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ORIGINAL PAPER

# Seedling production of *Physalis peruviana* from osmoprimed seeds under irrigation water salinity

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**Abstract:** Salinity limits seed germination and seedling growth by inducing osmotic and oxidative stress. However, seed osmoconditioning is a strategy aimed at mitigating these adverse effects. *Physalis peruviana* is a crop with high economic value, but management strategies to optimize seedling establishment are still limited. Therefore, this study aimed to evaluate the effect of osmotic conditioning of *P. peruviana* seeds on seedling production under salt stress. The experiment was conducted in a controlled environment at the Federal University of Campina Grande, located at the Center for Food Science and Technology in Pombal, Paraíba, Brazil. A randomized block design was used in a 2 × 4 factorial arrangement: first factor consisted of osmoprimed and non-osmoprimed seeds, and the second factor included four levels of electrical conductivity of irrigation water (ECw – 0.3, 1.2, 2.1, and 3.0 dS $m^{-1}$), with four replicates. The osmoprimed seeds were soaked in a PEG 6000 solution at -0.4 MPa. ECw levels negatively affected the emergence, growth, physiology, biomass, and quality of *P. peruviana* seedlings. Osmopriming the seeds with PEG 6000 solution promoted greater growth compared to non-osmoprimed seeds. While the osmopriming technique did not completely prevent the negative effects of salinity in the irrigation water, it did mitigate the detrimental impact on seedling emergence and leaf expansion in *P. peruviana*.

**Keywords:** Solanaceae, physalis, hydroconditioning, water salinity.

## Introduction

The presence of salts in water is one of the biggest challenges for sustainable agriculture (Arif et al., 2020), as it causes abiotic stress in crops. This problem is particularly evident in arid and semi-arid regions (Minhas et al., 2020), such as the Brazilian Northeast.

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In the semi-arid Northeast of Brazil, the scarcity of surface water makes the use of groundwater an essential alternative for irrigated agriculture (Minhas et al., 2020). However, approximately 160,000 wells in the region contain saline water, with electrical conductivity between 1.0 and 6.0 dS $m^{-1}$, especially in crystalline aquifers (Lessa et al., 2023).

The negative effects of salinity on seed germination occur by creating a lower osmotic potential that reduces water imbibition and/or through specific ion toxicity (Benadjaoud et al., 2022), causing harmful impacts on enzymes, proteins, cellular organelles, and plasma membranes, thereby reducing respiration and photosynthesis rates (Lei et al., 2021). Specifically for *Physalis peruviana* L., increasing the electrical conductivity of irrigation water (0.5 to 5.5 dS $m^{-1}$) negatively affects germination, growth, and gas exchange (Figueiredo et al., 2021).

The variety of uses for *P. peruviana* fruit, both in edible products and other applications, underscores its market value. Recently, the food industry has incorporated *P. peruviana* into a range of innovations, such as juices, dairy products, and jams (Ramadan, 2024). However, techniques that enable the production of high-quality seedlings using saline water are necessary to promote this crop in the semi-arid region of northeastern Brazil.

Polyethylene glycol (PEG) is an osmotic polymer that cannot penetrate seed cells, and due to its chemically inert nature, PEG does not harm seed embryos (Ma et al., 2024). When used in osmopriming, PEG creates a low-water-potential environment, slowing the rate of water absorption by the seeds and preventing visible germination (Bruce et al., 2007).

Seed osmopriming with PEG 6000 accelerates the germination process and enhances plant vigor by promoting enzymatic activation, increasing respiratory rates, and stimulating macromolecule production, allowing successive adaptation when exposed to stress conditions (Mirmazloum et al., 2020). Studies have shown that osmopriming improves seed tolerance to adverse conditions such as salt stress (Guo et al., 2022) and water stress (Silva et al., 2023). In the specific case of *P. peruviana*, Dutra et al. (2022) observed that water restriction caused less growth of shoot seedlings; however, when the seeds were subjected to a potential of -0.2 MPa, an increase in root length was observed. However, research under saline stress conditions during the seedling stage is necessary.

In this context, the present study tests the hypothesis that osmopriming *P. peruviana* seeds with a PEG 6000 solution improves germination and early growth under salt stress conditions, making the seedling vigor for subsequent stages. Thus, the aim was to evaluate the effect of osmotic conditioning of *P. peruviana* seeds on seedling production under salt stress.

## Materials and Methods

### Experimental location

The experiment was conducted in a greenhouse at the Federal University of Campina Grande, located at the Center for Food Science and Technology in Pombal (6° 46’ 58’’ S and 37° 48’ 46’’ W), Paraíba, Brazil. Climate conditions were monitored inside the greenhouse throughout the experimental period using a thermohygrometer model HT-208 (ICEL-Manaus, KMA Brasil Com. de Peças e Equipamentos Ltda., São Paulo, SP, Brazil). The mean temperature during the experiment was 35 ± 5°C, with an mean relative humidity of 40 ± 15%.

### Experimental design

The experimental design used was a randomized block design in a 2 × 4 factorial scheme: first factor consisted of osmoprimed and non-osmoprimed seeds, and the second factor included four levels of electrical conductivity of irrigation water (0.3 dS $m^{-1}$ – tap water, 1.2, 2.1, and 3.0 dS $m^{-1}$), with four replicates of eight plants each. The experiment was conducted in a

(Biochemical Oxygen Demand) BOD incubator, with treatments randomly distributed across all shelves. The experimental unit was a Petri dish with eight seeds.

The osmoprimed seeds were soaked in a PEG 6000 solution at -0.4 MPa at a seed-to-solution ratio of 1:5 (w/v). 50 seeds were placed per Petri dish (9 cm diameter), which was lined with two layers of filter paper moistened with 5 mL of the osmotic solution. After the 48-h priming period, seeds were rinsed with distilled water and dried at room temperature (25°C) until reaching their initial moisture content (standardized at approximately 10%) to ensure physiological stability.

**Development of the experiment**

The seeds of *P. peruviana* were extracted from ripe fruits obtained from a local retail market. Fruits were selected for uniformity in size and color to ensure a consistent seed lot. Prior to the experiment, a preliminary germination test was conducted, showing a germination rate higher than 90%, confirming the high physiological quality and vigor of the seed lot used.

Seeds of *P. peruviana* were osmoprimed in Petri dishes (14.6 cm in diameter and 2.1 cm in height) containing enough PEG 6000 solution to cover up to half the height of the seeds, leaving part of the surface exposed. The solution was adjusted to an osmotic potential of -0.4 MPa (Burlyn and Kaufman, 1973; Villela et al., 1991) and incubated in BOD (Biochemical Oxygen Demand incubator) chambers regulated at 25°C with a 12-h photoperiod. After 12 h of incubation, the seeds were washed under running water and dried on a bench in ambient conditions (25°C temperature and 60% relative humidity) for 30 min to remove surface moisture.

Three seeds of *P. peruviana* were sown at a depth of 0.5 cm in polyethylene bags (0.4-L capacity) containing a substrate composed of soil, sand, carbonized rice husk, and goat manure in a ratio of 1:1:1:2 (v/v/v/v). The chemical and physical analysis of the substrate is presented in Table 1. These analyses were conducted at the Soil Laboratory of the Federal University of Paraíba, Areia, Paraíba, Brazil.

Table 1. Chemical and physical analysis of the substrate used for the production of *Physalis peruviana* seedlings.

| pH ($H_2O$) | Sand | Silt | Clay | P | $K^+$ | $Na^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Al^{3+}$ | $H^+ + Al^{3+}$ | O.M. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| (1:2.5) | ---------($g\ kg^{-1}$)--------- | | | ($mg\ dm^{-3}$) | | -------------------($cmol_c\ dm^{-3}$)--------------- | | | | | ($g\ kg^{-1}$) |
| 6.6 | 881.0 | 153.0 | 38.0 | 389.9 | 198.8 | 0.39 | 4.05 | 2.13 | 0.00 | 0.00 | 21.36 |

pH – hydrogen potential; O.M. – organic matter; P, $K^+$, and $Na^+$ – phosphorus, potassium, and sodium extracted with Mehlich-1 solution; $Ca^{2+}$ and $Mg^{2+}$ – calcium and magnesium extracted with 1 M KCl solution; $Al^{3+}$ – aluminum extracted with 1 M KCl solution; $H^+ + Al^{3+}$ – potential acidity, extracted using the 0.5 mol $L^{-1}$ calcium acetate method buffered at pH 7.0.

Fifteen days after emergence, thinning was performed, leaving only the most vigorous seedling with three fully developed leaves.

A stock solution was prepared by adding sodium chloride (NaCl), dihydrate calcium chloride ($CaCl_2{\cdot}2H_2O$), and hexahydrate magnesium chloride ($MgCl_2{\cdot}6H_2O$) in a 7:2:1 (w/w/w) ratio (Medeiros, 1992) to irrigation water (Table 2). The electrical conductivity (EC) of the stock solution was 50 dS $m^{-1}$, following the relationship between EC and salt concentration (mg $L^{-1}$ = 640 × EC × 10), considering that the electrical conductivity of the irrigation water was 0.3 dS $m^{-1}$ (Rhoades et al., 2000). The saline solutions were stored in plastic containers (20-L capacity) and properly protected to prevent evaporation, rainwater entry, and contamination by solids.

Irrigation was carried out with the volume corresponding to that obtained from the water balance, determined according to Equation 1.

$$\mathrm{VI} = \frac{(\mathrm{Vw} - \mathrm{Vd})}{(1 - \mathrm{LF})} \quad (1)$$

Where: VI – volume of water applied in each irrigation, mL; Vw – volume of water applied in the previous irrigation, mL; Vd – volume drained in the previous irrigation, mL; LF – leaching fraction, decimal. An LF of 0.10 was adopted.

The EC of the drainage and substrate were monitored weekly.

Table 2. Chemical analysis of the supply water used in preparing saline solutions for irrigation.

| EC | pH | $K^+$ | $Ca^{2+}$ | $Mg^{2+}$ | $Na^+$ | $SO_4^{2-}$ | $CO_3^{2-}$ | $HCO_3^-$ | $Cl^-$ | SAR |
|---|---|---|---|---|---|---|---|---|---|---|
| (dS $m^{-1}$) | | --------------------------------(mmol$_c$ $L^{-1}$)----------------------------- | | | | | | | | (mmol $L^{-1}$)$^{0.5}$ |
| 0.3 | 7.0 | 0.3 | 0.2 | 0.6 | 1.4 | 0.2 | 0.0 | 0.8 | 1.3 | 2.21 |

EC – electrical conductivity of the irrigation water; pH – hydrogen potential; $K^+$ – potassium; $Ca^{2+}$ – calcium; $Mg^{2+}$ – magnesium; $Na^+$ – sodium; $SO_4^{2-}$ – sulfate; $CO_3^{2-}$ – carbonate; $HCO_3^-$ – bicarbonate; $Cl^-$ – chloride; SAR – sodium adsorption ratio {$SAR = Na^+/[(Ca^{2+} + Mg^{2+})/2]^{0.5}$}.

**Variables analyzed**

The emergence percentage (E, %) and emergence speed index (ESI) were evaluated through daily counts until stabilization. Emergence percentage was determined by the final count of emerged seedlings relative to the initial number of sown seeds, considering as emerged those seedlings with the potential to continue developing into normal plants. ESI was calculated through daily counts of emerged seedlings until complete stabilization, according to the Equation 2 proposed by Maguire (1962).

$$\mathrm{ESI} = \frac{G1}{D1} + \frac{G2}{D2} + \frac{G3}{D3} \ldots + \frac{Gn}{Dn} \quad (2)$$

Where: G1, G2, G3 … Gn – number of seedlings germinated in each count; D1, D2, D3 … Dn – number of days from sowing to the 1st, 2nd, 3rd ... nth count.

At 55 days after sowing (DAS), biometric, physiological, biomass, and seedling quality analyses were conducted. Three plants from each plot were evaluated, always excluding the border plants.

Plant height (PH, cm): measured from the soil to the apex using a ruler.

Number of leaves per plant: determined by simple manual counting.

Stem diameter (SD, mm): measured at the base of the plants using a digital caliper.

Leaf length (L, cm) and width (W, cm): were determined by measuring all marked leaves on each plant using a ruler. The L was defined as the distance from the point of petiole insertion on the leaf blade to the opposite end of the leaf, while the W was defined as the largest dimension perpendicular to the length axis. Based on the measurements of L and W, leaf area (LA, $cm^2$ per plant) was calculated using Equation 3 proposed by Reis et al. (2013).

$$\mathrm{LA} = \mathrm{L} \times \mathrm{W} \times \mathrm{f} \quad (3)$$

Where: f – form factor, dimensionless (the value 0.59 was used).

Root volume (RV, $cm^3$): measured by placing the roots in a graduated 1000 mL cylinder containing a known volume of water. The difference in water level provided a direct measurement of root volume, based on the equivalence of units (1 mL = 1 $cm^3$), according to Basso (1999).

Chlorophyll and carotenoid content: eight leaf discs were collected from the middle third of a leaf from each plot. The discs were ground in the dark with 10 mL of 80% acetone and $CaCO_3$. The solution was filtered and diluted with 80% acetone to a final volume of 25 mL. Then, the contents of chlorophyll a, chlorophyll b, and carotenoids were determined using a SP-1105 visible spectrophotometer (Bel Photonics, Piracicaba, SP, Brazil) at wavelengths of 663, 646, and 470 nm, respectively. Subsequently, calculations were performed according to Lichtenthaler (1987), and results were expressed in g $m^{-2}$.

Total chlorophyll was calculated as the sum of chlorophyll a and chlorophyll b.

Relative water content (RWC, %): leaf discs were collected from one plant per plot. The discs were immediately weighed on a semi-analytical balance to obtain fresh mass (FM, g), then incubated in deionized distilled water for 10 h. After this period, the leaf discs were removed, gently blotted dry to remove excess surface water, and weighed to obtain turgid mass (TM, g). The discs were then dried in an oven at 65°C for 48 h, and the dry mass (DM, g) was determined. RWC was calculated according to Equation 4 by Irigoyen et al. (1992).

$$\text{RWC (\%)} = \frac{(\text{FM} - \text{DM})}{(\text{TM} - \text{DM})} \times 100 \qquad (4)$$

Membrane integrity: was evaluated by electrolyte leakage (EL, %) according to Equation 5 (Lutts et al., 1996). Ten leaf discs (each 10 mm in diameter) were collected from the leaves of one plant per plot and placed in a beaker containing 40 mL of distilled water. The samples were then left to rest at 25ºC for 4 h. After the 4 h incubation period, the initial electrical conductivity of the solution was measured (EC1). The beakers containing the discs were then sealed with aluminum foil and placed in an oven at 90°C for 2 h. After cooling, the final electrical conductivity was measured (EC2). The values of EC1 and EC2 were measured using a benchtop conductivity meter model AK51 (Akso®, São Leopoldo, RS, Brazil).

$$\text{EL (\%)} = \frac{\text{EC1}}{\text{EC2}} \times 100 \qquad (5)$$

Dry mass determination: three *Physalis peruviana* seedlings per plot were collected and separated into shoots and roots. The plant parts were placed in kraft paper bags and dried in a forced-air circulation oven at 65ºC until constant weight (approximately 72 h). Subsequently, shoot dry mass (SDM, g) and root dry mass (RDM, g) were determined. Total dry mass (TDM, g) was obtained by summing SDM and RDM. All dry mass measurements were obtained using a digital balance.

Quality of *Physalis peruviana* seedlings: was evaluated using the Dickson quality index (DQI) (Dickson et al., 1960), calculated according to Equation 6.

$$\text{DQI} = \frac{\text{TDM}}{\frac{\text{PH}}{\text{SD}} + \frac{\text{SDM}}{\text{RDM}}} \qquad (6)$$

## Statistical analysis

The data were first subjected to the Shapiro-Wilk test for normality ($p \leq 0.05$), followed by analysis of variance using the F-test ($p \leq 0.05$). When significant effects were detected, polynomial regression analysis (linear and quadratic models) was performed for the levels of irrigation water electrical conductivity. For the factor of seed osmotic conditioning, means were separated using Tukey's test ($p \leq 0.05$). All statistical analyses were performed with the SISVAR 5.6 statistical program (Ferreira, 2019).

## Results and Discussion

According to the summary of the analysis of variance (Table 3), there was a significant interactive effect ($p \leq 0.01$) between the studied factors (osmotic conditioning and levels of irrigation water electrical conductivity – ECw) only for the emergence speed index and leaf area, indicating that both factors simultaneously influence these variables. The other variables were significant only when the factors were considered in isolation, except for the Dickson quality index, which was significant only for ECw. The osmotic conditioning of *P. peruviana* seeds resulted in a higher percentage of plant emergence compared to non-osmotically conditioned seeds, indicating an increase in the emergence percentage of 16.7% with osmotic conditioning (Figure 1A).

During osmotic conditioning, the seeds are partially hydrated, activating essential metabolic processes for germination, such as protein synthesis and enzyme activation (Tian et al., 2023). This treatment also facilitates the repair of cellular damage accumulated during storage and enhances the seeds' ability to absorb water (Nile et al., 2022). As a result, conditioned seeds are better prepared to germinate quickly and uniformly when sown, leading to a higher plant emergence rate.

Table 3. Summary of the analysis of variance for emergence percentage (E), emergence speed index (ESI), plant height (PH), number of leaves (NL), stem diameter (SD), leaf area (LA), root volume (RV), shoot dry mass (SDM), root dry mass (RDM), total dry mass (TDM), and Dickson quality index (DQI) of *Physalis peruviana* seedlings subjected to seed osmotic priming (osmopriming) and cultivated under different levels of electrical conductivity of irrigation water (ECw), at 55 days after sowing.

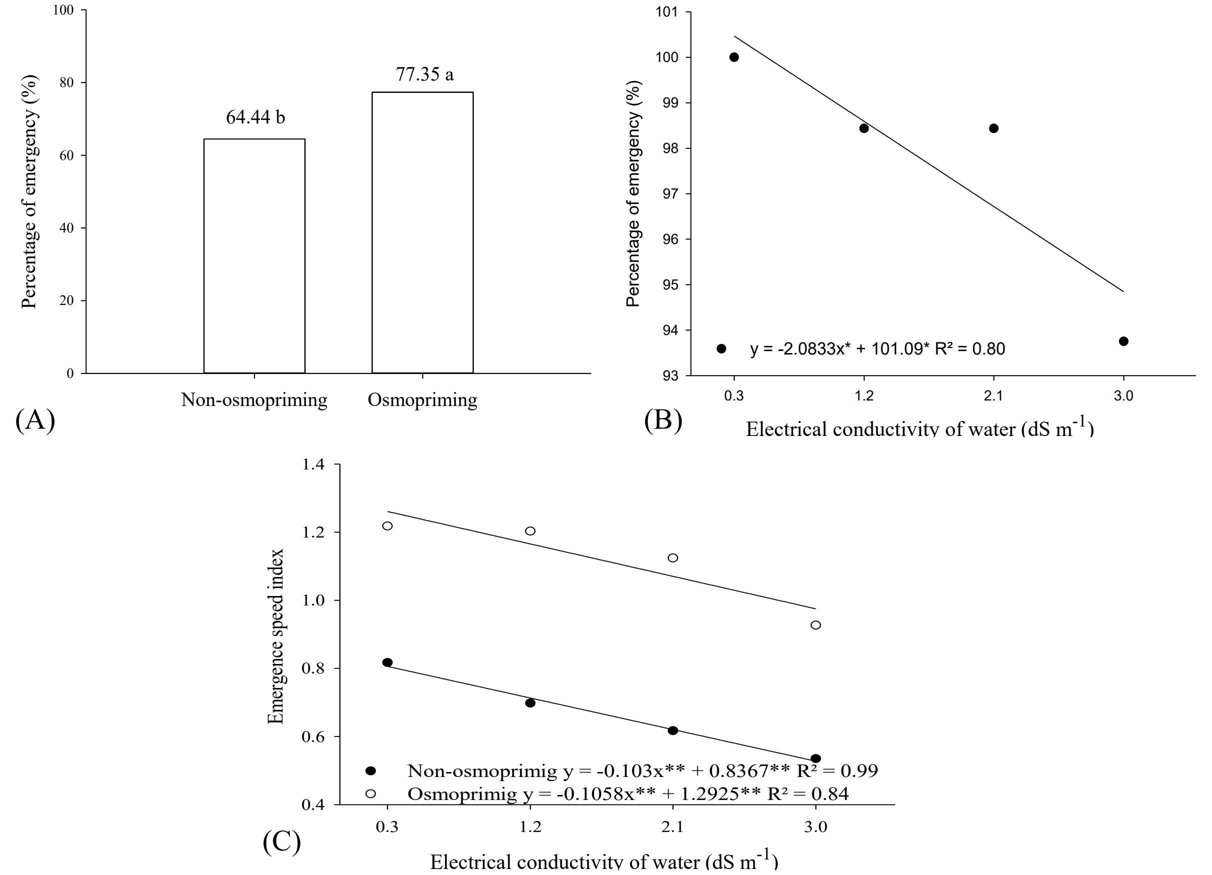
| Source of variation | DF | Mean squares | | | | | |
|---|---|---|---|---|---|---|---|
| | | E (%) | ESI | PH (cm) | NL | SD (mm) | LA ($cm^2$) |
| Osmopriming | 1 | 1323.98** | 1.62** | 48.84** | 7.39** | 0.63* | 3090.02** |
| ECw | 3 | 2452.62** | 0.12** | 106.95** | 15.98** | 2.97** | 20754.2** |
| Osmopriming × ECw | 3 | $65.27^{ns}$ | 0.008** | $1.426^{ns}$ | $0.15^{ns}$ | $0.03^{ns}$ | 357.82** |
| Block | 3 | $33.51^{ns}$ | $0.0003^{ns}$ | 17.02* | 1.89** | 2.14** | 333.38** |
| Error | 21 | 31.25 | 0.0007 | 0.62 | 0.24 | 0.10 | 60.11 |
| CV | | 7.88 | 13.07 | 6.51 | 6.73 | 8.17 | 15.94 |
| Mean | | 70.92 | 0.892 | 12.16 | 7.37 | 3.97 | 130.60 |
| | | RV ($cm^3$) | SDM (g) | RDM (g) | TDM (g) | DQI | |
| Osmopriming | 1 | 18.75* | 0.16** | 0.12** | 0.58** | $0.007^{ns}$ | |
| ECw | 3 | 179.97** | 0.83** | 0.93** | 3.53** | 0.13** | |
| Osmopriming × ECw | 3 | $2.35^{ns}$ | $0.02^{ns}$ | $0.002^{ns}$ | $0.01^{ns}$ | $0.001^{ns}$ | |
| Block | 3 | 13.69* | 0.05* | $0.01^{ns}$ | 0.07* | 0.008* | |
| Error | 21 | 2.92 | 0.01 | 0.007 | 0.02 | 0.001 | |
| CV | | 17.88 | 13.65 | 12.42 | 10.18 | 12.70 | |
| Mean | | 9.56 | 0.76 | 0.711 | 1.47 | 0.34 | |

DF – degree of freedom; CV – coefficient of variation; ns, * and ** – not significant, significant at $p < 0.05$ and significant at $p < 0.01$, respectively, by F-test.

Regarding seed emergence as a function of ECw, it was observed that the average values declined as ECw increased, resulting in a reduction in the emergence rate from 100 to 94.8% (a decline of 5.16%) between ECw levels of 0.3 and 3.0 dS $m^{-1}$ (Figure 1B). These results can be attributed to the decrease in water potential, which limits water absorption by the seeds, and to ionic toxicity, both of which inhibit germination and subsequent plant emergence when irrigated with saline solutions (Benadjaoud et al., 2022).

Similarly, in the ESI (Figure 1C), declines were observed for both osmotic conditioned and non-osmotic conditioned seeds as ECw increased. However, the osmotic conditioned seeds exhibited greater vigor compared to the non-osmotic conditioned seeds, with reductions of 22.61 and 34.76%, respectively, between the lowest and highest ECw levels evaluated. The vigor of seeds can be affected under saline conditions because such conditions induce oxidative stress, generating reactive oxygen species (ROS) that damage lipids, leading to lipid peroxidation of cell membranes, proteins, causing enzymatic deactivation and structural dysfunction, and nucleic acids, resulting in mutations and DNA breaks (Hasanuzzaman et al., 2021).

However, when osmotic conditioning is applied, the seeds can achieve a specific physiological state that allows for the control of the rate and amount of water absorption before initiating the germination process (Muhammad et al., 2023). This, in turn, ensures faster and more uniform germination, reduces imbibition time, intensifies the activation of pre-germinative enzymes, aids in the recovery of cell membranes, increases the production of metabolites, repairs DNA damage, and regulates osmosis (Marthandan et al., 2020; Tian et al., 2023).

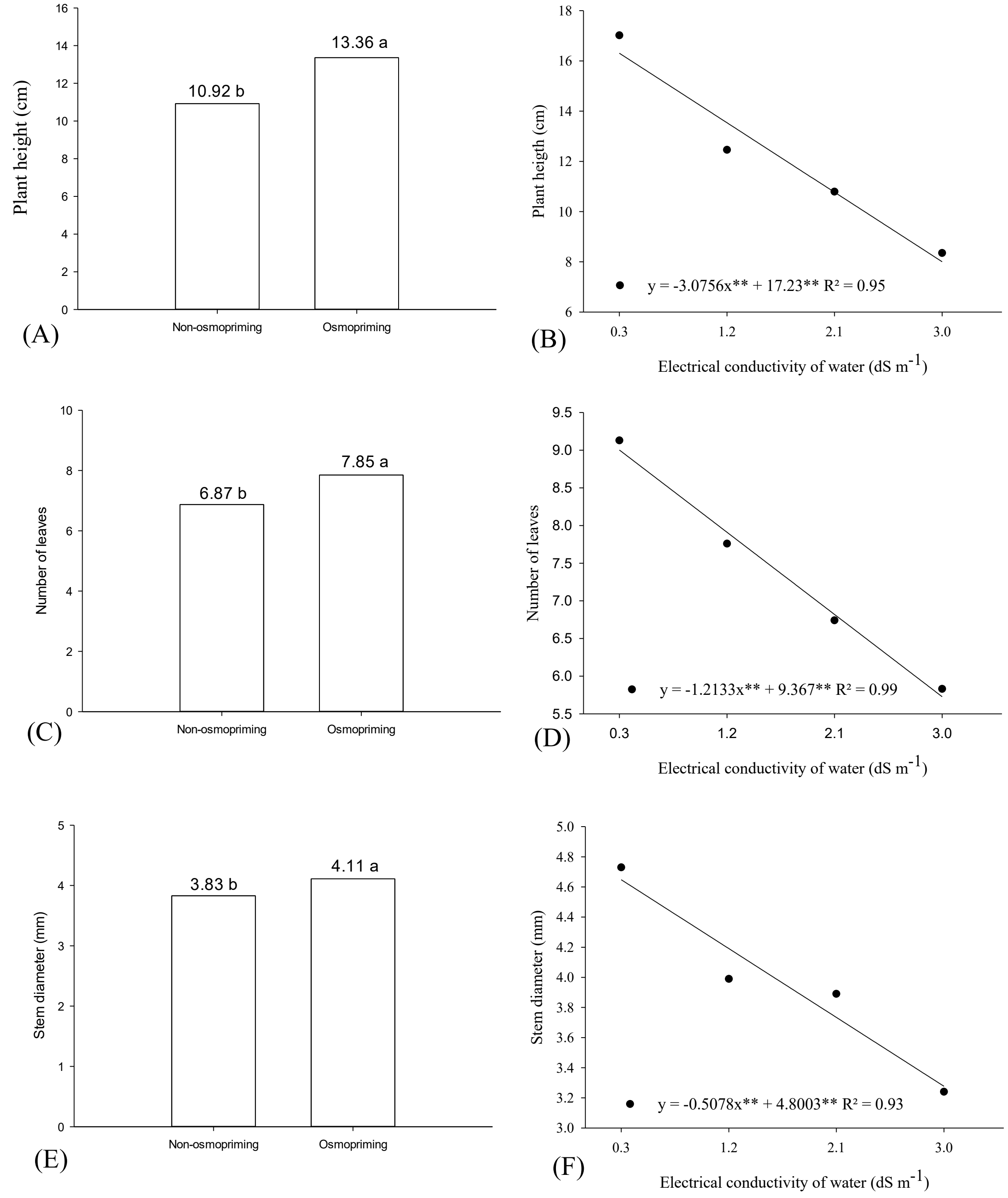


In Figure A, means followed by the same letter are not significantly different according to Tukey's test ($p \leq 0.05$); * and ** – significant at $p < 0.05$ and significant at $p < 0.01$, respectively, by F-test.

Figure 1. Isolated effects of seed osmotic priming (osmopriming) (A) and electrical conductivity levels of the irrigation water (B) on emergence percentage, and the interactive effect of both factors on emergence speed index (C) of *Physalis peruviana* seedlings.

Osmotically conditioned seeds resulted in seedlings with greater height compared to those that were not subjected to osmotic conditioning, showing an increase of 21.77% (Figure 2A). The enhanced growth of *P. peruviana* from osmotically conditioned seeds was attributed to the reduction in the time to emergence, which increased germinability, uniformity, and seedling vigor, thereby promoting vegetative development compared to non-osmotically conditioned seedlings. This occurs because the process hydrates the seeds to the extent that it intensifies biochemical processes, such as enzymatic activation and respiratory rate, stimulating germination and accelerating plant emergence and, consequently, its development (Wang et al., 2024).

The height of *P. peruviana* seedlings was significantly impacted by the increase in ECw, resulting in a reduction from 16.3 to 8.0 cm, which represents a decrease of 50.9% between ECw levels of 0.3 and 3.0 dS $m^{-1}$ (Figure 2B). This effect can be attributed to the rising ECw, which restricts the absorption of essential water and nutrients, thereby hindering cellular and metabolic growth. Furthermore, the resulting oxidative stress damages cell membranes and biomolecules, compromising plant development (Giannelli et al., 2023).



In Figures A, C, and E, means followed by the same letter are not significantly different according to Tukey's test ($p \leq 0.05$); ** – significant at $p < 0.01$ by F-test.

Figure 2. Isolated effects of seed osmotic priming (osmopriming) and electrical conductivity levels of the irrigation water on plant height (A and B, respectively), number of leaves (C and D, respectively), and stem diameter (E and F, respectively) of *Physalis peruviana* seedlings.

Osmoconditioning of the seeds resulted in a greater number of leaves (12.48%) in *P. peruviana* seedlings compared to those that were not osmoconditioned (Figure 2C).

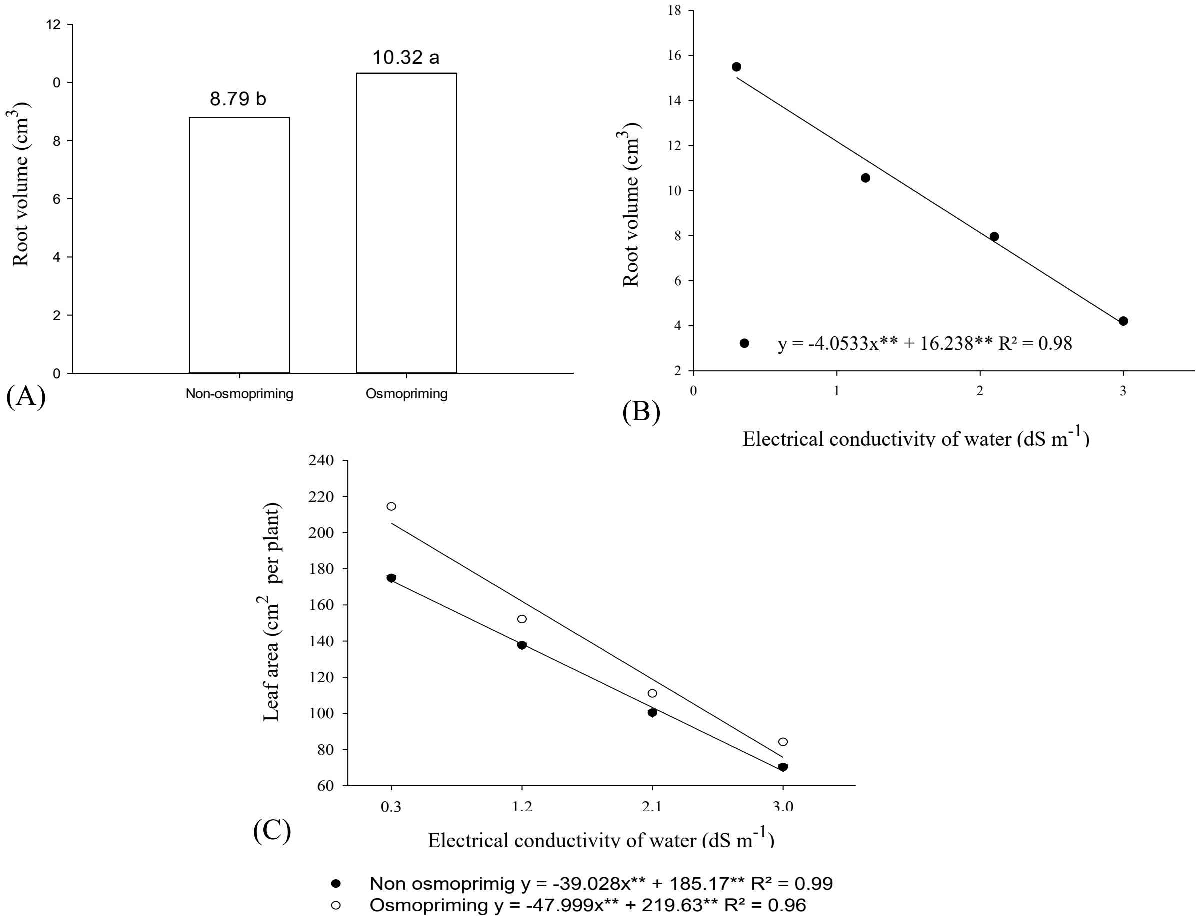
This pre-germinative treatment enhances water and nutrient absorption, activates and boosts metabolic and enzymatic processes (such as catalase, peroxidase, and superoxide dismutase) (Xia et al., 2016), and regulates osmotic substances like soluble sugars and proline (Salemi et al., 2019). These factors increase tolerance and promote more vigorous early growth, resulting in plants with a higher leaf count.

The number of leaves in *P. peruviana* decreased linearly from 9.0 to 5.8 as the ECw increased from 0.3 to 3.0 dS $m^{-1}$, representing a reduction of 35.5% (Figure 2D). When plants are subjected to saline stress, they close their stomata, the structures in the leaves responsible for gas exchange, which reduces transpiration rates and $CO_2$ uptake, consequently diminishing photosynthetic activity and carbon assimilation (Ahmed et al., 2024). This process results in lower energy and biomass production, negatively impacting leaf growth, as demonstrated by Sousa et al. (2024) in eggplant seedlings under saline conditions, which showed a decrease from 6.02 leaves (0.5 dS $m^{-1}$) to 3.14 leaves (4.5 dS $m^{-1}$).

Similar to height and leaf number, the stem diameter of the seedlings exhibited a comparable pattern. When the seeds underwent osmoconditioning, the diameter was statistically greater, showing an increase of 6.81% compared to the non-osmoconditioned seeds (Figure 2E). With the increase in ECw, there was a reduction of 29.52% in the stem diameter of *P. peruviana* seedlings, decreasing from 4.64 to 3.27 mm between ECw values of 0.3 and 3.0 dS $m^{-1}$ (Figure 2F). This effect is attributed to salt-induced damage, primarily resulting from hyperosmotic stress and ionic imbalance. The excessive accumulation of sodium ($Na^+$) and chloride ($Cl^-$) ions, along with the concomitant reduction of potassium ($K^+$) and calcium ($Ca^{2+}$), adversely affects plant development (Nikolić et al., 2023).

The root volume of seedlings from osmoconditioned seeds was greater than that of seedlings from non-osmoconditioned seeds (Figure 3A). This is because osmoconditioning accelerated germination and promoted more vigorous seedlings, positively influencing root volume (Ma et al., 2024). Conversely, when the seedlings were subjected to saline conditions, a decline in root volume was observed, decreasing from 15.02 $cm^3$ (0.3 dS $m^{-1}$) to 4.07 $cm^3$ (3.0 dS $m^{-1}$) (Figure 3B). This decline occurs because, as a strategy to acclimatize to salt stress, the plant redirects its energy to maintain restricted activities, limiting growth to avoid chlorophyll synthesis and minimize the production of reactive oxygen species (Liu et al., 2020).

The leaf area of *P. peruviana* seedlings demonstrated a marked decline with increasing ECw from 0.3 to 3.0 dS $m^{-1}$, decreasing from 173.46 and 205.23 $cm^2$ per plant to 68.08 and 75.63 $cm^2$ per plant. This represents reductions of 60.75 and 63.14% for seedlings derived from non-osmoconditioned and osmoconditioned seeds, respectively (Figure 3C). Under salt stress conditions, plant photosynthesis is adversely affected due to the excessive accumulation of reactive oxygen species (ROS). These ROS can interact with essential cellular components, resulting in oxidative damage characterized by lipid peroxidation, enzyme inactivation, protein oxidation, and the dysregulation of hormones and nutrients (Hasanuzzaman et al., 2021), ultimately leading to a reduction in leaf area (Megersa, 2022). Conversely, the osmoconditioning of seeds mitigated this decrease in leaf area by promoting osmotic regulation and enhancing the seedlings' antioxidant capacity, thereby facilitating their growth and alleviating the adverse effects of stress (Ma et al., 2024).

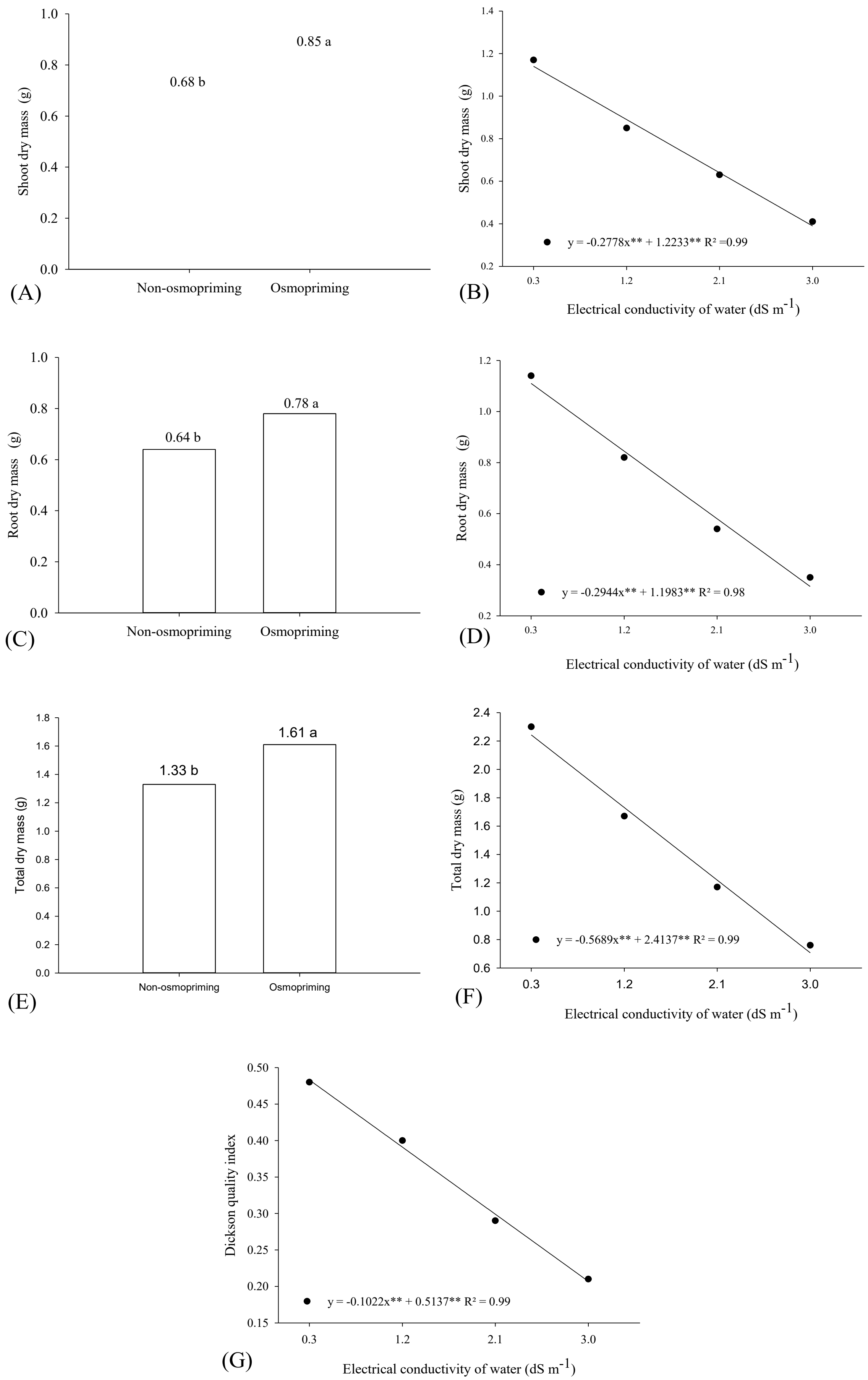


In Figure A, means followed by the same letter are not significantly different according to Tukey's test ($p \leq 0.05$); ** – significant at $p < 0.01$ by F-test.

Figure 3. Isolated effects of seed osmotic priming (osmopriming) (A) and electrical conductivity levels of the irrigation water (B) on root volume, and the interactive effect of both factors on leaf area (C) of *Physalis peruviana* seedlings.

The accumulation of shoot dry mass (Figure 4A), root dry mass (Figure 4C), and total dry mass (Figure 4E) was higher in seedlings subjected to osmoconditioning treatment. This increased dry mass accumulation in seedlings derived from osmoconditioning with PEG 6000 is attributed to the enhanced synthesis of macromolecules, such as nucleic acids and proteins, compared to non-osmoconditioned seeds (Mirmazloum et al., 2020).

Regarding the dry mass accumulation of seedlings under saline conditions, declines of 65.7, 72.6, and 68.5% were observed for shoot dry mass (Figure 4B), root dry mass (Figure 4D), and total dry mass (Figure 4F), respectively, when comparing the lowest and highest levels of ECw. Generally, the reduction in dry mass accumulation under saline conditions occurs because salt stress induces water imbalance and ionic toxicity, leading to growth cessation and impacting various physiological processes, which ultimately results in reduced dry mass accumulation (Hajihashemi et al., 2021).


Shoot dry mass (g)
1.0
0.8
0.6
0.4
0.2
0.0
0.68 b
0.85 a
Non-osmopriming
Osmopriming
(A)
Shoot dry mass (g)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
y = -0.2778x** + 1.2233** R² =0.99
0.3
1.2
2.1
3.0
(B)
Electrical conductivity of water (dS m-1)
Root dry mass (g)
0.64 b
0.78 a
Non-osmopriming
Osmopriming
(C)
Root dry mass (g)
y = -0.2944x** + 1.1983** R² = 0.98
(D)
Electrical conductivity of water (dS m-1)
Total dry mass (g)
1.33 b
1.61 a
Non-osmopriming
Osmopriming
(E)
Total dry mass (g)
y = -0.5689x** + 2.4137** R² = 0.99
(F)
Electrical conductivity of water (dS m-1)
Dickson quality index
0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
y = -0.1022x** + 0.5137** R² = 0.99
(G)
Electrical conductivity of water (dS m-1)

In Figures A, C, and E, means followed by the same letter are not significantly different according to Tukey's test ($p \leq 0.05$); ** – significant at $p < 0.01$ by F-test.

Figure 4. Isolated effects of seed osmotic priming (osmopriming) and electrical conductivity levels of the irrigation water (ECw) on shoot dry mass (A and B, respectively), root dry mass (C and D, respectively), total dry mass (E and F, respectively), and the effect of ECw on Dickson quality index (G) of *Physalis peruviana* seedlings.

The DQI of *P. peruviana* seedlings decreased by 57.1% between ECw of 0.3 and 3.0 dS m$^{-1}$, reaching a minimum quality value of 0.20 at the highest conductivity (Figure 4G). This index reflects seedling quality, indicating a certain resistance to saline conditions. However, the reduction in quality index is associated with the osmotic effects caused by $Na^+$ and $Cl^-$ ions, which, at high concentrations, disrupt the water balance in apoplastic and symplastic pathways (Bonacina et al., 2022). This disruption negatively impacts the absorption of water and nutrients, resulting in lower-quality seedlings.

The membrane integrity, relative water content, and photosynthetic pigments were not affected by osmotic conditioning. However, these variables were influenced by ECw levels (Table 4).

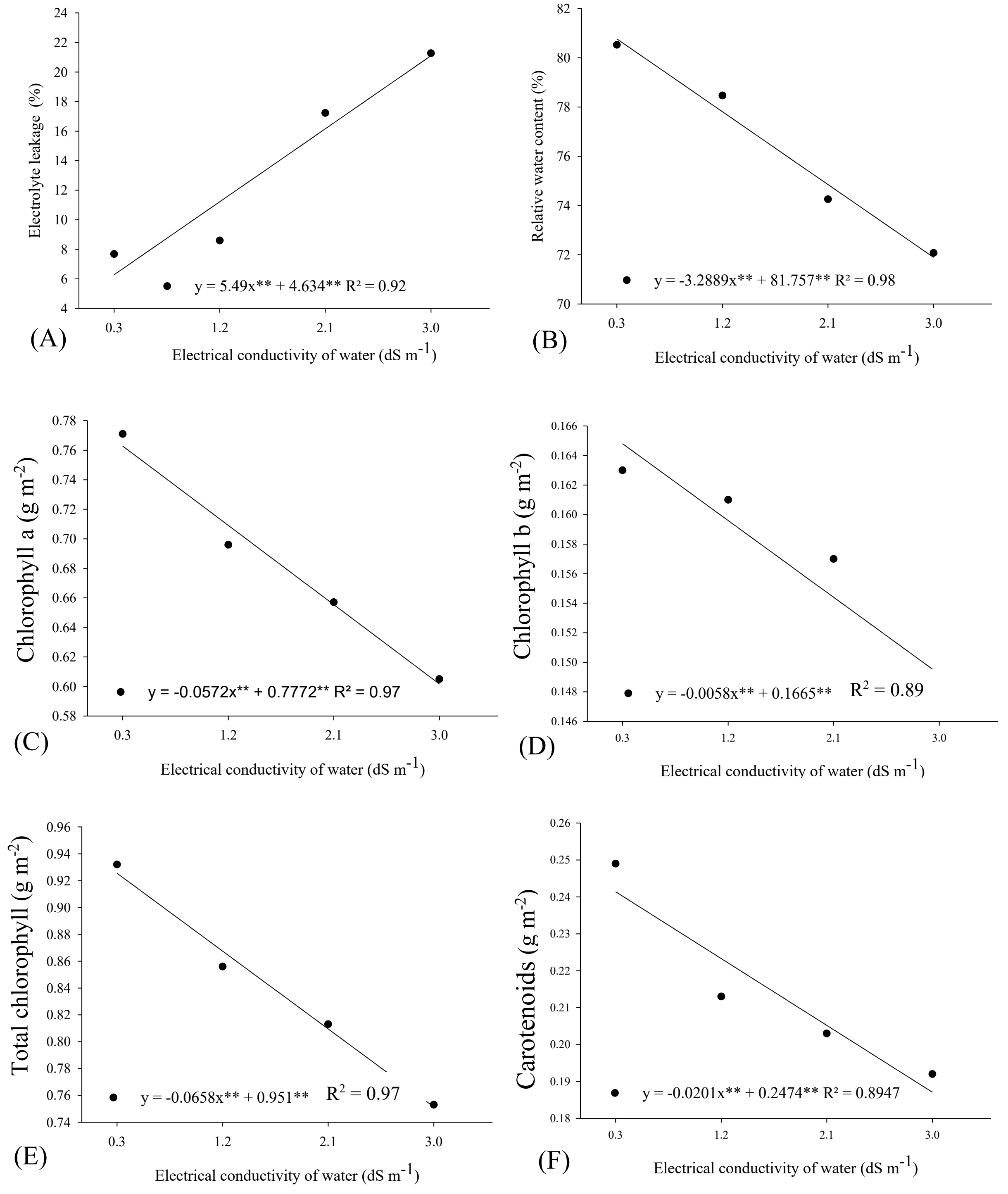
Table 4. Summary of the analysis of variance for electrolyte leakage (EL), relative water content (RWC), chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Total Chl), and carotenoids in *Physalis peruviana* seedlings subjected to seed osmotic priming (osmopriming) and cultivated under different levels of electrical conductivity of irrigation water (ECw), at 55 days after sowing.

| Source of variation | DF | Mean squares | | | | | |
|---|---|---|---|---|---|---|---|
| | | EL (%) | RWC (%) | Chl a | Chl b | Total Chl | Carotenoids |
| | | | | ----------------------(g m$^{-2}$)-------------------- | | | |
| Osmopriming | 1 | $0.442^{ns}$ | $0.110^{ns}$ | $0.002^{ns}$ | $0.0002^{ns}$ | $0.003^{ns}$ | $0.001^{ns}$ |
| ECw | 3 | 352.09** | 119.15** | 0.038** | 0.0003* | 0.045** | 0.004** |
| Osmopriming × ECw | 3 | $0.713^{ns}$ | $1.773^{ns}$ | $0.0009^{ns}$ | $0.00004^{ns}$ | $0.0009^{ns}$ | $0.0001^{ns}$ |
| Block | 3 | $2.672^{ns}$ | $7.785^{ns}$ | $0.0013^{ns}$ | $0.00009^{ns}$ | $0.0007^{ns}$ | $0.0003^{ns}$ |
| Error | 21 | 1.478 | 12.000 | 0.0013 | 0.00011 | 0.0012 | 0.0002 |
| CV | | 8.88 | 6.54 | 5.40 | 6.75 | 14.26 | 7.44 |
| Mean | | 13.69 | 76.33 | 0.682 | 0.157 | 0.84 | 0.214 |

DF – degree of freedom; CV – coefficient of variation; ns, * and ** – not significant, significant at $p < 0.05$ and significant at $p < 0.01$, respectively, by F-test.

The absence of significant effects of osmotic conditioning on photosynthetic pigments, relative water content, and electrolyte leakage—contrasting with the observed improvement in seedling growth—suggests that priming acted through pathways distinct from direct protection of the photosynthetic apparatus or maintenance of leaf water homeostasis. contrasting with the improvement in seedling growth, indicates that priming acted through pathways distinct from direct protection of the photosynthetic apparatus or leaf water homeostasis. It is likely that conditioning promoted an initial "metabolic vigor", optimizing biomass partitioning and resource use efficiency, or activated osmotic adjustment and antioxidant defense mechanisms that favor growth even under stress. However, these mechanisms did not reverse the inhibitory effects of salinity on pigment synthesis (Khan et al., 2022). Thus, improved growth emerges as a more sensitive indicator of the beneficial effect of priming than the isolated physiological variables evaluated. Nevertheless, salinity alone had a significant impact, similar to most vegetables that exhibit considerable effects on the photosynthetic apparatus when irrigated with highly saline water, including *Solanum lycopersicum* (Singh et al., 2016), *Capsicum annuum* (Melo et al., 2017), and *Cucumis melo* (Sousa et al., 2018).

The electrolyte leakage in *P. peruviana* seedlings increased with the addition of salts in the saline solution, rising from 6.48 to 17.40% when comparing the lowest (0.3 dS m$^{-1}$) and highest (3.0 dS m$^{-1}$) levels of ECw, representing an increase of 168.51% (Figure 5A).



** – significant at $p < 0.01$ by F-test.

Figure 5. Electrolyte leakage (A), relative water content (B), chlorophyll a (C), chlorophyll b (D), total chlorophyll (E), and carotenoids (F) of *Physalis peruviana* seedlings subjected to different electrical conductivity levels of irrigation water.

This increase is due to the rupture of cellular membranes caused by the excess of $Na^+$ and $Cl^-$ ions in the leaf tissue (Ahmed et al., 2024). This finding aligns with Silva et al. (2021), who reported that high salinity levels (0.5 to 4.5 dS $m^{-1}$) applied to the irrigation of *P. peruviana* seedlings damage essential cell structures, particularly the plasma membrane, increasing electrolyte leakage by 70%.

Consequently, the relative water content decreased with the increase in salts in the water, showing a decline of 10.99% as salinity rose from 0.3 to 3.0 dS $m^{-1}$ (Figure 5B). This decline is attributed to the excess solutes, $Na^+$ and $Cl^-$, which significantly alter the water status of the plants, reducing water absorption (Minhas et al., 2020).

The contents of chlorophyll a (Figure 5C), chlorophyll b (Figure 5D), total chlorophyll (Figure 5E), and carotenoids (Figure 5F) declined with the increase in salts, showing respective decreases of 18.50, 9.50, 19.07, and 22.48% as the ECw increased from 0.3 to 3.0 dS $m^{-1}$. The decline in chlorophyll content is attributed to increased activity of the enzyme chlorophyllase, which is responsible for chlorophyll degradation, likely caused by the higher translocation of chloride instead of nitrate due to the high salt concentration in the plants (Giordano et al., 2021).

In summary, osmoconditioning of *P. peruviana* seeds enhances germination and seedling growth. However, saline stress negatively impacts both the germination process and seedling development, with detrimental effects being more pronounced in the absence of osmoconditioning. This approach could be particularly relevant for cultivating this species in the northeastern semi-arid regions, where salinity poses a common challenge.

## Conclusions

The levels of irrigation water electrical conductivity negatively impacts the emergence, growth, physiology, biomass, and quality of *Physalis peruviana* seedlings. Osmoconditioning of seeds with PEG 6000 solution (-0.4 MPa) promoted greater growth compared to seeds without osmoconditioning.

The osmoconditioning technique did not inhibit but rather mitigated the deleterious effects of salinity in water on the emergence and leaf expansion in *P. peruviana*. These findings suggest that while osmoconditioning improves early establishment under saline conditions, its long-term effects on crop viability and productivity throughout the complete production cycle remain to be investigated.

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## References

Ahmed, M.; Tóth, Z.; Decsi, K. The impact of salinity on crop yields and the confrontational behavior of transcriptional regulators, nanoparticles, and antioxidant defensive mechanisms under stressful conditions: A review. International Journal of Molecular Sciences, v. 25, n. 5, 2654, 2024. https://doi.org/10.3390/ijms25052654

Arif, Y.; Singh, P.; Siddiqui, H.; Bajguz, A.; Hayat, S. Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. Plant Physiology and Biochemistry, v. 156, p. 64-77, 2020. https://doi.org/10.1016/j.plaphy.2020.08.042

Basso, S. M. S. Caracterização morfológica e fixação biológica de nitrogênio de espécies de *Adesmia* DC e *Lotus* L. Porto Alegre: Universidade Federal do Rio Grande do Sul, 1999. 268p. Tese de Doutorado.

Benadjaoud, A.; Dadach, M.; El-Keblawy, A.; Mehdadi, Z. Impacts of osmopriming on mitigation of the negative effects of salinity and water stress in seed germination of the aromatic plant *Lavandula stoechas* L. Journal of Applied Research on Medicinal and Aromatic Plants, v. 31, 100407, 2022. https://doi.org/10.1016/j.jarmap.2022.100407

Bonacina, C.; Cruz, R. M. S.; Nascimento, A. B.; Barbosa, L. N.; Gonçalves, J. E.; Gazim, Z. C.; Magalhães, H. M.; Souza, S. G. H. Salinity modulates growth, oxidative metabolism, and essential oil profile in *Curcuma longa* L. (Zingiberaceae) rhizomes. South African Journal of Botany, v. 146, p. 1-11, 2022. https://doi.org/10.1016/j.sajb.2021.09.023

Bruce, T. J. A.; Matthes, M. C.; Napier, J. A.; Pickett, J. A. Stressful "memories" of plants: Evidence and possible mechanisms. Plant Science, v. 173, n. 6, p. 603-608, 2007. https://doi.org/10.1016/j.plantsci.2007.09.002

Burlyn, E. M.; Kaufmann, M. R. The osmotic potential of polyethylene glycol 6000. Plant Physiology, v. 51, n. 5, p. 914-916, 1973. https://doi.org/10.1104/pp.51.5.914

Dickson, A.; Leaf, A. L.; Hosner, J. F. Quality appraisal of white spruce and white pine seedling stock in nurseries. The Forestry Chronicle, v. 36, n. 1, p. 10-13, 1960. https://doi.org/10.5558/tfc36010-1

Dutra, V. H.; Amorim, L. M. A.; Bernardo, A. M. G.; Alves, E. C.; Oliveira, C. M.; Dias, D. C. F. S. Qualidade fisiológica de sementes de *Physalis peruviana* sob condições de estresse hídrico. Research, Society and Development, v. 11, n. 2, e44011225997, 2022. http://dx.doi.org/10.33448/rsd-v11i2.25997

Ferreira, D. F. Sisvar: A computer analysis system to fixed effects split plot type designs. Revista Brasileira de Biometria, v. 37, n. 4, p. 529-535, 2019. https://doi.org/10.28951/rbb.v37i4.450

Figueiredo, F. R. A.; Nóbrega, J. S.; Fátima, R. T.; Ferreira, J. T. A.; Leal, M. P. S.; Melo, M. F.; Dias, T. J.; Albuquerque, M. B. Impact of biostimulant and saline water on cape gooseberry (*Physalis peruviana* L.) in Brazil. Physiology and Molecular Biology of Plants, v. 27, n. 9, p. 2141-2150, 2021. https://doi.org/10.1007/s12298-021-01058-3

Giannelli, G.; Potestio, S.; Visioli, G. The contribution of PGPR in salt stress tolerance in crops: Unravelling the molecular mechanisms of cross-talk between plant and bacteria. Plants, v. 12, n. 11, 2197, 2023. https://doi.org/10.3390/plants12112197

Giordano, M.; Petropoulos, S. A.; Rouphael, Y. Response and defence mechanisms of vegetable crops against drought, heat and salinity stress. Agriculture, v. 11, n. 5, 463, 2021. https://doi.org/10.3390/agriculture11050463

Guo, X.; Zhi, W.; Feng, Y.; Zhou, G.; Zhu, G. Seed priming improved salt-stressed sorghum growth by enhancing antioxidative defense. Plos One, v. 17, n. 2, e0263036, 2022. https://doi.org/10.1371/journal.pone.0263036

Hajihashemi, S.; Skalicky, M.; Brestic, M.; Pavla, V. Effect of sodium nitroprusside on physiological and anatomical features of salt-stressed *Raphanus sativus*. Plant Physiology and Biochemistry, v. 169, p. 160-170, 2021. https://doi.org/10.1016/j.plaphy.2021.11.013

Hasanuzzaman, M.; Raihan, M. R. H.; Masud, A. A. C.; Rahman, K.; Nowroz, F.; Rahman, M.; Nahar, K.; Fujita, M. Regulation of reactive oxygen species and antioxidant defense in plants under salinity. International Journal of Molecular Sciences, v. 22, n. 17, 9326, 2021. https://doi.org/10.3390/ijms22179326

Irigoyen, J. J.; Emerich, D. W.; Sánchez-Díaz, M. Water stress induced changes in concentrations of proline and total soluble sugars in nodulated alfalfa (*Medicago sativa*) plants. Physiologia Plantarum, v. 84, n. 1, p. 55-60, 1992. https://doi.org/10.1111/j.1399-3054.1992.tb08764.x

Khan, M. O.; Irfan, M.; Muhammad, A.; Ullah, I.; Nawaz, S.; Khalil, M. K.; Ahmad, M. A practical and economical strategy to mitigate salinity stress through seed priming. Frontiers in

Environmental Science, v. 10, 991977, 2022. https://doi.org/10.3389/fenvs.2022.991977

Lei, C.; Bagavathiannan, M.; Wang, H.; Sharpe, S. M.; Meng, W.; Yu, J. Osmopriming with Polyethylene glycol (PEG) for abiotic stress tolerance in germinating crop seeds: A review. Agronomy, v. 11, n. 11, 2194, 2021. https://doi.org/10.3390/agronomy11112194

Lessa, C. I. N.; Lacerda, C. F.; Cajazeiras, C. C. A.; Neves, A. L. R.; Lopes, F. B.; Silva, A. O.; Sousa, H. C.; Gheyi, H. R.; Nogueira, R. S.; Lima, S. C. R. V.; Costa, R. N. T.; Sousa, G. G. Potential of brackish groundwater for different biosaline agriculture systems in the Brazilian semi-arid region. Agriculture v. 13, n. 3, 550, 2023. https://doi.org/10.3390/agriculture13030550

Lichtenthaler, H. K. Chlorophylls and carotenoids: Pigment photosynthetic biomembranes. Methods in Enzymology, v. 148, p. 350-382, 1987. https://doi.org/10.1016/0076-6879(87)48036-1

Liu, L.; Huang, L.; Lin, X.; Sun, C. Hydrogen peroxide alleviates salinity-induced damage through enhancing proline accumulation in wheat seedlings. Plant Cell Reports, v. 39, n. 5, p. 567-575, 2020. https://doi.org/10.1007/s00299-020-02513-3

Lutts, S.; Kinet, J. M.; Bouharmont, J. NaCl-induced senescence in leaves of rice (*Oryza sativa*) cultivars differing in salinity resistance. Annals of Botany, v. 78, n. 3, p. 389-398, 1996. https://doi.org/10.1006/anbo.1996.0134

Ma, L.; Wei, J.; Han, G.; Sun, X.; Yang, X. Seed osmopriming with polyethylene glycol (PEG) enhances seed germination and seedling physiological traits of *Coronilla varia* L. under water stress. PloS One, v. 19, n. 5, e0303145, 2024. https://doi.org/10.1371/journal.pone.0303145

Maguire, J. D. Speed of germination—aid in selection and evaluation for seedling emergence vigor. Crop Science, v. 2, n. 2, p. 176-177, 1962. https://doi.org/10.2135/cropsci1962.0011183X000200020033x

Marthandan, V.; Geetha, R.; Kumutha, K.; Renganathan, V. G.; Karthikeyan, A.; Ramalingam, J. Seed priming: A feasible strategy to enhance drought tolerance in crop plants. International Journal of Molecular Sciences, v. 21, n. 21, 8258, 2020. https://doi.org/10.3390/ijms21218258

Medeiros, J. F. Qualidade de água de irrigação e evolução da salinidade nas propriedades assistidas pelo GAT nos Estados de RN, PB e CE. Campina Grande: Universidade Federal da Paraíba, 1992. 173p. Dissertação de Mestrado.

Megersa, H. G. Potential effects of salt stress on selected solanaceous crops (tomato (*Solanum esculentum* L.) and hot pepper (*Capsicum annuum* L.) production. Journal of Agricultural Science and Food Research, v. 13, n. 3, 1000494, 2022. https://doi.org/10.3389/2167-1044.22.13.494

Melo, H. F.; Souza, E. R.; Duarte, H. H. F.; Cunha, J. C.; Santos, H. R. B. Gas exchange and photosynthetic pigments in bell pepper irrigated with saline water. Revista Brasileira de Engenharia Agrícola e Ambiental, v. 21, n. 1, p. 38-43, 2017. https://doi.org/10.1590/1807-1929/agriambi.v21n1p38-43

Minhas, P. S.; Ramos, T. B.; Ben-Gal, A.; Pereira, L. S. Coping with salinity in irrigated agriculture: Crop evapotranspiration and water management issues. Agricultural Water Management, v. 227, 105832, 2020. https://doi.org/10.1016/j.agwat.2019.105832

Mirmazloum, I.; Kiss, A.; Erdélyi, É.; Ladányi, M.; Németh, É. Z.; Radácsi, P. The effect of osmopriming on seed germination and early seedling characteristics of *Carum carvi* L. Agriculture, v. 10, n. 4, 94, 2020. https://doi.org/10.3390/agriculture10040094

Muhammad, I.; Yang, L.; Ahmad, S.; Farooq, S.; Khan, A.; Muhammad, N.; Ullah, S.; Adnan, M.; Ali, S.; Liang, Q. P.; Zhou, X. B. Melatonin-priming enhances maize seedling drought tolerance by regulating the antioxidant defense system. Plant Physiology, v. 191, n. 4, p. 2301-2315, 2023. https://doi.org/10.1093/plphys/kiad027

Nikolić, N.; Ghirardelli, A.; Schiavon, M.; Masin, R. Effects of the salinity-temperature interaction on seed germination and early seedling development: a comparative study of crop and weed species. BMC Plant Biology, v. 23, n. 1, 446, 2023. https://doi.org/10.1186/s12870-023-04465-8

Nile, S. H.; Thiruvengadam, M.; Wang, Y.; Samynathan, R.; Shariati, M. A.; Rebezov, M.; Nile, A.; Venkidasamy, B.; Xiao, J.; Kai, G. Nano-priming as emerging seed priming technology for sustainable agriculture—recent developments and future perspectives. Journal of Nanobiotechnology, v. 20, n. 1, 254, 2022. https://doi.org/10.1186/s12951-022-01423-8

Ramadan, M. F. Introduction to goldenberry (*Physalis peruviana*): cultivation, processing, chemistry, and functionality. In: Ramadan, M. F (ed.). Handbook of goldenberry (*Physalis Peruviana*). Cambridge: Academic Press, 2024. p. 3-8. https://doi.org/10.1016/B978-0-443-15433-1.00001-7

Reis, L. S.; Azevedo, C. A. V.; Albuquerque, A. W.; Silva Junior, J. F. Índice de área foliar e produtividade do tomate sob condições de ambiente protegido. Revista Brasileira de Engenharia Agrícola e Ambiental, v. 17, n. 4, p. 386-391, 2013. https://doi.org/10.1590/S1415-43662013000400005

Rhoades, J. D.; Kandiah, A.; Mashali, A. M. Uso de águas salinas para produção agrícola. Campina Grande: UFPB, 2000. 117p. (Estudos FAO Irrigação e Drenagem, 48).

Salemi, F.; Esfahani, M. N.; Tran, L.-S. P. Mechanistic insights into enhanced tolerance of early growth of alfalfa (*Medicago sativa* L.) under low water potential by seed-priming with ascorbic acid or polyethylene glycol solution. Industrial Crops and Products, v. 137, p. 436-445, 2019. https://doi.org/10.1016/j.indcrop.2019.05.049

Silva, J. G.; Oliveira, O. H.; Lopes, K. P.; Cavalcante, J. A.; Hornke, N. F.; Moraes, D. M. Tolerance to irrigation water salinity in *Physalis peruviana* L. plants. Revista Ceres, v. 68, n. 6, p. 617-623, 2021. https://doi.org/10.1590/0034-737X202168060014

Silva, P. B.; Vaz, T. A. A.; Acencio, M. L.; Bovolenta, L. A.; Hilhorst, H. W. M.; Silva, E. A. A. Can osmopriming induce cross-tolerance for abiotic stresses in *Solanum paniculatum* L. seeds? A transcriptome analysis point of view. Seeds, v. 2, n. 4, p. 382-393, 2023. https://doi.org/10.3390/seeds2040029

Singh, M.; Sing, V. P.; Prasad, S. M. Responses of photosynthesis, nitrogen and proline metabolism to salinity stress in *Solanum lycopersicum* under different levels of nitrogen supplementation. Plant Physiology and Biochemistry, v. 109, p. 72-83, 2016. https://doi.org/10.1016/j.plaphy.2016.08.021

Sousa, V. F. O.; Costa, C. C.; Diniz, G. L.; Santos, J. B.; Bomfim, M. P. Physiological behavior of melon cultivars submitted to soil salinity. Pesquisa Agropecuária Tropical, v. 48, n. 3, p. 271-279, 2018. https://doi.org/10.1590/1983-40632018v4852495

Sousa, V. F. O.; Santos, A. S.; Sales, W. S.; Silva, A. J.; Gomes, F. A. L.; Dias, T. J.; Gonçalves-Neto, A. C.; Faraz, A.; Santos, J. P. O.; Santos, G. L.; Cruz, J. M. F. L.; Silva, L. D. R.; Araújo, J. R. E. S. Exogenous application of salicylic acid induces salinity tolerance in eggplant seedlings. Brazilian Journal of Biology, v. 84, e257739, 2024. https://doi.org/10.1590/1519-6984.257739

Tian, Y.; Gama-Arachchige, N. S.; Zhao, M. Trends in seed priming research in the past 30 years based on bibliometric analysis. Plants, v. 12, n. 19, 3483, 2023. https://doi.org/10.3390/plants12193483

Villela, F. A.; Doni Filho, L.; Siqueira, E. L. Tabela de potencial osmótico em função da concentração de polietileno glicol 6.000 e da temperatura. Pesquisa Agropecuária Brasileira, v. 26, n. 11/12, p. 1957-1968, 1991.

Wang, R.; Li, C.; Zeng, L.; Liu, L.; Xi, J.; Li, J. Polyethylene glycol priming enhances the seed germination and seedling growth of *Scutellaria baicalensis* Georgi under salt stress. Plants, v. 13, n. 5, 565, 2024. https://doi.org/10.3390/plants13050565

Xia, F. S.; Chen, L. L.; Yan, H. F.; Sun, Y.; Li, M. L.; Mao, P. S. Antioxidant and ultrastructural responses to priming with PEG in aged, ultra-dry oat seed. Seed Science and Technology, v. 44, n. 3, p. 556-568, 2016. https://doi.org/10.15258/sst.2016.44.3.12