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Article

Differential physiological and biochemical responses of two tomato cultivars to salt stress at the seedling stage

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Abstract: Soil salinity is a major abiotic stress that drastically hinders plant growth and development, resulting in lower crop yields and productivity. As one of the most consumed vegetables worldwide, tomato (*Solanum lycropersicum* L.) plays a key role in the human diet. The current study aimed to explore the differential tolerance level of two tomato varieties (Rio Grande and Agata) to salt stress. To this end, various growth, physiological and biochemical attributes were assessed after two weeks of 100 mM NaCl treatment. Obtained findings indicated that, although the effects of salt stress included noticeable reductions in shoots' and roots' dry weights and relative growth rate as well as total leaf area, for the both cultivars, Rio Grande performed better compared to Agata variety. Furthermore, despite the exposure to salt stress, Rio Grande was able to maintain an adequate tissue hydration and a high leaf mass per area (LMA) through the accumulation of proline. However, relative water content, LMA and proline content were noticeably decreased for Agata cultivar. Likewise, total leaf chlorophyll, soluble proteins and total carbohydrates were significantly decreased; whereas, malondialdehyde was significantly accumulated in response to salt stress for the both cultivars. Moreover, such negative effects were remarkably more pronounced for Agata relative to Rio Grande cultivar. Overall, the current study provided evidence that, at the early growth stage, Rio Grande is more tolerant to salt stress than Agata variety. Therefore, Rio Grande variety may constitute a good candidate for inclusion in tomato breeding programs for salt-tolerance and is highly recommended for tomato growers, particularly in salt-affected fields.

Keywords: tomato; salinity; growth, tolerance; relative water content; proline

1. Introduction

Salinity is considered as a major devastating environmental constraint that drastically decrease the agricultural productivity of soil and results in reduced crop yields, posing a major threat to global food security [1]. Worldwide, it is assumed that nearly 20% of agricultural land and 50% of farmland globally are affected by a varying degree of salinity [2]. In Tunisia, soil salinity is becoming an alarming condition as it affects almost 10% of the global area and 18% of the cultivable lands [3]. The scarcity of rains and the high evapotranspiration, particularly in arid regions, the poor irrigation water and the excessive use of chemical fertilizers as well as the leaching of salts in the irrigated lands due to anthropogenic activities are all factors responsible for soil salinity [4].

Salt stress negatively affects plant growth and development in many ways. It produces physiological drought, nutritional disorders and ion toxicities as well as overproduction of reactive oxygen species (ROS), leading to an oxidative stress [5]. All these effects trigger cellular damage, alteration of several metabolic processes and disturbance of the hormonal equilibrium as well as reduction of cell division and expansion, and even plant death [5,6]. Generally, plants are classified in two types regarding their tolerance to salt stress. Some plant, termed as halophytes, can grow in soil containing more than 200 mM NaCl. By contrast, most other plant species named as glycophytes are salt-sensitive, and their growth and productivity are adversely affected by soil salinity [7].

Tomato (*Solanum lycopersicum* L.) is an important crop plant playing a crucial role in the human diet. Tomato consumption and production are permanently increasing worldwide, due to the protective effects of lycopene that acts as anti-cancer and anti-oxidative product [8]. However, like other crop plants, tomato is frequently exposed to numerous environmental stresses, mainly soil salinity. Considering the tolerance ability, tomato is considered as moderately sensitive to salt constraint, as both growth and yield are negatively affected by salt stress [9]. Nevertheless, besides the salt concentration and stress duration, the impact of soil salinity on plant growth is also dependent on the plant species and even on the cultivar within the same species [10]. As far as tomato is concerned, several previous studies showed that tomato varieties differ widely in their responses to soil salinity, due to their genetic diversity [8,9]. Generally, breeding in tomato by producers is focused on several aspects. Along with quality traits, a great importance is given to breeding for abiotic stresses, particularly salt stress as it is the major threat to tomato production [9]. Thus, the assessment and analysis of the salinity effects on tomato plants constitutes a worth exploring direction to remediate this devastating stress and hence might be useful for selection of salt-tolerant varieties for tomato cultivation in salt-affected soils [11].

Keeping in view the increasing salinity concerns and the importance of tomato crop in the human nutrition, the aim of the current study was to compare the physiological and biochemical responses of two widely-cultivated tomato cultivars, Rio Grande and Agata, to salt stress.

2. Material and methods

2.1. Plant material and growth conditions

Seeds of two widely cultivated tomato (*Solanum lycopersicum*L.) cultivars in Tunisia (cvs. Rio Grande and Agata) [12,13] were germinated in Petri dishes containing filter papers soaked with distilled water for 1 week at 23 °C. Obtained seedlings were grown under controlled greenhouse conditions as described by Horchani et al. [14]. The culture medium contained macro- and micro-nutrients as described by Horchani et al. [15]. Salt treatment was applied, for the two used cultivars, one week after seedlings' transplantation. The concentration of 100 mM NaCl-salinity used in this study was selected based on previous published experiments [16] and was found in many Tunisiansalt-affected fields [3].

2.2. Vegetative growth and water status analysis

Growth-related parameters were determined after a two week-period of NaCl treatment. To this end, roots' and shoots' fresh weights (FW) were determined immediately following seedlings' harvest. Turgor weights (TW) were determined after immersion of the both plant organs for 4 h in closed Petri dishes filled with distilled water. After drying at 80 °C for 24 h, shoots and roots were weighted to determinate the dry weights (DW). Relative growth rate (RGR) was calculated as $(\ln DW_f - \ln DW_0)/\Delta t$[1], where DW_0 and DW_f are the initial and final dry weights, and Δt is the duration of NaCl treatment. Relative water content (RWC) was estimated as described by Sarker and Oba [17]. Leaf area (LA) and leaf mass per area (LMA) were determined as described by Horchani et al. [18].

2.3. K^+ and Na^+ contents determination

K^+ and Na^+ ions extraction was performed from dried leaves and roots using an acid mixture formed of HNO_3 and $HClO_4$, (3/1, v/v) as described by Wolf [19]. K^+ and Na^+ were assayed as described by Boulila-Zoghlami et al. [20].

2.4. Chlorophyll content determination

Chlorophyll content was determined as described by Horchani et al. [18]and calculated as: Chlorophyll (a + b) = $6.1\ OD_{665nm} + 20.04\ OD_{649nm}$ [21].

2.5. Soluble proteins' content determination

Total soluble proteins' contents were measured following the Bradford method [22] and estimated using a standard curve of bovine serum albumin.

2.6. Total carbohydrates' content determination

Total carbohydrates were analyzed using the anthrone-sulphuric acid method [23]. Briefly, approximately 0.1 g of dried leaf and root samples were homogenized in 5 mL of 80% ethanol. The mixture was heated for 30 min at 70 °C and then centrifuged at 6.000 g for 15 min. After separation of the supernatant and the pellet, this latter was resuspended in 5 mL of 80% ethanol and recentrifuged at 6.000 g for 10 min. Thereafter, 250 µl of the crude extract were combined with 5 mL of 0.2% (w/v) anthrone-sulphuric acid solution. The mixture was shaken, boiled at 70 °C for 10 min and then cooled on ice. The absorbance of the mixture was determined spectrophotometrically at 640 nm. A standard curve of glucose was used to determinate the total carbohydrates' contents.

2.7. Proline content determination

Proline contents were determined using the ninhydrin method [24]. Briefly, approximately 0.25g of fresh leaf and root samples was ground in 5 mL of 3% (w/v) aqueous sulphosalicylic acid. After centrifugation at 4 °C at 10.000 g for 10min, the obtained supernatant was added to a mixture containing 2 ml of glacial acetic acid and 2 mL of ninhydrin reagent. The obtained mixture was boiled at 100 °C for 1 h and the reaction was arrested by cooling at 4 °C. Thereafter, the absorbance of the upper layer was measured at 520 nm after addition of 4 ml of toluene to the reaction mixture. A calibration curve of D-proline was used to determinate the proline contents.

2.8. Malondialdehyde content determination

Leaf and root malondialdehyde (MDA) contents were determined following the reaction of thiobarbituric acid [25]. Approximately 0.1 g of plant tissue was ground in 1 mL of 0.25% thiobarbituric acid (TBA) in 10% trichloroacetic acid (TCA). The mixture was centrifuged at 10.000 g for 25 min at 4 °C and 0.2 mL aliquots of the obtained supernatant were mixed with 0.8 mL of 0.25% TBA in 20% TCA. After boiling at 95 °C for 30 min and cooling at 4 °C, samples were centrifuged at 10.000 g for 10 min at 4 °C and absorbance was read at 532 nm. Then, the non-specific absorbance was measured at 600 nm and subtracted from the first reading. MDA contents were determined using a standard curve of MDA.

2.9. Statistics

Statistical analyses were performed using the XLSTAT 2023 software. For all measurements, differences among treatments were compared using the analysis of variance (ANOVA) test. Results at a level of $P \leq 0.05$ were considered significantly different. Each experiment was performed in six replicates and results were presented as means ± S.D.

3. Results and discussion

3.1. Plant growth

3.1.1. Biomass production and relative growth rate

The changes in shoots' and roots' DW productions and RGRs as well as shoot/root ratios for Rio Grande and Agata cultivars over 2 weeks of salt stress treatment are shown in **Table 1**. In response to salt stress, both Rio Grande and Agata cultivars exhibited a decrease in DWs and RGRs. Such decreases were, however, more pronounced in Agata, relative to Rio Grande cultivar. Indeed, shoots' and roots' DWs were decreased by 27 and 35% as well as 43 and 46% for Rio Grande and Agata cultivars, respectively, relative to controls. Contrarily to Agata, for which no obvious effect was observed, the shoot/root ratio was increased by 17% for salt-stressed Rio Grande, as compared to control, indicating allocation of the dry matter to the aerial part for this latter tomato cultivar, under stressful conditions (**Table 1**). Shoots' and roots' RGRs were reduced by 33 and 26% as well as 55 and 50% relative to controls, for Rio Grande and Agata genotypes, respectively (**Table 1**). The decrease in growth-related parameters, i.e., DW production and RGR, was previously reported in Super Marmande and Red River tomato cultivars in response to a 100 mM NaCl-salinity [16] and could be attributed to the disturbance of the carbon-assimilating reactions and to the physiological drought known to be induced by salt stress [26,27]. Furthermore, as the aerial part of a plant is the major site of all its physiological and metabolic processes [28], the allocation of dry matter to this plant part for Rio Grande (**Table 1**) could be a possible explanation for the relative tolerance of this tomato cultivar to salt stress. A potentially positive effect of such a change is maintaining the shoot's ability to supply assimilates to roots and growing tissues, affecting thereby plant growth and survival under saline conditions [29].

Table 1. Effects of NaCl (100 mM) on dry weights (DW), shoot DW/root DW ratio and relative growth rates (RGR) of Rio Grande and Agata tomato cultivars.

		DW (g plant^{-1})		**Shoot/root ratio**	**RGR (day^{-1})**	
		Shoot	**Root**		**Shoot**	**Root**
Rio Grande	C	0.34 ± 0.03^{a}	0.20 ± 0.02^{a}	1.72 ± 0.03^{b}	0.052 ± 0.004^{a}	0.042 ± 0.002^{a}
	S	0.25 ± 0.04^{b}	0.13 ± 0.03^{b}	2.01 ± 0.04^{a}	0.035 ± 0.003^{b}	0.031 ± 0.003^{b}
Agata	C	0.35 ± 0.04^{a}	0.22 ± 0.02^{a}	1.60 ± 0.05^{c}	0.055 ± 0.005^{a}	0.040 ± 0.004^{a}
	S	0.20 ± 0.03^{b}	0.12 ± 0.01^{b}	1.66 ± 0.06^{c}	0.025 ± 0.004^{c}	0.020 ± 0.001^{c}

Note: a, b and c letters indicate significance between treatments. For each analyzed parameter, statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$). C: Control, S: Salinity.

3.1.2. Plant water status

It is known that salt stress induces a plant physiological drought in relation to a decrease of soil water potential [4]. As already reported for lucerne cv. Gabes [14] and durum wheat cv. Karim [30], our findings showed that salt stress significantly decreased shoots' and roots' RWCs by 32 and 24%, respectively, for Agata cultivar. However, the Rio Grande cultivar was able to avoid this salt stress-component, inasmuch as no decreases were observed in shoots' and roots' RWCs following salinity treatment (**Table 2**). Menezes et al. [31] stated that the RWC could be used as a parameter to compare the tolerance/sensitivity of crop plants to salinity, as it reflects the metabolic activities within plant tissues. Herein, since RWC was reduced for Agata and did not change for Rio Grande cultivar (**Table 2**), we presume that Agata is salt-sensitive; whereas Rio Grande is a moderately salt-tolerant cultivar.

Table 2. Effects of NaCl (100 mM) on relative water content (RWC) of Rio Grande and Agata tomato cultivars.

		RWC (%)	
		Shoot	**Root**
Rio Grande	C	82.5 ± 1.5^{a}	75.2 ± 1.0^{a}
	S	78.6 ± 2.2^{ab}	72.8 ± 2.3^{ab}
Agata	C	75.4 ± 2.3^{b}	68.8 ± 1.7^{b}
	S	53.2 ± 3.4^{c}	52.7 ± 1.6^{c}

Note: a, b and c letters indicate significance between treatments. For each analyzed parameter, statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$). C: Control, S: Salinity.

3.1.3. Leaf properties

The decrease in all growth-related characteristics, particularly LA, is a common behavior observed in several plants exposed to salt stress, mainly the sensitive ones [32]. Accordingly, our findings showed reduced LAs for the two salt-stressed-tomato cultivars. This decrease was, however, more prominent for Agata compared to Rio Grande cultivar. Indeed, reductions of 28 and 43% were observed for salt-stresses Rio Grande and Agata cultivars, respectively as compared to controls). Furthermore, since (i) no visual damages such as chloroses and necroses were observed in the leaves of two cultivars and (ii) only reduction in biomass production was noted, it is likely that after a 2-week period of salt treatment, the two tomato cultivars were still, according to the two-phase model established by Munns [33], at the first phase of salt stress and did not reach the second one. The significant decrease in DW production (**Table 1**) could be attributed, according to Pitann et al. [34], to the leaf-growth reduction (**Table 3**). As a consequence, the impairment of the growth of the two tomato cultivars can be ascribed mainly to the osmotic effect of salt stress and not to the toxic ion effects [35,36]. On the other hand, the LMA is a parameter used generally to relate the increases in LA and DW [17]. Results of the present study showed no effect of salt stress on the LMA for Agata genotype; whereas a significant increase of 49% was observed in the LMA of Rio Grande cultivar (**Table 3**). From these results, it could be suggested that salt stress provoked a leaf thickness for Rio Grande and not for Agata cultivar. In *Lyciumbarbarum*, Yao et al. [37] found that salt stress induced the expression of the expansin-like A (*EXLA2*) gene, which augmented the longitudinal expansion of cells of the palisade tissue leading thereby to increased leaves' thickness. The thickening of leaves could be considered as an adaptive strategy to salt stress as it reduces water loss and increases the plant's water retention capacity [37].

Table 3. Effects of NaCl (100 mM) on leaf area (LA) and leaf mass per area (LMA) of Rio Grande and Agata tomato cultivars.

		LA (cm^2 plant^{-1})	**LMA (g m^{-2})**
Rio Grande	C	25.5 ± 2.5^a	1.95 ± 0.30^b
	S	18.3± 1.3^b	2.90 ± 0.21^a
Agata	C	25.1 ± 0.8^a	1.79 ± 0.33^b
	S	14.2 ± 1.1^c	1.80 ± 0.51^b

Note: a, b and c letters indicate significance between treatments. For each analyzed parameter, statistically significant values are indicated by different letters (one way ANOVA test, $p< 0.05$). C: control, S: Salinity.

3.2. K^+ and Na^+ ion contents

The decrease in the K^+ content due to antagonism with Na^+ ions and thus in the K^+/Na^+ ratio is well known competitive processes that generally occur in salt-stressed plants [4]. Our findings showed that leaves' and roots' K^+ contents were remarkably decreased by salt stress, whereas Na^+ contents were significantly increased, with more pronounced effects obtained for Agata, relative to Rio Grande cultivar. As a consequence, leaves' and roots' K^+/Na^+ ratios were noticeably higher for Rio Grande than Agata cultivar (**Table 4**). In line to this, several previous studies stated that the maintain of a high K^+/Na^+ ratio in plant tissues is an indicator of its tolerance to salt stress [1,4,38]. Herein, taking into account the higher K^+/Na^+ ratios for Rio Grande relative to Agata cultivar, we presume that Rio Grande is more tolerant to salt stress as compared to Agata cultivar. It is noteworthy that, contrarily to that was observed for Agata, K^+/Na^+ ratio was significantly lower in leaves than in roots for Rio Grande cultivar (**Table 4**). These results indicate that, contrarily to Agata cultivar, Rio Grande excluded Na^+ ions from leaves, which are the major site of all plant metabolic processes [27]. As Na^+ exclusion from photosynthetic tissues is considered as one of the most important salt tolerance mechanisms [4,38], it can be suggested that Rio Grande is more tolerant to salt stress than Agata cultivar.

Table 4. Effects of NaCl (100 mM) on K^+ and Na^+ contents, and K^+/Na^+ ratios of Rio Grande and Agata tomato cultivars.

		K^+ (mmol g^{-1} DW)		**Na^+ (mmol g^{-1} DW)**		**K^+/Na^+ ratio**	
		Leaf	**Root**	**Leaf**	**Root**	**Leaf**	**Root**
Rio Grande	C	1.45 ± 0.07^a	1.18 ± 0.04^a	nd	nd	nd	nd
	S	0.95 ± 0.05^c	0.78 ± 0.09^b	1.20 ± 0.05^b	1.37 ± 0.03^a	0.75 ± 0.05^a	0.57 ± 0.07^a
Agata	C	1.32 ± 0.06^b	1.11 ± 0.05^a	nd	nd	nd	nd
	S	0.63 ± 0.05^d	0.61 ± 0.08^b	1.63 ± 0.04^a	1.25 ± 0.03^b	0.39 ± 0.04^b	0.49 ± 0.04^b

Note: a, b and c letters indicate significance between treatments. For each analyzed parameter, statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$). nd: not detected, C: control, S: salinity.

3.3. Total chlorophyll contents

As shown in **Figure 1**, our results indicated that, although chlorophyll contents were reduced by salt stress for the both tomato genotypes, the percentage of decrease was significantly much higher for Agata than Rio Grande cultivar (decreases of 54 and 26%, as compared to controls, respectively). Because of its positive correlation with the photosynthetic activity, the chlorophyll content of a plant can be used as an index of its tolerance to salt stress [39]. In wheat, Sairam et al. [40] found significantly higher decrease in chlorophyll content in the salt-sensitive cultivars relative to tolerant ones. Herein, taking into account our findings on total leaf chlorophyll contents (**Figure 1**), we presume that Rio Grande is more tolerant to salt stress as compared to Agata cultivar. The reduction in total chlorophyll content is a typical symptom of the oxidative stress, which occurs always following severe salt stress [41]. Such decrease could be explained either by the reduction in the activities of chlorophyll biosynthesis enzymes or by increased activity of chlorophyllase, enzyme responsible for chlorophyll degradation [42].

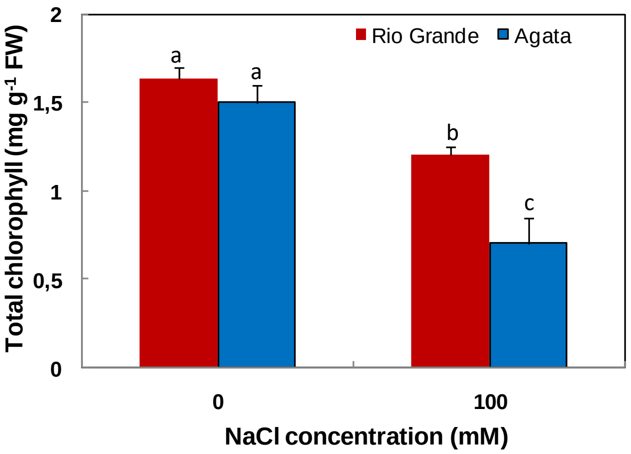

Figure 1. Total chlorophyll contents in leaves of tomato (cvs. Rio Grande and Agata) seedlings under salinity (100 mM NaCl).

Note: Statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$).

3.4. Soluble protein contents

The alteration of protein metabolism is one of the major consequences of salinity in plant tissues [43]. As can be seen in **Figure 2**, our results showed that leaves' and roots' protein contents were decreased by 28 and 30% as well as 42 and 46%, in salt-treated Rio Grande and Agata cultivars, respectively, with respect to controls. The decrease in protein contents in response to salt stress was reported in several plant species, such as *Broussonetia papyrifera* [44], *Medicago sativa* [14] and *Triticum durum* [30]. Such a decrease could be due to the decrease in biosynthesis or the increase in protein degradation by the proteolytic process in response to salt stress [45].

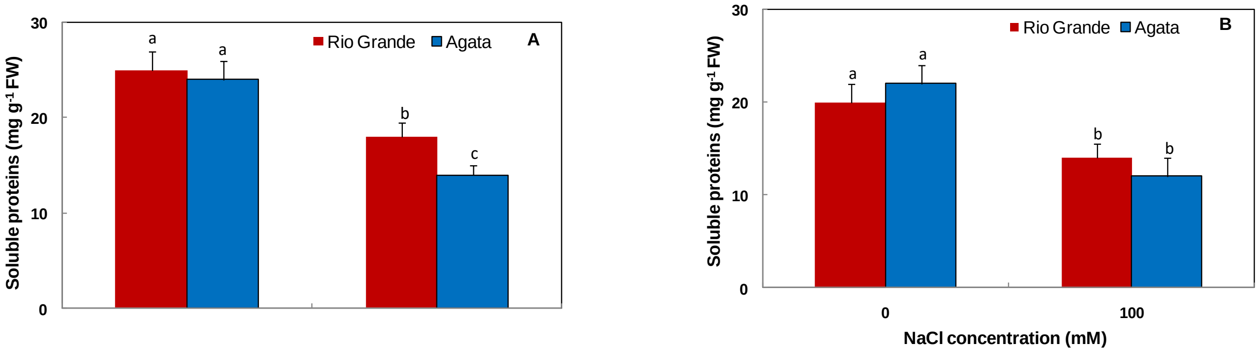

Figure 2. Protein contents in leavesandroots of tomato (cvs. Rio Grande and Agata) seedlings under under salinity (100 mM NaCl). **(A)** leaves; **(B)** roots.

Note: Statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$).

3.5. Total carbohydrates' and proline contents

Results relative to changes in total carbohydrates' and proline contents for the both tomato cultivars in response to salt stress are depicted in **Figure 3**. Salt stress significantly decreased carbohydrates' contents in leaves and roots by 37 and 39% as well as 50 and 40%, in salt-treated Rio Grande and Agata cultivars, respectively, with respect to controls (**Figure 3A,B**). The salt-induced decrease in total carbohydrates was already observed in many other plant species [25,29,30,36] and could be attributed to the reduction of the photosynthetic activities [45] and to the decrease of the chlorophyll content (**Figure 1**).

Our findings indicated that the effects of salt stress on proline contents were tomato variety-dependent. In fact, significantly increased leaves and roots' proline contents of 45 and 34%, respectively, were observed for the salt-stressed Rio Grande cultivar relative to control. However, significant decreases of 30 and 27% were observed in leaves' and roots' proline contents for Agata (**Figure 3C,D**). Proline is a compatible solute playing a crucial role in the osmoregulation of plants submitted to salt stress through lowering the plant osmotic potential below that of the soil solution and, hence, maintaining a driving gradient for water uptake [42]. Several studies showed that the induction of the osmotic adjustment process of a plant is a reliable indicator to its tolerance to salt stress [25,42]. Herein, keeping in view the results on proline contents, it may be suggested that Rio Grande is more tolerant to salt stress as compared to Agata variety. The role of proline in the mitigation of the osmotic component and physiological drought for salt-stressed Rio Grande variety is confirmed in our study by maintaining high shoots' and roots' RWCs, as compared to controls (**Table 1**).

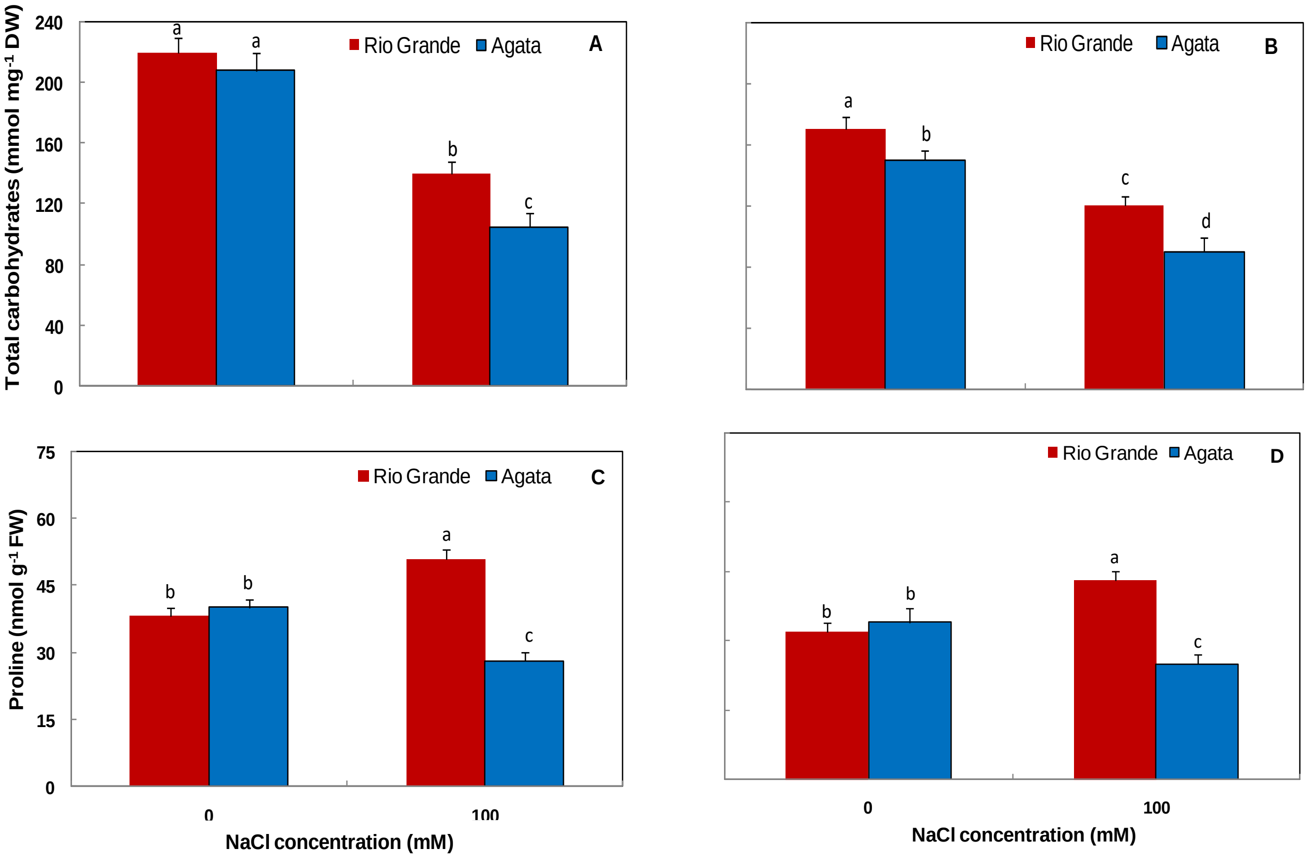

Figure 3. Total carbohydrates' and proline contents in leaves' and roots' of tomato (cvs. Rio Grande and Agata) seedlings under salinity (100 mM NaCl). **(A)** Total carbohydrates in leaves; **(B)** Total carbohydrates in roots; **(C)** Proline in leaves; **(D)** Proline in roots.

Note: Statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$).

3.6. Malondialdehyde contents

It is well known that salt stress generates an oxidative injury indicated by the overproduction of ROS. These ROS disturb all plant' processes both at molecular and biochemical levels [46]. The cellular MDA content reflects, generally, the extent of such oxidative damage in plant cells [47,48]and can be used as a physiological indicator for evaluating the plant's tolerance to salinity [16]. As for many other plant species such as Zea mays [49]and Vicia faba [50], our results indicated that salt stress provoked an oxidative stress for the both tomato cultivars. This oxidative stress is, however, more severe for Agata compared to Rio Grande variety. Indeed, leaves' and roots' MDA contents were increased by 278 and 311%, respectively relative to controls, for Agata. However, increases of only 110 and 125% were observed for Rio Grande (**Figure 4**). These results confirm, once again, that Rio Grande is more tolerant to salt stress than Agata.

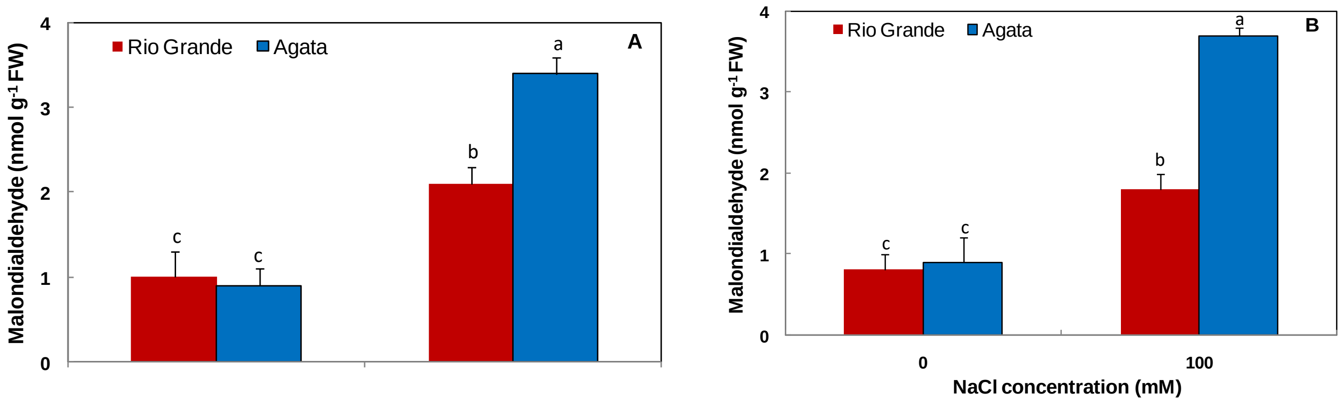

Figure 4. Malondialdehyde contents in leaves and roots of tomato (cvs. Rio Grande and Agata) seedlings under under salinity (100 mM NaCl). **(A)** leaves; **(B)** roots.

Note: Statistically significant values are indicated by different letters (one way ANOVA test, $p < 0.05$).

4. Conclusions

Illumination of the growth characteristics as well as the physiological and biochemical attributes, in response to soil salinity at the seedling stage, can be used as efficient criteria to select salt-tolerant varieties for tomato cultivation in salt-affected soils. As a whole, results of the current study provide strong arguments highlighting the significant level of tolerance of Rio Grande to salt stress, relative to Agata variety. Therefore, the Rio Grande variety could be highly recommended for tomato cultivation in salt-affected soils.

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