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Effect of Salicylic Acid on the Growth and Development of Sweet Pepper (*Capsicum annum* L.) under Standard and High EC Nutrient Solution in Aeroponic Cultivation

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Abstract: High electrical conductivity (EC) in cultivation systems with the recirculating nutrient solutions can affect plant growth and development. This study aimed to investigate the effect of salicylic acid (SA) on the selected physiological and biochemical parameters of sweet pepper (*Capsicum annum* L.) growing aeroponically at standard and high concentrations of nutritive solutions. Four experimental variants were tested: (1) plants cultivated under low EC conditions, (2) plants cultivated under low EC conditions and treated with foliar SA, (3) plants cultivated under high EC conditions, (4) plants cultivated under high EC conditions and treated with SA on leaves and roots. The obtained results revealed that exogenous SA, regardless of EC, reduced the formation of fruits with calcium deficiency symptoms. Furthermore, SA helps plants to cope with high EC nutrient stress through an increase in leaf SPAD index, maximum light-adapted chlorophyll fluorescence and PSII viability. Exogenous SA reduced the number of soluble proteins both under low and high EC; however, increased H_2O_2 content induced a defence mechanism reflected by the upregulation of antioxidant enzyme activity. The results of the study provide valuable information on the role of SA in the alleviation of the harmful effect of salinity under aeroponic cultivation.

Keywords: *osmotic stress*; *physiological disorder*; reactive oxygen species (ROS); photosynthetic activity

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1. Introduction

Sweet pepper (*Capsicum annuum* L.) is economically important for the worldwide vegetable industry. World production of pepper in 2020 was over 36 million tonnes and is still growing; European production was over 3.5 million tonnes, while in Poland, the annual harvest is approximately 159,000 tonnes [1–3]. Pepper fruits are a source of natural pigments and antioxidants, including vitamin C, flavonoids, phenolic acids, as well as carotenoids. Given the nutraceutical and anticancer properties of pepper compounds, they are important preventive factors against many diseases, e.g., cardiovascular disease, type II diabetes, and other aging-associated disorders [4–6]. Global demand for food, especially high-quality products, is increasing rapidly. However, agricultural areas and water resources are decreasing, mainly due to climate change. That is why any agronomic treatments with elicitors, including salicylic acid (SA), can positively influence the yielding of many species and reduce negative environmental impacts. However, appropriate concentrations and methods of elicitor application need to be determined to improve the effectiveness of this practice under different growing conditions [7,8].

A significant problem for pepper cultivation is the sensitivity of plants to environmental stresses, such as drought, salinity, oxygen deficit, low/high temperature, or excessive

radiation. Various unfavourable factors decrease yield and lead to the formation of non-commercial fruits. In the case of peppers, a major problem is a physiological disorder caused by a calcium deficiency in the pericarp cells, known as dry pepper fruit rot, or BER (blossom-end rot). BER significantly affects crop production also in tomatoes and watermelons [9]. It is often associated with calcium deficiency in the whole plant or in the fruit only. Calcium is an essential plant macronutrient. The plants evolved a mechanism involving interactions between the cell wall and the cytoplasm, where Ca^{2+} acts as an agent. The regulation of Ca^{2+} ions concentration in the cytoplasm, apoplast, and organelles of the cell is used by the plant as a signalling mechanism [10]. In addition, calcium stabilizes cell membrane components and pectins in the cell wall. Water uptake and transport play a crucial role in the uptake and distribution of calcium, which is supplied to the fruit mainly through the xylem [11]. Various abiotic stresses can cause a physiological BER disorder in fruits, through reduced calcium uptake by the roots and disturbed regulation of cellular calcium distribution.

In hydroponic and aeroponic cultivation, especially when the nutrient solution is recirculated, a common problem is an increase in the concentration of ions in the nutrient solution. Such manipulation can evoke abiotic stress. More specifically, higher ion concentration limits nutrient uptake and reduces crop production by increasing osmotic pressure [12]. In pepper, high electrical conductivity (EC) of nutrients in the medium was shown to reduce plant growth and net leaf photosynthesis [13]. According to Pérez-Vazquez et al. [14], EC of 3 dS m^{-1} or higher improves nutraceutical quality but decreases bell pepper yield.

According to Hagassou et al. [9], abiotic stress induces the production of reactive oxygen species (ROS) in the plant, leading to membrane breakdown and loss of cellular turgor. As reported by Rekhter et al. [15] and Ding and Ding [16], plant hormones (phytohormones) play an important role in the plant's response to biotic and abiotic stresses.

It was found that the treatment of pepper plants with salicylic acid (SA) reduced oxidative damage caused by salinity stress [17] and increased pepper fruit yield and quality [18]. SA is a plant hormone that controls growth and promotes seedlings' root formation, delays leaf senescence, induces flowering, and interacts with abscisic acid and jasmonates. In addition, it has a positive effect on photosynthesis [19]. Exogenous SA affects various processes, including stomatal closure, ion uptake and transport [20], cell membrane permeability, and intensity of photosynthesis, as well as plant growth [21]. Many studies indicated the positive effects of this hormone in stimulating plant growth under abiotic stress conditions. Furthermore, SA has been found to act as a key signalling molecule under drought, high temperature, and salinity stress conditions [22,23]. Its activity is essential for basal immunity and systemic acquired resistance [24,25] and, by regulating gene expression, SA leads to the synthesis of proteins affecting a number of metabolic processes [26]. However, the specific mechanism of action of SA is still not well understood. Additionally, SA may interact with several different stress-linked compounds, and so, its role in the regulation of plant responses is much more complex [27,28].

The aim of this study was to evaluate the effect of exogenous SA on fruit growth and quality of pepper cultivated in aeroponic conditions under standard and high nutrient solutions.

2. Materials and Methods

2.1. Location of Research

The study was conducted in the experimental greenhouses of the Warsaw University of Life Sciences in the Department of Vegetable and Medicinal Plants in the Institute of Horticultural Science (longitude 21° E, latitude 51°15′ N).

2.2. Plant Material and Growing Conditions

2.2.1. SA Concentration Optimized for Foliar and Root Treatment

In the first part, a test experiment was carried out to determine the appropriate concentration of SA for spray treatment (foliar) and by watering (root treatment). For this purpose,

pepper ('Palermo F1' cultivar) seeds, the same that was used in further studies, were sown on 25 August 2020 into 25 mm × 25 mm × 4 mm rockwool plugs soaked in nutrient solution with an EC of 1.4 dS m^{-1} and covered with expanded clay. Pepper seedlings were transplanted 14 days after sowing (DAS) into 100 mm × 100 mm × 65 mm rockwool seedling cubes soaked in nutrient solution with EC 2.5 dS m^{-1}, pH 5.5. The concentration of nutrients (mg L^{-1}) was as follows: N-NO_3-195, P-57, K-273, Mg-47, Ca-187, Fe-2, Mn-0.6, B-0.3, Cu-0.15, Zn-0.3, Mo-0.05. The day/night temperature averaged 22 °C/20 °C, RH (relative humidity) was 60–70%, and the average CO_2 concentration was 800 ppm.

Pepper plants were sprayed with SA (foliar) at four concentrations (1; 2; 5; 10 mmol SA), while the control plants were sprayed with water only (0 SA-f). SA was also applied at four concentrations (100; 150; 500; 1000 ppm SA) to the roots with a nutrient solution, and the control plants were watered with nutrient solution without salicylic acid (0 SA-r). There were 10 plants in each combination and 3 plants for each replicate. The first treatment of plants with salicylic acid was carried out on 21 DAS, followed by 24 and 27 DAS. Solutions for spray (1; 2; 5; 10 mmol SA) were supplemented with Tween 20 (0.05% (*v/v*), while for root application, 100; 150; 500; 1000 ppm SA was provided with the standard nutrient solution for pepper seedlings. Each plant was watered with SA-supplemented nutrient solution at the appropriate concentration for each combination as the plants in the control when a reduction of approximately 35% WC (water content) in the rockwool pot was recorded. In each combination, 30 DAS plants were tested. The height of the plant and the diameter of the shoot at 1 cm above the root neck were measured. The number of leaves and the fresh weight (d = 0.1 g) of the plant (leaves and stems) were also determined. The SPAD index of the relative chlorophyll content of the leaves was measured with a Minolta SPAD-502 apparatus. Based on the results obtained in this part, SA concentrations appropriate for pepper for foliar and root application were selected for further studies.

2.2.2. Aeroponic Growing System

Studies on the effect of SA on pepper fruit growth and quality under standard and high EC medium conditions in aeroponic cultivation were carried out on two terms. The sweet pepper cultivar 'Palermo F1' from Rijk Zwaan, with elongated and red-coloured fruit, was used for the study. Seed sowing on the first date (Term 1) was carried out on 7 April 2021 and on the second date (Term 2) on 14 July 2021. The seedling quilting treatment was performed on 14 DAS on both test terms. Seedlings were produced in 50 mm × 50 mm × 65 mm rockwool cubes and plants were fed with a standard nutrient solution for pepper seedlings with EC 2.5 dS m^{-1} pH 5.5. The concentration of nutrients and cultivation conditions were the same as in the section *SA concentration optimized for foliar and root treatment*.

Pepper seedlings were planted into the aeroponic system on both date 1 and date 2, on day 28 after sowing the seeds (28 DAS). The same method of pepper cultivation was used on both experimental dates. In the experimental growing chamber, microclimatic conditions were computer-controlled. The temperature was maintained at 20–23 °C during the day and 17–19 °C at night. Relative humidity was approximately 70–75%. The experiment was completed with 70 DAS on both terms (date 1–16 June 2021, date 2–22 September 2021). Plants with a properly developed root system, 4–5 fully developed leaves, free from diseases and pests were selected. The pepper plants were placed in openwork pots, which were then inserted into holes made on the top of special bottomless containers of 0.28 m × 0.36 m × 0.27 m in size. The containers had a capillary fed into the side wall ending in an atomizing nozzle, so that when the fertilization computer was activated, the nutrient solution was sprayed onto the plant roots. The nutrient solution then flowed down to the bottom of the bed and on to the collection container, where, when topped up with a new nutrient solution, it fed back into the pepper's root system. The containers were kept out of the sunlight and, in addition, were all covered with double-sided black and white plastic sheeting (Photo S1, Graph S1). Plants were grown in the growing chamber at a density of 2.5 plants per 1 m^2 of growing area.

2.3. Experimental Design and Treatments

The experimental design was completely randomized. The treatments included four different EC combinations and different treatments of the plants with SA.

Combinations tested:

(1) Low EC—plants were fed a standard nutrient solution for peppers with an EC of 3.3 dS m^{-1};
(2) Low EC + SA-f—plants were fed with a standard nutrient solution as in combination (1) and treated with foliar SA (SA-f);
(3) High EC—plants were fed with a nutrient solution 2 × concentrated compared to Low EC, with an EC of 7 dS m^{-1};
(4) High EC + SA-f + SA-r—plants were supplied with a nutrient solution as in the High EC combination (3), treated with foliar SA (SA-f) as in the combination (2), and SA was also applied to the roots (SA-r).

There were 20 plants in each of the four independent beds, fed with the nutrient solution in an aeroponic growing system. The nutrient concentration of the solution, EC, and pH were controlled and maintained at a uniform level suitable for the combination. Plants were cut and managed on two shoots. Immediately after planting the peppers into the aeroponic system, the plants were fed with a standard nutrient solution for peppers with the composition (mg L^{-1}): N-NO_3-195, P-57, K-273, Mg-47, Ca-187, Fe-2, Mn-0.6, B-0.3, Cu-0.15, Zn-0.3, Mo-0.05. The EC of the standard medium feeding the plants in the aeroponic system was 3.3 dS m^{-1}, and the pH was 6.2. The following fertilizers were used to prepare the concentrated media: $Ca(NO_3)_2 \times 4H_2O$; KNO_3; $MgSO_4 \times 7H_2O$, KH_2PO_4, $K_2SO_4 \times 2H_2O$, HNO_3, and Superba/Micromix from Yara International ASA.

Subsequently, on 35 DAS (0 DAT—0 days after treatment with high EC), the nutrient solution in the two combinations tested was changed, increasing the EC by adding twice as much concentrated nutrient solution as in the standard one. The EC of the nutrient solution in the combinations labelled High EC was about 7 dS m^{-1} (High EC and High EC + SA-f + SA-r). In the High EC + SA-f + SA-r combination, 100 ppm SA was added to the nutrient solution. The nutrient solution in each bed was circulated in a closed system (nutrient solution recirculation), the nutrient solution taken up by the plants was replenished daily with a new nutrient solution to a volume of 90 L^{-1}/bed, while once a week, the entire nutrient solution in each bed was replaced with a new nutrient solution. Plants in the combinations Low EC + SA-f and High EC + SA-f + SA-r (38 DAS) were sprayed with SA at a concentration of 5 mmol every 3 days (38–68 DAS). All plants were cut and managed on two fruiting shoots. The shoots left on the plant were wrapped with twine tied to wires stretched on each side of the bed. The first pruning treatment, clearing the plants of side shoots, oldest leaves, and excess flowers and fruit sets, was carried out on 42 DAS, and was repeated weekly thereafter, throughout the growing season, up to 70 DAS. During pruning, buds were removed from the plants, so that there was 1 bud in each internode. An equal number of buds were left on each plant and, for proper fruit nutrition, 2 leaves were left per bud. Eight test plants per combination were randomly selected for all analyses. All removed leaves, side shoots, and fruit set from the test plants were weighed on laboratory scales (d = 0.001 g). The results obtained were used to calculate the total plant weight produced during the 70 DAS period. At the termination of the experiment (70 DAS), the test plants were weighed. The green parts of the test plants (leaves and shoots), all fruit sets, and roots were weighed separately.

2.4. Evaluated Parameters

2.4.1. Morphological Characteristics

Morphological measurements were taken once a week for five weeks. The first plant measurements were taken on 35 DAS (0 DAT), followed by 42 DAS (7 DAT), 49 DAS (14 DAT), 56 DAS (21 DAT), and 63 DAS (28 DAT). Total plant height was measured and the number of fully developed leaves was counted. Up to 70 DAS (35 DAT), the number and

weight of pepper fruit set, and fruit set from the BER, as well as total plant mass produced (leaves, shoots and fruit) and root mass were determined. The ratio of plant weight to pepper root weight depending on the combination was calculated.

2.4.2. Chlorophyll Fluorescence and Chlorophyll Content (SPAD)

The effect of SA on the photosynthetic activity of peppers under high EC nutrient solution conditions was studied by measuring the chlorophyll *a* fluorescence of pepper leaves and the SPAD leaf greenness index, which is correlated with leaf chlorophyll content [29]. Measurements were made on three test plants, on the upper (5th) and lower (10th) fully developed leaf, counting from the top of the fruiting shoot of the plant.

Chlorophyll *a* fluorescence was measured with an FMS-2 fluorimeter (Hansatech Instruments Ltd., King's Lynn, Norfolk, England). Measurements were made in the current light. The saturating light source used was a built-in halogen lamp. The pulse intensity was 8000 µmol m^{-2} s^{-1}, and the pulse duration was 1 s. The following parameters were measured: Fs—steady-state fluorescence yield; Fm'—light-adapted fluorescence maximum; ΦPSII—PSII quantum yield. At the same locations on the pepper leaf after 30 min of leaf acclimatization to darkness by applying special clips, the leaves were illuminated with red light (3500 µmol m^{-2} s^{-1}), and the fluorescence of chlorophyll *a* was measured using a Pocket PEA chlorophyll fluorimeter (Hansatech Instruments Ltd., Pentney, UK). After leaf adaptation to darkness, the following chlorophyll fluorescence parameters were measured: Fv/Fm—maximum photochemical yield of PSII and PI (performance index) plant vitality concerning photosystem I and II [30,31]. The results of chlorophyll fluorescence measurements from the 5th and 10th leaves of the test plant were averaged.

SPAD chlorophyll content was measured using a Minolta SPAD 502 Plus portable meter (Konica Minolta Sensing, Inc., Osaka, Japan), at the same locations on the leaves as chlorophyll fluorescence. Five individual measurements were taken for each leaf and the results were averaged. Measurements were taken on each experimental date: 42 DAS, 49 DAS, 56 DAS, 63 DAS, 70 DAS.

2.4.3. Soluble Protein and H_2O_2 Content

Soluble protein content was determined using the Bradford method [32] and expressed in mg per g of fresh weight (FW).

The modified methodology of Wilmowicz et al. was used for H_2O_2 analysis [33]. Material for the study was collected on 42 DAS and 63 DAS from 5 test plants from each combination (pooled sample). Leaves were taken from the plants directly into bags made of aluminium foil, immediately placed in liquid nitrogen, and then frozen at −81 °C.

Pepper leaves (200 mg) were homogenized with 1 mL of 1% trichloroacetic acid. The homogenates were then centrifuged, the supernatants were transferred to new tubes and adjusted to pH 7.5 (with KOH). The samples were then centrifuged, and 1 mL of supernatant was mixed with 250 µL 3-(dimethylamino)-benzoic acid (19.8 mM) in 0.5 M buffer phosphate (pH 6.5), 230 µL 3-methyl-2-benzothiazolinone hydrazone (0.456 mM) and 20 µL peroxidase (0.25 U). Absorbance (590 nm) was measured and the total H_2O_2 content was expressed as µmol H_2O_2 per gram of fresh weight (µmol g^{-1} FW).

2.4.4. Assays of Antioxidant Enzymes

Extracts for measuring enzymatic activity were prepared by freezing the pepper leaves in liquid nitrogen. An amount of 0.2 g of material was weighed on an analytical scale (d = 0.001 g) and then, ground with 1 mL extraction buffer (50 mM potassium phosphate buffer, pH 7.6, 0.1 mM Na-EDTA). The homogenate was centrifuged at 15,000 rpm for 15 min and the supernatant was used for analyses.

Total SOD activity (U mg^{-1} protein) was investigated by monitoring the superoxide radical-induced nitro tetrazolium blue (NBT) reduction at 560 nm according to the method described by Giannopolitis and Ries [34], with some modifications. An amount of 1 mL of the reaction mixture contained 50 mM potassium phosphate buffer, pH 7.8, 6.5 mM

methionine, 50 µM NBT, 20 µM riboflavin, 10 µM EDTA, and 55 µL enzyme extract. This mixture was mixed and then incubated in the light for 15 min.

Total CAT activity (U mg^{-1} protein) was determined according to the Góth method [35]. For this purpose, 0.2 mL of protein extract was incubated in 1.0 mL of the substrate (65 pmoles per mL hydrogen peroxide in 60 mmol/L sodium potassium phosphate buffer, pH 7.4) at 37 °C for 60 s. Serum catalase activity was linear up to 100 kU/l. If the catalase activity exceeded 100 kU/l, the serum was diluted with phosphate buffer (2- to 1-fold) and the test was repeated. Under these conditions, one unit of catalase degraded 1 pmole of hydrogen peroxide/l min. The enzymatic reaction was stopped by adding 1.0 mL of 8.5 mole/l 3-amino-1,2,4-triazole. The hydrogen peroxide content of the reaction mixture was determined by polarographic analysis and used for calculations. The enzymatic reaction was stopped with 1.0 mL of 32.4 mmol/L ammonium molybdate and the yellow complex of molybdate and hydrogen peroxide was measured at 405 nm against blank.

2.5. Statistical Analysis

Statistical analysis was performed using one-factor and two-factor analysis of variance, ANOVA (Statistica, version 13, Warsaw, Poland). A detailed comparison of means was performed using the Tukey test at a significance level of $\alpha = 0.05$.

3. Results

3.1. SA Concentration for Foliar and Root Treatment

The SA concentrations used in the study for foliar and root treatment of peppers were selected based on the results of the conducted test (Supplementary Material, Tables S1 and S2). Pepper plants sprayed with SA at concentrations of 0 to 10 mmol L^{-1} were shorter, had fewer leaves, and had a lower SPAD index value than the control. Spraying peppers at the seedling stage with SA, regardless of the concentration used for the test, resulted in a significant reduction in plant height and a number of leaves compared to the control (Table S1). SA at a concentration of 10 mmol L^{-1} was toxic to peppers since they had stunted growth, the lowest weight, and few chlorotic leaves, which correlated with the lowest SPAD index values. Based on the results, a concentration of 5 mmol L^{-1}, the highest tested SA concentration tolerated by peppers, was selected for further studies using SA as a foliar spray on pepper plants (Table S1).

Tests for pepper tolerance to the root SA application showed that this SA at concentrations of 150 ppm and lower reduced plant growth, leaf number and weight, shoot diameter, and SPAD index compared to the control. In contrast, the treatment of roots with SA at a concentration of 1000 ppm was toxic to peppers (Table S2). Based on the results, a concentration of 100 ppm SA was selected for further studies with the use of SA for root treatment in pepper cultivation.

3.2. SPAD Index

The high EC of the nutrient solution used in 35 DAS in aeroponic pepper cultivation resulted in a lower SPAD index value in pepper leaves compared to the control (Figure 1). Plants from the control and the Low EC + SA-f and High EC + SA-f + SA-r combinations had a higher relative chlorophyll content in the leaves than those grown at the high EC of the nutrient solution (High EC). High EC of the nutrient solution had a lower effect on the SPAD index, especially in the leaves of younger peppers. Foliar application of SA and, at the same time, root application of SA at High EC of the nutrient solution resulted in an inhibition of the SPAD index value reduction (Figure 1).

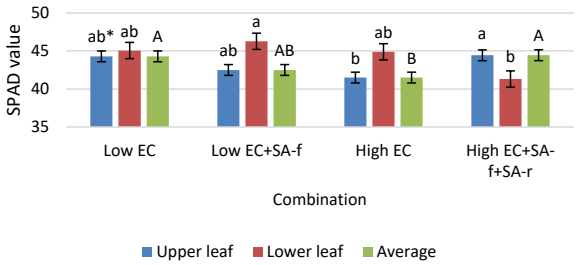

Figure 1. Effect of high EC nutrient solution and SA treatment in aeroponic cultivation on SPAD index in pepper leaves (average of two terms ± SE). * Mean values marked with the same letters do not differ significantly according to the Tukey HSD test at $\alpha = 0.05$. Lowercase letters indicate differences in the interaction of leaves × treatment, capital letters indicate differences between treatments (mean of two terms).

3.3. Morphological Characteristics

In the aeroponic method of cultivation, the application of a high EC nutrient solution on 35 DAS proved to be a stress factor for peppers. On the subsequent days of treatment with the high EC nutrient solution, after 21 DAT and after 28 DAT, a reduction in plant height and leaf number was observed (Figures 2 and 3). In contrast, spraying plants with SA in the combination with the high EC nutrient solution and the simultaneous addition of SA to the nutrient solution (High EC+SA-f+SA-r) did not reduce the negative effect of the high EC nutrient solution on plant height and leaf number (Figures 2 and 3). Plants cultivated under High EC and High EC + SA-f + SA-r combination were shorter and had fewer leaves than plants grown in the other experimental combinations. Peppers growing at Low EC were the highest and had most of the leaves (Figures 2 and 3).

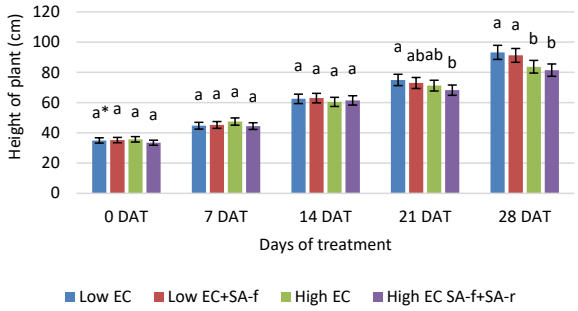

Figure 2. Effect of high EC nutrient solution and SA treatment in aeroponic cultivation on the height of plant in the following days after treating (DAT) pepper plant with high EC (average of two terms ± SE). * Means with different letters indicate a statistically significant difference according to the Tukey HSD test at $\alpha = 0.05$.

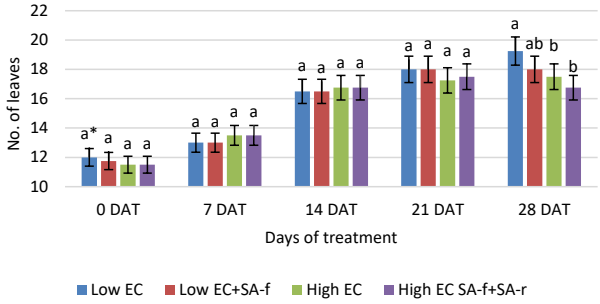

Figure 3. Effect of high EC nutrient solution and SA treatment in aeroponic cultivation on the number of leaves in the following days after treating (DAT) pepper plant with high EC (average of two terms ± SE). * Means with different letters indicate a statistically significant difference according to the Tukey HSD test at $\alpha = 0.05$.

The total weight of fruit sets produced in peppers after 70 DAS using the high EC stress of 35 DAS was the highest in the Low EC and High EC combinations (Table 1). There was no effect of the applied high EC of the nutrient solution in the aeroponic cultivation of peppers on the reduction of fruit set weight after 35 DAT compared to the control. In contrast, spraying of peppers grown with the standard nutrient solution (Low EC) with SA at a concentration of 5 mmol L^{-1}, resulted in a reduction in the total fruit set weight in pepper plants on 70 DAS.

Table 1. Effect of high EC nutrient solution and SA treatment in aeroponic cultivation on biometric characteristics of the pepper plant (average of two terms ± SE).

Parameter	Measurement Dates	Combinations of EC Medium and SA Treatment			
		Low EC	Low EC + SA-f	High EC	High EC + SA-f + SA-r
Total weight of set fruits (g/plant)	Term 1.	423.75 ± 51.45 a*	342.50 ± 38.39 b	421.25 ± 40.62 a	362.50 ± 23.36 ab
	Term 2.	713.75 ± 29.93 a	632.50 ± 38.39 b	711.25 ± 40.62 a	652.50 ± 23.36 ab
	Mean	568.75 ± 42.66 A	487.50 ± 45.71 B	566.25 ± 46.60 A	507.50 ± 40.69 AB
Total number of set fruits (No./plant)	Term 1.	3.75 ± 0.61 b	5.25 ± 0.67 ab	6.25 ± 0.70 a	5.75 ± 0.37 ab
	Term 2.	6.75 ± 0.36 b	8.25 ± 0.67 ab	9.25 ± 0.70 a	8.75 ± 0.37 ab
	Mean	5.25 ± 0.46 B	6.75 ± 0.60 AB	7.75 ± 0.62 A	7.25 ± 0.46 AB
Mean weight of fruit set (g)	Term 1.	113.00 ± 4.54 a	65.24 ± 5.43 b	67.40 ± 4.63 b	63.04 ± 5.90 b
	Term 2.	105.74 ± 2.16 a	76.67 ± 8.39 b	76.89 ± 3.56 b	74.57 ± 4.03 b
	Mean	109.38 ± 2.64 A	70.96 ± 4.95 B	72.15 ± 3.05 B	68.81 ± 3.71 B
Weight of set fruits with BER (g/plant)	Term 1.	423.75 ± 30.43 a	146.63 ± 52.47 b	87.5 ± 48.51 bc	0.00 ± 0.00 c
	Term 2.	448.75 ± 29.94 a	171.62 ± 52.47 b	112.5 ± 48.51 bc	25.00 ± 0.00 c
	Mean	436.25 ± 20.70 A	159.13 ± 35.99 B	100.00 ± 33.30 BC	12.50 ± 3.20 C
Number of set fruits with BER (No./plant)	Term 1.	3.75 ± 0.43 a	1.88 ± 0.48 b	1.25 ± 0.64 bc	0.00 ± 0.00 c
	Term 2.	4.75 ± 0.37 a	2.88 ± 0.48 b	2.25 ± 0.64 bc	1.00 ± 0.00 c
	Mean	4.25 ± 0.28 A	2.38 ± 0.35 B	1.75 ± 0.46 BC	0.50 ± 0.13 C
% set fruit with BER in total weight of set fruits (%)	Term 1.	18.4 ± 3.95a **	14.40 ± 11.24 b	12.50 ± 12.80 bc	0.00 ± 0.00 c
	Term 2.	16.30 ± 1.85 a	12.90 ± 6.74 b	11.50 ± 7.26 bc	8.10 ± 0.14 c
	Mean	17.50 ± 4.94 A	13.70 ± 6.54 B	12.10 ± 7.16 BC	6.80 ± 0.50 C
Total weight of plant (leaves, shoots, set fruits and roots) (g/plant)	Term 1.	1227.50 ± 65.14 a	1059.75 ± 42.59 ab	977.88 ± 73.71 b	969.25 ± 45.88 b
	Term 2.	1677.50 ± 56.25 a	1509.75 ± 42.59 ab	1427.88 ± 73.71 b	1419.25 ± 45.88 b
	Mean	1452.50± 69.65 A	1284.75 ± 64.97 AB	1202.88 ± 76.88 B	1194.25 ± 66.01 B
Weight of green parts of the plant (leaves, shoots and set fruits) (g/plant)	Term 1.	823.75 ± 83.19 a	672.50 ± 40.17 b	720.63 ± 71.17 ab	661.25 ± 43.39 b
	Term 2.	1123.75 ± 51.37 a	972.50 ± 40.17 b	1020.63 ± 71.17 ab	961.25 ± 43.39 b
	Mean	973.75 ± 52.27 A	822.50 ± 47.46 B	870.63 ± 62.16 AB	811.25 ± 48.77 B
Weight of roots (g/plant)	Term 1.	403.75 ± 19.58 a	387.25 ± 7.24 a	257.25 ± 31.35 b	308.00 ± 10.21 ab
	Term 2.	553.75 ± 8.92 a	537.25 ± 7.24 a	407.25 ± 31.35 b	458.00 ± 10.21 ab
	Mean	478.75 ± 20.30 A	462.25 ± 19.98 A	332.25 ± 28.80 B	383.00 ± 20.59 AB
Ratio of green parts of the plant to the weight of roots	Term 1.	2.04 ± 0.08 b	1.74 ± 0.02 c	4.29 ± 0.68 a	2.15 ± 0.09 b
	Term 2.	2.03 ± 0.06 ab	1.81 ± 0.01 b	2.73 ± 0.15 a	2.10 ± 0.06 ab
	Mean	2.03 ± 0.06 B	1.77 ± 0.03 C	3.51 ± 0.36 A	2.13 ± 0.07 B

* Means with different letters indicate a statistically significant difference according to the Tukey HSD test at α = 0.05. Lowercase letters indicate differences in the interaction of crop term × treatment, capital letters indicate differences between treatments (mean of two terms). ** data after Bliss transformation.

The number of fruit sets was lowest in the control and highest at high EC nutrient solution (Table 1). The mean weight of the pepper fruit set was highest in the control. The applied high EC of the nutrient solution (High EC) and the SA foliar (Low EC + SA-f) and foliar treatment with the simultaneous root treatment (High EC + SA-f + SA-r) reduced the average weight of pepper fruit set produced up to 70 DAS (Table 1). In contrast, the weight and number of fruits sets with BER symptoms were the highest in the control with standard Low EC of the nutrient solution. The foliar application of SA to the plants growing at Low EC of the nutrient solution up to 70 DAS, reduced the weight and number of fruit sets with BER. Additionally, the application of High EC of nutrient solution without SA resulted in lower weight and number of fruit sets with BER than in the control. Application of High EC and foliar and root application of SA at 5 mmol and 100 ppm, respectively, had the strongest effect on the reduction of the weight and number of fruit sets with BER, compared to the control. Foliar SA spraying of peppers grown at low nutrient EC decreased the number (by more than 40%) and weight (by about 60%) of fruit sets with BER symptoms compared to plants grown at low nutrient EC. At the same time, foliar and root application

of SA in plants grown at a high nutrient EC decreased the number (by about 70%) and weight (by more than 80%) of fruit sets with BER symptoms compared to plants supplied with a high nutrient EC (Table 1).

Peppers grown aeroponically at the low EC of the nutrient solution produced the highest mass of leaves, shoots, and fruit sets. The lowest values of these parameters were observed for plants from the High EC + SA-f + SA-r combination. It was found that the high EC of the nutrient solution had a negative effect on plant weight. Measurements made after 70 DAS showed that the root weight of plants growing under Low EC was the highest. The foliar application of SA in combination with the Low EC nutrient solution reduced the weight of leaves, shoots, and set fruits, but not root weight. When SA was applied by spray and to the roots in the stress combination (High EC + SA-f + SA-r), an increase in root weight was observed compared to the High EC combination. Total plant and root weights were highest in the Low EC and Low EC + SA-f combination and lowest in the High EC combination. The ratio of total aboveground weight (leaves, shoots, and fruit set) to roots was highest in the High EC combination and lowest in the Low EC + SA-f combination [Table 1].

3.4. Chlorophyll a Fluorescence

The use of high EC of the nutrient solution in pepper cultivation reduced chlorophyll *a* fluorescence parameters of pepper leaves such as Fs, Fm, and PI compared to the control and the other combinations (Table 2). On the other hand, when the nutrient solution was characterized by high EC and SA was applied to the leaves and roots, an increase in maximum light-adapted fluorescence Fm' and overall PSII—PI viability was observed, compared to plants untreated with SA (Table 2). SA-treated plants growing under optimal EC conditions also showed an increase in maximum light-adapted fluorescence Fm' compared to non-treated plants. The statistical analysis showed no significant differences between the combinations for the quantum yield of PSII—ΦPSII and the maximum photochemical yield of PSII—Fv/Fm (Table 2).

Table 2. Effect of high EC nutrient solution and SA treatment in aeroponic cultivation on chosen parameters of chlorophyll a fluorescence of pepper leaves (average of two terms ± SE).

Parameter	Combination			
	Low EC	**Low EC + SA-f**	**High EC**	**High EC + SA-f + SA-r**
Fs	484.66 ± 5.55 a*	493.66 ± 2.87 a	438.33 ± 4.50 b	486.00 ± 5.09 ab
Fm'	1763.66 ± 1.69 c	2003.33 ± 2.36 a	1649.67 ± 0.47 d	1835.33 ± 1.24 b
ΦPSII	0.72 ± 0.00 a	0.72 ± 0.03 a	0.74 ± 0.02 a	0.71 ± 0.01 a
Fv/Fm	0.80 ± 0.00 a	0.80 ± 0.01 a	0.79 ± 0.03 a	0.81 ± 0.00 a
PI	4.95 ± 0.17 a	4.78 ± 0.49 a	4.23 ± 1.00 b	4.67 ± 0.58 a

* Means with different lowercase letters in the same row indicate a statistically significant difference according to the Tukey test ($p \leq 0.05$).

3.5. Content of Soluble Protein and H_2O_2, the Activity of SOD and CAT

In order to precisely investigate the redox homeostasis in pepper leaves in response to different treatment combinations, the H_2O_2 content and activity of antioxidant enzymes: SOD and CAT were determined. In the first step, the soluble protein level was analysed and it was observed that it had a higher value when EC increased. The simultaneous treatment with SA to both low and high-EC-treated plants negatively influenced protein content. The foliar application of SA to the plants cultivated under low EC reduced protein level up to 14.58 mg g^{-1} FW (Figure 4A).

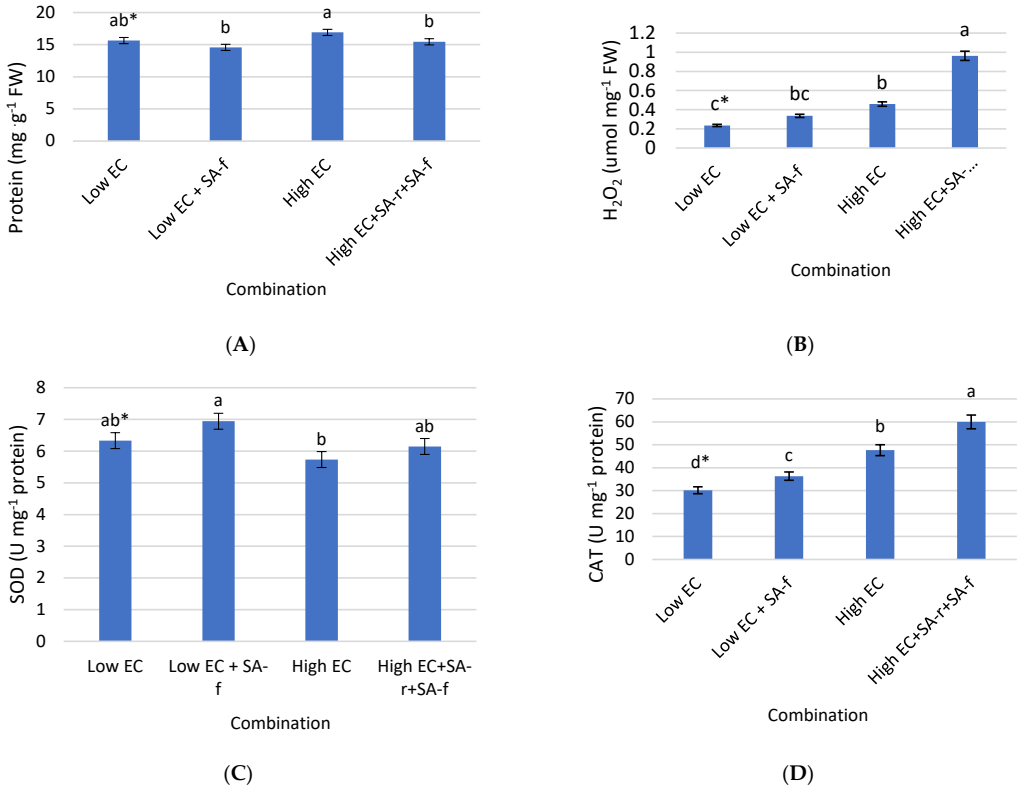

Figure 4. Effect of high EC nutrient solution and SA treatment in aeroponic cultivation on protein content (**A**), H_2O_2 level (**B**), activity of superoxide dismutase (SOD) (**C**) and catalase (CAT) (**D**) in pepper plants (average of two terms ± SE). * Means with different letters indicate a statistically significant difference according to the Tukey HSD test at $\alpha = 0.05$.

The activity of one enzyme responsible for H_2O_2 formation–SOD–fluctuated among different treatments. When EC was higher, the activity of the enzyme decreased. In turn, SA application upregulated SOD activity regardless of the EC value. The maximum activity was observed when leaves were subjected to the simultaneous action of low EC and exogenous SA (Figure 4C). The next step of analyses focused on the determination of the H_2O_2 compound in pepper leaves. As Figure 4B shows, a gradual increase in H_2O_2 content was observed when EC was higher. Strong accumulation of H_2O_2 was noted in plants cultivated under high EC and treated with SA. Then, it reached 0.9 µmol mg^{-1} FW. However, foliar SA spraying on leaves under low EC did not evoke such strong stimulatory effect. One of the antioxidative enzymes dismutating H_2O_2 is CAT; thus, its activity was also determined. A similar tendency for this parameter was observed as the H_2O_2 content. The increasing salt concentration of nutrients upregulated CAT up to ~45 µmol mg^{-1} FW. Moreover, exogenous SA accelerated the activity of the enzyme, especially when it was applied to plants cultivated under high EC. Under these conditions, CAT activity was the highest reaching 60 U mg^{-1} protein (Figure 4D).

4. Discussion

4.1. Selection of a Proper SA Concentration for Foliar and Root Treatment in Peppers

Based on the obtained results, it can be concluded that 5 mmol L^{-1} SA is the most effective for foliar application to pepper plants, since a higher concentration (10 mmol L^{-1}) of this compound evoked toxic effects. On the other hand, 100 ppm SA applied with a nutrient solution in hydro or aeroponic cultivation is recommended for root treatments. A higher concentration of SA (150 ppm) affected plant growth and development and was even toxic for pepper (1000 ppm). There were several reports concerning the positive role of SA in the regulation of the development of this species in hydroponic cultivation.

Ibrahim et al. [18] sprayed pepper leaves with SA at concentrations of 0, 0.5, 1.0, and 1.5 g L^{-1} on the 20th, 40th, and 60th day after transplanting and showed that the foliar application increased vegetative growth rate compared to the control. According to this study, the application of SA at a concentration of 1.5 g L^{-1} enhanced not only growth but also fruit quality and yield. Canakci [36] treated roots of pepper seedlings with different SA concentrations (0; 0.3; 1.5; 5; and 10 mmol) and selected 1.5 mmol SA as optimal for growth improvement.

4.2. Effect of SA on the Morphology, SPAD Index, and Chlorophyll Fluorescence of Pepper Cultivated under Different EC

A study by Vicente and Plasencia [27] proves that the regulatory role of SA depends on the concentration, the plant growth conditions, and the stage of development. It was experimentally confirmed that high concentrations of SA (>1 mM) have a negative effect on plant development and growth. In the present study, there was no positive effect of foliar SA on plant growth, number of leaves, or plant and root weight of peppers grown under standard EC conditions in aeroponic cultivation. In contrast, Souri and Tohidloo [37] showed that foliar application of SA increased plant height and leaf area in tomatoes, while Yildirim and Dursun [38] observed higher growth, yield, and better quality of fruits in this species. On the other hand, Kowalska and Smoleñ [39] reported no effect of salicylic acid on tomato fruit yield. Nevertheless, the most important result obtained in this study was that plants sprayed with SA formed fewer fruits with calcium deficiency symptoms (BER), which is the limiting factor for pepper productivity. Thus, this valuable data can be used to obtain high-quality products in aeroponic cultivation.

The application of a high concentration of the nutrient solution (7 dS m^{-1}) to peppers on 35 DAS under aeroponic conditions induced oxidative stress. According to Aktas et al. [40] and Ahmadi and Souri [41], high EC (5 dS m^{-1}) induced by NaCl, negatively affects pepper growth parameters. Salt stress is one of the main factors affecting plant growth and yield [42], which was confirmed by the obtained results. The exogenous SA applied as a spray and to the roots of plants growing under high EC nutrient reduced the weight and number of BERs, affected the increase in root weight of peppers, increased leaf SPAD values, maximum light-adapted fluorescence Fm' and overall PSII—PI viability compared to non-treated plants [43]. Studies by Tahjib-Ul-Arif et al. [44] and Oliveira et al. [45] showed that exogenous SA had a significant effect on cherry tomato fruit production. The authors revealed that SA optimizes plant uptake of nutrients, increases photosynthetic activity and biochemical processes, with consequent positive effects on plant growth and development under salt stress conditions. It cannot be ruled out that the SA-dependent regulation of crucial processes such as photosynthesis might contribute to the improvement of plant vitality and further better resistance to physiological disorders, such as BER. It is highly possible given the findings of Huang et al. [46], who showed that SA-treatment of *Dendrobium officinale* cultivated under stress conditions upregulated chlorophyll fluorescence parameters, including maximum photochemical PSII yield (Fv/Fm), which allowed the plant to adapt to the stress. Additionally, exogenous SA increased chlorophyll content under drought conditions [47] and salinity [48]. Osama et al. [43] suggested that the regulatory role of SA is connected to the prevention of the reduction of auxin and cytokinin levels, which leads to better cell division of the root apical meristem, thus contributing to the improvement of plant growth and yield. Furthermore, SA can alleviate salt stress by increasing water and nutrient absorption, membrane protection, as it can also interact with ROS signalling pathways and reduce oxidative stress [49].

4.3. SA-Dependent Effect on the Soluble Protein and H_2O_2 Content, SOD and CAT Activity in Pepper Cultivated under Different EC

Salinity, similarly to other stresses, stimulates the synthesis of proteins protecting plant tissues, which is a part of the defence mechanism induced in the plant to deal with adverse environments. That is why, as it was presented here, leaves of pepper cultivated under higher salt concentrations accumulate proteins. These findings are in line with

the results of Agamy et al. [50]. They show that salinity positively regulated soluble protein content in tomato leaves (~37%), even more, when SA was applied. Similarly, Ahmed et al. [51] suggested that the simultaneous action of salinity and SA increased proteins by about 5%. However, the study showed the opposite effect evoked by this plant hormone. Regardless of salt concentration, SA downregulated protein levels in pepper leaves. This is in accordance with previous studies of Shahba et al. [52] and El-Tayeb [53], indicating that SA reduced protein content under salt stress in tomato and barley. Collectively, SA treatment could exert various effects against stress in a species-dependent manner. Furthermore, it cannot be excluded that SA action in the alleviation of salinity stress could be related to the modulation of protein activity even more than their content. So, to better understand this phenomenon, the next analyses focused on the enzyme activity. Abiotic stress causes oxidative stress reflected by an imbalance in ROS generation and their scavenging, e.g., by antioxidant enzymes, such as SOD and CAT. It was not surprising that the content of H_2O_2, as one of the relatively stable ROS, increased under higher salinity. At the same time, SOD activity decreased. On the contrary, SOD activity was found to be upregulated under salt stress in tomato and wheat [54,55]. Based on the presented observations, it may be assumed that H_2O_2 could be formed in the SOD-independent pathway during salinity in pepper. The obtained results indicate that the production of H_2O_2 is stimulated by exogenous SA in pepper leaves, particularly when it was applied to the leaves and roots. Farhadi and Ghassemi-Golezani [56] observed an accumulation of H_2O_2 under salt stress in *Mentha pulegium*, but exogenous SA reversed this effect. A similar trend was noted by Alsahli et al. [55] in wheat; however, 75 mM SA upregulated H_2O_2 content. Concentration-dependent effect of exogenous SA can explain the extensive H_2O_2 production in pepper leaves. Moreover, a strong accumulation of H_2O_2 in the leaves subjected to salinity and double SA application to leaves and roots might be related to its transport from the place of application to the leaves since this molecule has the ability to diffuse across membranes [57]. Such a scenario is possible, given the enzymatic activity of CAT responsible for H_2O_2 detoxification. A high level of this kind of ROS is correlated with increasing CAT activity in every experimental variant suggesting that this enzyme is activated by salinity and exogenous SA and could detoxify such high amounts of H_2O_2 and helps the plant to alleviate stress and survive. The positive role of SA in salinity-evoked antioxidant responses was reported in tomato [58] and rice [59].

The effect of SA treatment of peppers both at low EC and under stress conditions caused by high EC of the nutrient solution in the aeroponic growing system was positive. Stress conditions cause disorders in plant metabolism, resulting in an increased production of ROS. This results in the activation of signalling cascades, leading to acclimatization to the affected conditions [60]. ROS could interact with SA during the stress response. Slight increases in ROS concentrations are thought to induce defence mechanisms, while very high concentrations induce death by cell damage [60,61]. One example of a known signalling function of ROS is the involvement of H_2O_2 in the regulation of stomatal movements [62,63], which could increase Ca transport in xylem tissues and, consequently, reduce the occurrence of BER in SA-treated plants, as was shown in SA-treated peppers.

5. Conclusions

The use of SA in aeroponic cultivation affects the growth and development of peppers. Peppers cultivated in a high concentration of the nutrient solution (EC of about 7dS m^{-1}) showed symptoms of oxidative stress. SA reduced the number and weight of fruit set with calcium deficiency symptoms. The results of the study indicate that the effect of SA in the alleviation of salinity stress in pepper is related to increasing the leaf SPAD index, a maximum light-adapted fluorescence—Fm' and overall PSII viability—PI. Oxidative balance is disrupted by high EC, while exogenous SA activates CAT, which detoxifies high amounts of ROS and helps the plant to alleviate stress.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13030779/s1, Table S1. Effect of SA foliar spraying on chosen pepper plant parameters depending on acid concentration (mean ± SD); Table S2. Effect of SA root-applied on chosen pepper plant parameters depending on acid concentration (average of two terms ± SD); Table S3. Effect of solution with different EC and SA treatment in hydroponic cultivation on height and number of leaves (average of two terms ± SD); Photo S1. (A) Cultivation of peppers in an aeroponic system, where upside-down containers with nozzles for spraying nutrient solution (one for each plant) onto the roots were covered with black and white film, and a container for nutrient solution was installed at the beginning of each bed, which was automatically pumped into the nozzles and fed to the plants (B). A sweet pepper plant cut into two fruiting shoots; Graph S1. Diagram of the conduct of the experiment. Four growing beds, one individual aeroponic system for each combination (20 plants each). Randomly selected test plants for physiological and biochemical measurements are marked (See Photo S1).

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References

1. Sikha, S.; Sunil, P.; Arti, J.; Sujata, B. Impact of water-deficit and salinity stress on seed germination and seedling growth of *Capsicum annuum* 'Solan Bharpur'. *Int. Res. J. Biol. Sci.* **2013**, *2*, 9–15.
2. FAOSTAT. Available online: www.fao.org/faostat/en/#home (accessed on 15 December 2022).
3. Wu, L.; Yang, H.; Li, Z.; Wang, L.; Peng, Q. Effects of Salinity-Stress on Seed Germination and Growth Physiology of Quinclorac-Resistant *Echinochloa crus-galli* (L.) Beauv. *Agronomy* **2022**, *12*, 1193. [CrossRef]
4. Zhang, Y.J.; Gan, R.Y.; Li, S.; Zhou, Y.; Li, A.N.; Xu, D.P.; Li, H.B. Antioxidant phytochemicals for the prevention and treatment of chronic diseases. *Molecules* **2015**, *20*, 21138–21156. [CrossRef] [PubMed]
5. Zaki, N.; Hasib, A.; Eddine, K.C.; Dehbi, F.; El Batal, H.; Ouatmane, A. Comparative Evaluation of the Phytochemical Constituents and the Antioxidant Activities of Five Moroccan Pepper Varieties (*Capsicum Annuum* L.). *JCBPS* **2017**, *7*, 1294–1306.
6. Sanati, S.; Razavi, B.M.; Hosseinzadeh, H. A review of the e_ects of *Capsicum annuum* L. and its constituent, capsaicin, in metabolic syndrome. *Iran. J. Basic Med. Sci.* **2018**, *21*, 439–448.
7. García-Mier, L.; Guevara-González, R.G.; Mondragón-Olguín, V.M.; Del Rocío Verduzco-Cuellar, B.; Torres-Pacheco, I. Agriculture and Bioactives: Achieving Both Crop Yield and Phytochemicals. *Int. J. Mol. Sci.* **2013**, *14*, 4203–4222. [CrossRef]
8. Munshi, M.H.; Issak, H.; Kabir, K.; Hosain, M.T.; Fazle Bari, A.S.M.; Rahman, M.S.; Tamanna, M. Enhancement of growth, yield and fruit quality of sweet pepper (*Capsicum annuum* L.) by foliar application of salicylic acid. *Int. J. Biosci.* **2020**, *17*, 49–56.
9. Hagassou, D.; Francia, E.; Ronga, D.; Buti, M. Blossom end-rot in tomato (*Solanum lycopersicum* L.): A multi-disciplinary overview of inducing factors and control strategies. *Sci. Hortic.* **2019**, *249*, 49–58. [CrossRef]
10. Hepler, P.K.; Winship, L.J. Calcium at the Cell Wall-Cytoplast Interface. *J. Integr. Plant Biol.* **2010**, *52*, 147–160. [CrossRef]
11. Hocking, B.; Tyerman, S.D.; Burton, R.A.; Gilliham, M. Fruit calcium: Transport and physiology. *Front. Plant Sci.* **2016**, *7*, 569. [CrossRef]
12. Ding, X.; Jiang, Y.; Zhao, H.; Guo, D.; He, L.; Liu, F.; Zhou, Q.; Nandwani, D.; Hui, D.; Yu, J. Electrical conductivity of nutrient solution influenced photosynthesis, quality, and antioxidant enzyme activity of pakchoi (*Brassica campestris* L. ssp. Chinensis) in a hydroponic system. *PLoS ONE* **2018**, *13*, e0202090. [CrossRef]
13. Ding, X.; Zhang, H.; Qian, T.; He, L.; Jin, H.; Zhou, Q.; Yu, J. Nutrient Concentrations Induced Abiotic Stresses to Sweet Pepper Seedlings in Hydroponic Culture. *Plants* **2022**, *11*, 1098. [CrossRef]
14. Pérez-Vazquez, E.L.; Monserrat Gaucín-Delgado, J.; Ramírez-Rodríguez, S.C.; de los Ángeles Sariñana-Aldaco, M.; Zapata Sifuentes, G.; Zuñiga-Valenzuela, E. Conductividad eléctrica De La solución Nutritiva Efecto En El Rendimiento Y La Calidad nutracéutica De Pimiento morrón. *Rev. Mex. De Cienc. Agrícolas* **2020**, *11*, 1669–1675. [CrossRef]

15. Rekhter, D.; Lüdke, D.; Ding, Y.; Feussner, K.; Zienkiewicz, K.; Lipka, V.; Wiermer, M.; Zhang, Y.; Petit-Houdenot, Y. Isochorismate-derived biosynthesis of the plant stress hormone salicylic acid. *Science* **2019**, *365*, 498–502. [CrossRef]
16. Ding, P.; Ding, Y. Stories of Salicylic Acid: A Plant Defense Hormone. *Trends Plant Sci.* **2020**, *25*, 549–565. [CrossRef]
17. Veloso, L.L.A.; Lima, G.S.; Silva, A.A.R.; Souza, L.P.; Lacerda, C.N.; Silva, I.J.; Chaves, L.H.G.; Fernandes, P.D. Attenuation of salt stress on the physiology and production of bell peppers by treatment with salicylic acid. *Semin. Ciências Agrárias Londrina* **2021**, *42*, 2751–2768. [CrossRef]
18. Ibrahim, A.; Abdel-Razzak, H.; Wahb-Allah, M.; Alenazi, M.; Alsadon, A.; Dewir, Y.H. Improvement in Growth, Yield, and Fruit Quality of Three Red Sweet Pepper Cultivars by Foliar Application of Humic and Salicylic Acids. *HortTechnology* **2019**, *29*, 170–178. [CrossRef]
19. Mahdavian, K.; Ghorbanli, M.; Kalantari, K.M. Role of Salicylic Acid in Regulating Ultraviolet Radiation Induced Oxidative Stress in Pepper Leaves. *Russ. J. Plant Physiol.* **2008**, *55*, 560–563. [CrossRef]
20. Abou El-Yazied, A. Effect of foliar application of salicylic acid and chelated zinc on growth and productivity of sweet pepper (*Capsicum annuum* L.) under autumn planting. *Res. J. Agric. Biol. Sci.* **2011**, *7*, 423–433.
21. Haytova, D. A review of foliar fertilization of some vegetables crops. *Annu. Rev. Res. Biol.* **2013**, *3*, 455–465.
22. Shaar-Moshe, L.; Blumwald, E.; Peleg, Z. Unique Physiological and Transcriptional Shifts under Combinations of Salinity, Drought, and Heat. *Plant Physiol.* **2017**, *174*, 421–434. [CrossRef] [PubMed]
23. Torun, H. Time-course analysis of salicylic acid effects on ROS regulation and antioxidant defense in roots of hulled and hulless barley under combined stress of drought, heat and salinity. *Physiol. Plant.* **2018**, *165*, 169–182. [CrossRef] [PubMed]
24. Kim, D.S.; Hwang, B.K. An important role of the pepper phenylalanine ammonia-lyase gene (PAL1) in salicylic acid-dependent signalling of the defence response to microbial pathogens. *J. Exp. Bot.* **2014**, *65*, 2295–2306. [CrossRef] [PubMed]
25. Huang, W.; Wang, Y.; Li, X.; Zhang, Y. Biosynthesis and Regulation of Salicylic Acid and N-Hydroxypipecolic Acid in Plant Immunity. *Mol. Plant.* **2020**, *13*, 31–41. [CrossRef] [PubMed]
26. Janda, T.; Szalai, G.; Pál, M. Salicylic Acid Signalling in Plants. *Int. J. Mol. Sci.* **2020**, *21*, 2655. [CrossRef]
27. Vicente, M.R.S.; Plasencia, J. Salicylic acid beyond defence: Its role in plant growth and development. *J. Exp. Bot.* **2011**, *62*, 3321–3338. [CrossRef]
28. Dempsey, D.A.; Klessig, D.F. How does the multifaceted plant hormone salicylic acid combat disease in plants and are similar mechanisms utilized in humans? *BMC Biol.* **2017**, *15*, 23. [CrossRef]
29. Baker, N.R.; Rosenqvist, E. Applications of chlorophyll fluorescence can improve crop production strategies: An examination of future possibilities. *J. Exp. Bot.* **2004**, *55*, 1607–1621. [CrossRef]
30. Strasser, R.J. The Fluorescence Transient as a Tool to Characterize and Screen Photosynthetic Samples. In *Probing Photosynthesis: Mechanism, Regulation and Adaptation*; Yunus, M., Pathre, U., Mohanty, P., Eds.; CRC Press: Boca Raton, FL, USA, 2000; pp. 445–483.
31. Sieczko, L.; Dąbrowski, P.; Kowalczyk, K.; Gajc-Wolska, J.; Borucki, W.; Janaszek-Mańkowska, M.; Kowalczyk, W.; Farci, D.; Kalaji, H.M. Early detection of phosphorus deficiency stress in cucumber at the cellular level using chlorophyll fluorescence signals. *J. Water Land Dev.* **2022**, 176–186. [CrossRef]
32. Bradford, M.M. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal. Biochem.* **1976**, *72*, 248–254. [CrossRef]
33. Wilmowicz, E.; Frankowski, K.; Glazinska, P.; Kesy, J.; Kopcewicz, J. Involvement of ABA in flower induction of *Pharbitis nil*. *Acta So. Bot. Pol.* **2011**, *80*, 21–26. [CrossRef]
34. Giannopolitis, C.N.; Ries, S.K. Superoxide Dismutases: I. Occurrence in Higher Plants. *Plant Physiol.* **1977**, *59*, 309–314. [CrossRef]
35. Góth, L. A simple method for determination of serum catalase activity and revision of reference range. *Clin. Chim. Acta* **1991**, *196*, 143–152. [CrossRef]
36. Canakci, S. Effects of Salicylic Acid on Growth, Biochemical Constituents in Pepper (*Capsicum annuum* L.) Seedlings. *PJBS* **2011**, *14*, 300–304. [CrossRef]
37. Souri, M.K.; Tohidloo, G. Effectiveness of different methods of salicylic acid application on growth characteristics of tomato seedlings under salinity. *Chem. Biol. Technol. Agric.* **2019**, *6*, 26. [CrossRef]
38. Yildirim, E.; Dursun, A. Effect of foliar salicylic acid applications on plant growth and yield of tomato under greenhouse conditions. *Acta Hort.* **2009**, *807*, 395–400. [CrossRef]
39. Kowalska, I.; Smoleń, S. Effect of foliar application of salicylic acid on the response of tomato plants to oxidative stress and salinity. *J. Elem.* **2013**, *18*, 239–254. [CrossRef]
40. Aktas, H.; Abak, K.; Cakmak, I. Genotypic variation in the response of pepper to salinity. *Sci. Hortic.* **2006**, *110*, 260–266. [CrossRef]
41. Ahmadi, M.; Souri, M.K. Growth characteristics and fruit quality of chili pepper under higher electrical conductivity of nutrient solution induced by various salts. *AJAS* **2020**, *42*, 143–152. [CrossRef]
42. Kamanga, R.M.; Mndala, L. Crop abiotic stresses and nutrition of harvested food crops: A review of impacts, interventions and their effectiveness. *Afr. J. Agric. Res.* **2019**, *14*, 118–135.
43. Osama, S.; Sherei, M.; Al-Mahdy, D.A.; Bishr, M.; Salama, O. Effect of salicylic acid foliar spraying on growth parameters, γ-pyrones, phenolic content and radical scavenging activity of drought stressed *Ammi visnaga* L. plant. *Ind. Crops Prod.* **2019**, *134*, 1–10. [CrossRef]

44. Tahjib-Ul-Arif, M.; Siddiqui, M.N.; Sohag, A.A.M.; Sakil, M.A.; Rahman, M.M.; Polash, M.A.S.; Mostofa, M.G.; Tran, L.S.P. Salicylic acid-mediated enhancement of photosynthesis attributes and antioxidant capacity contributes to yield improvement of maize plants under salt stress. *J. Plant Growth Regul.* **2018**, *37*, 1318–1330. [CrossRef]
45. Oliveira, V.K.N.; Lima, G.S.; Soares, M.D.M.; Soares, L.A.A.; Gheyi, H.R.; Silva, A.A.R.; Paiva, F.J.S.; Mendonca, A.J.T.; Fernandes, P.D. Salicylic acid does not mitigate salt stress on the morphophysiology and production of hydroponic melon. *Braz. J. Biol.* **2022**, *82*, e262664. [CrossRef]
46. Huang, C.; Wang, D.; Sun, L.; Wei, L. Effects of exogenous salicylic acid on the physiological characteristics of Dendrobium officinale under chilling stress. *Plant Growth Regul.* **2016**, *79*, 199–208. [CrossRef]
47. Tang, Y.; Sun, X.; Wen, T.; Liu, M.; Yang, M.; Chen, X. Implications of terminal oxidase function in regulation of salicylic acid on soybean seedling photosynthetic performance under water stress. *Plant Physiol. Biochem.* **2017**, *112*, 19–28. [CrossRef] [PubMed]
48. Ghassemi-Golezani, K.; Farhangi-Abriz, S. Foliar sprays of salicylic acid and jasmonic acid stimulate H+-ATPase activity of tonoplast, nutrient uptake and salt tolerance of soybean. *Ecotoxicol. Environ. Saf.* **2018**, *166*, 18–25. [CrossRef]
49. Saleem, M.; Fariduddin, Q.; Castroverde, C.D.M. Salicylic acid: A key regulator of redox signalling and plant immunity. *Plant Physiol. Biochem.* **2021**, *168*, 381–397. [CrossRef]
50. Agamy, R.A.; Hafez, E.E.; Taha, T.H. Acquired resistant motivated by salicylic acid applications on salt stressed tomato (*Lycopersicum esculentum* Mill.). *Am. Eur. J. Agric. Environ. Sci.* **2013**, *13*, 50–57.
51. Ahmed, H.B.; Dhaou, N.; Wasti, S.; Mimouni, H.; Zid, E. Effects of Salicylic Acid on the Growth and Some Physiological Characters in Salt Stressed Tomato Plants (*Solanum Lycopersicum*). *J. Life Sci.* **2011**, *5*, 838–843.
52. Shahba, Z.; Baghizadeh, A.; Ali, V.S.M.; Ali, Y.; Mehdi, Y. The salicylic acid effect on the tomato (*Lycopersicon esculentum* Mill.) sugar, protein and proline contents under salinity stress (NaCl). *J. Biophy. Struct. Bio.* **2010**, *2*, 35–41.
53. El–Tayeb, M.A. Response of barley grains to the interactive effect of salinity and salicylic acid. *Plant Growth Regul.* **2005**, *45*, 215–224. [CrossRef]
54. Krantev, A.; Yordanova, R.; Janda, T.; Szalai, G.; Popova, L. Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. *J. Plant Physiol.* **2008**, *165*, 920–931. [CrossRef]
55. Alsahli, A.; Mohamed, A.K.; Alaraidh, I.; Al-Ghamdi, A.; Al-Watban, A.; El-Zaidy, M.; Alzahrani, S.M. Salicylic acid alleviates salinity stress through the modulation of biochemical attributes and some key antioxidants in wheat seedlings. *Pak. J. Bot.* **2019**, *51*, 1551–1559. [CrossRef]
56. Farhadi, N.; Ghassemi-Golezani, K. Physiological changes of Mentha pulegium in response to exogenous salicylic acid under salinity. *Sci. Hortic.* **2020**, *267*, 109325. [CrossRef]
57. Petrov, V.D.; Van Breusegem, F. Hydrogen peroxide—A central hub for information flow in plant cells. *AoB Plants* **2012**, *2012*, 1–13. [CrossRef]
58. Rodrıguez-Rosales, M.; Kerkeb, L.; Bueno, P.; Donaire, J. Changes induced by NaCl in lipid content and composition, lipoxygenase, plasma membrane H+-ATPase and antioxidant enzyme activities of tomato (*Lycopersicon esculentum* Mill) calli. *Plant Sci.* **1999**, *143*, 143–150. [CrossRef]
59. Jini, D.; Joseph, B. Physiological mechanism of salicylic acid for alleviation of salt stress in rice. *Rice Sci.* **2017**, *24*, 97–108. [CrossRef]
60. Gechev, T.S.; van Breusegem, F.; Stone, J.M.; Denev, I.; Laloi, C. Reactive oxygen species as signals that modulate plant stress responses and programmed cell death. *BioEssays* **2006**, *28*, 1091–1101. [CrossRef]
61. Van Breusegem, F.; Dat, J.F. Reactive oxygen species in plant cell death. *Plant Physiol.* **2006**, *141*, 384–390. [CrossRef]
62. Bhattacharjee, S. Reactive oxygen species and oxidative burst: Roles in stress, senescence and signal transduction in plants. *Curr. Sci.* **2005**, *89*, 1113–1121.
63. Pitzschke, A.; Hirt, H. Mitogen-activated protein kinases and reactive oxygen species signaling in plants. *Plant Physiol.* **2006**, *141*, 351–356. [CrossRef] [PubMed]