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Generational Mean Analysis of Salt Tolerance during Osmotic Phase in Maize Seedling

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Abstract

This study details the nature and magnitude of the genetic effects associated with various quantitative characters (morphological and hydric relations) measured in maize seedlings during the osmotic phase of saline stress (100 mM NaCl). Three lines with differential behavior in salt stress: SC2 (tolerant), AFE (susceptible) and LP3 (moderately tolerant) were used to obtain contrasting crosses (SC2 × AFE) and (SC2 × LP3). An analysis of six generational means (P_1, P_2, F_1, F_2, BC_1 and BC_2) was applied for each cross. First a scaling test was applied and then a three and six-parameter genetic models were used to estimate various genetic components. In none of the traits studied there was evidence of adequacy to the three parameter model, which indicates important epistatic effects in genetic expression. The dominant genetic effects were greater than the additive ones for all the characters evaluated. LG showed positive and significant differences for [h] in both crosses, indicating the presence of hybrid vigor and its possible use in the improvement. Low value of [d] and high of [h] both significant in SC2 × AFE, indicates existence of genes dispersion between the parental lines. While, for the cross SC2 × LP3, the low and significant value of [d] and not significant value of [h], indicate greater genetic similarity. In the SC2 × LP3 cross, the negative interaction [l] confirms ambidirectional dominance, while for SC2 × LP3 the positive sign indicates directional dominance. The analysis of tolerance to salinity in the osmotic phase showed a complex polygenic inheritance for the traits used, determined by simple and interaction effects of different magnitudes and significance according to the cross considered.

Keywords

Maize, Salinity, Osmotic Stress Tolerance, Genetic Effects, Generation Means Analysis

1. Introduction

Saline soils are one of the abiotic factors that have had the greatest negative impact on world agriculture [1]. Salinity affects some of the physiological and biochemical processes of plants and reduces their yield. The identification of tolerant crops could be an effective strategy for overcoming this saline stress.

Munns's biphasic model explains the reduction of plants growth produced by salt stress [2]. The first phase consists in a mechanism osmotic which occurs when the plants are affected by a high concentration of salt that exists outside the tissues producing a hydric stress. Secondly, the ionic phase is produced by an increase of Na^+ intracellular. This sodium can be stored in old leaves that then are removed and/or in roots (mechanism associated with ionic stress). Another tissue tolerance mechanism consists in Na^+ compartmentalization to prevent its toxicity.

Maize has been classified as moderately sensitive to salt [3] and its mechanism of salt tolerant is the exclusion of Na^+ [4]. However, other mechanisms above proposed could be also inducing its tolerance [5]. Collado *et al.* [6] probed the existence of osmotic tolerance mechanisms, studying the effects of salinity on growth and the water relations in the seedlings of 13 maize inbred lines. In this way, the identification of genotypes with contrasting behavior could be applied to genetic studies and breeding programs. The osmotic phase can last several hours or days before reaching toxic levels of Na^+ concentration. Plants tolerant to osmotic stress are those that maintain their rate of growth during the first days of exposure to salinity [5]. This response can be seen as adaptive feature that reduces the loss of water by transpiration or as a reduction in stomatal efficiency by partial or total closure of the stomata [7]. Thus, the improvement in tolerance to the osmotic stress could involve two opposing strategies. The first one is to select plants with lower leaf area, which avoids water stress and is associated with improvement of stomatal efficiency. The second strategy, on the contrary, is to select plants with greater leaf area and capacity to intercept light, which is related to the improvement of the efficiency of the absorption of water from the roots [7].

Tolerance to abiotic stress in general and to salinity stress in particular is under polygenic control [8]. Due to their quantitative nature, traits related to salinity cannot be studied in a simpler way. The efficiency of a breeding program depends, to a large extent, on knowledge of the type of gene action involved in the expression of each character [9]. For this reason, it is necessary to conduct a genetic experiment that involves segregating populations obtained from the crossing of materials with contrasting characters and to use methods of quantitative genetics [10].

Specialized biometrical techniques are required to establish the type of genetic variability associated with traits related to tolerance. Generational mean analysis is a simple but useful technique for estimating gene effects for a polygenic trait, its greatest merit lying in the ability to estimate epistatic genetic effects such as

additive × additive, dominance × dominance and additive × dominance [11] [12]. It is based on the mean of six generations: P_1, P_2, F_1, F_2, BC_1 and BC_2. Information derived from these analyses can be further utilized for the formulation of an effective breeding strategy. In addition to gene effects, breeders are also able to estimate how much of character variation is genetic and to what extent this variation is heritable, since the efficiency of selection depends mainly on additive genetic variance, influence of the environment and interaction between genotype and environment [13].

The aim of this study is to determine the heritability of morphological and physiological traits in maize seedlings with respect to salt tolerance in the osmotic phase, using generational mean analysis for two different crosses between Tolerant × Non-Tolerant inbred lines.

2. Materials and Methods

2.1. Plant Material

Three inbred lines with differing growth responses to NaCl stress during the osmotic phase were used in this investigation: SC2 exhibits high tolerance to salinity; while AFE is susceptible and LP3 display moderately tolerant [6] (**Table 1**).

In the first season (2012-2013), the three lines were intercrossed (by hand emasculation and pollination techniques) to produce two F_1 crosses. The SC2 line was used as a female tester; two crosses were obtained: SC2 × AFE and SC2 × LP3. In the second season (2013/2014), F_1 plants of each cross were selfed and backcrossed to the two parents to obtain F_2, BC_1 and BC_2 generations, respectively. In this season, parents and F_1 seeds were also multiplied in order to decrease the effects of pre-replication factors on the VE estimation [12].

During the 2014/2015 growing season, parents, F_1, F_2, BC_1 and BC_2 generations of the two crosses were grown in two separate assays in a randomized complete block design. Since the non-segregating generations represent the homogeneous population while the segregating generations represent the heterogeneous population, the sample size (*i.e.* number of plants analyzed) varied as follows: 20 plants in each P_1, P_2 and F_1 generations; 60 plants for the F_2 generations; and 30 plants in each BC_1 and BC_2 generations.

2.2. Hydroponic System

The surfaces of maize seeds were sterilized with a 1% sodium hypochlorite solution for 5 minutes before experimentation, and then rinsed with distilled water. Pre-germinated caryopses were transferred to pots containing perlite. These pots were put in trays with a 1/4 strength Hoagland's solution. The full-strength nutrient solution had the following composition: in $mol \cdot m^{-3}$, $Ca(NO_3)_2$, 2.5; KH_2PO_4, 0.1; K_2SO_4, 0.5; $MgSO_4$, 0.6; $CaCl_2$, 5; in $mmol \cdot m^{-3}$, H_3BO_4, 1; $MnSO_4$, 2; $ZnSO_4$, 0.5; $CuSO_4$, 0.3; $NH_4MO_7O_{24}$, 0.005; Fe-EDTA, 200. Daily increments of 1/4 of concentration in the nutrient solution were made until the complete solution was reached; the pH of the solution was maintained at 6. The solutions

Table 1. Food and Agriculture Organization of the United Nations (FAO) maturity: Short is less than 500, Medium is between 500 and 700, Large is more than 700; type and color of grain (O: Orange, Y: Yellow, F: Flint, D: Dent) and behavior in salt (Susceptible, moderately susceptible, tolerant) of each genotype (inbred lines).

Genotypes	Color grain	Type of grain	FAO maturity	Tolerance
AFE	O	F	Large	Susceptible
LP3	O	F	Medium	Mod. Tolerant
SC2	O	F	Short	Tolerant

were renewed every three days. The experiment was carried out in a controlled environment room at 25˚C, with 16 h day length.

2.3. Treatments

Two treatments were used: 0 and 100 mM NaCl [14] [15] [16] [17]. The final concentration was reached by a gradual increment of 25 mM NaCl every two days [18] [19]. After 14 days of treatment, the seedlings were harvested.

2.4. Measurement

The following traits were measured:

Leaf length, in cm: The length of 4th leaf was measured every 2 days after completing the salinity (4 measurements in total: L1; L2; L3 and L4).

Leaf Growth (LG): Rate of growth between the first and the last measurement (in cm).

Root Length (RL) in cm.

Shoot Dry Mass (SDM) and **Root Dry Mass (RDM)**, were obtained after drying in an oven at 70˚C until constant weight was achieved.

Total Dry Mass (TDM) was obtained by SDM plus RDM.

Relative water content (RWC) was determined on cut leaves using the method of Mata & Lamattina [20] through the application of the following formula:

RWC(%): (FW − DW)/((TW − DW) × 100 where FW = fresh weight, obtained immediately after cutting pieces of leaf; DW = dry weight, obtained by drying the sample in an oven to constant weight; and TW = weight of turgor, determine once the pieces of leaf were rehydrated for 2 hours.

Leaf Water Loss (LWL) was measured according to the method used by Xing *et al.* [21]. The fresh weight of pieces of leaf was recorded (W1), then these pieces were left to evaporate at room temperature for 2 hours, resulting in weigh (W2). The following formula was applied: LWL = (W1 − W2)/W1 × 100

Stability of membrane (IE) was determined on the 6th leaf with the use of a conductivity meter (Consort C931). A piece of leaf was cut, weighed and washed with distilled water; then this piece was placed in a tube with 10 ml of distilled water and left to incubate for a period of 24 hours [22] [23]. After incubation, the sample was left to stabilize to room temperature and the conductivity of the solution (*M*1) was measured. The samples were autoclaved for 15 minutes to kill

the tissue, left to cool at room temperature and the conductivity of solutions was once again measured (*M*2). The stability index was obtained from the following formula:

$$IE = M1/M2 * 100$$

2.5. Statistical and Genetic Analysis

A scaling test with the three-parameter genetic model [24] [25] was used for generation mean analysis. The model [13] was employed as follows:

$$Y = m + \alpha[d] + \beta[h] + \alpha 2[i] + 2\alpha\beta[j] + \beta 2[l]$$

where Y = generation mean, m = mean of all possible homozygous lines which can be derived from a cross, [*d*], [*h*], [*i*], [*j*] *and* [*l*] = net directional effects of loci contributing to additive, dominance, additive × additive, additive × dominance, and dominance × dominance components, respectively, and α and β = coefficients of genetic parameters.

Thus individual scaling tests (*A*, *B*, *C* and *D*) were employed to test their compatibility with the additive-dominance model, where:

$$A = 2BC_1 - P_1 - F_1 \qquad B = 2BC_2 - P_2 - F_1$$
$$C = 4F_2 - 2F_1 - P_1 - P_2 \qquad D = 2F_2 - BC_1 - BC_2$$

The *A*, *B*, *C* and *D* standard error were tested with the *t*-test. Besides, the significance of *A* and *B* scales indicate the presence of all types of non-allelic gene interactions. The significance of *C* scale suggests [*dd*] type of epistasis. The significance of *D* scale reveal [*aa*] gene interaction, significance of *C* and *D* scales indicate [*aa*] and [*dd*] type of gene interactions [12] (Kearsey and Pooni, 1996).

- The significance of scaling tests indicated the inadequacy of the three-parameter genetic model. A six-parameter genetic model was then used to estimate various genetic components. The Joint scaling test of Cavalli [26] was used to determine the presence or absence of non-allelic interactions. The genetic model of six parameters (*m*, *d*, *h*, *i*, *j* and *l*) was computed according to Jinks and Jones [27] (**Table 2**).
- Potence ratio (*P*) was estimated as follows [28]:

$$P = (F_1 - MP)/[0.5 \times (P_2 - P_1)]$$

where: F_1 = the first generation mean, P_1 = the mean of the first parent, P_2 = the mean of the better parent and *MP* = mid-parents value. Complete dominance occurs when potence ratio is equal to (+1) or (−1), partial dominance when the ratio is between (+1) and (−1) and over-dominance if the ratio exceeds (±1).

- Heterosis (*H*) was expressed as the percentage deviation of F_1 mean performance from mid-parents according to Singh and Chaudhary [29] as follows:

$$H_{MP} = [(F_1 - MP)/MP] * 100$$

Significance of *H* was determined by a *t*-test [30].

- Inbreeding depression (%) was estimated according to Singh and Chaudhary [29] as follows:

Table 2. The α and β coefficients used for the construction of different models in generation means analysis.

Generations	Genetic effects					
	m	[*d*]	[*h*]	[*i*]	[*j*]	[*l*]
$\bar{P}_1$	1	1	0	1	0	0
$\bar{P}_2$	1	−1	0	1	0	0
$\bar{F}_1$	1	0	1	0	0	1
$\bar{F}_2$	1	0	0.5	0	0	0.25
$\overline{BC}_1$	1	0.5	0.5	0.25	0.25	0.25
$\overline{BC}_2$	1	−0.5	0.5	0.25	−0.25	0.25

$$ID = \left[\left(F_1 - F_2\right)/F_1\right] * 100$$

- Phenotypic coefficient of variation (*PCV*) and genotypic coefficient of variation (*GCV*) were estimated using the formula suggested by Singh and Chaudhary [29] as follows:

$$PCV = \left(S_{F2}/X_{F2}\right) * 100$$

$$GCV = \left(S_{F2}^2 - S_E^2\right) * 100$$

- Broad and narrow sense heritability were estimated using the formula proposed by Burton [31] and Warner [32]:

$$H_{BS} = S_G^2/S_P^2 \quad \text{and} \quad H_{NS} = S_a^2/S_P^2$$

- The expected genetic advance from selection was calculated using the formulae proposed by Johanson *et al.* [33]. The predicted genetic advance was expressed as percentage of F_2 mean.

$$\Delta G = 2.0627 * H_{NS} * S_{F2} \quad \text{and} \quad \Delta G\% = \left(\Delta G/F_2\right) * 100$$

All statistical analyses were carried out using Genes software [34] and Microsoft Excel spreadsheets.

3. Results and Discussion

Effects of generations in NaCl salinities were tested using variance analysis [35]. The six generations were significantly different ($P < 0.01$) in RL, RDM, SDM, TDM, L2, L3 and LG. For SC2 × AFE, there was significant ($P < 0.05$) difference of LWL between generations, while for RWC and IT the differences were not significant. For SC2 × LP3 the six generations were significantly different ($P < 0.01$) in RL, RDM, SDM, TDM, L3, LG, LWL, RWC and IT; whereas the differences were significant at the 5% level of probability ($P < 0.05$) in LG and not significant in L2 (**Table 3**).

It was this significant difference between generations, therefore, that made the application of generational mean analysis possible.

Mean values and their standard errors for the analyzed traits were presented in **Table 4**.

Table 3. Variance analysis of two crosses of maize exposed to 100 mM of NaCl. Mean Squares for LR: length root; RDM: root dry mass; SDM: shoot dry mass; L2: leaf length in the 2nd measured, L3: leaf length in the 3rd measured; LG: rate of growth between the first and the last measure; LWL: leaf water loss; RWC: relative water content and IT: index of tolerance.

	SC2 × AFE		SC2 × LP3	
Traits	**Generations**	**Error**	**Generations**	**Error**
RL	73.1**	12	149.1**	15.8
RDM	225.7**	9.3	172.1**	7.9
SDM	335.8**	37.3	342.0**	40.7
TDM	958.1**	59.3	735.2**	59.6
L2	65.4**	11.8	2.71ns	1.9
L3	93.4**	14.6	20.55**	6.0
LG	134.7**	16.4	25.5*	9.8
LWL	235.4*	81.9	446.4**	54.9
RWC	0.02ns	0.02	0.01**	0.002
IT	0.09ns	0.36	0.35**	0.009

*, **: Significant at the 0.05 and 0.01 probability levels, respectively; ns: not significant.

For SC2 × AFE, the results indicated that F_1's means were close to the higher parent for RDM, TDM, LWL; while for RL and LG the F_1 means were close to the lowest parent value, indicating partial or total dominance in these traits. The F_1 generation means were greater than the one of the parents for L2, L3, LG and RL, indicating the presence of over-dominance. There were no significant differences in RWC and IT between generations.

For SC2 × LP3, the *F*1's means were close to the lowest parent for LWL and RL, indicating partial or total dominance. While, for the remaining traits the F_1 generation means were greater than the one of the parent, indicating the presence of over-dominance (Table 5).

The Potence ratio was calculated to determine the nature and degree of dominance for all studied characters (Table 5). The results indicated that P ratio values exceeded the unity in most of the studied traits indicating over-dominance towards one of the parents. However, the fact that P was less than −1 or +1 signals partial dominance in: RL (−0.89) and RWC (−0.73) for SC2 × LP3 and RDM (0.94), SDM (−0.11), LWL (0.77) and RWC (−0.23) for SC2 × AFE. This estimation of P does not constitute a measure of dominance but indicates, rather, that the parent who has the largest number of dominant alleles is the most powerful in the cross. In the case that the sign is negative, the dominant parent is the one with the lowest value.

The *PCV* was greater than *GCV* for all studied traits in both crosses (Table 5). These results indicate that the environment had an important role in the expression of these traits. Genetic coefficient of variation points to the existence of genetic variability in various quantitative traits. *GCV* together with heritability

Table 4. Means and standard errors of the six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) in the two crosses for: LR (length root), RDM (root dry mass), SDM (shoot dry mass), TDM (total dry mass), L2 (2nd length leaf), L3 (3rd length leaf), LG (leaf growth), LWL (leaf water loss), RWC (relative water content) and IT (index of tolerance). Means compared using LSD test.

Traits	SC2 × AFE					
	P_1	P_2	F_1	F_2	RC_1	RC_2
LR	27.07 ± 0.89a	24.04 ± 0.96b	23.36 ± 0.92bc	23.17 ± 0.44bc	21.50 ± 0.63c	21.89 ± 0.67bc
RDM	16.87 ± 0.88a	10.58 ± 0.82c	15.22 ± 0.85ab	14.83 ± 0.38b	10.48 ± 0.56c	9.14 ± 0.59c
SDM	28.66 ± 1.81a	23.50 ± 1.58bc	25.87 ± 1.58ab	24.26 ± 0.72b	20.69 ± 1.04cd	17.68 ±1.12d
TDM	44.07 ± 2.57a	34.68 ± 2.22bc	42.88 ± 2.43a	39.14 ± 0.97ab	30.77 ± 1.43c	26.69 ± 1.48d
L2	21.50 ± 1.09bc	20.09 ± 1.09c	26.16 ± 0.99a	21.87 ± 0.44bc	22.42 ± 0.63b	20.29 ± 0.67c
L3	27.47 ± 1.10bcd	29.39 ± 1.06ab	32.06 ± 1.10a	26.60 ± 0.48cd	25.35 ± 0.75d	27.84 ± 0.70bc
LG	23.61 ± 1.04b	25.57 ± 1.17ab	21.02 ± 1.08b	21.18 ± 0.51c	23.06 ± 0.74b	26.62 ± 0.81a
LWL	59.91 ± 2.61a	51.81 ± 2.42b	59.91 ± 2.73a	54.23 ± 1.14ab	50.67 ± 1.85b	52.83 ± 1.74b
RWC	0.96 ± 0.04a	0.95 ± 0.04a	0.97 ± 0.04a	0.96 ± 0.02a	0.95 ± 0.03a	0.90 ± 0.03a
IT	0.63 ± 0.19a	0.62 ± 0.18a	0.62 ± 0.19a	0.76 ± 0.08a	0.68 ± 0.12a	0.65 ± 0.12a
Traits	SC2 × LP3					
	P_1	P_2	F_1	F_2	RC_1	RC_2
LR	26.79 ± 1.15a	19.59 ± 1.20d	20.00 ± 1.15cd	23.39 ± 0.55b	26.22 ± 0.67a	22.41 ± 0.67bc
RDM	15.71 ± 0.85c	12.19 ± 0.85d	22.99 ± 0.78a	16.23 ± 0.38c	18.53 ± 0.47b	16.55 ± 0.48c
SDM	22.02 ± 1.92c	20.09 ± 1.92c	28.94 ± 1.55ab	28.06 ± 0.78b	28.64 ± 1.11b	32.06 ± 1.05a
TDM	37.60 ± 2.33c	31.98 ± 2.33c	50.84 ± 1.87a	44.60 ± 0.95b	47.23 ± 1.34ab	48.57 ± 1.27a
L2	14.93 ± 0.74a	13.83 ± 0.74a	13.62 ± 0.68a	13.84 ± 0.32a	13.59 ± 0.42a	14.80 ± 0.41a
L3	20.04 ± 0.68a	19.59 ± 0.66ab	19.25 ± 0.63b	19.27 ± 0.32b	19.48 ± 0.42b	21.26 ± 0.41b
LG	20.05 ± 0.95b	21.69 ± 0.90ab	22.94 ± 0.84 a	22.41 ± 0.43a	23.19 ± 0.55a	23.54 ± 0.52a
LWL	69.69 ± 2.14a	63.78 ± 1.85b	63.08 ± 1.85b	63.22 ± 0.97b	60.94 ± 1.40b	71.66 ± 1.40a
RWC	0.97 ± 0.01ab	0.94 ± 0.01bc	0.94 ± 0.01bc	0.96 ± 0.01ab	0.92 ± 0.01c	0.98 ± 0.01a
IT	0.68 ± 0.02b	0.71 ± 0.02b	0.99 ± 0.02a	0.60 ± 0.01c	0.66 ± 0.02b	0.69 ± 0.02b

Values followed with same letters within a column are not significantly different at $P < 0.05$.

ratio would provide the best indication of the amount that was gained by the selection [36].

Heterosis relative to mid-parent for the traits studied in both crosses showed few significant values (Table 5). Positive and highly significant H values were found for RDM and TDM in SC2 × LP3, indicating that dominance direction was toward the better respective parent. In SC2 × AFE, LR showed a negative and highly significant heterosis signals that dominance direction was toward the lower parents while for L2 the dominance was in opposite direction.

Broad sense heritability estimates ranged from 45.08 (for TDM) to 65.09 (for L2) in cross SC2 × AFE, and from 36.48 (LWL) to 84.41 (L2) in cross SC2 × LP3 (Table 5).

Table 5. Potence ratio (P), Heterosis %, Inbreeding depression (ID), phenotypic (*PCV*) and genotypic (*GCV*) coefficient of variability, broad (HBS) and narrow (HNS) sense heritability, genetic advance (ΔG) and genetic advance as percentage of F_2 mean ($\Delta G\%$) calculated in both crosses for the traits with showed significant differences between treatments: LR: length root; RDM: root dry mass; SDM: shoot dry mass; TDM: total dry mass; L2: leaf length in the 2nd measured, L3: leaf length in the 3rd measured; LG: rate of growth between the first and the last measure; LWL: leaf water loss.

Traits	Hybrid	P	Heterosis %		ID	*PCV*	*GCV*	Hb	Hn	ΔG	ΔG%
			MP	*MP*%							
LR	SC2 × AFE	−1.89	−4.56*	−17.31	−6.63	13.84	10.79	60.80	16.11	0.91	3.91
	SC2 × LP3	−0.89	−3.19	−13.76	−16.98	18.92	15.78	69.55	20.93	1.72	7.36
RDM	SC2 × AFE	0.94	2.34	17.82	3.94	24.08	18.07	56.29	126.44	8.42	56.58
	SC2 × LP3	5.14	9.05*	64.87	29.42	20.20	15.96	62.37	57.49	3.50	21.59
SDM	SC2 × AFE	−0.11	−0.23	−0.83	9.45	26.95	20.30	56.74	101.97	12.52	51.06
	SC2 × LP3	14.62	8.77	43.45	3.02	25.73	19.87	59.63	40.38	5.42	19.31
TDM	SC2 × AFE	1.17	4.92	13.29	6.71	23.57	15.83	45.08	114.26	19.59	50.04
	SC2 × LP3	5.71	16.05*	46.13	12.26	19.09	14.40	56.93	27.00	4.27	9.58
L2	SC2 × AFE	8.35	6.04*	30.05	16.41	18.35	14.80	65.09	43.81	3.09	14.11
	SC2 × LP3	−1.37	−0.75	−5.25	−1.62	22.48	20.65	84.41	95.47	5.52	39.88
L3	SC2 × AFE	−3.77	3.63	12.76	17.03	15.51	10.69	47.55	20.13	1.46	5.48
	SC2 × LP3	−2.47	−0.56	−2.82	−0.09	16.13	13.72	72.37	99.82	5.76	29.91
LG	SC2 × AFE	−2.56	−2.43	−10.22	0.93	19.98	16.01	64.26	85.71	6.36	30.05
	SC2 ×LP3	−2.53	2.07	9.92	2.33	15.73	12.07	58.88	41.03	2.69	12.00
LWL	SC2 × AFE	0.77	3.75	6.81	7.72	19.27	14.38	55.68	62.34	12.11	22.33
	SC2 × LP3	−1.24	−3.65	−5.47	−0.21	13.87	8.38	36.48	104.20	16.98	26.86

*Significant at the 0.05 probability level.

Narrow-sense heritabilities in cross SC2 × AFE ranged from 16.11 (RL) to 85.71 (LG), and from 20.93 (RL) to 99.82 (L3) in cross SC2 × LP3. For several traits the H_N was greater than H_B, which can be attributed to the fact that most genetic models assume absence of epistasis while estimating components of genetic variation. However, when [*i*] and [*j*] epistasis are present, the results are biased. These biased estimates and the amount and type of epistasis present in crop species can have major consequences for both the reliability of prediction and the design of breeding programs [37].

The fact that the H_N values were lower than those obtained for the H_B confirms the existence of dominance and/or epistatic effects. These findings reveal the nature of gene action in these traits, where non-additive gene effects were found to have a great role. Such results are in agreement with those obtained by several investigators: Rafiq *et al.* [38]; Asadabadi *et al.* [39]; Kere *et al.* [40]; Ali *et al.* [41] and Hassan *et al.* [42].

Genetic advance % ranged from 3.91 (RL) to 56.58% (RDM) in the first cross, and from 7.36 (RL) to 39.88% (L2) in the cross SC2 × LP3 (Table 5). However, for several traits the Genetic advance was overestimated because the H_N was biased.

The individual scaling tests of Mather [24] and Hayman and Mather [25] were employed to test compatibility with the additive-dominance model. The results for the scaling test indicated that A, B, C and D were significant or highly significant in both crosses for the most of the traits (**Table 6**). These results would indicate the inadequacy of the additive-dominance model and complicate the interpretation of the gene effects involved in the heritance of traits because of an increase of gene interaction effects (epistasis) [13]. Similar results were obtained by Kere *et al.* [40]; Hassan and El-Said [42], who reported significant scaling tests for several traits in saline soils. Saha and Amirul [43], on the other hand, found non-significant results for traits measured on salinity stress in rice, which proved a good fit for the additive-dominance model. As a consequence, we applied the six parameters model to test the significance of additive/dominance effects and their interactions ([*i*], [*j*] and [*l*]).

On account of the presence of epistasis, generation mean analyses were carried out according to Hayman [25]. **Table 6** presents the estimates of the six parameters: additive [*d*], dominance [*h*], additive × additive [*i*], additive × dominance [*j*] and dominance × dominance [*l*] and means [*m*]. The additive, dominance and epistatic types of gene interaction in each cross for different traits were found to be different from each other.

The results indicated that mean effect [*m*] of each cross was significant for all characters, which implies a difference in these characters among the parents and indicates that all the traits were quantitatively inherited under a salinity stress.

Additive effects [*d*] were significant for all the traits in both crosses, except SDM for the SC2 × LP3 cross; L2 for the SC2 × AFE cross and for L3, LG, RWC in both crosses. The non-significance in those cases may be attributed to large error variance [44]. The lack of significance of the principal effects for the characters of L2 and L3, however, can also be attributed to the brevity of the lapse of time between one measurement and the next (2 days). The traits L3 for the SC2 × AFE and LG for the SC2 × LP3 showed negative additive effects. The negative or positive signs for additive effects depend on which parent is chosen as P_1 [44] [45].

The [*d*] values were statistically significant for both crosses. But, in all the cases, SC2 × AFE had higher values than SC2 × LP3, which could indicate a greater degree of dispersion of genes between the two parents of SC2 × LP3 [12].

Negative values of dominance effects [*h*] were registered for almost all the characters in SC2 × AFE, except LG, which showed a positive and significant value in both crosses. The significance for LG can be explained by the amount of time that elapsed before its measurement (10 days). SC2 × LP3, to the contrary, had positive and significant [*h*] effects for all the traits. The L3 traits in SC2 × AFE, LR and LWL in SC2 × LP3 and L2 and RWC in both crosses, on the other hand, showed non-significant value for [*h*]. With regard to the negative value of [*h*] observed for some studied traits indicated that the alleles responsible for less value of traits were over dominant over the alleles controlling high value [45].

Table 6. Scaling test and Generation means analysis in the two crosses. Six parameters model: Additive and multiplicative genetic effects for the traits: LR (length root), RDM (root dry mass), SDM (shoot dry mass), TDM (total dry mass), L2 (2nd length leaf), L3 (3rd length leaf), LG (leaf growth), LWL (leaf water loss), RWC (relative water content) and IT (index of tolerance).

Trait	Hybrid	Scaling Test				Genetic Effects					
		A	B	C	D	m	[*d*]	[*h*]	[*i*]	[*j*]	[*l*]
LR	SC2 × AFE	**	**	ns	**	34.73**	2.41**	−33.01**	−8.36**	−6.28**	20.08**
	SC2 ×LP3	**	**	**	ns	19.51**	3.60**	15.06ns	3.68ns	0.41ns	−14.57**
RDM	SC2 × AFE	**	**	ns	**	33.96**	2.5**	−57.87**	−20.82**	−2.14ns	39.39**
	SC2 × LP3	**	**	**	ns	8.72**	1.76**	15.77**	5.23**	0.44ns	−1.49ns
SDM	SC2 × AFE	**	**	ns	**	48.62**	2.11**	−74.87**	−21.32**	1.79ns	53.33**
	SC2 × LP3	**	**	**	ns	11.03*	0.6ns	50.22**	9.14ns	−8.05*	−32.32**
TDM	SC2 × AFE	**	**	**	**	77.95**	4.22**	−119.27**	−40.92**	0.42ns	83.27**
	SC2 × LP3	**	**	**	**	21.60**	2.81*	62.76**	13.18*	−8.30ns	−33.53**
L2	SC2 × AFE	ns	**	**	ns	22.14**	0.72ns	−5.13ns	−2.03ns	2.80ns	9.15*
	SC2 × LP3	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
L3	SC2 × AFE	**	**	**	**	28.46**	−0.96ns	−11.05ns	−0.03ns	−3.05ns	14.64**
	SC2 × LP3	**	**	**	ns	15.42**	0.23ns	11.58*	4.39*	−4.01**	−7.74**
LG	SC2 × AFE	**	**	ns	**	11.32**	0.95ns	29.36**	12.48**	6.01**	−19.31**
	SC2 × LP3	**	**	**	ns	17.03**	−0.82ns	15.59*	3.84ns	0.93ns	−9.68*
LWL	SC2 × AFE	**	ns	ns	ns	64.94**	4.89**	−36.67*	−9.92ns	−14.09**	30.49*
	SC2 × LP3	**	**	**	ns	54.38**	2.95*	26.64ns	12.35*	−27.35**	−17.94*
RWC	SC2 × AFE	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
	SC2 × LP3	**	**	**	ns	1.01**	0.02ns	−0.12ns	−0.06ns	−0.15**	0.05ns

*, **: Significant at the 0.05 and 0.01 probability levels, respectively; ns, not significant; nc: non-calculated.

In all the cases where [*h*] were significant, dominance gene effect was higher than additive gene effect for all traits studied in both crosses, indicating a predominant role of the dominant component of gene action in the inheritance of these traits. The contribution of the parent to dominance effect varies according to the trait. The sign for dominance effect is a function of the F_1 mean value in relation to the mid parental value and indicates which parent is contributing to the dominance effect [45]. The absence of significant values for [*h*] component, on the other hand, signal non-dominance genetic differences or the presence of ambidirectional dominance between the both parents; and dominance effect seem not to be important in the genetic control of these crosses [46].

The statistically significant values of [*h*] were higher on the SC2 × AFE, which could indicate the presence of greater ambidirectionality in the effects of dominance in SC2 × LP3, and for this reason the values were lower [12].

Significant [*i*] gene effects were detected for RL, RDM, SDM, TDM and LG for SC2 × AFE; and in SC2 × LP3 for RDM, TDM, L3 and LWL. The [*l*] interaction was significant for all the traits evaluated except for L2 in SC2 × LP3 and

RWC in both crosses. Significant [*j*] interaction was detected for RL, LG and LWL for SC2 × AFE; while, in SC2 × LP3 were significant SDM, L2, L3 and LWL.

Among the interactions, [*l*] interaction was larger than [*i*] and [*j*] except for RDM, L2 in SC2 × AFE; and for LWL in SC2 × LP3.

The signs associated with estimates of [*i*], [*j*] and [*l*] types of epistasis indicate the direction in which the gene effect influences the mean of the population. Positive or negative form of [*i*] interaction shows association and dispersion of alleles in parents, respectively [13]. Therefore, negative and significant values of [*i*] in this study showed the dispersion of alleles in parents for all the traits evaluated, except for TDM and L3 in SC2 × LP3 and LG for SC2 × AFE, which showed association of alleles in parents. The negative sign of [*l*] interaction shows the presence of ambidirectional dominance. In the present study, this ambidirectionality was observed for most traits, except RL, SDM, TDM, L2, L3 and LWL for SC2 × AFE, which showed positive sign of [*l*] interaction and therefore directional dominance.

With four exceptions, all the other signs of [*i*] and [*j*] type of detected epistasis were negative, which suggests an interaction between increasing and decreasing alleles, thus providing evidence of some level of dispersion in the inbred parents. A negative sign for each of these two parameters suggests that it would be possible to further improve the level of the corresponding traits. The dominance [*h*] and dominance × dominance [*l*] effects were in the opposite direction, suggesting that duplicate-type epistasis occurred in most cases and indicating predominantly dispersed alleles at the interacting loci [27]. This kind of epistasis generally hinders improvement through selection and, hence, a higher degree of dominance and [*l*] type of interaction effects should not be expected. It also indicated that selection should be delayed for several generations (single seed descent) until a high level of gene fixation is attained.

However, the presence of significant estimates for additive [*d*] and [*i*] gene effects in several traits in the crosses indicates that some additive or additive × additive type of gene action may also be operative in the inheritance of this trait.

The values of the gene effects of epistasis for RDM, SDM, TDM, LG and LWL in SC2 × AFE were elevated and significant. In SC2 × LP3, on the other hand, elevated epistasis values were found in L3 and LWL. These results could explain the overestimation of H_N and ΔG%.

Since one or more kinds of epistatic effects were detected for all the traits, estimates of the additive and dominance components for these traits may be biased due to nonorthogonality, if estimated using procedures that assume no epistatic [37]. For this reason, the estimates of epistasis obtained are likely to be of minimum value. The assumption of no epistasis is one of the most common in quantitative genetic models [47]. The amount and type of epistasis present in crop species can have major consequences on both the reliability of prediction and the design of breeding programs.

The difficulty in using generational mean analysis to estimate genetic effect resides in the balance effect of the segregating loci. Additive gene effects, or interaction effects related to additive effects, are conditioned by the degree of dispersion among parents for the trait being analyzed. In the case of dominance effect, the final effect comes from the sum of the individual dominant effects at each locus. We can therefore conclude that additive effect may be low on account of gene dispersion, in the same way that dominance effect may be low due to the ambidirectionality of the dominance.

4. Conclusions

The variable for LG (leaf growth) showed positive and significant differences for [*h*] in both crosses, indicating the presence of hybrid vigor which can be exploited in a program of improvement.

For the variable RL (root length), the comparison of the genetic effects assessed in both crosses enabled us to determine that there was a greater dispersion of genes between the SC2 and AFE lines, which could be seen through the lower value of [*d*] obtained in their cross. The lack of significance for the genetic effect [*h*] for SC2 × LP3 would point a higher genetic resemblance between them. This seems logic since LP3 line is moderate tolerant to salt.

The three traits associated with the biomass (RDM, SDM and TDM) displayed superior values of [*d*] and [*h*] in the SC2 × AFE cross, which would indicate a greater association of genes and genetic divergence between these lines. This was to be expected given that both lines were selected for their contrasting tolerance to saline stress in a previous experiment. The SC2 line displayed an increased growth of the aerial part and root as a strategy for salt tolerance through a more efficient absorption of water and higher rate of photosynthesis. In SC2 × AFE, the negative and significant values that were obtained for [*h*] indicate that the AFE line possesses dominant genes for diminishing the production of dry matter, whereas SC2 line provides the genes that increase it. In the SC2 × LP3 cross, on the other hand, the positive sign for [*h*] indicates that the dominant genes come from the tolerant parent (SC2) and therefore the heterosis could be exploited.

The analysis of the variables for hydric relations (LWL and RWC) showed different behavior. The LWL trait displayed significant differences in both crosses, whereas RWC did not. This could be attributed to the fact that LWL is associated with the loss of water through the epidermis of the leaf determined by the thickness of the cuticle (secondary transpiration). Given that this characteristic is of a constitutive nature, it is expected not to vary under saline stress. RWC, on the other hand, is associated with the diminishment of the Ψo of the tissues and is subject to modifications throughout the crop cycle according to the Ψo in the soil. In our experiment, ten days of salinization were insufficient to display significant differences.

The results of the present study show that both additive and non-additive

types of gene action (dominance and epistasis) are important in controlling the inheritance of the studied traits. The crossing of SC2 × AFE displayed high and significant interaction effects for the majority of the variables. It is impossible to obtain unbiased estimates of pooled additive or dominance effects when epistasis is of major importance in the inheritance of a trait.

The analysis of the tolerance to osmotic stress associated with salinity showed complex polygenetic inheritance for the variables used in this study, as demonstrated by the presence of simple principal effects and/or the interaction of different importance according to the cross in consideration.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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