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NaCl 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 were subjected to 150 mM and 0 mM NaCl and evaluated. The test was carried out for 20 days in a germination chamber with constant darkness, temperature of 25±2 °C and relative humidity of 80±4%. At the seedling stage, 22 wild tomato lines with the best performance in the germination test and 2 commercial hybrids were evaluated for 12 days in a floating raft system. Concentrations of 175 mM and 0 mM NaCl were used. Seventeen tolerant genotypes were identified at one of both developmental stages, while one genotype showed tolerance at 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 or as potential rootstocks.

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

1. Introduction

Ten percent of the Earth's land surface (950 million ha) and 50 % of its agricultural land (230 million ha) are affected by salts [1]; this condition is responsible for significant crop yield losses, with an annual value of up to $30 billion [2]. Salt-affected areas are increasing due to the use of saline water and intensive use of groundwater for irrigation, excessive application of chemical fertilizers and irrational crop rotation [3]; therefore, one of the current challenges facing agriculture is to increase crop production under salinity 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 of enzymes and respiratory disorders [4]. 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 [5–7]. 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. [8,9].

Plant salinity tolerance is directly associated with the phenological stage, the affected plant organ, the duration and severity of the stress, and the environmental factors that cause it [10–13]. The genetic component is also of great importance since wild tomatoes with salt tolerance have multiple regulatory mechanisms of Na^+ accumulation, including regulation of ion uptake and distribution, osmoregulation, and efficient antioxidant defense [10,14,15].

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 [16], since the use of uncharacterized accessions may indicate that commercial cultivars have greater tolerance to salinity [17–19]. 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* [2,20–25].

Some *S. pimpinellifolium* accessions have high salt tolerance, making them potential candidates for breeding [2,26], since being closely related to *S. lycopersicum* they have been used as a donor to commercial tomato of many important traits [26]. *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 seawater [24].

Given the great genetic variation of wild species and especially those native to Mexico, one of the centers of domestication of this species [27], 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 [28].

Because commercial tomato breeding has focused on the development of disease-resistant cultivars with commercial fruit quality [29], 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 an alternative that is 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 Tomato Breeding Program (PMGT) greenhouses operated by the Universidad Autónoma Chapingo (UACh) located at NL 19°30′0.0″ and WL 98°53′00 and 2247 masl.

The genotypes evaluated were 52 lines derived from wild tomato populations of the PMGT and the Wild Tomato Breeding Program of the Colegio de Postgraduados (LOR lines), as well as three commercial hybrids used as controls: Imperial® (Enza Zaden), Reserva® (Vilmorin) and Topanga® (Rogers Seeds).

2.1. Germination salt tolerance test

Fifty-two wild tomato lines and the commercial hybrids Imperial® (Enza Zaden) and Reserva® (Vilmorin) 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). For its preparation, distilled water, and reagent quality NaCl with 99.3 % purity were used. The experimental unit consisted of a 5.5 cm diameter Petri dish, with 25 seeds and filter paper as 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) in constant darkness, a temperature of 25±2 °C and relative humidity 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 germination rate (GR), according to the formula proposed by Maguire (1962)[30]:

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

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.

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 2 commercial hybrids were evaluated: Imperial Imperial® (Enza Zaden) and Topanga® (Rogers Seeds). The experiment was conducted under greenhouse conditions. 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 x 1.2 m and 20 cm high, covered with polyethylene and with a capacity of 500 liters of nutrient solution. The nutrient solution used was 0.589 $kg \cdot m^{-3}$ $Ca(NO^3)^2$, 0.101 $kg \cdot m^{-3}$ KNO^3, 0.123 $kg \cdot m^{-3}$ KH^2PO^4, 0.171 $kg \cdot m^{-3}$ $MgSO^4$, 0.033 $kg \cdot m^{-3}$ librel mix, 0.012 $kg \cdot m^{-3}$ $FeSO^4$, 0.007 $kg \cdot m^{-3}$ borax and 0.022 $kg \cdot m^{-3}$ H^2SO^4. Transplanting to the floating raft system was performed 20 days after sowing.

Four days after transplanting (DAT), NaCl was applied to the nutrient solution to achieve the concentration of 175 mM NaCl (15.9 $dS \cdot m^{-1}$); likewise, a treatment without salt application (0 mM NaCl) was considered.

The experimental unit consisted of 5 seedlings of which the three central ones were evaluated. A randomized complete block experimental design 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 with ImageJ software (v1.4.3.67; National Institutes of Health).

The evaluated traits were subjected to 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, $\beta =$ parameter indicating plant height growth rate, $e =$ 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 (CONxGEN), except for RL in CON. This indicates differential effects caused by salt stress, and by genotypic differences; in addition, some genotypes had different behavior 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 condition (150 mM NaCl) during germination.

SV	DF	GP	ESI	SL	RL	NP	SDM	RDM	TOTDM
GEN	53	2017.9*	10.6*	5.0*	1.9*	124.3*	231.4*	9.9*	331.6*
CON	1	31051.4*	1095.4*	399.5*	0.0001	3667.1*	2065.7*	22.8*	2386.1*
GENxCON	53	628.7*	5.4*	2.3*	2.0*	37.7*	60.3*	3.6*	96.0*
ERROR	148	94.0	0.7	0.8	0.9	9.1	12.4	1.2	16.9
TOTAL	255								
CV		13.6	20.7	19.7	55.8	23.0	25.2	39.4	24.5
MEAN		70.9	4.2	4.6	1.7	13.1	13.9	2.8	16.9

GEN: genotype, CON: concentration, GP: germination percentage, EVI: emergence speed index, 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 $\alpha \leq 0.05$.

Mean comparisons of NaCl concentrations (Table 2) indicated that the 150 mM dose decreased ($\alpha \leq 0.05$) all evaluated traits, except for RL (Table 2). SL reduced its expression by 46 % and the dry weights SDM, RDM and TOTDM by 37, 33 and 31 %, respectively. It is striking that decreases in RDM were detected ($\alpha \leq 0.05$); however, the length of this structure (RL) was not modified.

Table 2. Mean comparisons of NaCl concentrations and percentage reduction due to the salt stress effect of traits evaluated in 54 tomato lines during germination.

CON (mM)	GP	ESI	SL	RL	NP	SDM	RDM	TOTDM
0	78.7 a	5.9 a	5.5 a	1.7 a	16.1 a	16.0 a	3.0 a	19.0 a
150	58.2 b	1.4 b	2.9 b	1.7 a	8.2 b	10.7 b	2.5 b	13.4 b
HSD	2.4	0.2	0.2	0.2	0.7	0.9	0.3	1.0
Decrease %	26.0	75.9	46.4	0	49.0	37.5	33.3	31.5

CON: concentration, GP: germination percentage, ESI: emergence speed index, 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, $\alpha \leq 0.05$).

Salt stress reduced GP by 26 % ($\alpha \leq 0.05$) and ESI by 75 % ($\alpha \leq 0.05$), 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 (Table 2).

Mean comparisons of the genotype x NaCl concentration (GENxCON) interactions are presented in Table 3, which includes 14 genotypes with outstanding performance, 7 with the highest susceptibility and the commercial hybrid Imperial.

The genotypes that did not decrease the expression of their traits significantly ($\alpha \leq 0.05$) when changing from 0 mM to 150 mM NaCl were considered as those with the best performance under salinity. The genotypes found in this category were: CJ106, CM32, CM39, LOR119, LOR124, LOR129, LOR130, LOR37, LOR46, LOR78, LOR83, LOR85, SS2 and SS3. In contrast, those genotypes with significant decreases in most of their traits when subjected to the saline condition were considered susceptible to NaCl. These genotypes were: CM19, CM58, CM63 and Imperial. The rest of the lines had intermediate tolerance.

Table 3. 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.

GEN	CON	GP	ESI	RL	NP	SDM	RDM	TOTDM	
CJ106	0	91 a	5.7 a	1.1 a	15 a	8 a	1.6 a	10.5 a	Tolerant
CJ106	150	80 a	2.1 a	2.1 a	8 a	4 a	1.7 a	6.1 a	
	%	12	64	0	47	50	0	41.9	
CM32	0	93 a	5.3 a	2.4 a	23 a	13 a	3.7 a	17.4 a	Tolerant
CM32	150	68 a	2.6 a	3.1 a	16 a	11 a	1.6 a	13.4 a	
	%	27	51	0	29	15	57	23	
CM39	0	71 a	3.3 a	0.7 a	8.7 a	4 a	0.6 a	4.7 a	Tolerant
CM39	150	44 a	1.1 a	1.4 a	3 a	15 a	1.2 a	16.9 a	
	%	38	66	0	65	0	0	0	
LOR119	0	25 a	1.5 a	0.5 a	2.7 a	2 a	0.4 a	2.5 a	Tolerant
LOR119	150	44 a	1.1 a	1.7 a	4 a	6 a	2.1 a	8.8 a	
	%	0	27	0	0	0	0	0	
LOR124	0	23 a	1.3 a	0.5 a	2.7 a	3 a	0.2 a	3.8 a	Tolerant
LOR124	150	32 a	0.7 a	0.5 a	4 a	4 a	0.9 a	5 a	
	%	0	44	0	0	0	0	0	
LOR129	0	45 a	2.5 a	0.6 a	3.7 a	4 a	0.5 a	5.3 a	Tolerant
LOR129	150	32 a	0.9 a	1 a	2 a	2 a	0.9 a	3.8 a	
	%	29	66	0	45	50	0	28.3	
LOR130	0	33 a	2.1 a	1.4 a	6.3 a	7 a	1.5 a	8.9 a	Tolerant
LOR130	150	25 a	0.6 a	0.6 a	2.3 a	3 a	0.9 a	4.6 a	
	%	24	71	57	63	57	40	48.3	
LOR137	0	40 a	2.1 a	0.7 a	4.3 a	3 a	0.1 a	3.2 a	Tolerant
LOR137	150	40 a	1.1 a	0.5 a	1 a	2 a	1.1 a	3.4 a	
	%	0	49	19	77	33	0	0	
LOR146	0	28 a	1.7 a	1 a	6 a	5 a	0.7 a	6.3 a	Tolerant
LOR146	150	12 a	0.3 a	0.4 a	1 a	2 a	0.1 a	2.6 a	
	%	57	84	61	83	60	86	58.7	
LOR78	0	27 a	2.1 a	0.6 a	3.3 a	2 a	0.2 a	2.6 a	Tolerant
LOR78	150	24 a	0.5 a	1 a	1.7 a	2 a	0.4 a	2.5 a	
	%	10	74	0	50	0	0	3.85	
LOR83	0	20 a	1.3 a	0.2 a	1 a	6 a	0.9 a	7 a	Tolerant
LOR83	150	32 a	0.8 a	0.4 a	2 a	2 a	0.9 a	3.4 a	
	%	0	42	0	0	67	0	51.4	
LOR85	0	91 a	5.8 a	2.3 a	16 a	14 a	3.3 a	18 a	Tolerant
LOR85	150	87 a	2.2 a	2.8 a	14 a	15 a	3.7 a	18.9 a	
	%	4.4	62	0	8.5	0	0	0	
SS2	0	55 a	3.9 a	1 a	12 a	14 a	1.9 a	16 a	Tolerant
SS2	150	60 a	1.6 a	1 a	8.5 a	14 a	3.2 a	17.7 a	
	%	0	59	0	31	0	0	0	

SS3	0	73	a	4.4	a	1.3	a	16	a	19	a	3.8	a	23	a	Tolerant
SS3	150	76	a	1.8	a	3.3	a	7.7	a	15	a	3.6	a	19.1	a	
	%	0		59		0		53		21		5.3		17		
CM19	0	99	a	7.5	a	4.8	a	23	a	37	a	9.2	a	46.8	a	Susceptible
CM19	150	6	b	0.1	b	0.9	a	1.5	b	2	b	0.1	b	2.6	b	
	%	94		99		82		94		95		99		94.4		
CM58	0	96	a	4.7	a	1.5	a	22	a	22	a	4.6	a	27.1	a	Susceptible
CM58	150	12	b	0.2	b	0.8	a	1	b	1	b	0.1	a	1.1	b	
	%	88		96		45		96		95		98		95.9		
CM63	0	79	a	5.7	a	1.9	a	18	a	21	a	3.9	a	25.6	a	Susceptible
CM63	150	10	b	0.2	b	1.3	a	2	b	2	b	0.1	a	2.7	b	
	%	87		97		30		89		90		97		89.5		
IMPERIAL	0	89	a	3.8	a	1.6	a	18	a	25	a	2.3	a	27.8	a	Susceptible
IMPERIAL	150	24	b	0.4	a	2.5	a	3	b	4	b	0.1	a	5	b	
	%	73		90		0		84		84		96		82		
HSD		43.9		4		4.3		13.6		16		5.1		18.8		

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 (%), ESI: emergence speed index, 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.

Linear correlations (Table 4) 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 ESI 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) and of the GENxCON interaction (Table 3).

Table 4. Linear correlations between pairs of traits evaluated in 54 tomato lines under salinity conditions.

	CON	**GP**	**ESI**	**SL**	**RL**	**NP**	**SDM**	**RDM**
GP	-0.36 *							
ESI	-0.71 *	0.74 *						
SL	-0.65 *	0.63 *	0.73 *					
RL	0.02	0.37 *	0.18 *	0.31 *				
NP	-0.49 *	0.85 *	0.79 *	0.68 *	0.35 *			
SDM	-0.28 *	0.69 *	0.61 *	0.64 *	0.33 *	0.75 *		
RDM	-0.11	0.68 *	0.48 *	0.51 *	0.43 *	0.66 *	0.80 *	
TOTDM	-0.25 *	0.71 *	0.59 *	0.62 *	0.35 *	0.76 *	0.98 *	0.85 *

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

3.2. Development of tomato seedlings under salinity conditions

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

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PH (α≤0.05), so the genotypes have different behavior across NaCl concentrations. The coefficients of variation (CV) were low, less than 21 %, 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 condition (175 mM NaCl) during seedling stage.

SV	DF	APDM		RDM		LA		RL		PH		β	
CON	1	101.89	*	0.07	*	8955313.33	*	11085.97	*	1263.22	*	0.3290	*
BLO(CON)	4	0.08		0.01		4127.31		20.11		0.64		0.0002	
GEN	24	8.03	*	0.29	*	280216.77	*	66.01	*	66.17	*	0.0020	*
GENxCON	22	1.35	*	0.02	*	63215.33	*	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, GEN*CON: genotype*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 α≤0.05.

Mean comparisons of the CON factor (Table 6) indicate that the 175 mM concentration reduced (α≤0.05) all evaluated variables except RDM. APDM was reduced by 46 %, 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 (α≤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 (α≤0.05) with respect to the absence of NaCl.

Table 6. Mean comparisons by concentration and percentage reduction of ratios under saline condition with respect to the control of traits evaluated in 24 tomato lines under saline and control conditions.

CON (mM)	APDM		RDM		LA		RL		PH		β	
0	3.86	a	0.50	a	891.27	a	43.88	a	15.63	a	0.14	a
175	2.07	b	0.55	a	362.26	b	25.26	b	9.34	b	0.04	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, α≤0.05).

Regarding the CONxGEN interaction, Table 7 presents the comparison of means between the two NaCl concentrations within each of the genotypes. CJ106, CM3 and QUIMH3-1 did not differ (α≤0.05) when going from 0 to 175 mM NaCl in four of the six variables evaluated; that is, these genotypes can be considered as the most tolerant to NaCl exposure. In contrast, Claudia, CM29, CM46, Imperial, L47B1, L47S8, LOR133, *Pimpinellifolium* and SS3 had statistical differences in 5 of the 6 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 7. Mean comparisons of GEN x C 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		
CJ106	0	1.66	a	0.29	a	386.71	a	44.61	a	9.83	a	0.17	a	Tolerant
CJ106	175	1.08	a	0.30	a	210.59	a	24.56	b	6.79	a	0.07	b	
	%	34.79		0.00		45.54		44.94		30.93		58.75		
QUIMH3-1	0	1.77	a	0.24	a	650.72	a	42.38	a	10.33	a	0.18	a	Tolerant
QUIMH3-1	175	1.22	a	0.36	a	238.39	b	26.78	a	6.50	a	0.07	b	
	%	31.36		0.00		63.37		36.81		37.09		64.16		
CM3	0	1.25	a	0.21	a	311.24	a	39.05	a	7.67	a	0.13	a	Tolerant
CM3	175	1.06	a	0.26	a	188.81	a	19.53	b	5.71	a	0.05	b	
	%	15.00		0.00		39.34		49.98		25.55		65.37		
CM46	0	6.61	a	0.77	a	1412.89	a	45.42	a	23.17	a	0.17	a	Susceptible
CM46	175	3.02	b	0.75	a	518.67	b	25.19	b	12.75	b	0.07	b	
	%	54.31		2.27		63.29		44.54		44.96		60.08		
IMPERIAL	0	6.50	a	0.72	a	1402.12	a	50.23	a	19.00	a	0.11	a	Susceptible
IMPERIAL	175	3.30	b	0.84	a	535.86	b	28.25	b	12.29	b	0.03	b	
	%	49.23		0.00		61.78		43.76		35.31		69.51		
L47B1	0	3.47	a	0.35	a	988.49	a	43.42	a	15.33	a	0.15	a	Susceptible
L47B1	175	1.88	b	0.35	a	318.59	b	21.82	b	8.04	b	0.03	b	
	%	45.74		0.00		67.77		49.75		47.55		78.93		
L47S8	0	3.05	a	0.43	a	635.10	a	41.17	a	15.83	a	0.10	a	Susceptible
L47S8	175	1.44	b	0.39	a	219.81	b	23.56	b	9.04	b	0.03	b	
	%	52.63		8.72		65.39		42.78		42.89		67.43		
LOR133	0	3.24	a	0.35	a	805.70	a	47.08	a	18.67	a	0.22	a	Susceptible
LOR133	175	1.67	b	0.41	a	301.07	b	25.19	b	7.42	b	0.05	b	
	%	48.61		0.00		62.63		46.49		60.27		76.89		
PIMP	0	6.55	a	0.98	a	1161.11	a	51.09	a	26.92	a	0.21	a	Susceptible
PIMP	175	2.64	b	0.81	a	464.18	b	24.99	b	13.79	b	0.07	b	
	%	59.77		16.92		60.02		51.08		48.76		65.59		
SS3	0	5.63	a	0.64	b	1245.29	a	42.11	a	22.92	a	0.16	a	Susceptible
SS3	175	3.60	b	1.02	a	707.41	b	32.99	a	14.13	b	0.06	b	
	%	36.10		0.00		43.19		21.66		38.36		61.45		
CLAUDIA	0	4.78	a	0.63	a	1085.98	a	45.57	a	16.00	a	0.15	a	Susceptible
CLAUDIA	175	2.58	b	0.72	a	469.99	b	25.37	b	11.00	b	0.05	b	
	%	45.97		0.00		56.72		44.33		31.25		65.11		
CM29	0	4.49	a	0.59	a	1055.07	a	38.77	a	16.83	a	0.16	a	Susceptible
CM29	175	2.29	b	0.52	a	414.65	b	19.94	b	9.13	b	0.04	b	
	%	49.05		11.86		60.70		48.56		45.79		73.87		
HSD		1.29		0.37		206.61		16.67		4.56		2.03		

Means with the same letter vertically do not differ statistically (Tukey, α≤0.05). GEN: genotype, CON: concentration, %: reduction percentage, APDM: aerial part dry matter, RDM: root dry matter, LA: leaf area, RL:

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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 8) indicated that the evaluated variables are strongly associated with each other positively, and negatively 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 8. 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 $\alpha \leq 0.05$.

4. Discussion

4.1. Germination test

Seed germinated before NaCl generated seedlings with lower RDM ($\alpha \leq 0.05$). However, the length of this structure (RL) was not modified; that is, the root elongated its cells in search of favorable conditions, a situation that contrasts with Baranova et al. [31] who detected the inhibition of cell elongation during germination under a saline condition.

The significant decrease in germination speed and seed development during germination is due to the inhibition of water uptake caused by NaCl [8,12]. This leads to the 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 [17,32,33].

In our research, GP decreased 26 % with 150 mM NaCl; in contrast, the Rio Grande variety, when subjected to 85 mM NaCl, decreased by only 6.4 % compared to the control, while, in 171 and 257 mM NaCl, the germination percentage on the third day was 2.0 and 0.8 %, respectively [34].

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 [9,14,15]. 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].

Under concentrations of 112 mM NaCl (10.2 $dS \cdot m^{-1}$), *Solanum peruvianum* accessions have been identified with greater tolerance than *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 [38].

One of the processes involved in salt tolerance is associated with the regulation of water potential by osmotic regulation, through the synthesis of amino acids, sugars and other osmoregulators [39]. 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 germination rate, which is a reliable and easy to verify indicator. With 0 and 150 mM, the time required to reach 50 % germination was 2.45 days in the control, while with 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 [40]. Increasing the concentration (50, 100 and 150 mM) of salt delayed seed germination of four tomato cultivars; at 150 mM, after 10 days of incubation, only one of the evaluated cultivars achieved 50 % germination [41]. NaCl concentrations of 50, 100 and 200 mM NaCl reduced the rate and percentage of tomato seed germination, which may be due to the deterioration of enzymatic activity by Na^+ and Cl^- ion toxicity [42], while with 0 and 4 $dS{\cdot}m^{-1}$, they managed to germinate at 5.3 and 8.34 days after sowing, respectively [43].

Low NaCl concentrations induce seed dormancy, since, with increasing salinity concentrations, the germination speed and germination percentage decreased, but 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 [44,45].

Previous studies have indicated the negative root: stem relationship in terms of increasing salt concentration, that is, stem growth is restricted while root growth is less hindered [44], whereas in this study the RL:SL ratio showed a positive relationship, although of low magnitude.

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 [45].

PH reduced ($\alpha \leq 0.05$) its expression in saline conditions since this stress causes reductions in plant height and changes in the number and size of leaves. This is caused by the toxicity of Na^+ and Cl^- ions and the nutritional imbalance induced by salinity [46]. Likewise, root length is severely affected; in a rhizogenesis study at a concentration of 150 mM conducted by Bogoutdinova et al. [4]. on two tomato lines, a significant decrease in root length was observed in both genotypes.

Sánchez et al. [47] observed that leaf area decreased by 33 % in the Raf cultivar under a salinity level of 11 $dS{\cdot}m^{-1}$. Likewise, De Pascale et al. (2012) [48] indicate that saline water with electrical conductivity of 4.4 $dS{\cdot}m^{-1}$ used in tomato irrigation reduced leaf area by 47.55 % with respect to the control.

SanJuan-Lara et al. [13] evaluated the response of 48 lines obtained by individual selection in a native tomato population at five levels of electrical conductivity (4, 6, 8, 8, 10 and 12 $dS{\cdot}m^{-1}$) at 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 morphology and growth habits [49]. 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 [50]. The lower tolerance of the cultivars may be due to excessive sodium accumulation in the cells which rapidly causes osmotic stress and cell death [51].

The above is 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 [52].

During the seedling stage, tomato is more sensitive to high salt concentrations compared to later growth stages [53]. 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 an increasing salinity concentration [54], resulting in reduction percentages of up to 40 %.

In a study by Sánchez et al. [47], tomato seedlings of the Raf cultivar were exposed to a salinity level of 5.5 $dS \cdot m^{-1}$ where they obtained 2708 cm^2 of leaf area, while at 11 $dS \cdot m^{-1}$ their leaf area decreased to 1815 cm^2.

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 mainly genetics and the developmental stage play an important role in tolerance and/or susceptibility to salinity.

A total of 17 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 the variables evaluated.

Native tomato species play an important role in the identification and use of tolerant genotypes since they can be used as a genetic resource for obtaining commercial genotypes with salt tolerance or as potential rootstocks.

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