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Does the Source of Nitrogen Affect the Response of Tomato Plants to Saline Stress?

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Abstract

The aim of the present study was to investigate the effects of the source of nitrogen (N) nutrition on the response of tomato (*Solanum lycopersicum* L. cv. Rio Grande) plants to saline stress (100 mM NaCl). To this end, plant growth, chlorophyll and carbohydrate levels, ion contents as well as N compounds and main N-metabolizing enzymes (nitrate reductase and glutamine synthetase) were analyzed in salt-treated and control plants grown in the presence of either NO_3^-, NH_4^+, or the mixture of NO_3^- and NH_4^+. Our results showed that plant growth declined under saline stress but NO_3^--fed plants were less sensitive to salinity than NH_4^+-fed plants. This different sensitivity was due mainly to a better maintenance of root growth and root nitrate reductase activity in NO_3^--fed plants. Concomitantly, leaf chlorophyll content was significantly decreased, regardless of the N source. Salinity affects the uptake of several nutrients in a different way, depending on the N source. Thus, sodium was accumulated mainly in NH_4^+-fed plants, especially in roots, displacing other cations such as $NH_4^+$and potassium. It is concluded that the N source is a major factor affecting tomato responses to saline stress, plants being more sensitive when NH_4^+ is the source used. The different sensitivity is discussed in terms of a competition for energy between N assimilation and sodium exclusion processes.

Key Words: Tomato, Nitrogen, Salinity, Growth

Introduction

Plants are constantly challenged by environmental constraints that reduce growth and crop yield. Among the adverse environmental factors commonly encountered by land plants, salinity is one of the most significant abiotic stresses [1].

Soil salinity is considered a major factor threatening crop production in arid and semiarid regions, where soil salt content is naturally high and precipitation can be insufficient for leaching [2]. In Tunisia, like many regions of the world, soil salinity is one of the most important abiotic stresses limiting plant growth and development. In fact, 1.5 million ha (10% of the whole territory and 18% of the arable lands) are affected by salinity [1].

In contrast to the situation with halophytes, for which a salt tolerance mechanism has been widely identified, the physiology of salt tolerance for glycophytes is still debated vigorously [3]. Although most crop species are glycophytes, there is a wide spectrum of salt sensitivity. Thus, tomato plants are considered as a salt-sensitive species [4]. Besides interspecific differences in salt sensitivity, there are others factors that can affect the response of plants to salt-stress. Thus, the form in which nitrogen (N) is supplied to salt-stressed plants can influence the salinity response, although recent literature on this subject is inconclusive. Thus, some authors have described, a greater sensitivity when ammonium (NH_4^+) is the N form used [5], similar effects, regardless of the source of N nutrition [6] or an even greater sensitivity to salinity when plants were grown with nitrate (NO_3^-) [7].

The detrimental effects of salinity on plant growth may be divided into three broad categories: i) a reduction in the osmotic potential of the soil solution that reduces the amount of water available to the plant, ii) specific Na^+ toxicity, and iii) inhibition of the uptake of several nutrients causing nutrient imbalances in the plant [8]. Each of the different components of salt stress affects different aspects of plant metabolism, and can be influenced in a different way by the N source.

Plants grown under saline conditions absorb large amounts of Na^+. These ions have detrimental effects on plant metabolism and in most instances, growth inhibition in salt-sensitive species, even at low salinity, is caused primarily by its toxicity [9]. Plants are presumed to have mechanisms to avoid this Na^+ accumulation, which involve sequestration of Na^+ into vacuoles and/or exclusion of these ions to the apoplast [3]. NaCl evacuation from the cytosol to the external and vacuolar lumen implies an increase of the maintenance energy costs [10]. The control of Na^+ accumulation might be important physiological processes conferring salt tolerance in plants [11], and this control can be related to N nutrition since the source of N nutrition can lead to differences in the accumulation patterns of these ions [5]. Nutrient imbalances can result in salt-stressed plants in various ways. Imbalances may result from the effect of salinity on nutrient availability, competitive uptake, transport or partitioning within the plant [12]. Various interactions of Cl^- and Na^+ with the uptake of different ions have been widely described: Na^+ interacts with Ca^{2+} and with K^+, and Cl^- with NO_3^- [13]. Na^+ uptake also suppresses NH_4^+

uptake [14]. Thus, it appears that the effect of salinity on nutrient imbalance is dependent on the N source.

In this study, we investigated the effects of the source of N on the response of tomato plants (*Solanum lycopersicum* L. cv. Rio Grande), a salt sensitive species, to a moderate salt stress (100 mM NaCl). Plant growth, chlorophyll concentration, and carbohydrate levels, as well as N compounds and ion contents were analyzed in salt-treated and control plants grown in the presence of either NO_3^-, NH_4^+, or the mixture of NO_3^- and NH_4^+. In addition, the activities of two major enzymes involved in N metabolism (nitrate reductase and glutamine synthetase) were analyzed in roots and leaves of salt-treated and control plants.

Material and Methods

Plant material and culture conditions

Tomato (*Solanum lycopersicum* L. cv. Rio Grande) seeds were germinated on filter paper moistened with distilled water at 23°C in the dark. Six days after germination, seedlings were grown hydroponically in a growth chamber (16 h light at 23°C/8 h dark at 18°C with an irradiance of 350 µmol m^{-2} s^{-1}, and 75-80% relative humidity). Each seedling was placed in a 25 mL vermiculite plug on a polystyrene tray floating nutrient solution, with six plants per 10 L tank [15]. At this moment, saline and nitrogen treatments were initiated. Plants were fed either with the basic nutrient solution (2.5 mM for each N source), with 5 mM nitrate supplied as $Ca(NO_3)_2$, or 5 mM ammonium supplied as $(NH_4)_2SO_4$. Salt treatments consisted of 0 mM (control) and 100 mM (saline) NaCl. The pH of the solutions was controlled daily and restored to 5.8 as in Horchani *et al.* [16]. The nutrient solutions were renewed twice a week to restore nutrients to their original concentrations. The micronutrient composition of the nutrient solution was as described by Saglio and Pradet [17].

Vegetative growth analysis

Growth parameters were evaluated 21 d after salt-treatment application. Plants were harvested and separated into roots and shoots. Roots were washed in distilled water. Fresh weights (FW) were immediately determined for roots and shoots. Dry weights (DW) were obtained by weighing the plant material after drying at 80°C until a constant mass was reached. Water content (WC) was calculated as (FW – DW) / DW.

Ions, chlorophyll and sugar determination

Ions were extracted from dried plant material (50 mg DW) in an acid mixture (HNO_3:$HClO_4$, 3/1, v/v). K^+ was assayed by flame emission photometry (Corning, UK). Na^+, Ca^{2+}, and Mg^{2+} were determined by atomic absorption spectrophotometry (Perkin Elmer, Courtaboeuf, France). Chlorophyll measurement was performed according to Wintermans and Mots [18], and total chlorophyll concentration was calculated as in Horchani *et al.* [19]. Total soluble carbohydrates were extracted in 80% (v/v) methanol and assayed in leaves and roots using the anthrone-sulfuric acid method as described in Horchani *et al*. [20].

Nitrogen compounds assay

Root and leaf samples were ground thoroughly with mortar and pestle in 500 mM Tris-HCl (pH 7.5), and centrifuged at 20,000 g for 10 min. The supernatant was analyzed for nitrate, nitrite, and total soluble proteins. Ammonium was extracted using 6% (w/v) TCA as in Horchani *et al.* [19]. Nitrate and ammonium were assayed spectrophotometrically in sample extracts by the salicylic acid-sulfuric acid method [21] and the phenol-hypochlorite method [22], respectively. Total soluble proteins were measured according to Bradford [23] using γ-globulin as a standard.

Enzyme assays

Nitrate reductase (NR) and glutamine synthase (GS) activities were extracted and assayed as described in Horchani *et al.* [24].

Statistics

Statistical data analysis was made using the Student's t-test. The results are given as means with standard errors of at least six replicates per treatment. The significance of differences between the control and the treatment mean values was determined at the significance level of $p<0.05$. Experiments were replicated two to three times.

Results

Vegetative growth analysis

Saline and nitrogen (N) treatments were applied, in the present study, at the moment of plant transplanting. The changes in the root and shoot dry weights (DW), in shoot-to-root ratio and in root and shoot water contents (WC) were investigated after a 21-d period of either control or saline conditions. Under control conditions, the use of NH_4^+ as a sole N source (Horchani *et al.,* 2010b) or in the presence of NO_3^- led to a significant increase in root and shoot biomass production compared to NO_3^--fed plants. Contrary to shoot-to-root ratio, root and shoot WC were significantly increased for NH_4^+ and NO_3^- + NH_4^+-fed plants compared to plants grown with NO_3^- (Table 2).

Plants grown under saline conditions produced less root biomass than control plants, this effect being more pronounced in NH_4^+ or NO_3^- + NH_4^+-fed plants that in those fed with NO_3^- alone. No differences were observed in shoot dry matter reduction, due to saline stress between both sources of N (Table 2). The use of NO_3^- as a sole N source had no effect on shoot-to-root ratio. In NH_4^+ and NO_3^- + NH_4^+ nutrition, the marked negative effect of salinity on root growth is illustrated by a significantly higher shoot-to-root ratio in salt-treated compared to control plants (Table 2).

Salt-treated plants grown under NH_4^+ showed a slight lower root and shoot WC, compared to control plants. By contrast, root and shoot WC were slightly increased by salinity for NO_3^--fed plants. No obvious differences were observed for plants grown in the presence of the two N forms (Table 2).

Table 1. Macroelement content of the nutrient solution. Values are expressed in mM

	N-source		
	NO_3^-	NH_4^+	NO_3^- + NH_4^+
K_2HPO_4	1.00	1.00	1.00
KCl	0.20	0.20	0.20
$MgSO_4.7H_2O$	0.64	0.64	0.64
$Ca(NO_3)_2.4H_2O$	2.50	0.00	1.25
$(NH_4)_2SO_4$	0.00	2.50	1.25
$CaSO_4.2H_2O$	0.00	2.50	1.25

Table 2. Dry weight (DW) and water content (WC) of control (C) and salt-treated (T) tomato *(Solanum lycopersicum* L. cv. Rio Grande) plants grown for three weeks under 5 mM NO_3^-, 5 mM NH_4^+ or 2.5 mM NO_3^- + 2.5 mM NH_4^+. Values are the mean ± S.D. from six measurements. *The significance of differences between the control and the treatment mean values was determined by the Student's t-test at the significance level of $p<0.05$

		N-source		
	Treatment	NO_3^-	NH_4^+	NO_3^-+ NH_4^+
Root DW (g^{-1} plant)	C	0.25 ± 0.03	0.37 ± 0.05	0.38 ± 0.06
	T	0.18 ± 0.01*	0.14 ± 0.04*	0.16 ± 0.04*
Shoot DW (g^{-1} plant)	C	1.35 ± 0.15	1.97 ± 0.21	1.89 ± 0.16
	T	1.12 ± 0.11	1.74 ± 0.25	1.77 ± 0.27
Shoot/Root ratio	C	6.13	4.80	4.97
	T	6.22	12.42*	11.06*
Root WC (ml g^{-1}DW)	C	12 ± 1.4	16 ± 2.1	17 ± 1.1
	T	16 ± 0.9*	12 ± 1.3*	16 ± 2.3
Shoot WC (ml g^{-1}DW)	C	17 ± 0.8	22 ± 2.5	21 ± 1.9
	T	20 ± 1.1*	17 ± 2.1*	20 ± 1.5

Ions, chlorophyll and sugar determination

Roots and leaves were analysed for their Na^+, K^+, Ca^{2+} and Mg^{2+} contents (Fig. 1). Root and leaf Na^+ content were significantly increased in plants grown under saline conditions. By contrast, K^+, Ca^{2+} and Mg^{2+} contents were significantly decreased. These effects were more pronounced in NH_4^+ or NO_3^- + NH_4^+-fed plants in comparison to those fed with NO_3^- alone.

Chlorophyll content was significantly decreased in salt-treated compared to control plants. This effect being more pronounced in NH_4^+-fed plants in comparison to those fed with NO_3^- + NH_4^+ or NO_3^- alone (Table 3).

Under control conditions, roots and leaves of NH_4^+ or NO_3^- + NH_4^+-fed plants showed higher carbohydrate concentrations than did the roots and the leaves of NO_3^--fed plants. In NH_4^+ nutrition, saline treatment decreased root and leaf carbohydrate concentrations by 34% and 21%, respectively, whereas no significant effects were observed when plants were grown in the presence of NO_3^- alone or in the presence of the two N forms (Table 3).

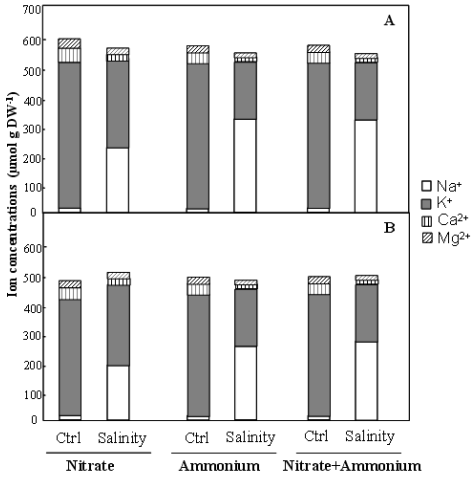

Figure 1. Mineral content in roots (A) and leaves (B) of tomato plants as affected by nitrogen nutrition (5 mM NO_3^-, 5 mM NH_4^+ or 2.5 mM NO_3^-+ 2.5 mM NH_4^+) and salinity (0 and 100 mM NaCl). Values represent the mean (n = 6)

Table 3. Total leaf chlorophyll, and root and leaf carbohydrate concentrations of control (C) and salt-treated (T) tomato *(Solanum lycopersicum* L. cv. Rio Grande) plants grown for three weeks under 5 mM NO_3^-, 5 mM NH_4^+ or 2.5 mM NO_3^- + 2.5 mM NH_4^+. Values are the mean ± S.D. from six measurements. *The significance of differences between the control and the treatment mean values was determined by the Student's t-test at the significance level of $p<0.05$

		N-source		
	Treatment	NO_3^-	NH_4^+	NO_3^-+ NH_4^+
Total chlorophyll (mg g^{-1} FW)	C	0.65 ± 0.08	1.43 ± 0.12	1.12 ± 0.07
	T	0.41 ± 0.05*	0.52 ± 0.06*	0.76 ± 0.09*
Root carbohydrates (nmol mg^{-1} DW)	C	72 ± 3.4	124 ± 5.1	87 ± 7.7
	T	66 ± 4.2	82 ± 8.1*	74 ± 6.5
Leaf carbohydrates (nmol mg^{-1} DW)	C	235 ± 9.3	270 ± 13.6	265 ± 9.8
	T	224 ± 10.2	213 ± 5.7*	251± 11.3

Table 4. Nitrate, ammonium and soluble-protein concentrations in roots and leaves of control (C) and salt-treated (T) tomato *(Solanum lycopersicum* L. cv. Rio Grande) plants grown under three N-nutrition regimes (5 mM NO_3^- , 5 mM NH_4^+, 2.5 mM NO_3^- + 2.5 mM NH_4^+) for 21 d. Values are the means of six replicates ± S.D. *Significant differences between the control and the treatment means according to the Student's t-test at $p < 0.05$. 'nd' denotes 'not detected'

		N-source		
	Treatment	NO_3^-	NH_4^+	NO_3^-+ NH_4^+
Root nitrate content	C	48 ± 2.5	nd	36 ± 1.8
(µmol g^{-1} FW)	T	43 ± 4.1	nd	41 ± 4.7
Leaf nitrate content	C	27 ± 1.5	nd	25 ± 3.4
(µmol g^{-1} FW)	T	13 ± 2.3*	nd	12 ± 0.9*
Root ammonium content	C	0.4 ± 0.05	3.1 ± 0.15	0.9 ± 0.12
(µmol g^{-1} FW)	T	0.3 ± 0.07	1.8 ± 0.21*	0.6 ± 0.08*
Leaf ammonium content	C	0.2 ± 0.02	1.3 ± 0.31	0.8 ± 0.07
(µmol g^{-1} FW)	T	0.1 ± 0.02*	0.8 ± 0.15*	0.5 ± 0.05*
Root protein content (mg g^{-1} FW)	C	6.1 ± 0.8	8.3 ± 1.3	6.5 ± 0.9
	T	4.3 ± 0.6*	4.1 ± 1.0*	4.6 ± 0.7*
Leaf protein content (mg g^{-1} FW)	C	2.2 ± 0.2	3.1 ± 0.7	2.7 ± 0.4
	T	1.6 ± 0.2*	1.5 ± 0.4*	1.7 ± 0.3*

Table 5. Nitrate reductase (NR) and glutamine synthetase (GS) activities in roots and leaves of control (C) and salt-treated (T) tomato *(Solanum lycopersicum* L. cv. Rio Grande) plants grown under three N-nutrition regimes (5 mM NO_3^- , 5 mM NH_4^+, 2.5 mM NO_3^- + 2.5 mM NH_4^+) for 21 d. Values are the means of six measurements ± S.D. *Significant differences between the control and the treatment means according to the Student's t-test at $p < 0.05$

		N-source		
	Treatment	NO_3^-	NH_4^+	NO_3^-+ NH_4^+
Root NR activity (nmol NO_2^- formed min^{-1} g^{-1} FW)	C	18.4 ± 2.5	2.1 ± 1.4	13.5 ± 1.8
	T	21.2 ± 3.1	2.4 ± 1.1	9.1 ± 0.9*
Leaf NR activity (nmol NO_2^- formed min^{-1} g^{-1} FW)	C	13.7 ± 1.5	1.3 ± 1.0	10.6 ± 1.4
	T	9.1. ± 1.3*	0.9 ± 1.3	7.2 ± 0.7*
Root GS activity (nmol GHM min^{-1} g^{-1} FW)	C	20.9 ± 1.2	40.1 ± 2.5	35.7 ± 2.2
	T	16.3 ± 1.7*	29.8 ± 2.1*	25.1 ± 1.1*
Leaf GS activity (nmol GHM min^{-1} g^{-1} FW)	C	14.2 ± 0.7	31.3 ± 1.3	31.8 ± 1.7
	T	11.6 ± 1.0*	23.8 ± 1.5*	22.5 ± 1.5*

Nitrogen compounds analysis

When plants grew with NO_3^-, it was observed that NO_3^- was accumulated mainly in roots, whereas it was not detected in tissues of plants grown with NH_4^+. Salinity decreased shoot NO_3^- accumulation and it had no any effect on root NO_3^- accumulation under NO_3^- as well as N mixed nutrition (Table 4). Tomato plants accumulated NH_4^+ mainly in their roots. Moreover, this accumulation was greater in NH_4^+-fed plants compared with plants grown under NO_3^- + NH_4^+ or with NO_3^- alone. Leaf NH_4^+ content was significantly decreased by salinity, regardless of the N source. Root NH_4^+ content was significantly decreased in salt-treated plants compared to control plants, under NH_4^+ and N mixed nutrition, whereas no obvious difference was observed under NO_3^- nutrition. Soluble protein concentrations were significantly decreased by salinity in roots and leaves, regardless of the N source (Table 4).

Nitrate reductase and glutamine synthetase activities

Activities of nitrate reductase (NR) and glutamine synthetase (GS) were assayed in roots and leaves of control and salt-treated tomato plants grown for 21 d under the three N-nutrition regimes (Table 5). Under NO_3^--nutrition, leaf and root GS activities were slightly decreased in salt-treated compared to control plants. Simultaneously, leaf NR activity was significantly decreased, whereas no obvious difference was observed in root NR activity. Under NH_4^+ and N-mixed nutrition, root and leaf GS activities were significantly decreased in salt-treated compared to control plants. Concomitantly, root and leaf NR activities were slightly decreased, under N-mixed nutrition. A low constitutive level of root and leaf NR was observed, under NH_4^+ nutrition without any exogenous added NO_3^- (Table 5).

Discussion

The conclusions from the numerous studies on the response of plants grown with different N sources (NO_3^-or NH_4^+) to salt stress are variable. Thus, a higher sensitivity to salinity in NH_4^+-fed plants has been described [5], no effect of N source on the response to salt stress [25], and a greater sensitivity to salinity when plants were grown with NO_3^- [7]. To explain these different results, it is important to recognise that plant species vary in their sensitivity to NH_4^+ [26] and this could cause different responses to salt stress under different N sources. In a previous work [24], we have shown that tomato plants (*Solanum lycopersicum* L. cv. Rio Grande) are tolerant to NH_4^+ nutrition since this N source ameliorated the plant growth, compared with NO_3^--fed plants. Thus, we have investigated, in this work, the effect of a 100 mM salt treatment in tomato plants grown with both sources of N nutrition. Our results showed that NH_4^+-fed plants were more sensitive to salinity than NO_3^--fed plants since growth inhibition by salt was greater in NH_4^+-fed plants. Salinity may decrease biomass production, due to a low soil water potential, specific Na^+ and Cl^- toxicity, or inhibition of the uptake of several nutrients causing nutrient imbalances in the plant [8]. To determine whether a water deficit or ion toxicity/ imbalance, or both, is the predominant constraint on plant growth, it is important to take into account the salinity level and the duration of exposure to stress. Thus, in plants exposed to high salinity levels for short periods, water deficit is the principal constraint, whereas in plants exposed for long periods, which is more typical of field conditions, ion toxicity and imbalance are more important [27]. Plant species differ greatly in their growth response to salinity, thus, tomato plants have been described as a salt sensitive species and a 100 mM NaCl-salinity produces visible symptoms of salt damage [4]. This study was done at the same salinity level (100 mM NaCl), but for a longer period (21 days), so that the observed growth reduction could have been the result of an ion toxicity/imbalance rather than a water deficit. This was confirmed by the fact that the water relations changed slightly under saline stress (Table 2), whereas ion content was affected significantly (Fig. 1; Table 4).

Stressed-plants accumulated chloride and sodium, and this accumulation could have a negative effect on plant metabolism [28]. Our results show that tomato plants grown

under saline conditions absorbed large amounts of Na^+, mainly the NH_4^+-fed plants, which accumulated this cation in their roots, displacing other cations such as K^+ and NH_4^+. These differences in ion content could be, at least in part, responsible for the greater sensitivity of NH_4^+-fed plants to saline stress.

Salinity interferes with N acquisition and utilisation [29]. Saline conditions can influence the different steps of N metabolism, such as uptake, reduction, and protein synthesis, that may be responsible, at least in part, for the observed reduction in plant growth rate. This effect on N metabolism and growth may vary with different N sources [7]. Our results showed that NO_3^- and NH_4^+ uptake was decreased by salinity. Previous works demonstrated that salinity affects NO_3^- uptake at two levels: by direct competition of Cl^- with NO_3^-, and at the level of the membrane and/or the membrane proteins by changing plasmalemma integrity [30]. Inhibition of NH_4^+ uptake by salinity could be due to direct competition with Na^+ and to the depolarising effect of NaCl on the plasmalemma [31]. These changes in N uptake are correlated with a decrease in NO_3^- and NH_4^+ contents (Table 4) and a decrease in NR and GS activities (Table 5), under NH_4^+ nutrition.

We have found a close relationship between root growth inhibition, Na^+ accumulation in roots (Fig. 1) and a decrease in root protein content of NH_4^+-fed plants (Table 4) under saline conditions. In attempting to explain this fact, it is important to take into account that both NH_4^+ accumulation and Na^+ extrusion are energy-dependent processes.

Nitrate uptake and assimilation appear to be energetically more expensive than the uptake and assimilation of NH_4^+, not least because the NO_3^- ion is reduced to NH_4^+ after uptake [32]. However, despite this extra cost of assimilation, the energetic balance is not at all clear. NO_3^- ions can accumulate in vacuoles, so most plant species can tolerate high NO_3^- concentrations without any sign of toxicity. However, most authors observe that NH_4^+ absorbed by the plant must be rapidly metabolised into organic N compounds [26] since high amount of free NH_4^+ can be toxic. The assimilation of NH_4^+ takes place mainly in the roots which avoids the accumulation of NH_4^+ ions in the leaves requiring a high energy cost of producing carbon skeletons through respiration, in order to incorporate this NH_4^+ into organic N [24].

Under saline conditions, tomato plants accumulated Na^+, mainly in the roots of NH_4^+-fed plants, displacing other cations such as K^+ and NH_4^+. At the cellular level, plants can export Na^+ from the cytoplasm to the extracellular space via plasmalemma Na^+/H^+ antiports, with H^+-ATPases operating at the plasmalemma providing the H^+ electrochemical gradient [33]. Thus, in roots of NH_4^+-fed plants, two processes are competing for the energy: NH_4^+ assimilation and Na^+ exclusion. This fact is reflected by a decrease in protein content in the roots (Table 4) and an increase in Na^+ content (Fig. 1). Na^+ is an ion that is toxic for different aspects of plant metabolism [34]. However, Na^+ toxicity depends on its cellular compartmentation. Thus, the Na^+ toxic effect is less when this cation is accumulated in the vacuoles than when it is accumulated in the cytosol. Although Na^+ is assumed to be accumulated mainly in the vacuole, the capacity of compartmentation is dependent on the species and the N source. Thus, tomato plants are glycophytes and their compartmentation may begin to break down under saline conditions [35]. On the other hand, studies done with tomato showed that the intracellular compartmentation capacity of NH_4^+-grown plants was considerably less than that of NO_3^--grown plants [26].

In summary, the salt-sensitivity of tomato plants grown with NH_4^+ was found to be greater than that of NO_3^--fed plants, due to a reduction in root growth. This fact was correlated with a greater Na^+ accumulation in roots of NH_4^+-fed plants. The competition for ATP by N assimilation and Na^+ exclusion could be responsible, at least in part, for this difference in sensitivity, dependent on the N nutrition.

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