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Cucurbita Rootstocks Improve Salt Tolerance of Melon Scions by Inducing Physiological, Biochemical and Nutritional Responses

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Abstract: A hydroponic experiment was conducted to assess whether grafting with *Cucurbita* rootstocks could improve the salt tolerance of melon scions and to determine the physiological, biochemical, and nutritional responses induced by the rootstocks under salt stress. Two melon (*Cucumis melo* L.) cultivars (Citirex and Altinbas) were grafted onto two commercial *Cucurbita* rootstocks (Kardosa and Nun9075). Plants were grown in aerated nutrient solution under deep water culture (DWC) at two electrical conductivity (EC) levels (control at 1.5 dS m^{-1} and salt at 8.0 dS m^{-1}). Hydroponic salt stress led to a significant reduction in shoot and root growths, leaf area, photosynthetic activity, and leaf chlorophyll and carotenoid contents of both grafted and nongrafted melons. Susceptible plants responded to salt stress by increasing leaf proline and malondialdehyde (MDA), ion leakage, and leaf Na^+ and Cl^- contents. Statistically significant negative correlations existed between shoot dry biomass production and leaf proline (r = −0.89), leaf MDA (r = −0.85), leaf Na^+ (r = −0.90), and leaf (r = 0.63) and root (r = −0.90) ion leakages under salt stress. Nongrafted Citirex tended to be more sensitive to salt stress than Altinbas. The *Cucurbita* rootstocks (Nun9075 and Kardosa) significantly improved growth and biomass production of grafted melons (scions) by inducing physiological (high leaf area and photosynthesis), biochemical (low leaf proline and MDA), and nutritional (low leaf Na^+ and ion leakage and high K^+ and Ca^{++} contents) responses under salt stress. The highest growth performance was exhibited by the Citirex/Nun9075 and Citirex/Kardosa graft combinations. Both *Cucurbita* cultivars have high rootstock potential for melon, and their significant contributions to salt tolerance were closely associated with inducing physiological and biochemical responses of scions. These traits could be useful for the selection and breeding of salt-tolerant rootstocks for sustainable agriculture in the future.

Keywords: photosynthesis; chlorophyll; proline; ion leakage; susceptibility

1. Introduction

Salinity is the one of the major environmental stress factors limiting crop growth and productivity in many arid and semiarid regions, in spite of the advanced management techniques developed in recent decades [1]. Worldwide, up to 20% of arable land and up to 50% in irrigated areas is detrimentally affected by salinity, while in Turkey almost 4 million hectares of land has salinity problems [2]. As long

as the current situation in salinization remains, half of the presently cultivated agricultural land may be lost by 2050 [3]. Crops that are grown under excessively saline conditions usually exhibit shorter life cycles or limited plant growth and biomass yield [4]. Internal damages and metabolic disturbances [5], ion toxicity [6], water deficiency in older leaves and carbohydrate deficiency in younger leaves [7], and reductions in root growth, nutrient uptake [8], photosynthetic activity [9,10], and protein synthesis are some of the major problems exhibited by crops grown under salt stress conditions.

As a horticultural crop, melon (*Cucumis melo* L.) has economic significance in the world due to its intensive and wide cultivation particularly in arid and semiarid regions. Global melon production was almost 31.6 million tons (Mt) in 2018 [11], and the main producing countries were China (16 Mt), Turkey (1.8 Mt), Iran (1.6 Mt), and Egypt (1.06 Mt). As melon is an arid and semiarid region crop, several studies have focused on the salt stress problems of melon and have determined that melon is a salt-sensitive or moderately tolerant crop in terms of yield and fruit quality characteristics [12,13]. To improve the salt tolerance of melon for sustainable agriculture production, integrated management strategies that take into consideration improved soil and crop management practices are necessary. Moreover, another way to avoid or reduce salt stress impacts and hinder yield losses in melon production affected by salt stress in high-yielding susceptible cultivars (as scions) would be to graft them onto resistant genotypes (as rootstocks) capable of improving the salt tolerance of the scions. Some studies [7–9] have revealed that *Cucurbita* genotypes exhibit salt tolerance and may therefore be used as rootstocks to improve the growth and yield of some horticultural crops (i.e., cucumber and melon) under salt stress. Grafting onto suitable rootstocks is an important technique in the horticultural area for the suitable cultivation of some Cucurbitaceae and Solanaceae species in Japan, Korea, China, and some other Asian and European countries [14]. Previously, other studies [15–18] were carried out to determine the contribution of grafting to several abiotic stress tolerance mechanisms of many plant species. However, no comprehensive hydroponic studies were found in the literature with regard to the salinity problem of melon plants. Therefore, the aim of the present study was to evaluate whether grafting with hybrid *Cucurbita maxima* × *Cucurbita moschata* rootstocks could improve the salt tolerance of melon scions and to determine the physiological, biochemical, and nutritional responses induced by *Cucurbita* rootstocks under hydroponic salt stress.

2. Materials and Methods

2.1. Plant Material, Treatments, and Experimental Design

A hydroponic trial was set up using an aerated deep water culture (DWC) technique in a fully automated climate room in the Plant Physiology Laboratory of Erciyes University's Faculty of Agriculture, Department of Soil Science and Plant Nutrition, in Kayseri, Turkey. For the vegetation period, the room temperatures were maintained at 25/22 °C (day/night) with a relative humidity of 65–70%. The supplied photon flux in the growth chamber was almost 350 µmol m^{-2} S^{-1} with an intensity of 16/8 h (light/dark) photoperiod. As plant materials, two melon cultivars [Galia type (Citirex F1) and standard type (Kirkagac Manisa Altinbas)] were used as scions, while two commercial *Cucurbita* hybrid (*Cucurbita maxima* × *C. moschata*) cultivars (Kardosa and Nun9075) were used as rootstocks. Maintaining homogeneity among the germinated seedlings is very crucial in a hydroponic study. Therefore, melon seeds were sown 1 week earlier than rapidly growing *Cucurbita* hybrid rootstocks' seeds in multipots containing a mixture of peat (pH: 6.0–6.5) and perlite in a 2:1 (*v*/*v*) ratio for 2 weeks. When the seedlings reached the stage of three or four true leaves, the melon scions were grafted by using the cleft grafting technique onto the *Cucurbita* rootstocks. As control plants, the nongrafted melon varieties were used. For the healing and acclimatization process, the grafted plants were transferred to double-layered and shaded plastic growth boxes and placed in the growth chamber for 7 days. When the healing and acclimatization process was completed, the grafted and nongrafted control plants were removed from the growth medium of the multipots. The roots were washed without root damage, and the stem of each seedling was carefully covered with a thin sponge. After that,

each seedling was placed onto the cover of 8 L plastic pots filled with nutrient solution (modified Hoagland) in the fully automated climate chamber. The sufficiently dissolved oxygen (8.0 mg/L) in nutrient solution was supplied by using a continuously working air pump.

The trial was set up in a completely randomized block design (RBD) with four replicated blocks and two plants of each ungrafted cultivar and cultivar by rootstock combination in each block treated with one of two different electrical conductivity (EC) levels (control at 1.5 dS m^{-1} and salt at 8.0 dS m^{-1}). The salt stress was created by adding NaCl in nutrient solution. The salt application was done gradually in an increasing manner (2 dS/m per day) 5 days after transplanting. The total growth period of the plants from transplant into 8 L plastic pots to final harvest was 42 days after treatment (DAT). To prepare the nutrient solution for the hydroponic experiment, analytical grade (99% pure) chemicals with distilled water were used according to the Hoagland (modified) formulation. In the solution, 2000 µM nitrogen was supplied by using 75% calcium nitrate ($Ca(NO_3)_2$) and 25% ammonium sulfate ($(NH_4)_2SO_4$) as the N sources. Moreover, the composition of the basic nutrient solution was as follows (µM): $CaSO_4$ (1000), K_2SO_4 (500), $MgSO_4$ (325), KH_2PO_4 (250), NaCl (50), H_3BO_3 (8.0), Fe-EDDHA (80), $ZnSO_4$ (0.4), $CuSO_4$ (0.4), $MnSO_4$ (0.4), $MoNa_2O_4$ (0.4). All the nutrients were replaced to prior concentrations when the N concentration in the solution fell from 2.0 mM to below 1.0 mM. Daily nitrogen concentration was checked by nitrate test strips (Merck, Darmstadt, Germany) with the aid of a NitracheckTM reflectometer. Distilled water was added every 2 days to replenish the water lost to evaporation, and the solution was changed weekly.

2.2. Harvest, Shoot, and Root Dry Weight Measurements

At the final harvest, the plants were separated into leaves, stems, and roots. To determine the dry biomass, plant tissues were dried in a forced-air oven at 70 °C for 72 h. They were then weighed on an electronic digital scale. The sum of aerial vegetative plant parts (leaves + stems) is equal to total shoot biomass. To calculate the shoot-to-root ratio, the sum of leaf and stem dry weights was divided by the total root dry weight.

2.3. Leaf Area and Photosynthetic Activity Measurements

Prior to the harvest, nondestructive measurements of the leaf-level CO_2 gas exchange (µmol CO_2 m^{-2} s^{-1}) were performed using a portable photosynthesis system (LI-6400XT; LI-COR Inc., Lincoln, NE, USA). The leaf net photosynthesis measurement (photosynthetically active radiation (PAR) = 1000 µmol m^{-2} s^{-1}, CO_2 at 400 µmol mol^{-1}) was performed on the youngest fully expanded leaves, using four replicate leaves per treatment in the third and fifth weeks of the growth period. Leaf area of the plants was measured destructively during the harvesting process by using a portable leaf-area meter (LI-3100, LI-COR. Inc., Lincoln, NE, USA). Total leaf area was recorded as cm^2.

2.4. Leaf Total Chlorophyll and Carotenoid Content Measurements

A day before harvesting, 100 mg of fresh leaf samples from each replication of the two treatments was taken to measure the leaf total chlorophyll and carotenoid contents using UV–VIS spectroscopy. The samples were put into 15 mL capped containers where 10 mL of 95% (*v*/*v*) ethanol was added. Afterward, to allow for the extraction of the leaf pigments, the samples were held overnight in darkness at room temperature. Measurements were done using a spectrometer (UV/VS T80+, PG Instruments Limited, UK) at wavelengths of 470, 648.6, and 664.2 nm. Total chlorophyll (a-Total-Chlo) and total carotenoids (b-TC) were estimated from the spectrometric readings using the formulae described by Lichtenthaler [19]:

(a) Total-Chlo (mg/g plant sample) = [5.24 WL664.2 − 22.24 WL648.6 × 8.1]/ weight plant sample (g)
(b) TC (mg/g plant sample) = [(4.785 WL470 + 3.657 WL664.2) − 12.76 WL648.6 × 8.1]/ weight plant sample (g).

(Note: WL470, WL648.6, and WL664.2 refer to spectrometric readings at wavelengths 470, 648.6, and 664.2 nm, respectively).

2.5. Proline Contents and Lipid Peroxidation Measurements

The proline contents were measured according to the method described by Bates et al. [20]. To homogenize the plant material, 3% aqueous sulfosalicylic acid was used. After centrifugation of the homogenate mixture at 10,000 rpm, the proline contents were determined in supernatant. To prepare the reaction mixture, 2 mL of acid ninhydrin and 2 mL of glacial acetic acid were used and then boiled at 100 °C for 1 h. Afterwards, the reaction was terminated in an ice bath. For the extraction of the reaction mixture, 4 mL of toluene was used, and then the absorbance was read at 520 nm. Membrane lipid peroxidation was characterized by the main product of lipid peroxidation, the malondialdehyde (MDA) concentration, which was determined according to the method described by Lutts et al. [21].

2.6. Leaf and Root Electrolyte Leakage Measurements

Electrolyte leakage (EL) in leaves and roots was measured according to the method described by Lutts et al. [22]. The youngest fully expanded leaves were used for the EL measurements in between 1100 and 1500 h every 48 h with three replications per treatment. Leaf disks (1 cm^2) were excised from young fully expanded leaves using a cork borer. To clean leaf surface contamination, samples were washed three times with distilled water. Afterwards, the samples were placed in individual stoppered vials containing 10 mL of distilled water.

EL determination in plant roots was done by taking fresh root tips (2 cm in length) from each treatment at the final harvest. The root samples containing 10 mL of distilled water were placed on a shaker (100 rpm) for 24 h at room temperature (25 °C) for incubation. After incubation, the first electrical conductivity (EC1) reading in the solution was performed. After a while, the same samples were placed in an autoclave at 120 °C for 20 min. After termination of the autoclave process, the samples were left at room temperature for cooling, and then the second electrical conductivity (EC2) reading was performed in the solution. The EL was expressed as EL = (EC1/EC2) × 100.

2.7. Mineral Analysis Measurements

To determine mineral element composition, 0.5 g dried leaf tissues were used. Potassium (K^+), calcium (Ca^{++}), and sodium (Na^+) contents were measured by dry ashing at 400 °C for 4.5 h. After that, the ash samples were dissolved in 5 mL of 20% (*v*/*v*) HCl, which was then filtered. The filtered solutions were then diluted with distilled water to a volume 50 mL. An amount of 10 mL was used for inductively coupled plasma atomic emission spectroscopy (ICP-AES) analysis. The ICP-AES results were converted into percentages (%) and parts per million (ppm). Chloride (Cl^-) was determined by precipitation as AgCl and titration according to the method described by Johnson and Ulrich [23].

2.8. Statistical Analysis

Statistical analysis of the data was performed using the PROC GLM procedure of the SAS Statistical Software (SAS for Windows 9.1, SAS Institute Inc., Cary, NC, USA). A two-factor analysis of variance was performed to study the effects of genotype or grafting combination and salt and their interactions on the variables analyzed. The levels of significance are represented at $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), or n.s. as not significant (*F*-test and Pearson correlation coefficients). Differences between the treatments were analyzed using Duncan's multiple range test ($p < 0.05$).

3. Results

3.1. Results and Discussion

3.1.1. Changes in Shoot and Root Biomass Productions and Partitioning

The results indicated that shoot and root dry matter and the shoot-to-root ratio of melon plants were affected significantly ($p < 0.001$) by salt, graft combination, and salt × graft combination interaction (Table 1). Irrespective of the graft combinations, shoot and root growths were affected detrimentally by hydroponic salt stress, and thus significant reductions were found in shoot (49.9%) and root (17.6%) dry matter and shoot-to-root ratio (45.8%) of melon plants under salt stress as compared with the control conditions. It is well-known that crop growth decreased with rising salinity level. Corroborative results were demonstrated in several studies conducted with melon [4,9], watermelon [24,25], cucumber [8], tomato [26], eggplant [27], and pepper [10] under salt stress. Our results clearly indicated that grafting with the *C. maxima* × *C. moschata* hybrid rootstocks had pronounced positive effects on the improvement of growth of melon scions under control and particularly salt stress conditions.

Table 1. Shoot and root dry weight and shoot-to-root ratio of melon graft combinations under control (1.5 dS m^{-1}) and salt stress (8.0 dS m^{-1}) conditions.

Graft Combination	Shoot Dry Weight (g $plant^{-1}$)		Root Dry Weight (g $plant^{-1}$)		Shoot-to-Root Ratio (g g^{-1})	
(Scion/Rootstock)	**Control**	**Salt**	**Control**	**Salt**	**Control**	**Salt**
Altinbas	14.67 e[z]	6.03 f	4.24 a	2.91 cd	3.52 ef	2.05 f
Altinbas/Nun9075	28.02 ab	13.82 e	3.02 bc	3.22 b	9.41 b	4.32 de
Altinbas/Kardosa	25.83 b	15.51 de	2.71 cd	2.81 cd	9.52 b	5.52 cd
Citirex	20.92 c	4.53 f	3.63 ab	1.23 f	5.70 cd	3.83 ef
Citirex/Nun9075	29.04 a	17.51 d	2.31 de	3.20 b	12.81 a	5.52 cd
Citirex/Kardosa	28.12 ab	16.14 de	2.11 e	2.41 de	13.43 a	6.72 c
***F*-test**						
Graft combination	***		***		***	
Salt	***		***		***	
Graft comb. × salt	***		***		***	

[z] Values denoted by different letters are significantly different between graft combinations within columns at $p < 0.05$. Significance of main and interaction effects *F* values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

Significant differences were found between the two melon cultivars and their graft combinations. Nongrafted Citirex showed significantly higher shoot dry matter than nongrafted Altinbas under control conditions, whereas both melon cultivars did not differ significantly in shoot dry matter under salt stress (Table 1). However, shoot dry matter reductions of Citirex (78.5% decline) tended to be more than those of Altinbas (59.2% decline) under salt stress. This might be due to root morphological differences between the two melon cultivars. Nongrafted Altinbas showed a significantly higher root dry matter than Citirex under salt stress (Table 1). Furthermore, Altinbas exhibited similar root dry matter as Nun9075 and Kardosa rootstocks under salt stress. These indicated that Altinbas has a vigorous root system compared with Citirex. The shoot dry matter of Citirex was increased by 288.8% in Citirex/Nun9075 and 257.7% in Citirex/Kardosa graft combinations, whereas the increase in the shoot dry matter of Altinbas was 130.1% in Altinbas/Nun9075 and 158.3% in Altinbas/Kardosa graft combinations under salt stress.

This was also shown by the significantly higher shoot-to-root ratios of Citirex/Nun9075 and Citirex/Kardosa graft combinations under salt stress. The graft combination Altinbas/Nun9075 and nongrafted Altinbas showed significantly lower shoot-to-root ratios in control and salt stress conditions. All the results clearly indicated that grafting with the *Cucurbita maxima* × *C. moschata* hybrid rootstocks significantly improved the salt tolerance of both melon (scions) cultivars. However, the contribution

of both rootstocks to salt tolerance was much higher for Citirex (high sensitivity) than for Altinbas (less sensitivity). Grafted plants usually have strong and vigorous root systems [24], and thus, improved crop growth performance of grafted melons might be the result of more water and nutrient uptake that caused an increase in leaf area and photosynthetic activity of leaves under salt stress.

3.1.2. Changes in Leaf Area, Photosynthesis, Chlorophyll, and Carotenoid Contents

The results indicated that the leaf area, photosynthetic activity of leaves, total chlorophyll content, and carotenoid content of melon plants were affected significantly by salt and graft combination (Table 2). An interaction between salt and graft combination was found only in the total leaf area and carotenoid content. Irrespective of the graft combinations, similar shoot and root biomass reductions under salt stress led to a significant decline in leaf area formation (49.1%), photosynthesis (9.1%), chlorophyll content (14.8%), and carotenoid content (20.4%) of melon plants. This also explains why the shoot and root dry biomass productions (Table 1) of both melon cultivars and their graft combinations were detrimentally affected by hydroponic salt stress, since crop biomass production and yield is strongly dependent on leaf area formation and leaf photosynthetic activity [28]. Our results also correspond to those from the study of Colla et al. [24], who found that salinity decreased the photosynthesis of grafted and nongrafted watermelon plants grown in a hydroponic system. Similar results were also demonstrated with grafted and nongrafted pepper plants under saline conditions [10].

Table 2. Leaf area, photosynthesis, chlorophyll content (a+b), and carotenoid content of melon graft combinations under control (1.5 dS m^{-1}) and salt stress (8.0 dS m^{-1}) conditions.

Graft Combination	Leaf Area (cm^2 $plant^{-1}$)		Photosynthesis (μmol m^{-2} s^{-1})		Chlorophyll (a + b) (mg gr^{-1})		Carotenoid (mg gr^{-1})	
(Scion/Rootstock)	**Control**	**Salt**	**Control**	**Salt**	**Control**	**Salt**	**Control**	**Salt**
Altinbas	3843 d[z]	1767 g	43.4 c	39.2 d	1.72 bc	1.47 d	0.25 ef	0.22 g
Altinbas/Nun9075	4418 c	2459 f	46.1 ab	43.9 bc	1.87 ab	1.59 cd	0.32 ab	0.24 efg
Altinbas/Kardosa	4342 c	2634 f	46.1 ab	42.5 c	2.03 a	1.54 cd	0.35 a	0.23 efg
Citirex	4450 c	1117 h	44.8 bc	38.0 d	1.68 cd	1.49 d	0.26 de	0.22 fg
Citirex/Nun9075	5583 a	3312 e	48.0 a	47.1 ab	1.85 ab	1.62 cd	0.30 bc	0.26 ef
Citirex/Kardosa	4954 b	2749 f	46.1 ab	42.6 c	1.74 bc	1.62 cd	0.29 cd	0.24 efg
***F*-test**								
Graft combination	***		***		*		***	
Salt	***		***		***		***	
Graft comb. × salt	***		n.s.		n.s.		***	

[z] Values denoted by different letters are significantly different between graft combinations within columns at $p < 0.05$. Significance of main and interaction effects F values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***), with n.s. meaning not significant.

That study showed that the photosynthetic activity of pepper leaves decreased as a result of the reduction in chlorophyll and carotenoid contents as salinity level increased in nutrient solution. Similar to our study, a substantial decline in the chlorophyll content of leaves was reported for several horticultural species, such as melon [5] and tomato [26], under salt stress conditions. Furthermore, significant variations existed between grafted and nongrafted melon plants regarding measured parameters at control and salt stress conditions (Table 2). The grafted melons produced 16.3% and 93.43% higher leaf area than the nongrafted melons under control and salt stress conditions, respectively. This clearly indicated that the rootstock contributions to leaf area development of scions (melon) were substantially higher under salt stress than under control conditions. As a result, the reduction in the total leaf area of nongrafted melons was 65.2%, whereas the reduction in grafted melons was only 42.2%. The grafted melons showed 11.7% higher photosynthetic activity than the nongrafted ones under salt stress. This might be due to higher chlorophyll (7.4%) and carotenoid contents (9.4%) of the grafted melons as compared with the nongrafted ones under salt stress. Our results corroborated those of a study that showed that the leaf area of nongrafted watermelon (cv. Tex) was significantly improved

when it was grafted onto two commercial rootstocks, Macis [*Lagenaria siceraria* (Mol.) Standl.] and Ercole (*Cucurbita maxima* Duchesne × *Cucurbita moschata* Duchesne), under salt stress conditions [20].

In our study, significant genotypic variation existed regarding leaf area formation between the two nongrafted melon cultivars under salt stress. Under control conditions, Altinbas and Citirex had similar leaf areas, whereas significantly higher total leaf area was exhibited by Altinbas than Citirex under salt stress. This clearly indicated a significant genotype × salt interaction. The Altinbas total leaf area was reduced by 54.1% under salt stress, whereas the reduction in total leaf area of Citirex was 74.9%. As shown by shoot and root dry matter productions (Table 1), Altinbas can be characterized as a salt-tolerant cultivar due to maintaining high leaf area under salt stress as compared with the salt-sensitive cultivar Citirex (Table 2). On the other hand, the salt-sensitive cultivar Citirex exhibited significantly higher leaf area formation, photosynthetic activity, leaf chlorophyll content, and carotenoid content when it was grafted on Nun9075 and Kardosa rootstocks under salt stress. Although similar rootstock contributions to leaf area formation, photosynthesis, total leaf chlorophyll content, and carotenoid content were recorded with Altinbas/Nun9075 and Altinbas/Kardosa graft combinations under salt stress, the increases were lower than those in graft combinations with Citirex. These results clearly indicated that the two melon cultivars had contrasting salt tolerances (Citirex: sensitive, Altinbas: tolerant) and therefore responded significantly differently when they were grafted with both tolerant rootstocks.

3.1.3. Changes in Proline, Lipid Peroxidation, and Root and Leaf Ion Leakages

The proline content (Figure 1A), lipid peroxidation (MDA) (Figure 1B), and ion leakages in roots (Figure 1C) and leaves (Figure 1D) of melon plants were affected significantly ($p < 0.001$) by salt, graft combination, and salt × graft combination interaction. Regardless of the graft combination, salt stress led to a significant increase in proline (59.1%) and MDA (31.3%) contents and leaf (56.8%) and root (36.7%) ion leakages of salt-treated melons as compared with controls (Figure 1A–D). These are common responses of plants that usually exhibit tolerance strategies as shown in studies with melon [29], cucumber [30], pepper [10,31], and tomato [32]. However, there were significant differences between grafted and nongrafted melons regarding biochemical responses under both control and salt stress conditions (Figure 1A–D). Irrespective of the cultivars, grafted melons produced 24.4%, 2.9%, 0.53%, and 9.1% lower proline, MDA, leaf ion leakage, and root ion leakage, respectively, than nongrafted melon plants under control conditions. Similar contributions of rootstocks to the biochemical responses of melon plants were also observed under salt stress. However, the plants responded much more under salt stress, such that grafted melons produced 27.6%, 29.6%, 13.5%, and 13.2% lower proline, MDA, leaf ion leakage, and root ion leakage, respectively, than nongrafted melon plants. Our results clearly indicated that grafting with the *Cucurbita maxima* × *C. moschata* rootstocks had pronounced contributions to the biochemical responses of the scions (melon) under both control and salt stress conditions. Similar results were observed when the experiment was conducted using different Iranian melon landraces [29].

Nongrafted Altinbas showed significantly higher proline, MDA, and leaf ion leakage than Citirex under control conditions, whereas the root ion leakage of Altinbas was significantly lower than that of Citirex. Without salt stress, significantly lower root ion leakage could be the result of the vigorous root system of Altinbas (Table 1), which leads to its characterization as salt tolerant. However, under salt stress, opposite results were found between the two melon cultivars. Citirex showed significantly higher proline, slightly higher MDA, and significantly higher root ion leakage than Altinbas. This might be due to the sensitivity of the response of Citirex to salt stress. This was confirmed by the results, which revealed that Citirex had increased proline, MDA, leaf ion leakage, and root ion leakage by 231.6%, 80.3%, 91.6%, and 32.7%, respectively, whereas the increase in proline, MDA, leaf ion leakage, and root ion leakage of Altinbas was 97.3%, 43.6%, 58.2%, and 50.1%, respectively, under salt stress as compared with control conditions. Similarly, greater responses were exhibited by Citirex in shoot

and root growth (Table 1), leaf area formation, photosynthesis, and photosynthetic pigment contents (Table 2) under salt stress.

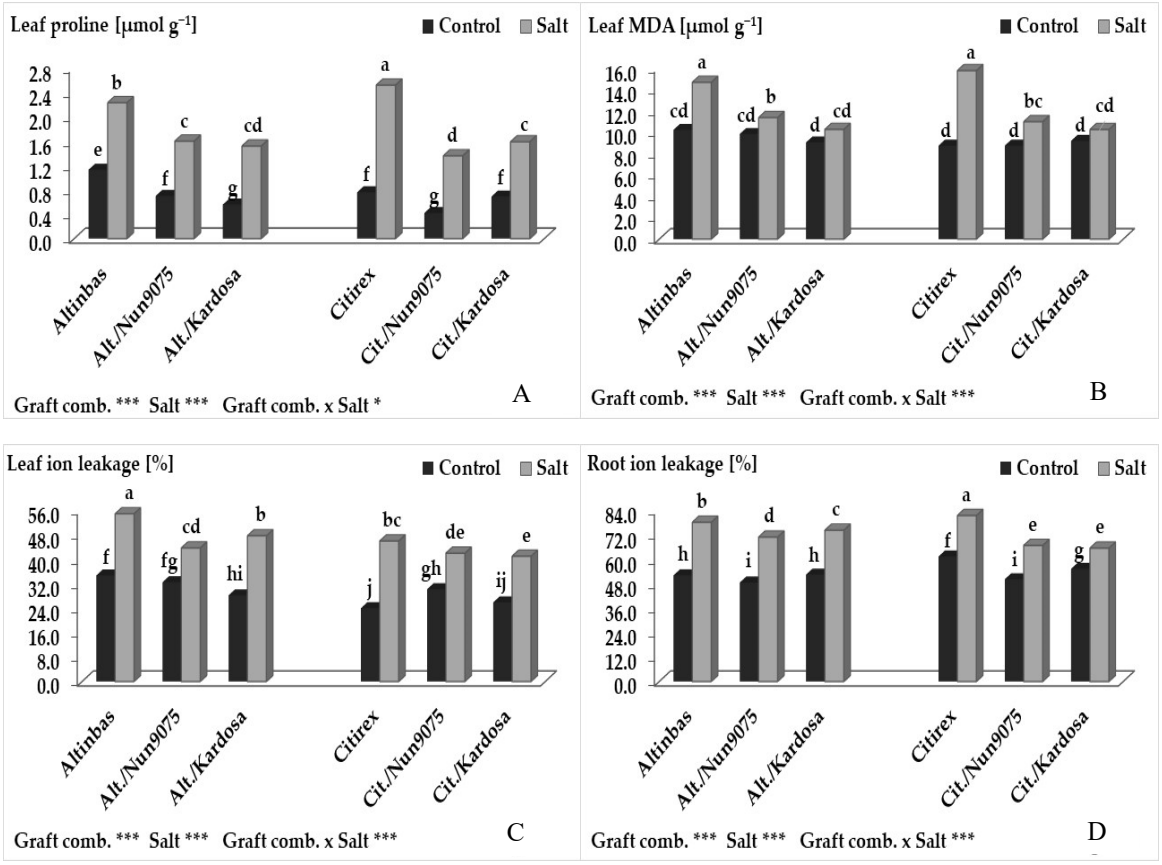

Figure 1. Leaf proline (**A**), malondialdehyde (MDA) (**B**), leaf ion leakage (**C**), and root ion leakage (**D**) of melon graft combinations under control (1.5 dS m^{-1}) and salt stress (8.0 dS m^{-1}) conditions. Values denoted by different letters are significantly different between graft combinations within columns. Significance of main and interaction effects *F* values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

All of the results clearly indicated that Citirex is a salt-sensitive cultivar, whereas Altinbas is a salt-tolerant cultivar. Our results corroborate those from the study of Yasar et al. [27], who concluded that MDA content in leaf tissues of salt-tolerant eggplant genotypes was twofold lower than that of salt-sensitive eggplant genotypes under salt stress. Similar results were also demonstrated by the study of Lutts et al. [21], who elucidated that MDA content was lowest in salt-tolerant rice genotypes, whereas a salt-sensitive rice genotype exhibited the highest MDA content under salt stress.

Interestingly, irrespective of the cultivar, the proline, MDA, leaf ion leakage, and root ion leakage were significantly reduced when they were grafted with Nun9075 and Kardosa rootstocks under salt stress (Figure 1A–D). Although significant reductions existed when Altinbas was grafted onto both rootstocks, significantly lower proline, MDA, leaf ion leakage, and root ion leakage were exhibited only in Citirex/Nun9075 and Citirex/Kardosa graft combinations under salt stress. One of the indicators of tolerance to salt stress is low absolute or proportional ion leakages, which was demonstrated in studies conducted with rice [21], cucumber [30], pepper [31], tomato [32], and melon [29]. Our results again confirmed that grafting with tolerant *Cucurbita maxima* × *C. moschata* rootstocks had pronounced positive effects on the biochemical responses that contribute to the tolerance mechanisms of sensitive scions (melons) under salt stress.

3.1.4. Changes in Leaf Na^+, Cl^-, K^+, and Ca^{++} Uptakes

The leaf Na^+, Cl^-, K^+, and Ca^{++} uptakes of melon plants was significantly ($p < 0.001$) affected by salt, graft combination, and salt × graft combination interaction (Table 3). Irrespective of the graft combination, leaf Na^+ and Cl^- concentrations of melon plants increased by 1137.5% and 1392.3%, respectively, under salt stress as compared with control conditions. It is well-known that Na^+ and Cl^- uptakes of leaves increase with increasing salinity level. A study by Colla et al. [8] demonstrated that the Cl^- concentration of cucumber leaves increased by 300% with salt application regardless of genotype. Similar increases in Na^+ and Cl^- concentrations in leaves have been reported in melon [33], watermelon [25], and pumpkin [6] grown under salt stress. However, we observed significant differences between grafted and nongrafted melons regarding leaf Na^+ and Cl^- uptakes under both control and salt stress conditions (Table 3).

Table 3. Leaf Na^+, Cl^-, K^+, and Ca^{++} contents of melon graft combinations under control (1.5 dS m^{-1}) and salt stress (8.0 dS m^{-1}) conditions.

Graft Combination	Leaf Na^+ (%)		Leaf Cl^- (mg gr^{-1})		Leaf K^+ (%)		Leaf Ca^{++} (%)	
(Scion/Rootstock)	Control	Salt	Control	Salt	Control	Salt	Control	Salt
Altinbas	0.36 f[z]	3.29 a	18.1 f	207 c	3.30 ab	1.25 e	0.40 gh	0.94 e
Altinbas/Nun9075	0.11 g	1.51 d	17.2 f	252 a	3.37 a	3.08 bc	0.50 fg	2.33 b
Altinbas/Kardosa	0.10 g	1.71 c	14.4 f	265 a	3.20 bc	3.02 c	0.36 h	2.17 c
Citirex	0.15 g	2.77 b	15.3 f	150 e	3.36 a	2.27 d	0.40 c	1.29 d
Citirex/Nun9075	0.13 g	1.05 e	12.1 f	225 b	3.37 a	3.14 bc	0.53 f	2.79 a
Citirex/Kardosa	0.08 g	1.50 d	11.3 f	178 d	3.15 bc	3.07 bc	0.42 gh	2.68 a
***F*-test**								
Graft combination	***		***		***		***	
Salt	***		***		***		***	
Graft comb. × salt	***		***		***		***	

[z] Values denoted by different letters are significantly different between graft combinations within columns at $p < 0.05$. Significance of main and interaction effects *F* values: $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

Irrespective of the cultivars, grafted melons exhibited 58.1% and 19.8% lower Na^+ and Cl^- uptakes, respectively, than nongrafted melon plants under control conditions. Similar contributions of rootstocks to Na^+ exclusion were observed, whereas an opposite response was observed in Cl^- uptake in grafted plants under salt stress. Consequently, the grafted melons exhibited 52.1% lower Na^+ uptake than the nongrafted ones under salt stress. However, under the same conditions, the grafted plants showed the opposite, a higher Cl^- uptake (28.7%) than that of the nongrafted melon plants. Excluding the toxic ion in roots and retaining salt in the root and not transporting it to shoots are known biochemical responses of salt-tolerant genotypes [34,35]. In agreement with this characterization, our results clearly confirmed that with the two tolerant *Cucurbita maxima* × *C. moschata* rootstocks, Na^+ uptake might be excluded by the roots, and thus the leaf Na^+ content of the scions (melon) was significantly reduced under salt stress. On the other hand, higher leaf Cl^- uptake of the grafted plants than that of the nongrafted plants disagrees with the salt tolerance characterization studies of Acosta-Motos et al. [34] and Zhu and Bie [35]. However, the study of Colla et al. [33] reported that grafted melon plants had higher leaf Cl^- contents than nongrafted ones under salt stress, which was corroborated by our results. In our study, this result might be due to maintenance of a higher leaf area and photosynthetic activity (Table 2) of the grafted melon plants as compared with the nongrafted ones under salt stress. Chloride can play an essential role in photosynthetic activity by controlling stomatal conductance [36] and osmoregulation [37]. Therefore, the increase in leaf area of the grafted melons with high chloride uptake may be a result of enhancement in cell division rates and cell extension [38].

Irrespective of the graft combination, the leaf K^+ concentration of the melon plants was reduced by 20.1%, whereas the leaf Ca^{++} concentration increased by 353.3% under salt stress as compared with

that under control conditions. The reduction in leaf K^+ uptake under salt stress could be the result of high Na^+ uptake, which usually causes a disruption in ion activities [39] and a specific competition with K^+ for binding sites [40]. Moreover, highly significant differences were found between grafted and nongrafted melon plants regarding leaf Na^+, K^+, and Ca^{++} uptakes under salt stress. As compared with nongrafted melon cultivars, leaf Na^+ uptake was significantly reduced (52.1%), whereas leaf K^+ (75.1%) and Ca^{++} (123.2%) uptakes significantly increased in all graft combinations under salt stress. This indicates that the increase in leaf K^+ might be the result of indirect contributions of substantial Ca^{++} uptake of the grafted plants under salt stress. High Ca^{++} content can maintain membrane stability in roots and leaves by limiting the adverse effects of Na^+ ions on the membrane [41] and leads to decreased Na^+ uptake and increased K^+ uptake [42]. Yetisir and Uygur [43] reported that *Cucurbita* and *Lagenaria* rootstocks expressed mechanisms to avoid physiological damage caused by excessive accumulation of Na^+ ion in leaves and hence showed higher performance than watermelon under salinity stress. In agreement with this study, our results clearly indicated that grafting with two tolerant *Cucurbita maxima* × *C. moschata* rootstocks (Nun9075 and Kardosa) led to an increase in leaf K^+ and Ca^{++} ions and hence caused a decline in the leaf Na^+ ion of the two melon cultivars under salt stress. This might be a useful strategy for preserving membrane stability and maintaining K^+ balance for increasing the tolerance of plants to salt stress [44].

3.1.5. Correlation between Shoot and Root Growths and the other Parameters under Salt Stress

Irrespective of the graft combination, the correlation coefficients between shoot and root dry biomass productions, leaf area formation, and the other parameters of melon plants under salt stress conditions are shown in Table 4. Shoot dry weight and leaf area of salt stress plants were significantly negatively correlated with leaf proline, leaf MDA, leaf Na^+, and leaf and root ion leakages. Similar negative correlations between root dry matters were recorded only with leaf MDA and root ion leakage.

Table 4. Irrespective of the graft combination, the correlation coefficients between shoot and root dry biomass productions, leaf area formation, and other parameters of melon plants under salt stress (8.0 dS m^{-1}) condition.

	Correlation Coefficients under Salt Stress		
Parameters	**Shoot Dry Weight**	**Root Dry Weight**	**Leaf Area**
Shoot dry weight	1.00	0.506 *	0.954 ***
Root dry weight	0.506 *[z]	1.00	0.655 **
Shoot-to-root ratio	0.858 ***	0.005 n.s.	0.717 ***
Leaf area	0.954 ***	0.655 **	1.00
Photosynthesis	0.860 ***	0.644 **	0.852 ***
Chlorophyll	0.653 **	0.215 n.s.	0.583 *
Carotenoid	0.681 **	0.199 n.s.	0.696 **
Leaf proline	−0.896 ***	−0.446 n.s.	−0.816 ***
Leaf MDA	−0.851 ***	−0.501 *	−0.818 ***
Leaf Na	−0.903 ***	−0.262 n.s.	−0.783 ***
Leaf Cl^-	0.541 *	0.712 ***	0.547 *
Leaf K^+	0.831 ***	0.096 n.s.	0.699 **
Leaf Ca^{++}	0.935 ***	0.298 n.s.	0.866 ***
Leaf electrolyte	−0.628 **	0.134 n.s.	−0.504 *
Root electrolyte	−0.900 ***	−0.491 *	−0.895 ***

[z] Levels of significance are represented by $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***) with n.s. meaning not significant (Pearson correlation coefficient, $n = 18$).

On the other hand, all physiological (leaf area, photosynthesis, and chlorophyll and carotenoid contents) and nutritional (leaf K, Ca, and Cl) parameters were significantly positively correlated with shoot dry weight and leaf area under salt stress. All of these results clearly indicated that salt tolerance was closely associated with high shoot biomass production with an extensive photosynthetically

active leaf area formation, but conversely with substantially lower leaf proline, leaf MDA, leaf Na^+, and leaf and root ion leakages. This might be due to common tolerance responses of grafted plants that were usually exhibited as salt tolerance strategies in studies carried out with rice [21], melon [29], cucumber [30], pepper [10,31], and tomato [32].

4. Conclusions

One of the most prevalent abiotic stress factors, salinity usually has harmful effects on crop productive capacity by decreasing yield and quality, particularly in arid and semiarid regions of the world. To solve this problem, grafting with salt-tolerant rootstocks can be an effective management strategy for improving the salt tolerance of crop plants. In this short-term hydroponic experiment, two melon cultivars were grafted onto two different commercial *Cucurbita maxima* × *C. moschata* hybrid rootstocks to assess plant growth performance under control (1.5 dS m^{-1}) and salt stress (8.0 dS m^{-1}) conditions. Results indicated that the shoot and root growths of grafted and nongrafted melon plants were detrimentally affected by salt stress. Significant reductions were recorded in some agronomic and physiological plant responses under salt stress. On the other hand, susceptible plants responded to salt stress by increasing leaf proline and malondialdehyde (MDA), ion leakage, and leaf Na^+ and Cla^- contents. As a result, significant negative correlations existed between shoot dry biomass production and leaf proline (r: −0.89 ***), leaf MDA (r: −0.85 ***), leaf Na^+ (r: −0.90 ***), leaf ion leakage (r: 0.63 *), and root ion leakage (r: −0.90 ***) under salt stress. The two melon cultivars differed significantly in salt tolerance. Nongrafted Citirex tended to be more sensitive than Altinbas to salt stress. The *Cucurbita* rootstock genotypes (Nun9075 and Kardosa) significantly improved the growth and biomass production of the grafted melon scions by inducing physiological (high leaf area and photosynthesis), biochemical (low leaf proline and MDA), and nutritional (low leaf Na and ion leakages and high K^+ and Ca^{++}) responses under salt stress. The highest plant growth performance was exhibited by Citirex/Nun9075 and Citirex/Kardosa graft combinations. All of these suggest that these *Cucurbita* cultivars have a high rootstock potential for melon, and their significant contributions to salt tolerance were closely associated with inducing beneficial plant physiological and biochemical responses of melon scions. Consequently, these traits could be useful for the selection and breeding of salt-tolerant rootstocks for sustainable agriculture in the future.

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