world. However, this practice may cause limitations to growth and development, depending on the tolerance level of the crop. Applying strategies that minimize salt stress in crops is therefore essential, and, in this respect, salicylic acid can act as an antioxidant and enhance the plant's tolerance to salt stress. The objective of this study was to examine the effects of foliar application of salicylic acid on the physiology and production components of naturally colored cotton cv. BRS Jade grown under salt stress. The plants were cultivated on lysimeters in outdoor conditions at the Agro-Food Science and Technology Center, Federal University of Campina Grande, located in Pombal - PB, Brazil. The experiment was laid out in a randomized block design with a 5 × 5 factorial arrangement consisting of five irrigation-water electrical conductivity levels (ECw: 0.3, 1.8, 3.3, 4.8, and 6.3 dS m⁻¹) and five concentrations of salicylic acid (SA: 0, 1.5, 3.0, 4.5, and 6.0 mM), with

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three replicates. Irrigation with water with salinity levels from 0.3 dS m⁻¹ reduced gas exchange, the synthesis of photosynthetic pigments, and the number of bolls in cotton cv. BRS Jade. Salinity levels from 0.3 dS m⁻¹ induced stomatal closure and reduced transpiration, CO₂ assimilation rate, the levels of photosynthetic pigments, and production components of cotton cv. BRS Jade. The salicylic acid concentrations of 2.6 and 2.7 mM increased CO₂ assimilation rate and stomatal conductance, respectively, in the cotton plants. Foliar application of salicylic acid did not mitigate the effects of salt stress on gas exchange, the synthesis of photosynthetic pigments, or production components of cotton.

Key words: *Gossypium hirsutum* L. Plant hormone. Salt stress.

Resumo

O uso de águas salinas na agricultura irrigada vem se tornando uma realidade em diversas regiões do mundo, entretanto, dependendo do nível de tolerância da cultura ocorrem limitações no crescimento e desenvolvimento. Dessa forma, o uso das estratégias que minimizem o estresse salino nas culturas é fundamental, nesta perspectiva, o ácido salicílico pode atuar como antioxidante e contribuir na tolerância das plantas ao estresse salino. Neste sentido, objetivou-se avaliar os efeitos da aplicação foliar de ácido salicílico na fisiologia e nos componentes de produção do algodoeiro naturalmente colorido cv. BRS Jade cultivado sob estresse salino. As plantas foram conduzidas em lisímetros sob condições de céu aberto, no Centro de Ciências e Tecnologia Agroalimentar pertencente à Universidade Federal de Campina Grande, Pombal-PB. O delineamento utilizado foi em blocos casualizados, em esquema fatorial 5 × 5, sendo cinco níveis de condutividade elétrica da água de irrigação - CEa (0,3; 1,8; 3,3; 4,8 e 6,3 dS m⁻¹) e cinco concentrações de ácido salicílico - AS (0; 1,5; 3,0, 4,5 e 6,0 mM) com três repetições. A irrigação com água a partir de 0,3 dS m⁻¹ reduziu as trocas gasosas, a síntese de pigmentos fotossintéticos e o número de capulhos do algodoeiro cv. BRS Jade. A irrigação com água a partir de 0,3 dS m⁻¹ induziu o fechamento estomático e diminuiu a transpiração, a taxa de assimilação de CO₂, os teores de pigmentos fotossintéticos e os componentes de produção do algodoeiro cv. BRS Jade. As concentrações de ácido salicílico de 2,6 e 2,7 mM proporcionaram aumento na taxa de assimilação de CO₂ e condutância estomática, respectivamente, das plantas de algodão. A aplicação foliar de ácido salicílico não amenizou os efeitos do estresse salino sobre as trocas gasosas, a síntese de pigmentos fotossintéticos e os componentes de produção do algodoeiro.

Palavras-chave: Estresse salino. Fitormônio. *Gossypium hirsutum* L.

Introduction

Colored-fiber cotton stands out as one of the crops with high economic and social potential in the semi-arid region of Northeast Brazil, where it contributes to employment and income generation through the fixation of labor in rural areas. It is also highlighted for its environmental appeal, as it dispenses with

the industrial dyeing step, which produces a large volume of waste, compromising the environment (Silva et al., 2017; Lima et al., 2017). Despite the agricultural potential of this region for cotton farming, its irregular rainfall distribution at times with prolonged periods of drought and rain events concentrated in some months of the year limits the development and production of crops (Soares et al., 2023).

The scarcity of water resources in the Brazilian semi-arid region involves quantitative and qualitative aspects that lead to restrictions on its use for both human and animal consumption and irrigation (Lima et al., 2018). A high concentration of salts (sodium, mainly) is commonly found in water sources in this region, which reduces their quality and consequent use in agriculture (Dias et al., 2019). Salinity is one of the main abiotic stresses that limit physiological mechanisms of plants e.g., synthesis of photosynthetic pigments, gas exchanges, and production itself due to the osmotic effects that restrict the availability of water and nutrients (Soares et al., 2018a; Sá et al., 2019; Lima et al., 2022).

Excess salts can cause nutritional imbalance, since high concentrations of sodium in the soil solution compromise nutrient absorption, affecting the uptake of ions such as Ca^{2+} , Mg^{2+} , and K^+ by the plant (Cruz et al., 2018). Salt stress also induces the accumulation of reactive oxygen species, which can alter cellular metabolism, leading to oxidative cell destruction (Denaxa et al., 2020). Nonetheless, the tolerance and/or sensitivity of a plant to salt stress varies depending on the species, cultivar, cationic and/or anionic nature of the water, intensity and duration of the stress, irrigation management, as well as soil and climatic conditions in the region (Bezerra et al., 2018; Pinheiro et al., 2022).

Several studies have investigated the irrigation of cotton with different water salinity levels (Santos et al., 2016; Silva et al., 2017; Soares et al., 2018a,b; Dias et al., 2020). Overall, these studies showed that colored-fiber cotton cultivars are sensitive to salt stress from the water electrical conductivity level of 0.7 dS m^{-1} and that salinity delays and reduces emergence, alters gas exchanges,

reduces growth and production components, and compromises some fiber quality characteristics.

Among the strategies used to mitigate the effects of salt stress on plants, foliar application of salicylic acid (SA) is highlighted. Salicylic acid acts as a signaling molecule and a non-enzymatic antioxidant that induces plant tolerance to salt stress through the regulation of physiological processes, in addition to providing protection against biotic and abiotic stresses such as salinity (Hayat et al., 2010; Silva et al., 2020). Foliar application of SA plays an important role in stomatal regulation, seed germination, ion uptake, cell membrane permeability, and photosynthetic rate including photosynthetic pigment synthesis; and increases the activity of enzymatic and non-enzymatic antioxidants (El-Taher et al., 2022). In this respect, several authors have reported that the exogenous application of SA increases the plant's tolerance to salt stress, as observed in tomato (Javaheri et al., 2012), maize (Bagheri, 2014), soursop (Silva et al., 2020), acerola (Dantas et al., 2021), and okra (Mendonça et al., 2022).

In view of the foregoing, the present study was undertaken to examine the effects of foliar application of SA on the physiology and production components of naturally colored cotton cv. BRS Jade grown under salt stress.

Material and Methods

The study was developed at the Center of Agro-Food Science and Technology (CCTA) at the Federal University of Campina Grande (UFCG), located in the municipality of Pombal - PB, Brazil, ($6^{\circ}47'20'' \text{ S}$, $37^{\circ}48'01''$

W, 194 m above sea level). Figure 1 shows the meteorological data collected during the

experiment, between March 30 and July 17, 2021.

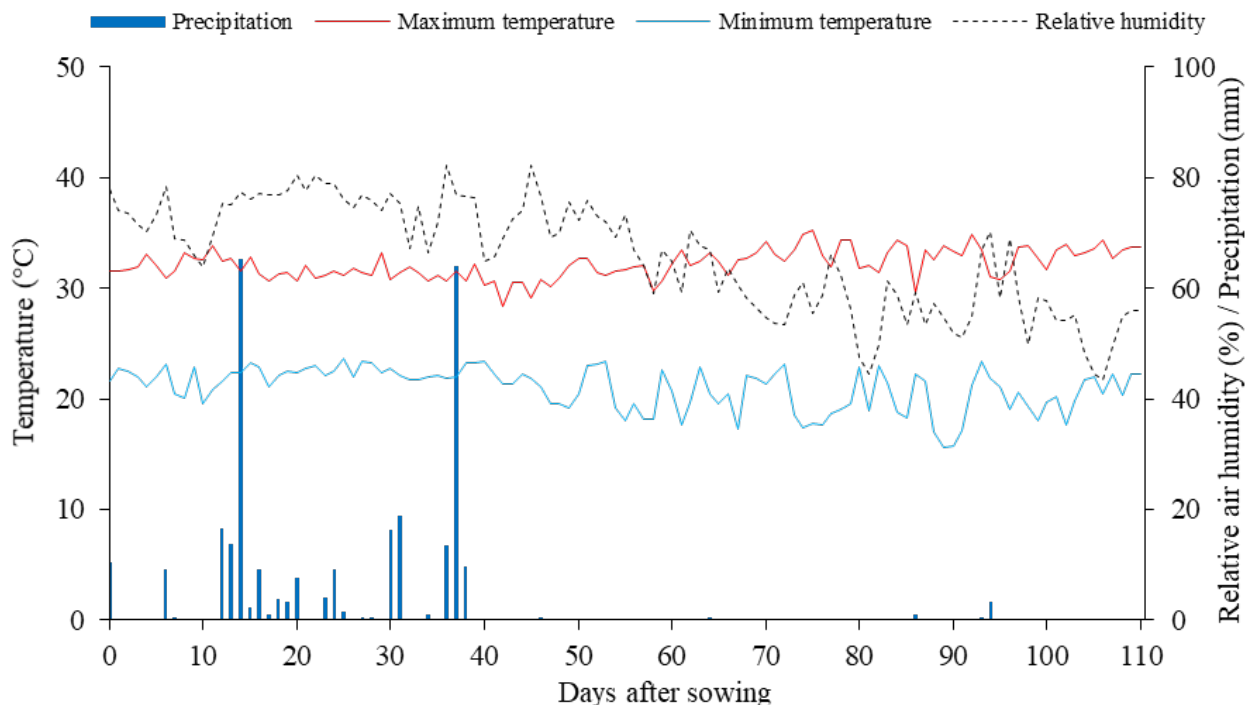


Figure 1. Maximum and minimum temperatures, precipitation, and relative humidity of air data during the experiment.

A randomized-block experimental design was adopted with a 5×5 factorial arrangement that corresponded to five levels of electrical conductivity in the irrigation water (ECw: 0.3, 1.8, 3.3, 4.8, and 6.3 dS m⁻¹) and five concentrations of salicylic acid (SA: 0, 1.5, 3.0, 4.5, and 6.0 mM), with three replicates and one plant per plot. The SA concentrations used in this study were based on the study conducted with soursop (Silva et al., 2019a), whereas the salt levels were established according to the studies of Souza et al. (2018) and Dias et al. (2020).

The plants were grown in 20-L plastic pots adapted with lysimeters. At the base of the pots, two holes were drilled into which

transparent (drains 16 mm in diameter) were installed (Figure 2). The end of the drain inside the lysimeter was lined with non-woven geotextile fabric (Bidim OP 30) to avoid clogging with soil material. Below each drain was a container to collect the drained water to estimate water consumption by the plants. The pots were arranged in outdoor conditions in single rows spaced 1.2 m apart, with plants spaced 1.0 m apart in the row. The pots were filled with a layer of 0.5 kg of gravel followed by 23.5 kg of a Regosol (Psamments) from the rural area of the municipality of Pombal - PB, Brazil. The chemical and physical characteristics of soil (Table 1) were obtained as proposed by Teixeira et al. (2017).

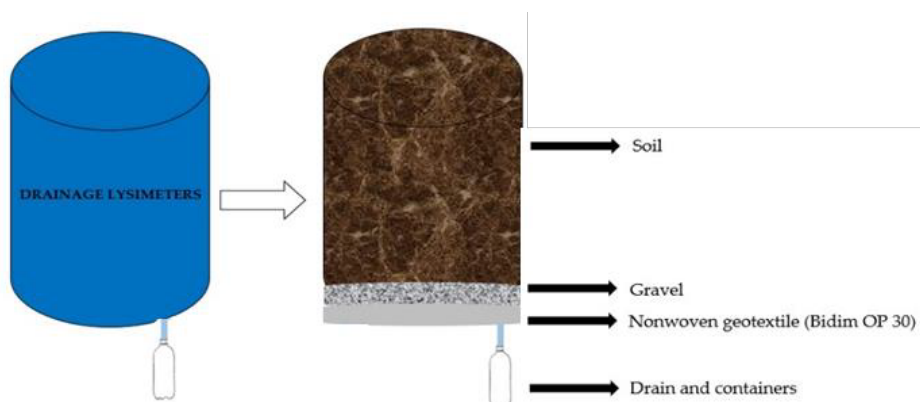


Figure 2. Illustration of the details of drainage lysimeters and layers after filling.

Table 1
Chemical and physical characteristics of the soil used in the experiment, before the treatments were applied

| Chemical characteristics | | | | | | | | | |
|--|----------------------------|-----------------------------|------------------|-----------------|------------------|------------------|--|------|-------------------------------|
| pH (H ₂ O) (1:2.5) | OM dag kg ⁻¹ | P (mg kg ⁻¹) | K ⁺ | Na ⁺ | Ca ²⁺ | Mg ²⁺ | H ⁺ + Al ³⁺ % | ESP | ECse (dS m ⁻¹) |
| 7.00 | 3.80 | 11.99 | 0.38 | 0.09 | 2.42 | 5.84 | 0.0 | 1.05 | 0.75 |
| Physical characteristic | | | | | | | | | |
| Particle size fraction (g kg ⁻¹) | | | Texture class | Moisture (kPa) | | AW | Total porosity % | AD | PD |
| Sand | Silt | Clay | | 33.42 | 1519.5 | | | | |
| 853.00 | 130.70 | 16.30 | SL | 11.60 | 4.23 | 6.93 | 47.23 | 1.50 | 2.69 |

pH (H₂O) = potential of hydrogen; OM = organic matter; ESP = exchangeable sodium percentage; ECse = electrical conductivity of the saturation extract at 25 °C. Ca²⁺ and Mg²⁺ extracted with 1 M KCl at pH 7.0; Na⁺ and K⁺ extracted using 1 M NH₄OAc at pH 7.0; H⁺ and Al³⁺ extracted with 0.5 M CaOAc at pH 7.0; SL = sandy loam; AW = available water; AD = apparent density; PD = particle density.

The seeds of colored cotton cv. BRS Jade originated from the National Cotton Research Center (CNPA) at Embrapa Algodão. Cultivar BRS Jade is a light brown-fiber variety, with high fiber yield potential (approximately 41%) and a high production yield that exceeds 4500 kg ha⁻¹. The cultivar has high productive potential in the *cerrado* and semiarid environments and good fiber

characteristics, with 28.6 mm fiber length, 83.7% uniformity, and 29.2 gf tex⁻¹ resistance (Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA], 2015).

At sowing, five seeds were distributed equidistantly in each lysimeter, at a depth of 2 cm. After seedling emergence, thinning was performed in two stages: when the plants exhibited two and three pairs of definitive

leaves, respectively, leaving one plant per container in the last thinning. Prior to sowing, the seeds were treated with Trichodermit SC 1306® at a concentration of 48 g L⁻¹. Before adding the seeds to the mixture, Trichodermit SC 1306® was stirred in a 2-L beaker until a homogeneous mixture was formed. The seeds were immersed in the Trichodermit SC 1306® mixture for a period of 8 h.

Salicylic acid concentrations were prepared by dissolving salicylic acid A.R. in 30% ethyl alcohol. Foliar application of SA began 10 days after plant emergence and was subsequently repeated every 12 days, by spraying and so as to completely wet the leaves (abaxial and adaxial surfaces). Applications were performed from 17h00. To prevent the drift of SA, the plants were isolated with a plastic curtain.

The waters were prepared so as to have an equivalent Na:Ca:Mg ratio of 7:2:1, using the salts NaCl, CaCl₂·2H₂O, and MgCl₂·6H₂O (the ratio that predominates in water sources used for irrigation on small farms in northeast Brazil [Medeiros, 1992]). The relation between EC_w and salt concentration (Richards, 1954) shown in Eq. 1 was considered for the preparation of the waters in the laboratory:

$$A = 640 \times EC_w \dots\dots\dots(1),$$

where A = amount of salts to be applied (mg L⁻¹); and EC_w = water electrical conductivity (dS m⁻¹).

Irrigation was performed daily at 17h00, by applying the volume corresponding to that obtained by the principle of drainage lysimetry (Bernardo et al., 2013), determined by Eq. 2:

$$VI = \frac{(V_p - V_d)}{(1 - LF)} \dots\dots\dots(2),$$

where VI = volume of water to be applied (mL); V_p = volume applied in the previous irrigation event (mL); V_d = volume of water drained (mL); and LF = leaching fraction of 0.20.

Nitrogen (N), phosphorus (P₂O₅), and potassium (K₂O) fertilization was carried out following recommendations for pot trials (Novais et al., 1991), using 100, 150, and 300 mg kg⁻¹ of N, K₂O, and P₂O₅, respectively, via fertigation, at 10-day intervals. Fertilizer applications started at 15 days after sowing (DAS). Urea (45% N) and potassium chloride (60% K₂O) were used as sources of nitrogen and potassium, respectively. Monoammonium phosphate was used as a source of phosphorus, considering the amount of N (12%) added via monoammonium phosphate at a rate of 300 mg of P₂O₅ kg⁻¹ of soil.

Micronutrient fertilization was performed weekly, on the abaxial and adaxial sides of the leaves, using a backpack sprayer (Jacto XP®, Jacto) with a capacity of 12 L, working pressure (maximum) of 88 psi (6 bar), and JD 12P nozzle, employing solutions containing 1.0 g L⁻¹ of Ubyfol® [(N (15%), P₂O₅ (15%), K₂O (15%), Ca (1%), Mg (1.4%), S (2.7%), Zn (0.5%), B (0.05%), Fe (0.5%), Mn (0.05%), Cu (0.5%), and Mo (0.02%)]. The applications took place at 12-day intervals with an average mixture volume of 200 mL was used per plant per application.

Pest control was carried out using contact and systemic insecticides of the neonicotinoid (Acetamiprid) and pyrethroid (Phenpropathrin) chemical groups. Disease control (Ramularia blight) was achieved with a systemic-action fungicide (Fenpropimorph)

of the chemical group of morpholines. These applications were performed with a backpack sprayer (Jacto XP®, Jacto) with a capacity of 12 L, working pressure (maximum) of 88 psi (6 bar), and JD 12P nozzle. To control weeds on the lysimeters, manual weeding was carried out during the experimental period to avoid interspecific competition for water and nutrients, favoring the full development of the crop.

At 90 DAS, the effects of treatments on the crop were measured through gas exchanges, by evaluating stomatal conductance (g_s , $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), transpiration (E , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), intercellular CO_2 concentration (C_i , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and CO_2 assimilation rate (A , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). The A/E and A/C_i ratios were then used to determine instantaneous water use efficiency ($iWUE$, $[\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] [\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}]^{-1}$) and instantaneous carboxylation efficiency (iCE , $[\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}] [\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}]^{-1}$). Gas exchange was determined using an infrared gas analyzer (LCpro - SD, ADC Bioscientific, UK). Readings were taken between 07h00 and 10h00, on the third fully expanded leaf counted from the apical bud, under natural conditions of air temperature and CO_2 concentration and using an artificial source of radiation of $1,200 \mu\text{mol m}^{-2} \text{ s}^{-1}$. This value was established from the curve of photosynthetic response to light and by determining the point of photosynthetic light saturation (Fernandes et al., 2021).

Photosynthetic pigment levels (chlorophylls a, b, and total, as well as carotenoids) were also determined at 90 DAS following Arnon (1949), using five leaf discs (5 mm in diameter) collected from the third

leaf counted from the apex. In the laboratory, each sample received 6.0 mL of 80% acetone A.R. After preparation, the samples were kept for 48 h in a refrigerated environment under dark conditions. Using these extracts, the chlorophyll and carotenoid contents in the solutions were determined with a spectrophotometer at the absorbance wavelengths (ABS) of 470, 647, and 663 nm, as shown in Eqs. 3, 4, 5, and 6:

$$\text{Chl } a = 12.21 \text{ ABS}_{663} - 2.81 \text{ ABS}_{646} \dots\dots\dots(3)$$

$$\text{Chl } b = 20.13 \text{ ABS}_{646} - 5.03 \text{ ABS}_{663} \dots\dots\dots(4)$$

$$\text{Car} = (1000 \text{ ABS}_{470} - 1.82 \text{ Chl } a - 85.02 \text{ Chl } b)/198 \dots\dots\dots(5)$$

$$\text{Chl } T = (17.3 \text{ ABS}_{646} + 7.18 \text{ ABS}_{663}) \dots\dots\dots(6)$$

where Chl a: chlorophyll a; Chl b: chlorophyll b; Car: carotenoids; and Chl T: chlorophyll total.

The chlorophyll a and b and carotenoid contents found in the leaves were expressed in mg g^{-1} of fresh weight (FW).

The cotton was harvested manually when 60% of the bolls were open. Harvesting started at 80 DAS and ended at 110 DAS. At the time of harvest, the number of bolls per plant was determined and cottonseed weight was quantified according to the treatments using a scale with 0.01-g precision.

Data were analyzed for normality (Shapiro-Wilk test) and homoscedasticity (Bartlett test) and subsequently subjected to analysis of variance by the F test ($p \leq 0.05$). When significant results were obtained, regression analysis was performed ($p \leq 0.05$) for water salinity levels (SL) and SA using SISVAR-ESAL statistical software version 5.6 (Ferreira, 2019).

Results and Discussion

There was a significant SL × SA interaction effect on intercellular CO₂ concentration, transpiration, and instantaneous carboxylation efficiency (Table 2). The irrigation-water salinity level

significantly influenced all gas exchange variables. On the other hand, SA analyzed in isolation significantly affected the stomatal conductance, transpiration, and instantaneous carboxylation efficiency of the cotton plants at 90 DAS.

Table 2

Summary of the analysis of variance referring to the intercellular CO₂ concentration (*C_i*), stomatal conductance (*g_s*), transpiration (*E*), CO₂ assimilation rate (*A*), instantaneous carboxylation efficiency (*iCE*), and instantaneous water use efficiency (*iWUE*) of cotton cv. BRS Jade irrigated with saline water and foliar application of salicylic acid

| Source of variation | DF | Mean square | | | | | |
|----------------------|----|----------------------|----------------------|-------------------|--------------------|---------------------|-------------------|
| | | <i>C_i</i> | <i>g_s</i> | <i>E</i> | <i>A</i> | <i>iCE</i> | <i>iWUE</i> |
| Salinity level (SL) | 4 | 2105.6* | 0.09** | 31.9** | 219.3** | 0.010* | 5.6** |
| Linear regression | 1 | 2.4 ^{ns} | 0.36** | 143.1** | 853.4** | 0.004** | 20.4** |
| Quadratic regression | 1 | 4867.2* | 0.001 ^{ns} | 3.7* | 13.5 ^{ns} | 0.001 ^{ns} | 0.9 ^{ns} |
| Salicylic acid (SA) | 4 | 1304.9 ^{ns} | 0.02* | 5.2** | 99.6* | 0.005 ^{ns} | 1.8 ^{ns} |
| Linear regression | 1 | 902.8 ^{ns} | 0.02 ^{ns} | 8.2* | 57.9 ^{ns} | 0.001 ^{ns} | 1.4 ^{ns} |
| Quadratic regression | 1 | 3233.2 ^{ns} | 0.03* | 11.1** | 133.9* | 0.001 ^{ns} | 0.4 ^{ns} |
| SL × SA interaction | 16 | 1906.4** | 0.01 ^{ns} | 1.3** | 40.5 ^{ns} | 0.009** | 2.2 ^{ns} |
| Blocks | 2 | 612.6 ^{ns} | 0.01 ^{ns} | 0.1 ^{ns} | 33.4 ^{ns} | 0.003 ^{ns} | 1.4 ^{ns} |
| Residual | 48 | 795.9 | 0.007 | 0.7 | 35.9 | 0.003 | 1.4 |
| CV (%) | | 18.9 | 19.1 | 13.1 | 18.9 | 25.6 | 22.6 |

^{ns}, *, and ** = not significant and significant at $p \leq 0.05$ and $p \leq 0.01$, respectively. DF = degrees of freedom; CV = coefficient of variation.

The water electrical conductivity levels linearly increased the intercellular CO₂ concentration (*C_i*) of the cotton plants subjected to the SA concentrations of 0, 1.5, and 3.0 mM. According to the regression equations, *C_i* increased by 6.31, 10.48, and 14.94%, respectively, at the respective SA concentrations (Figure 3). Between the water salinity levels of 0.3 and 6.3 dS m⁻¹, *C_i*

increased by 37.88, 62.88, and 89.68% in the plants treated with 0, 1.5, and 3.0 mM SA, respectively. As for the plants that received the SA concentrations of 4.5 and 6.0 mM, the maximum estimated *C_i* values (173.90 and 156.92 μmol CO₂ m⁻² s⁻¹) were obtained under irrigation with water with 2.9 and 2.6 dS m⁻¹ salinity, respectively.

Despite the partial closure of the stomata observed in this study based on the stomatal conductance (g_s) results (Figure 4A), the plants' C_i increased (Figure 3). However, the uptake of CO_2 from the external environment by the plants did not reflect on its assimilation (Figure 5A). It is noteworthy that this reduction was caused by the action of factors of non-stomatal origin, that is, the unavailability of ATP and NADPH in the

Calvin cycle and/or inhibition of the ribulose-1,5-bisphosphate carboxylase/oxygenase enzyme activity (Lima et al., 2020). Dias et al. (2020) evaluated gas exchanges in white-fiber cotton cv. BRS 368 RF irrigated with water with increasing salinity levels (ECw ranging from 0.7 to and 6.7 dS m^{-1}) and also found that ECw from 0.7 dS m^{-1} provided a linear increase in the plants' C_i , at 77 days after sowing.

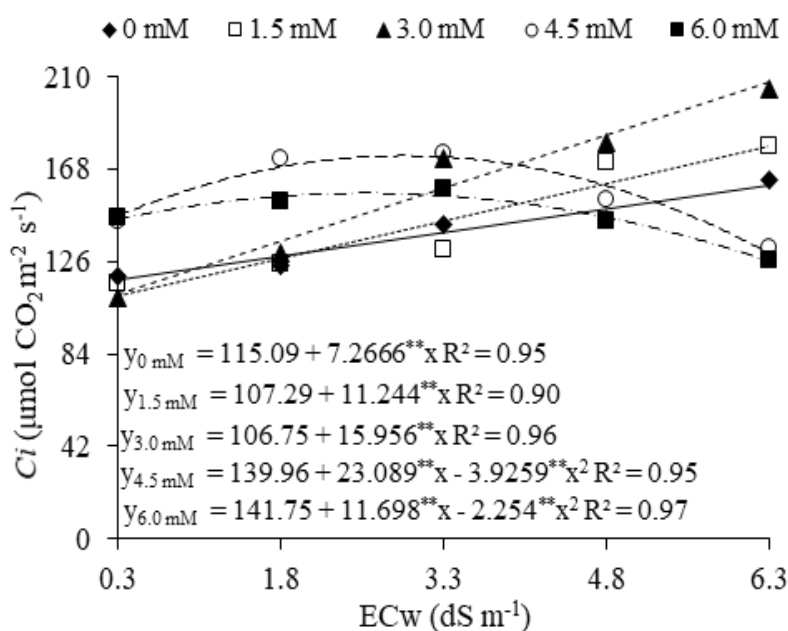


Figure 3. Intracellular CO_2 concentration (C_i) in cotton cv. BRS Jade as a function of the interaction between water electrical conductivity levels (ECw) and salicylic acid concentrations (SA).

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

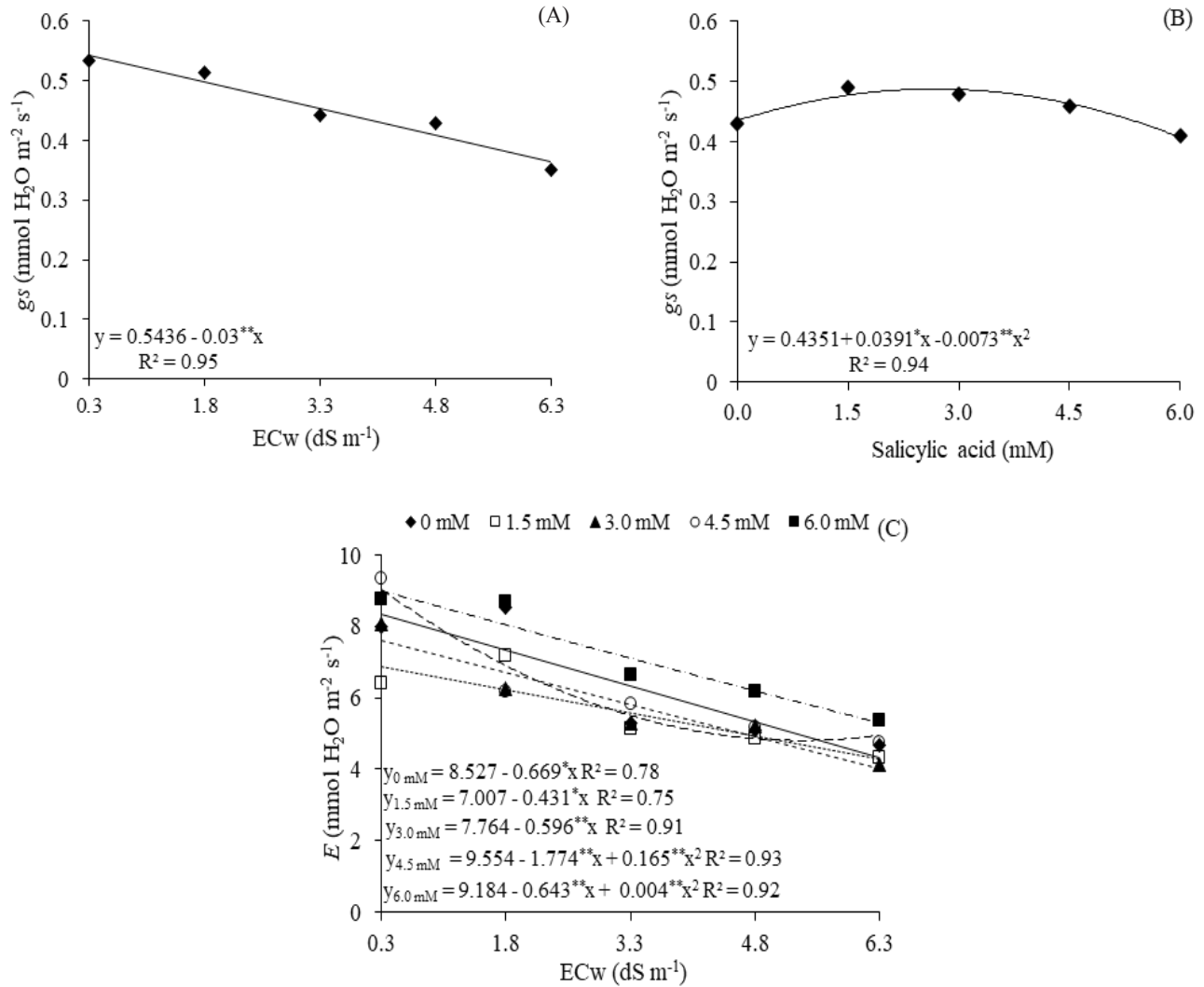


Figure 4. Stomatal conductance (g_s) of cotton cv. BRS Jade as a function of water electrical conductivity levels (ECw, A) and salicylic acid concentrations (SA, B); and transpiration (E , C) as a function of the interaction between ECw and SA.

* and ** = significant at $p \leq 0.05$ and $p \leq 0.01$, respectively.

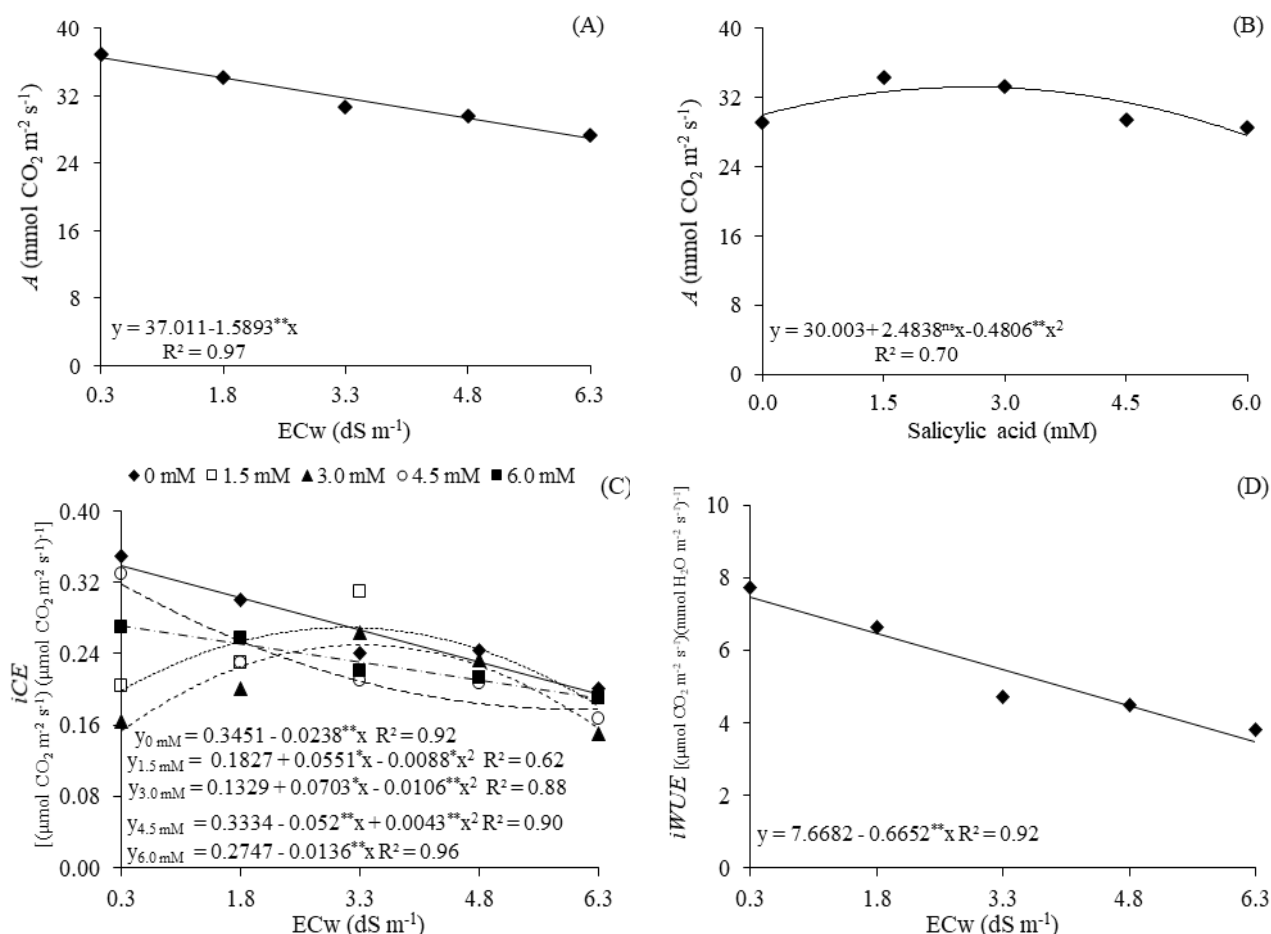


Figure 5. CO₂ assimilation rate (*A*) of cotton cv. BRS Jade as a function of water electrical conductivity levels (ECw), A) and salicylic acid concentrations (SA), B); Instantaneous water use efficiency (*iWUE*, D) as a function of ECw; and instantaneous carboxylation efficiency (*iCE*, C) as a function of the interaction between ECw and SA.

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

Stomatal conductance in the cotton plants decreased linearly, by 5.5%, with each unit increase in ECw (Figure 4A). Between plants irrigated with the highest salinity level (6.3 dS m⁻¹) and those grown under the lowest ECw (0.3 dS m⁻¹), a 33.7% reduction was observed in *g_s* (0.18 mmol H₂O m⁻² s⁻¹). In an experiment evaluating the gas exchanges of white fiber cotton cv. BRS 368 RF irrigated with saline water (0.7 to 6.7 dS m⁻¹), Dias et al. (2020) described a 9.48% reduction in *g_s*

with each unit increase in ECw. The smaller reductions in *g_s* observed in the present study in comparison with the results reported by Dias et al. (2020) may be related to the seasons and weather conditions where the study was done. Normally, under low relative humidity and high temperature conditions, plants tend to close their stomata to avoid excessive water loss to the atmosphere, a situation observed in the present study. The study by Dias et al. (2020) was developed

in Campina Grande - PB, Brazil, a region characterized by milder temperatures and high relative humidity. According to Lira et al. (2018), the reduction in g_s in response to increases in ECw is an important strategy for plants to avoid severe dehydration and maintain high cellular water potential, since osmotic stress limits water availability.

The SA concentrations influenced the g_s of the cotton plants (Figure 4B), with those that received the foliar application of 2.7 mM standing out with the highest g_s value ($0.49 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). Plants under foliar application with the SA concentration of 2.7 mM showed a 12% higher g_s ($0.052 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) than those grown under 0 mM SA. Salicylic acid plays an important role in regulating various physiological and developmental processes in plants, including stomatal opening (Souri & Tohidloo, 2019).

The transpiration (E) of cotton plants subjected to the SA concentrations of 0, 1.5, and 3.0 mM decreased linearly, by 7.84, 6.15, and 7.67%, respectively, per unit increase in ECw (Figure 4C). In the plants grown under the ECw of 6.3 dS m^{-1} , E was 47.07, 39.90, and 46.05% lower compared to those irrigated with water with 0.3 dS m^{-1} salinity, under foliar application of 0, 1.5, and 3.0 mM SA. However, plants subjected to foliar application of 4.5 and 6.0 mM SA obtained estimated maximum E values of 8.39 and $8.73 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively, under irrigation with an ECw of 0.3 dS m^{-1} . The minimum values (4.92 and $5.29 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) were estimated at the ECw of 6.7 dS m^{-1} in plants that received 4.5 and 6.0 mM SA, respectively.

The decrease in E can be partially attributed to stomatal closure (Figure 4A) as a plant strategy to avoid water loss through transpiration, a mechanism that also leads to

a reduction in CO_2 assimilation rate (Time et al., 2018). Nonetheless, the application of SA at a concentration of 0.8 mM increased E even when the plant was irrigated with saline water. Under salt stress conditions, SA can act to reduce Na^+ and Cl^- ions and increase the K^+/Na^+ ratio, improving gas exchanges (Gunes et al., 2007; Tufail et al., 2013). According to Nahar et al. (2016), the replacement of Na^+ with K^+ , exclusion of Na^+ , and retention of intracellular K^+ are important mechanisms for plant tolerance to salt stress.

The increase in irrigation-water salinity levels negatively affected the CO_2 assimilation rate (A) (Figure 5A) of the cotton plants, which declined by 4.29% with each unit increase in ECw. A 26.1% reduction in A ($9.54 \text{ mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was observed between the highest (6.3 dS m^{-1}) and the lowest (0.3 dS m^{-1}) salinity levels. These A results corroborate those found by Silva et al. (2019b) in a study with cotton cultivars BRS 368 RF and BRS Safira under salt stress (ECw ranging from 1.5 to 7.5 dS m^{-1}), where a 5.1% decrease was observed per unit increase in ECw. The authors attributed this result to the decline in stomatal conductance and transpiration, a process that can restrict the transfer of CO_2 to the leaf and contribute to the reduction of A .

Salicylic acid concentrations up to 2.6 mM increased A (Figure 5B). According to the regression equation for this variable, plants that received 2.6 mM SA stood out with the highest A value ($33.2 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). From the SA concentrations of 0 to 2.6 mM, A increased by 9.63% ($3.2 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). At adequate concentrations, SA can induce plants to produce antioxidant compounds such as enzymes and proteins that act to remove reactive oxygen species and improve photosynthetic activity (Safeer et al., 2019).

The interaction between the factors (SL × SA) also significantly affected the instantaneous carboxylation efficiency (*iCE*) of cotton cv. BRS Jade. Plants subjected to foliar application of 0 and 6.0 mM SA showed a linear reduction in their *iCE* (Figure 5C), which decreased by 6.89 and 4.95%, respectively, with each unit increase in EC_w. Comparing the *iCE* of plants cultivated under lowest level of EC_w (0.7 dS m⁻¹) with those that received water with a EC_w of 6.3 dS m⁻¹, decreases of 40.57 and 28.72% were observed at the SA concentrations of 0 and 6.0 mM, respectively. In the plants that received the SA concentrations of 1.5, 4.5, and 6.0 mM, the *iCE* data fit the quadratic regression model (Figure 5C), with maximum values [0.269, 0.249, and 0.299 (μmol CO₂ m⁻² s⁻¹) (μmol CO₂ m⁻² s⁻¹)⁻¹] estimated under the EC_w of 3.30, 3.60, and 0.7 dS m⁻¹, respectively.

The decline in *iCE* may be related to the inhibition of ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) activity caused by the accumulation of salts in leaf tissues, mainly Na⁺ and Cl⁻. Coupled with other environmental factors, these ions favor the oxygenation of RuBisCO and an increase in the photorespiratory pathway, reducing carbon compounds (Lima et al., 2019a). According to Khalvandi et al. (2021), the increase in stomatal conductance provided by the application of SA can contribute to the availability of carbon for the photosynthesis process and regulate metabolic processes associated with the absorption and/or fixation of carbon in the chloroplast. In addition, SA helps maintain the integrity of the photosynthetic apparatus, contributing to better RuBisCO activity (Nazar et al., 2015), a mechanism that may be responsible for increasing *iCE* under salt stress.

The increase in EC_w induced a linear decrease in *iWUE* (Figure 5D), which declined by 8.67% per unit increase in EC_w. Plants irrigated with water of higher salinity (6.3 dS m⁻¹) showed a 53.43% reduction in this variable [3.99 (μmol CO₂ m⁻² s⁻¹) (mmol H₂O m⁻² s⁻¹)⁻¹] compared with those cultivated under an EC_w of 0.3 dS m⁻¹. The decrease in *iWUE* is also related to the effects of salinity, stemming from the alteration in the osmotic potential of the soil solution that reduced water and nutrient absorption by the plants. This situation possibly induced partial stomatal closure, which likely impaired CO₂ absorption and, consequently, photosynthesis (Roque et al., 2022). It is important to point out that during gas exchange, the absorption of CO₂ from the external environment through the stomata also results in water loss, and in an attempt to mitigate this loss, the plant restricts the entry of CO₂. Thus, *iWUE* indicates the amount of CO₂ that the plant fixes per unit of water that is lost in this process (Suassuna et al., 2014).

In a study developed with colored-fiber cotton cv. BRS Rubi under salt stress (EC_w: 5.1 to 9.1 dS m⁻¹), Lima et al. (2017) also found that an increase in EC_w levels resulted in a quadratic decrease in *iWUE*, with a minimum value of 3.66 [(μmol CO₂ m⁻² s⁻¹) (mmol H₂O m⁻² s⁻¹)⁻¹] obtained in plants subjected to the water salinity level of 9.1 dS m⁻¹. According to these authors, the reduction in *iWUE* was caused by the low availability of water in the soil due to osmotic effects that induce stomatal closure and, consequently, a decline in leaf transpiration and CO₂ assimilation.

The summary analysis of variance (Table 3) revealed a significant effect of salinity levels on chlorophylls *a* (Chl *a*), *b* (Chl *b*), and total (Chl *T*); carotenoids; number of bolls per plant; and seed weight (CSW)

of cotton cv. BRS Jade at 90 DAS. Salicylic acid concentrations significantly influenced Chl *a* and CSW. The interaction between the factors (SL × SA) only significantly affected the CSW of the cotton plants.

Regarding the levels of Chl *a* in cotton cv. BRS Jade (Figure 6A), the highest estimated value of 15.42 mg g⁻¹ FW was obtained in plants subjected to the EC_w of 2.5 dS m⁻¹. From this electrical conductivity level, there was a decrease in this variable, which reached a minimum value of 10.00 mg g⁻¹ FW in plants irrigated with water with

the highest salinity (6.3 dS m⁻¹). A 2.384 mg g⁻¹ FW reduction in Chl *a* was observed between the water salinity levels of 0.3 and 6.3 dS m⁻¹. Chlorophyll contents tend to decrease under salt stress conditions, which can be attributed to pigment destruction and instability of the pigment-protein complex. In addition, osmotic stress causes strong damage to chloroplast membranes, increasing membrane permeability or the loss of membrane integrity (Nobrega et al., 2020).

Table 3

Summary of analysis of variance referring to chlorophylls *a* (Chl *a*), *b* (Chl *b*), and total (Chl *T*), carotenoids (Car), number of bolls per plant (NBP), and seed weight (CSW) of cotton cv. BRS Jade irrigated with saline water and foliar application of salicylic acid

| Source of variation | DF | Mean square | | | | | |
|----------------------|----|---------------------|--------------------|---------------------|--------------------|--------------------|--------------------|
| | | Chl <i>a</i> | Chl <i>b</i> | Chl <i>T</i> | Car | NBP | CSW |
| Salinity level (SL) | 4 | 69.01** | 1.84* | 230.04** | 4.25* | 9.28* | 104.64** |
| Linear regression | 1 | 128.86** | 4.30* | 597.96** | 10.14** | 15.36* | 15.62* |
| Quadratic regression | 1 | 143.59** | 1.55 ^{ns} | 60.36* | 2.38* | 1.21 ^{ns} | 117.25** |
| Salicylic acid (SA) | 4 | 24.26* | 0.65 ^{ns} | 19.47 ^{ns} | 1.17 ^{ns} | 18.71** | 78.83** |
| Linear regression | 1 | 0.65 ^{ns} | 0.18 ^{ns} | 0.08 ^{ns} | 0.63 ^{ns} | 62.72** | 111.69** |
| Quadratic regression | 1 | 3.51* | 1.30 ^{ns} | 29.46* | 1.80 ^{ns} | 1.71 ^{ns} | 2.64 ^{ns} |
| SL × SA interaction | 16 | 10.69 ^{ns} | 0.31 ^{ns} | 10.25 ^{ns} | 1.00 ^{ns} | 1.68 ^{ns} | 36.38** |
| Blocks | 2 | 11.29 ^{ns} | 0.56 ^{ns} | 3.03 ^{ns} | 0.41 ^{ns} | 3.00 ^{ns} | 2.43 ^{ns} |
| Residual | 48 | 6.46 | 14.68 | 5.92 | 0.55 | 2.11 | 4.04 |
| CV (%) | | 18.82 | | 14.05 | 14.52 | 9.90 | 3.15 |

^{ns}, *, and ** = not significant and significant at $p \leq 0.05$ and $p \leq 0.01$, respectively. DF = degrees of freedom; CV = coefficient of variation.

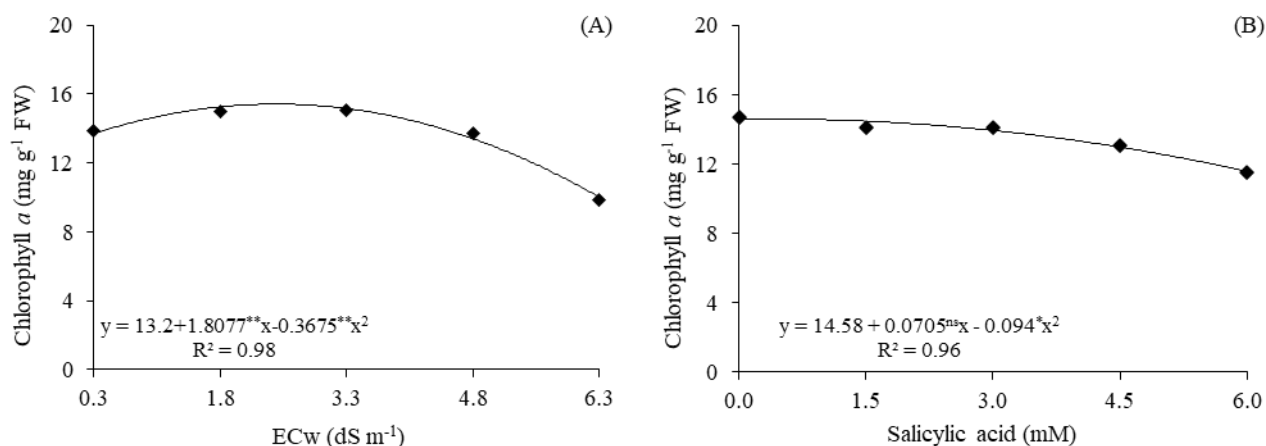


Figure 6. Chlorophyll *a* content in cotton cv. BRS Jade as a function of water electrical conductivity levels (ECw, A) and salicylic acid concentrations (B)

^{ns}, *, and ** = not significant and significant at $p \leq 0.05$ and $p \leq 0.01$, respectively.

Salicylic acid concentrations significantly affected the Chl *a* contents of the cotton plants (Figure 6B), with a maximum estimated value of 14.59 mg g⁻¹ FW obtained at the SA concentration of 0.4 mM. On the other hand, the minimum Chl *a* value of 11.61 mg g⁻¹ FW was observed in plants sprayed with 6.0 mM SA (Figure 6B). The beneficial effects of applying SA at low concentrations may be related to the prevention of auxin oxidation (Vicente & Plasencia, 2011) and elimination of reactive oxygen species (ROS) in plant cells. A reduction in ROS prevents plants from oxidative damage and osmotic stress, maintaining the mechanism of photosynthesis and synthesis of photosynthetic pigments (Naz et al., 2022).

The Chl *b* contents of cotton cv. BRS Jade plants decreased linearly, by 2.43%, with each unit increase in water salinity levels (Figure 7A). A decrease of 0.672 mg g⁻¹ FW

(14.72%) in Chl *b* was observed between the plants irrigated with the lowest water salinity level (0.3 dS m⁻¹) and the ECw of 6.3 dS m⁻¹. The salinity of the irrigation water caused the chlorophyll total contents of cotton cv. BRS Jade to decrease quadratically (Figure 7B), with a maximum estimated value of 20.296 mg g⁻¹ FW found in plants subjected to the ECw of 1.2 dS m⁻¹. There was a sharp decline from this salinity level, with the lowest Chl *T* content occurring under the ECw of 6.3 dS m⁻¹ (11.598 mg g⁻¹ FW). In a study examining quantum efficiency and levels of photosynthetic pigments of naturally colored cotton genotypes under irrigation with water with different salinity levels (ECw of 0.8 and 5.3 dS m⁻¹), Veloso et al. (2023) concluded that irrigation with 5.3 dS m⁻¹ reduced the synthesis of photosynthetic pigments, at 60 DAS.

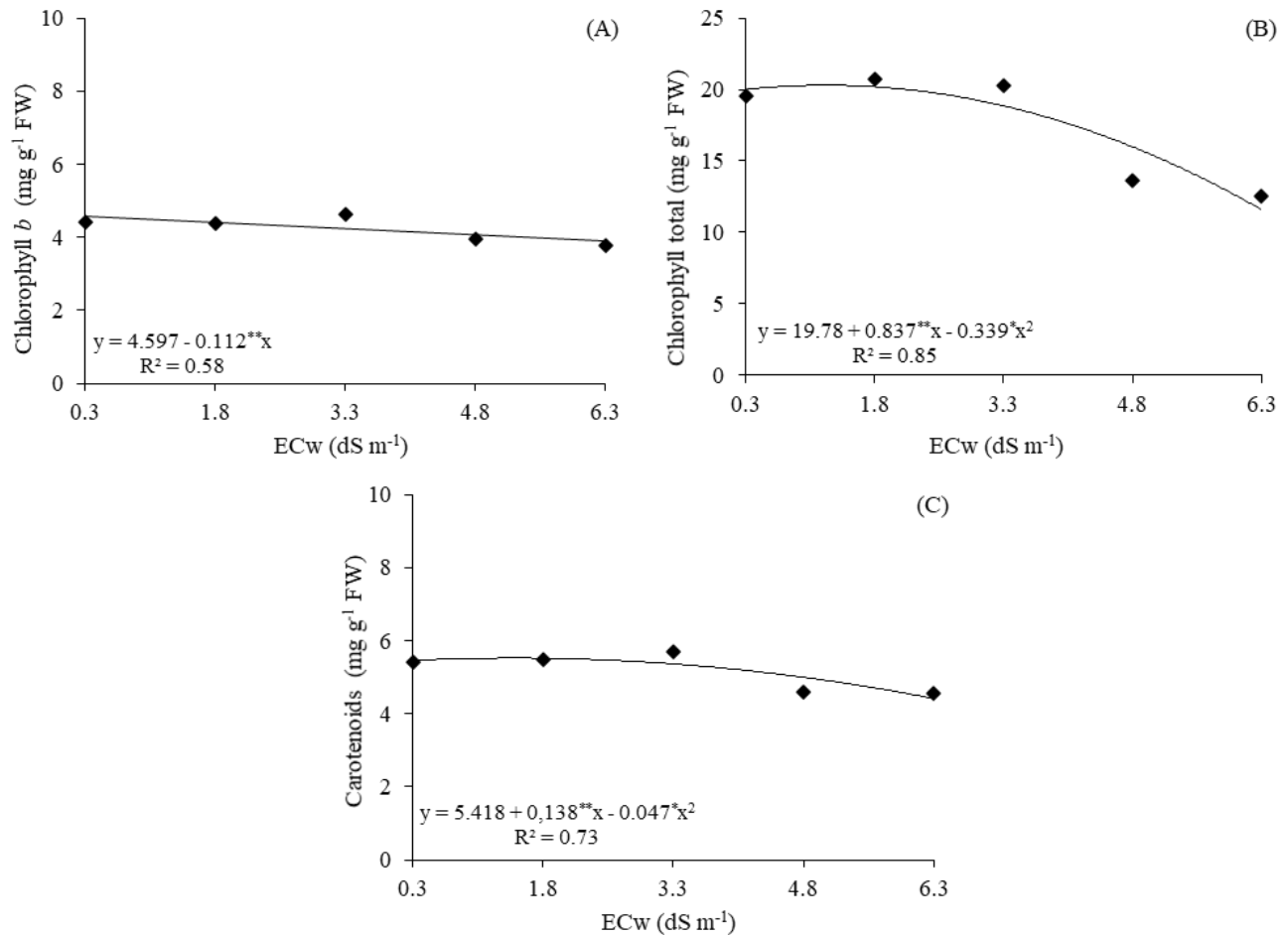


Figure 7. Chlorophyll *b* (A), chlorophyll total (B), and carotenoid (C) contents in cotton cv. BRS Jade as a function of water electrical conductivity levels (ECw).

* and ** = significant at $p \leq 0.05$ and $p \leq 0.01$, respectively.

The increase in ECw levels also had a quadratic effect on the carotenoid contents of cotton cv. BRS Jade (Figure 7C), which reached a maximum value of 5.52 mg g⁻¹ FW in plants subjected to an estimated ECw of 1.5 dS m⁻¹ and a minimum of 4.42 mg g⁻¹ FW at the ECw of 6.3 dS m⁻¹. The reduced biosynthesis of carotenoids can be attributed to the fact that salt stress causes the production of photosynthetic pigments to decrease, inducing the degradation of β -carotene and a reduction in the carotenoid content, which

are integrated components of thylakoids that participate in the absorption and transfer of light to chlorophyll (Dias et al., 2019).

Lima et al. (2020) conducted an experiment to determine the effects of different irrigation-water electrical conductivities (ranging from 0.3 to 3.5 dS m⁻¹) on chloroplast pigments in passion fruit cv. BRS Rubi do Cerrado and, unlike the current results, found that the carotenoid contents increased with salinity, at 40 DAS.

On the other hand, in a study evaluating the effects of irrigation with saline water on the West Indian cherry crop, Dias et al. (2019) observed that the EC_w of 3.8 dS m⁻¹ resulted in a decline in carotenoid synthesis. According to these authors, the decrease in carotenoid contents can be considered a mechanism of acclimatization of the plants to salt stress, in an attempt to conserve energy and, consequently, capture less light energy and thus reduce the flow of electrons to the electron transfer chain, preventing possible photo-oxidative stress.

The number of bolls per plant (NBP) in cotton cv. BRS Jade (Figure 8A) decreased linearly, by 2.21%, with each unit increase in EC_w. Plants subjected to irrigation with water with 6.3 dS m⁻¹ salinity exhibited a 13.37% lower NBP than those that were irrigated with an EC_w of 0.3 dS m⁻¹. The reduction in the

number of bolls is the result of the deleterious effects of excess salts on the CO₂ assimilation process (Figure 5A), which reduce the osmotic potential of the soil solution, affecting water and nutrient absorption by the plants. This results in the partial use of carbohydrates by other metabolic pathways (Abdelhamid et al., 2013; Lima et al., 2019b), such as the synthesis of compatible solutes (trehalose, glycine betaine, proline, among others) and repair of oxidative damage caused by salt stress and maintenance of cellular homeostasis. Lima et al. (2017) investigated gas exchange and production components in colored-fiber cotton cv. BRS Rubi as a function of irrigation with saline water (EC_w from 5.1 to 9.1 dS m⁻¹) and concluded that the CO₂ assimilation rate and the total number of seeds per plant were the most sensitive variables to the effects of salt stress.

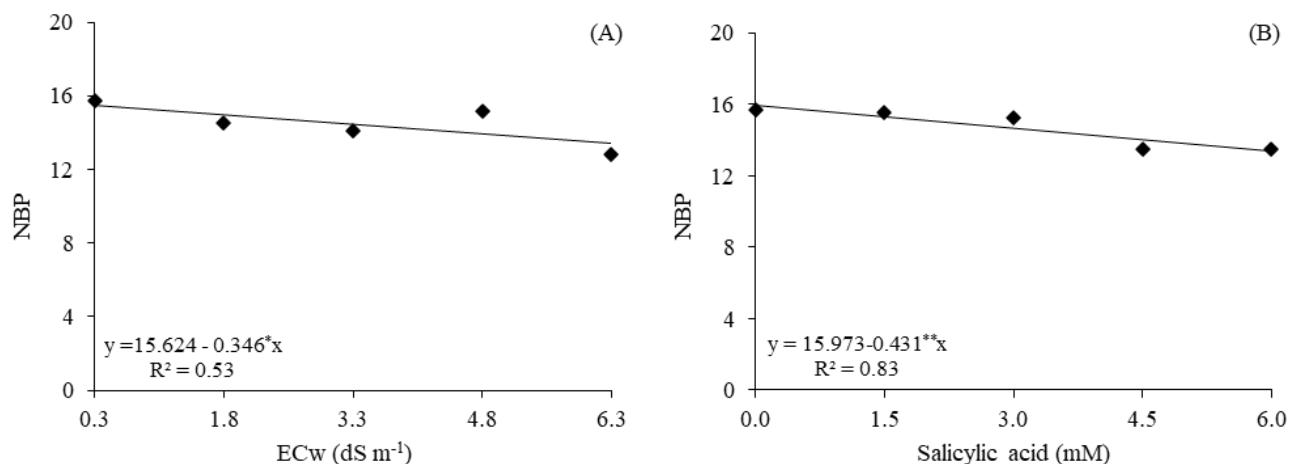


Figure 8. Number of bolls per plant in cotton cv. BRS Jade as a function of water electrical conductivity levels (EC_w) - A and salicylic acid concentrations (B).

* and ** = significant at $p \leq 0.05$ and $p \leq 0.01$, respectively.

The NBP of cotton cv. BRS Jade decreased linearly as the SA concentrations were increased. According to the regression equation (Figure 8B), NBP decreased by 2.69% per unit increase in SA concentration. Between the foliar application of 6.0 mM and the control treatment (0 mM), a reduction of 16.99% was observed in this variable. Salicylic acid application has a controversial role in plant growth and development, depending on its concentration, species, form and frequency of application, and plant development stage (Silva et al., 2020; Koo et al., 2020). The role of SA in the physiology and production of plants is limited to low concentrations, since at high concentrations it can induce oxidative damage, reducing tolerance against abiotic stresses such as salt (Kumar et al., 2022) by lowering the photosynthetic rate and RuBisCO activity.

Unlike NBP (Figure 8), the interaction between the factors (SL \times SA) significantly affected cottonseed weight (Figure 9). In the plants under foliar application with 0, 1.5, 3.0, 4.5, and 6.0 mM SA, CSW decreased linearly, by 2.70, 3.09, 1.70, 1.87, and 2.43%, per unit increase in water electrical conductivity. Between the lowest water salinity level (0.7 dS m⁻¹) and the level of 6.3 dS m⁻¹, the application of the SA concentrations of 0, 1.5, 3.0, 4.5, and 6.0 mM caused CSW to decrease by 15.45, 17.70, 9.63, 10.64, and 13.87%, respectively. This decrease in production reflects the changes observed in gas exchange especially CO₂ assimilation rate and is related to the difficulty of plants in absorbing water and nutrients due to the excess of salts that directly interferes with soil water potential. In a study with cotton cv. BRS Jade, Souza et al. (2018) concluded that increasing water salinity from 1.7 to 6.8 dS m⁻¹ reduced CSW by 61.03%.

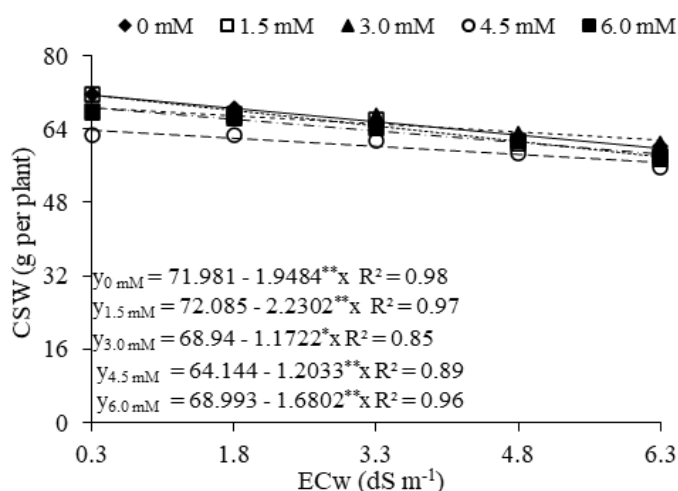


Figure 9. Seed weight (CSW) of cotton cv. BRS Jade as a function of the interaction between water electrical conductivity levels (ECw) and salicylic acid concentrations (SA).

* and ** = significant at $p \leq 0.05$ and $p \leq 0.01$, respectively.

Conclusions

Irrigation with water of electrical conductivity from 0.3 dS m⁻¹ induces stomatal closure and reduces transpiration, the CO₂ assimilation rate, and the levels of photosynthetic pigments in cotton cv. BRS Jade at 90 days after sowing.

Water salinity levels from 0.3 dS m⁻¹ reduce the number of bolls and seed weight in cotton cv. BRS Jade.

The salicylic acid concentrations of 2.6 and 2.7 mM increase CO₂ assimilation rate and stomatal conductance, respectively, in cotton plants.

Foliar application of salicylic acid does not mitigate the effects of salt stress on gas exchange, the synthesis of photosynthetic pigments, or production components of cotton cv. BRS Jade.

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