

Growth, yield and fruit quality of Mexican tomato landraces in response to salt stress

Peter LADEWIG^{1a}, Libia I. TREJO-TÉLLEZ^{2b},
Roselia SERVÍN-JUÁREZ¹, Adriana CONTRERAS-OLIVA¹,
Fernando C. GÓMEZ-MERINO^{2*}

¹College of Postgraduates in Agricultural Sciences Campus Córdoba, Manuel León, Amatlán de los Reyes, Veracruz, Mexico; peter.ladewig@yahoo.de; roseliasj@colpos.mx; adricon@colpos.mx

²College of Postgraduates in Agricultural Sciences Campus Montecillo, Montecillo, State of Mexico, Mexico; tlibia@colpos.mx; fernandg@colpos.mx (*corresponding author)

^{ab}These authors contributed equally to the work

Abstract

The Mexican tomato landraces ‘Campeche’, ‘Oaxaca’, ‘Puebla’, and ‘Veracruz’, and the commercial hybrid ‘Vengador’ were evaluated in response to four levels of NaCl (0, 30, 60 and 90 mM) applied through the nutrient solution in a hydroponic system under greenhouse conditions. Yield and dry biomass weight of roots, stems and leaves were reduced by increasing salinity stress, while fruit quality characteristics were improved, with the magnitude of the changes being genotype-dependent. The landrace ‘Veracruz’ produced the lowest yield, 1.06 t ha⁻¹ under control conditions and 0.59 t ha⁻¹ when treated with 90 mM NaCl, amounting to a 44% reduction that was, however, the lowest yield decrease among all genotypes tested. Paradoxically, ‘Veracruz’ was the only landrace displaying a reduction in the root/shoot ratio when exposed to high salinity, indicating more sensitivity to salinity as compared to the other landraces and the hybrid tested. ‘Campeche’ performed the poorest in response to salinity with the most pronounced yield reductions, recording 71.1%, 80.1% and 89.6% yield decreases when comparing plants exposed to 30, 60 and 90 mM to the control, respectively. Although at each salinity level the ‘Veracruz’ fruits showed the highest °Brix value as compared to the other landraces and the hybrid, ‘Oaxaca’ and ‘Puebla’ fruits had a greater increase in °Brix between the control and 90 mM NaCl (109.2% and 110.4%, respectively). With 90 mM NaCl, ‘Oaxaca’ fruits also registered the highest decrease in pH (6.1%) and the highest increase in total soluble sugars (106.7%) with respect to the control.

Keywords: abiotic stress; heirloom; sodium chloride; *Solanum lycopersicum*; salt tolerance

Introduction

Salinity due to the excessive accumulation of salt in the rhizosphere is a global problem and is considered to be one of the most widespread causes of soil degradation and yield limitation, with sodium chloride (NaCl) being the most abundant and soluble salt (Manaa *et al.*, 2011; Ladeiro, 2012). Recent data on the global extent

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of salinity-affected area is rare and existing data shows a wide range of values. It is estimated that 23% of all cultivated area is affected by salinity and 5% by secondary salinity, as a result of human activities (Tanji and Wallender, 2012). Efforts to reclaim land affected by salinity and maintain nutrient balances are costly and energy intensive with only temporary success, so the introduction of salt-tolerant crop species capable of producing economic yields is a creditable alternative (Singh *et al.*, 2012).

The tomato plant is considered moderately sensitive to salinity and according to Singh *et al.* (2012), most commercial cultivars display yield reduction at high salinity implied by electrical conductivity values above 2.5 dS m^{-1} , but large variation among genotypes exists in regard to response to salinity (Manaa *et al.*, 2011; Oztekin and Tuzel, 2011). In tomato the increasing salinity reduces the dry biomass of leaves, stems, fruits and roots (Agong *et al.*, 2004; Parvin *et al.*, 2015); furthermore, it can positively modulate tomato fruit metabolism and improve the sensorial/nutritional value of the production (D'Amico *et al.*, 2003).

Mexico as the place of final domestication of the tomato provides a high diversity of genetic resources of wild and native tomato varieties that allow discovering abiotic stress tolerance traits, including salt tolerance (Blanca *et al.*, 2012; Velasco-Alvarado *et al.*, 2017). Before the release of the first commercial tomato hybrid cultivar in 1946, breeding was performed with open pollinated varieties which could be considered landraces or heirlooms (Bai and Lindhout, 2007). Interestingly, high-density production of Mexican native tomato landraces is reported for the states of 'Veracruz' and 'Puebla' in the years before 1948 (Jenkins, 1948). While most tomatoes produced nowadays in Mexico are commercial hybrid cultivars of the 'Roma', round and cherry types, there is little documentation of the production of native tomato landraces, locally named "tomate criollo". These tomatoes are sold regionally and vary widely in shape, size, flavor and names. Velasco-Alvarado *et al.* (2017) classified some of these traditional native varieties according to fruit size and shape. There have been recent attempts to describe the agronomic diversity of Mexican native landraces from the states of 'Oaxaca' and 'Puebla' in regard to total soluble solids and yield, among other parameters. Some of these landraces show superior values of total soluble solids and even yields comparable to commercial hybrids (Bonilla-Barrientos *et al.*, 2014). Sanjuan-Lara *et al.* (2015), in a study on young tomato plants of native varieties collected in the state of Puebla, reported significant differences in plant growth in response to salt stress. While synthesis and accumulation of phytochemicals in tomato fruits mainly depends on the genetic material, agronomical practices and the environment (including salinity) may modify such properties as well (Rouphael *et al.*, 2012). Salinity induces changes in physiology and metabolism that affect the final crop yield (Pompeiano *et al.*, 2016). It was demonstrated that two landraces, exhibiting very different fruit metabolic profiles, are able to avoid, at least partially, the loss of fruit yield induced by salinity and at the same time they can improve fruit quality (Massaretto *et al.*, 2018). Local tomato varieties represent a reservoir of genetic traits useful to improve the quality of the fruits of plants grown under stress conditions (Moles *et al.*, 2019). Consequently, native tomato genotypes may display different responses in growth and in fruit quality characteristics, which, at the same time are influenced by salinity. Therefore, in this study we analyzed the impact of salinity on dry weight, yield and fruit quality of four Mexican native tomato genotypes, which were chosen because they are the best known and the most consumed in the center of the country. These genotypes were compared to a commercial 'Roma-Saladette' type cultivar in hydroponics under greenhouse conditions.

Materials and Methods

Experimental conditions

The experiment was conducted at the College of Postgraduates in Agricultural Sciences Campus Montecillo in Texcoco, State of Mexico, Mexico ($19^{\circ} 27' 38.3'' \text{ N}$ and $98^{\circ} 54' 24'' \text{ W}$, at 2243 masl), under greenhouse condition, with mean daytime/night temperatures of $25^{\circ}\text{C}/15^{\circ}\text{C}$, mean photosynthetically active radiation (PAR) of 275 W m^{-2} , and mean relative humidity of 65%.

Tomato genotypes

The plants were obtained by germination of seeds originating from collections of traditional native landraces in four states of Mexico: Campeche, Oaxaca, Puebla and Veracruz, of the types kidney, ribbed kidney-shaped, chino criollo (bell pepper-shaped) and citlale (star-tomato), respectively, and one commercial hybrid of the 'Roma-Saladette' type, 'Vengador' (Syngenta; Basel, Switzerland). Details on these genotypes are given in Table 1.

Table 1. Characteristics of tomato (*Solanum lycopersicum*) genotypes analyzed in response to salt stress under greenhouse conditions

Commercial name	Fruit shape type	Plant habit	Fruit length (cm)	Equatorial diameter (cm)	Fruit weight (g)
'Campeche'	Kidney	Indeterminate	4.0-6.0	5.0-7.8	55.0-85.0
'Oaxaca'	Ribbed kidney	Indeterminate	4.5-6.5	5.2-7.5	50.0-80.0
'Puebla'	Bell pepper	Indeterminate	5.0-7.0	5.5-7.8	55.0-80.0
'Veracruz'	Cherry	Determinate	1.4-2.0	1.5-2.2	3.0-4.5
'Vengador'	Saladette	Indeterminate	7.5-9.5	6-2-8.2	100.0-120.0

Seeds of the five aforementioned tomato genotypes were sown in germination trays filled with peat moss-based substrate and irrigated with tap water. Twenty days after sowing plantlets were irrigated with Steiner solution at 50%. Plants were transplanted at 45 days after sowing (35 days of age on average) into 10-L black polyethylene bags filled with an inert local volcanic gravel (locally named tezontle), with particle size between 1 and 20 mm. Plastic bags containing the inert gravel as substrate were placed in four double rows, 160 cm between double rows and 35 cm between plants (35,714 plants ha⁻¹), and were supported with heavy nylon string. Suckers were cut when appearing and lower leaves when drying out. Steiner solution was increased to 75% at the moment of transplant and to 100% 15 days after transplantation with a final electrical conductivity of 2.4 dS m⁻¹. The nutrient solution was prepared according to Steiner (1984) for macronutrients, having the following composition in mol_e m⁻³: 12 NO₃⁻, 1 H₂PO₄⁻, 7 SO₄²⁻, 7 K⁺, 9 Ca²⁺ and 4 Mg²⁺. Micronutrients were supplied from a commercial product at the following concentrations in mg L⁻¹: 5 Fe, 2.3 Mn, 0.47 Zn, 0.19 Cu, 0.43 B and 0.17 Mo.

Treatments and experimental design

Twenty-five days after transplanting, plants of each of the five genotypes were treated with 30, 60 and 90 mM NaCl added in the 100% Steiner nutrient solution, which increased the electrical conductivity to 5.4, 8.4 and 11.4 dS m⁻¹, respectively. A solution without NaCl was used as control. Each treatment in each genotype had 10 replicates, which were distributed in a greenhouse in a completely randomized experimental design. The experimental unit was a 10-L black polyethylene bag filled with the inert gravel and containing a single tomato plant. The nutrient solution with the corresponding NaCl concentration was supplied with an open drip irrigation system. The daily irrigation volume per experimental unit was 800 mL distributed in 8 irrigations of 100 mL.

Evaluated variables

After 102 days of treatment plants were harvested and divided into leaves, stems, and root, which were dried at 65 °C until constant weight in a forced air-drying oven (Riossa HCF-125D; Guadalajara, Jalisco, Mexico). Dry weight of stems and leaves was combined to obtain shoot dry weight, which was then used together with root dry weight to calculate root/shoot ratio.

Fully-ripe fruits harvested during the cultivation stage were weighed directly afterwards. Yield and yield decrease were calculated using the fruit weights obtained.

After weighing, fruits were frozen at -80 °C for analysis of total soluble solids (°Brix), total soluble sugars and pH value of fruit juice. For these analyses five randomly picked fruits, at full maturity stage, belonging to

landraces Oaxaca, Puebla, and Campeche, as well as for the hybrid Vengador were blended, with five replications; they were then filtered and pH was measured with a digital pH-meter (J.T. Baker Conductronic PC18; Phillipsburg, NJ, USA) and °Brix with a hand refractometer (Atago N-1E; Tokyo, Japan) in filtered juice. In the case of the landrace Veracruz, 20 fruits (not only five) were used because of the small fruit size.

The concentration of total soluble sugars in fruits was measured in 1.0 g of fruit pulp using the method described by Southgate (1976). Absorbance was determined at a wavelength of 620 nm in a Genesys™ 10S spectrophotometer (Thermo Fisher Scientific; Santa Clara, CA, USA). Glucose was used as standard in the preparation of the calibration curve.

Statistical analysis

All data were subjected to analysis of variance (ANOVA) using the GLM procedure of SAS ver. 9.3 (SAS Institute, 2011) to detect principal effects of NaCl and genotype and the interaction effect of both variation sources. Means comparison was performed with Tukey's range test. Predetermined significance level was set up with alpha equal to 0.05.

Results

Yield and relative yield

Yield per plant decreased for all genotypes with increasing salinity levels. With the exception of 'Puebla' and 'Vengador' genotypes, differences between 30, 60 and 90 mM NaCl were not significant among genotypes tested (Figure 1A).

Under control conditions (i.e. absence of salt stress), 'Vengador' showed the highest yield (30.3 t ha⁻¹), followed by 'Campeche' (28.4 t ha⁻¹), 'Oaxaca' (28.3 t ha⁻¹), 'Puebla' (21.3 t ha⁻¹) and 'Veracruz' (1.06 t ha⁻¹). This order changes when applying NaCl. At the 30 mM level, 'Oaxaca' had the highest yield (14.9 t ha⁻¹), followed by 'Vengador' (14.8 t ha⁻¹), Puebla (13.1 t ha⁻¹), 'Campeche' (8.2 t ha⁻¹) and 'Veracruz' (0.79 t ha⁻¹). Among all five genotypes evaluated, 'Vengador' recorded the highest yield at both 60 and 90 mM NaCl, whereas 'Veracruz' had the lowest (Figure 1A). However, when exposed to 30 mM NaCl, the landraces 'Veracruz', 'Puebla', 'Oaxaca' and 'Campeche', and the cultivar 'Vengador' showed decreased yields of 26.0, 38.5, 47.4, 71.1 and 51.0%, respectively, in comparison to the control. When 90 mM NaCl were applied, the landrace 'Veracruz' showed the lowest decrease in yield with a 44.0% reduction, while 'Campeche' showed the highest decrease with 89.6%, both in comparison to the control (without NaCl) (Figure 1B).

Dry biomass

The landrace 'Puebla' displayed the lowest dry biomass weight of leaves among all genotypes evaluated, regardless of the salt stress levels tested. In all genotypes tested but 'Oaxaca', dry biomass of leaves in the evaluated genotypes did not show a statistical difference between the control and the 30 mM NaCl treatment. When applying 60 and 90 mM NaCl, leaf dry biomass weight in 'Vengador' was reduced by 45.1 and 55.5%, respectively, as compared to the control; in 'Campeche' by 25.3 and 41.1%; in 'Oaxaca' by 42.2 and 61.1%; in 'Puebla' by 28.1 and 31.2%; and in 'Veracruz' by 38.8 and 46.1%, in all cases, as compared to their respective controls (Figure 2A).

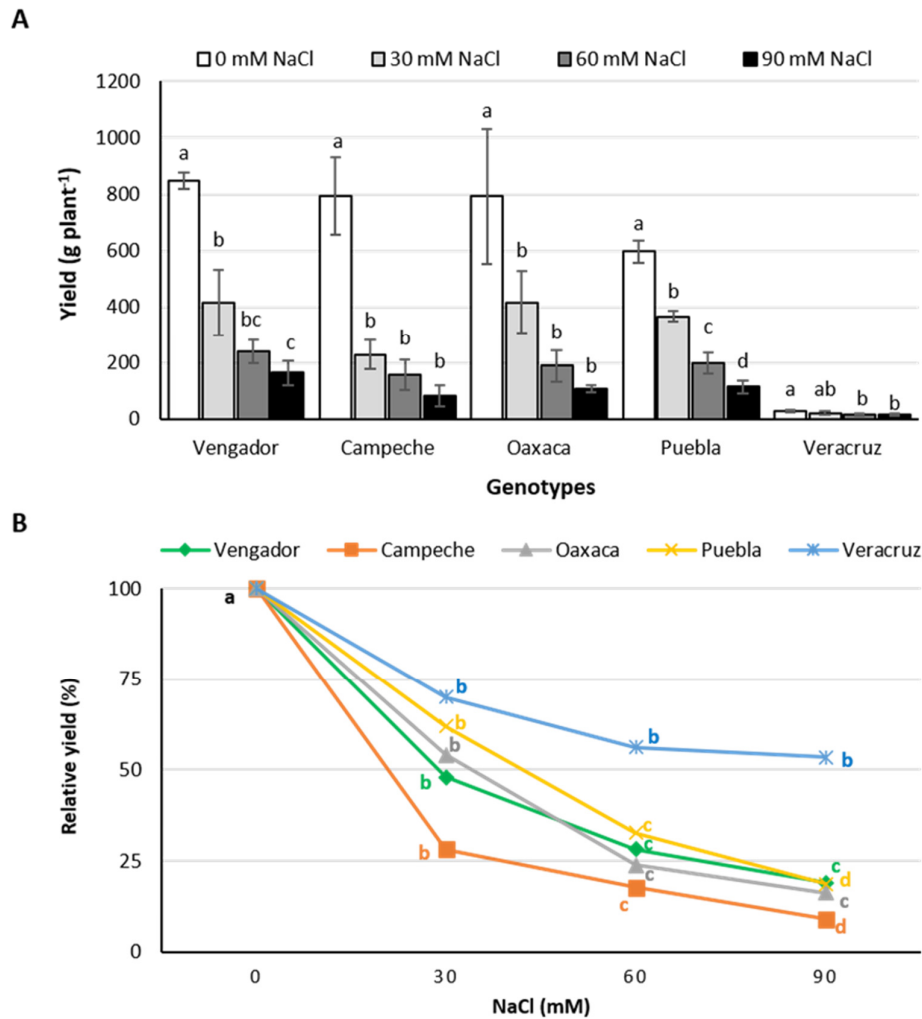


Figure 1. Yield (A) and relative yield of five tomato genotypes (B) in response to increasing concentrations of NaCl in the hydroponic nutrient solution. Means with different letters in each subfigure and genotype indicate statistical differences (Tukey, $p \leq 0.05$)

Regarding stem dry biomass weight, the genotypes ‘Campeche’ and ‘Puebla’ displayed significant reductions as compared to the control only when testing 90 mM NaCl. Conversely, the landrace ‘Oaxaca’ showed a higher sensitivity in comparison to the other genotypes, and displayed significant reductions at all salt stress levels tested, as compared to the control. When exposed to 60 and 90 mM NaCl, the genotypes ‘Vengador’ and ‘Veracruz’ significantly reduced stem dry biomass weight by 43.2 and 59.7%, and by 37.3 and 44.5%, respectively, as compared to their respective controls (Figure 2B).

In ‘Campeche’ and ‘Oaxaca’, root dry biomass weight was not significantly affected by NaCl. In ‘Puebla’, only the application of 90 mM NaCl significantly reduced dry biomass weight as compared to the control, by 66.4%. The genotypes ‘Vengador’ and ‘Veracruz’ displayed significant reductions in dry biomass weight when plants were treated with 60 and 90 mM NaCl, with reductions of 59.1 and 59.2%, and of 62.7 and 79.5%, respectively, as compared to the control. It is worth mentioning that the landrace Veracruz displayed the highest root biomass weight among all genotypes tested (Figure 2C).

In this study, the root/shoot ratio declined sharply in the landraces ‘Veracruz’ and ‘Puebla’ with increasing salinity, but only in ‘Veracruz’ were these declines significant as compared to the control. This reduction observed in the landrace ‘Veracruz’ resulted from the drastic decrease in the dry biomass as the salt

stress increased. The ratio remained stable in ‘Vengador’ and ‘Campeche’, while it showed high variability in ‘Oaxaca’, with no significant effects of the NaCl levels tested (Figure 3).

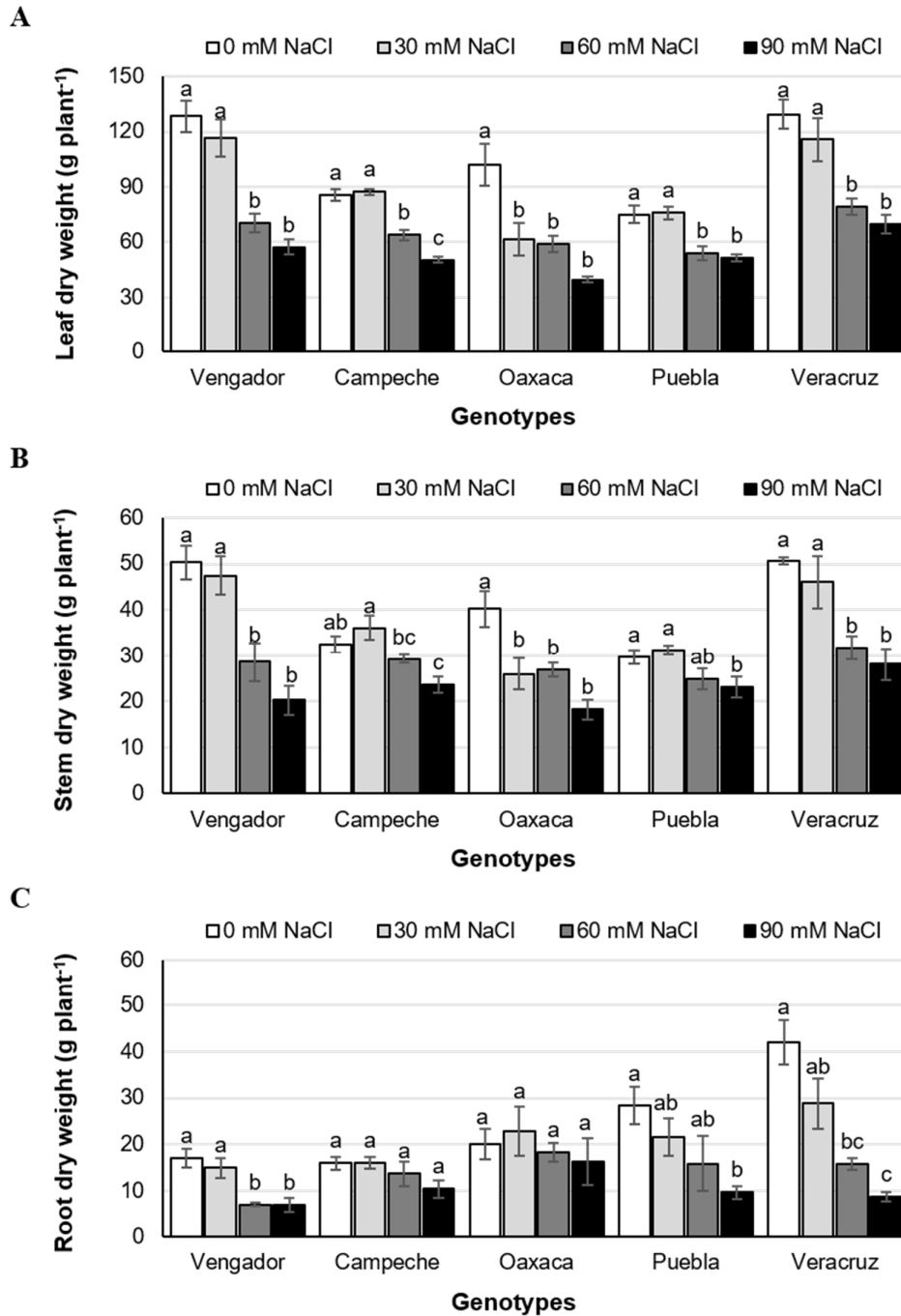


Figure 2. Dry weight of leaves (a), stems (b) and root (c) of five tomato genotypes in response to increasing concentrations of NaCl in the hydroponic nutrient solution. Means with different letters in each subfigure and genotype indicate statistical differences (Tukey, $p \leq 0.05$)

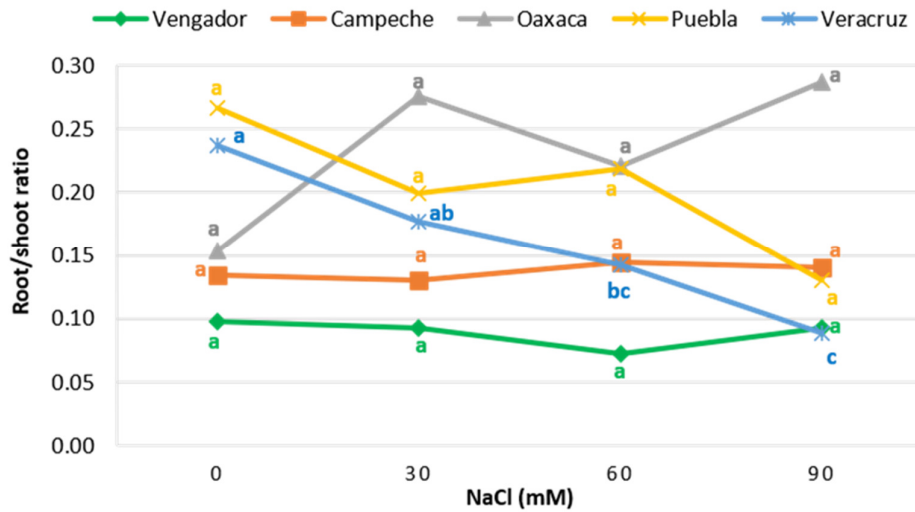


Figure 3. Root/shoot ratio of five tomato genotypes in response to increasing concentrations of NaCl in the nutrient solution in hydroponics

Means with different letters in each genotype indicate statistical differences (Tukey, $p \leq 0.05$)

Fruit quality

The NaCl levels caused a significant increase in total soluble solids at all concentrations evaluated, though those increases showed high variation among genotypes. In ‘Campeche’, treatments did not affect total soluble solids. In the commercial hybrid ‘Vengador’, the mean values of total soluble solids were statistically similar between the three levels of NaCl tested (30, 60 and 90 mM NaCl). However, these NaCl treatments significantly increased the mean value of this reference variable (total soluble solids) compared to the control. On the other hand, total soluble solids increased in ‘Oaxaca’, ‘Puebla’ and ‘Veracruz’ as the NaCl in the nutrient solution rose; when exposed to 90 mM NaCl, the percentage increases were 109.2, 110.4 and 41.2%, respectively, as compared to their respective controls (Figure 4A).

Salinity significantly decreased pH values of fruit juice in all genotypes evaluated. Nonetheless, control plants of the landraces ‘Puebla’ and ‘Veracruz’ did not show differences in fruit juice pH as compared to those treated with 60 mM NaCl. Fruits of ‘Oaxaca’ plants treated with 90 mM NaCl displayed the highest decrease (6.1%), while those of ‘Puebla’ exhibited the lowest decrease (1.4%) in juice pH (Figure 4B).

Great variability among genotypes tested was observed in relation to total soluble sugars. In ‘Vengador’, ‘Campeche’ and ‘Puebla’ the highest concentration of soluble sugars was recorded with 30 mM NaCl, with increases of 33.7%, 32.5% and 78.1%, respectively, in comparison to their controls. In ‘Vengador’ and ‘Campeche’, the application of 60 and 90 mM NaCl did not affect soluble sugars. ‘Oaxaca’ and ‘Veracruz’ registered the highest concentrations of total soluble sugars when exposed to 90 mM NaCl, with increases of 106.7% and 31.5%, respectively, as compared to their respective controls (Figure 4C).

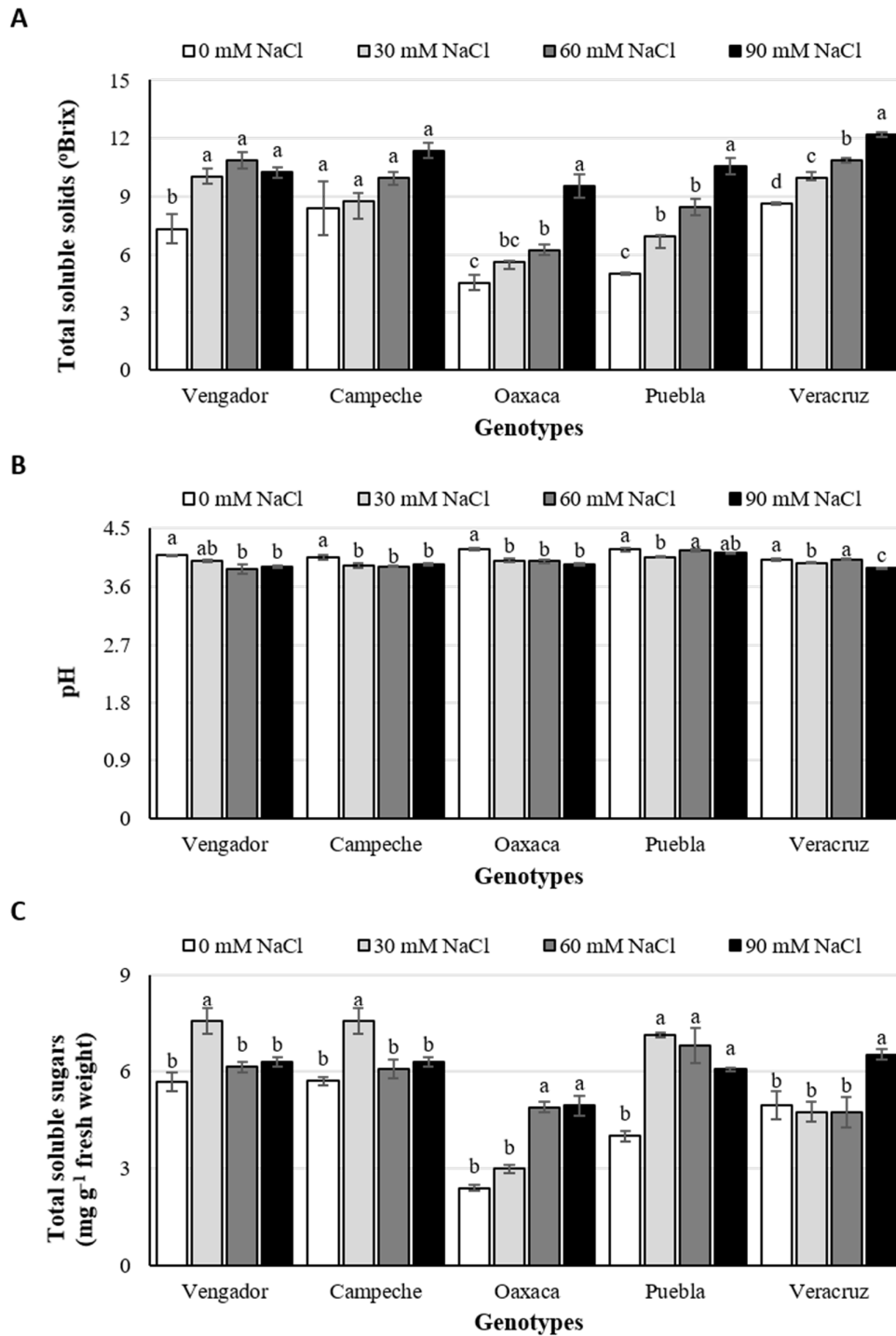


Figure 4. Total soluble solids (a), pH (b) and total soluble sugars (c) of five tomato genotypes in response to increasing concentrations of NaCl in the hydroponic nutrient solution. Means with different letters in each subfigure and genotype indicate statistical differences (Tukey, $p \leq 0.05$)

Discussion

Yield and relative yield

Salinity causes three major effects in plants. Firstly, plants suffer from water deficit (osmotic stress) due to low water potential in the rhizosphere. The Na⁺ and Cl⁻ ions which are absorbed excessively by plant roots cause ion toxicity. As well, these ions trigger nutrient imbalance caused by lowered uptake of other essential nutrients or reduced shoot transport and distribution within the plant. A specific growth inhibition process would be hard to link to one of these three effects as they impact plant organs in different ways and shift according to plant developmental stage, genotype and environmental conditions (Eckhard *et al.*, 2012). In this study, all genotypes tested (the landraces and the hybrid) exhibited significant yield reductions when exposed to salt stress (Figure 1A). With the highest NaCl level tested (90 mM), 'Vengador' was the genotype with the highest yield as compared to the rest of the genotypes. In general, this tendency provides evidence of high yield performance of modern hybrid cultivars even at elevated salinity stress conditions (Figure 1A). Magán *et al.* (2008) demonstrated different yield responses for two commercial cultivars exposed to various electrical conductivities influenced by NaCl.

Interestingly, we could observe different sensitivity levels of the genotypes evaluated when comparing their responses to the respective controls. 'Veracruz' showed the lowest reduction in yield under salinity stress and thus displayed the highest salinity tolerance regarding yield, followed by 'Puebla'. 'Vengador' and 'Oaxaca'. 'Campeche' proved to be the most sensitive genotype to NaCl exposure under these experimental conditions (Figure 1B). Tomato genotypes with high yields under control conditions as well as large-fruited genotypes tend to be more negatively affected by increasing NaCl stress (Caro *et al.*, 1991), which is in full agreement with the results of this study. Accordingly, Bolarín *et al.* (1993) showed that tomato cultivars, including landraces, may display similar responses with decreasing yield as salinity levels increase, though differences among genotypes are evident.

Depending on tomato cultivar, yield reduction at 50 mM NaCl compared with the control may be linked to a decreased number of fruits per plant, but not for all cultivars studied (Nouck *et al.*, 2016). Plants exposed to salinity stress over several months may show reduced formation of flowers, resulting in reduced fruit set (Munns and Tester, 2008). The landrace 'Veracruz' was the only small-fruited genotype in this investigation and displayed irregular growth. In traditional production systems plants are grown in bushy forms with higher potential yields. Instead, in this study all plants were grown as usual in modern production systems for comparative and reproducible reasons. Tomato genotypes display different tolerance to salinity. Genotypes resistant to high salinity are used as rootstocks to improve salinity tolerance and therefore productivity. The small-fruited botanical variety cerasiforme (such as the 'Veracruz' genotype), widely dispersed in Mexico, is considered more tolerant to salt stress than most commercial cultivars. This botanical variety was less affected when exposed to 35, 70 and 140 mM NaCl than commercial cultivars were (Caro *et al.*, 1991; Di Gioia *et al.*, 2013; Nouck *et al.*, 2016), which is in full agreement with the findings of this research.

Water flow into fruits is affected by high salinity levels due to lower water potential in the plant, thereby directly affecting the fruit expansion rate (Johnson *et al.*, 1992). Fruit growth rate declined due to reduction of predawn water potential in tomato fruit as a result of the application of Ca salt, as compared to control plant (Hossain and Nonami, 2012). The xylem plays a pivotal role in water and nutrient influx to tomato trusses, with more than 75% being transported by xylem in the first eight weeks of truss development (Windt *et al.*, 2009). According to Hossain and Nonami (2010), size of the growth-induced water potential and the hydraulic conductance are crucial factors that regulate fruit cell expansion. Indeed, tomato fruit growth is strongly correlated with xylem functionality, water uptake rate and expansion of cells in fruit pericarp (Hossain and Nonami, 2011). Furthermore, transpiration flux and growth flux have additive relations suggesting that water fluxes for growth and transpiration rate are linearly superimposed (Nonami and Hossain, 2010). Tomato plants exposed to salt stress show a reduced xylem exudation flow by a factor of 17 to 20 compared to control

plants (without salt stress), and ion concentrations in the xylem sap may rise by a factor of 2 to 3 in plants exposed to 50 mM NaCl (Kafkafi, 1991).

Dry biomass

Total plant dry weight of tomato plants decreases due to reduced growth with increasing salinity stress levels (Maggio *et al.*, 2007). Osmotic stress rapidly affects plants and is then followed by an ionic effect of excessive Na⁺ and Cl⁻ ion uptake up to toxic concentrations, which may cause cell death in older leaves and results in reduced carbohydrate production (Munns and Tester, 2008). Osmotic stress in general slows carbon accumulation, has negative effects on plant tissue expansion and leads to reduced cell number (Tardieu *et al.*, 2011). In this experiment, a significant reduction in dry biomass weight was observed when plants were treated with 90 mM NaCl. In the genotypes Vengador and Oaxaca, plants exposed to 90 mM NaCl exhibited a 55.1 and 61.1% reduction in dry biomass as compared to the control (Figure 2A), while regarding stem dry biomass the highest reduction was observed in Vengador, with a 59.7% decrease as compared to the control (Figure 2B). Conversely, Veracruz showed the highest decrease in root dry biomass, with a 79.5% decrease as compared to the control (Figure 2C).

Regarding the dry weight decrease in roots, shoots and leaves, there is significant variation among cultivars and a landrace evaluated (Pérez-Alfocea *et al.*, 1993). Root and shoot dry weight of salt-tolerant tomato cultivars may not be affected by salinity concentrations of up to 200 mM NaCl, while moderately tolerant and sensitive cultivars show decreased dry weight with increasing salinity stress at different intensities (Nouck *et al.*, 2016).

A more efficient assimilates supply and an integrated root protection system provided by sugars and antioxidants can result in a significantly higher root/shoot ratio of salt-tolerant tomato landraces (Moles *et al.*, 2016). These observations are contrary to those reported by Maggio *et al.* (2007), who observed an increasing root/shoot ratio with increasing salinity levels. Plants in the above-mentioned research were younger than those evaluated in this study, but Cruz and Cuartero (1990) showed that plants at various stages of development tend to increase their root/shoot ratio. Tuna *et al.* (2007) demonstrated an increased root/shoot ratio for one tomato cultivar exposed to 75 mM NaCl with plants harvested at fruit-set stage. Pérez-Alfocea *et al.* (1993) showed root and shoot dry weight decline in response to NaCl stress, and this decline is more evident when plants are exposed to this stress for a longer time, while the intensity of dry weight decrease depends on the selected genotype. Root and shoot dry weight are negatively affected by increased salinity, but salinity decreases shoot dry weight to a greater extent than root dry weight (Cuartero and Fernández-Muñoz, 1999; Munns and Tester, 2008). Root/shoot ratio may vary greatly among tomato genotypes in response to salinity stress and this ratio may be a crucial factor to determine salinity tolerance and selection of elite genotypes for breeding proposes (Dasgan *et al.*, 2002; Nouck *et al.*, 2016). In this research, root/shoot ratio was only influenced by treatments in the Veracruz genotype, where the increase in NaCl concentration was negatively related to root/shoot ratio (Figure 3). Salinity tolerance is controlled by various mechanisms, leading to an improved or worsened plant performance during plant growth (Foolad and Lin, 1997). Tomato tolerance to salinity at a certain stage of plant development is not necessarily connected to salt tolerance at another stage of development (Foolad, 2007). This circumstance makes comparisons with other investigations difficult because not only is each study subject to different climate conditions and cultivation methods, but plants are also evaluated at different stages of development with different duration of salinity treatments at different concentrations.

Fruit quality

In response to salinity, osmotic adjustment is achieved by higher fruit electrical conductivity, °Brix and total titratable acidity (Agong *et al.*, 1997). Indeed, as a result of exposure to salinity, increased acidity and total soluble solids have been reported with increasing electrical conductivity, which improve tomato fruit quality (Cuartero and Fernández-Muñoz, 1999; Brasiliano *et al.*, 2006; Magán *et al.*, 2008). Accordingly, in all genotypes evaluated under these experimental conditions, °Brix values were positively correlated with the NaCl

concentrations tested (Figure 4A). In tomato fruits, soluble solids are found in a range of 4.5 to 8.5% on a fresh basis (André *et al.*, 2005). With the exception of 'Veracruz', which exhibited 8.64% soluble solids, all other control plants of the genotypes tested produced fruits with soluble solids contents within the aforementioned range. With the highest NaCl level tested (90 mM NaCl), Veracruz maintained the highest total soluble solids content with a mean of 12.2 °Brix, followed by Campeche and Puebla (Figure 4A). The results of this work confirm that while landraces usually cannot compete with modern hybrid cultivar yields (Jenkins, 1948; Caro *et al.*, 1991; Brugarolas *et al.*, 2009), they may provide different flavors and nutrient properties, as well as represent a crucial source of genetic variability for breeding approaches.

It is well documented that salinity reduces the pH value of tomato fruits (Coban *et al.*, 2020), which was also observed in this research (Figure 4B). Furthermore, total soluble sugars increased as the NaCl concentration in the nutrient solution increased (Figure 4C). Fruits with high acidity and sugar concentration are perceived as full in flavor, while those with high acidity and low sugar concentration present a tart flavor and sweet fruits without acidity are tasteless (Grierson and Kader, 1986). Tomato cultivars and especially landraces tend to exhibit considerable variation in their fruit sugar-and-acid profile (Casals *et al.*, 2015).

Under salt stress, the increase in soluble solids seems to be related to an increase in soluble sugar accumulation, reduced fruit water content and reduced fruit cell size causing a concentration of soluble solids (Mitchell *et al.*, 1991; Saito *et al.*, 2008). Increased values of total soluble solids and acidity are an active adaptation of plants to salinity to maintain water uptake under osmotic stress conditions (Hasegawa *et al.*, 2000).

Under these experimental conditions, the genotype Veracruz was the most tolerant to salt stress, among all genotypes tested, since the reduction of the relative yield was the lowest (Figure 1B), while the concentration of soluble solids (12.2, Figure 4A), acidity (3.89, Figure 4B) and total soluble sugars were high (6.52 mg g⁻¹ fresh weight, Figure 4C). Furthermore, 'Veracruz' was the only genotype in which the root/shoot ratio was reduced in response to salinity (Figure 3), since root dry biomass was reduced to a greater extent than leaf and stem dry biomass (Figure 2A, B and C).

Because of the genetic erosion of this horticultural species, the recovery of locally adapted landraces could play a pivotal role in avoiding, at least in part, production losses and simultaneously improving fruit quality (Massaretto *et al.*, 2018). Importantly, Moles *et al.* (2019) reported the feasible use of tomato landraces as a target to select interesting genetic traits to improve fruit quality under stress conditions, which is in full agreement with the findings of this research. Furthermore, metabolites and secondary antioxidants are involved in the process of salt stress adaptation, thereby increasing salinity tolerance in tomato landraces (Sumalan *et al.*, 2020).

Conclusions

Tomato, a crop plant considered moderately sensitive to salinity, may display a wide range of tolerance to salinity depending on genotype. In this study, 'Veracruz' had the lowest fruit yield and 'Vengador' the highest for all NaCl treatments tested. Nevertheless, in regard to yield decrease percentage, 'Veracruz' demonstrated the highest tolerance to salinity. Dry biomass weight of roots, stems and leaves were significantly reduced in all genotypes tested, especially when exposed to 60 and 90 mM NaCl. Although at each salinity level evaluated the Veracruz fruits showed the highest °Brix value as compared to the rest of the genotypes, 'Oaxaca' and 'Puebla' fruits had a greater increase between the control and 90 mM NaCl (109.2% and 110.4%, respectively). With 90 mM NaCl, 'Oaxaca' fruits also registered the highest decrease in pH (6.1%) and the highest increase in total soluble sugars (106.7%) with respect to the control. In summary, the tomato genotypes tested displayed different responses to salt stress, with 'Veracruz' standing out as a promising landrace useful for further breeding programs. Importantly, salinity improved some tomato fruit quality, and thus a certain level of salt that does not reduce yield significantly could be recommended in order to increase fruit quality.

Authors' Contributions

Conceptualization: LITT and FCGM; Formal analysis: PL and LITT; Funding acquisition: LITT, and FCGM; Investigation: PL and ACO; Methodology: LITT and FCGM; Supervision: LITT, RJS and FCGM; Validation: LITT and FCGM; Writing - original draft: PL, LITT and FCGM; Writing - review and editing: LITT, FCGM, RJS and ACO. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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