Study of genetic control of salinity tolerance in bread wheat cv. Kavir-using generation mean analysis

S. Z. Ravari[1], H. Dehghani[2*] and H. Naghavi[3]

[1 and 3] Kerman Agricultural and Natural Resources Research and Education Center, Agricultural Research, Education and Extension Organization (AREEO), Kerman, Iran.
[2]Faculty of Agriculture, Tarbiat Modares University, Tehran, Iran.
*Corresponding author Email address:dehghanr@modares.ac.ir

Received: February 2017
Accepted: August 2017

ABSTRACT

Ravari, S. Z., H. Dehghani, H. and Naghavi, H. 2017. Study of genetic control of salinity tolerance in bread wheat cv. Kavir-using generation mean analysis. **Crop Breeding Journal 7 (1 & 2): 57-66.**

Kavir wheat is one of the salinity tolerant cultivars that have been improved in Iran. In this research, F_1, BC_1, BC_2 and F_2 generations derived from a cross between Kavir × Arta and Kavir × Moghan3 (Arta and Moghan3 are susceptible to salinity) were evaluated through generation mean analysis in non-stress and salinity stress conditions in a randomized complete block design with three replications at the Agriculture Research Center of Kerman. The irrigation water salinity was 0.63 and 15 dS/m in non-stress and stress conditions, respectively. The salinity of farm soil was 2.1 dS/m in both conditions. The traits of flowering and maturity time, plant height, flag leaf relative water content, amount of Na^+ and K^+ in flag leaf, yield per plant and hundred seed weight were recorded for each treatment during the growth season and after harvest. The frequency distribution showed that Kavir was the superior parent in terms of the amount of Na^+ while Arta and Moghan3 were the superior parent in terms of the amount of K^+ and K^+/Na^+ in non-stress conditions. The concentration of Na^+ decreased and the concentration of K^+ and K^+/Na^+ increased in Kavir in stress conditions, while this condition was contrary in Arta and Moghan3. These results showed that when the plant encounters stress, some genes will be activated, which will result in a decrease in the concentration of Na^+ and increase K^+ uptake. Scale test results rejected the adequacy of the additive-dominance model and confirmed the presence of epistatic effects for these traits (except for K^+/Na^+ in stress conditions) in both environments. None of these tests were significant for the K^+/Na^+ in stress conditions. This result showed that the K^+/Na^+ was affected by additive × additive gene effect and the adequacy of the three-parametric models in the joint scaling test also confirmed this.

Key words: wheat, salinity, tolerance, generation mean analysis.

INTRODUCTION

Lack of food puts the agricultural sector under the most pressure. By 2050, global food production must increase 50% to meet the increasing population (Dehdari et al., 2007). Wheat makes a major contribution towards providing the human protein requirements. To meet food demand, it is necessary to increase wheat production either by increasing the yield per unit area or by increasing the cultivated areas. In either way, in the arid and semi-arid regions of the world, including Iran, soil salinity is one of the major abiotic stresses affecting germination, crop growth and productivity that impair normal growth and limits realization of the yield potential of modern wheat varieties (Sairam et al., 2002; Di Caterina et al., 2007). These occur as a result of water shortage caused by the negative potential of the soil solution, ion toxicity associated excessive absorption of Na^+ and Cl^- ions and nutrient ion imbalance when the excess of Na^+ or Cl^- leads to a diminished uptake of K^+, Ca^{2+} and NO_3^- (Krishnasamy et al., 2014; Oyiga et al., 2017). In wheat, salt tolerance is associated with low rates of transport of Na^+ to the shoot, with high selectivity for K^+ over Na^+ (Munns et al., 2006; Chen et al., 2007). Bread wheat is affected by a low rate of Na^+ accumulation and an enhanced K^+/Na^+ discrimination, a character that is controlled by a locus on chromosome 4D (Gorham et al., 1997; Munns et al., 2006).

Breeding for salt tolerance offers more promising, energy efficient, economical, and socially acceptable approach to solving these problems than other processes of soil amelioration. Salinity tolerance is a complex quantitative trait and the selection of a successful breeding program to produce tolerant cultivars depends on understanding the genetic structure of the population under study.

One of these methods is the generation mean analysis .This model is free from the limitations of other models and can estimate the genetic markers needed for each trait (Mather and Jinks, 1971). In this way, in addition to estimates of additive and dominance gene effects, the effects of epistasis can also be estimated using the scale test. Previous studies on wheat have revealed that salinity tolerance in this crop is controlled by additive and non-additive gene effects (Singh and Singh, 2000; Munns and James, 2003). In an experiment conducted on salt tolerance inheritance in barley, generation mean analysis revealed that dominance and epistasis gene action contribute to the control of K^+, Na^+ and K^+/Na^+ (Farshadfar et al., 2008). The aim of this study was to investigate the genetic control of the traits associated with salinity tolerance in the Kavir variety.

MATERIALS AND METHODS

This study utilized two crossing blocks "Kavir × Arta" and "Kavir × Moghan3". "Kavir" (P_1) was used as a tolerant variety while "Arta and Moghan3" (P_2) were employed as susceptible varieties (Ravari et al., 2016a; Ravari et al., 2016b). F_1 and parents were used to produce F_2 and backcross generations in the crosses. Then P_1, P_2, F_1, BC_1, BC_2 and F_2 derived from each cross were evaluated through generation mean analysis in two randomized complete block designs with three replications at the Agriculture and Natural Resources Research Center of Kerman. Each block contains two lines of each parent, F_1, BC_1, BC_2 and ten F_2 lines in a total of 20 lines, each line with a length of one meter, with row-to-row intervals of 0.2m and ten seeds in each line (totaling 60 seeds each of P_1, P_2, F_1, BC_1, BC_2 and 300 seeds of F_2 in each design). Two irrigation salinity levels for design 1 (non-stress) and design 2 (stress); 0.631 dSm^{-1} and 15 dSm^{-1} were used, respectively. Based on soil sample analysis, the required fertilizer was applied before sowing (120 $kgNha^{-1}$ and 30 kg Pha^{-1}). Nitrogen was applied in three equal parts at the sowing, tillering and anthesis stages. The traits of flowering time (days to flowering), maturity (days to maturity) and plant height were recorded during the growth season. Fresh mass (FM), turgid mass (TM) and dry mass of 10 flag leaves were measured at the time of pollination in each of the treatments and then flag leaf relative water content (RWC) was calculated using equation (1) (Weatherley, 1950).

$$RWC = \frac{fm - dm}{tm - dm} \times 100 \qquad (1)$$

Similarly, 10 leaves at the bottom of the flag leaves in the same plants were cut off and Na^+ and K^+ were measured.. These two elements were measured with the flame Photometry method (FP) (Tandon, 1995). After harvest, yield per plant and hundred seed weight were measured for each treatment. After obtaining the relevant data, a weighted least square analysis (Mather and Jinks, 1982) was performed on the generation means, commencing with the simplest model using parameter "m" only and the reversed variance within each generation ($weight = \frac{1}{s^2}$) was used as weight. Generation mean analysis was performed in those variables for which the weighted least square analysis showed significant differences between generations, using the methodology proposed by Mather and Jinks (1971):

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

where Y, m, d, h, i, l and j represent the mean for one generation, mean of all generations, sum of additive effects, sum of dominance effects, sum of additive × additive, sum of additive × dominant and sum of dominant × dominant interactions, respectively. Also α, β, 2αβ, α^2, β^2 are the coefficients for the additive, dominant effects and their interactions in the model, respectively. The following six parameters: m (average effect), d (additive), h (dominance), i (additive × additive), j (additive × dominance) and l (dominance × dominance) were estimated after testing the adequacy of the three parameter models through the joint scaling test. Further models of increasing complexity were considered to fit, if the chi square value was significant. The best-fitted model was the one which had significant estimates of all parameters along with a non-significant chi square value. The broad-sense and narrow-sense heritability of all traits calculated based on Warner (1952) formulas,

$h^2_{bs} = \{[V_{F_2} - (V_{P_1} \times V_{P_2} \times V_{F_1})0.33]/V_{F_2}\}$ and

$h^2_{ns} = \{[2V_{F_2} - (V_{BC_1} + V_{BC_2})]/V_{F_2}\}$,

respectively.

Data were analyzed using SAS ver. 9.2 (SAS Institute, 2011).

RESULTS AND DISCUSSION

The homogeneity of variance test results showed that the variances were not homogeneous in two crosses in two environments (Table 1). Also, weighted least square analysis results showed that six generations were significantly ($P \leq 0.01$) different for all traits measured in both stress and non-stress conditions in two crosses (Table 1). Due to the significant difference between generations, generation mean analysis for these traits was

Table 1. Weighted least square analysis for six generations in two conditions at the two crosses, Kavir × Arta, Kavir × Moghan3

Cross	Environment	S.O.V	df	Yield grain	Plant height	100KW	Na^+	K^+	K^+/Na^+	RWC	HD	MD
Kavir × Arta	Non-stress	Replication	2	0.07	2.7	0.04	0.037	0.59	0.99	0.45	0.78	4.37
		Generation	5	1.149**	95**	0.38**	0.19**	5.98**	23.4**	3.21**	64.53**	23.9**
		Error	10	0.2	1.54	0.02	0.0017	0.4	0.33	0.11	0.28	0.12
	χ^2			131.78**	789.13	89.14*	167.23**	371.5**	530.1**	120.7**	88.6**	89.77**
	Stress	Replication	2	0.229	13.52	0.3	0.098	0.4	2.5	0.34	7.8	0.46
		Generation	5	5.47**	69.41**	2.13**	2.27**	10.7**	58.58**	8.69**	85.2**	45.8**
		Error	10	0.14	0.6	0.59	0.45	0.27	2.9	2.23	1.58	1.8
	χ^2			121.35	333.43**	184.11**	410.3**	428.4**	381.17**	298.3**	230**	76.8*
Kavir × Moghan3	Non-stress	Replication	2	0.11	3.49	1.01	1.23	0.336	2.06	1.11	15.3	2.45
		Generation	5	1.95**	130.5**	0.619**	0.73**	11.99**	23.39**	4.54**	120.18**	35.1**
		Error	10	0.28	2.23	0.067	0.023	3.43	2.75	1.55	22.77	0.728
	χ^2			71.66**	35.58**	25.34**	44.18**	34.19**	84.12**	71.33**	81.45**	56.2**
	Stress	Replication	2	0.139	18.82	0.48	5.34	2.61	2.5	3.44	10.88	0.59
		Generation	5	6.02**	96.5**	0.225**	3.65**	19.52**	63.8**	5.95**	315.8**	91.28**
		Error	10	0.19	1.06	0.08	0.89	4.43	6.47	2.04	2.58	2.51
	χ^2			30**	13.13**	15.8**	55.9**	34.2**	28.18**	54.5**	34.2**	22.22**

Table 2. A, B, C and D scale tests for the studied traits in two stressed and non-stressed environments and two crosses, Kavir × Arta, Kavir × Moghan3

Cross	Environment	Test	Trait								
			maturity	Heading date	RWC	K^+/Na^+	K^+	Na^+	100KW	Plant Height	Grain Yield
Kavir × Arta	Non-stress	A	$0.44^{**} \pm 1.3$	2.48 ± 2.11	2.21 ± -1.82	2.47 ± -0.6	3.95 ± 2.4	0.43 ± 1.02	0.9 ± -0.64	$2.6^{**} \pm 5.8$	$0.5^{**} \pm 1.5$
		B	$2.8^{**} \pm 6.86$	2.7 ± -2.64	2.16 ± 1.76	2.65 ± 1.02	1.8 ± 0.01	0.08 ± 0.08	0.35 ± 0.38	$0.1^{**} \pm -1.7$	$0.5^{*} \pm 1.7$
		C	3.78 ± -1.25	$0.9^{**} \pm 2.9$	$1.4^{**} \pm -3.1$	4.1 ± 2.15	1.2 ± 0.1	2.02 ± 1.07	1.21 ± 0.02	2.6 ± 0.37	0.62 ± 0.62
		D	3.24 ± -1.34	$0.1^{**} \pm 3.1$	$0.72^{**} \pm 4.3$	$0.6^{**} \pm -1.3$	$0.8^{**} \pm 2.6$	$0.1^{**} \pm 3.1$	0.61 ± 0.17	2.8 ± 0.57	1.3 ± -0.09
	Stress	A	$0.9^{**} \pm -2.4$	$2.2^{**} \pm 6.1$	1.07 ± -0.21	5.4 ± 2.45	1.62 ± 1.1	1.1 ± -0.44	0.27 ± 0.78	4.6 ± 1.4	1.1 ± 0.54
		B	$2^{**} \pm -11.1$	$2.1^{**} \pm -12$	3.04 ± -0.81	4.1 ± -2.57	1.2 ± -1.42	1.1 ± -0.53	0.24 ± -0.5	4.8 ± -1.7	$0.9^{**} \pm -2.4$
		C	4.11 ± -1.11	1.16 ± 0.37	$0.62^{**} \pm 1.1$	3.3 ± -0.07	0.6 ± 0.6	1.25 ± 0.98	1.83 ± 0.22	4.2 ± 0.21	$4.7^{*} \pm 1.9$
		D	4.32 ± -0.23	4.56 ± 0.87	$0.34^{**} \pm 1.4$	0.7 ± -0.85	$0.3^{**} \pm 1.3$	$0.1^{**} \pm 1.9$	0.92 ± 0.18	$1.4^{**} \pm 4.2$	2.3 ± 0.9
Kavir × Moghan3	Non-stress	A	$0.15 \pm 2.1^{**}$	$0.2 \pm 2.3^{**}$	2.14 ± 0.24	1.4 ± -1.22	0.4 ± 0.34	3.44 ± 0.54	$1.1^{**} \pm 2.2$	$0.7 \pm 3.5^{**}$	$0.5^{**} \pm 1.21$
		B	$5.4^{**} \pm 21.4$	1.6 ± 1.26	0.25 ± 0.11	1.31 ± 1.06	0.1 ± 1.3	1.2 ± -0.41	2.42 ± 0.19	$0.8^{**} \pm 3.1$	$1.2^{**} \pm 3.43$
		C	5.23 ± 1.32	8.56 ± 4.24	$0.8^{**} \pm -3.1$	$1.6 \pm 4.1^{**}$	1.3 ± 0.02	1.8 ± 1.2	2.4 ± -2.16	2.2 ± -0.51	0.9 ± 0.84
		D	1.81 ± 0.32	$5.1^{**} \pm -9.1$	6.7 ± 4.89	$0.4^{**} \pm 0.9$	$0.3 \pm 1.2^{**}$	$1.4 \pm -3.3^{**}$	3.95 ± 0.19	1.4 ± 0.08	0.8 ± -0.78
	Stress	A	2.81 ± 1.45	3.22 ± 1.63	$1.72^{**} \pm 7.1$	0.46 ± -0.2	2.2 ± 0.88	2.9 ± -0.73	$1.5^{**} \pm 3.2$	$0.6^{*} \pm 1.58$	$0.4^{**} \pm 1.91$
		B	1.92 ± 0.89	$4^{**} \pm 10.1$	2.17 ± -2.1	0.82 ± 0.36	$0.1^{**} \pm 3.7$	$2.7^{**} \pm 9.1$	1.35 ± 0.37	1.3 ± 1.49	2.3 ± 0.73
		C	$3.32^{**} \pm 8.2$	3.1 ± -0.51	12.6 ± 11.1	1.22 ± 1.18	2.3 ± 0.52	6.3 ± -1.52	6.46 ± 1.49	3.2 ± -1.59	3.1 ± -0.35
		D	14.1 ± -11.2	1.65 ± 1.45	$0.11^{**} \pm 1.8$	5.54 ± 3.19	0.55 ± 0.3	4.23 ± 0.93	3.16 ± 0.81	1.2 ± 0.29	$1.2^{**} \pm 4.3$

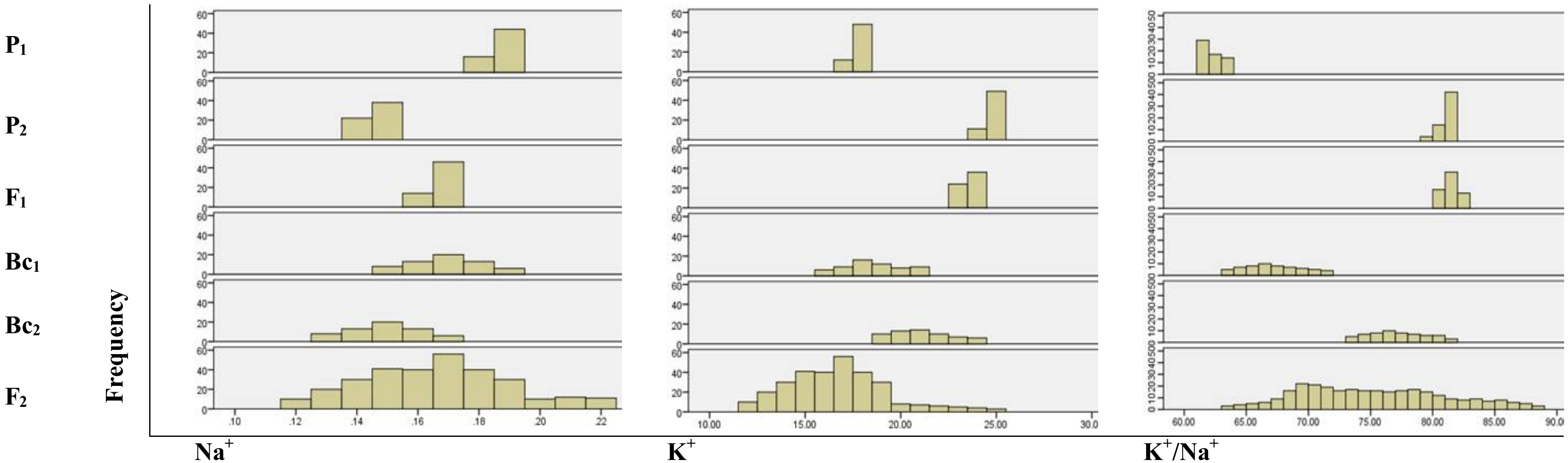

Fig. 1 Distribution of traits of Na^+, K^+ and K^+/Na^+ in six generations studied in Non-stressed environments for Kavir × Arta

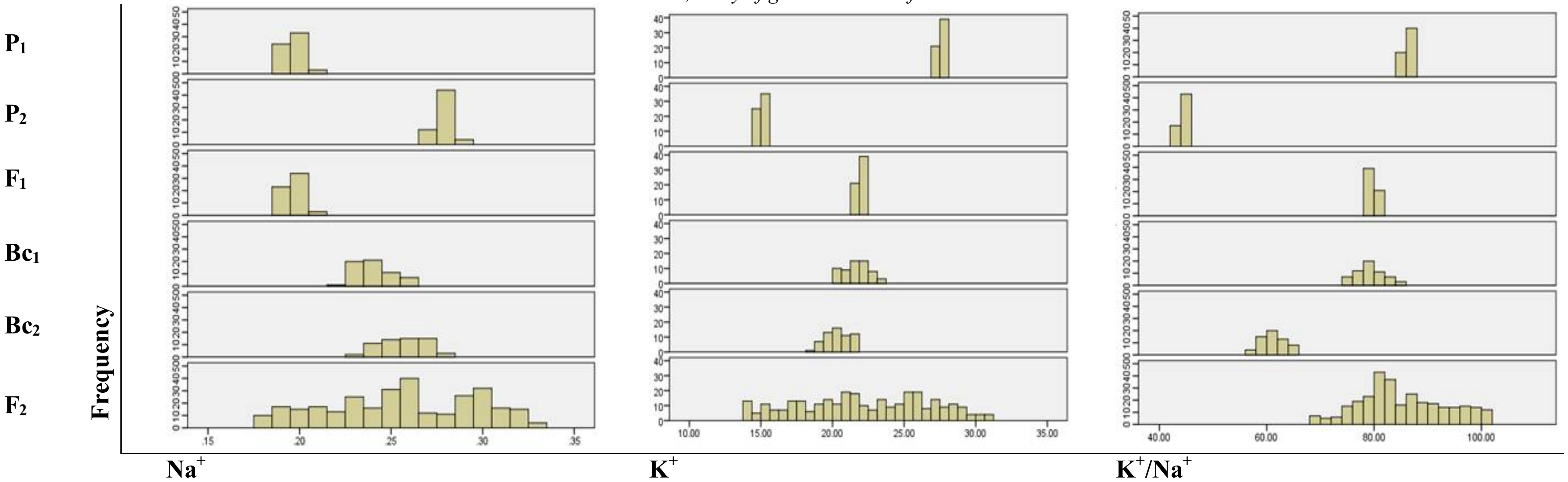

Fig. 2 Distribution of traits of Na^+, K^+ and K^+/Na^+ in six generations studied in Stressed environments for Kavir × Arta

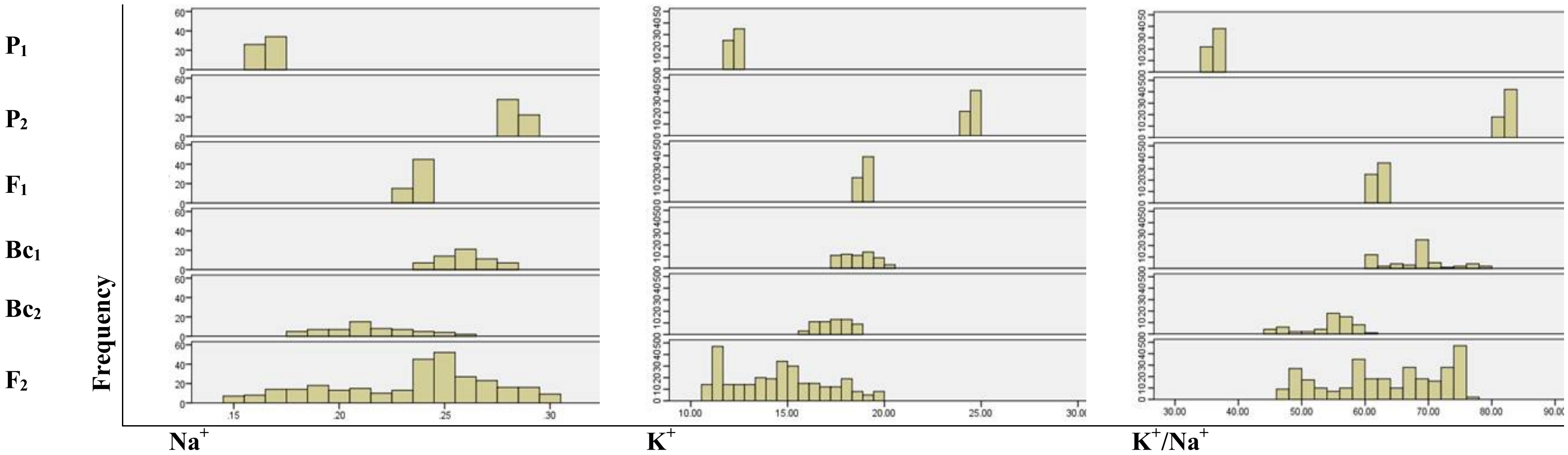

Fig. 3. Distribution of traits of Na^+, K^+ and K^+/Na^+ in six generations studied in Non-stressed environments for Kavir × Moghan3

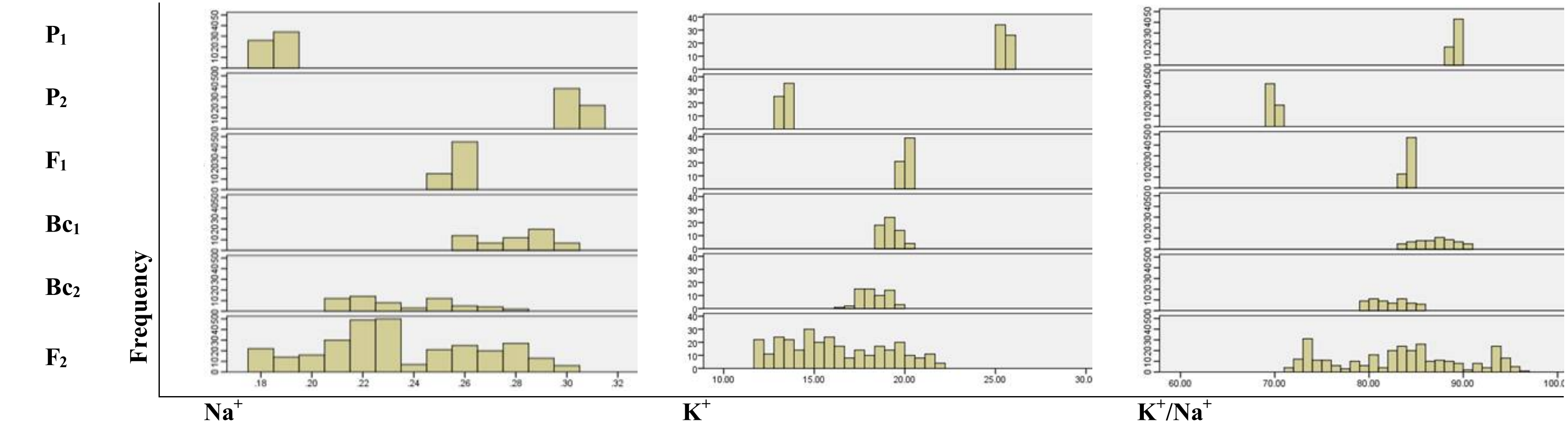

Fig. 4. Distribution of traits of Na^+, K^+ and K^+/Na^+ in six generations studied in Stressed environments for Kavir × Moghan3

possible in both stress and non-stress conditions.

The frequency distribution generation results showed that Kavir variety was the superior parent in terms of the amount of Na^+ while Arta (sensitive) was the superior parent in terms of the amount of K^+ and K^+/Na^+ in Kavir × Arta cross in non-stress conditions. However, in the Kavir × Moghan3 cross, the concentration of Na^+, K^+ and K^+/Na^+ in Moghan3 (sensitive variety) was higher than Kavir. The average concentration of K^+ and K^+/Na^+ in F_1 was more than that of the F_2 populations and can be caused by the adverse effects of inbreeding (Figures 1 and 3). The concentration of Na^+ reduced and K^+ and K^+/Na^+ increased in Kavir under stress conditions; this situation is contrary to the results obtained for Arta and Moghan3 (Figures 1, 2, 3 and 4). These results show that genes are activated in the salt tolerant plant when it is faced with stress (Avinash and Bakti, 2017; Jian-Xiang, et al., 2007) which results in a decrease in the concentration of Na^+ and an increase in K^+ uptake by the plant. The results of the scaling tests (A, B, C and D) in both stress and non-stress conditions in both crosses showed that at least one of the scales for most traits was significant (Table 2), and this means rejecting the null hypothesis (H_0: A, B, C and D = 0) and thus, the adequacy of the additive × dominance effects are rejected and the epistatic effects are confirmed.

In non-stress conditions for some traits, such as yield, plant height, days to heading, days to maturity and K^+/Na^+ more than one scale were significant and this means that these traits are affected by the combined effects of epistasis. Regarding traits of Na^+ and K^+ content, D was significant and this means that Na^+ and K^+ were affected by additive × additive and K^+/Na^+ was affected by additive × additive and dominance × dominance effects of genes. The significant trend of scales in the stress conditions were different. Differences of gene action from the non-stress to stress conditions showed that another gene or genes are activated to protect the plant from stress when the plant is exposed to stress (Gorham, 1990; Flowers and Yeo, 1995). Any of the scaling tests for the K^+/Na^+ ratio were insignificant under stress conditions in two crosses. This indicates that this trait is influenced by the dominance × additive effects of genes. None of the gene effects for kernel weight was insignificant in the different environments.

In order to ensure the results of the scaling test (A, B, C and D), the joint scaling test was also performed (Table 3). In non-stress conditions, only a three-parameter model was fitted for hundred seed weight, and for the remaining traits the three-parameter model was not fitted. The six-parameter model fitted the traits of yield, plant height and flowering date (Table 3). The results of the joint scaling test showed that in non-stress conditions, epistatic effects play a role in controlling all traits except the 100KW. Lack of significance of the genetic effects on 100KW trait in the Kavir × Arta cross and its significance at the Kavir × Moghan3 cross indicates that the two parents of Arta and Moghan3 were different for this trait. The lack of significance of these effects suggests that the two parents, Kavir and Arta, have been heavily bred in relation to the 100KW trait, or are likely to carry similar genes.

Table 3. Estimation of mean and genetic components for the studied traits in two environments for Kavir × Arta cross

Environment	Traits	m	a	d	aa	ad	dd	χ^2
	Yield	9.77**±0.32	-0.7**±0.05	-3.8**±0.8	-2**±0.3	1.25**±0.22	3.1**±0.5	0.00
	Plant height	99.6**±2.7	-1.3**±0.28	42.8**±5.1	7.35**±2.7	4.3**±0.96	35.2**±3.1	0.00
	100KW	3.53**±0.59	0.34±0.42	-0.02±1.5	-	-	-	6.26
	Na^+	0.24**±0.01	0.03±0.001	0.2**±0.04	-0.3**±0.01	-	0.09**±0.02	3.58
Non-stress	K^+	18.5**±1.14	-1.2**±0.06	-	-	-0.81±0.03	2.7**±1.27	3.49
	K^+/Na^+	87.1**±2.3	-1.1**±0.04	18.3**±4.1	-	-5.51**±1.3	-	9.46
	RWC	0.84**±0.03	0.09**±0.01	3.49**±0.05	-0.1**±0.03	-	0.31**±0.03	10.86
	HD	157.4**±1.4	3.47**±0.08	10.6**±2.2	13.4**±0.48	2.17**±0.15	21.3**±3.2	0.00
	MD	219.2**±1.34	4.04**±0.44	-11.9**±3.4	-	7.16**±1.31	4.16**±0.41	11.32
	Yield	5.85**±1.9	2.37**±0.47	-	-	6.24**±1.94	-	11.19
	Plant height	74.65**±1.79	-3.2**±0.64	3.31**±0.61	3.7**±1.25	8.02**±0.68	7.92**±0.23	0.00
	100KW	2.78**±0.57	-	-	-	-	-	2.41
	Na^+	0.53**±0.04	-0.1**±0.01	-0.5**±0.02	-0.2**±0.04	-	-	11.11
Stress	K^+	25.4**±1.12	1.12**±0.11	-18.3**±2.9	-6.7**±1.12	-	-	8.76
	K^+/Na^+	57.08**±3.2	12.58**±0.13	-	-	-	-	14.9
	RWC	1.92**±0.11	1.08**±0.04	-1.2**±0.32	4.24**±0.91	-	1.34**±0.11	11.2
	HD	151.4**±2.12	-15.8**±0.52	-2.1**±0.15	42.3**±3.34	-	6.99**±0.52	12.29
	MD	188.4**±1.8	9**±0.44	-33.6**±3.9	-	6.24**±0.98	34.6**±2.29	6.77

**:Significant at 1%, m: Mean generation, a: Additive effect, d: Dominance effect, aa: Additive × Additive effect, ad: Additive × Dominance effect

For the K^+/Na^+, the three-parameter model was fitted in stress conditions. The adequacy of the 3 parametric model means that there is no epistatic gene effects for K^+/Na^+ in the stress conditions and this trait is influenced by the additive-dominance effects of the genes. The six-parameter model fit

Table 4. Estimation of mean and genetic components for the studied traits in two environments for Kavir × Moghan3 cross

Environment	Traits	m	a	d	aa	ad	dd	χ^2
Non-stress	Yield	15.88**±0.22	0.6**±0.15	-14.4**±0.8	-6.8**±0.32	-	7.96**±0.55	10.54
	Plant height	126.1**±2.77	7.95**±0.28	-13.1**±5.8	-7.3**±2.76	18.5**±0.9	6.72**±3.1	0.00
	100KW	3.2**±0.07	0.63**±0.01	2.94**±0.2	0.63**±0.08	-	-1.49**±3.1	13.34
	Na^+	0.15**±0.03	-0.5**±0.001	-	0.06**±0.003	-	-	8.27
	K^+	28.1**±0.83	1.94**±0.05	-9.5**±1.7	-7.4**±0.84	-	-	11.66
	K^+/Na^+	93.1**±2.44	-2.7**±0.05	-10.7**±4.8	-	1.9**±0.39	8.5**±2.34	6.43
	RWC	1.05**±0.03	0.23**±0.01	-4.3**±2.2	-0.12**±0.03	-	0.25**±0.06	5.21
	HD	205.1**±0.08	-130.3**±2.4	-43.7±1.1	-	87.6**±1.34	2.13**±0.08	9.53
	MD	229.2**±1.4	4.16**±0.09	-26.4**±3.1	-10.8**±1.2	-5.42**±0.64	15.3**±1.73	0.00
Stress	Yield	13.8**±0.31	1.66**±0.11	-17.1**±0.7	-7.5**±0.29	1.89**±0.25	10.4**±0.5	0.00
	Plant height	74.4**±1.47	6.39**±0.37	9.34**±3.39	9.98**±1.43	-	-	13.19
	100KW	2.77**±0.12	0.3**±0.05	-	-	0.36**±0.1	-	8.76
	Na^+	0.37**±0.02	0.03**±0.001	-0.2**±0.03	0.08**±0.01	0.04**±0.001	0.13**±0.02	0.00
	K^+	22.1**±1.14	1.22**±0.06	-16.1**±2.3	-5.4**±1.14	-	12.1**±1.27	4.57
	K^+/Na^+	56.5**±3.6	14.4**±3.2	-	-	-	-	6.64
	RWC	0.76**±0.28	0.31**±0.08	-	-	-0.44**±0.11	-	12.78
	HD	151.1**±1.19	4.61**±0.07	-	-6.2**±1.91	-	-	14.44
	MD	236.2**±1.79	5.1**±0.07	-25.7**±3.5	-12.6**±1.7	-8.7**±0.45	13.7**±1.9	0.00

**:Significant at 1%, m: Mean generation, a: Additive effect, d: Dominance effect, aa: Additive × Additive effect, ad: Additive × Dominance effect

only the performance trait while four and five parameter models fit other traits.

Estimation of components of variance and calculating the heritability of traits in two conditions showed that, the broad-sense and narrow-sense heritability of all traits, except the 100KW, were relatively high. The low heritability of seed weight based on the previous result was predictable because due to the low genetic variation in this trait, it was not significant to estimate variance components in any two parents. The inheritance of most traits in the stress medium was somewhat lower, but the K^+ and K^+/Na^+ ratios still had a relatively high heritability.

Studies have shown that Na^+, K^+ and K^+/Na^+ (especially K^+/Na^+) are the important traits in relation to salinity tolerance in wheat (Abu et al., 2017). The results of the studies by Khan et al. (2009) and Benito et al. (2014) also showed that the K^+/Na^+ ratio was influenced by the additive effects of genes and has high narrow-sense heritability. The plant's ability to maintain potassium uptake is also important in high salinity as well as sodium ion excretion. This trait is called the K^+/Na^+ discrimination in the family of cereals. Studies have shown that the relationship between this trait with agronomic traits and salinity tolerance is very strong (Cuin et al., 2011; Shabala and Cuin, 2008).

One of the mechanisms of salt tolerance observed in glycophytic plants, including wheat, is the prevention of sodium ion entry into the root and, consequently, other organs of the plant, or sodium excretion in some way from these organs and decreasing its concentration, while increasing the concentration of Potassium ion in plant organs through its active absorption when the plant is exposed to salt stress (Krishnasamy et al., 2014).

The results of molecular studies also indicate the importance of Na^+, K^+ and K^+/Na^+ in relation to salinity tolerance in wheat. The results of the cDNA library review by Yu *et al*. (2007) revealed a TaNHX2 gene on this bread wheat line. This gene reduces the destructive concentration of Na in the cytoplasm by removing Na^+ from the cell, through the Na^+/H^+ antiporter action of the plasmid membrane, or Na^+ storage inside the vacuole through the Na^+/H^+ antiporter action of the vacuole membrane. This action is carried out by H^+-ATPase and H^+-PPiase enzymes, which create an electrochemical gradient and transfer the sodium ion into the vacuole, reduce its negative effects in the plant by decreasing its concentration in plant cells.

The results of this experiment also showed that this trait has a relatively high heritability. Therefore, the genotype with high K^+/Na^+ ratio can be tolerated to salinity. The concentration of these ions and their ratio in plant organs, including the flag leaf of the plant's time of stress, can be considered as an important indicator in the detection of a tolerant plant (Hamada et al., 2001; Fukuda et al., 2004)

Based on the results of this experiment, the following recommendations are proposed regarding the improvement of tolerance to salinity in wheat.

The selection of appropriate parents plays a very important role in the success or failure of the breeding program. Therefore, parents should be selected in such a way so that they differ in terms of the important traits associated with salt tolerance (such as Na^+, K^+ and K^+/Na^+ ratio), leading to their capacity to create a high level of diversity in the segregating generations. In the assessment stage for parents and generations in the field or in the greenhouse, the salinity of the irrigation water must not be too high, so that on the one hand, it does not cause the plants to die and, on the other hand, the tension is created to a degree that reveals the difference between tolerant and sensitive plants in segregating generations.

The next important point is to choose the correct breeding method. In relation to traits such as Na^+ and K^+ levels that are affected by additive × additive effects of genes, this effect is a fixable component of genetics, the hybridization and recurrent selection method followed by a pedigree or cross-breeding method, with an appropriate selection of tolerant plant, is suitable but for traits that are affected by the dominance × dominance of the gene effects, selection should be postponed to advanced generations in order to stabilize the effects of the gene.

REFERENCES

Abu, H., R. H. Hafizur, S. Nurealam, M. Khatun, I. Rabiul, and A. Abdullah. 2017. Evaluation of wheat genotypes for salt tolerance based on some physiological traits. Journal of Crop Science and Biotechnology. 18: 333-340.

Avinash, M. and T. Bhakti. 2017. Halophytes: Potential resources for salt stress tolerance genes and promoters. Frontiers in plant Science. 8: 1-10.

Benito, B., R. Haro, A. Amtmann, T.A. Cuin, and I. Dreyer. 2014. The twins K^+ and Na^+ in plants. Journal Plant Physiolgy. 171: 723–731.

Chen, C., C. Tao, H. Peng, and Y. Ding. 2007. Genetic analysis of salt stress responses in asparagus bean (*Vigna unguiculata* L. ssp. Sesquipedalis verdc.). Journal of Heredity. 98: 655-665.

Cuin, T. A., J. Bose, G. Stefano, D. Jha, M. Tester, and S. Mancuso. 2011. Assessing the role of root plasma membrane and tonoplast Na^+/H^+ exchangers in salinity tolerance in wheat: in planta quantification methods. Plant Cell Environment. 34: 947–961.

Dehdari, A., A. Rezaii, M. and S. A. Meibodi. 2007. Genetic control of salinity tolerance in wheat using generation mean analysis. Science and Technology of Agriculture and Natural Resources. 40: 179-191.

Di Caterina, R., M. M. Giuliani, T. Rounno, A. De Caro, and Z. Flagella. 2007. Influence of salt stress on seed yield and oil quality of two sunflower hybrids. Annals of Applied Biology. 151: 145-154.

Farshadfar, E., M. Aghaie Sarbarzah, M. Sharifi, and A. Yaghotipour. 2008. Assessment of salt tolerance inheritance in barley via generation mean analysis. Journal of Biology Science. 8: 461-465.

Flowers, T. J., and A. R. Yeo. 1995. Breeding for salt tolerance in crop plants-Where next? Australian Journal Plant Physiolgy. 22: 875–884.

Fukuda, A., A. Nakamura, A. Tagiri, H. Tanaka, A. Miyao, H. Hirochika, and Y. Tanaka. 2004. Function, intracellular localization and the importance in salt tolerance of a vacuolar Na^+/H^+ antiporter from rice. Plant Cell Physiology. 45: 146-159.

Gorham, J. 1990. Salt tolerance in the Triticeae: K^+/Na^+ discrimination in (Agilops species). Journal of Experimental Botany. 41: 615-621.

Gorham, J., J. Bridges, J. Dubcovsky, J. Dvorak, P.A. Hollington, M.C. Luo, and J. A. Khan. 1997. Genetic analysis and physiology of a trait for enhanced K^+/Na^+ discrimination in wheat. New Phytol. 137: 109-116.

Hamada, A., M. Shono, T. Xia, M. Ohta, Y. Hayashi, A. Tanaka, and T. Hayakawa. 2001. Isolation and characterization of a Na^+/H^+ antiporter gene from the halophyte *Atriplex gmelini*. Plant Molecular Biology. 46: 35–42.

Jian-Xiang, L., S. Renu, C. Ping, and H. H. Stephen. 2007. Salt stress responses in arabidopsis utilize a signal transduction pathway related to endoplasmic reticulum stress signaling. The Plant Journal. 51: 897-909.

Khan, J. A. 1997 Genetic analysis and physiology of a trait for enhanced K^+/Na^+ discrimination in wheat. New Phytol. 137: 109-116.

Khan, M.A., M. U. Shirazi, M. A. Khan, S. M. Mujtaba, E. Islam, S. Mumtaz, A. Shereen, R. U. Ansari, and M. Y. Ashraf. 2009. Role of proline, K/Na ratio and chlorophyll content in salt tolerance of wheat (*Triticum aestivum* L.). Pakistan Journal Botany. 41: 633–638.

Krishnasamy, K., R. Bell, and Q. Ma. 2014. Wheat responses to sodium vary with potassium use efficiency of cultivars. Frontiers in Plant Science. Plant Nutrition, 5: 1-10.

Mather, K., and J. L. Jinks. 1971. Biometrical genetics. Cornell University Press, Ithaca, New York.

Mather, K., and J. L. Jinks. 1982. Biometrical genetics, 3rd ed. Chapman and Hall, London.

Munns, R. and R. A. James. 2003. Screening methods for salinity tolerance: a case study with tetraploid wheat. Plant and Soil. 253: 201-218.

Munns, R., A.J. Richard, and L. Andre. 2006. Approaches to increasing the salt tolerance of wheat and other cereals. Journal of Experimental Botany. 57: 1025-1043.

Oyiga, B. C., R.C. Sharma, J. Sen, M. Baum, F. C. Ogbonnaya, J. Leon, and A. Ballvora. 2017. Identification and characterization of salt tolerance of wheat germplasm using a multivariable screening approach. Journal of Agronomy and Crop Science. 202: 472-485.

Ravari, S. Z., H. Dehghani, and H. Naghavi. 2016a. Assessment of salinity indices to identify Iranian wheat varieties using an artificial neural network. Annals Applied Biology. 168: 185-194.

Ravari, S. Z., H. Dehghani, and H. Naghavi. 2016b. Assessing salinity tolerance of bread wheat varieties using tolerance indices based on K^+/Na^+ ratio of flag leaf. Cereal Research. 6:133-144.

Sairam, R. K., K. V. Rao, and G. C. Srivastava. 2002. Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress, antioxidant activity and osmolyte concentration. Plant Science. 163: 1037-1046.

SAS Institute Inc., (2011). SAS/STAT user’s guide, second edition. SAS institute Inc., Cary, Nc.

Shabala, S., and T. A. Cuin. 2008. Potassium transport and plant salt tolerance. Physiol. Plant. 133: 651–669.

Singh, S., and M. Singh. 2000. Genotypic basis response to salinity stress in some crosses of spring wheat *Triticum aestivum* L. Euphytica, 115: 209-214.

Tandon, H. L. S. 1995. Estimation of sodium and potassium. *In*: Methods of Analysis of Soils, Plants, Water and Fertilizers, FDCO, New Delhi. 62-63.

Warner, J. N. 1952. A method for estimation heritability. Agronomy Journal. 44: 427-430.

Weatherley, P. E. 1950. Studies in water relations of cotton plants I: The field measurement of water deficit in leaves. New Phytology. 49: 81-87.

Yu, J. N., J. Huang, Z. N. Wang, J. S. Zhang, and S. Y. Chen. 2007. An Na^+/H^+ antiporter gene from wheat plays an important role in stress tolerance. Journal of Biosciences. 32: 1153-1161.