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Sodium Chloride Tolerance during Germination and Seedling Stages of Tomato (*Solanum lycopersicum* L.) Lines Native to Mexico

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Abstract: Tomato is considered moderately sensitive to salinity, which detracts from the quality and yield of its fruit; therefore, wild populations have been used as a genetic resource. The aim of this research was to identify lines derived from wild tomato populations with tolerance to salinity during the germination and seedling stages. During germination, 52 wild lines and 2 commercial hybrids (Imperial®, Reserva®) were subjected to treatment with 150 mM and 0 mM NaCl and evaluated. The test was carried out for 20 days in a germination chamber with constant darkness, a temperature of 25 ± 2 °C and relative humidity conditions of 80 ± 4%. At the seedling stage, 22 wild tomato lines with the best performance in the germination test and 2 commercial hybrids (Imperial®, Topanga®) were evaluated for 12 days in a floating raft system. Concentrations of 175 mM and 0 mM of NaCl were used. During germination, the saline condition decreased the germination percentage (65.2%), speed of germination (88.2%), steam length (72.5%), root length (46.56%), number of normal plants (59.5%), stem dry matter (68.78%), root dry matter (61.99%), and total dry matter (67.1%). At the seedling stage, this condition decreased ($p < 0.05$) the aerial part dry matter (46.37%), leaf area (59.35%), root length (42.43%), final plant height (40.24%), and growth rate (71.42%). Seventeen tolerant genotypes were identified in one of the two developmental stages, while one genotype showed tolerance in both stages. These results indicate that there are different response mechanisms in each developmental stage. Native tomatoes play an important role in the identification of tolerant genotypes since they can be used as genetic resources for obtaining commercial genotypes with salt tolerance.

Keywords: salt tolerant genotypes; wild tomato; developmental stages; seed germination

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1. Introduction

In total, 9% of the Earth's land surface (more than 424 million hectares of topsoil and 833 million hectares of subsoil) are salt-affected and 50% of its agricultural land is affected by salts [1]; this condition is responsible for significant crop yield losses, with an annual value of up to USD 30 billion [2]. In Mexico, the irrigated agricultural area is 9.23 million hectares, out of which 60% is affected by sodium and salinity. whereas from the rainfed agricultural area, 8.91 million hectares, 19.7%, suffers from these conditions [3], indicating that almost a fifth of the agricultural land area faces these problems. Salt-affected areas are increasing due to the use of saline water and the intensive use of groundwater for irrigation, the excessive application of chemical fertilizers, and irrational crop rotation [4]; therefore, one of the current challenges facing agriculture is to increase crop production under saline conditions. One of the strategies being followed to address this problem is the development of salt stress-tolerant varieties.

Excess soil salinity generates ionic stress in plants due to the increase in toxic ions such as Na^+ and Cl^- that alter the ionic balance of the cell membrane, causing organ destruction, alterations in protein synthesis, structural changes to enzymes, and respiratory disorders [5]. Osmotic stress is also generated due to the limited availability of water resulting from the increase in osmotic pressure, which decreases growth by inhibiting water uptake by the roots, which in turn generates oxidative damage and may cause plant death [6–8]. Some agronomically important traits adversely affected by salt stress include germination, leaf development, leaf area, plant height, root length, dry matter accumulation, photoassimilate production, etc. [9,10].

Plant salinity tolerance is directly associated with the phenological stage, the affected plant organ, the duration and severity of stress, and the environmental factors that cause it [11–14]. The genetic component is also of great importance since wild tomatoes with salt tolerance have multiple regulatory mechanisms of Na^+ accumulation, including osmoregulation, regulation of ion uptake and distribution, and efficient antioxidant defense [11,15,16].

Wild tomato species represent a valuable genetic resource for improving commercial varieties since genetic variability in cultivated tomato is scarce; however, it is necessary to initially characterize native materials to identify the type of tolerance they may possess [17], since the use of uncharacterized accessions may indicate that commercial cultivars have greater tolerance to salinity [18–20]. This is especially true in the case of wild species phylogenetically related to tomato, which have greater resistance to salts; such is the case of *Solanum sitiens*, *Solanum pimpinellifolium*, *Solanum galapaguense*, *Solanum cheesmaniae*, *Solanum chilense*, and *Solanum peruvianum* [2,21–26].

Some *S. pimpinellifolium* accessions have high salt tolerance, making them potential candidates for breeding [2,27], since, being closely related to *S. lycopersicum*, they have been used as a donor of many important traits for commercial tomato [27]. *S. galapaguense* and *S. cheesmaniae*, wild species endemic to the Galapagos Islands, have been harnessed to transfer salinity tolerance, so that improved plants can be irrigated with one-third of seawater [25].

Wild tomato populations are still very frequently observed, and it is possible to find them in a cultivated form, as well as with tolerance and promoted growth. In fact, wild tomato has shown a strong ability to disperse and overrun perturbated areas; it is used as food, in the preparation of sauces, and as a medicinal plant [28]. Ramírez-Ojeda et al. [29] identified areas of high diversity in wild tomato populations. These areas also reflect high-diversity climate conditions, which coincide with known areas of great diversity and the regional use of wild tomatoes.

Given the great genetic variation in wild species and especially those native to Mexico, one of the centers of domestication of this species [30], information on its tolerance to salts is still scarce since its study initially requires phenotypic characterization and subsequently the identification of specific genes that confer resistance to this condition. Therefore, the evaluation of phenotypic traits of a plant, such as its architecture and biochemical properties, is key to explaining plant growth and yield under salt stress conditions [31]. The limited study of native materials is due to their low commercial importance, and hence their scarce cultivation, despite their extraordinary culinary and nutraceutical characteristics. Thus, they are used mainly for local consumption in regional stews, associated with the cultural richness of the different cultures in the country.

Because commercial tomato breeding has focused on the development of disease-resistant cultivars with commercial fruit quality [32], tolerance to abiotic stresses has not been decisively addressed; moreover, the difficulty of identifying this tolerance in conventional germplasm forces us to resort to wild populations as alternatives that are still far from being properly addressed in view of the wide diversity of native and wild tomatoes.

This research aimed to identify lines, derived from wild tomato populations, with tolerance to salinity during germination and seedling stages for their probable use in breeding.

2. Materials and Methods

The experiments were established in greenhouses operated by the Universidad Autónoma Chapingo (UACh) located at NL 19°29′23″ and WL 98°52′26″, and 2264 masl.

The genotypes evaluated were lines derived from wild tomato populations of the PMGT and the Wild Tomato Breeding Program of the Colegio de Postgraduados (Table A1), as well as three commercial hybrids used as controls: Imperial® (Enza Zaden, San Juan Bautista, CA, USA), Reserva® (Vilmorin, Salinas, CA, USA), and Topanga® (Rogers Seeds, Yuma, AZ, USA). The evaluated lines were derived from wild population by means of individual selection and maintained by selfing.

2.1. Germination Salt Tolerance Test

Fifty-five wild tomato lines and the commercial hybrids Imperial® (Enza Zaden, San Juan Bautista, CA, USA) and Reserva® (Vilmorin, Salinas, CA, USA) were evaluated using a sodium chloride concentration of 150 mM (13.7 $dS \cdot m^{-1}$), as well as a control with the absence of NaCl (0 mM). The used NaCl concentration was selected based on previous laboratory tests and various investigations [5,15,33–39]. Since the concentration of 150 mM of NaCl was not a lethal dose, it allowed us to discriminate tolerant genotypes from those that were susceptible. The Imperial variety has an indeterminate growth habit and is preferred for greenhouse production systems; it has large fruits (260 g), and is of the round type and red in color, with high commercial quality, a long shelf life, high firmness, and high yield. The Reserva variety has the same characteristics, although its fruit is a medium-sized saladette type (120 g) and develops better in temperate to cold environments.

The experimental unit consisted of a 5.5 cm diameter Petri dish, with 25 seeds and filter paper as a substrate, saturated with 2 mL of distilled water or with the saline solution (150 mM). A completely randomized experimental design with four replicates was used. The germination test was carried out for 20 days in a germination chamber (LAB-TECH INC Model D-7140, Mexico city, MEX) in constant darkness, with a temperature of 25 ± 2 °C and relative humidity condition of 80 ± 4%.

Germinated seeds were counted daily for 20 days. A seed was considered germinated when radicle protrusion occurred. At the end of the test, the following were evaluated: germination percentage (GP), stem length (SL, in cm), root length (RL, in cm), number of normal plants (NP), accumulated stem dry matter (SDM, in mg), accumulated root dry matter (RDM, in mg), total dry matter (TOTDM, in mg), and speed of germination (SG), in accordance with the formula proposed by Maguire [40]:

$$SG = \sum_{i=1}^{n} \frac{X_i}{d_i}$$

where n = number of counts performed during the test; X_i = number of seeds germinated between count $i-1$ and count i; d_i = number of days after sowing at count i.

An analysis of variance and Tukey's multiple comparison test ($\alpha \leq 0.05$) were performed on the evaluated traits. Additionally, Pearson linear correlations were obtained for each pair of variables. The SAS statistical package, version 9.1, was used.

2.2. Salt Tolerance Test in Seedlings

Twenty-two wild tomato lines (with the best performance in the germination test) and two commercial hybrids were evaluated: Imperial® (Enza Zaden, Enkhuizen, the Netherlands) and Topanga® (Rogers Seeds, Yuma, AZ, USA). The Topanga variety has a semi-indeterminate habit, and is of the irregular semi-round type, with intermediate performance in greenhouse production systems. The experiment was conducted in a greenhouse

covered with 30% shade plastic. The minimum, maximum, and average temperatures recorded were 6.2 °C, 34.3 °C, and 21.3 °C, respectively. The relative humidity ranged from 17.2 to 80.0%, with an average of 61.9%; radiation ranged from 23.6 to 500.8 μmol·s^{-1}, with an average of 114.2 μmol·s^{-1}.

The genotypes were planted in 200-cavity polystyrene trays with Oasis® peat foam substrate. Transplanting was carried out in a floating raft system (expanded polystyrene plates) in wooden boxes measuring 2.4 m × 1.2 m and 20 cm high, covered with polyethylene and with a capacity of 500 L of nutrient solution. The nutrient solution used was composed of 0.589 kg·m^{-3} of $Ca(NO_3)_2$, 0.101 kg·m^{-3} of KNO_3, 0.123 kg·m^{-3} of KH_2PO_4, 0.171 kg·m^{-3} of $MgSO_4$, 0.033 kg·m^{-3} of librel mix, 0.012 kg·m^{-3} of $FeSO_4$, 0.007 kg·m^{-3} of borax, and 0.022 kg·m^{-3} of H_2SO_4. Transplanting in the floating raft system was performed 20 days after sowing.

Four days after transplanting (DAT), NaCl was applied to the nutrient solution to achieve a concentration of 175 mM of NaCl (15.9 dS·m^{-1}); likewise, a treatment without salt application (0 mM NaCl) was considered. The 175 mM NaCl concentration was obtained by considering the molecular weight of NaCl (58.4398), multiplied by 0.175. This corresponds to adding 10.227 g of NaCl to a liter of nutritive solution. The selection of this NaCl concentration was based on previous tests and the results from Bogoutdinova et al. [5], Sanjuan-Lara et al. [14], Ávila-Amador et al. [37], Wafa'a [41], and Saeed et al. [42]. The floating raft system used with this concentration allowed the survival of seedlings for 12 days after the application of treatments used to discriminate tolerant and susceptible genotypes.

The experimental unit consisted of 5 seedlings, of which the three central ones were evaluated. A randomized complete block experimental design with three replicates was used for each NaCl concentration.

Seedling height (SH, in cm) was recorded from three EU seedlings every three days. At the end of the trial, 12 days after the application of NaCl (16 DAT), the following were quantified: root length (RL, in cm), aerial part dry matter (APDM, in g), and root dry matter (RDM, in g). Leaf area (LA, in cm^2) was determined by capturing digital photographs and processing them with ImageJ software (v1.4.3.67; National Institutes of Health, Bethesda, MD, USA).

The evaluated traits were subjected to an analysis of variance as a series of experiments (NaCl concentrations) in a randomized complete block design; additionally, Tukey's test ($\alpha \leq 0.05$) was performed, and Pearson linear correlations were obtained for each pair of variables.

Plant height (PH) was measured on four occasions (3, 6, 9, and 12 DAT); a regression analysis with the exponential model was performed for each experimental unit:

$$E[PH] = e^{-\beta X}$$

where E[PH] = expectancy for plant height; X = days after transplanting; β = the parameter indicating the plant height growth rate; e = the natural logarithm base (e = 2.718281828).

Statistical analyses were obtained with the SAS package, version 9.1.

3. Results

3.1. Germination under Salinity Conditions

The analysis of variance (Table 1) showed significance ($\alpha \leq 0.05$) in all traits evaluated for concentration (CON), genotypes (GEN), and their interaction (GENxCON), except for RL in CON. This indicates differential effects caused by salt stress, and by genotypic differences; in addition, some genotypes had different behaviors across NaCl concentrations. Coefficients of variation were high due to the high-level salt stress, which increased variations within treatments.

Table 1. Sources of variation (SV), degrees of freedom (DF), and mean squares (MS) of the analysis of variance of traits evaluated in 54 tomato lines under saline conditions (150 mM NaCl) during germination.

SV	DF	GP	SG	SL	RL	NP	SDM	RDM	TOTDM
GEN	56	1507.2 *	8.7 *	6.79 *	1.89 *	1031.4 *	234.9 *	9.50 *	332.2 *
CON	1	300,642.0 *	2922.0 *	1472.80 *	62.25 *	220,422.0 *	13,144.0 *	405.93 *	17,869.0 *
GENxCON	56	1525.4 *	3.9 *	2.82 *	2.34 *	1286.9 *	82.2 *	4.85 *	128.0 *
ERROR	228	298.2	0.7	0.97	0.85	636.6	16.8	1.50	26.3
TOTAL	341								
CV		28.2	22.4	27.00	65.74	42.1	34.7	50.49	35.8
MEAN		61.3	3.7	3.64	1.41	59.9	11.8	2.43	14.3

GEN: genotype; CON: concentration; GP: germination percentage; SG: speed of germination; SL: stem length; RL: root length; NP: normal plants; SDM: stem dry matter; RDM: root dry matter; TOTDM: total dry matter; CV: coefficient of variation. * Significant with a value of $\alpha \leq 0.05$.

Mean comparisons of NaCl concentrations (Table 2) indicated that the 150 mM dose decreased ($\alpha \leq 0.05$) all evaluated traits. Salt stress reduced the GP by 65.2% and the SG by 88.2%, causing the germination period to extend to 20 days in most genotypes evaluated. In contrast, in the absence of stress, germination occurred within 10 days. SL and RL reduced by 72.5% and 46.56%, respectively, and the dry weights, SDM, RDM, and TOTDM, reduced by 68.78%, 61.99%, and 67.1%, respectively.

Table 2. Mean comparisons of NaCl concentrations and percentage reductions due to the salt stress effect on traits evaluated in 57 tomato lines during germination.

CON (mM)	GP	SG	SL	RL	NP	SDM	RDM	TOTDM
0	91.0 ± 0.79 a	6.61 ± 0.15 a	5.71 ± 0.07 a	1.83 ± 0.06 a	85.3 ± 1.24 a	18.02 ± 0.59 a	3.51 ± 0.13 a	21.5 ± 0.70 a
150	31.7 ± 2.74 b	0.81 ± 0.07 b	1.56 ± 0.14 b	0.98 ± 0.10 b	34.5 ± 2.81 b	5.63 ± 0.61 b	1.34 ± 0.14 b	7.1 ± 0.77 b
HSD	3.7	0.22	0.21	0.20	5.4	0.87	0.26	1.1
Decrease %	65.2	88.2	72.50	46.56	59.5	68.78	61.99	67.1

CON: concentration; GP: germination percentage; SG: speed of germination; SL: stem length; RL: root length; NP: normal plants; SDM: stem dry matter; RDM: root dry matter; TOTDM: total dry matter; HSD = honest significant difference. Means with the same letter within columns do not differ statistically (Tukey, $\alpha \leq 0.05$).

Linear correlations (Table 3) indicated that the evaluated traits are strongly associated with each other in a positive way ($\alpha \leq 0.05$), because they assess seed vigor during germination, which is reduced in the presence of NaCl, hence the negative correlations with this factor, especially with SG and SL ($\alpha \leq 0.05$). These results agree with what is indicated by the comparisons of means of the NaCl concentration factor (Table 2).

Table 3. Linear correlations between pairs of traits evaluated in 57 tomato lines under salinity stress.

	CON	GP	SG	SL	R	NP	SDM	RDM
GP	−0.74 *							
SG	−0.87 *	0.82 *						
SL	−0.81 *	0.9 *	0.86 *					
RL	−0.35 *	0.66 *	0.46 *	0.63 *				
NP	−0.66 *	0.75 *	0.50 *	0.77 *	0.56 *			
SDM	−0.61 *	0.79 *	0.69 *	0.82 *	0.58 *	0.68 *		
RDM	−0.51 *	0.78 *	0.65 *	0.75 *	0.66 *	0.62 *	0.87 *	
TOTDM	−0.60 *	0.81 *	0.74 *	0.82 *	0.61 *	0.69 *	0.99 *	0.90 *

CON: concentration; GP: germination percentage; SG: speed of germination; SL: stem length; RL: root length; NP: normal plants; SDM: stem dry matter; RDM: root dry matter; TOTDM: total dry matter. * Significant at $\alpha \leq 0.05$.

Mean comparisons of the genotype x NaCl concentration interactions (GENxCON) of 19 selected genotypes are presented in Table 4, which includes 12 genotypes with outstanding performance, and 7 genotypes with the highest susceptibility (the information of the 57 genotypes is presented in Table A2.

Table 4. Mean comparisons of the genotype x NaCl concentration (GENxCON) interaction of tomato genotypes selected exposed to two NaCl concentrations (0 and 150 mM). Comparisons are between concentrations within each genotype during germination stage.

GEN	CON	GP	SG	SL	RL	NP	SDM	RDM	TOTDM
					TOLERANT				
CJ103-1	0	98.7 ± 1.33 a	10.4 ± 1.51 a	7.82 ± 0.27 a	2.02 ± 0.09 a	93.22 ± 1.39 a	38.2 ± 2.04 a	5.83 ± 0.81 a	44.03 ± 1.35 a
CJ103-1	150	98.7 ± 1.33 a	2.7 ± 0.15 b	5.44 ± 1 a	3.38 ± 1.21 a	73 ± 4.72 a	33.73 ± 2 a	5.9 ± 1.15 a	39.63 ± 3.12 a
%		0	74	30	−67	22	12	−1	10
CJ106	0	90.7 ± 1.33 a	5.7 ± 0.45 a	4.28 ± 0.23 a	1.09 ± 0.1 a	66.21 ± 7.59 a	8.83 ± 1.45 a	1.66 ± 0.17 a	10.5 ± 1.56 a
CJ106	150	80 ± 4.61 a	2.1 ± 0.12 b	1.78 ± 0.21 a	2.14 ± 0.78 a	40.45 ± 4.78 a	4.4 ± 0.65 a	1.73 ± 0.31 a	6.13 ± 0.55 a
%		128	63	58	−96	39	50	−4	42
CJ83	0	86.7 ± 1.33 a	7.5 ± 0.64 a	5.53 ± 0.21 a	1.57 ± 0.3 a	89.32 ± 3.95 a	24.03 ± 1.21 a	4.76 ± 0.43 a	28.8 ± 1.62 a
CJ83	150	77.3 ± 4.8 a	1.5 ± 0.19 b	2.86 ± 0.62 a	1.66 ± 0.49 a	43.87 ± 13.7 a	19.4 ± 2.49 a	3.83 ± 0.69 a	23.23 ± 1.8 a
%		11	80	48	−6	51	19	20	19
CM15-1	0	100 ± 0 a	11.1 ± 0.44 a	5.84 ± 0.49 a	1.8 ± 0.25 a	88 ± 6.11 a	31.76 ± 1.32 a	6.73 ± 1.41 a	38.5 ± 2.74 a
CM15-1	150	93.3 ± 3.52 a	2.9 ± 0.56 b	5.05 ± 0.49 a	2.33 ± 1.15 a	82.77 ± 10.9 a	26.16 ± 1.83 a	7 ± 0.86 a	33.16 ± 1.73 a
%		7	74	13	−30	6	18	−4	1
CM53	0	89.3 ± 3.52 a	7.4 ± 0.31 a	6.32 ± 0.03 a	1.27 ± 0.35 a	88.16 ± 3.71 a	24.03 ± 0.76 a	3.66 ± 1.12 a	27.7 ± 0.41 a
CM53	150	61.3 ± 28.8 a	1.9 ± 0.93 b	3.28 ± 1.64 a	1.83 ± 1.11 a	53.76 ± 30.1 a	15.33 ± 7.69 a	3.26 ± 1.65 a	18.6 ± 9.31 a
%		31	74	48	−44	39	36	11	33
LOR122	0	80.0 ± 8.0 a	5.4 ± 0.86 a	5.08 ± 0.34 a	1.67 ± 0.32 a	72.34 ± 7.19 a	6.6 ± 0.97 a	1.4 ± 0.47 a	8 ± 1.31 a
LOR122	150	42.7 ± 13.1 a	1.1 ± 0.39 b	1.94 ± 0.31 a	1.41 ± 0.08 a	54.24 ± 12.4 a	2.93 ± 0.08 a	0.76 ± 0.71 a	3.7 ± 0.8 a
%		47	80	62	16	25	56	45	54
LOR133	0	81.3 ± 5.81 a	5.3 ± 0.67 a	5.41 ± 0.24 a	2.12 ± 0.12 a	66.03 ± 3.31 a	9.2 ± 0.85 a	1.86 ± 0.54 a	11.06 ± 0.67 a
LOR133	150	28.0 ± 12.2 a	0.6 ± 0.26 b	2.96 ± 0.31 a	1.3 ± 0.33 a	88.03 ± 30.2 a	4.1 ± 1.17 a	1.1 ± 0.63 a	5.2 ± 1.8 a
%		66	89	45	39	−33	55	41	53
LOR85	0	90.7 ± 3.52 a	5.8 ± 0.66 a	5.94 ± 0.22 a	2.32 ± 0.57 a	69.02 ± 1.23 a	14.7 ± 0.55 a	3.36 ± 0.23 a	18.06 ± 0.53 a
LOR85	150	86.7 ± 5.33 a	2.2 ± 0.31 b	4.7 ± 0.58 a	2.75 ± 0.95 a	66.28 ± 2.72 a	15.13 ± 0.81 a	3.76 ± 1.18 a	18.9 ± 0.73 a
%		4	62	21	−19	4	−3	−12	−5
LOR87	0	92.0 ± 0.0 a	6.7 ± 0.5 a	6.51 ± 0.28 a	1.28 ± 0.31 a	60.86 ± 5.02 a	15.86 ± 1.26 a	3.06 ± 0.85 a	18.93 ± 2.11 a
LOR87	150	84.0 ± 6.11 a	2.1 ± 0.18 b	4.21 ± 0.12 a	3.78 ± 0.28 a	52.26 ± 1.21 a	10.23 ± 2.94 a	3.33 ± 0.61 a	13.56 ± 3.49 a
%		9	68	35	−194	14.	36	−9	28
LOR89	0	90.7 ± 1.33 a	7.0 ± 0.38 a	5.86 ± 0.19 a	1.51 ± 0.31 a	74.96 ± 1.68 a	12.66 ± 1.16 a	2.03 ± 0.31 a	14.7 ± 0.86 a
LOR89	150	72.0 ± 10.6 a	1.8 ± 0.36 b	3.31 ± 0.83 a	1.52 ± 0.37 a	57.39 ± 14.7 a	9.4 ± 3.35 a	2.93 ± 1.03 a	12.33 ± 3.89 a
%		21	74	44	−0.4	23	26	−44	16
LOR90	0	88.0 ± 6.11 a	6.9 ± 0.45 a	6.63 ± 0.43 a	1.48 ± 0.19 a	78.39 ± 2.82 a	15.63 ± 1.59 a	3.03 ± 0.14 a	18.66 ± 1.49 a
LOR90	150	69.3 ± 3.52 a	1.8 ± 0.09 b	5.33 ± 0.34 a	1.18 ± 0.37 a	38.62 ± 2.59 a	12 ± 1.96 a	2.53 ± 0.49 a	14.53 ± 1.61 a
%		21	74	20	20	51	23	16	22
SS3	0	76.0 ± 5.81 a	4.4 ± 0.49 a	6.21 ± 0.29 a	1.31 ± 0.09 a	88.16 ± 9.39 a	19.23 ± 4.43 a	3.8 ± 0.28 a	23.03 ± 4.69 a
SS3	150	73.3 ± 9.23 a	1.8 ± 0.31 a	4.28 ± 0.83 a	3.26 ± 0.68 a	38.72 ± 9.12 a	15.5 ± 0.41 a	3.63 ± 0.62 a	19.13 ± 0.71 a
%		4	60	31	−150	57	19	4	17
					Susceptible				
CJ102	0	100 ± 0 a	6.5 ± 0.57 a	5.84 ± 0.1 a	1.74 ± 0.16 a	97.33 ± 1.33 a	23.33 ± 0.63 a	4.13 ± 0.61 a	27.46 ± 0.82 a
CJ102	150	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 a	0 ± 0 b	0 ± 0 b	0 ± 0 a	0 ± 0 b
%		100	100	100	100	100	100	100	100
CJ103-2	0	98.7 ± 1.33 a	5.7 ± 0.8 a	4.85 ± 0.29 a	1.79 ± 0.49 a	91.72 ± 6.38 a	19.83 ± 1.5 a	4.33 ± 0.43 a	24.16 ± 1.76 a
CJ103-2	150	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 a	0 ± 0 b	0 ± 0 b	0 ± 0 a	0 ± 0 b
%		100	100	100	100	100	100	100	100
CM19	0	98.7 ± 1.33 a	7.5 ± 0.31 a	6.62 ± 0.16 a	4.82 ± 1.03 a	94.66 ± 5.33 a	37.6 ± 1.13 a	9.23 ± 0.69 a	46.83 ± 1.82 a
CM19	150	4.0 ± 2.31 b	0.1 ± 0.03 b	0.5 ± 0.25 b	0.57 ± 0.31 b	66.66 ± 33.3 a	1.7 ± 1.01 b	0.06 ± 0.03 b	1.76 ± 1.03 b
%		96	99	92	88	30	95	99	96
CM29	0	98.7 ± 1.33 a	7.6 ± 0.66 a	6.26 ± 0.54 a	2.04 ± 0.21 a	98.66 ± 1.33 a	30.5 ± 1.02 a	5.36 ± 0.61 a	35.86 ± 0.46 a
CM29	150	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 a	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
%		100	100	100	100	100	100	100	100
CM43	0	100 ± 0 a	7.1 ± 0.11 a	5.91 ± 0.21 a	2.41 ± 0.18 a	98.66 ± 1.33 a	21.56 ± 0.36 a	5.1 ± 0.49 a	26.66 ± 0.84 a
CM43	150	1.3 ± 1.33 b	0.1 ± 0.02 b	0 ± 0 b	0 ± 0 a	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b
%		99	99	100	100	100	100	100	100
CM58	0	96.0 ± 4 a	4.7 ± 0.62 a	4.86 ± 0.54 a	1.45 ± 0.14 a	92.78 ± 3.95 a	22.5 ± 1.76 a	4.66 ± 1.07 a	27.16 ± 2.83 a
CM58	150	5.3 ± 3.52 b	0.1 ± 0.06 b	0.24 ± 0.24 b	0.26 ± 0.26 a	11.11 ± 11.1 a	0.33 ± 0.33 b	0.03 ± 0.03 b	0.36 ± 0.36 b
%		94	98	95	82	88	99	99	99
Habro	0	97.3 ± 1.33 a	6.0 ± 0.31 a	5.78 ± 0.31 a	3.91 ± 0.52 a	80.88 ± 3.42 a	16.43 ± 5.28 a	3.86 ± 1.21 a	20.3 ± 6.5 a
Habro	150	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 b	0 ± 0 a	0 ± 0 b	0 ± 0 a	0 ± 0 b
%		100	100	100	100	100	100	100	100

Means with the same letter vertically and within each genotype did not differ statistically (Tukey, $\alpha \leq 0.05$). GEN: genotype; %: percentage decrease; GP: germination percentage (%); SG: speed of germination; SL: stem length (cm); RL: root length (cm); NP: number of normal plants; SDM: stem dry matter (mg); RDM: root dry matter (mg); TOTDM: total dry matter (mg); HSD: honestly significant difference.

3.2. Development of Tomato Seedlings under Saline Conditions

The analyses of variance of the seedling NaCl tolerance test (Table 5) indicated that at least one genotype (GEN) and NaCl concentrations (CON) had different behaviors ($\alpha \leq 0.05$) in all traits evaluated. The interaction of both factors (GENxCON) showed significance for the APDM, RDM, LA, and PH ($\alpha \leq 0.05$), so the genotypes have different

behaviors across NaCl concentrations. The coefficients of variation (CV) were low, at less than 21.5%, so the information generated can be considered reliable.

Table 5. Sources of variation (SV), degrees of freedom (DF), and mean squares (MS) of the analysis of variance of traits evaluated in 24 tomato lines under saline conditions (175 mM NaCl) during the seedling stage.

SV	DF	APDM	RDM	LA	RL	PH	β
CON	1	101.89 *	0.07 *	8,955,313.33 *	11,085.97 *	1263.22 *	0.3290 *
BLO(CON)	4	0.08	0.01	4127.31	20.11	0.64	0.0002
GEN	23	8.03 *	0.29 *	280,216.77 *	66.01 *	66.17 *	0.0020 *
GENxCON	23	1.35 *	0.02 *	63,215.33 *	27.52	10.22 *	0.0007
ERROR	92	0.13	0.01	3337.05	22.01	1.69	0.0003
CV		13.72	19.32	10.72	14.90	11.36	21.5100
MEAN		2.67	0.54	538.59	31.47	11.44	0.0810

SV: source of variation; DF: degrees of freedom; CON: concentration; G: genotype; BLO(CON): nested block in concentration; GENxCON: Genotype x Concentration; CV: coefficient of variation; APDM: aerial part dry matter; RDM: root dry matter; LF: leaf area; RL: root length; PH: final plant height; β: PH growth rate. * Significant with $\alpha \leq 0.05$.

Mean comparisons of the CON factor (Table 6) indicate that the 175 mM concentration reduced ($\alpha \leq 0.05$) all evaluated variables except RDM. APDM was reduced by 46%, which was attributed to a 59% reduction in LA and a 40% decrease in PH, while RDM had no significant reduction. The β coefficient, which represents the PH daily growth rate, decreased ($\alpha \leq 0.05$) by 71%, and was the trait most affected by NaCl. The trend of increasing RDM under salt stress is striking, although such differences were not significant ($\alpha \leq 0.05$) with respect to the absence of NaCl.

Table 6. Mean comparisons for the NaCl concentration of the response in saline medium divided by the response of the control for traits evaluated in 24 tomato lines.

CON (mM)	APDM	RDM	LA	RL	PH	β
0	3.86 ± 0.25 a	0.50 ± 0.03 a	891.27 ± 47.831 a	43.88 ± 0.62 a	15.63 ± 0.70 a	0.14 ± 0.005 a
175	2.07 ± 0.08 b	0.55 ± 0.02 a	362.26 ± 14.959 b	25.26 ± 0.654 b	9.34 ± 0.21 b	0.04 ± 0.001 b
HSD	0.14	0.04	31.53	2.20	0.39	0.007
Decrease %	46.37	−10	59.35	42.43	40.24	71.42

CON: concentration; APDM: aerial part dry matter; RDM: root dry matter; LA: leaf area; RL: root length; PH: final plant height; β: PH growth rate; HSD = honest significant difference. Means with the same letter within columns do not differ statistically (Tukey, $\alpha \leq 0.05$).

Pearson correlations (Table 7) indicated that the evaluated variables are strongly associated with NaCl concentration, especially plant height growth rate (β), RL, and LA ($\alpha \leq 0.05$). Increases in PH corresponded with increases in APDM and LA ($\alpha \leq 0.05$). They also indicated that APDM had a strong association with LA.

Table 7. Linear correlations between pairs of traits evaluated in 24 tomato wild lines under salinity conditions.

	CON	APDM	RDM	LA	RL	PH
APDM	−0.57 *					
RDM	0.09	0.64 *				
LA	−0.74 *	0.92 *	0.44 *			
RL	−0.84 *	0.62 *	0.22 *	0.73 *		
PH	−0.64 *	0.88 *	0.49 *	0.86 *	0.66 *	
β	−0.89 *	0.52 *	−0.04	0.68 *	0.80 *	0.69 *

CON: concentration; APDM: aerial part dry matter; RDM: root dry matter; LA: leaf area; RL: root length; PH: final plant height; β: PH growth rate. * Significant with $\alpha \leq 0.05$.

Regarding the GENxCON interaction, Table 8 presents the comparison of means between the two NaCl concentrations within each of the genotypes (Table A2). CJ106, CM3, and QUIMH3-1 did not differ ($\alpha \leq 0.05$)under treatment with 0 to 175 mM NaCl in four of the six variables evaluated; that is, these genotypes can be considered the most tolerant to NaCl exposure. In contrast, Claudia, CM29, CM46, Imperial, L47B1, L47S8, LOR133, *Pimpinellifolium*, and SS3 had statistical differences in five of the six traits evaluated, making them the genotypes with the lowest tolerance. The commercial hybrids did not tolerate the saline condition, and, in general, the native lines performed better in this condition.

Table 8. Mean comparisons of GENxCON interaction of 24 selected tomato genotypes exposed to two salinity concentrations (0 and 175 mM). Comparisons are between concentrations within each genotype during seedling stage.

GEN	CON	APDM	RDM	LA	RL	PH	β
				Tolerant			
CJ106	0	1.66 ± 0.27 a	0.29 ± 0.09 a	386.7 ± 48.3 a	44.6 ± 3.2 a	9.83 ± 1.00 a	0.17 ± 0.031 a
CJ106	150	1.08 ± 0.03 a	0.30 ± 0.03 a	210.6 ± 8.6 a	24.6 ± 2.9 b	6.79 ± 0.30 a	0.07 ± 0.006 b
%		34.79	−5.26	45.5	44.9	30.93	58.75
QUIM3-1	0	1.77 ± 0.23 a	0.24 ± 0.03 a	650.7 ± 45.5 a	42.4 ± 3.1 a	10.33 ± 0.16 a	0.18 ± 0.011 a
QUIM3-1	150	1.22 ± 0.09 a	0.36 ± 0.04 a	238.4 ± 14.4 b	26.8 ± 0.9 a	6.50 ± 0.14 a	0.07 ± 0.006 b
%		31.36	−51.04	63.4	36.8	37.09	64.16
CM3	0	1.25 ± 0.03 a	0.21 ± 0.02 a	311.2 ± 22.9 a	39.1 ± 0.8 a	7.67 ± 0.33 a	0.13 ± 0.006 a
CM3	150	1.06 ± 0.16 a	0.26 ± 0.05 a	188.8 ± 31.2 a	19.5 ± 2.4 b	5.71 ± 0.14 a	0.05 ± 0.005 b
%		15.00	−22.62	39.3	49.9	25.55	65.37
				Susceptible			
CM46	0	6.61 ± 0.86 a	0.77 ± 0.11 a	1412.9 ± 59.2 a	45.4 ± 1.6 a	23.17 ± 1.83 a	0.17 ± 0.003 a
CM46	150	3.02 ± 0.21 b	0.75 ± 0.08 a	518.7 ± 37.0 b	25.2 ± 5.2 b	12.75 ± 0.32 b	0.07 ± 0.004 b
%		54.31	2.27	63.3	44.5	44.96	60.08
IMPERIAL	0	6.50 ± 0.45 a	0.72 ± 0.18 a	1402.12 ± 18.2 a	50.2 ± 0.4 a	19.00 ± 0.20 a	0.11 ± 0.026 a
IMPERIAL	150	3.30 ± 0.07 b	0.84 ± 0.02 a	535.9 ± 8.6 b	28.3 ± 1.8 b	12.29 ± 0.25 b	0.03 ± 0.005 b
%		49.23	−16.78	61.8	43.8	35.31	69.51
L47B1	0	3.47 ± 0.61 a	0.35 ± 0.04 a	988.5 ± 78.8 a	43.4 ± 1.2 a	15.33 ± 0.33 a	0.15 ± 0.017 a
L47B1	150	1.88 ± 0.09 b	0.35 ± 0.04 a	318.6 ± 22.7 b	21.8 ± 1.9 b	8.04 ± 0.28 b	0.03 ± 0.006 b
%		45.74	0.00	67.8	49.8	47.55	78.93
L47S8	0	3.05 ± 0.06 a	0.43 ± 0.03 a	635.1 ± 40.1 a	41.2 ± 3.4 a	15.83 ± 0.50 a	0.10 ± 0.008 a
L47S8	150	1.44 ± 0.21 b	0.39 ± 0.08 a	219.8 ± 32.6 b	23.6 ± 2.5 b	9.04 ± 0.14 b	0.03 ± 0.002 b
%		52.63	8.72	65.4	42.8	42.89	67.43
LOR133	0	3.24 ± 0.25 a	0.35 ± 0.04 a	805.7 ± 4.7 a	47.1 ± 4.7 a	18.67 ± 1.33 a	0.22 ± 0.037 a
LOR133	150	1.67 ± 0.05 b	0.41 ± 0.02 a	301.1 ± 13.1 b	25.2 ± 2.5 b	7.42 ± 0.18 b	0.05 ± 0.003 b
%		48.61	−19.57	62.6	46.5	60.27	76.89
PIMP	0	6.55 ± 0 a	0.98 ± 0.02 a	1161.1 ± 5.8 a	51.1 ± 2.7 a	26.92 ± 0.08 a	0.21 ± 0.012 a
PIMP	150	2.64 ± 0.14 b	0.81 ± 0.09 a	464.2 ± 23.9 b	25.0 ± 1.6 b	13.79 ± 0.51 b	0.07 ± 0.008 b
%		59.77	16.92	60.0	51.1	48.76	65.59
SS3	0	5.63 ± 0.26 a	0.64 ± 0.04 b	1245.2 ± 91.4 a	42.1 ± 0.9 a	22.92 ± 0.08 a	0.16 ± 0.003 a
SS3	150	3.60 ± 0.17 b	1.02 ± 0.03 a	707.4 ± 45.5 b	32.9 ± 0.9 a	14.13 ± 0.48 b	0.06 ± 0.002 b
%		36.10	−61.02	43.2	21.7	38.36	61.45
CLAUDIA	0	4.78 ± 0.68 a	0.63 ± 0.17 a	1085.9 ± 87.3 a	45.6 ± 1.8 a	16.00 ± 0.33 a	0.15 ± 0.001 a
CLAUDIA	150	2.58 ± 0.12 b	0.72 ± 0.04 a	469.9 ± 21.9 b	25.4 ± 2.5 b	11.00 ± 0.58 b	0.05 ± 0.001 b
%		45.97	−13.49	56.7	44.3	31.25	65.11
CM29	0	4.49 ± 0.06 a	0.59 ± 0.02 a	1055.0 ± 5.0 a	38.8 ± 0.2 a	16.83 ± 0 a	0.16 ± 0.011 a
CM29	150	2.29 ± 0.09 b	0.52 ± 0.03 a	414.7 ± 4.5 b	19.9 ± 2.7 b	9.13 ± 0.08 b	0.04 ± 0.006 b
%		49.05	11.86	60.7	48.7	45.79	73.87
HSD		1.29	0.37	206.6	16.7	4.56	2.03

GEN: genotype; CON: concentration; %: reduction percentage; APDM: aerial part dry matter; RDM: root dry mater; LA: leaf area; RL: root length; PH: final plant height; β: PH growth rate; HSD: honest significant difference. Means with the same letter within columns do not differ statistically (Tukey, $\alpha \leq 0.05$).

4. Discussion

4.1. Germination Test

All evaluated characters were highly susceptible to saline concentration, since their expression decreased by more than 50%, where germination speed and stem length were the most affected, with reductions greater than 72%.

The significant decrease in germination speed and seed development during germination is due to the inhibition of water uptake caused by NaCl [9,13]. This leads to a reduction in the germination percentage and prolongs the germination period by more than 50% with 80 mM NaCl, and by almost twice as long with 190 mM NaCl [18,34,35].

In our research, GP decreased 65.2% with 150 mM NaCl; in contrast, the Rio Grande variety, when subjected to 85 mM NaCl treatment, decreased by only 6.4% compared with the control, while under treatment with 171 and 257 mM NaCl, the germination percentages on the third day were 2.0 and 0.8%, respectively [43].

There are multiple mechanisms that explain the salt tolerance of wild tomatoes, such as the regulation of Na^+ and Cl^- ion absorption and distribution, osmoregulation, and antioxidant defense [10,15]. Likewise, wild tomatoes have shown advantages over commercial varieties under salt stress conditions (3, 6, 9, and 10.2 $dS{\cdot}m^{-1}$), highlighting their importance as a genetic reservoir for tolerance to this condition [35,37,44].

Under concentrations of 112 mM NaCl (10.2 $dS{\cdot}m^{-1}$), *Solanum peruvianum* accessions were identified with greater tolerance than that of *S. pimpinellifolium* and *S. lycopersicum*, showing greater germination and plumule and root growth [35]. At 150 mM (13.7 $dS{\cdot}m^{-1}$) NaCl, significant reductions in germination percentage and biomass production occur; however, at this concentration, *Solanum chilense* and *Solanum peruvianum* showed outstanding performance [36].

One of the processes involved in salt tolerance is associated with the regulation of water potential via osmotic regulation, through the synthesis of amino acids, sugars, and other osmoregulators [45]. These results and those of our research indicate the possibility of selecting salinity-tolerant genotypes during germination, as there is variation in the responses of the genotypes to this condition, so it is necessary to identify the mechanisms and their association with visual and physiological characteristics for improvement.

One of these mechanisms is the speed of germination, which is a reliable and easy-to-verify indicator (Maguire). With concentrations of 0 and 150 mM, the time required to reach 50% germination was 2.45 days in the control, while with a concentration of 150 mM it took 8.51 days; susceptible genotypes further decreased their germination speed. Research on the subject reports germination delays of 100% due to inefficient regulatory processes [46]. Increasing the concentration (50, 100, and 150 mM) of salt delayed the seed germination of four tomato cultivars; at 150 mM, after 10 days of incubation, only one of the evaluated cultivars achieved 50% germination [38]. NaCl concentrations of 50, 100, and 200 mM NaCl reduced the speed and percentage of tomato seed germination, which may have been due to the deterioration of enzymatic activity under Na^+ and Cl^- ion toxicity [47], while with 0 and 4 $dS{\cdot}m^{-1}$, they managed to germinate at 5.3 and 8.34 days after sowing, respectively [39].

Low NaCl concentrations induce seed dormancy since, with increasing salinity concentrations, the germination speed and germination percentage decreased, but the mean germination time increased, while high concentrations inhibit germination due to the decrease in the water potential gradient between the seeds and the surrounding medium; coupled with this, the osmotic and toxic effects of NaCl reduce enzymatic activity and ABA content [48,49].

Previous studies have indicated the negative root–stem relationship in terms of increasing salt concentrations; that is, stem growth is restricted while root growth is less hindered [48], whereas in this study, the RL:SL ratio showed a positive relationship (0.63), and was high, which is attributed to high expression in the roots of transporters, such as HKT1:2, which participate in the transfer of Na^+ from the shoot to the root [50]. Thus,

growth inhibition is due to the toxicity of Cl^- and Na^+ ions and the nutritional imbalance they generate [51].

Our results (Table 7), like those of Ludwiczak et al. [52], show that the greater sensitivity to salt in aerial and/or root growth is a particular genotypic response, because the effects of salt on the morphology of the different organs of plants occur at all stages of development and negatively affect diverse organs such as the stem, root, and leaves (size, weight, and dry matter), and characteristics like the percentage and speed of germination and the root/shoot ratio [53].

4.2. Development of Tomato Seedlings under Salinity Conditions

Tukey's mean comparisons of the evaluated traits (Table 6) indicate that the 175 mM concentration reduced ($\alpha \leq 0.05$) all evaluated variables except for RDM. APDM was reduced by 46%, while RDM had no significant reduction. Considering that salt stress also implies osmotic stress, similar to that caused by drought, the low water availability could have contributed to modifying the relationship between the growth of the aerial part and that of the root, since the latter continued its development in search of water in deeper areas, while the aerial part stopped its growth [49]. However, these results suggest that ionic stress could affect plant performance due to high NaCl concentrations [51].

PH was reduced ($\alpha \leq 0.05$) in saline conditions since this type of stress causes reductions in plant height and changes in the number and size of leaves. This could be due to the toxicity of Na^+ and Cl^- ions and the nutritional imbalance induced by salinity [51]. Likewise, the root length of tomato lines was severely reduced at a concentration of 150 mM [5].

During the first hours of exposure to salts, stomatal closure and inhibition of cell expansion occur, mainly in the growth buds. Therefore, in prolonged periods of salt-induced stress, leaves decrease their growth, become stunted, and frequently turn blue-green. This is due to the increase in respiration and the activity of the chlorophyllase enzyme, which decreases chloroplast activity, photosynthesis, and chlorophyll content, triggering chlorosis symptoms (CIATs). Similarly, metabolic disorders ensue and decrease the efficiency and speed of these process, leading to premature senescence and ultimately cell death [53,54].

By reducing the availability of soil water, salinity causes a decrease in the water and osmotic potential of the plant to maintain water absorption via the root [55]; however, in the face of high concentrations or prolonged stress conditions, plant growth is compromised, causing a decrease in fresh weight and dry matter accumulation [56]. We observed a similar phenomenon in our study, as the provided saline conditions decreased the dry weight of the aerial plant tissue, affecting overall development by reducing leaf size, plant height, and leaf number.

Leaf area decreased by 33% in the Raf cultivar under a salinity level of 11 $dS{\cdot}m^{-1}$ [57]. Likewise, saline water with an electrical conductivity of 4.4 $dS{\cdot}m^{-1}$ used in tomato irrigation reduced leaf area by 47.55% with respect to that of the control [58].

SanJuan-Lara et al. [14] evaluated the response of 48 lines obtained via individual selection in a native tomato population at five levels of electrical conductivity (4, 6, 8, 8, 10, and 12 $dS{\cdot}m^{-1}$) in the seedling stage, finding that salinity reduced the number of leaves by 12%, stem diameter by 17%, leaf area by 38%, and plant height by 40%, some percentages being similar to those obtained in the present study.

According to the above, it is possible that tomato genotypes have various strategies to tolerate salinity depending on their morphology and growth habits [59]. Plant tolerance to salt is mediated by several biochemical pathways that favor the retention and/or acquisition of water, the protection of chloroplast functions, and the maintenance of ion homeostasis [53]. The lower tolerance of the cultivars may be due to excessive sodium accumulation in the cells, which rapidly causes ionic stress and cell death [60].

The above occur because there are phenotypic differences in the size of the fruits and vegetative organs, with leaves exhibiting the greatest differences in size and morphology. This phenotypic divergence has been shown to be an important factor determining the

ability of wild species to thrive in extreme environments [61]. During the seedling stage, tomato is more sensitive to high salt concentrations compared with when it is in the later growth stages [41].

To design an experiment that will assist in the selection of salt-tolerant genotypes, it is necessary to consider the phenological stage of the crop, since through the development of a particular genotype, the susceptibility to this condition is variable due to the expression of specific genes at each stage [52,53] Another factor to consider is the degree of stress to be applied, which must be selected to avoid the lethality of the plants, although it must be high enough so that in a short time it can allow tolerance levels to be assessed through characters such as dry matter accumulation, chlorophyll concentration, structure length, leaf area, etc., and other traits such as the plant tissue concentration of antioxidants, chlorine, sodium, enzymes, nutrients, flavonoids, phytohormones, sugars, and proteins, among others [10,54,62,63]. Tolerance mechanism activity is highly dependent on the level of salinity. For example, Na^+ exclusion is more effective under high salinity conditions, while osmotic tolerance may be the most important tolerance mechanism under moderate salinity [53].

Additionally, managing stress levels is essential; if it is too high, the variation in the response of a genotype will increase too much, even in the same condition, resulting in estimates of experimental error with lower precision, preventing the detection of statistical differences between treatments. Similarly, it is necessary to consider that in production on saline soils or with the use of saline water, conditions that are increasingly common in agriculture, the presence of this stress will be continuous during the development of the crop. Thus, the maintenance of growth, dry matter accumulation, and yield will be primary indicators for the selection of genotypes tolerant to continuous salt stress. Despite the above, it is also necessary to quantify the damage caused by salt stress using physiological indicators to identify diverse tolerance mechanisms.

At the seedling stage, decreased stem and root length, as well as reduced wet and dry weights of the aerial part and root, occur with increasing salinity concentrations [42], resulting in a reduction in percentages of up to 40%.

In a study by Sánchez et al. [57], tomato seedlings of the Raf cultivar were exposed to a salinity level of 5.5 $dS{\cdot}m^{-1}$, under which they showed 2708 cm^2 of leaf area, while at 11 $dS{\cdot}m^{-1}$, their leaf area decreased to 1815 cm^2.

Plants adapt to salt stress through multiple biochemical and molecular pathways, where Na^+ and K^+ transporters across the plasma membrane play an important role, especially the HKT and HAK families of transporters [64].

Salinity induces Ca^+ accumulation, which is a rapid signal for detecting this condition. This occurs by means of Ca^+-dependent proteins that decode Ca^+ input routes to the cytoplasm, such as the hypersensitive salt route (SOS) dependent on Ca^+ that activates antiporters Na^+/H^+ and K^+/H^+ to expel salt and improve tolerance to this condition [54].

Osmotic adjustment is used to reduce osmotic stress, as a means by which to aid the plants in absorbing water and maintaining turgor in cells by increasing the solute concentration, which plays a protective role in stabilizing the structure of biological macromolecules. Osmotic regulators mainly include inorganic ions and organic substances such as sugar, complex sugars, proline, glycinbetaine, polyamines, and late embryogenesis abundant (LEA) proteins [65–67].

Saline stress induces the production of reactive oxygen species (ROS) in apoplasts, chloroplasts, mitochondria, and peroxisomes of the plant [62]. The MAPK3 gene can increase tolerance to salts via the RBOH1-dependent anti-oxidant system [68]. Melatonin also decreases the production of ROS by balancing the distribution of electron flow in photosynthesis and promoting the activity of enzymes involved in the ascorbate-glutathione cycle [69]. Superoxide dismutase is the most efficient enzyme of ROS eliminating, converting O_2 into H_2O_2 and subsequently into H_2O. Flavonoids and phytohormones (ABAs) also play an important role as antioxidants [63].

Epigenetic modifications are molecular mechanisms that regulate gene expression under salt stress, conferring adaptations to unfavorable conditions. In tomato, eleven

DNA methyltransferase genes have been identified (MET, MET1, CMT2, CMT3, CMT4, DRM5, DRM6, DRM7, DRM8, DNMT2, and METL). These genes are regulated by salt stress, suggesting that they are involved in the adaptive response to this stress [9]. In the PI365967 accession of *S. pimpinellifolium*, 86 genes involved in sallicylic acid signaling, the SOS pathway, transcriptional regulation, and ROS removal have been identified, suggesting the role of multiple strategies for tolerance to salt in wild species [11].

5. Conclusions

Salinity produces negative effects on germination and the early developmental stages of tomato seedlings. Furthermore, the results of this study suggest that the effects of salinity differ depending on the cultivar, where genetics and the developmental stage, mainly, play an important role in tolerance and/or susceptibility to salinity.

During germination, the saline condition decreased the germination percentage (65.2%), speed of germination (88.2%), steam length (72.5%), root length (46.56%), normal plants number (59.5%), stem dry matter (68.78%), root dry matter (61.99%), and total dry matter (67.1%).

At the seedling stage, 175 mM NaCl decreased the aerial part dry matter (46.37%), leaf area (59.35%), root length (42.43%), final plant height (40.24%), and growth rate (71.42%).

In total, 15 tolerant genotypes were identified at both developmental stages, while one genotype (CJ106) showed tolerance at both stages studied. These genotypes showed the best response in terms of the variables evaluated.

The plant morphology and physiological responses expressed by the native tolerant genotypes are associated with tolerant mechanisms, such as osmotic adjustments, genetic resistance, the production of antioxidants, and the expression of specific genes that avoid the modification of metabolic processes due to diverse saline stress conditions.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Origins of evaluated lines, derived from wild tomato populations of Mexico.

Genotype	Location	Municipality	State	Program
Catemaco	Mercado	Catemaco	Veracruz	UACh
Chapopote	Unknown			UACh
CJ102	Martínez de la Torre	Martínez de la Torre	Veracruz	UACh
CJ103-1	Unknown			UACh
CJ103-2	Unknown			UACh
CJ106	Huitzuco	Huitzuco	Guerrero	UACh
CJ81	Ecatlán	Jonotla	Puebla	UACh
CJ83	Totonaca	Totonaca	Veracruz	UACh
CM10	Ecatlán	Zozocolco de Hidalgo	Veracruz	UACh

Table A1. *Cont.*

Genotype	Location	Municipality	State	Program
CM11	La Esperanza	San Martín Chalchicuautla	San Luis Potosí	UACh
CM15-1	Unknown			UACh
CM15-2	Unknown			UACh
CM19	San Blas Atempa	San Blas Atempa	Oaxaca	UACh
CM2	El Solar San Juan	Chichiquila	Puebla	UACh
CM22	San José Monte Verde	Santa María Nativitas	Oaxaca	UACh
CM29	Santiago Cuixtla	Santos Reyes Nopala	Oaxaca	UACh
CM3	El Solar San Juan	Chichiquila	Puebla	UACh
CM31	Ecatlán	Zozocolco de Hidalgo	Veracruz	UACh
CM32	Santiago Cuixtla	Santos Reyes Nopala	Oaxaca	UACh
CM36	Oventic	Larráizar	Chiapas	UACh
CM37	Shuchila	Ocosingo	Chiapas	UACh
CM39	Cerano	Cerano	Guanajuato	UACh
CM40	Cerano	Cerano	Guanajuato	UACh
CM42	Coetzalan	Coetzalan	Veracruz	UACh
CM43	Cuerámaro	Cuerámaro	Guanajuato	UACh
CM44	Cerano	Cerano	Guanajuato	UACh
CM45	Juquila	Juquila	Oaxaca	UACh
CM46	Santo Domingo Alboradas	Tlacolula	Oaxaca	UACh
CM5	San Francisco Chamizal	Misantla	Veracruz	UACh
CM53	Palenque	Palenque	Chiapas	UACh
CM55	Huichapan	Huichapan	Hidalgo	UACh
CM58	Unknown		Chiapas	UACh
CM59	Unknown		Chiapas	UACh
CM63	Unknown			UACh
S. habrocaites	Unknown			UACh
Huasave	Gusave	Guasave	Sinaloa	UACh
LOR107	Altepexi	Altepexi	Puebla	CP
LOR111	Zinacantepec	Zinacantepec	Puebla	CP
LOR115	Unknown			CP
LOR122	Huauchinango	Huauchinango	Puebla	CP
LOR133	Sta. María Temaxcalapa	Santa María Temaxcalapa	Oaxaca	CP
LOR134	Unknown			CP
LOR85	Altepexi	Altepexi	Puebla	CP
LOR87	Altepexi	Altepexi	Puebla	CP
LOR89	Chimalhuacán	Chimalhuacán	México	CP
LOR90	Altepexi	Altepexi	Puebla	CP
S. pimpinellifollium	Unknown			UACh
QUIMH1-1	Quimixtla	Tlanchinol	Hidalgo	UACh
QUIMH3-1	Quimixtla	Tlanchinol	Hidalgo	UACh
QUIMH3-2	Quimixtla	Tlanchinol	Hidalgo	UACh
SILVNVO9	Unknown			UACh
SS3	Necaxa	Necaxa	Puebla	UACh
SS4	Palenque	Palenque	Chiapas	UACh
SS5	Unknown			UACh
Tonatico	Tonatico	Tonatico	México	UACh

Table A2. Mean comparisons of the GENxC interaction of 24 selected tomato genotypes exposed to two salinity concentrations (0 and 175 mM). Comparisons are between concentrations within each genotype.

GEN	CON	APDM	RDM	LA	RL	PH	β
CHAPOPOTE	0	2.17 ± 0.15 a	0.28 ± 0.02 a	490.96 ± 12.63 a	49.65 ± 3.84 a	10.91 ± 2.25 a	0.17 ± 0.015 a
CHAPOPOTE	175	1.25 ± 0.03 a	0.43 ± 0.04 a	255.6 ± 4.67 b	32.71 ± 4.49 b	6.12 ± 0.14 b	0.04 ± 0.005 b
%		42.05	−56.25	47.93	34.10	43.89	72.35
CJ106	0	1.66 ± 0.27 a	0.28 ± 0.09 a	386.71 ± 48.27 a	44.61 ± 3.17 a	9.83 ± 1 a	0.17 ± 0.032 a
CJ106	175	1.08 ± 0.03 a	0.3 ± 0.03 a	210.59 ± 8.61 a	24.56 ± 2.97 b	6.79 ± 0.3 a	0.07 ± 0.006 b
%		34.78	−5.26	45.54	44.93	30.92	58.75

Table A2. *Cont.*

GEN	CON	APDM	RDM	LA	RL	PH	β
CJ83-1	0	4.97 ± 0.32 a	0.63 ± 0.03 a	1048.18 ± 53.62 a	45.02 ± 5.75 a	16.75 ± 0.75 a	0.13 ± 0.003 a
CJ83-1	175	3.11 ± 0.13 b	1.03 ± 0.06 a	542.95 ± 30.93 b	33.36 ± 2.81 a	11.79 ± 0.35 b	0.05 ± 0.006 b
%		37.27	−62.20	48.20	25.88	29.60	62.16
CLAUDIA	0	4.77 ± 0.68 a	0.63 ± 0.17 a	1085.98 ± 87.28 a	45.57 ± 1.78 a	16.00 ± 0.33 a	0.14 ± 0.0001 a
CLAUDIA	175	2.58 ± 0.12 b	0.71 ± 0.04 a	469.99 ± 21.91 b	25.37 ± 2.47 b	11.00 ± 0.58 b	0.05 ± 0.001 b
%		45.96	−13.49	56.72	44.32	31.25	65.11
CM15-1	0	6.56 ± 0.11 a	1.08 ± 0.08 a	1303.66 ± 45.26 a	40.91 ± 2.21 a	19.16 ± 1.33 a	0.13 ± 0.004 a
CM15-1	175	3.08 ± 0.11 b	0.91 ± 0.06 a	527.8 ± 17.84 b	30.08 ± 2.92 a	13.12 ± 0.77 b	0.05 ± 0.012 b
%		52.93	15.66	59.51	26.46	31.52	59.31
CM29	0	4.48 ± 0.06 a	0.59 ± 0.02 a	1055.07 ± 5.02 a	38.76 ± 0.15 a	16.83 ± 0 a	0.15 ± 0.011 a
CM29	175	2.28 ± 0.09 b	0.52 ± 0.03 a	414.65 ± 4.51 b	19.93 ± 2.66 b	9.12 ± 0.08 b	0.04 ± 0.006 b
%		49.05	11.86	60.69	48.56	45.79	73.87
CM3	0	1.25 ± 0.03 a	0.21 ± 0.02 a	311.24 ± 22.86 a	39.04 ± 0.79 a	7.66 ± 0.33 a	0.13 ± 0.006 a
CM3	175	1.06 ± 0.16 a	0.25 ± 0.05 a	188.81 ± 31.2 a	19.53 ± 2.37 b	5.71 ± 0.14 a	0.04 ± 0.005 b
%		15.00	−22.61	39.33	49.97	25.55	65.36
CM46	0	6.61 ± 0.86 a	0.77 ± 0.11 a	1412.89 ± 59.2 a	45.41 ± 1.54 a	23.16 ± 1.83 a	0.17 ± 0.003 a
CM46	175	3.02 ± 0.21 b	0.75 ± 0.08 a	518.67 ± 37.0 b	25.18 ± 5.2 b	12.75 ± 0.32 b	0.06 ± 0.004 b
%		54.31	2.27	63.29	44.54	44.94	60.07
IMPERIAL	0	6.49 ± 0.45 a	0.71 ± 0.18 a	1402.12 ± 18.2 a	50.23 ± 0.36 a	19 ± 2 a	0.11 ± 0.026 a
IMPERIAL	175	3.29 ± 0.07 b	0.83 ± 0.02 a	535.86 ± 8.62 b	28.24 ± 1.79 b	12.29 ± 0.25 b	0.03 ± 0.005 b
%		49.23	−16.78	61.78	43.76	35.31	69.51
L3	0	2.32 ± 0.14 a	0.26 ± 0.07 a	881.97 ± 37.12 a	38.76 ± 1.02 a	17.25 ± 1.41 a	0.16 ± 0.009 a
L3	175	1.21 ± 0.09 a	0.22 ± 0.02 a	202.64 ± 15.08 b	20.03 ± 1.36 b	8.29 ± 0.36 b	0.04 ± 0.005 b
%		47.62	15.09	77.02	48.32	51.93	73.61
L47B1	0	3.46 ± 0.61 a	0.35 ± 0.04 a	988.49 ± 78.84 a	43.41 ± 1.19 a	15.33 ± 0.33 a	0.15 ± 0.017 a
L47B1	175	1.88 ± 0.09 b	0.35 ± 0.04 a	318.59 ± 22.76 b	21.81 ± 1.94 b	8.04 ± 0.28 b	0.03 ± 0.006 b
%		45.74	0.00	67.77	49.75	47.55	78.93
L47S8	0	3.04 ± 0.06 a	0.43 ± 0.03 a	635.1 ± 40.1 a	41.16 ± 3.43 a	15.83 ± 0.5 a	0.1 ± 0.008 a
L47S8	175	1.44 ± 0.21 b	0.39 ± 0.08 a	219.81 ± 32.56 b	23.55 ± 2.52 b	9.04 ± 0.14 b	0.03 ± 0.002 b
%		52.62	8.72	65.38	42.77	42.89	67.43
L52	0	4.11 ± 0.31 a	0.5 ± 0.06 a	877.4 ± 26.86 a	43.66 ± 1.69 a	11 ± 0.66 a	0.13 ± 0.023 a
L52	175	1.9475 ± 0.11 b	0.41 ± 0.03 a	306.54 ± 14.54 b	18.66 ± 0.91 b	6.95 ± 0.31 a	0.04 ± 0.004 b
%		52.67	18.50	65.06	57.25	36.74	67.52
L69	0	1.72 ± 0.57 a	0.18 ± 0.11 a	541.11 ± 12.52 a	39.73 ± 4.64 a	11.83 ± 1 a	0.15 ± 0.051 a
L69	175	1.14 ± 0.08 a	0.19 ± 0.03 a	181.79 ± 11.26 b	16.21 ± 1.19 b	6.08 ± 0.09 b	0.03 ± 0.009 b
		33.91	−5.55	66.40	59.21	48.59	75.92
LOR133	0	3.24 ± 0.25 a	0.34 ± 0.04 a	805.7 ± 4.72 a	47.08 ± 4.65 a	18.66 ± 1.33 a	0.21 ± 0.037 a
LOR133	175	1.66 ± 0.05 b	0.41 ± 0.02 a	301.07 ± 13.08 b	25.194 ± 2.52 b	7.41 ± 0.18 b	0.05 ± 0.003 b
		48.61	−19.56	62.63	46.48	60.26	76.88
LOR134	0	2.55 ± 0.06 a	0.39 ± 0.01 a	620.91 ± 20.24 a	45.209 ± 0.38 a	13.91 ± 1.41 a	0.16 ± 0.001 a
LOR134	175	1.6 ± 0.04 a	0.53 ± 0.03 a	311.79 ± 11.46 b	31.788 ± 3.15 a	6.91 ± 0.17 b	0.03 ± 0.005 b
		37.25	−35.89	49.78	29.68	50.29	75.81
LOR85	0	5.24 ± 1.24 a	0.7 ± 0.15 a	1433.8 ± 146.77 a	42.3 ± 0.16 a	16.58 ± 4.91 a	0.12 ± 0.047 a
LOR85	175	2.89 ± 0.16 b	0.702 ± 0.06 a	496.49 ± 27.96 b	27.31 ± 3.31 a	11.83 ± 0.15 b	0.04 ± 0.001 b
		44.89	−0.35	65.37	35.42	28.64	60.36
LOR89	0	3.06 ± 0.31 a	0.36 ± 0.1 a	808.77 ± 83.08 a	43.47 ± 0.77 a	12.08 ± 0.91 a	0.12 ± 0.023 a
LOR89	175	2.22 ± 0.05 a	0.59 ± 0.03 a	411.7 ± 12.24 b	25.47 ± 1.77 b	8.91 ± 0.29 a	0.05 ± 0.007 b
		27.56	−64.58	49.09	41.41	26.20	59.19
PIMP	0	6.55 ± 0 a	0.97 ± 0.02 a	1161.11 ± 5.85 a	51.08 ± 2.74 a	26.91 ± 0.08 a	0.21 ± 0.01 a
PIMP	175	2.63 ± 0.14 b	0.81 ± 0.09 a	464.18 ± 23.86 b	24.99 ± 1.58 b	13.79 ± 0.51 b	0.07 ± 0.008 b
		59.77	16.92	60.02	51.07	48.76	65.58
QUIMH3-1	0	1.77 ± 0.23 a	0.24 ± 0.03 a	650.72 ± 145.58 a	42.38 ± 3.05 a	10.33 ± 0.16 a	0.18 ± 0.013 a
QUIMH3-1	175	1.21 ± 0.09 a	0.36 ± 0.04 a	238.39 ± 14.39 b	26.78 ± 0.85 a	6.5 ± 0.14 a	0.06 ± 0.006 b
		31.35	−51.04	63.36	36.81	37.09	64.16
SILNVO9	0	3.13 ± 0.31 a	0.42 ± 0.05 a	583.52 ± 6.92 a	43.86 ± 1.98 a	11.75 ± 0.08 a	0.1 ± 0.004 a
SILNVO9	175	1.41 ± 0.06 b	0.31 ± 0.02 a	206.12 ± 7.35 b	19.76 ± 0.89 b	8.21 ± 0.18 a	0.02 ± 0.007 b
		55.18	26.78	64.67	54.93	30.14	78.33
SS3	0	5.63 ± 0.26 a	0.63 ± 0.04 b	1245.29 ± 91.43 a	42.11 ± 0.92 a	22.91 ± 0.08 a	0.15 ± 0.003 a
SS3	175	3.59 ± 0.17 b	1.02 ± 0.03 a	707.41 ± 45.51 b	32.99 ± 0.93 a	14.12 ± 0.48 b	0.06 ± 0.002 b
		36.10	−61.02	43.19	21.66	38.36	61.45
SS4	0	4.07 ± 0.11 a	0.75 ± 0.02 a	871.17 ± 3.79 a	47.58 ± 1.51 a	13.83 ± 0.16 a	0.11 ± 0.013 a
SS4	175	2.29 ± 0.06 b	0.75 ± 0.03 a	366.45 ± 15.42 b	25.16 ± 1.58 b	9.37 ± 0.2 a	0.04 ± 0.004 b
		43.61	0.66	57.93	47.11	32.22	60.33
TOPONGA	0	3.84 ± 0.01 a	0.46 ± 0.005 a	788.65 ± 87.42 a	42.11 ± 0.67 a	17.58 ± 2.41 a	0.13 ± 0.006 a
TOPONGA	175	1.98 ± 0.09 b	0.56 ± 0.04 a	296.3 ± 14.34 b	27.72 ± 1.71 a	10.16 ± 0.27 b	0.02 ± 0.004 b
		48.50	−21.51	62.42	34.17	42.17	77.84

GEN: genotype; CON: concentration; %: reduction percentage; APDM: aerial part dry matter; RDM: root dry mater; LA: leaf area; RL: root length; PH: final plant height; β: PH growth rate; HSD: honest significant difference. Means with the same letter within columns do not differ statistically (Tukey, $\alpha \leq 0.05$).

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