

Article

Salicylic Acid Modulates Morphophysiological Responses of *Paubrasilia echinata* Seedlings Irrigated with Saline Water

Thayná Kelly Formiga de Medeiros ^{1,*}, Francisco Thiago Coelho Bezerra ^{1,2},
Gleyse Lopes Fernandes de Souza ¹, Marcos Vinícius da Silva ³, Maria Beatriz Ferreira ³,
Dayane Gomes da Silva ¹, Daniela Rosário de Mello ¹, Robevania da Silva Alves Almeida ¹,
Francisco Eudes da Silva ¹, Igor Eneas Cavalcante ¹, Alberício Pereira de Andrade ⁴, Olaf Andreas Bakke ⁵,
Ivonete Alves Bakke ⁵ and Riselane de Lucena Alcântara Bruno ¹

- ¹ Postgraduate Program in Agronomy, Federal University of Paraíba, Areia 58397-000, PB, Brazil; thiago_bezerra@uvanet.br (F.T.C.B.); gleyse.souza@academico.ufpb.br (G.L.F.d.S.); anedgomes22@gmail.com (D.G.d.S.); daniela.mello@academico.ufpb.br (D.R.d.M.); robervania.alves@gmail.com (R.d.S.A.A.); fes@academico.ufpb.br (F.E.d.S.); iec@academico.ufpb.br (I.E.C.); lanebruno.bruno@gmail.com (R.d.L.A.B.)
 - ² Academic Unit of Agronomy of Ibiapaba, State University of Vale do Acaraú, São Benedito 62370-000, CE, Brazil
 - ³ Chapadinha Science Center, Federal University of Maranhão, Chapadinha 65500-000, MA, Brazil; mv.silva@ufma.br (M.V.d.S.); mb.ferreira@ufma.br (M.B.F.)
 - ⁴ Postgraduate Program in Animal Science and Pastures, Federal University of Agreste of Pernambuco, Garanhuns 55292-270, PE, Brazil; albericio.andrade@ufape.edu.br
 - ⁵ Postgraduate Program in Forest Sciences, Federal University of Campina Grande, Patos 58708-110, PB, Brazil; olaf.andreas@professor.ufcg.edu.br (O.A.B.); ivonete.alves@professor.ufcg.edu.br (I.A.B.)
- * Correspondence: thayna.formiga2@academico.ufpb.br

Abstract

Rising salt concentration in water induces osmotic stress and ionic toxicity, compromising photosynthesis, growth, and survival of threatened species such as *Paubrasilia echinata* and highlighting the need for stress-mitigating compounds such as salicylic acid. This study evaluated the effect of salicylic acid on the morphophysiological responses of *P. echinata* seedlings irrigated with saline water. Treatments were arranged in a 2 × 3 factorial scheme, with two electrical conductivity levels of irrigation water (0.5 and 6.0 dS m^{−1}) and three salicylic acid concentrations (0, 2, and 3 mM), randomized across 24 experimental plots containing five plants each in a randomized complete block design. Analyses included growth, relative water content, chlorophyll indices and fluorescence of seedlings. Irrigation water with an electrical conductivity of 6.0 dS m^{−1} reduced leaf number by 9.09% and PSII efficiency by 26.94%. Under saline conditions, salicylic acid at 2 and 3 mM increased root dry matter by 49.28% and 60.29%, respectively. The highest total chlorophyll index (79.03) was obtained at 2 mM, whereas leaf area peaked at 734.74 cm² per plant at 3 mM. Salicylic acid enhances salt tolerance in *P. echinata*. At 2 mM, it improves seedling morphophysiological traits and may support restoration in salinized sites.

Keywords: plant stress; bioregulator; brazilwood; climate change; salinity stress



Academic Editor: Hui Xia

Received: 11 June 2026

Revised: 3 July 2026

Accepted: 6 July 2026

Published: 8 July 2026

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1. Introduction

The Atlantic Forest is a global biodiversity hotspot [1], and approximately 82% of the tree species in this biome are threatened with extinction [2]. Among them, the endemic tree *Paubrasilia echinata*, popularly known as brazilwood, stands out with its high ecological,

historical, economic, and cultural value [3]. Due to intense exploitation since the beginning of the XVI century and the degradation and fragmentation of its natural distribution area, this tree is currently classified as an endangered species [4]. Its distribution ranges from Northeastern to Southeastern Brazil, thriving in inland mesophytic ombrophilous forests and coastal environments associated with sandy soils, or in dry habitats, such as semideciduous forests and rock outcrops [5].

According to the Intergovernmental Panel on Climate Change [6,7], sea level rise associated with climate change intensifies the risk of saltwater intrusion into low-altitude coastal aquifers, increasing the salinization of soils and groundwater in coastal ecosystems. This process represents a growing threat to natural vegetation, as the increase in salt concentration in soil and water may compromise plant growth and development [8].

Increases in salt content reduce the water potential of the soil solution, which hinders water absorption by roots [9]. In such conditions, the plants need to expend a great amount of metabolic energy to maintain osmotic gradients and cellular metabolism by energy-demanding biochemical and physiological adjustments associated with changes in ionic balance [10] and physiological responses that include a reduction in leaf area and stomatal conductance. Ultimately, this compromises the photosynthetic rate and plant growth [11], as observed in *P. echinata* seedlings subjected to water deficit, in which there was a reduction in growth variables, biomass, relative water content and chlorophyll indices [12]. Salt stress may also affect electron transport and the activity of photosystem II (PSII), responsible for the oxidation of water molecules at the oxygen-evolving complex and the generation of electrons during photosynthesis [13].

Excessive uptake and accumulation of Na^+ in cells cause ionic imbalance, lipid peroxidation, and damage to cellular membranes [14,15]. The substitution of potassium (K^+) by Na^+ results in a reduction in the K^+/Na^+ ratio and affects essential metabolic processes, such as enzymatic activity and photosynthesis. Excess Na^+ promotes the generation of reactive oxygen species, which intensifies oxidative damage [16]. These effects are particularly critical during seed germination and seedling establishment, although impacts may persist in subsequent phases of plant development [17].

An important growth regulator involved in the modulation of plant reaction to biotic and abiotic stresses is the salicylic acid (SA) [18], a key phenolic compound that regulates plant growth and development [19,20]. In woody species exposed to salt stress, SA has been reported to increase relative water content, chlorophyll content, photosynthetic performance, PSII efficiency, and biomass production while reducing membrane damage, as demonstrated in *Torreya grandis* cv. *Merrillii* [21] and *Anacardium occidentale* L. [22]. In contrast, under non-stress conditions, the effects of SA vary depending on the species and applied concentration and may either stimulate or inhibit plant growth [19]. Contrasting responses have been reported for *Schinus terebinthifolius* R. and *Cedrela fissilis* V. seedlings, indicating that the effects of SA are species-specific and concentration-dependent [23].

The SA can increase plant tolerance to salinity through the activation of antioxidant enzymes, maintenance of ionic balance, and regulation of the expression of stress-responsive genes [24]. SA plays an important role in regulating plant tolerance to abiotic stresses, promoting protection against damage induced by these factors and modulating aspects of the plant life cycle [25]. Under saline conditions, its action contributes to the reduction of oxidative damage, maintenance of cellular integrity, and minimization of the deleterious effects caused by excess salts on essential physiological and biochemical processes [26].

Paubrasilia echinata is threatened with extinction and occurs in environments potentially vulnerable to the intensification of soil and water salinization. Investigating the tolerance of this species to salinity, as well as mitigatory strategies to overcome saline conditions, may help to establish protocol for seedling production and ecological restoration programs when

the available water or the soil presents high levels of salts. However, information on the morphophysiological responses of *P. echinata* to saline irrigation and on the potential of SA to mitigate salt stress remains scarce. Because the effects of this regulator are species- and concentration-dependent, its evaluation in *P. echinata* is warranted. Therefore, this study provides the first comprehensive evaluation of the effects of SA on the morphophysiological responses of *P. echinata* seedlings under saline irrigation. Thus, this study aimed to evaluate the effects of salicylic acid on growth, relative water content, chlorophyll indices, and chlorophyll fluorescence of *P. echinata* seedlings irrigated with saline water.

2. Materials and Methods

2.1. Study Area

The experiment was conducted in a greenhouse (6°57'59" S, 35°42'57" W, and 506 m above sea level), from August to December 2025, at the Center for Agricultural Sciences (CCA) of the Federal University of Paraíba (UFPB), in the municipality of Areia, Paraíba State, Brazil. During the experimental period, air temperature and relative humidity were automatically monitored and recorded every 10 min using a digital thermo-hygrometer (Datalogger LI-1400, LI-COR®, Lincoln, NE, USA). Manipulation of these data allowed the estimation of the daily mean values for maximum, minimum, and average air temperature, as well as maximum, minimum, and average relative humidity (Figure 1).

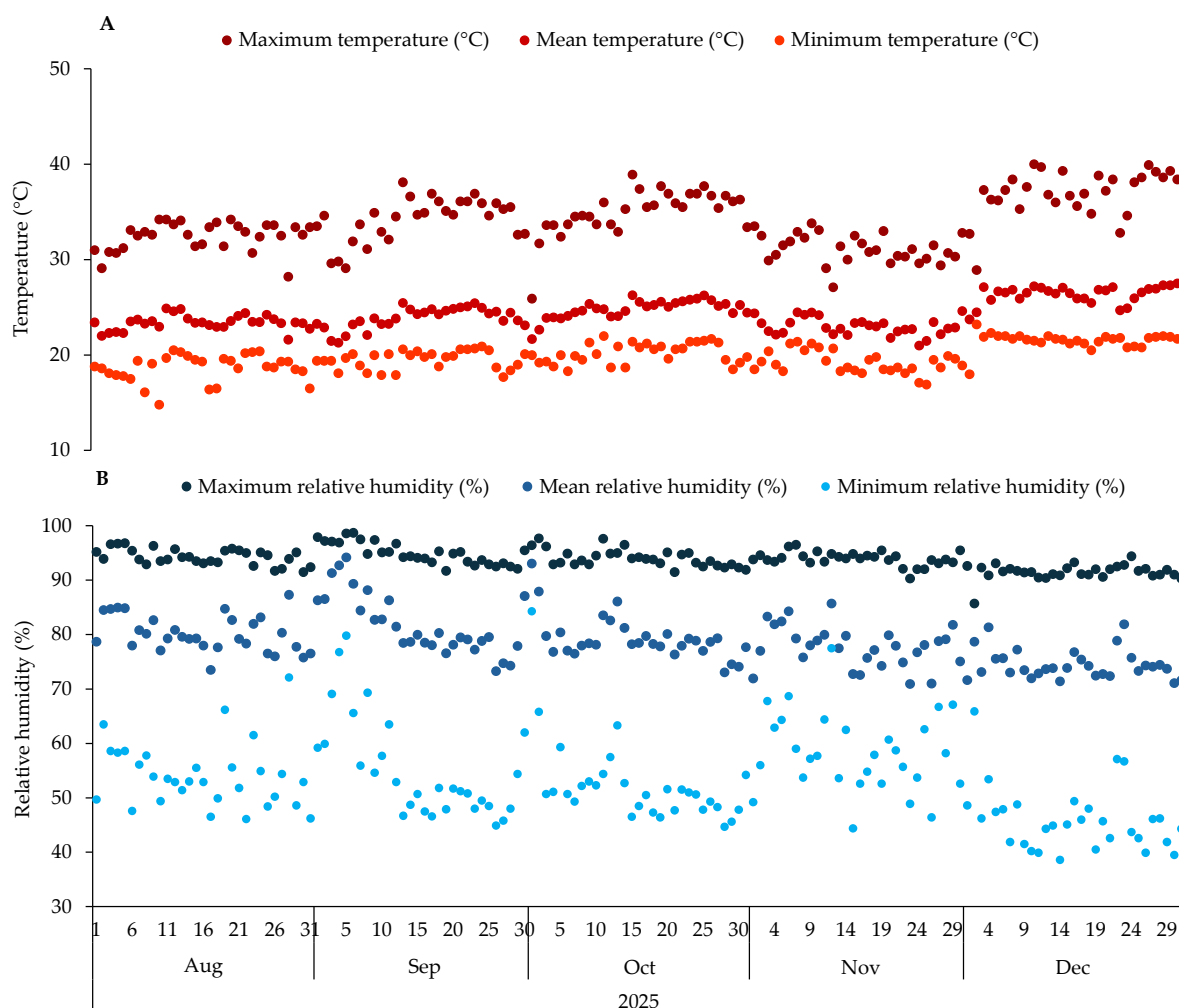


Figure 1. Daily maximum, mean, and minimum air temperature (A) and relative humidity (B) of the experimental period.

2.2. Treatments and Statistical Design

The treatments were organized in a scheme 2×3 factorial design [two levels of EC of irrigation water (0.5 and 6.0 dS m⁻¹) and three levels of SA (0, 2, and 3 mM)], totaling six treatments. The treatments were distributed in four randomized blocks, and each experimental unit contained five plants.

The selected irrigation water electrical conductivity levels were chosen to represent contrasting irrigation conditions. The EC of 0.5 dS m⁻¹ corresponds to low-salinity water commonly used for seedling production, whereas 6.0 dS m⁻¹ represents a saline irrigation condition capable of imposing physiological constraints on the development of forest seedlings, without causing generalized loss of viability [27].

2.3. Experimental Procedures

The seeds used for seedling production came from trees of the small variant morphotype [3,28] located at a fragment of the UFPB/CCA Atlantic Forest Reserve (6°57'59" S latitude, 35°42'57" W longitude, and 506 m altitude).

Seed treatment comprised immersion in a 1% sodium hypochlorite solution for 1 min, thorough rinsing with distilled water, and sowing in 128-cell polystyrene trays. Each 5 cm × 5 cm × 6 cm cell, filled with a commercial substrate based on pine bark (MecPlant®, Telêmaco Borba, Paraná State, Brazil), received one seed positioned sub-superficially in the substrate (Figure 2).

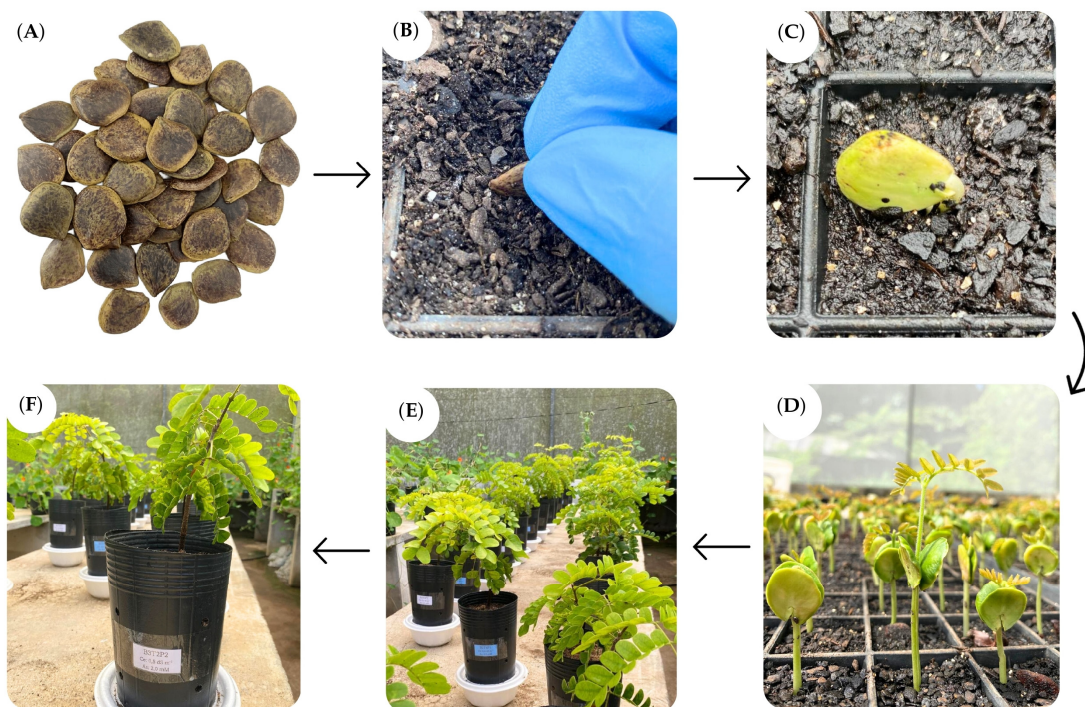


Figure 2. Details of the *P. echinata* seedling production: (A) seeds; (B) manual sowing in the pine bark-based substrate; (C) seedling emergence four days after sowing in a 5 cm × 5 cm × 6 cm cell; (D) seedlings eight days after emergence; (E) overview of the seedlings used in the experiment; and (F) a seedling in an individual plastic container with a developing seedling in greenhouse conditions.

The commercial pine bark-based substrate presents pH = 5.0, general moderate macronutrient contents, base saturation (V%) of 46.76%, and aluminum saturation of 0.00%, indicating no Al³⁺ toxicity (Table 1). The organic matter content of 55.60 g kg⁻¹ contributes to the adequate physical structure of the substrate.

Table 1. Chemical characterization of the substrate used in the production of *P. echinata* seedlings.

pH	P	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	SB	H ⁺ +Al ³⁺	Al ³⁺	CEC	V	ESP	OM
	mg dm ⁻³	----- cmol _c dm ⁻³ -----								--- % ---		g kg ⁻¹
5.0	233.27	8.9	8.9	0.06	0.25	18.11	20.62	0.00	38.73	46.76	0.15	55.60

pH (hydrogen potential) in water (1:2.5); P (phosphorus), K⁺ (potassium), and Na⁺ (sodium) extracted using Mehlich 1; Ca²⁺ (calcium), Mg²⁺ (magnesium), and Al³⁺ (aluminum) extracted using 1 M KCl; H⁺ + Al³⁺ (hydrogen plus aluminum) extracted using 0.5 M calcium acetate at pH 7.0; SB (sum of bases) = K⁺ + Na⁺ + Ca²⁺ + Mg²⁺; CEC (cation exchange capacity) = SB + H⁺ + Al³⁺; V (base saturation) = (SB/CEC) × 100; ESP (exchangeable sodium percentage) = (Na⁺/CEC) × 100; OM (organic matter) = organic carbon × 1.724, Walkley-Black method.

Seedling emergence began four days after sowing, and the first two true leaves were visible at day seven. Transplantation from the tray cells to the black plastic containers occurred at day 15 after sowing, when the plants showed two true leaves fully expanded, and the mean ± standard error for seedling height and stem diameter at substrate level were, respectively, (6.72 ± 1.16) cm and (1.33 ± 0.20) mm. The plastic material was 350 µm thick, and the container height and diameter were 20 cm and 9 cm, respectively, filled with 1.1 dm³ of soil (Table 2).

Table 2. Chemical characterization of the soil used in the production of *P. echinata* seedlings.

pH	P	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	SB	H ⁺ +Al ³⁺	Al ³⁺	CEC	V	ESP	OM
	mg dm ⁻³	----- cmol _c dm ⁻³ -----								--- % ---		g kg ⁻¹
6.9	56.3	15.0	4.4	0.80	1.88	22.08	1.5	0.00	23.58	93.64	3.62	55.60

pH (hydrogen potential) in water (1:2.5); P (phosphorus), K⁺ (potassium), and Na⁺ (sodium) extracted using Mehlich 1; Ca²⁺ (calcium), Mg²⁺ (magnesium), and Al³⁺ (aluminum) extracted using 1 M KCl; H⁺ + Al³⁺ (hydrogen plus aluminum) extracted using 0.5 M calcium acetate at pH 7.0; SB (sum of bases) = K⁺ + Na⁺ + Ca²⁺ + Mg²⁺; CEC (cation exchange capacity) = SB + H⁺ + Al³⁺; V (base saturation) = (SB/CEC) × 100; ESP (exchangeable sodium percentage) = (Na⁺/CEC) × 100; OM (organic matter) = organic carbon × 1.724, Walkley-Black method.

Addition of monoammonium phosphate (MAP, 60.8% P₂O₅ and 10.8% N) and potassium sulfate (K₂SO₄, 50% K₂O and 18% S) increased N, P and K in the substrate to 100, 300 and 150 mg kg⁻¹, respectively [29].

The experiment used 120 healthy 547-day-old seedlings, grown in protected (greenhouse) conditions, with an initial mean height and mean leaf number of 21.03 ± 6.33 cm and 9 ± 1, respectively. The 2 × 3 factorial treatments [two levels of EC of irrigation water (0.5 and 6.0 dS m⁻¹) × three levels of SA (0.0, 2.0, and 3.0 mM)] were applied during the experimental period of 122 days, and the initial differences in seedling height were controlled by the distributed in four randomized blocks, and each experimental unit contained five plants.

2.4. Irrigation Management

The irrigation water came from a tubular well located at Sítio Chã da Pia, in the municipality of Areia, Paraíba, Brazil, and from the regular municipal water supply system of Areia, Paraíba State, Brazil, and analyzed for its chemical characteristics (Table 3). The water from the tubular well had its high electrical conductivity reduced from 18.34 to 6.00 dS m⁻¹ by adding the proper amount of water from the regular municipal supply system (electrical conductivity of 0.5 dS m⁻¹), in batches of 50 L in a plastic container. The electrical conductivity values were checked using a digital conductivity meter (model CD-850, Instrutherm Instrumentos de Medição Ltda., São Paulo, SP, Brazil).

Ordinary daily irrigation of the *P. echinata* seedlings lasted for 547 days after transplanting to the 1.1 dm³ containers, and sought to keep the substrate moisture close to field capacity (i.e., water addition in each plastic container stopped at the onset of drainage of excess water). Subsequently, 0.5 and 6.0 dS m⁻¹ water substituted the ordinary daily irrigation regimen during the next 122 days; the seven spray events of the SA solutions,

applied late in the afternoon on the entire abaxial and adaxial leaf surfaces, occurred at days 30, 45, 60, 75, 90, 105 and 120 after the beginning of the water salinity treatments. SA solutions were prepared by dissolving SA in 5 mL of absolute ethyl alcohol 5% (v/v), followed by adjustment of the volume to 100 mL with distilled water.

Table 3. Chemical attributes of the water used to irrigate the *P. echinata* seedlings.

Water	ECwi	pH	Ca ²⁺	Mg ²⁺	Na ⁺	K ⁺	Cl [−]	CO ₃ ^{2−}	HCO ₃ [−]	SO ₄ ^{2−}	SAR	Classification
	dS m ^{−1}		mmol _c L ^{−1}								%	
Non-saline	0.50	7.3	0.65	0.80	1.37	0.20	2.00	0.00	2.50	0.24	1.60	C ₂ S ₁
Saline	18.34	8.0	35.50	56.75	44.38	0.38	158.00	0.00	3.50	5.13	6.54	C ₄ S ₂

ECwi = electrical conductivity of the water (dS m^{−1}); pH (potential of hydrogen); SAR = sodium adsorption ratio, $\text{Na}^+ / [0.5(\text{Ca}^{2+} + \text{Mg}^{2+})]^{0.5}$; C₂S₁ = class of moderate risk of salinization and low risk of sodification of the soil; C₄S₂ = class with very high risk of salinization and moderate risk of sodification of the soil [30].

2.5. Variables Analyzed

Growth and physiological data collection occurred at day 122 after the start of the treatments. The considered growth variables were: stem diameter at the substrate level (mm), measured using a digital caliper; number of leaves, leaflets, and pinnae; leaf area (cm²), determined from leaf images processed using ImageJ[®] software (version 1.54, National Institutes of Health, Bethesda, MD, USA); shoot and root length (cm), measured with a millimeter ruler; and root volume (cm³), determined according to Archimedes' principle [31], in which roots were washed to remove substrate residues, dried with paper towels, and then immersed in a 50 mL graduated cylinder containing distilled water, with root volume corresponding to the displaced water indicated in the water column. Shoot, root and total dry matter mass (g) were determined separately after drying the fresh material in a forced-air circulation oven at 65 °C [32]. In addition, the Dickson Quality Index (DQI) of each seedling was calculated [33] according to the following equation:

$$\text{DQI} = \text{TDMM} / [(\text{LAP} / \text{DGL}) + (\text{SDMM} / \text{RDMM})] \quad (1)$$

In the above equation, TDMM is the total dry matter mass (g); LAP is the length of the aerial part (cm); DGL is the diameter at ground level (mm); SDMM is the shoot dry matter mass (g); and RDMM is the root dry matter mass (g).

The following physiological variables were evaluated: relative water content, leaf index of chlorophyll a (LICa), b (LICb) and total (LICt) indexes, and chlorophyll a/b ratio (LICa/LICb). Measurements were taken on the third pair of leaves from the plant apex under natural photoperiod, between 7:00 and 9:00 a.m., using a portable chlorophyll activity meter (ChlorofiLOG, CFL 1030, Falker[®], Porto Alegre, Rio Grande do Sul State, Brazil).

Estimation of the relative water content [RWC(%)] followed the methodology proposed by [34]: ten 10-mm-diameter leaf discs, collected from the fourth fully expanded leaf of each seedling had their fresh mass (FM) determined in a semi-analytical balance (accurate to the of 0.001 g), followed by immersion in distilled water for 24 h, removal of excess water from disc surface with paper towel, weighing to obtain their turgid mass (TM), and dried at 65 °C for 24 h in a forced-air circulation oven to determine their dry mass (DM). The RWC (%) of each seedling was calculated using the following equation:

$$\text{RWC} (\%) = [(\text{FM} - \text{DM}) / (\text{TM} - \text{DM})] \times 100 \quad (2)$$

On the third pair of leaves from the plant apex under natural, between 7:00 and 9:00 a.m., after 30 min of dark adaptation using leaf clips, the following parameters were measured: initial fluorescence (F₀), maximum fluorescence (F_m), variable fluorescence

(Fv), maximum quantum efficiency of photosystem II ($\text{MQE}_{\text{PSII}} = F_v/F_m$), and the ratio between competing photochemical and non-photochemical quantum yields in PSII ($\text{ratio}_{\text{photochem/non-photochem quantum yields in PSII}} = F_v/F_0$), using a modulated fluorometer (OptiSciences Inc., model OS-30p, Hudson, NY, USA).

2.6. Statistical Analysis

Data were tested for normality of residuals and homogeneity of variances using the Shapiro–Wilk and Levene tests, respectively, considering $p \leq 0.05$. Subsequently, the results were subjected to the analysis of variance (ANOVA), adopting a significance level of $p \leq 0.05$. When a significant effect was detected ($p \leq 0.05$), means were compared using the F-test ($p \leq 0.05$) for factors with two levels or Tukey's test ($p \leq 0.05$) for factors with three or more levels. Multivariate analysis using principal component analysis (PCA) was performed to identify variation patterns and interrelationships among the evaluated variables. Correlation analyses were conducted based on Pearson's correlation coefficients. The statistical analyses were run using the R software, version 4.5.2 [35].

3. Results

3.1. Morphological and Growth Responses to Salinity and Salicylic Acid

The increase in the electrical conductivity of the irrigation water from 0.5 to 6.0 dS m^{-1} reduced shoot growth and leaf expansion in *P. echinata* seedlings. Morphological differences were observed among SA concentrations under both irrigation conditions (Figure 3).

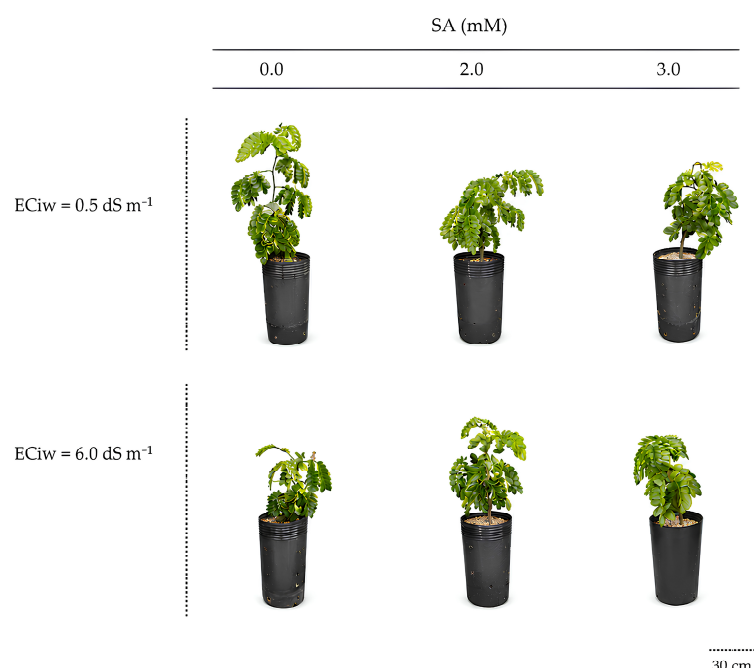


Figure 3. Morphological appearance of *P. echinata* seedlings at 669 days of age, in response to irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m^{-1}) and salicylic acid (SA) concentrations (0.0; 2.0 and 3.0 mM).

Irrigation water electrical conductivity, SA concentrations, or the interaction between these factors showed no significant effect ($p > 0.05$) on diameter at ground level, number of pinnae, and length of the aerial part, and resulted in mean $\pm$ standard error values of 6.48 ± 0.17 mm, 50.33 ± 2.35 pinnae, and 29.07 ± 5.49 cm, respectively.

Changes in the irrigation water electrical conductivity ($F = 5.70$; $p = 0.0306$) and SA concentration ($F = 8.50$; $p = 0.0034$) affected the number of leaves. The increase in electrical conductivity from 0.5 to 6.0 dS m^{-1} decreased the average number of leaves from 11 to

10, a 9.09% reduction (Figure 4A), while SA concentration of 2.0 mM significantly decreased the average number of leaves (9 leaves) compared to the observed at 0.0 and 3.0 mM (11 leaves), equivalent to 18.18% reduction in the number of leaves (Figure 4B).

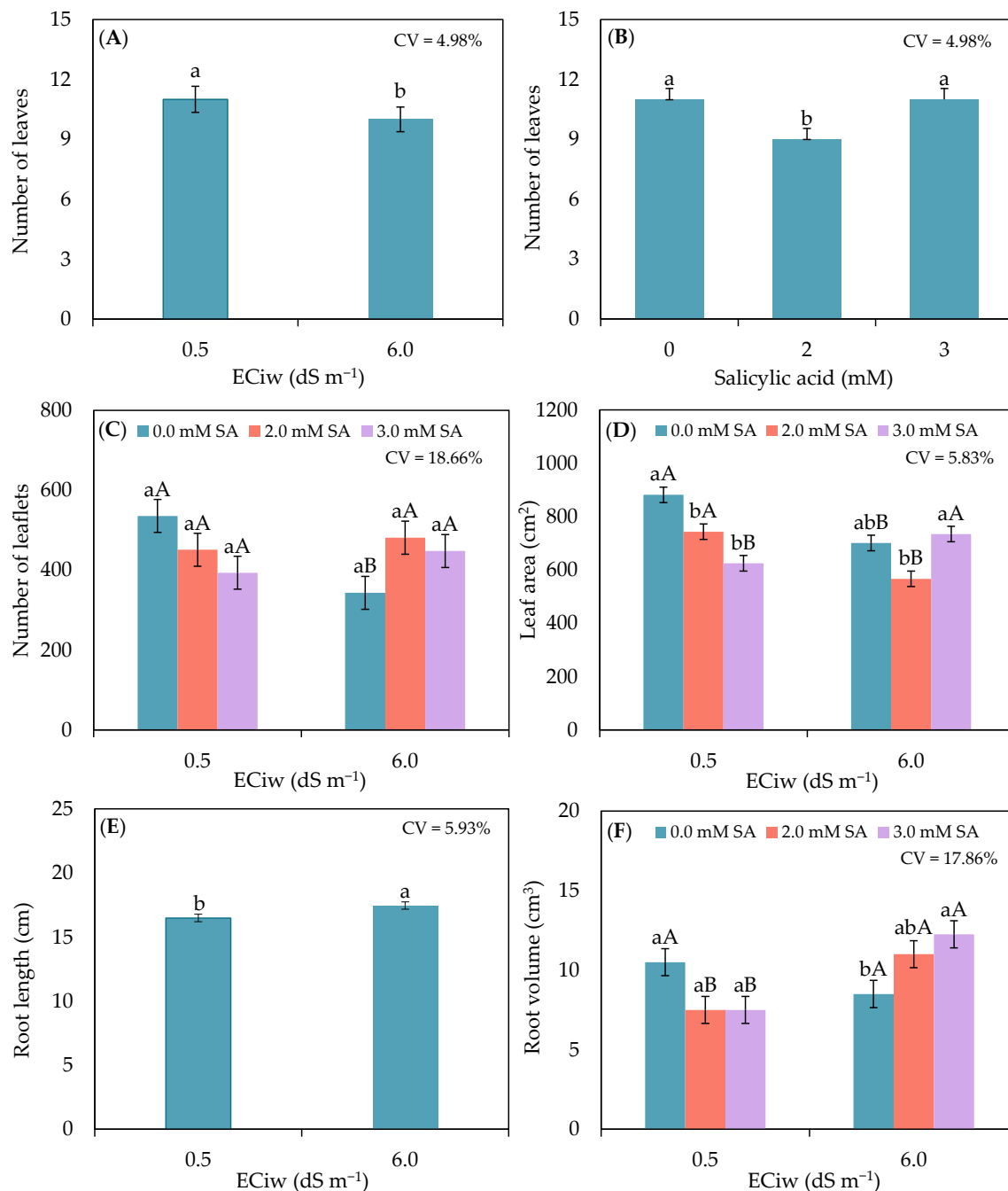


Figure 4. Mean values $\pm$ standard error for number of leaves (A) and root length (E) according to the irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m⁻¹), number of leaves according to salicylic acid concentrations (SA) (0.0; 2.0 and 3.0 mM) (B), number of leaflets (C), leaf area (D), and root volume (F) according to the ECiw $\times$ SA in *P. echinata* seedlings. For isolated effects, means followed by the same lowercase letter among SA concentrations (Tukey test, $p \leq 0.05$) or levels of irrigation water electrical conductivity (F test, $p \leq 0.05$) not differ from each other. For the ECwi $\times$ SA interactions, means followed by the same lowercase letter among SA concentrations at the same electrical conductivity water (Tukey test, $p \leq 0.05$) and uppercase letter among levels of irrigation water electrical conductivity at the same SA concentration (F test, $p \leq 0.05$) do not differ from each other. CV = Coefficient of variation.

For the number of leaflets, the interaction between irrigation water electrical conductivity and SA concentrations was significant ($F = 5.45$; $p = 0.0166$). Increase in the electrical conductivity from 0.5 to 6.0 dS m⁻¹ reduced the number of leaflets from 536 to 343 leaflets only in the absence of SA application (0 mM), corresponding to a 36.01% reduction. Regardless of irrigation water electrical conductivity, no differences were observed among SA concentrations (Figure 4C).

For leaf area, the interaction between irrigation water electrical conductivity and SA concentrations showed a significant effect ($F = 16.20$; $p = 0.0065$). The highest leaf area was recorded under irrigation with 0.5 dS m⁻¹ water and without SA application (881.46 cm²), with a reduction of 20.46% when irrigated with 6.0 dS m⁻¹ water in the absence of SA (701.08 cm²). At the 2 mM concentration, under irrigation with 0.5 dS m⁻¹ water, leaf area was 743.45 cm², decreasing to 566.75 cm² under irrigation with 6.0 dS m⁻¹ (a reduction of 23.77%). In contrast, at the 3 mM concentration, the highest leaf area was obtained under irrigation with 6.0 dS m⁻¹ water (734.74 cm²), which was 17.51% higher than that obtained under 0.5 dS m⁻¹ water (625.27 cm²). Under irrigation with 0.5 dS m⁻¹ water, the average leaf area value (881.46 cm²) observed in the absence of SA decreased significantly to 743.45 cm² and 625.27 cm² (no significant difference between these values) for SA concentrations of 2 and 3 mM, corresponding to reductions of 15.66% and 29.06%, respectively. In contrast, under irrigation with 6.0 dS m⁻¹ water, leaf area without SA application (701.08 cm²) did not differ from that under 2 mM (566.75 cm²) and 3 mM (734.74 cm²); however, a reduction in leaf area (22.86%) was observed with SA application at 2 mM compared to 3 mM (Figure 4D).

The average root length increased 6.06% ($F = 5.62$; $p = 0.0316$), from 16.49 cm to 17.49 cm as a result of the irrigation of seedlings with water with 0.5 and 6.0 dS m⁻¹ electrical conductivity, respectively (Figure 4E).

The irrigation water electrical conductivity $\times$ SA interaction was significant ($F = 8.88$; $p = 0.0028$). The increase in electrical conductivity from 0.5 to 6.0 dS m⁻¹ increased root volume in plants sprayed with 2 and 3 mM SA solutions. Under irrigation with 0.5 dS m⁻¹ water, root volumes at 2 and 3 mM were 7.50 cm³, whereas under irrigation with 6.0 dS m⁻¹ water, they were 11.00 and 12.25 cm³, representing increases of 46.67% and 63.33%, respectively. Under irrigation with 0.5 dS m⁻¹ water, SA concentrations did not affect root volume. Under irrigation with 6.0 dS m⁻¹ water, the root volume obtained with 2 mM SA (11.00 cm³) did not differ from those at 0 mM (8.50 cm³) and 3 mM (12.25 cm³); however, the application of SA at 3 mM promoted an increase in root volume of 44.12% compared to the treatment without SA (Figure 4F).

3.2. Biomass Accumulation and Seedling Quality

Shoot and stem dry matter mass were not influenced by irrigation water electrical conductivity, SA concentrations, and the interaction between these factors was not significant ($p > 0.05$), showing overall mean values of 14.32 ± 2.29 g and 4.33 ± 0.22 g, respectively. In contrast, the interaction between these factors was significant for root dry matter mass ($F = 11.70$; $p = 0.0009$). Irrigation with 0.5 dS m⁻¹ water resulted in root dry matter mass values of 8.25, 6.94, and 7.33 g plant⁻¹ at SA concentrations of 0, 2, and 3 mM, respectively. When irrigated with 6.0 dS m⁻¹ water, these values were 6.27, 9.36, and 10.05 g plant⁻¹, corresponding to a reduction of 24.00% and increases of 34.87% and 37.11%, respectively. Under irrigation with 0.5 dS m⁻¹ water, SA concentrations did not significantly affect root dry matter mass. Under irrigation with 6.0 dS m⁻¹ water, SA applications promoted increases in root dry matter mass, with higher values observed at 2 mM (9.36 g plant⁻¹) and 3 mM (10.05 g plant⁻¹), which were 49.28% and 60.29% higher, respectively, than the

value obtained without SA application ($6.27 \text{ g plant}^{-1}$) (Figure 5A), with no significant difference between the root biomass averages for the 2 and 3 mM SA levels.

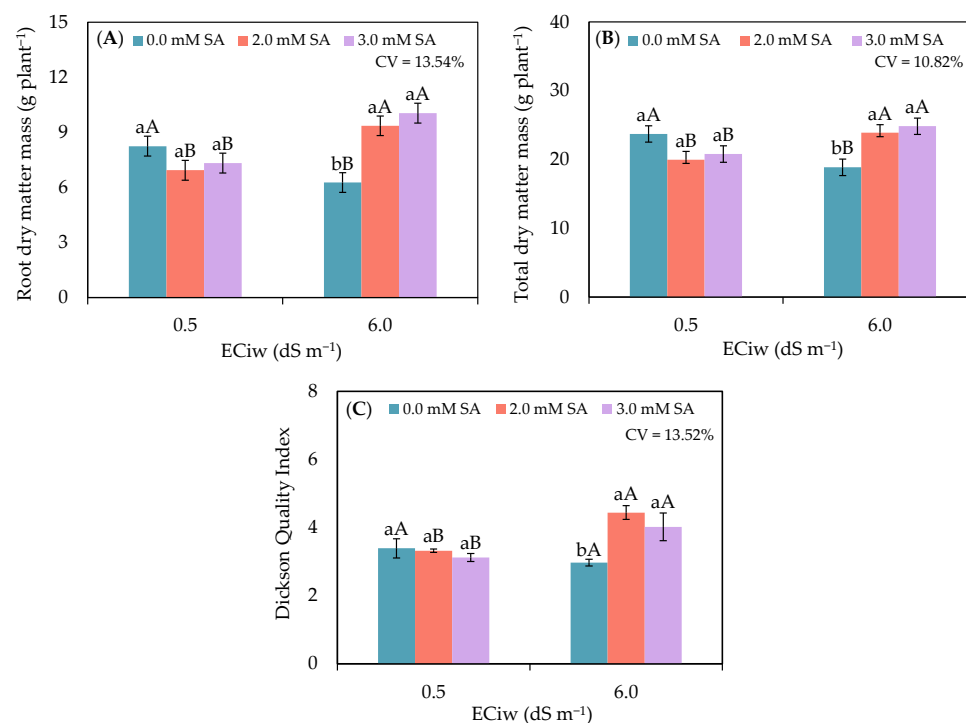


Figure 5. Mean values $\pm$ standard error for root dry mass (A), total dry mass (B), and Dickson Quality Index (C) of *P. echinata* seedlings according to the interaction between irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m^{-1}) and salicylic acid (SA) concentrations (0.0; 2.0 and 3.0 mM). Means followed by the same lowercase letter among SA concentrations at the same electrical conductivity (Tukey test, $p \leq 0.05$) and uppercase letter among levels of irrigation water electrical conductivity at the same SA concentration (F test, $p \leq 0.05$) do not differ from each other. CV = Coefficient of variation.

For total dry matter mass, an interaction between irrigation water electrical conductivity and SA concentrations was observed ($F = 9.13$; $p = 0.0026$). Under irrigation with 0.5 dS m^{-1} water, total dry mass values were 23.71 , 19.97 , and $20.80 \text{ g plant}^{-1}$ at SA concentrations of 0, 2, and 3 mM, respectively, with a respective reduction to $18.86 \text{ g plant}^{-1}$ and increases to 23.88 and $24.83 \text{ g plant}^{-1}$ for the 6.0 dS m^{-1} irrigation water use. These values correspond to a reduction of 20.45% (23.71 g vs. 18.86 g) and increases of 19.58% (19.97 g vs. 23.88 g) and 19.37% (20.80 g vs. 24.83 g), respectively. Under irrigation with 0.5 dS m^{-1} water, SA concentrations did not affect the total dry matter mass seedlings. Under irrigation with 6.0 dS m^{-1} water, SA applications promoted increases in total dry mass at 2 mM ($23.88 \text{ g plant}^{-1}$) and 3 mM ($24.83 \text{ g plant}^{-1}$), which did not differ from each other and were 26.62% and 31.65% higher, respectively, than the value obtained without SA application ($18.86 \text{ g plant}^{-1}$) (Figure 5B).

For the Dickson Quality Index, the interaction between irrigation water electrical conductivity and SA concentrations was significant ($F = 6.01$; $p = 0.0121$). Irrigation with water at 6.0 dS m^{-1} did not affect the index in the absence of SA application, whereas at concentrations of 2 and 3 mM, an increase was observed. Under irrigation with 0.5 dS m^{-1} water, Dickson Quality Index values were 3.32 and 3.12 at SA concentrations of 2 and 3 mM, respectively, increasing to 4.44 and 4.02 under irrigation with 6.0 dS m^{-1} water, corresponding to index value increases of 33.73% and 28.85%, respectively. Under irrigation with 0.5 dS m^{-1} water, SA concentrations had no significant effect on Dickson Quality Index and resulted in mean $\pm$ standard error value of 3.26 ± 0.10 . Under irrigation with

6.0 dS m⁻¹ water, SA applications promoted increases in the Dickson Quality Index, with higher values at 2 mM (4.44) and 3 mM (4.02), which did not differ from each other and were 49.50% and 35.35% higher, respectively, than the value obtained without SA application (2.97) (Figure 5C).

3.3. Plant Water Status

The relative water (RW%) content was negatively affected by irrigation water electrical conductivity (F = 21.36; *p* = 0.0013), and decreased from 77.94% to 68.43% when using water with electrical conductivity of 0.5 and 6.0 dS m⁻¹, respectively, corresponding to a reduction of 12.2% in RW% (Figure 6).

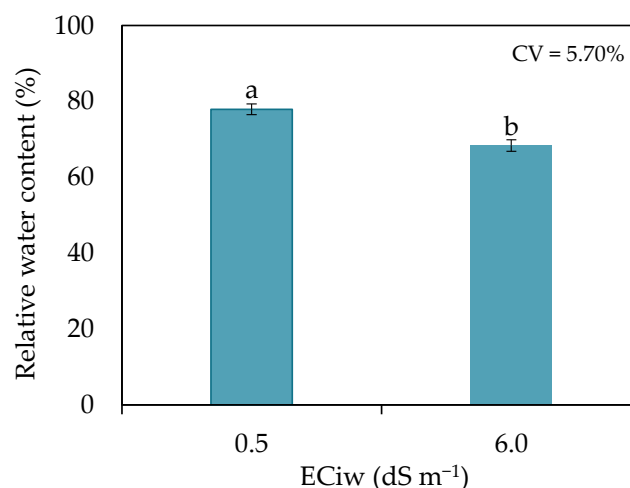


Figure 6. Mean values $\pm$ standard error for relative water content of leaves of *P. echinata* seedlings according to the irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m⁻¹). Means followed by the same letter do not differ from each other (F test, *p* $\leq$ 0.05).

3.4. Photosynthetic Pigments and Chlorophyll Indices

For the leaf index of chlorophyll a (ICLa), the interaction between irrigation water electrical conductivity and SA concentrations was significant (F = 8.26; *p* = 0.0038). Irrigation with water at 6.0 dS m⁻¹ reduced the leaf index of chlorophyll a only when associated with SA application at the concentration of 3 mM, decreasing from 47.65 under irrigation with 0.5 dS m⁻¹ water to 37.61 under irrigation with 6.0 dS m⁻¹ water, corresponding to a reduction of 21.07%. Under irrigation with 0.5 dS m⁻¹ water, the SA showed no significant effect on the leaf index of chlorophyll a and resulted in mean $\pm$ standard error value of (47.79 $\pm$ 0.81). In contrast, under irrigation with 6.0 dS m⁻¹ water, the application of SA at 3 mM reduced the leaf index of chlorophyll a to 37.61, which was 24.11% and 20.54% lower than the values obtained, respectively, at 0 mM (49.56) and 2 mM (47.33), which did not differ from each other (Figure 7A).

For the leaf index of chlorophyll b, the interaction between irrigation water electrical conductivity and SA concentrations was also significant (F = 36.70; *p* < 0.0001). Irrigation with water at 6.0 dS m⁻¹ reduced the leaf index of chlorophyll b when associated with SA application at concentrations of 0 and 3 mM, decreasing from 29.94 and 34.73 under irrigation with 0.5 dS m⁻¹ water to 20.25 and 22.40 under irrigation with 6.0 dS m⁻¹ water, corresponding to reductions of 32.36% and 35.50%, respectively. In contrast, under the application of 2 mM SA, the leaf index of chlorophyll b under irrigation with 0.5 dS m⁻¹ water was 27.86, increasing to 31.70 under irrigation with 6.0 dS m⁻¹ water, corresponding to an increase of 13.78%. Under irrigation with 0.5 dS m⁻¹ water, the highest leaf index of chlorophyll b was obtained at 3 mM SA (34.73), which was, respectively, 15.99% and 24.66% higher than the values observed at 0 mM (29.94) and 2 mM (27.86), which did not

differ from each other. Under irrigation with 6.0 dS m^{-1} water, the highest leaf index of chlorophyll b occurred at 2 mM SA (31.70), which was, respectively, 56.54% and 41.52% higher than the 0 mM (20.25) and 3 mM (22.40) values, which did not differ from each other (Figure 7B).

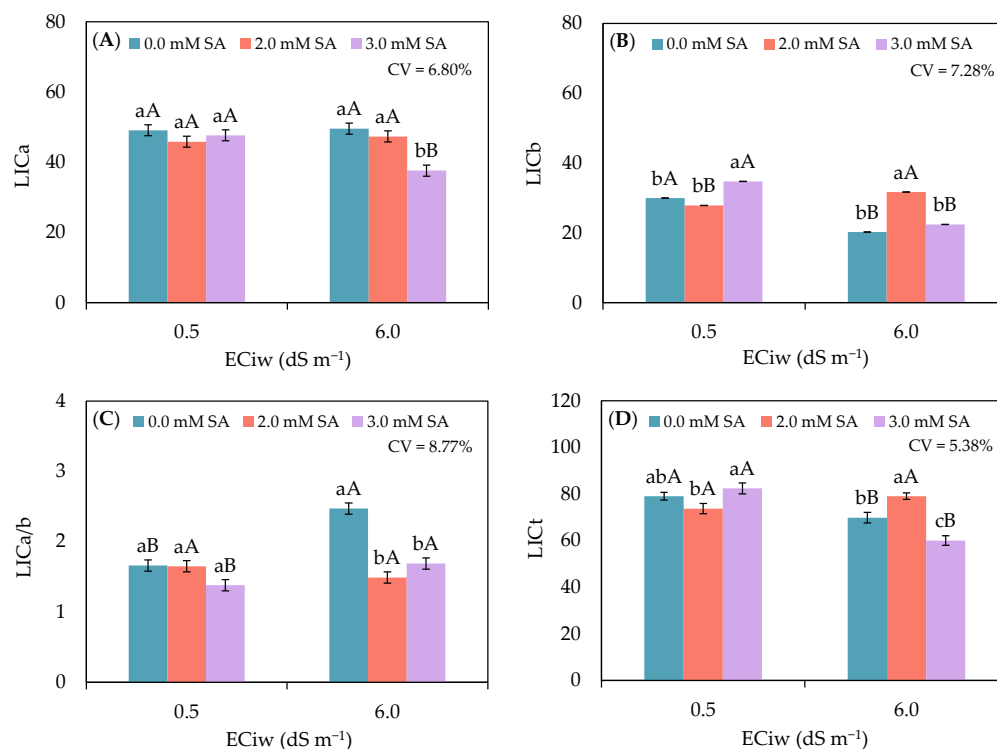


Figure 7. Mean values $\pm$ standard error for leaf index of chlorophyll a (LICa) (A), b (LICb) (B), a/b ratio (LICa/b) (C), and total (LICt) (D) indices in *P. echinata* seedlings according to the interaction between irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m^{-1}) and salicylic acid (SA) concentrations (0.0; 2.0 and 3.0 mM). Means followed by the same letter, lowercase among SA concentrations at the same irrigation electrical water conductivity (Tukey test, $p \leq 0.05$) and uppercase among levels of irrigation water electrical conductivity at the same SA concentration (F test, $p \leq 0.05$), do not differ from each other. CV = Coefficient of variation.

For the chlorophyll a/b ratio, the interaction between irrigation water electrical conductivity and SA concentrations ($F = 20.45$; $p < 0.0001$) was also significant. Under irrigation with 0.5 dS m^{-1} water, values of 1.66 and 1.38 were obtained for the chlorophyll a/b ratio when associated with SA applications at concentrations of 0 and 3 mM, respectively, with increases under irrigation with 6.0 dS m^{-1} water to 2.47 and 1.69, corresponding to increases of 48.79% and 22.46%, respectively. The chlorophyll a/b ratio values did not differ with SA application under irrigation with 0.5 dS m^{-1} water; however, under irrigation with 6.0 dS m^{-1} water, the highest ratio was observed in the absence of SA application (2.47), with reductions of 39.68% and 31.58%, respectively, at concentrations of 2 mM (1.49) and 3 mM (1.69), which did not differ from each other (Figure 7C).

For the leaf total chlorophyll index, the interaction between irrigation water electrical conductivity and SA concentrations was significant ($F = 24.20$; $p < 0.0001$). Irrigation with water at 6.0 dS m^{-1} reduced the leaf total chlorophyll index in plants treated with SA at concentrations of 0 and 3 mM. Under irrigation with 0.5 dS m^{-1} water, leaf total chlorophyll index was 79.01 at 0 mM and 82.38 at 3 mM, decreasing 11.64% and 27.15%, respectively, to 69.81 and 60.01 under irrigation with 6.0 dS m^{-1} water. Under irrigation with 0.5 dS m^{-1} water, the application of SA at 3 mM increased leaf total chlorophyll index from 73.7 at 2 mM to 82.38 at 3 mM, representing an increase of 11.78%. Under irrigation

with 6.0 dS m^{-1} water, the highest leaf total chlorophyll index was observed at 2 mM SA (79.03), followed by the absence of SA (69.81), whereas the lowest value was recorded at 3 mM (60.01). The values at 2 mM were 13.21% and 31.69% higher than those observed in the absence of SA and at 3 mM , respectively, while the absence of SA resulted in a 16.33% higher index than at 3 mM (Figure 7D).

3.5. Chlorophyll Fluorescence and Photochemical Efficiency of PSII

Initial chlorophyll a fluorescence was influenced only by irrigation water electrical conductivity ($F = 19.88$; $p = 0.0005$), and increased 23.71%, from 71.54 to 88.50, when the electrical conductivity of irrigation water increased from 0.5 to 6 dS m^{-1} (Figure 8A).

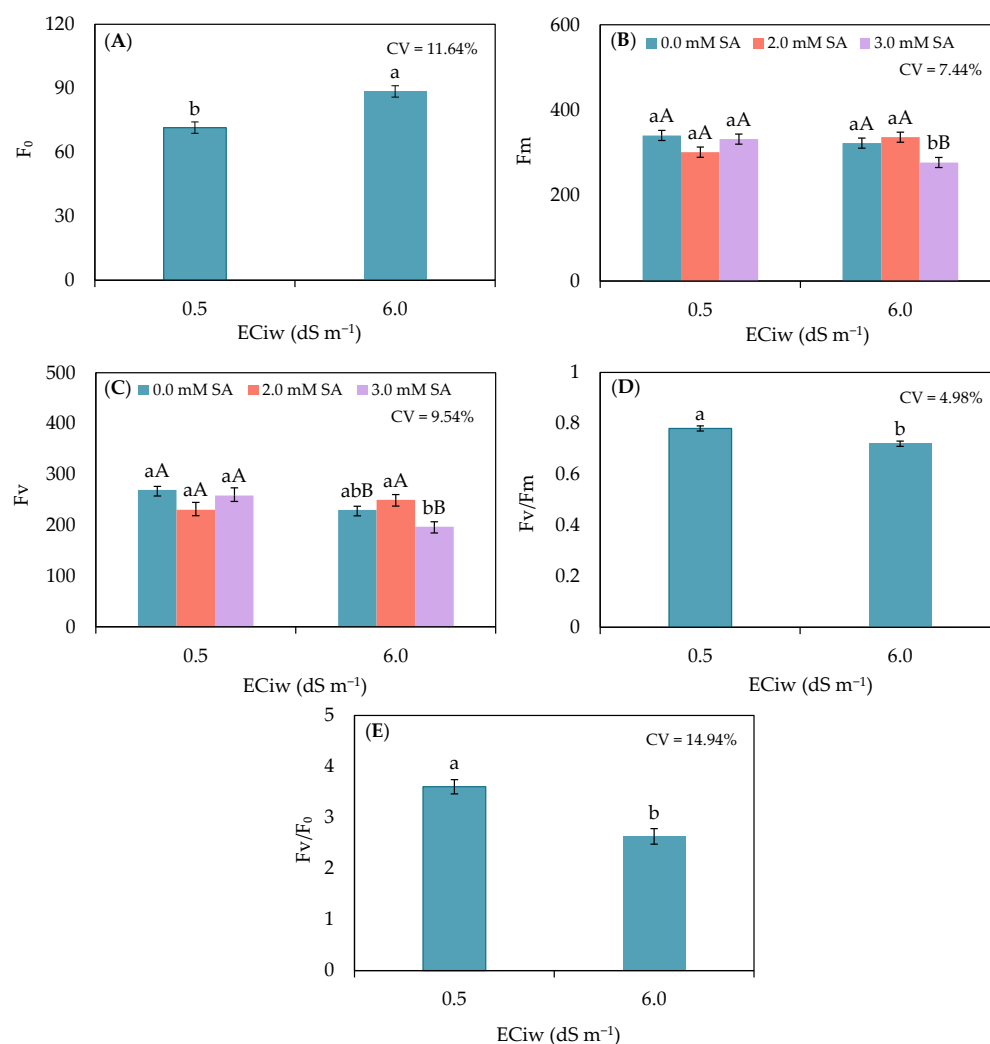


Figure 8. Mean values $\pm$ standard error for minimum fluorescence (F_0) (A), maximum quantum efficiency of PSII ($\text{MQE}_{\text{PSII}} = F_v/F_m$) (D), and potential photochemical efficiency of PSII (F_v/F_0) (E) according to irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m^{-1}), and for maximum fluorescence (F_m) (B) and variable fluorescence (F_v) (C) according to the interaction between irrigation water electrical conductivity (ECiw) (0.5 and 6.0 dS m^{-1}) and salicylic acid (SA) concentrations (0.0 ; 2.0 and 3.0 mM) in *P. echinata* seedlings. For isolated effects, means followed by the same lowercase letter among levels of irrigation water electrical conductivity do not differ from each other (F test, $p \leq 0.05$). For interactions, means followed by the same lowercase letter among SA concentrations at the same electrical conductivity of irrigation water (Tukey test, $p \leq 0.05$) and uppercase letter among levels of irrigation water electrical conductivity at the same SA concentration (F test, $p \leq 0.05$) do not differ from each other. CV = Coefficient of variation.

For maximum chlorophyll a fluorescence, the interaction between irrigation water electrical conductivity and SA concentrations was significant ($F = 7.23$; $p = 0.0063$). Irrigation with water at 6.0 dS m^{-1} reduced maximum chlorophyll a fluorescence only when associated with SA application at the concentration of 3 mM, decreasing from 332.25 under irrigation with 0.5 dS m^{-1} water to 277.50 under irrigation with 6.0 dS m^{-1} water, corresponding to a reduction of 16.48%. Under irrigation with 0.5 dS m^{-1} water, maximum chlorophyll a fluorescence values did not differ from 0, 2 and 3 mM SA concentrations and resulted in mean $\pm$ standard error value of (323.10 ± 7.16) . However, under irrigation with 6.0 dS m^{-1} water, the application of 3 mM SA reduced maximum chlorophyll a fluorescence to 277.50, which was 14.09% and 17.63% lower than, respectively, the values obtained without SA application (323.00) and at 2 mM (336.88), which did not differ from each other (Figure 8B).

For the variable maximum chlorophyll a fluorescence, the interaction between irrigation water electrical conductivity and SA concentrations was significant ($F = 6.72$; $p = 0.0083$). Irrigation with water at 6.0 dS m^{-1} reduced variable maximum chlorophyll a fluorescence when associated with SA at concentrations of 0 and 3 mM, decreasing from 269.47 and 258.68 under irrigation with 0.5 dS m^{-1} water to 230.20 and 196.87 under irrigation with 6.0 dS m^{-1} water, corresponding to reductions of 14.57% and 23.89%, respectively. Under irrigation with 0.5 dS m^{-1} water, values of variable maximum chlorophyll a fluorescence did not differ among SA concentrations and resulted in mean $\pm$ standard error value of (251.59 ± 6.73) . However, under irrigation with 6.0 dS m^{-1} water, variable maximum chlorophyll a fluorescence without SA application (230.20) did not differ from the values under application of 2 mM (249.89) and 3 mM (196.87); however, the value at 3 mM was lower than that obtained at 2 mM by 21.22% (Figure 8C).

Irrigation water electrical conductivity influenced the maximum quantum efficiency of PSII ($\text{MQE}_{\text{PSII}} = F_v/F_m$) ($F = 13.34$; $p = 0.0024$) and the potential photochemical efficiency of PSII ($\text{PPE}_{\text{PSII}} = F_v/F_0$) ($F = 26.38$; $p = 0.0001$). The maximum quantum efficiency of PSII decreased under irrigation with 6.0 dS m^{-1} water, from 0.78 under 0.5 dS m^{-1} to 0.72 under 6.0 dS m^{-1} , corresponding to a reduction of 7.69% (Figure 8D). The potential photochemical efficiency of PSII also decreased under irrigation with 6.0 dS m^{-1} water, from 3.60 under 0.5 dS m^{-1} to 2.63 under 6.0 dS m^{-1} , corresponding to a reduction of 26.94% (Figure 8E).

The multivariate analysis grouped the evaluated morphophysiological variables of *P. echinata* seedlings into three principal components, which explained 83.57% of the total data variance (Table 4).

The first principal component (PC1) explained 38.89% of the total variance and represented the physiological response of *P. echinata* seedlings to saline irrigation, integrating variables related to photosynthetic performance, leaf water status, and root development (Table 4). The variables with the highest contribution ($\text{eigenvector}^2 \times 100$) in this component were potential photochemical efficiency of PSII (F_v/F_0) (10.57%), relative water content (9.85%), maximum quantum efficiency of PSII (F_v/F_m) (8.97%), initial fluorescence (F_0) (8.58%), variable fluorescence (F_v) (8.48%), total chlorophyll index (8.21%), chlorophyll a index (6.65%), root volume (5.96%), and root length (5.57%), associated with seedlings exhibiting higher physiological efficiency, whereas root morphological traits showed an opposite contribution pattern along PC1. In contrast, under saline irrigation, seedlings exhibited lower physiological efficiency, together with an increase in root length and a reduction in root dry mass, indicating a potential adaptive adjustment of plants to salt stress. The direction of the eigenvectors indicates that PC1 describes a physiological gradient in which variables related to photosynthetic efficiency (F_v/F_0 , F_v/F_m , F_v , and chlorophyll indices) and leaf water status are associated with one side of the component, whereas root morphological traits are positioned in the opposite direction. Biologically,

this component indicates that the maintenance of photosynthetic performance under saline conditions is associated with adaptive adjustments in the root system, highlighting the coordination between physiological functioning and root responses to salt stress. Overall, PC1 reflects the balance between photosynthetic performance and adaptive root responses under saline conditions.

Table 4. Eigenvalues and eigenvector matrix of the first three principal components (PC1, PC2, and PC3) from the PCA of morphophysiological variables of *P. echinata* seedlings subjected to different salinity levels and SA concentrations.

	PC1	PC2	PC3
Eigenvalue (λ)	8.556	6.402	3.428
Explained variance (%)	38.89	29.10	15.58
Accumulated variance (%)	38.89	67.99	83.57
Eigenvectors ¹			
Diameter at ground level (DGL)	0.0618	−0.1476	0.1590
Length of the aerial part (LAP)	0.0712	0.0290	0.4140
Number of pinnae (NP)	0.0159	0.3314	−0.1163
Number of leaves (NL)	0.0618	−0.0009	0.3651
Number of leaflets (NLf)	0.0373	0.3365	0.1481
Leaf area (LA)	0.0712	0.0290	0.4140
Root length (RL)	− 0.2360	0.2129	−0.1654
Root volume (RV)	− 0.2442	0.2515	0.0493
Dry matter mass of the aerial part (DMMAP)	−0.0575	0.3636	0.1406
Root dry matter mass (RDMM)	− 0.2142	0.3000	0.0565
Total dry matter mass (TDMM)	−0.1538	0.3452	0.0982
Dickson Quality Index (DQI)	− 0.2075	0.2650	−0.1368
Relative water content (RWC)	0.3138	0.0930	0.0394
Leaf index of chlorophyll a (LICa)	0.2579	−0.0494	− 0.2795
Leaf index of chlorophyll b (LICb)	0.2175	0.2241	−0.1186
Leaf index of chlorophyll a: leaf index of chlorophyll b ratio (LICa/b)	−0.0887	− 0.2895	−0.0725
Leaf total chlorophyll index (LICt)	0.2865	0.1255	−0.2311
Initial fluorescence (F_0)	− 0.2929	−0.0642	−0.2176
Maximum fluorescence (F_m)	0.2298	0.1168	− 0.3153
Variable fluorescence (F_v)	0.2911	0.1202	−0.1967
Maximum quantum efficiency of PSII (F_v/F_m)	0.2995	0.1701	0.1014
Potential photochemical efficiency of PSII (F_v/F_0)	0.3252	0.1104	0.0393

¹ The adopted criterion to detect the representative variables of the components was based on values higher than the modulus of the relation $0.5\lambda - 0.5$, and these variables can be identified by the bold highlighted values in each eigenvector [36]. The percentage contribution of each variable to the component was calculated by $\text{eigenvector}^2 \times 100$.

The second principal component (PC2) accounted for 29.10% of the total variance and represented biomass accumulation and seedling quality, being mainly associated with growth-related traits. The variables with the highest contribution ($\text{eigenvector}^2 \times 100$) in this component were shoot dry mass (13.22%), total dry mass (11.91%), number of leaflets (11.32%), number of pinnae (10.98%), root dry mass (9.00%), and Dickson quality index (7.02%). These results indicate that biomass accumulation was associated with changes in plant allometry and biomass allocation. The loading pattern of PC2 indicates a biological gradient associated with biomass accumulation, in which the positive loadings of shoot dry mass, total dry mass, number of leaflets, number of pinnae, root dry mass, and Dickson quality index reflect coordinated biomass accumulation, structural development, and improved seedling quality. Overall, PC2 reflects biomass accumulation and seedling structural quality under the evaluated treatments.

application was associated with a broader set of adjustments, involving simultaneous changes in physiological parameters and plant resource allocation.

The fourth group (purple color), associated with the treatment 3SA–6.0ECiw, was positioned in relation to growth variables, indicating greater biomass accumulation under high salinity with the application of the highest dose of SA. In contrast, it was positioned in the opposite direction of physiological variables, suggesting a trade-off between growth and photochemical performance and reflecting a distinct resource allocation strategy compared to the other treatments.

4. Discussion

Salt stress affects plant osmotic balance, restricts water uptake, induces cellular toxicity, and intensifies oxidative stress, resulting in limitations to plant growth and physiological functionality [37], as observed in the present study, with a reduction in the number of leaves, leaflets, and leaf area under saline irrigation. Salinity interferes with cell division and expansion, as well as causing osmotic and ionic imbalance, factors that limit the development of leaf structures [37,38]. For seedlings of *Pityrocarpa moniliformis* irrigated with water at an electrical conductivity of 8 dS m^{−1}, [33] reported reductions in leaf number and leaf area [27].

Decrease in leaf formation is a recurrent adaptive adjustment, as it contributes to reducing the transpiratory surface area and, consequently, water loss, favoring the maintenance of plant water status [39]. This process is limited by restricted water uptake due to excess salts in irrigation water [40], as observed in the present study, with a reduction in relative water content in cells from seedlings irrigated with saline water. Shoot dry mass did not differ between the two irrigation water electrical conductivity levels. Thus, although saline irrigation promoted reductions in the number of leaves, leaflets, and leaf area, this decrease did not result in lower biomass accumulation. This result indicates that biomass accumulation was maintained despite reductions in leaf area.

An increase in root length was observed under saline irrigation. Salinity tends to accumulate in the upper soil layers as a consequence of irrigation and evaporation, which can limit water and nutrient uptake by roots in these layers [41]. In this context, increased root length, especially toward deeper soil layers, favors the exploration of less saline soil layers, a strategy that may be beneficial to plants growing in saline conditions [10].

However, even with long roots, *P. echinata* seedlings irrigated with saline water showed lower mass and similar volume compared to those irrigated with non-saline water, indicating the formation of less dense roots and lower biomass per unit volume. This response may indicate an adaptive adjustment of the root system under saline conditions, which may maintain or even increase water and nutrient uptake capacity, even when total root mass is reduced under salt stress [42]. Roots with lower density and greater specific length exhibit higher soil exploration capacity per unit of carbon invested [43].

The reduction in total chlorophyll content under saline irrigation is associated with increased production of reactive oxygen species, which promote degradation of photosynthetic pigments and compromise chloroplast integrity [44]. Under salt stress, the light energy absorbed may exceed the capacity of the photosynthetic apparatus to utilize or safely dissipate it, promoting the accumulation of excitation energy and enhancing the production of reactive oxygen species in chloroplasts [45]. The resulting oxidative pressure promotes photoinhibition, thereby impairing the functionality of photosystem II (PSII). Under these conditions, the maintenance of PSII activity depends on the continuous turnover of the D1 protein, a core component of the PSII reaction center. When the rate of damage exceeds the repair capacity, photodamaged reaction centers accumulate, reducing the stability and functionality of chlorophyll-containing complexes [46]. In addition, oxidative stress

and photoinhibition may induce adjustments in the light-harvesting complex II (LHCII), including its reorganization or reduction, as a photoprotective mechanism to limit excess light absorption. However, this response also decreases the light-harvesting efficiency of the photosynthetic apparatus [47]. Furthermore, salinity may inhibit chlorophyll biosynthesis through alterations in nitrogen metabolism [48] and reduced availability of essential nutrients, such as magnesium, resulting in lower chlorophyll accumulation [49]. Because chlorophyll *b* is predominantly associated with LHCII, structural changes in these complexes may alter the chlorophyll *a/b* ratio and decrease light-harvesting efficiency [50,51]. Consequently, the reduction in total chlorophyll, together with the impairment of photosynthetic processes under salinity, may limit photosynthetic capacity and ultimately plant growth under salt stress [50,52].

Under salt stress conditions, photosystem II (PSII) reaction centers may be damaged or inactivated, compromising energy transfer and electron flow, resulting in greater dissipation of absorbed energy as fluorescence [53]. Reductions in variable fluorescence and in the F_v/F_m ratio indicate decreased electron transport capacity and impairment of PSII photochemical efficiency [54,55]. Likewise, lower F_v/F_0 values indicate greater non-photochemical energy dissipation and/or damage to PSII reaction centers [56,57]. In the present study, the increase in F_0 associated with reductions in F_v , F_v/F_m , and F_v/F_0 under saline irrigation indicates damage or inactivation of PSII reaction centers, resulting in reduced photochemical efficiency.

In the present study, an increase in initial fluorescence (F_0) was observed, associated with a reduction in variable fluorescence (F_v), and F_v/F_m and F_v/F_0 ratios under saline irrigation, indicating damage or inactivation of PSII reaction centers, with a consequent reduction in photochemical efficiency and an increase in non-photochemical energy dissipation.

Regarding the effect of SA, a reduction in leaf area was observed in seedlings irrigated with low-salinity water (0.5 dS m^{-1}). However, for the other variables evaluated, SA concentrations did not promote significant changes under non-saline irrigation conditions. This result reinforces the effect of SA associated with stress attenuation, widely described as an important regulator of plant metabolism, acting mainly in the induction of defense mechanisms and tolerance to abiotic stresses such as salinity [24,58], with positive responses related to growth, water status, gas exchange, PSII efficiency, ionic homeostasis ($\uparrow K^+$, $\downarrow Na^+$), and antioxidant enzyme activity, thereby reducing oxidative damage [59,60]. Considering the role of SA as a defense signaling molecule [24], under non-stress conditions, the activation of defense responses may promote the redirection of resources from growth to protective processes, reflecting the role of SA in modulating the balance between growth and defense [61], which may result in neutral or negative effects on plant development.

Under salt stress conditions, the increase in root volume and root mass observed in *P. echinata* seedlings treated with SA is consistent with previous reports associating this regulator with improved ionic homeostasis. SA has been associated with reduced Na^+ accumulation and the maintenance of adequate K^+ levels in plant tissues, contributing to the preservation of cellular integrity and metabolic activity under salinity. In addition, this hormone may influence plasma membrane proton pump activity, favoring the maintenance of the electrochemical gradient required for selective ion transport, which is essential for root growth in saline environments [24]. These combined effects may enhance root system growth and biomass accumulation, contributing to greater soil exploration and increased tolerance to salt stress. Similar responses have been reported in other plant species; in wheat under saline conditions, for example, SA application, either alone or in combination with other regulators, increased ATP content and H^+ -ATPase activity in roots and reduced Na^+ accumulation [62,63]. Studies have also shown that SA application can promote root

development in different plant species under salt stress conditions, resulting in increased root biomass [64,65].

The application of 2 mM SA reduced the number of leaves. Under saline irrigation, the number of leaflets did not differ between the 2 and 3 mM doses. However, leaf area was reduced at 2 mM, whereas the 3 mM concentration promoted greater leaf expansion. These results indicate that plants treated with 2 mM exhibited smaller leaflets, suggesting a limitation in cell expansion. Overall, these findings demonstrate that the response to SA is concentration- and stress-dependent. The effectiveness of this regulator varies according to the applied dose, potentially promoting distinct effects on plant growth, ranging from inhibition to stimulation, depending on stress intensity and concentration used. The greater leaf expansion observed at the 3.0 mM concentration under saline irrigation may be associated with the ability of SA to promote ionic homeostasis by reducing Na^+ accumulation and maintaining adequate K^+ levels in plant tissues [24]. These mechanisms may contribute to osmotic adjustment, maintenance of cell turgor, and leaf cell expansion, ultimately resulting in greater leaf area [66].

Shoot dry mass was not influenced by salinity or by SA concentrations. This result indicates that aboveground biomass accumulation in *P. echinata* seedlings remained stable under the evaluated conditions, even in the presence of reduced leaf area expansion, alterations in the photosynthetic apparatus, and reduced root dry mass under saline irrigation. In this context, coordinated resource allocation is observed, allowing a balance between growth and defense, with dynamic adjustments in the use of assimilates [67]. Biomass distribution among vegetative organs exhibits high plasticity and is strongly influenced by environmental conditions, potentially resulting in changes in growth and biomass accumulation in leaves and roots as an adaptive strategy [68].

Root dry mass was reduced under saline irrigation. However, the application of SA at concentrations of 2 and 3 mM promoted increases in root and total dry mass, as well as in the Dickson Quality Index, with no significant difference between SA concentrations. The increase in root dry mass and total dry mass promoted by SA under saline irrigation may be associated with its ability to enhance ionic homeostasis by reducing Na^+ accumulation and maintaining adequate K^+ levels in plant tissues, thereby preserving cellular integrity and metabolic activity under saline conditions [24]. This response has been associated with the stimulation of plasma membrane H^+ -ATPase activity, which maintains the electrochemical gradient required for selective ion transport, favoring K^+ uptake while restricting excessive Na^+ accumulation in plant cells [62,63]. The maintenance of ionic balance also contributes to preserving membrane stability and metabolic activity, thereby supporting root growth under saline conditions [24,59,60]. SA has also been associated with improved plant growth, water status, gas exchange, PSII photochemical efficiency, and antioxidant enzyme activity, thereby reducing oxidative damage and promoting biomass accumulation under salt stress [59,60].

The increase in root dry mass and total dry mass promoted by SA was directly reflected in the Dickson Quality Index, as this index integrates morphological traits related to seedling growth and biomass distribution. The Dickson Quality Index is an important indicator of seedling quality and is widely used to identify more vigorous seedlings. This index is associated with higher survival rates and better growth performance after transplanting in several plant species [69]. Values equal to or greater than 0.20 are considered indicative that the seedling meets quality standards [32]. In this context, all treatments showed Dickson Quality Index values above 0.20, including seedlings under saline irrigation without SA application. However, the application of this regulator under saline conditions increased the Dickson Quality Index, indicating improved seedling quality. The maintenance of adequate Dickson Quality Index values, even under saline irrigation, suggests that the

species possesses adaptive mechanisms of stress tolerance, which may be enhanced by SA application.

Irrigation of seedlings with saline water impacted the photosynthetic pigments, with a more pronounced reduction in chlorophyll contents, especially in the absence of regulators, highlighting the negative impact of salt stress on chloroplast integrity and photosynthetic efficiency. This effect is associated with increased production of reactive oxygen species, which accelerate chlorophyll degradation and compromise chloroplast integrity [51,70]. However, SA application at a concentration of 2.0 mM mitigated the deleterious effects of salinity, promoting increases in chlorophyll b and total chlorophyll, as well as a reduction in the chlorophyll a/b ratio, indicating greater efficiency in light capture and adaptation of the photosynthetic apparatus. The relative increase in chlorophyll b under stress is often interpreted as an adaptive mechanism that enhances light absorption and improves photosynthetic performance in response to oxidative stress [70]. Previous studies have reported that SA acts as a signaling molecule that induces antioxidant defense systems, enhancing the activity of enzymes involved in reactive oxygen species detoxification. This response reduces oxidative damage to thylakoid membranes and photosynthetic pigments, thereby contributing to the preservation of chloroplast integrity and photosynthetic function under salt stress [24]. Similar results have been reported for other plant species, in which SA application under salt stress promoted increases in chlorophyll b content and maintenance of photosynthetic pigments [65,71–73].

On the other hand, the 3.0 mM concentration promoted a reduction in chlorophyll a and total chlorophyll contents; however, this response was not accompanied by a decrease in shoot, root, or total dry mass. It also did not compromise growth, as leaf area expansion was observed. This behavior suggests a concentration-dependent morphophysiological adjustment [24], reflecting modulation of the growth–defense balance [61]. Thus, although the 3.0 mM concentration did not promote the same increase in photosynthetic pigments observed at 2.0 mM, there is no evidence of phytotoxic effects, but rather a differential modulation of the physiological response to salt stress.

Given the reduction in chlorophyll indices observed under saline irrigation and with the application of 3 mM SA, a decrease in both variable and maximum chlorophyll a fluorescence was recorded. Reductions in maximum chlorophyll a fluorescence [74] and variable chlorophyll a fluorescence [75] are associated with alterations in the functioning of the photosynthetic apparatus. These reductions indicate damage or inefficiency of PSII in the photosynthetic system [74,75]. These results suggest that the 3 mM concentration promoted functional modulation of the photosynthetic apparatus, without evidence of irreversible structural damage, since plant growth was not compromised.

The 2 mM treatment showed higher photochemical efficiency and greater stability of the photosynthetic apparatus, even with reduced leaf expansion, indicating a better physiological adjustment. In contrast, 3 mM favored greater leaf area expansion, but with reductions in chlorophyll indices and fluorescence parameters. Shoot, root, and total dry mass did not differ among the SA concentrations applied. The results indicate that the 2 mM concentration of SA enabled a better physiological adjustment to salt stress, characterized by higher photochemical efficiency and maintenance of PSII stability, despite the lack of a marked increase in leaf expansion, while still preserving shoot, root, and total dry mass, which did not differ from those obtained under 3 mM SA.

This pattern suggests that the 2 mM concentration of SA promoted a more efficient physiological adjustment to salinity, contributing to the maintenance of electron transport efficiency under stress conditions [24]. On the other hand, the 3 mM concentration induced greater leaf expansion, but this was accompanied by reductions in chlorophyll contents and fluorescence parameters. These results indicate distinct morphophysiological

responses depending on SA concentration. This is consistent with the dose-dependent role of SA in modulating the growth–defense balance [61]. Thus, although both concentrations maintained biomass production, the 2 mM dose demonstrated greater efficiency in the functional adjustment of the photosynthetic apparatus under saline conditions, while the 3 mM concentration promoted greater leaf expansion despite reductions in chlorophyll indices and fluorescence parameters. Overall, irrigation with saline water induced osmotic and ionic stress in *P. echinata* seedlings, resulting in reductions in the number of leaves, chlorophyll content, and PSII efficiency, whereas SA application promoted morphophysiological adjustments that improved seedling performance under saline conditions (Figure 10).

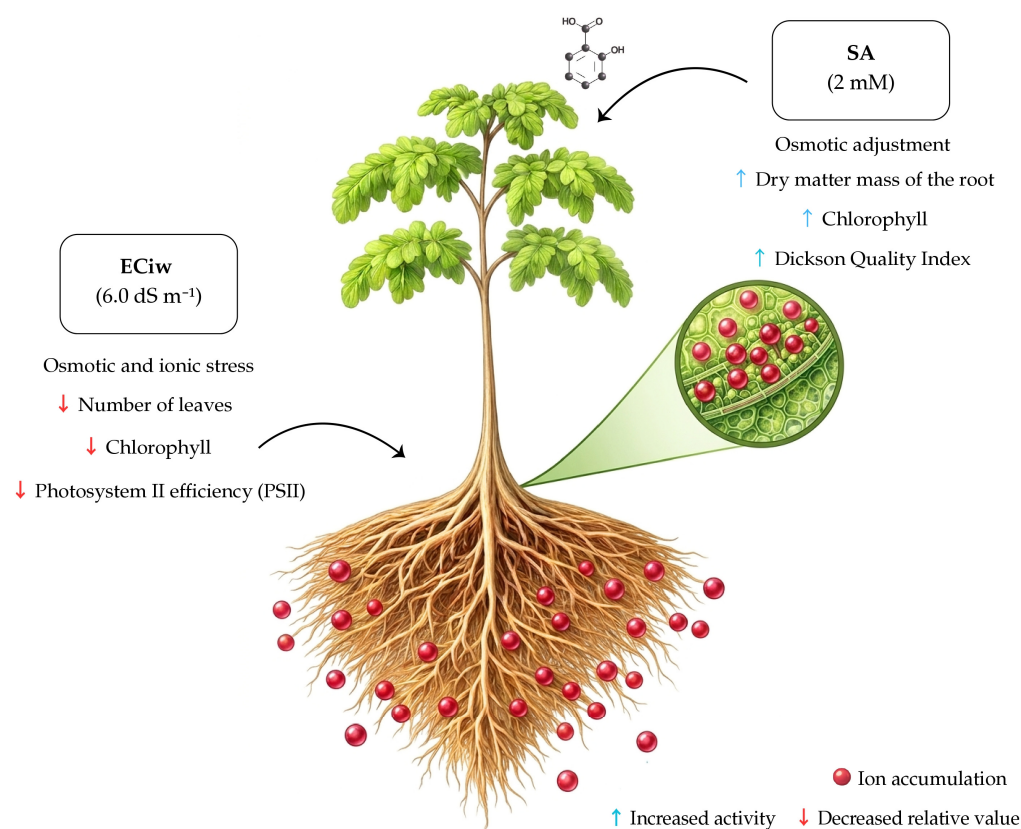


Figure 10. Morphophysiological responses of 669-day-old *P. echinata* seedlings to irrigation with saline water ($\text{ECiw} = 6.0 \text{ dS m}^{-1}$) and application of salicylic acid ($\text{SA} = 2 \text{ mM}$). Arrows indicate increase ($\uparrow$) or decrease ($\downarrow$) in activity or relative values compared to the daily irrigation treatment (control $\text{ECiw} = 0.5 \text{ dS m}^{-1}$).

High electrical conductivity of the irrigation water (6.0 dS m^{-1}) induced osmotic and ionic stress, resulting in reductions in the number of leaves, chlorophyll content, and photosystem II (PSII) efficiency resulting under saline conditions in the root zone. The application of 2 mM SA promoted morphophysiological adjustments associated with increased chlorophyll content, biomass accumulation, and improved Dickson Quality Index.

This study provides the first comprehensive evaluation of the effects of SA on the morphophysiological responses of *P. echinata* seedlings under saline irrigation. Unlike previous studies, which have primarily focused on the responses of this species to water deficit, the present study demonstrates that SA mitigates the effects of salt stress through dose-dependent morphophysiological responses without improving seedling performance under non-saline conditions. Under saline irrigation, the 2 mM concentration promoted greater physiological adjustment, as evidenced by enhanced photochemical stability and maintenance of photosynthetic efficiency, whereas the 3 mM concentration favored leaf

expansion but was associated with lower photosynthetic efficiency. These findings expand the current understanding of the responses of *P. echinata* to salt stress and demonstrate that the effectiveness of SA depends on both stress intensity and the applied concentration.

The present results provide a scientific basis for optimizing salicylic acid use during the production of *P. echinata* seedlings under saline conditions and may support decision-making in restoration programs involving salt-affected areas. However, the effectiveness of salicylic acid is influenced by factors such as stress intensity, plant developmental stage, and environmental conditions, which may alter plant responses. Therefore, further studies under natural environments are needed to evaluate the optimal application frequency and timing, as well as the long-term effects of salicylic acid on the establishment, growth, and survival of this perennial species in salt-affected ecosystems.

5. Conclusions

Irrigation with saline water (6.0 dS m^{-1}) reduces the growth of *Paubrasilia echinata* seedlings and compromises photosystem II, although the maintenance of shoot dry mass indicates the activation of adaptive mechanisms to stress.

Under non-saline conditions, SA application did not improve seedling performance. However, under saline irrigation, the 2 and 3 mM SA concentrations mitigate the deleterious effects of salts and improve seedling quality. Although seedling shoot, root, and total dry masses were similar in the range of 0 to 3 mM SA concentration, the physiological responses differed according to the applied dose. The 2 mM dose provides better physiological adjustment, with greater photochemical stability, whereas the 3 mM dose favors greater leaf expansion, but with lower photosynthetic efficiency. These results demonstrate that SA enhances tolerance to saline irrigation through dose-dependent morphophysiological responses.

The ability to tolerate salt stress, combined with improvements in morphophysiological adjustments promoted by the application of 2 mM SA under saline conditions, indicates that *P. echinata* has potential for establishment in areas subject to salinization, with its tolerance to such environments enhanced by the use of this regulator. These findings support ecological restoration programs, especially in reforestation areas of the Atlantic Forest Biome exposed to adverse water conditions, contributing to the conservation and maintenance of this endangered endemic tree.

Author Contributions: Conceptualization, T.K.F.d.M., F.T.C.B., G.L.F.d.S., M.V.d.S., M.B.F., I.A.B. and R.d.L.A.B.; data curation, T.K.F.d.M., F.T.C.B., I.A.B. and R.d.L.A.B.; formal analysis, T.K.F.d.M., F.T.C.B., G.L.F.d.S., M.V.d.S., M.B.F., I.A.B. and R.d.L.A.B.; funding acquisition, T.K.F.d.M., I.A.B. and R.d.L.A.B.; investigation, T.K.F.d.M., F.T.C.B., G.L.F.d.S., I.A.B. and R.d.L.A.B.; methodology, T.K.F.d.M., F.T.C.B., G.L.F.d.S., M.V.d.S., M.B.F., D.G.d.S., D.R.d.M., I.A.B. and R.d.L.A.B.; project administration, T.K.F.d.M., I.A.B. and R.d.L.A.B.; resources, T.K.F.d.M., F.T.C.B., G.L.F.d.S., M.V.d.S., M.B.F., O.A.B., I.A.B. and R.d.L.A.B.; software, T.K.F.d.M., F.T.C.B., G.L.F.d.S., D.G.d.S., D.R.d.M., R.d.S.A.A., I.E.C., I.A.B. and R.d.L.A.B.; supervision, T.K.F.d.M., F.T.C.B., I.A.B. and R.d.L.A.B.; validation, T.K.F.d.M., F.T.C.B., G.L.F.d.S., R.d.S.A.A., F.E.d.S., I.E.C., A.P.d.A., I.A.B. and R.d.L.A.B.; visualization, T.K.F.d.M., F.T.C.B., G.L.F.d.S., M.V.d.S., M.B.F., D.G.d.S., D.R.d.M., R.d.S.A.A., F.E.d.S., I.E.C., A.P.d.A., O.A.B., I.A.B. and R.d.L.A.B.; writing—original draft, T.K.F.d.M., F.T.C.B., G.L.F.d.S., I.A.B. and R.d.L.A.B.; writing—review and editing, T.K.F.d.M., F.T.C.B., G.L.F.d.S., M.V.d.S., M.B.F., D.G.d.S., D.R.d.M., R.d.S.A.A., F.E.d.S., I.E.C., A.P.d.A., O.A.B., I.A.B. and R.d.L.A.B. All authors have read and agreed to the published version of the manuscript.

Funding: This study was financed in part by the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES)—Finance Code 001.

Data Availability Statement: All data generated and/or analyzed during the present study are available in the manuscript, and the corresponding authors have no objection to making the data and materials available upon reasonable request.

Acknowledgments: The authors would like to thank the Coordination for the Improvement of Higher Education Personnel (CAPES, Brasília, Brazil) for the doctoral scholarship of the first author and the Graduate Program in Agronomy at the Federal University of Paraíba.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

Al ³⁺	Exchangeable Aluminum
ANOVA	Analysis of Variance
C2S1	Class of Salinization/Sodicity Risk
C4S2	Class of Salinization/Sodicity Risk
Ca ²⁺	Calcium Ion
CEC	Cation Exchange Capacity
Cl [−]	Chloride Ion
CO ₃ ^{2−}	Carbonate Ion
CV	Coefficient of Variation
DM	Dry Mass
DGL	Diameter at Ground Level
DMMAP	Dry Matter Mass of the Aerial Part
DQI	Dickson Quality Index
ECiw	Electrical Conductivity of Irrigation Water
ESP	Exchangeable Sodium Percentage
FM	Fresh Mass
F ₀	Minimum Fluorescence
F _m	Maximum Fluorescence
F _v	Variable Fluorescence
F _v /F _m	Maximum Quantum Efficiency of PSII
F _v /F ₀	Potential Photochemical Efficiency of PSII
H ⁺ + Al ³⁺	Potential Acidity
HCO ₃ [−]	Bicarbonate Ion
K ⁺	Potassium Ion
LA	Leaf Area
LAP	Length of the Aerial Part
LICa	Leaf Chlorophyll a Index
LICa/b	Ratio of Chlorophyll a to Chlorophyll b Index
LICb	Leaf Chlorophyll b Index
LICt	Total Leaf Chlorophyll Index
Mg ²⁺	Magnesium Ion
Na ⁺	Sodium Ion
NL	Number of Leaves
NLf	Number of Leaflets
NP	Number of Pines
OM	Organic Matter
P	Phosphorus
PCA	Principal Component Analysis
pH	Hydrogen Ion Concentration
PSII	Photosystem II
RL	Root Length
RWC	Relative Water Content

RV	Root Volume
SA	Salicylic Acid
SAR	Sodium Adsorption Ratio
SB	Sum of Bases
SO ₄ ^{2−}	Sulfate Ion
TDMM	Total Dry Matter Mass
TM	Turgid Mass
V	Base Saturation

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