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Hydrogen peroxide (H_2O_2) improves ion homeostasis in coriander plants under salt stress[1]

Peróxido de hidrogênio (H_2O_2) melhora a homeostase iônica em plantas de coentro sob estresse salino

Petterson C. C. Silva[2*], Hans R. Gheyi[2], Héssica S. Evangelista[3], Karine da S. de Deus[3] & André D. de Azevedo Neto[3]

[1] Research developed at Universidade Federal do Recôncavo da Bahia, Cruz das Almas, BA, Brazil
[2] Universidade Federal de Campina Grande/Programa de Pós-Graduação em Engenharia Agrícola, Campina Grande, PB, Brazil
[3] Universidade Federal do Recôncavo da Bahia/Programa de Pós-Graduação em Engenharia Agrícola, Cruz das Almas, BA, Brazil

HIGHLIGHTS:

Seed priming with H_2O_2 increases salt tolerance in coriander plants subjected to 50 mM NaCl.
H_2O_2 priming improves ionic balance, contributing to ion homeostasis.
Na^+ and Cl^- contents have an opposite relationship with the shoot fresh mass and shoot dry mass.

ABSTRACT: Priming with hydrogen peroxide (H_2O_2) contributes positively to the increase of salt tolerance in plants. Thus, this study aims to evaluate the effect of H_2O_2 as an attenuator of the negative effects induced by salinity on coriander plants grown in a hydroponic system. The coriander seeds were pretreated with different H_2O_2 concentrations (0.1, 1, 10, and 100 mM). The coriander plants were grown in nutrient solutions without presence of NaCl for control treatment (T1), while the other five treatments received 50 mM NaCl: T2 (absence of H_2O_2 in seed pretreatment), T3, T4, T5, and T6 corresponding to seed pretreatment with H_2O_2 at concentrations of 0.1, 1, 10, and 100 mM, respectively, in a completely randomized design with four replicates. In general, salinity reduced the production of shoot fresh and dry mass of coriander plants. However, the pretreatment with H_2O_2 significantly increased the salt tolerance of plants. H_2O_2 acted as a metabolic signal, improving the ion homeostasis by decreasing Na^+ and/or Cl^- contents and increasing K^+ content in leaves. The multivariate analysis revealed an opposite effect between the Na^+ and K^+ contents, in addition, to indicating that these results can directly affect the growth of coriander plants.

Key words: *Coriandrum sativum* L., reactive oxygen species, salt tolerance, hydroponic system

RESUMO: O pré-tratamento com peróxido de hidrogênio (H_2O_2) contribui positivamente para o aumento da tolerância ao sal em plantas. Assim, este estudo tem como objetivo avaliar o efeito do H_2O_2 como atenuador do efeito negativo induzido pela salinidade em plantas de coentro cultivadas em sistema hidropônico. As sementes de coentro foram pré-tratadas com diferentes concentrações de H_2O_2 (0,1, 1, 10 e 100 mM). As plantas de coentro foram cultivadas em soluções nutritivas sem a presença de NaCl para o tratamento controle (T1), enquanto nos outros cinco tratamentos receberam 50 mM de NaCl: T2 (ausência de H_2O_2 no pré-tratamento das sementes), T3, T4, T5 e T6 correspondendo ao pré-tratamento de sementes com H_2O_2 nas concentrações de 0,1, 1, 10 e 100 mM, respectivamente, em delineamento inteiramente casualizado com quatro repetições. Em geral, a salinidade reduziu a produção de massa fresca e seca da parte aérea das plantas de coentro. No entanto, o pré-tratamento com H_2O_2 aumentou significativamente a tolerância das plantas ao sal. O H_2O_2 atuou como sinalizador metabólico, melhorando a homeostase iônica diminuindo o teor de Na^+ e/ou Cl^- e aumentando o teor de K^+ nas folhas. A análise multivariada revelou um efeito oposto entre os teores de Na^+ e K^+, além disso, indicou que esses resultados podem afetar diretamente o crescimento das plantas de coentro.

Palavras-chave: *Coriandrum sativum* L., espécies reativas de oxigênio, tolerância ao sal, sistema hidropônico

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* Corresponding author - E-mail: petter.ufrb@gmail.com
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Introduction

In the Brazilian semiarid region, groundwater resources are a source of water for irrigation systems in periods of fresh water scarcity (Nunes et al., 2022). However, due to geological factors, brackish waters are common in underground reserves (Akter et al., 2020).

To solve this problem, some studies have sought to evaluate the feasibility of using brackish waters in hydroponic cultivation of several crops (Silva et al., 2020a; Santos et al., 2021; Silva et al., 2022a). These studies have demonstrated that hydroponic cultivation is a viable technique to minimize the negative effects of salinity when compared to field conditions (Leal et al., 2020). However, crops still show significant reductions in growth and production under saline conditions, especially leafy vegetables.

As mentioned, Silva et al. (2020a) reported that an increase in nutrient solution salinity significantly reduces coriander production. Silva et al. (2021) affirm that one of the main factors for the reduction of plant growth with the use of brackish waters is the salt-induced ion imbalance. Therefore, several studies have been looking for alternatives to minimize the negative effects caused by salinity on plants. One of these alternatives is the priming of seeds with hydrogen peroxide (H_2O_2) (Shalaby et al., 2021; Silva et al., 2021).

H_2O_2 is a reactive oxygen species (ROS) that, at adequate concentrations, can act as a metabolic signal, inducing a series of reactions that can provide plants with acclimation to different stress conditions (Shalaby et al., 2021). In several species, H_2O_2 has been shown to be able to minimize the negative effects caused by salinity (Silva et al., 2019; Silva et al., 2020b), but little is known on its effects on leafy vegetables.

Thus, this study aims to evaluate the effect of H_2O_2 as an attenuator of the negative effect induced by salinity on coriander plants grown in a hydroponic system.

Material and Methods

The experiment was conducted in a greenhouse consisting of a simple arch, with ceiling height of 3.0 m, a width of 7.0 m and a length of 28 m, with sides covered with black screen and covered with 150-µm-thick polyethylene, in the experimental area of the Programa de Pós-Graduação em Engenharia Agrícola of the Universidade Federal do Recôncavo da Bahia (UFRB), in the municipality of Cruz das Almas, Bahia state, Brazil (12° 40’ 19” S, 39° 6’ 23” W, and mean altitude of 220 m). The climate is classified as tropical hot and humid (Af) according to the Köppen classification (Alvares et al., 2013). During the experimental assay, the average minimum temperature, maximum temperature, and relative humidity of the air were 21.6 and 34.5 °C, and 84.5%, respectively.

Coriander seeds (cv. ‘Verdão’), obtained from the TopSeed line™ (Agristar, Santo Antônio de Posse, SP, Brazil), were sown in discardable plastic cups (50 mL capacity, with holes at the bottom) filled with coconut fiber as substrate, and the plants were maintained under these conditions during all the experiment. Twelve seeds per cup were sown. The H_2O_2 priming of the seed was previously established by continuously irrigating the seeds with different concentrations of H_2O_2 (0.1, 1, 10, and 100 mM) for 36 hours, under dark conditions. In addition, seeds for two other treatments without H_2O_2 (without salt stress – control and with salt stress) were irrigated with distilled water for 36 hours.

After the period of pretreatment, the cups with the seeds were taken to the greenhouse. After germination (five days after sowing), thinning was carried out, leaving only eight seedlings per cup. Seedlings were irrigated with 25 mM NaCl, except the control treatment which was irrigated with municipal supply water (electrical conductivity of 0.3 dS m^{-1}). After 15 days of the sowing, plants were transferred to a hydroponic system in polyethylene pots (Figure 1) containing 15 L of nutrient

Figure 1. Overview of the assay with coriander cultivation 20 days after transplanting in a floating hydroponic system

solution according to the formulation by Furlani et al. (1999). The aeration system consisted of an air compressor with a flow rate of 18,000 L h^{-1} (Resun, GF-180), activated by an analog timer every three hours and kept on for a period of 15 min.

The experiment was carried out in a completely randomized design with four replicates (containing eight plants in each bunch), with a total of six treatments. The coriander plants were grown in nutrient solutions without presence of NaCl for control treatment (T1), while the other five treatments received 50 mM NaCl, namely T2 (absence of H_2O_2 in seed pretreatment), T3, T4, T5, and T6 corresponding to seed pretreatment with H_2O_2 at concentrations of 0.1, 1, 10, and 100 mM, respectively. The doses of NaCl and H_2O_2 were selected based on the reduction of fresh and dry mass reported in previous studies (Silva et al., 2020a). During the experiment, the replacement of water consumed by coriander plants was carried out with municipal supply water, and the pH values in the nutrient solutions were measured daily. In general, the pH values oscillated within the range recommended for hydroponic cultivation, i.e., between 6.0 and 6.5.

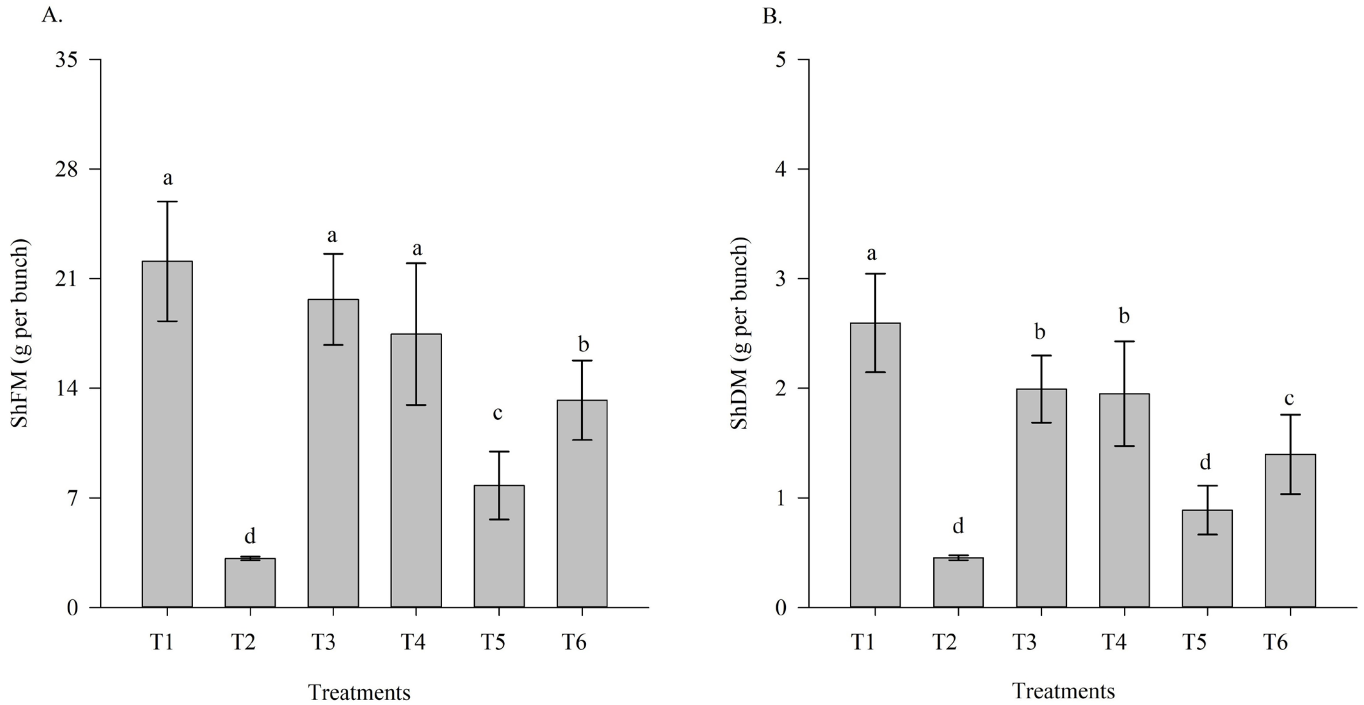
At the end of the experiment (35 days after sowing – DAS), the plants were harvested to determine shoot fresh mass (ShFM, g per bunch). The material was dried in an oven at 65 °C for 72 hours (until a constant mass was obtained), and then the plants were weighed on a precision balance to quantify shoot dry mass (ShDM, g per bunch).

For the determination of contents of sodium (Na^+), potassium (K^+), and chloride (Cl^-), extracts of leaf samples were prepared in deionized water following the methodology described by Azevedo Neto et al. (2020). For this, 0.1 g of dried powdered plant sample was added in 10 mL of deionized water. The tubes were heated to 95 °C in a water bath for one hour and then centrifuged at 5.000 × g for 5 min. The supernatants were filtered in a quantitative filter paper for further analysis. Na^+ and K^+ contents were determined in a Q498M2 flame photometry (Quimis, Diadema, SP, BR), as described by Faithfull (2002). In sequence, the K^+/Na^+ ratio was calculated. The Cl^- content was determined in a UV-VIS spectrophotometer, model 2000 UV (Bel Engineering, Piracicaba, SP, Brazil), following the methodologies described by Gaines et al. (1984), using a solution of mercury thiocyanate in absolute methanol plus iron nitrate at 20.2%.

The data were first tested for normality (Shapiro-Wilk test) and then subjected to analysis of variance (ANOVA), using the F test ($p \leq 0.05$). The significant results were compared using the Scott-Knott mean test ($p \leq 0.05$), using the statistical software SISVAR, 5.6 version (Ferreira, 2019). In addition, all data were transformed ($\sqrt{x}$) and subjected to principal component analysis (PCA). In order to describe the magnitude of the relationships among the variables analyzed, the Pearson correlation coefficient (r) was calculated, using the program SigmaPlot 14.0, for both analyses.

Results and Discussion

All variables analyzed (shoot fresh mass – ShFM, shoot dry mass – ShDM, chloride content – Cl^-, sodium content – Na^+, potassium content – K^+, and K^+/Na^+ ratio) were significantly affected by the treatments tested ($p \leq 0.01$). Coriander plants grown under salt stress without H_2O_2 (T2) reduced their ShFM (Figure 2A) and ShDM (Figure 2B) by 85 and 82%, respectively, when compared to the control treatment (T1). However, the H_2O_2 seed priming (at all concentrations), even under saline conditions, increased on average 4.7-fold the ShFM of coriander



Means ± standard deviation. Bars with the same letter do not differ statistically from each other, by the Scott-Knott's test ($p \leq 0.05$). Treatments: T1 - control (absence of H_2O_2 and absence of NaCl); T2 - salt stress without H_2O_2 (absence of H_2O_2 and presence of 50 mM of NaCl); T3 - 0.1 mM H_2O_2 + 50 mM NaCl; T4 - 1 mM H_2O_2 + 50 mM NaCl; T5 - 10 mM H_2O_2 + 50 mM NaCl; T6 - 100 mM H_2O_2 + 50 mM NaCl

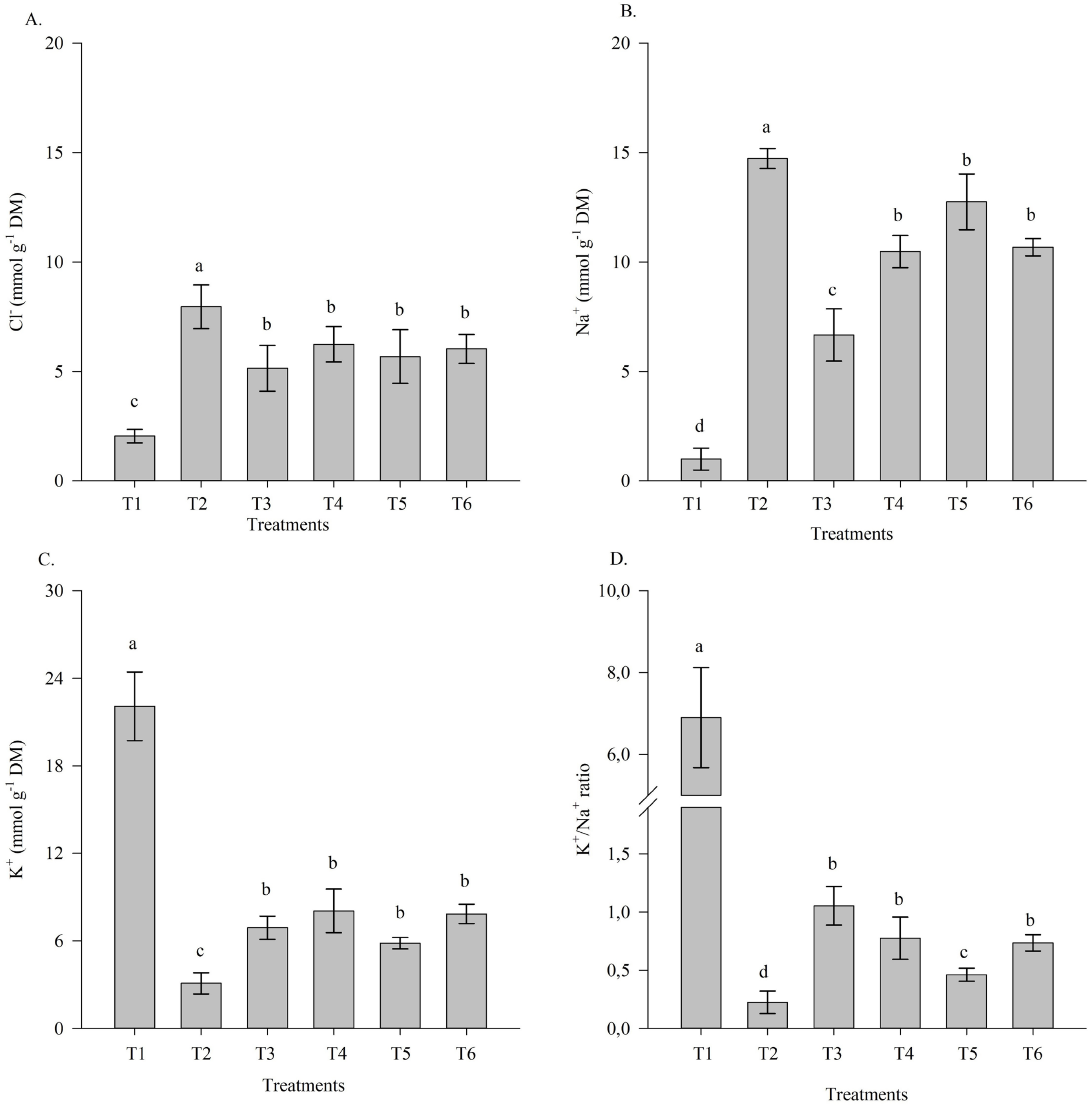
Figure 2. Effect of salt stress and H_2O_2-seed priming on the shoot fresh mass - ShFM (A) and shoot dry mass - ShDM (B) of coriander plants grown in a floating hydroponic system

plants in comparison to T2. The treatments T3 and T4 showed similar values to those ones of the control treatment (Figure 2A), indicating, that optimal concentrations are crucial to trigger the signaling role of H_2O_2. As for ShDM, H_2O_2 priming increased it on average 4-fold when compared to T2, except for T5 treatment, which showed similar values (Figure 2B).

These results confirm the hypothesis of this study, that H_2O_2 seed priming mitigates the harmful effects of salinity, increasing salt tolerance and improving the growth of coriander plants, mainly with the use of lower concentrations (0.1 and 1 mM H_2O_2). Similar results were reported in sunflower (Silva et al., 2019; Silva et al., 2020b; Silva et al., 2022b), in maize (Araújo et al., 2021), and in zucchini (Dantas et al., 2022).

Several studies report on the role of H_2O_2 as a metabolic signal in decreasing the negative effects of various stresses (Habib et al., 2021; Shalaby et al., 2021). This effect is named crosstalk by physiologists, and the majority of the studies affirm that this mechanism is related to pathways triggered by using mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs) (Qiao et al., 2021).

With regard to inorganic solutes, in general, salinity increased Cl^- (Figure 3A) and Na^+ contents (Figure 3B) in leaves of coriander plants, especially in the treatment without H_2O_2, which showed, respectively, increases of around 3.9



Means ± standard deviation. Bars with the same letters do not differ statistically from each other, by the Scott-Knott's test ($p \leq 0.05$). Treatments: T1 - control (absence of H_2O_2 and absence of NaCl); T2 - salt stress without H_2O_2 (absence of H_2O_2 and presence of 50 mM of NaCl); T3 - 0.1 mM H_2O_2 + 50 mM NaCl; T4 - 1 mM H_2O_2 + 50 mM NaCl; T5 - 10 mM H_2O_2 + 50 mM NaCl; T6 - 100 mM H_2O_2 + 50 mM NaCl

Figure 3. Effect of salt stress and H_2O_2 seed priming on Cl^- (A), Na^+ (B), and K^+ (C) contents and on K^+/Na^+ ratio (D) in leaves of coriander plants grown in a floating hydroponic system

and 4.5-fold when compared to the control treatment (T1). In contrast, when compared to T2, the H_2O_2 priming decreased Cl^- and Na^+ contents on average by 27 and 31%, respectively. Among the H_2O_2 primed treatments, the T3 (0.1 mM H_2O_2 + 50 mM NaCl) had the expressive reduction of Na^+ content, corresponding to 55% in comparison to T2 (Figure 3B).

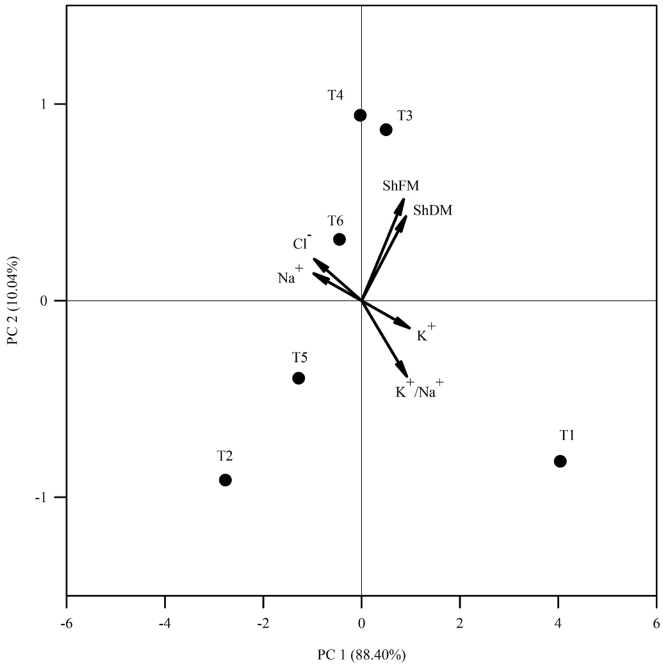
High concentrations of Cl^- and Na^+ in the root zone can cause ion toxicity in plants (Geilfus, 2018; Ketehouli et al., 2019). Several studies reported the role of Cl^- on the degradation of chlorophylls, pigments responsible for the photosynthesis process and which can adversely affect plant growth (Geilfus, 2018; Zhang et al., 2019). In addition, the high salt concentration causes nutrient deficiency symptoms, due to nutrient imbalance with a decrease in the content of K^+ (Keisham et al., 2018; Wu et al., 2018). The K^+ content (Figure 3C) and K^+/Na^+ ratio (Figure 3D) in leaves of coriander plants showed a strong decrease induced by salinity (50 mM NaCl in the nutrient solutions), but these reductions were comparatively less expressive in plants obtained from H_2O_2-primed seeds.

Compared to the control treatment (T1), the decrease of the K^+ content (Figure 3C) and K^+/Na^+ ratio (Figure 3D) observed in T2 was 86 and 97%, respectively. On the other hand, other treatments from H_2O_2-primed seeds showed an increase in K^+ content and K^+/Na^+ ratio, on average 132 and 239%, respectively, when compared to T2.

The increase in the K^+ content of leaves, observed in plants primed with H_2O_2, contributes to plant growth (Silva et al., 2020b; Silva et al., 2021). Taha et al. (2020) reported that the K^+ increase in leaves is related to plant development, chlorophyll synthesis, and stomata movement and reduces the uptake and movement of toxic ions, such as Na^+ and Cl^-. In addition, Wu et al. (2018) affirm that an indication of salt-tolerant species is related to the control of long-distance K^+ transport, either due to its more efficient xylem loading and delivery to the shoot, or minimizing the extent of K^+ recirculation in the phloem. Yao et al. (2021) reported that maintaining a high level of cellular K^+/Na^+ ratio contributes to decreasing Na^+ replacement in K^+ channels in different biological activities.

The principal component analysis (PCA) showed that, for all variables studied, the principal component 1 (PC1) was responsible for the largest variance observed in the data (88.40%), while the principal component 2 (PC2) was responsible for only 10.04% of this variance (Figure 4).

Taken together, Figure 4 and Table 1 show that, from the distribution of the treatments and loads of PCA, there was a positive relationship between PC1 and the traits K^+, K^+/Na^+, ShFM, and ShDM, and a strong relationship between PC2 and



Treatments: T1 - Control (absence of H_2O_2 and absence of NaCl); T2 - Salt stress without H_2O_2 (absence of H_2O_2 and presence of 50 mM of NaCl); T3 - 0.1 mM H_2O_2 + 50 mM NaCl; T4 - 1 mM H_2O_2 + 50 mM NaCl; T5 - 10 mM H_2O_2 + 50 mM NaCl; T6 - 100 mM H_2O_2 + 50 mM NaCl

Figure 4. Principal component analysis of the Cl^-, Na^+, K^+ contents, K^+/Na^+ ratio, shoot fresh mass - ShFM, and shoot dry mass - ShDM in leaves of coriander plants grown in a floating hydroponic system

the traits ShFM and ShDM. In addition, the position of the control treatment in PC1 in relation to the other treatments confirms that salinity strongly reduced plant growth, followed by treatments from H_2O_2-primed seeds with higher values of K^+, K^+/Na^+, ShFM, and ShDM, and lower values of Na^+ and Cl^-, when compared to plants of the treatment under salt stress without H_2O_2 (T2). Therefore, confirming that H_2O_2 priming increased the salt tolerance of coriander plants.

In Table 1 the correlation coefficients (r) describe the degree of correlation among the variables measured. Cl^- and Na^+ contents had a strong positive correlation with each other. However, in relation to the other variables, both the Cl^- and Na^+ content showed a negative correlation. On the other hand, K^+ content and K^+/Na^+ ratio had a positive correlation with the variables related to growth (ShFM and ShDM).

Silva et al. (2021) reported that the relationship between ion homeostasis and growth in plants primed with H_2O_2 is related to the signaling role of this agent on the negative regulation of absorption and transport of Na^+ and the decrease of K^+ losses in plants. K^+ is crucial for plants from the early phase of

Table 1. Component loadings of principal component analysis (PCA) and Pearson's correlation coefficients (r) of the variables analyzed in coriander plants under the effect of salt stress and H_2O_2-seed priming cultivated in a floating hydroponic system

Variables	Component loadings		Pearson's correlation coefficients (r)					
	PC1	PC2	Cl^-	Na^+	K^+	K^+/Na^+	ShFM	ShDM
Chloride content (Cl^-)	-0.96	0.21	1					
Sodium content (Na^+)	-0.97	0.14	0.967**	1				
Potassium content (K^+)	0.97	-0.14	-0.960**	-0.944**	1			
Potassium content/sodium content ratio (K^+/Na^+)	0.91	-0.38	-0.951**	-0.952**	0.951**	1		
Shoot fresh mass (ShFM)	0.85	0.51	-0.719*	-0.767*	0.761*	0.587*	1	
Shoot dry mass (ShDM)	0.90	0.43	-0.771*	-0.820**	0.822**	0.669*	0.992**	1

PC1 – Principal component 1; PC2 – Principal componente 2. *, ** - Significant at $p \leq 0,05$ and $p \leq 0,01$, respectively growth to vegetative growth and under-stressed environments. It contributes to cation-anion balance, osmoregulation, water movement, energy transfer, and many other processes, mitigating various abiotic stresses (Hasanuzzaman et al., 2018).

In summary, this study showed that it is possible to use saline water in hydroponic cultivation. However, to reduce the deleterious effects caused by salinity, it is necessary to use conditioning agents such as H_2O_2.

Conclusions

1. Salinity caused by 50 mM NaCl decreased the growth of coriander plants. However, seed priming with H_2O_2 for 36 hours increases salt tolerance, mainly at a concentration of 0.1 mM H_2O_2.

2. The increases of K^+ and K^+/Na^+ ratio are related to salt tolerance in coriander plants pretreated with H_2O_2 via seed.

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