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Investigation of genetic structure and gene action in bread wheat affected by salt stress

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Abstract

In order to study the effect of NaCl salinity on wheat genetic structure and gene action, F_1, BC_1P_1, BC_1P_2, F_2, and F_3 generations were produced in the greenhouse by crossing a sensitive bread wheat cultivar (Arta) with the salt tolerant (Bam) parent. A split plot experiment was conducted in greenhouse based on randomized complete block design at 0, 125 and 250 mM NaCl in the sand culture. The three salinity levels (0, 125 and 250 mM NaCl) were arranged as the main plots and seven generations were included in the subplots. Agronomic traits including plant height and shoot biomass together with physiological traits such as KNa^{-1} discrimination ratio and electrolyte leakage were measured. Regression method was used to estimate the effects and variances. Generation means were reduced for all traits in the salt stress condition except for electrolyte leakage which was increased in this environment. Only additive effects were present for plant height at 125 mM NaCl and for KNa^{-1} at 250 mM NaCl. Furthermore, both additive effects and additive by additive epistasis governed the control of plant height at the non-saline condition. High broad sense heritability and moderate narrow sense heritability were observed for most of the measured traits under different salinity levels. In conclusion, the notable amount of heritable variation obtained for several characters, especially KNa^{-1}, suggest the possibility of developing genotypes having suitable agronomic characters and the traits related to salt tolerance in the F_2 population under study.

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Introduction

Salinity has affected and continues to affect land area in the world (Flowers, 2004). High salt stress causes homeostasis change in water potential and ion distribution, molecular damage, growth stop, and even death (Zhu, 2001). Salt stress adversely affects plant growth by osmotic stress, toxicity and nutrient deficiency (Munns, 2006). Because of its importance, breeders are interested to investigate salt tolerance and associated mechanisms in many plant species (Sreenivasulu *et al.,* 2000; Baba and Fujiyama, 2003; Lopez-Aguilar *et al.*, 2003). Graminaceous crops are influenced by sodium toxicity under saline conditions and consequently their protein synthesis and enzyme activation are damaged (Tester and Davenport, 2003). Bread wheat (*Triticum aestivum* L.) is a major food crop in most countries of the world which suffer saline soils, and therefore, increasing salinity tolerance in this plant is necessary. The wheat is commonly considered as moderate salt tolerant with threshold EC of 6-8 dSm^{-1} (60-80 mM NaCl), having salt tolerance higher than corn but lower than barley (Hillel, 2000). Based on Francois *et al.* (1986), yield is decreased 3% per unit of EC.

Identification of plant salt tolerance mechanisms and breeding of new cultivars are some of the most effective strategies for reducing salinity problems. Because of its global importance as a crop, by far the greatest attention to selection and breeding for salinity tolerance has been given to bread wheat, however, the progress has not been so impressive. Colmer *et al.* (2006) have summarized results of large international collections of wheat that have been screened by breeders in the hydroponic culture. Many Iranian wheat accessions were screened for grain yield at salinity condition in the field site in California (Jafari-Shabestari *et al.*, 1995). However, no new salt-tolerant wheat cultivar was developed from these programs.

Hybridization is a useful tool for making genetic variation within the crop species to estimate gene effects. Lyon's (1941) study on *Lycopersicum* is one of the first researches to evaluate the inheritance of salinity tolerance in a cross between *Lycopersicon esculentum* and *L. pimpinellifolium*. He showed that fruit yield in the hybrid was more affectedby salinity than the parents.

Generation mean analysis is one of the methods for determining the type of gene action in a cross between two parents. This technique helps to understand the performance of selected parents and the potential ofthe resulting population to employ either for heterosis exploitation or pedigree selection (Singh and Chaudhary, 1985). Parents involved in hybridization must combine well with each other. Also, selection of parents from different geographic regions having different traits correlated with salinity tolerance can help to better comprehend with the salinity inheritance.

Genetics of salt tolerance is complex in different species. Correlated traits might be determined by a number of genes with additive and dominance effects (Flowers, 2004). Bohnert and Jensen (1996) reported that salt tolerance was controlled by multiple genes and regulated by different types of proteins. In wheat, previous research has revealed that salt stress is controlled by additive and non-additive gene effects (Singh and Singh, 2000; Munns and James, 2003). Dhanda and Sethi (1998) showed that traits under study were controlled by additive and incomplete dominance in the normal environment and by non-additive effects, especially overdominance, in the stress condition because of the genotype×environment interaction.

The aim of this research was to study the genetics of several agronomic characters and the traits related to salt tolerance in bread wheat via generation mean analysis under normal and salinity (NaCl) conditions.

Material and methods

Plant materials and green house experimental conditions

Seeds of F_1, F_2, F_3, BC_1P_1 and BC_1P_2 generations were produced in the greenhouse by crossing a sensitive bread wheat cultivar (Arta) with the salt tolerant

(Bam) parent. Seeds were soaked in benomil (2 gr liter^{-1}) for 10 minute. In order to provide uniform seed germination, the seeds were placed on paper sheets in 4°C for 12 h. After 7 days, the seedlings with uniform size were transplanted into sand culture. Two, four and seven days after transplanting, the Hoagland solution (Hoagland and Arnon1950) was added with 1/4, 1/2 and full strength, respectively. The Hoagland solutionhad the following composition per grl^{-1}: KH_2PO_4, 0.14; KNO_3, 0.51; $Ca(NO_3)_24H_20$, 2.5; $MgSO_47H_2O$ 0.5; Fe- EDTA, 0.03; H_3BO_3, 0.007; $MnCl_24H_20$, 0.002; $ZnSO_47H_20$, 0.005; $CuSO_45H_20$, 0.001; H_2MoO_4, 0.006.The solution was changed every 14 days.

NaCl was added in the Hoagland solution after 50 days of transplanting when plants were in the stem elongation stage (GS 30-39 in Zadocks scale). Parents and their progeny were in the same phonological stage when the stress was started. The experiment was conducted with a light intensity of 600 lE m^{-2} s^{-1} for 14 h with light and dark temperatures of 25°C and 18°C, respectively, and the relative humidity of 60%.
The experiment was conducted as split plot based on completely randomized design with two replications. The three salinity levels [0, 125 and 250 mM NaCl (equalized to 50% sea water)] were included in the main plots and seven generations were arranged as subplots. Recorded EC were1.9 $\pm$ 0.18, 10.5 $\pm$ 0.2 and 19.5$\pm$ 0.74 for 0, 125 and 250 mM NaCl, respectively.

Evaluated traits

During the growth period, shoot biomassper plant (gr), plant height (cm), KNa^1discriminationratio and electrolyte leakage were measured. KNa^{-1} ratio and electrolyte leakage were measured in all generations, except F_3. For measuring shoot biomass per plant and plant height in the non-segregating generations [(P_1, P_2) and F_1] 5 and 10 plants were used per subplot, respectively. In the segregating generations (F_2, F_3, and backcrosses) 50, 50 and 20 plant were used, respectively. For physiological traits (KNa^{-1}ratio and electrolyte leakage) 5, 10, 15 and 30 plants were used for parents, F_1, backcrosses and F_2, respectively. Shoot biomass was recorded after oven-drying at 72°C for 48 h.

In the end of experiment, the harvested flag leaf was weighed and digested in 7.2 M HNO_3. The digested plant material was filtered, diluted with distilled water in the 50 ml falcon, and then analyzed for Na^+ and K^+ concentration using flame photometer (Varian FS 220). Electrolyte leakage (EL) was measured using the portable electrical conductivity meter. Electrolyte leakage was recorded in the third leaf after 20 days of salt stress by takingfive disks of 5 mm diameter. Disks were transferred to a falcon with 15 ml distilled water. Then, 100 microliter of the solution was used to record EC_1. Thereafter, the falcons were placed in 120°C for 20 minute for recording EC_2 and finally EL was calculated by $EC_1EC_2^{-1}$.

Statistical analysis

Depending on the characters, six or seven generations were used to estimate the genetic parameters (Mather and Jinks, 1982). At first, adequacy of the additive-dominant model was tested by the following scaling tests:

$A = 2BC_1P_1 - F_1 - P_1$

$B = 2BC_1P_2 - F_1 - P_2$

$C = 4F_2 - 2F_1 - P_1 - P_2$

Then, six-parameter models including m (average), a (additive), d (dominance), aa (additive×additive), ad (additive×dominance) and dd (dominance×dominance) were fit after testing adequacy of the three-parameter models by joint scaling test. These parameters were estimated by the multiple regression method.

Furthermore, additive genetic variance (σ^2_A) and dominance genetic variance (σ^2_D) were estimated by the regression method using the weights in Table 1.

Environmental variance (σ^2_e), genetic variance (σ^2_G) and phenotypic (σ^2_P) variance were estimated as described by Mather and Jinks (1982) using the following equations:

$\sigma^2_e = 0.25 (\sigma^2P_1 + \sigma^2P_2 + 2\sigma^2F_1)$

$\sigma^2_G = \sigma^2_A + \sigma^2_D$

$\sigma^2_P = \sigma^2_A + \sigma^2_D + \sigma^2_e$

Broad-sense (h^2_b) and narrow-sense (h^2_n) heritability were estimated using the following formulae:

$h^2_b = \sigma^2_G / \sigma^2_P$

$h^2_n = \sigma^2_A / \sigma^2_P$

Degree of dominance was estimated by the following formula:

Degree of dominance = d/a

Results

Means and variances

Means and variances for each generation at different salinity treatments are shown in Table 2. Salinity stress reduced shoot biomass per plant, plant height, and KNa^{-1}. Electrolyte leakage was increased by imposing the salinity treatments in all generations.

Table 1. Matrix of weights for σ^2_A and σ^2_D for the generations under study.

Generation	σ^2_A	σ^2_D
F_2	1	1
BC_1P_1	0.5	1
BC_1P_2	0.5	1
F_3	1.5	0.75

Table 2. Mean and variance ofagronomic and physiological traits of wheat under study.

Generation	Trait	Mean	Variance	Trait	Mean	Variance
P_1	PH (0)	85.1	16.7292	BIO (0)	5.5	7.16337
	PH (125)	71.8	7.2	BIO (125)	4.3	4.18763
	PH (250)	49.0	8	BIO (250)	3.5	5.18863
P_2	PH (0)	66.4	25.3	BIO (0)	3.5	3.92477
	PH (125)	63.8	10.25	BIO (125)	2.1	0.31273
	PH (250)	14.1	5.55357	BIO (250)	0.8	0.02777
F_1	PH (0)	85.3	5.65909	BIO (0)	3.5	1.87238
	PH (125)	70.6	5.63	BIO (125)	3.0	0.69393
	PH (250)	15.3	3.15152	BIO (250)	1.3	0.25215
F_2	PH (0)	79.0	647.17	BIO (0)	5.6	41.0959
	PH (125)	64.9	199.316	BIO (125)	4.7	7.5525
	PH (250)	18.3	149.67	BIO (250)	1.7	1.92963
BC_1P_1	PH (0)	93.8	176.107	BIO (0)	5.2	15.0461
	PH (125)	72.8	97.4221	BIO (125)	3.3	4.45459
	PH (250)	18.0	74.0435	BIO (250)	2.3	1.39374
BC_1P_2	PH (0)	73.4	424.042	BIO (0)	4.8	13.7787
	PH (125)	67.5	96.4854	BIO (125)	3.0	1.92191
	PH (250)	15.5	28.2692	BIO (250)	1.6	0.22083
F_3	PH (0)	95.0	352.572	BIO (0)	6.6	42.346
	PH (125)	74.4	247.968	BIO (125)	4.4	8.49264
	PH (250)	22.7	213.21	BIO (250)	2.7	1.22198
P_1	KNa^{-1} (0)	6.72	0.50925	EL (0)	0.217	0.00383
	KNa^{-1} (125)	0.87	0.01841	EL (125)	0.266	0.00252
	KNa^{-1} (250)	0.66	0.01224	EL (250)	0.739	0.00194
P_2	KNa^{-1} (0)	6.04	2.11881	EL (0)	0.586	0.00582
	KNa^{-1} (125)	0.97	0.00306	EL (125)	0.600	0.06607
	KNa^{-1} (250)	0.45	0.00255	EL (250)	0.799	0.00188
F_1	KNa^{-1} (0)	5.84	0.93059	EL (0)	0.505	0.00893
	KNa^{-1} (125)	0.94	0.07818	EL (125)	0.280	0.00666
	KNa^{-1} (250)	0.56	0.00594	EL (250)	0.952	0.00366
F_2	KNa^{-1} (0)	4.99	5.2317	EL (0)	0.382	0.03305
	KNa^{-1} (125)	1.03	0.2506	EL (125)	0.350	0.07418
	KNa^{-1} (250)	0.60	0.06284	EL (250)	0.771	0.03204
BC_1P_1	KNa^{-1} (0)	7.97	6.78355	EL (0)	0.419	0.03535
	KNa^{-1} (125)	0.86	0.17149	EL (125)	0.259	0.08896
	KNa^{-1} (250)	0.61	0.05671	EL (250)	0.771	0.08189
BC_1P_2	KNa^{-1} (0)	6.08	3.25497	EL (0)	0.530	0.05916
	KNa^{-1} (125)	0.93	0.1606	EL (125)	0.518	0.51784
	KNa^{-1} (250)	0.57	0.0373	EL (250)	0.582	0.01318

Description: PH (plant height), Bio (biomass), SE (standard error), EL (electrolyte leakage), 0 (0 mM NaCl), 125 (125 mM NaCl), 250 (250 mM NaCl).

Scaling tests

Scaling tests were not significant for plant height at 125 mM, KNa^{-1} ratio at 250 mM and electrolyte leakage at 0 and 125 mM NaCl levels suggesting the lack of epistasis for the above mentioned traits at these conditions. However, scaling tests were significant for other traits at different salinity conditions (Table 3).

Table 3. Results of scaling tests A, B and C for the studied traits under different salinity conditions.

	Scaling tests					
Trait	A	SE	B	SE	C	SE
PH(0)	17.15	3.61	-4.85	5.49	-6.21	8.52
PH(125)	3.10	2.68	0.66	2.70	-7.35	4.81
PH(250)	-28.42	2.36	1.46	1.54	-20.76	4.16
BIO(0)	1.23	1.24	2.67	1.11	6.46	2.32
BIO(125)	-0.66	0.77	0.87	0.41	6.25	1.09
BIO(250)	-0.30	0.67	1.12	0.16	-0.09	0.77
KNa^{-1}(0)	3.37	1.01	0.27	0.84	-4.47	1.20
KNa^{-1}(125)	-0.10	0.13	-0.04	0.16	0.42	0.16
KNa^{-1}(250)	0.00	0.10	0.12	0.08	0.15	0.11
EL(0)	0.12	0.07	-0.03	0.09	-0.29	0.19
EL(125)	-0.03	0.11	0.16	0.09	-0.03	0.12
EL(250)	-0.15	0.11	-0.59	0.05	-0.36	0.08

Description: PH (plant height), Bio (biomass), SE (standard error), EL (electrolyte leakage), 0 (0 mM NaCl), 125 (125 mM NaCl), 250 (250 mM NaCl),SE (standard error).

Models and genetic effects

The results of r^2, adjusted r^2 (r^2_{adj}), F and chi-square (χ^2) statistics for the selected models are shown in Table 4 and the estimates of genetic effects are presented in Table 5. All models had non-significant χ^2 statistics, indicating that the selected models fitted the data obtained for different characters. However, some of the genetic effects were not significant in the selected models, probably due to small sample size. Only additive effects were included in the model for plant height at 125 mM NaCl and for KNa^{-1}at 250 mM NaCl. Furthermore, both additive effects and additive by additive epistasis governed the control of plant heightat the non-saline condition. In other models dominance effect were also responsible for the genetic control of the traits under study at different NaCl concentrations. Except for two models (for plant height at 125 mM NaCl and for KNa^{-1}at 250 mM NaCl.) epistatic effects were also present in the genetic control of studied characters.

Table 4. Selected regression models for the characters under study at different salinity conditions based on joint scaling test.

		Regression			Joint scaling test	
Model	Trait	r^2	r^2adj	F	χ^2	df
[m][a][aa]	PH(0 mM NaCl)	0.73	0.59	5.29^{+}	2.103^{ns}	4
[m][a]	PH(125 mM NaCl)	0.46	0.35	4.25^{+}	0.770^{ns}	5
[m][a][d][ad][dd]	PH(250 mM NaCl)	0.998	1.00	281^{*}	0.094^{ns}	2
[m][a][d][aa][ad][dd]	BIO(0 mM NaCl)	0.999	0.997	378^{+}	0.001^{ns}	1
[m][a][d][aa]	BIO(125 mM NaCl)	0.82	0.64	4.47^{+}	0.242^{ns}	3
[m][a][d][aa][ad]	BIO(250 mM NaCl)	0.96	0.88	12.38	0.091^{ns}	2
[m][a][d][aa][dd]	KNa^{-1}(0 mM NaCl)	0.807	0.036	1.05	0.14^{ns}	1
[m][a][d][aa][dd]	KNa^{-1}(125 mM NaCl)	0.986	0.93	17.87	0.0^{ns}	1
[m][a]	KNa^{-1}(250 mM NaCl)	0.865	0.832	25.71^{*}	0.01^{ns}	4
[m][a][d]	EL(0 mM NaCl)	0.909	0.85	14.91^{+}	0.019^{ns}	3
[m][a][d]	EL(125 mM NaCl)	0.954	0.923	30.86^{*}	0.011^{ns}	3
[m][a][d][ad][dd]	EL(250 mM NaCl)	0.916	0.58	2.71	0.008^{ns}	1

Description: PH (plant height), Bio (biomass), EL (electrolyte leakage)

**, *, $^{+}$ Probability levels at 0.01, 0.05 and 0.1, respectively.

^{ns}Not significant.

Heritability and other genetic parameters

Results of estimates for genetic components of variance and other parameters are shown in Table 6. Genetic variances were reduced from the control to the salt stress condition for all characters except electrolyte leakage. Broad sense heritability was high for all studied traits except for shoot biomass and grain yield per plant at 250 mM NaCl. Narrow sense heritability was moderate to high for all traits except shoot biomass (at 250mMNaCl), grain yield (at 250mMNaCl), KNa^{-1} ratio (at 0 and 250mMNaCl) and electrolyte leakage (at all conditions). Most of the estimates of degrees of dominance were in the over dominance range except for plant height (at 250mMNaCl), grain yield (at 250mMNaCl), KNa^{-1} ratio (at 0 and 250mMNaCl) and electrolyte leakage (at all conditions).

Table 5. Estimates of additive, dominance and epistatic effects and their standard errors for the studied traitsof wheat under different salinity conditions.

Trait	m	SE	a	SE	d	SE	aa	SE	ad	SE	dd	S.E
PH(0)	86.33**	3.31	11.56+	4.22	-35.24	56.97	-10.60+	6.02	22.00	29.23	21.03	43.89
PH(125)	69.39**	1.24	4.27+	2.07	1.36	4.22						
PH(250)	31.55**	0.62	17.44**	0.63	-41.17**	2.92	-0.89	2.44	-29.89**	2.84	24.97*	2.94
Bio(0)	7.34*	0.13	1.04*	0.05	-2.82+	0.40	-2.84*	0.13	-1.44+	0.20	-0.99+	0.31
Bio(125)	5.14**	0.69	0.94+	0.36	-2.24+	1.04	-2.04+	0.80	-1.54	2.56	1.30	3.84
Bio(250)	2.90+	0.38	1.36+	0.22	-1.64+	0.57	-0.76	0.44	-1.43	0.98	0.61	1.99
KNa^{-1}(0)	6.47*	0.76	0.65	0.62	19.33	11.67	8.12	4.81	3.10	3.76	-11.76	7.21
KNa^{-1} (125)	1.48**	0.09	-0.06+	0.01	-1.24+	0.20	-0.56+	0.08	-0.05	0.36	0.70+	0.13
KNa^{-1} (250)	0.57**	0.01	0.09*	0.02	0.02	0.04						
EL(0)	0.40**	0.0331	-0.17*	0.033	0.10+	0.061						
EL(125)	0.44**	0.0259	-0.19**	0.026	-0.15+	0.048						
EL(250)	0.77*	0.0545	-0.03	0.054	-0.43	0.254	0.28	0.34	0.44	0.244	0.61	0.259

Description: PH (plant height), Bio (biomass),SE (standard error), EL (electrolyte leakage), 0 (0 mM NaCl), 125 (125 mM NaCl), 250 (250 mM NaCl)

**, * and +Probability levels at 0.01, 0.05 and 0.1, respectively.

Discussion

Salinity reduced the mean of agronomic traits and KNa^{-1}discrimination ratio. Other researchers have also reported the adverse effects of salinity on protein synthesis and enzyme activation (Tester and Davenport, 2003), water potential (Zhu, 2001), ion distribution (Zhu, 2001), plant growth (Zhu, 2001; Munns, 2006) and consequently on yield and its components and also K uptake (Kausar *et al.*, 2013; Tuna *et al.*, 2013). The increased electrolyte leakage at saline condition suggests the membrane damage caused by salinity as it was reported also by Tuna *et al.* (2013). These results indicate the importance of breeding for salt tolerance in wheat and other plant species (Sreenivasulu *et al.*, 2000; Baba and Fujiyama 2003; Lopez-Aguilar *et al.*, 2003) as the most effective strategy of dealing with adverse effects of salinity. Hybridization is regarded as a useful method to generate genetic variation for selecting the salt tolerant genotypes.

In this study different genetic effects governed the traits under study under different salinity conditions. For example, additive and additive × additive effect controlled plant height at 0 and 125 mM NaCl, however, additive effects together with dominance effects and ad and dd interactions were responsible in the inheritance of the plant height at 250 mM NaCl. Additive and additive × additive effects can be exploited in the breeding programs. However, in most of the models, dominance and ad and dd epistatic effects governed the genetic control of the traits under

study, including KNa^{-1} ratio, at different NaCl concentrations. Dashti *et al.* (2010) also reported additive, dominance and epistatic effects for KNa^{-1}. Some traits such as plant height (at 250 mM NaCl) were controlled by duplicate epistasis while complementary effect was observed in the control of shoot biomass (at normal condition) depending on the signsof main effects and epistatic interactions (Kearsey and Pooni, 1998). The presence of non-additive effects in the models implies that these effects should be considered in the breeding programs for salt tolerance by producing hybrid varieties if the barriers in the hybrid seed production are improved. However, according to Mather and Jenkis (1982) linkage disequilibrium could bias the estimation of genetic effects especially epistasis. Since we used early segregating generations, such as F_2 and F_3, in our study, the presence of bias in estimating epistasisis highly probable and some part of the epistatic genetic effects should be attributed to linkage disequilibrium.

Table 6. Estimates of variance components and other related parameters for the wheat traits under study.

Parameter	PH (0)	PH (125)	PH (250)	BIO (0)	BIO (125)	BIO (250)	KNa^{-1} (0)	KNa^{-1} (125)	KNa^{-1} (250)	EL (0)	EL (125)	EL (250)
σ^2_e	13.3368	7.1775	4.9642	3.7082	1.4721	1.4302	1.1223	0.0445	0.0067	0.0069	0.0056	0.0028
$\sigma^2_P F_2$	647.17	199.316	149.67	41.0959	7.5525	1.92963	5.2317	0.2506	0.06284	0.03305	0.07418	0.03204
σ^2_G	405.7243	176.9390	140.9913	29.6794	5.4886	0.3034	7.2131	0.2061	0.0562	0.0308	0.0961	0.1290
σ^2_A	181.7642	153.1225	138.8711	26.4054	4.2229	0	0	0.1582	0.0123	0	0	0
σ^2_D	223.9601	23.8164	2.1202	3.2740	1.2656	0.3034	7.2131	0.0479	0.0439	0.0308	0.0961	0.1290
h^2_b	0.9682	0.9610	0.9660	0.8889	0.7885	0.1750	0.8653	0.8226	0.8939	0.8169	0.9243	0.9131
h^2_n	0.43	0.83	0.95	0.79	0.61	0.00	0.00	0.63	0.20	0.00	0.00	0.00
d/a	-3.04	0.32	-2.36	-2.71	-2.38	-1.20	29.73	-20.66	0.22	-0.58	0.79	14.33

Description: PH (plant height), BIO (shoot biomass), KNa^{-1} (KNa^{-1} discrimination), EL (electrolyte leakage), 0 (0 mMNaCl), 125 (125mMNaCl), 250 (250mMNaCl), σ^2_e(error variance), σ^2_P (phenotypic variance), σ^2_G (genetic variance), σ^2_A(additive genetic variance), σ^2_D(dominance genetic variance h^2_b(broad sense heritability),h^2_n(narrow sense heritability), d/a (degree of dominance).

In this study negative estimates of variance components were assumed to be zero (Robinson *et al.* 1955). Some researchers report these negative signs in their study for special purposes (Dudley and Moll, 1969; Hallauer and Miranda, 1988). Genetic variances for salt stress condition were lower than that of the salt-free environment for most of the traits under study. This indicates that salt stress may have prohibited the expression of some genes governing the traits measured in this research program.

High broad sense heritability and moderate to high narrow sense heritability for most of the characters were observed in this study. This indicates that there is appreciable amount of heritable variation, especially for KNa^{-1} discrimination ratio, in the generated F2 population for breeding agronomically feasible and probably salt tolerant genotypes, although the estimates may be biased upward by the epistasis interaction observed in the generation mean analysis. However, for initiation of an efficient breeding program other populations from different crosses should be included in the program.

As it was mentioned earlier, over dominance was observed for most of characters at different salinity conditions, suggesting the important role of dominance in controlling the traits under study. However, the estimates may be biased upwardly by the epistasis and/or linkage disequilibrium. Linkage disequilibrium could bias the estimation of degree of dominance, especially in the early segregating generations, so that an incomplete or complete dominance is estimated falsely as overdominant

genetic effect. Linkage disequilibrium has been suggested as the possible cause of this apparent overdominance or pseudo-overdominance.

In conclusion, the considerable amount of heritable variation for important agronomic traits and also KNa^{-1}, imply the possibility of extracting suitable lines for agronomic characters and the traits related to salt tolerance in the F_2 population under study. However, the existence of non-additive effects in governing the above mentioned traits suggest the production of hybrid varieties if the hybrid seed can be producedin the breeding programs.

References

Baba T, Fujiyama G. 2003. Short-term response of rice and tomato to NaCl stress in relation to ion transport. Soil Scienc and Plant Nutrition **49**, 513-519. http://dx.doi.org/10.1080/00380768.2003.10410040

Bohnert HJ, Jensen RG. 1996. Metabolic engineering for increased salt tolerance–the next step. Functional Plant Biology **23,** 661-667. http://dx.doi.org/10.1071/PP9960661

Colmer T, Munns R, Flowers T. 2006. Improving salt tolerance of wheat and barley: future prospects. Animal Production Science **45,** 1425-1443. http://dx.doi.org/10.1071/EA04162

Dashti H, Naghavi M, Tajabadipour A. 2010. Genetic analysis of salinity tolerance in a bread wheat cross. Journal of Agricultural Science and Technology **12,** 347-356.

Dhanda S, Sethi G. 1998. Inheritance of excised-leaf water loss and relative water content in bread wheat (*Triticum aestivum*). Euphytica **104,** 39-47. http://dx.doi.org/10.1023/A:1018644113378

Dudley J, Moll R. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Science **9,** 257-262.

Flowers T. 2004. Improving crop salt tolerance. Journal of Experimental Botany **55,** 307-319. http://dx.doi.org/10.1093/jxb/erh003

Francois L, Maas E, Donovan T, Youngs V. 1986. Effect of salinity on grain yield and quality, vegetative growth, and germination of semi-dwarf and durum wheat. Agronomy Journal **78,** 1053-1058. http://dx.doi.org/10.2134/agronj1986.00021962007800060023x

Hallauer AR, Miranda JF. 1988. Quantitative genetics in maize breeding. Iowa State Univ. Press, Ames, IA.

Hillel D. 2000. Salinity management for sustainable irrigation: integrating science, environment, and economics. World Bank Publications.

Hoagland DR, Arnon DI. 1950. The water-culture method for growing plants without soil. *Circular*. California Agricultural Experiment Station 347.

Jafari-Shabestari J, Corke H, Qualset CO. 1995. Field evaluation of tolerance to salinity stress in Iranian hexaploid wheat landrace accessions. Genetic Resources and Crop Evolution **42,** 147-156. http://dx.doi.org/10.1007/BF02539518

Kausar F, Shahbaz M, Ashraf M. 2013. Protective role of foliar-applied nitric oxide in *Triticumaestivum* under saline stress. Turkish Journal of Botany **37,** 1155-1165. http://dx.doi.org/10.3906/bot-1301-17

Kearsey MJ, Pooni HS. 1998. The genetical analysis of quantitative traits. Stanley Thornes Publishers, Ltd.

López-Aguilar R, Orduño-Cruz A, Lucero-Arce A, Murillo-Amador B, Troyo-Diéguez E. 2003. Response to salinity of three grain legumes for potential cultivation in arid areas. Soil Science and Plant Nutrition **49,** 329-336. http://dx.doi.org/10.1080/00380768.2003.10410017

Lyon CB. 1941. Responses of two species of tomatoes and the F1 generation to sodium sulphate in the nutrient medium. Botanical Gazette, 107-122.

Mather K, Jinks JL. 1982. Biometrical genetics, Chapman and Hall, New York.

Munns R, James RA, Läuchli A. 2006. Approaches to increasing the salt tolerance of wheat and other cereals. Journal of Experimental Botany **57,** 1025-1043.
http://dx.doi.org/10.1093/jxb/erj100

Robinson H, Comstock R, Harvey P. 1955. Genetic variances in open pollinated varieties of corn. Genetics **40,** 45-60.

Singh RF, Chaudhary BD. 1985. Biometrical methods in quantitative genetic analysis. Kalyani Publishers, New Dehli.

Sreenivasulu N, Grimm B, Wobus U, Weschke W. 2000. Differential response of antioxidant compounds to salinity stress in salt-tolerant and salt-sensitive seedlings of foxtail millet (*Setariaitalica*). Physiologia Plantarum **109**, 435-442.
http://dx.doi.org/10.1034/j.13993054.2000.100410.x

Tester M, Davenport R. 2003. Na^+ tolerance and Na^+ transport in higher plants. Annals of Botany **91**, 503-527.
http://dx.doi.org/10.1093/aob/mcg058

Tuna AL, Kaya C, Altunlu H, Ashraf M. 2013. Mitigation effects of non-enzymatic antioxidants in maize (*Zea mays* L.) plants under salinity stress. Australian Journal of Crop Science **7,** 1181.

Zhu J K. 2001. Plant salt tolerance. Trends in Plant Science **6,** 66-71.