Summer squash morphophysiology under salt stress and exogenous application of H₂O₂ in hydroponic cultivation

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Abstract

Summer squash is a vegetable of significant acceptance in the market due to its economic and nutritional importance, with the potential for expansion in the food industry. In this context, this study aimed to evaluate the gas exchange and growth of summer squash plants subjected to a saline nutrient solution and exogenous application of hydrogen peroxide. The study was conducted in a greenhouse in Pombal – PB. The cultivation system used was the Nutrient Film Technique (NFT) hydroponic system. The experimental design was completely randomized, in a 4 x 4 factorial arrangement, whose treatments consisted of four levels of electrical conductivity of the nutrient solution - ECns (2.1, 3.1, 4.1, and 5.1 dS m⁻¹) and four concentrations of hydrogen peroxide - H₂O₂ (0, 20, 40, and 60 μM), with three replications. The increase in the nutrient solution salinity from 2.1 dS m⁻¹ reduced the leaf area and transpiration of the summer squash plants. Hydrogen peroxide at a concentration of 40 μM increased the root length, the instantaneous carboxylation efficiency, and the CO₂ assimilation rate when the plants were subjected to the saline solution of 2.1 dS m⁻¹. Also, the application of 60 μM H₂O₂ mitigated the effect of salt stress on the internal CO₂ concentration and stomatal conductance of the summer squash plants.

Keywords: Cucurbita pepo, stress signaling, electrical conductivity, nutrient solution

Introduction

The tropical and subtropical climatic conditions of Brazil favor vegetable cultivation in protected environments throughout the year. However, water shortage in the Brazilian Northeast hinders agricultural production, with annual rainfall in the semiarid region ranging from 240 and 800 mm, besides high temperature and evaporation conditions that accelerate reduction of water volume in reservoirs (Melo Filho et al., 2019).

The distribution of water with low salt concentrations has priority for human consumption, while other water sources of inferior quality become an alternative for irrigation, such as water with high electrical conductivity (Santos et al., 2018).

Salinity is an aggravating factor for agricultural crops when the salt contents are above the tolerance limit, causing growth reduction and production losses. The increase in the Na⁺ and Cl⁻ ions reduces water and nutrient uptake due to the low osmotic potential, affecting plant metabolism and resulting in changes in growth and gas exchange, which compromises the photosynthetic efficiency (Santana Júnior et al., 2020).

Considering that the water sources available for irrigation present high salt concentrations, the hydroponic system becomes a viable alternative for cultivation in this region, allowing rational water use with approximately 70% saving compared to other systems, besides allowing the control of electrical conductivity, pH, and providing efficiency in the use of fertilizers (Sausen et al., 2020).

Another alternative to minimize the effect of salt stress on plants is the exogenous application of hydrogen peroxide (H₂O₂), which induces the process of plant acclimation, imposing moderate previous stress that results in metabolic changes that may afterward induce tolerance to more severe stress conditions (Gondim et al., 2011). According to Carvalho et al. (2011), hydrogen
peroxide stimulates the production of proteins and soluble carbohydrates, inducing osmotic adjustment in plants and improving water and nutrient uptake under salt stress conditions.

The effects of salt stress and the use of elicitors have been studied in crops such as maize (Silva et al., 2016), passion fruit (Silva et al., 2019), and cashew (Souza et al., 2019). However, studies with summer squash (Cucurbita pepo L.) under hydroponic cultivation conditions are still incipient, besides being a crop of economic importance for small producers, ranking among the ten vegetables of greatest economic value rich in iron, calcium, and fibers (Matos et al., 2017).

In this perspective, this study aimed to evaluate the growth and gas exchange of summer squash plants grown in saline nutrient solutions and subjected to exogenous application of hydrogen peroxide in a hydroponic system.

**Material and Methods**

The study was conducted from January to February 2020 in a greenhouse belonging to the Center of Sciences and Agrifood Technology (CCTA) of the Federal University of Campina Grande (UFCG), located in Pombal, Paraíba, at the geographic coordinates 6°46’13” S and 37°48’6” W, with a mean elevation of 184 m.

This study evaluated four salinity levels of the nutrient solution - ECns [2.1, 3.1, 4.1, and 5.1 dS m⁻¹] and four hydrogen peroxide concentrations - H₂O₂ (0, 20, 40, and 60 μM) applied via foliar spraying, distributed in a completely randomized design in a 4 x 4 factorial arrangement with three replications.

The NFT (Nutrient Film Technique) hydroponic system was structured with PVC pipes with 100 mm diameter and 6 m length, composed of four subsystems spaced 0.8 m apart, each containing three channels spaced 0.4 m apart. In the channels, the spacing was 0.5 m between plants and 1.0 m between treatments.

The channels were placed on racks 0.6 m high with a 4% slope to allow the flow of the nutrient solution. At the lowest portion of each bench of the hydroponic system, there was a 150 L polyethylene recipient to collect and conduct the nutrient solution to the channels. The nutrient solution was driven to the channels using a 35 W pump at a flow rate of 3 L per min. The circulation of the nutrient solution was scheduled with a timer, with an intermittent flow of 30 min at every hour.

The nutrient solution used was proposed by Hoagland & Arnon (1950). The stock solution was composed of the macronutrient concentrations of 136.09, 101.10, 236.15, and 246.49 g L⁻¹ of KH₂PO₄, KNO₃, Ca(NO₃)₂.4H₂O, and MgSO₄.7H₂O, respectively, in addition to 3.10, 1.70, 0.22, 1.25, 13.9, and 13.9 g L⁻¹ of H₃BO₃, MnSO₄.4H₂O, ZnSO₄.7H₂O, CuSO₄.5H₂O, (NH₄)₂MoO₄.4H₂O, 4H₂O, FeSO₄, and EDTA – Na, respectively.

Sowing was performed in 200 mL polyethylene containers, with a coconut fiber substrate, arranged in trays. From germination until the emergence of the first true leaf, a 50% concentration of the recommended solution was used, after which the fiber was removed and the seedlings were transplanted directly in the hydroponic system, then using nutrient solution of 100% concentration.

The saline solutions used for irrigation were obtained by adding the non-iodized sodium chloride (NaCl), calcium chloride (CaCl₂.2H₂O), and magnesium chloride (MgCl₂.6H₂O) salts to the nutrient solution prepared with tap water from Pombal, Paraiba, in a ratio of 7:2:1, respectively, in order to obtain the desired electrical conductivity values. These values correspond to the salt proportions commonly found in the waters used for irrigation in the semi-arid Northeast region of Brazil (Medeiros, 1992).

The total replacement of the solution occurred every eight days, with daily verification of electrical conductivity and pH, and adjustment of the solution whenever necessary through the addition of tap water with ECw of 0.3 dS m⁻¹, always maintaining the EC in accordance with the treatments and the pH within 6.5 and 7.0 through the addition of 0.1 M KOH or HCl. The plants were monitored, and phytosanitary practices were performed whenever necessary.

The hydrogen peroxide stock solution was obtained by diluting 30% H₂O₂ in deionized water, stored in plastic bottles wrapped in aluminum foil, and conserved under at 23 ºC. After transplantation, the seedlings received the exogenous application of hydrogen peroxide via foliar spraying, which was performed late in the afternoon with a manual sprayer in order to obtain a complete wetting of the leaves (abaxial and adaxial surfaces), at an eight-day interval according to the respective treatments, totaling three applications. The mean volume sprayed on the summer squash leaves was 8 mL per plant. During the application of the treatments, a cardboard structure was used to avoid wetting of neighboring plants.

Gas exchange was evaluated at 46 days after emergence through the following variables: stomatal conductance - gs (mol H₂O m⁻² s⁻¹), CO₂ assimilation rate - A (μmol m⁻² s⁻¹), transpiration - E (mmol H₂O m⁻² s⁻¹),

Comunicata Scientiae, v.12: e3464, 2021
and internal CO₂ concentration – Ci (µmol mol⁻¹), using a portable infrared gas analyzer (IRGA), model LCPro+ Portable Photosynthesis System®. After data collection, the instantaneous water-use efficiency - WUEi - A/E (µmol m² s⁻¹) [mmol H₂O m⁻² s⁻¹]⁻¹ and instantaneous carboxylation efficiency - CEi - A/Ci (µmol m² s⁻¹) (µmol mol⁻¹)⁻¹ were quantified.

Growth was measured at the same time through the analysis of the main stem length – MSL (cm), using a graduated ruler to measure the distance between the base of the plant and the apical meristem. The leaf area – LA (cm²) was determined based on the width of the leaves (>5 cm) and was estimated by the equation LA= 47.3647+0.6211W², as suggested by Fialho et al. (2011), where W corresponds to leaf width. The number of leaves – NL was obtained by counting all the fully-expanded leaves with a minimum length of 5 cm, except for the cotyledons. Root volume – RV (cm³) was measured following the methodology described by Basso (1999), by placing the roots in a graduated cylinder containing a known volume of water. The difference directly provided the root volume by unit equivalence (1 mL = 1 cm³). Root length – RL (cm) was determined with a graduated ruler as the distance between the base of the plant and the apex of the longest root.

The collected data were subjected to analysis of variance by the F-test at 0.05 probability; when significant, polynomial regression analysis (linear and quadratic) was performed for the saline nutrient solution and hydrogen peroxide concentrations using the statistical software SISVAR - ESAL (Ferreira, 2014).

**Results and Discussion**

There was a significant effect of the interaction between the electrical conductivity of the nutrient solution (ECns) and hydrogen peroxide concentrations (H₂O₂) on the internal CO₂ concentration (Ci), stomatal conductance (gs), CO₂ assimilation rate (A), instantaneous water-use efficiency (WUEi), and instantaneous carboxylation efficiency (CEi) of the summer squash plants (Table 1). Individually, the salinity levels significantly influenced the Ci, E, gs, A, and CEi of the summer squash plants at 46 days after emergence (DAE). In turn, hydrogen peroxide had no significant effect on the studied variables, except for CEi.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>Mean squares</th>
</tr>
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<tbody>
<tr>
<td>Source of variation</td>
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<td></td>
</tr>
<tr>
<td>Saline nutrient solution (SNS)</td>
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<td>0.012**</td>
</tr>
<tr>
<td>Linear Regression</td>
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</tr>
<tr>
<td>Quadratic Regression</td>
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<tr>
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<td>Quadratic Regression</td>
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<td>0.08**</td>
</tr>
<tr>
<td>Interaction (SNS x H₂O₂)</td>
<td>9</td>
<td>0.009**</td>
</tr>
<tr>
<td>CV (%)</td>
<td></td>
<td>11.05</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>231.46</td>
</tr>
</tbody>
</table>

The interaction between factors significantly affected the stomatal conductance (gs) of the summer squash plants (Figure 1A). By the unfolding of the interaction, it is noted that the plants that did not receive the foliar application of H₂O₂ (0 µM) along with the ECns of 2.1 dS m⁻¹ obtained the maximum value of 0.43 mol H₂O m⁻² s⁻¹. In the plants that received 20, 40, and 60 µM of H₂O₂, the maximum values were obtained with the nutrient solution salinities of 3.6, 2.1, and 2.1 dS m⁻¹, respectively. The reduction in the gs is caused by osmotic adjustment as the plants under salt stress activate their defense system to induce partial stomatal closure, reducing water loss to the atmosphere and the uptake of toxic ions, consequently limiting CO₂ entry, which affects the photosynthetic rate (Lima et al., 2019). The reduction in the gs was also observed by Oliveira et al. (2017) for cowpea under irrigation with saline water, in which the salinity levels of 2.5 and 5.0 dS m⁻¹ reduced the gs by 34 and 72%, respectively, at 20 days after planting.
Figure 1B, it is observed that the highest internal CO$_2$ concentration ($C_i$) of the plants exposed to the estimated nutrient solution salinity of 3.7 dS m$^{-1}$ and exogenous application of 60 mM H$_2$O$_2$ was equivalent to 269.9 mol H$_2$O m$^{-2}$ s$^{-1}$. In turn, the lowest internal CO$_2$ concentration (335.04 mol H$_2$O m$^{-2}$ s$^{-1}$) was verified in the plants cultivated with 2.1 dS m$^{-1}$ and in the absence of H$_2$O$_2$. According to Sousa et al. (2019), the increase in salinity negatively influences stomatal opening, affecting the $C_i$ due to the low stomatal conductance and CO$_2$ assimilation as a function of the decrease in the leaf area and the photochemical damage caused by the Na$^+$ and Cl$^-$ ions. Melo et al. (2017), in a study with bell pepper under irrigation with saline water (ECw from 0 to 9.0 dS m$^{-1}$), obtained a maximum value of 229.80 mmol CO$_2$ mol$^{-1}$ for the internal CO$_2$ concentration of pepper bell plants irrigated with 3.0 dS m$^{-1}$.

The increase in the conductivity of the saline solution negatively affected transpiration ($E$) in the summer squash plants (Figure 2), with a 5.64% decrease per unit increase in the ECns. When comparing the transpiration of the plants cultivated under ECns of 5.1 dS m$^{-1}$ in relation to those under 2.1 dS m$^{-1}$, a decrease of 1.08 mol H$_2$O m$^{-2}$ s$^{-1}$ is observed. The decrease in $E$ occurs due to the low water potential of the roots as a function of salt stress, considering that salt causes the partial closure of stomata to avoid leaf dehydration and water loss to the atmosphere (Lima et al., 2017). Guimarães et al. (2019), in a study with lettuce grown under salt stress, verified a linear reduction of transpiration equivalent to 48 and 32.2% under the electrical conductivity levels of the nutrient solution of 1.6 and 7.6 dS m$^{-1}$, respectively, at 14 and 21 days after transplanting.

Regarding the CO$_2$ assimilation rate ($A$) of the summer squash (Figure 3A), the plants cultivated without foliar application of H$_2$O$_2$ (0 μM) obtained the maximum value of 26.33 mol H$_2$O m$^{-2}$ s$^{-1}$ when grown under the nutrient solution salinity of 2.1 dS m$^{-1}$. In the plants that received the exogenous application of 20, 40, and 60 μM H$_2$O$_2$, the maximum estimated values were obtained in the plants grown under the ECns of 3.0, 2.1, and 3.3 dS m$^{-1}$, respectively. The decrease in the CO$_2$ assimilation rate is related to the reduction in stomatal conductance as the control of the opening and closure of stomata favors CO$_2$ entry in the leaf mesophyll, contributing to increase the internal CO$_2$ concentration, that is, the substrate for photosynthesis (Taiz et al., 2017). Ribeiro et al. (2020) verified a 23.8% reduction in the CO$_2$ assimilation rate in watermelon plants cultivated under salt stress (0.5 to 4.0 dS m$^{-1}$). The authors observed a maximum value of 4.19 μmol CO$_2$ m$^{-2}$ s$^{-1}$ and a minimum of 3.19 μmol CO$_2$ m$^{-2}$ s$^{-1}$ in plants cultivated under water salinity of 0.50 dS m$^{-1}$ and 3.49 dS m$^{-1}$, respectively.
Comunicata Scientiae, v.12: e3464, 2021
Dantas et al. (2021) Summer squash morphophysiology under...

Figure 3. CO₂ assimilation rate - A (A), instantaneous water-use efficiency - WUEi (B), and instantaneous carboxylation efficiency (CEi) – (C) of summer squash plants as a function of the interaction between salinity levels of the nutrient solution - ECns and the exogenous application of hydrogen peroxide – H₂O₂ in hydroponic cultivation, at 46 days after emergence. Pombal, PB, 2020.

With regard to instantaneous water-use efficiency– WUEi (Figure 3B), the data of the plants that received the exogenous application of 20, 40, and 60 μM H₂O₂ obtained better adjustment with the quadratic model, and the equations (Figure 3B) reveal the maximum estimated values of 6.1, 4.78, and 4.48 [(µmol m⁻² s⁻¹) (µmol mol⁻¹)⁻¹] in the plants grown under the ECns of 5.1, 2.1, and 5.1 dS m⁻¹. The reduction in the WUEi can be attributed to the increase in the concentration of soluble salts in the nutrient solution, hindering their uptake and use by the plant due to stomatal closure, as well as being related to the amount of carbon fixed by the plant, considering that this process results in water loss at each molecule fixed, while the ideal is CO₂ assimilation with minimal water loss, in which the reduction in the WUEi occurs as a function of the increase in CO₂ assimilation and transpiration (Taiz et al., 2017; Guimarães et al., 2019).

The instantaneous carboxylation efficiency (CEi) of the summer squash plants was significantly affected by the interaction between the ECns levels and H₂O₂ concentrations. Through the regression equations (Figure 3C), it is verified that the data were better adjusted to the quadratic model. The plants cultivated under the H₂O₂ concentrations of 0, 20, 40, and 60 μM obtained the CEi values of 0.13, 0.11, 0.14, and 0.10 [(µmol m⁻² s⁻¹) (µmol mol⁻¹)⁻¹] under the ECns of 2.1, 2.7, 2.1, and 2.1 dS m⁻¹, respectively. The reduction in the CEi is related to low CO₂ fixation in the carboxylation process of the leaf mesophyll cells, being essential for the regeneration of the RuBisCO enzyme in the Calvin cycle; when salt stress in the plants is severe, it compromises the efficiency of photosynthesis and increases the internal CO₂ concentration (Taiz et al., 2017; Dias et al., 2019).

There was a significant interaction between nutrient solution salinity and hydrogen peroxide concentrations for main stem length (MSL) and root length (RL) (Table 2). The factors had no significant effect on the number of leaves (NL) and root volume (RV).
Table 2. Summary of the analysis of variance for the main stem length (MSL), number of leaves (NL), leaf area (LA), root length (RL), and root volume (RV) of summer squash plants cultivated with saline nutrient solution and exogenous application of hydrogen peroxide in a hydroponic system, at 46 days after emergence. Pombal, PB, 2020.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>MSL</th>
<th>NL</th>
<th>LA</th>
<th>RL</th>
<th>RV</th>
</tr>
</thead>
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<tr>
<td>Saline nutrient solution (SNS)</td>
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<td>0.000*</td>
<td>0.349**</td>
<td>0.000*</td>
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<td>0.737*</td>
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<td>0.000*</td>
<td>0.113*</td>
<td>0.000*</td>
<td>0.064*</td>
<td>0.447**</td>
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<td>Quadratic Regression</td>
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<td>0.450**</td>
<td>0.415*</td>
<td>0.469**</td>
<td>0.420**</td>
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<tr>
<td>Hydrogen peroxide (H₂O₂)</td>
<td>3</td>
<td>0.447**</td>
<td>0.549**</td>
<td>0.007*</td>
<td>0.006*</td>
<td>0.397**</td>
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<td>0.168**</td>
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<tr>
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<td>0.006*</td>
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<td></td>
<td>91.05</td>
<td>21.23</td>
<td>11690.7</td>
<td>84.43</td>
<td>151.97</td>
</tr>
</tbody>
</table>

*ns, **, respectively not significant and significant at p < 0.05 and p < 0.01; DF= Degrees of freedom; CV= Coefficient of variation.

The main stem length (MSL) of the summer squash plants decreased quadratically as a function of the increase in the nutrient solution salinity, regardless of the hydrogen peroxide concentration, at 46 days after emergence (Figure 4A). For the plants cultivated under the ECns of 2.1 dS m⁻¹ and without H₂O₂ application (0 μM), the maximum estimated value was 115.52 cm. For the plants cultivated under the ECns of 3.1, 4.1, and 5.1 dS m⁻¹, the maximum values were 99.75, 88, and 79.37 cm when using the respective H₂O₂ concentrations of 60, 60, and 20 μM. The reduction in plant growth can be attributed to the increase in salinity, affecting plant metabolism, inducing osmotic imbalance, and hindering water and nutrient uptake, which unleashes changes in gas exchange characteristics (Andrade et al., 2019), although hydrogen peroxide mitigates stress in plants grown under salinity levels higher than 2.1 dS m⁻¹. Decreased plant growth under salt stress was also observed by Albuquerque et al. (2016) when irrigating cucumber plants with ECw levels from 0.6 to 3.0 dS m⁻¹, verifying a reduction in plant height equivalent to 13.5% per unit increase in water salinity.

![Figure 4A](image1.png)

![Figure 4B](image2.png)

The interaction between nutrient solution salinity and hydrogen peroxide significantly influenced root length (RL) in the summer squash plants (Figure 4B), whose data were better adjusted to the quadratic model. Based on the regression equations (Figure 4B), the summer squash plants that received the H₂O₂ concentrations of 0, 20, 40, and 60 μM obtained the maximum root length values when under the ECns levels of 2.1, 4.1, and 4.6 dS m⁻¹, respectively. On the other hand, the lowest RL values were obtained when the plants received the foliar applications of 0, 20, 40, and 60 μM H₂O₂ and ECns of 4.3, 2.1, 5.1, and 2.1 dS m⁻¹. Plants decrease water uptake under salt stress conditions, in which the Cl⁻ and Na⁺ ions influence the partial closure of stomata and consequently the CO₂ concentration in the substomatal chamber, affecting the CO₂ assimilation rate as well as plant nutrition and hormones (Taiz et al., 2017). However, at low concentrations, hydrogen peroxide emits signals inducing the plant to produce organic compounds that reduce the reactive oxygen species, boosting the
growth of the root system and consequently increasing the available area for water and nutrient uptake (Silva et al., 2019). Oliveira et al. (2019), evaluating cowpea root length under salt stress (ECw of 0.8 and 4.0 dS m⁻¹), reported that the increase in salinity reduced root length when the plants were irrigated with 4.0 dS m⁻¹.

The leaf area of the summer squash plants (Figure 5A) decreased linearly with the increase in the salinity levels of the nutrient solution, with an 8.62% decrease per unit increase in the ECns. When comparing the LA of the plants grown under the ECns of 5.1 dSm⁻¹ to those cultivated under 2.1 dS m⁻¹, it is possible to note a decrease of 4,387 cm². The reduction in the leaf area of the plants grown under salt stress conditions is considered an adaptation mechanism of the plant as the entry of Na⁺ and Cl⁻ ions affects cell division and elongation, resulting in the reduction of stomatal conductance; under these conditions, plant transpiration is reduced and these ions are carried through the xylem, maintaining cell turgidity (Taiz et al., 2017). The results found in this study agree with those found by Dias et al. (2019) when studying arugula growth under salt stress (ECw from 0.5 to 4.5 dS m⁻¹), obtaining a 78.33% reduction in the leaf area when the plants were subjected to the electrical conductivity of water of 4.5 dS m⁻¹ in relation to the lowest salinity level (0.5 dS m⁻¹).

Regarding the hydrogen peroxide concentrations, a quadratic behavior is observed for the leaf area (Figure 5B), verifying a maximum value of 12,983 cm² and a minimum of 12983.20 cm² in the plants that received the H₂O₂ concentrations of 42 and 0 μM, respectively. For Silva et al. (2016), the beneficial effect of the exogenous application of hydrogen peroxide occurs due to the activation of the defense system of the plant through the production of antioxidant enzymes, soluble carbohydrates, and NO₃ under stress conditions, making the plant tolerant to the Na⁺ and Cl⁻ ions, constituting a positive process of plant acclimation for reducing the damage to the cell membranes and allowing growth and expansion. Silva et al. (2019) verified that the hydrogen peroxide concentrations of 25 and 50 μM had a beneficial effect on the leaf area of soursop seedlings at 145 days after sowing, mitigating salt stress and obtaining a maximum value of 311.82 cm² at the concentration of 50 μM associated with the ECw of 2.17 dS m⁻¹.

**Conclusions**

Hydrogen peroxide concentrations up to 40 μM promote greater main stem length and root length in summer squash plants grown under nutrient solution salinity of 2.1 dS m⁻¹ in hydroponic cultivation.

The leaf area of summer squash plants is reduced with the increase in salinity and hydrogen peroxide concentrations above 42 mM.

The 40 μM concentration mitigated salt stress regarding the instantaneous carboxylation efficiency of the squash plants cultivated in the hydroponic system under the nutrient solution salinity of 2.1 dS m⁻¹. Furthermore, the H₂O₂ concentration of 60 μM reduced the effect of the salts on the internal CO₂ concentration and stomatal conductance.

The CO₂ assimilation rate of summer squash plants cultivated in the hydroponic system is reduced with the increase in the nutrient solution salinity from 2.1 dS m⁻¹ and the exogenous application of hydrogen peroxide above 40 mM.

**References**


Summer squash morphophysiology under...
Dantas et al. (2021) Summer squash morphophysiology under...


Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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