

## Genetic analysis of salt tolerance in vegetative stage in wheat (*Triticum aestivum*)

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### Abstract

Identification of genetic control of salt tolerance at the growth stage provides useful information for constructing breeding programs for wheat. Inheritance of salinity tolerance was studied in a cross between 'Tabasi' (P1) a tolerant and 'Ghods' (P2) a susceptible bread wheat (*T. aestivum*) cultivar, F<sub>1</sub>, F<sub>2</sub> and backcross generations (BC1 and BC2) under saline conditions (EC=14 dS m<sup>-1</sup>) in a greenhouse. Eight characters were recorded: biological dry weight (DW), heading date (HD), plant height (PH), K<sup>+</sup> concentration (K<sup>+</sup>), Na<sup>+</sup> concentration (Na<sup>+</sup>), K<sup>+</sup>/Na<sup>+</sup> ratios, total number of tillers per plant (NT) and ratio of fertile tillers per total tillers in each plant (RFT). Generation mean analysis of these traits revealed the involvement of additive and non-additive type gene effects in controlling most of the traits. The epistatic effects [i] for DW, Na<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup> and PH, [j] for DW and PH, [l] for DW, Na<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup>, NT, PH and HD were significant. Additive [d] effects were significant for all measured traits and dominance [h] effects were significant for all except K<sup>+</sup> and RFT. High narrow sense heritability (0.60) was estimated for K<sup>+</sup>/Na, indicating this may be used as a useful indicator index for the selection of salt tolerant genotypes at the vegetative growth stage in wheat. In consideration of demonstrable additive and non-additive effects in controlling measured traits, recurrent selection followed by pedigree breeding may prove useful in improving salinity tolerance in vegetative stage wheat.

**Keywords:** selection, salinity, gene effects, heritability.

**Abbreviations:** DW= dry weight, HD= heading date, PH= plant height NT= total number of tillers per plant and RFT= ratio of fertile tillers per total tillers in each plant, K<sup>+</sup>=K<sup>+</sup> concentration, Na<sup>+</sup>= Na<sup>+</sup> concentration.

### Introduction

Salinity is a major factor limiting plant growth and leads to lower agricultural production in arid and semi-arid regions (Bai et al, 2011). Agricultural productivity is severely affected by soil salinity because salt levels harmful to plant growth affect large terrestrial areas. Damaging effects of salt accumulation in agricultural soils have influenced ancient and modern civilizations. It is estimated that 20% of the irrigated land in the world is presently affected by salinity (Yeo, 1999; Yamaguchi and Blumwald, 2005). Iran's climate is mostly arid and semi-arid (Majidi et al, 2011). About 12.5% percent of the land in Iran has salt in water or soil (Zohary, 1973), so tolerance to salinity stresses is a key topic to consider for crop improvement. Wheat is the most important, widely adapted and consumed food cereal in Iran. It is necessary to increase wheat production in Iran by raising the wheat grain yield. One of the most efficient ways to increase wheat yield is to improve the salt tolerance of wheat genotypes. Identification of plant mechanisms for salt tolerance and breeding new cultivars are the best strategies for reducing salinity effects in agriculture (Forster et al, 1999; Yamaguchi and Blumwald, 2005). Salt tolerance of crops may vary according to their growth stage (Mass and Poss, 1989). In general, cereal plants are the most sensitive to

salinity during the vegetative stage and less sensitive during the flowering and grain-filling stages (Mass and Grieve, 1994). To plan efficient breeding programs for developing salt tolerant varieties, information on the genetic basis of salt tolerance, mode of inheritance, magnitude of gene effects and their mode of action are necessary. Na<sup>+</sup> concentration in shoots and K<sup>+</sup>/Na<sup>+</sup> discrimination are used to study salt tolerance in bread wheat (Gorham, 1990; Munns and James, 2003; Munns et al., 2006). Previous works on wheat showed that salinity tolerance in this crop is controlled by additive and non-additive gene effects (Singh and Singh, 2000; Dehdari et al., 2007; Dashti et al., 2010). Generation means analysis, provides an opportunity to estimate genetic components and measure epistasis. This also helps us to understand the performance of the parents used in the crosses and potentials for the crosses to be used either for heterosis exploitation or pedigree selection (Sharma et al., 2003, Farshadfar et al., 2001). This methods previously indicated that a simple genetic model (including additive and dominance effects) is sufficient for Na<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> ratio determination in a cross between two cultivars of wheat (Dehdari et al., 2007). In an experiment conducted on inheritance of salt tolerance in barley, generation mean

**Table 1.** Analysis of variance for eight agro-physiological traits in wheat.

Source of variation	Degree of freedom	Mean square							
		DW	Na <sup>+</sup>	K <sup>+</sup>	K <sup>+</sup> /Na <sup>+</sup>	PH	NT	RFT	HD
Generation	5	7.16**	1111.72**	817.09*	506.43**	2299.56**	32.09**	0.192	464.93**
Error	228	1.05	27.54	200.19	49.25	89.54	10.12	0.12	43.96

DW= dry weight, HD= heading date, PH= plant height, NT= total number of tillers per plant and RFT=relative fertile tillers per plants. \* and \*\* indicating significant at 0.05 and 0.01 probability levels, respectively.

**Table 2.** Difference between parental means for eight agro-physiological traits in wheat.

Parents	DW	HD	PH	Na <sup>+</sup>	K <sup>+</sup>	K <sup>+</sup> /Na <sup>+</sup>	NT	RFT
P1	2.77	30.55	40.90	5.51	47.23	9.98	6.62	0.332
P2	0.95	22.36	25.34	19.36	33.25	2.70	4.42	0.176
P1-P2	1.82**	8.9**	15.57**	-13.83**	13.98**	7.24**	250*	0.156*

DW= dry weight, HD= heading date, PH= plant height, NT= total number of tillers per plant and RFT=relative fertile tillers per plants. \* and \*\* indicating significant at 0.05 and 0.01 probability levels, respectively.

analysis revealed that dominance and epistasis gene action contribute to control of K<sup>+</sup>, Na<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> (Farshadfar et al., 2008). In order to obtain more precise estimates of gene effects of wheat cultivars under salinity condition, generation mean analysis was used to determine the genetic control of salinity tolerance during vegetative growth of bread wheat using F1, F2 and backcross populations derived from crosses between 'TABASI' (P1) as salt tolerant and 'GHODS' (P2) as salt sensitive genotypes.

## Results and discussion

### Mean comparison

There were significant differences among the means of generations for all of the traits except the RFT (Table 1). This indicates the presence of genetic diversity in this material. Comparison of parents by t-test (Table 2) showed that TABASI (P1) was significantly different with GHODS (P2) for all the traits. The P1 had higher tolerance under salinity condition than P2, as also reported in a previous study (Poustini and Siosemardeh, 2004). The F1 hybrid deviated to better once of the mean parents (Table 4), indicating heterosis relative to mean parents which may be used to help develop hybrid varieties.

### Relationship between traits

Significant positive correlation was found between K<sup>+</sup>/Na<sup>+</sup> ratio (as a salinity tolerance index) with DW, NT and PH (Table 3). This indicate that an increase in K<sup>+</sup>/Na<sup>+</sup> may have caused increasing tiller number and plant heights, resulting in increased dry weight. A significant negative correlation found between K<sup>+</sup>/Na<sup>+</sup> and Na<sup>+</sup> concentration while K<sup>+</sup>/Na<sup>+</sup> was positively correlated with K<sup>+</sup>. This result agrees with results reported by Dehdari et al., 2005, Poustini and Siosemardeh, 2004 and Dashti et al, 2010. Relative fertile tillers per plants (RFT) negatively correlated with NT, indicating that increasing total tiller may reduce the ability of spike production in plants. A negative correlation was observed between Na<sup>+</sup> with RFT, NT and PH, indicating that Na<sup>+</sup> reduces the growth of wheat (Poustini and Siosemardeh, 2004; Rashid et al, 1999; Dashti et al, 2010).

### Generation mean analysis

The joint scaling test (Mather and Jinks, 1982) was employed to estimate the mean [m], additive[d], dominance [h], additive × additive [i], additive × dominance [j] and

dominance × dominance [l] effects and values. The best model was selected using the non-significant chi square ( $\chi^2$ ) value and lowest standard error for all traits (Table 5). For RFT and K<sup>+</sup>, two parameters m and [d] were shown to be the best fit of the observed to the expected generation means and Inter-allelic interaction was not significant. The genetic variation between generations was explained alone by additive effects in these two traits. But for all other traits, both additive and non-additive gene effects are involved to explain genetic variation between generation means (Table 5). Six-parameter models were fitted only for DW and PH, a 5-parameter model was fitted for Na<sup>+</sup> and K<sup>+</sup>/Na<sup>+</sup> and 4-parameter models for HD and NT. The [h] and [l] components showed signs in the opposite direction for DW, Na<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup>, NT, HD and PH, indicating the presence of duplicate epistasis in these traits as mentioned by Adeniji et al. (2007) and Farshadfar et al. (2001). These results agree with results reported by Dashti et al (2010) about HD, Na<sup>+</sup> and NT in a cross between 'Roshan' (salt tolerant) and 'Falat' (salt sensitive). The epistatic effect [j] was significant in DW and PH, indicating that these effects are not fixable by selection under selfing conditions (Farshadfar et al., 2001). The genetic models fitted for DW, Na<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup> and PH indicate that [i] gene effects are significant. This suggests that selection should be carried out in later generations and the interaction should be fixed by selection under selfing conditions. But negative additive × additive interaction [i] for DW, K<sup>+</sup>/Na<sup>+</sup> and PH in this cross indicates a potential for reduction of these traits along fixation additive effects in subsequent generations (Singh and Narayanan, 1993). For RFT and K<sup>+</sup> only [d] was significant, therefore additive type of gene action is important in inheritance of this trait and selection through selfing will be effective (Table 5). The results of heritability estimates showed a moderate (0.2-0.5) broad and narrow sense heritability for DW, Na<sup>+</sup>, PH, RFT. These results indicate that for these traits, environmental effects have a larger contribution than genetic effects. But high heritability (0.5<) for K<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup>, NT and HD (Table 6) indicates this selection may be more effective for improving salt tolerance genotypes. The average dominance ( $\sqrt{H/D}$ ) for all traits was lower than one, except for RFT and HD. This indicates the presence of partial or incomplete dominance types of gene action in the inheritance of these traits (Table 6). Selection of these characters must therefore be delayed until the F3 or F4 generation. This delay permits a loss of non-additive genetic variance through inbreeding, so that the additive genetic variance can be more clearly evaluated (Farshadfar et al., 2001). The amount of  $\sqrt{H/D}$  for RFT and

**Table 3.** Pearson coefficients of correlation between eight agro-physiological traits in wheat.

	DW	Na <sup>+</sup>	K <sup>+</sup>	K <sup>+</sup> /Na <sup>+</sup>	PH	NT	RFT
DW	1						
Na <sup>+</sup>	-0.34**	1					
K <sup>+</sup>	0.11 <sup>ns</sup>	-0.22**	1				
K <sup>+</sup> /Na <sup>+</sup>	0.33**	-0.66**	0.27**	1			
PH	0.39**	-0.41**	-0.09 <sup>ns</sup>	0.27**	1		
NT	0.55**	-0.26**	0.15*	0.28**	0.24**	1	
RFT	-0.07 <sup>ns</sup>	-0.21**	-0.07 <sup>ns</sup>	-0.06 <sup>ns</sup>	0.07 <sup>ns</sup>	-0.32**	1
HD	-0.12 <sup>ns</sup>	-0.03 <sup>ns</sup>	0.21**	0.11 <sup>ns</sup>	-0.21**	-0.13 <sup>ns</sup>	0.11 <sup>ns</sup>

DW= dry weight, HD= heading date, PH= plant height, NT= total number of tillers per plant and RFT=relative fertile tillers per plants. \* and \*\* indicating significant at 0.05 and 0.01 probability levels, respectively.

**Table 4.** Means and standard deviations for eight traits of wheat in different generations.

Generation	Number of plant	DW	Na <sup>+</sup>	K <sup>+</sup>	K <sup>+</sup> /Na <sup>+</sup>	PH	NT	RFT	HD
P1	12	2.77±1.32	5.51±2.6	47.23±14.49	9.94±4.52	40.90±7.88	6.92±2.8	0.332±0.19	30.56±4.16
P2	25	0.95±0.80	19.36±7.5	33.25±15.23	2.70±2.71	25.34±6.72	4.42±2.1	0.176±0.28	22.36±4.79
F1	7	1.39±0.53	5.71±2.3	43.25±14.50	8.01±5.02	46.12±8.42	3.38±2.0	0.467±0.33	22.00±4.04
F2	125	1.71±1.06	6.04±5.2	41.25±21.91	10.80±7.97	45.61±10.2	6.14±3.5	0.250±0.37	20.57±7.12
BC <sub>1</sub>	33	1.24±1.01	6.50±4.15	45.35±21.36	9.07±7.63	36.74±9.75	6.03±2.8	0.310±0.33	25.70±7.18
BC <sub>2</sub>	32	1.28±0.97	15.0±5.45	34.27±16.01	3.98±5.50	39.23±8.6	5.58±3.2	0.256±0.36	19.70±6.35

DW= dry weight, HD= heading date, PH= plant height, NT= total number of tillers per plant and RFT=relative fertile tillers per plants. \* and \*\* indicating significant at 0.05 and 0.01 probability levels, respectively.

HD is higher than one that shows a over dominance gene effect for these traits indicating that selection must be delayed until F3 and F4 (same as other characters). But RFT and HD traits have a severe inbreeding depression in early selfing generations. In this study an additive type of gene action for Na<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup> and other studied traits was found. This indicated that selection is effective along homozygosis trend. Selection for lower Na<sup>+</sup> leaf content should increase K<sup>+</sup>/Na<sup>+</sup> ratio and consequently increasing salt tolerance. The F parameter is an indicator of correlation between D and H over all loci. If F is zero or positive it means that dominant genes are in the parent with high performance, while negative F indicates those dominant genes are in the low performance parent (Kersay and Pooni, 1996). The F value for DW, K<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup> and HD is positive, hence most of the genes responsible for these traits are dominant in 'Tabasi', meaning a prevalence of dominant alleles, while the F value for Na<sup>+</sup>, PH and RFT was negative (Table 6), indicating that recessive alleles were more prevalent than dominant alleles for these characters or genes controlling these characters are dominant in 'Ghods' (Farshadfar et al., 2001, Singh and Lal, 2009). Overall, generation mean analysis revealed additive and non-additive types of gene effects in most of the traits studied. The models suggests that complex epistatic effects are important in controlling salinity tolerance characters, particularly K<sup>+</sup>/Na<sup>+</sup> and leaf tissue Na<sup>+</sup> concentration. The magnitude and significance of the estimates for [i] and [I] indicated epistatic genes are important in the basic mechanism of traits involved salt tolerance inheritance in the wheat cross studied. Hayman (1960) has indicated when epistasis is of major importance in the inheritance of a trait, it is impossible to obtain unbiased estimates of pooled additive or dominance effect. However these effects of genes could be important in heterosis. The existence of additive effects and moderately high narrow sense heritability ( $h^2_n > 0.5$ ) in controlling K<sup>+</sup>, K<sup>+</sup>/Na<sup>+</sup> and NT in this study indicated that the

recurrent selection followed by a pedigree breeding system may be useful for improving salinity tolerance in wheat.

## Material and methods

### Plant materials and experimental procedure

This experiment was conducted in a greenhouse at Vali-Asr University in Rafsanjan, Iran. Two parental lines including 'TABASI' (P1) a salt tolerant and 'GHODS' (P2) a salt sensitive bread wheat cultivar (Poustini and Siosemardeh, 2004; Dehdari et al., 2005) were crossed in 2010. The F1 generations and parents were used to produce F2 and backcrosses. These six generations; P<sub>1</sub>, P<sub>2</sub>, F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub> (P<sub>1</sub> × F<sub>1</sub>) and BC<sub>2</sub> (P<sub>2</sub> × F<sub>1</sub>) were evaluated in an unbalanced and completely randomized design in greenhouse conditions. Five seeds were sown in each 20-cm-diameter pot with approximate 2 kg soil. The numbers of plants were studied in each of P1, P2, F1, F2, BC1 and BC2 generations were 12, 25, 7, 125, 33 and 32 respectively. In order for plant vernalization, the pots were taken outside the greenhouse and exposed to cold weather for 7 weeks. The pots were returned inside the greenhouse after vernalization and salinity treatment was applied. The amount of NaCl needed to reach to 14dSm<sup>-1</sup> was computed as suggested by Richard (1954) and the salt was added to soils three times via irrigation water. In order to maintain soil salinity in a constant level of EC =14 during the growth period, pots were irrigated with distilled water without leaching.

The data on total biological dry weight (DW), days to heading date (HD), plant height (PH), total number of tillers per plant (NT) and ratio of fertile tillers per total tillers in each plant (RFT), were recorded for all single plants in each generation. Dried tissues of the four upper-most leaves of each plant were ashed at 500 °C, dissolved in 2N hydrochloric acid (HCl) and made to volume with hot distilled water. Na<sup>+</sup> and K<sup>+</sup> concentrations were determined

**Table 5.** Genetic effects for eight traits of wheat evaluated in six generations.

Trait	m	[d]	[h]	[i]	[j]	[l]	$\chi^2$
DW	3.66±0.65**	0.908±0.20**	-5.55±1.78**	-1.80±0.62**	-1.88±0.64**	3.28±1.20**	0.00 <sup>ns</sup>
HD	26.52±0.76**	4.37±0.69**	-16.27±3.41**	-	-	11.75±3.98**	4.62 <sup>ns</sup>
PH	64.20±5.98**	7.78±1.32**	-56.30±15.30**	-31.09±5.83**	-20.67±5.26**	38.22±11.99*	0.00 <sup>ns</sup>
Na <sup>+</sup>	-5.47±3.04**	-7.43±0.68**	34.9±8.17**	18.22±2.99**	-	-23.71±5.44**	1.15 <sup>ns</sup>
K <sup>+</sup>	40.62±1.26**	8.10±2.20**	-	-	-	-	1.21 <sup>ns</sup>
K <sup>+</sup> /Na <sup>+</sup>	24.31±4.27**	3.84±0.64**	-37.75±11.27**	-17.82±4.25**	-	21.45±7.93**	0.67 <sup>ns</sup>
NT	5.53±0.43**	1.01±0.38**	3.93±1.80**	-	-	-6.09±1.99**	1.45 <sup>ns</sup>
RFT	0.26±0.02**	0.07±0.03*	-	-	-	-	3.16 <sup>ns</sup>

DW= dry weight, HD= heading date, PH= plant height, NT= total number of tillers per plant and RFT=relative fertile tillers per plants.

**Table 6.** Heritability and components of F<sub>2</sub> variance for the eight traits in wheat.

Traits	D	H	Ew	F	$\sqrt{H/D}$	$h^2_b$	$h^2_n$
DW	0.57	0.40	0.74	0.08	0.84	0.34	0.25
Na <sup>+</sup>	14.31	5.95	18.39	-12.48	0.64	0.32	0.26
K <sup>+</sup>	495.88	66.27	215.74	199.92	0.36	0.55	0.52
K <sup>+</sup> /Na <sup>+</sup>	77.15	21.51	19.57	27.96	0.53	0.69	0.61
PH	78.1155	10.88	62.26	21.10	0.37	0.40	0.38
NT	12.77	3.08	5.09	-2.39	0.49	0.58	0.52
RFT	0.07	0.07	0.08	-0.02	1.02	0.39	0.26
HD	19.03	91.83	18.22	11.23	2.19	0.64	0.19

DW= dry weight, HD= heading date, PH= plant height, NT= total number of tillers per plant and RFT=relative fertile tillers per plants. D = additive variance effects, H = dominance variance effects, Ew = environmental variance, F = joint contribution (association) on all the loci.

by flame photometry. K<sup>+</sup>/Na<sup>+</sup> ratio was computed as salinity tolerance criteria.

#### Statistical Analysis

Analysis of variance, correlation and generation mean was done using MINITAB software. Generation mean analysis was done using the Mather and Jinks model (1982) as follows:

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

where y, m, d, h, i, l and j represent mean of generation, mean of all generation, sum of additive effects, sum of dominance effect, sum of additive × additive (complementary), sum of additive × dominant (duplicate) and sum of dominant × dominant interactions, respectively.

The terms  $\alpha$ ,  $\beta$ ,  $\alpha^2$ ,  $2\alpha\beta$  and  $\beta^2$  represent coefficients of genetic parameters. A weighted least square analysis was performed on the generation means. Six parameters including m, d, h, i, j and l were estimated after testing adequacy three parameter models through joint scaling. Further models of increasing complexity were fitted if the chi-square value was significant. The best fit model was the one which had significant estimates of all parameters along with non-significant chi-square value. Broad-sense and narrow-sense heritability were estimated according to Warner (1952);

$$h_b^2 = [V_{F2} - (V_{P1} + V_{P2} + 2V_{F1})/4]/V_{F2}$$

$$h_n^2 = [2V_{F2} - (VB_1 + VB_2)]/V_{F2}$$

Components of variation for the six generations were calculated by the formula of Mather and Jinks (1982) as;

$$D = 4V_{F2} - 2(V_{B1} + V_{B2})$$

$$H = 4(V_{B1} + V_{B2} - V_{F2} - V_E)$$

$$Ew = (V_{P1} + V_{P2} + 2V_{F1})/4$$

$$F = V_{B1} - V_{B2}$$

Where,  $V_{F2}$ ,  $V_{F1}$ ,  $VB_1$ ,  $VB_2$ ,  $V_{P1}$  and  $V_{P2}$  are variance of F<sub>2</sub>, F<sub>1</sub>, BC<sub>1</sub>, BC<sub>2</sub>, P<sub>1</sub> and P<sub>2</sub>, D = additive variance effects, H = dominance variance, Ew = environmental variance, and F = joint contribution (association) on all loci.

#### Acknowledgement

The authors are grateful to Vali-E-Asr University for the financial support of this work from grant of 1389.

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