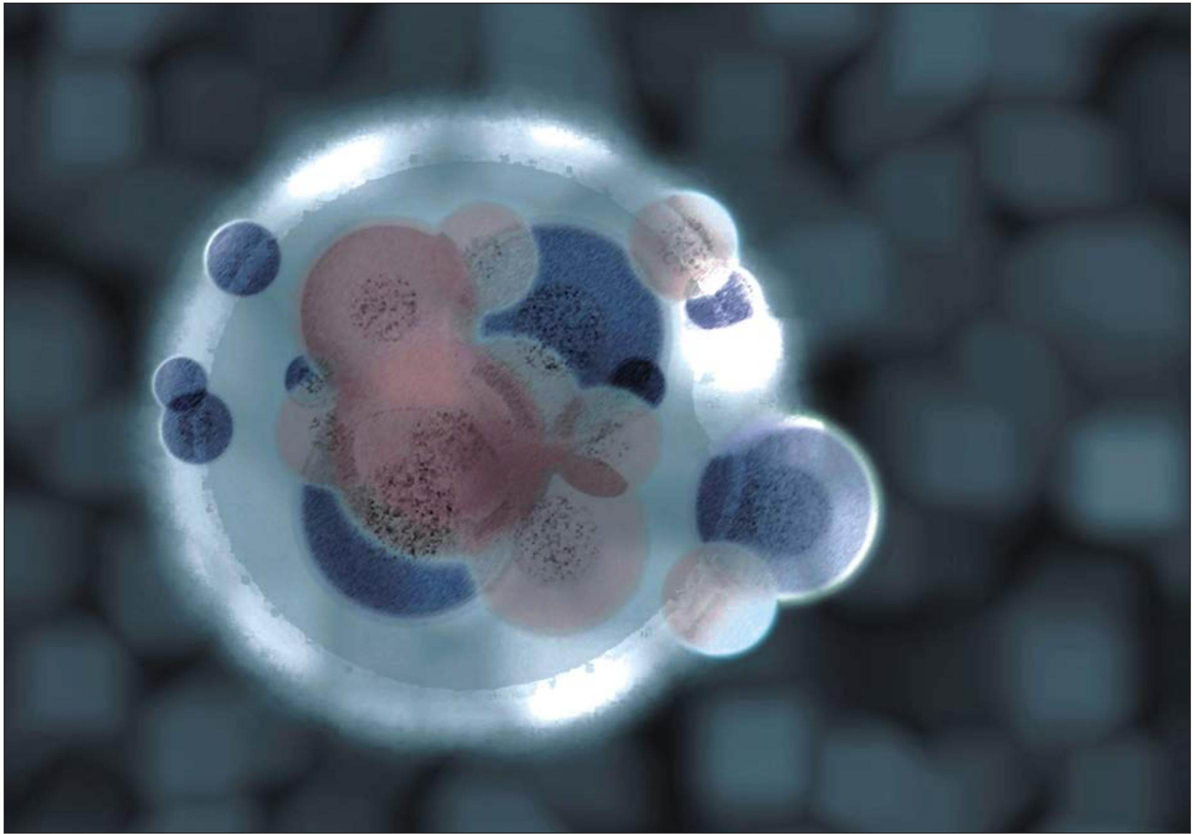

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Assessment of Salt Tolerance Inheritance in Barley via Generation Mean Analysis

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Abstract: In order to estimate additive and dominance components of genetic variance and detection of non-allelic interaction for the salt tolerance criteria in barley, 7 generations (P_1, P_2, F_1, F_2, F_3, BC_1, BC_2) derived from the cross Wiesel burger/Abor×Lokus/Bda and the check were used in a split plot design with two replications in hydroponic culture. Significant differences were found between both salinity levels and genotypes for all the characters investigated. Mean generation analysis indicated the involvement of additive, dominance and epistatic type of gene action in the inheritance of leaf weight (additive, dominance and epistasis), biomass (additive and epistasis), K^+, Na^+ and K^+/Na^+ (dominance and epistasis). Heritability estimate was low for K^+ and Na^+, moderate for shoot length, leaf weight, biomass and K^+/Na^+ and high for root length. Over dominance type of gene action was found for shoot length, biomass, K^+, Na^+ and K^+/Na^+, while partial dominance for root length and leaf weight.

Key words: Barley (*Hordeum vulgare*), salt tolerance, generation mean analysis, gene action

INTRODUCTION

Salinity is considered as a major limiting factor for crop plants especially in arid and semi-arid regions (Forster *et al*., 1990; Munns *et al*., 2002). Developments of salt tolerant varieties which can be adapted to a wide range of environmental stresses is the ultimate goal of plant breeders in barley improvement programs (Sabaghpour *et al*., 2003). Improving salt tolerance is therefore a major objective in plant breeding programs for arid and semi-arid regions (Farshadfar *et al*., 2007).

To formulate an efficient breeding program for developing salt-tolerant varieties, it is essential to understand the mode of inheritance, the magnitude of gene effects and their mode of action (Farshadfar *et al*., 2001; Sharma, 1998). Many workers developed genetic models for the estimation of different genetic effects (Gamil and Saheal, 1986; Kearsey and Pooni, 1996). However, the majority of these genetic models are basically additive-dominance models or simply additive models.

The epistatic or non-allelic interactions are largely ignored so as to have a simplified interpretation of genetic variation. But, it has now been established that such inter-allelic interactions are of frequent occurrence in the control of trait-expression for continuous variation. Thus, inferences drawn from additive models are likely to be based to an unknown extent. That is why, Jinks *et al*. (1969) suggested: it is no longer possible to Justify the use of a biometrical genetical analysis which does not have a built in test for epistasis. To be on safe side, it is therefore, rather essential to test the presence or absence of non-allelic interaction i.e., to carry out test of additivity or epistasis (Sharma, 1998; Kearsey and Pooni, 1996; Singh and Chaudhary, 1995; Farshadfar, 1998).

More than one procedure is available to test the deviation from additive models, i.e. to detect epistatic effects. These are: W_r-V_r tests of additivity (Hayman, 1954), the triple test cross test (Kearsey and Jinks, 1968), test of epistasis (Jinks *et al*., 1969), computation of interaction per se (Jinks and Jones, 1958) and scaling test (Mather, 1949; Hayman, 1954; Jinks and Jones, 1958).

We know that phenotypic mean is consummated by additive (a), dominance (d) and interaction effects (i) of genes in point.

The interaction effect is again of two kinds: (i) complementary (aa) and (ii) duplicate (ad and dd) at digenetic level.

The analysis of generation mean provides the opportunity first to detect the presence or absence of epistasis (by scaling test) and when present, it measures them appropriately. It also determines the components of heterosis in terms of gene-effects and some other statistics. Such as potence ratio, levels of dominance, number of effective factors, etc. (Kearsey and Pooni, 1996; Singh and Narayanan, 1993; Farshadfar, 1998; Farshadfar *et al*., 2001, 2007).

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The objectives of the present investigation were to genetic analysis of salt tolerance criteria in barley, to detection of non-allelic interaction for the characters investigated and to the estimation of additive and dominance components of genetic variance for the traits not influenced by epistasis.

MATERIALS AND METHODS

The experimental materials consisted of 7 generations (P_1, P_2, F_1, F_2, F_3, BC_1 and BC_2) derived from crosses between Wiesel burger/Abor cultivar (P_2 = salt tolerant) and Lokus/Bda (P_1 = salt sensitive) in the experimental farm of Dryland Agricultural Research Institute, Sararood, Kermanshah, Iran in 2003 and 2004. The parents (P_1 and P_2), the first (F_1) and second (F_2) generation hybrids and the first ($P_1 \times F_1$ = BC_1) and second ($P_2 \times F_1$ = BC_2) backcrosses together with check (Sararood = adaptable to the region) were grown in the green house of college of Agriculture, Razi University, Kermanshah, Iran. A split plot design based on completely randomized design (CRD) with two replications was carried out using hydroponic culture. Salinity was the main plot with three levels (0, 75 and 150 μmol of NaCl L^{-1} and genotypes were considered as sub-plot with 8 levels (parents, subsequent generations and control).

From each genotype 70 seeds were selected, surface sterilized with 5% calcium hypochlorite for 3 min, rinsed in distilled water and placed on sterile blotting paper in petriplates. They were germinated at 27°C and then transferred into growth chamber. At two leaves stage, 30 seedlings with roots of approximately 5 cm length from each genotype were selected and transferred into the tanks.

Hogland solution was the basic nutrient stock solution used in the Hydroponic culture system (Gorham, 1990). Saline solution was made for each treatment using NaCl and $CaCl_2$ salts with the pH of 5.45 to 5.55. The plantlets were hanged in the solution in such a way that roots were immersed in the aerated solution. The tanks were kept in growth chamber at 16-24°C, 300 μmol m^{-3} sec^{-1} light intensity, 18/6 h (light/darkness) and 45-50% relative humidity (Forster *et al.*, 1990).

Plants were grown in tanks for 2-3 weeks (2-3 leaf stage of seedling), the saline solution was gradually added to the container in such a way that final concentration was obtained after 4 days.

Five plants from fully expanded leaf (the 5th leaf) of each genotype were selected and the traits root length (RL), shoot length (SL), 5th leaf weight (LW) and biomass (Bio) were measured. The fully expanded leaf blade samples from each genotype were collected, rinsed in distilled water for 5 sec and dried at 70°C. The samples were ground with a mortar and pestle, dissolved in 10% acetic acid and 0.1% nitric acid and kept at room temperature for 24 h for complete digestion. Each sample was diluted 1:6 with acid solution and analyzed by flame photometer and the concentration of Na^+, K^+ and the ratio of K^+/Na^+ were determined.

Statistical analysis: Analysis of variance, mean comparison and correlation analysis was done using SPSS and MSTAT-C software.

Generation mean analysis was performed using the Mather and Jinks method (1982). In this method the mean of each character is indicated as follows:

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

where, Y = the mean of one generation, m = the mean of all generation, [d] = the sum of additive effects, [h] = the sum of dominance effects, [i] = the sum of additive×additive interaction (complementary), [l] = the sum of dominance×dominance interaction (duplicate), [j] = sum of additive×dominance and α, β, 2α β and β^2 are the coefficients of genetic parameters. The genetic parameters (m, [d], [h], [i], [j], [l]) were tested for significance using a t-test. The adequacy of the additive dominance model was determined by χ^2-test. Broadsense and narrowsense heritability were estimated by Warnner (1952) and Allard (1960) formulas:

$$H_b^2 = [V_{F2} - (V_{P1} + V_{P2} + V_{F1})/3] / V_{F2}$$

$$H_n^2 = [2V_{F2} - (V_{BC1} + V_{BC2})] / V_{F2}$$

The components of F_2 variance were obtained by the following formula (Farshadfar, 1998):

$$D = 4V_{F2} - 2(V_{BC1} + V_{BC2})$$

$$H = 2V_{F2} - 2D - 2E$$

$$E = 1/3(V_{P1} + V_{P2} + V_{F1})$$

$$F = V_{BC1} + V_{BC2}$$

where, V means variance.

RESULTS AND DISCUSSION

The results of analysis of variance (Table 1) revealed significant differences for salinity levels and generations

Table 1: Analysis of variance for various characters investigated

SOV	df	Mean square						
		RL	SL	LW	Bio	K^+	Na^+	K^+/Na^+
Saline factor (A)	2	1177.40**	17.63**	0.189**	1.86**	21.20**	0.236^{ns}	178.42**
Error	3	25.90	0.353	0.002	0.017	0.226	0.048	3.67
Genotype (B)	7	78.68**	36.07*	0.031**	0.417**	3.78**	0.462**	12.45*
A×B	14	22.40*	26.18^{ns}	0.123**	0.122**	1.22**	0.108**	2.86^{ns}
Error	21	8.11	14.50	0.003	0.018	0.213	0.025	4.002

*,**, ns: Significant at 0.05, 0.01 level of probability and non-significant, respectively

Table 2: Mean comparison between sub-main plots (genotypes) for various characters investigated

Characters*	Genotypes							
	P_1	P_2	F_1	F_2	BC_1	BC_2	F_3	Control
RL	21.36cd	30.88a	20.69d	24.80bc	20.30d	27.07b	22.80cd	22.74cd
SL	8.63ab	5.58b	5.81b	12.64a	10.12ab	6.51b	8.97ab	6.38b
LW	0.11b	0.25a	0.16a	0.18a	0.19a	0.20a	0.05b	0.24a
Bio	0.63d	0.93b	0.72cd	0.83bc	0.65d	0.61d	0.44e	1.30a
K^+ (ppm)	1.34c	2.47b	2.27b	1.97b	2.14b	2.51b	0.54d	3.31a
Na^+ (ppm)	0.47c	1.19a	0.43cd	0.68b	0.55bc	0.52bc	0.26d	0.52bc
K^+/Na^+ (ppm)	3.07bc	2.88c	4.70abc	3.24bc	5.59ab	6.13a	3.06bc	6.08a

*: Common letter(s) mean no significant difference

Table 3: Correlation coefficients between the characters studied

Characters	RL	SL	LW	Bio	K^+	Na^+	K^+/Na^+
RL	1.00						
SL-0.08	1.00						
LW	0.65**	-0.20	1.00				
Bio	0.63**	-0.14	0.82**	1.00			
K^+	0.68**	-0.22	0.95**	0.86**	1.00		
Na^+	0.006	-0.17	0.27	0.04	0.08	1.00	
K^+/Na^+	0.65**	-0.11	0.56**	0.59**	0.70**	-0.38**	1

**: Significant at 1% level of probability

Table 4: Estimates of genetic components of the mean for the characters studied

Characters	m	[d]	[h]	[i]	[j]	[l]	χ^2
RL	25.07±1.87**	3.950±0.84**	-34.12±7.76**	-28.10±7.67**	3.95±1.03**	27.95±8.45**	$4.04^{ns}0.80^{ns}$
SL	8.92±3.12**	-1.650±0.27**	97.10±4.9**	-	-	-	-
LW	0.17±0.04**	-0.400±0.024*	0.34±0.17*	0.31±0.16*	-	-0.51±0.22**	0.0037^{ns}
Bio	0.43±0.045**	0.045±0.016**	-	-	-	-0.56±0.206**	0.0044^{ns}
K^+	2.00±0.233**	$-0.315±0.42^{ns}$	3.17±1.35**	2.66±1.25**	-	-4.25±2.18**	0.082^{ns}
Na^+	1.50±0.195**	$0.110±0.113^{ns}$	-2.62±0.81**	-2.87±0.81**	-	2.93±0.91**	0.035^{ns}
K^+/Na^+	1.36±0.17**	$0.287±0.51^{ns}$	9.48±1.32**	9.13±1.23**	-	-10.80±2.36**	0.592^{ns}

*,**, ns: Significant at 5%, 1% level of probability and non-significant, respectively

for all the characters investigated indicating the presence of genetic variability and possibility of selection for salt tolerance (Baghizadeh *et al*., 2003). The genotype×salt tolerance interaction was also significant, except for SL and K^+/Na^+ displaying their similar response and different responses of other traits. Mean comparison (Table 2) between the genotypes showed that P_1 and P_2 have significant differences for most of the traits. The F_1 hybrid, BC_1 and BC_2 exhibited the highest heterosis over the best parent, although it was not significant for F_1 and BC_2 and significant for BC_1 for the criteria of salt tolerance (K^+/Na^+) (Schachtman and Munns, 1992; Deal *et al*., 1999). Most of the K^+ uptake belonged to the control (Sararood). Most of the Na^+ uptake was attributed to P_2 which is salt tolerant.

High significant correlation coefficient (Table 3) was found between RL, LW and Bio with K^+ and K^+/Na^+ indicating that these traits enhance salt tolerance in barley through correlated response. Omielan *et al.*(1991) showed that K^+/Na^+ ratio was highly correlated with biomass, RL and LW (Farshadfar *et al.,* 2007).

Generation mean analysis: The joint scaling test (Mather and Jinks, 1982; Farshadfar, 1998) was employed to estimate the mean (m), additive effect (d), dominance effect (h), additive×additive (i), additive×dominance (j) and dominance×dominance (l) values. The best dominance-additive model was selected using non-significant Chi-square test (χ^2) and the lower standard level (Table 4).

The dominance-additive model was adequate and fitted for all the characters investigated. All the genetic components of the mean were significant for root length indicating that besides additive and dominance gene effects, epistasis is also involved in the inheritance of RL.

Table 5: Genetic parameters and components of variation for various characters investigated

Characters	D	H	EW	$\sqrt{H/D}$	H_b^2
RL	22.40	-1.96	3.31	0.29	0.76
SL	4.48	-6.04	1.65	1.16	0.27
LW	0.007	-0.006	0.004	0.93	0.35
Bio	0.015	0.017	0.005	1.06	0.39
K^+	0.95	5.25	0.49	2.35	0.12
Na^+	0.202	1.152	0.34	2.38	0.12
K^+/Na^+	0.12	-2.12	0.58	4.20	0.41

The contribution of dominance effect (h) and epistasis (I) is greater than additive effect. As the sign of h and l is opposite, hence duplicate epistasis is involved (Farshadfar *et al*., 2001; Zahravi, 1999). Significancy of (j) revealed that selection through selfing is not effective for improvement of root length (Farshadfar *et al*., 2001; Sharifi, 2005).

For shoot length (d) and (h) were significant but inter-allelic interaction was not significant, therefore the genetic of SL is under the control of dominance and additive type of gene action, but the contribution of dominance effect is greater (Honarnejad and Tarang, 2000). The components [d], [h], [i] and [l] were significant for leaf weight exhibited the involvement of additive, dominance and epistatic effect in the control of leaf weight. The opposite sign of [h] and [l] displayed duplicate epistasis. As [j] was not significant and the contribution of [d] was greater than [h], hence selection under selfing can be effective for the breeding of leaf weight (Farshadfar *et al*., 2001; Sharifi, 2005).

For the biomass only [d] and [l] were significant, therefore additive type of gene action and epistasis are important in the inheritance of this trait and selection through selfing will be effective (Khalifa, 1982).

The components [h], [i] and [l] were significant for the characters K^+, Na^+ and K^+/Na^+ indicating the role of dominance and epistasis in the control of these salt tolerance criteria. As the sing of [h] and [l] is opposite, hence duplicate type of epistasis is involved. This complementary interaction increases the variation between the generations and in the segregating population (Farshadfar *et al*., 2007).

Heritability and genetic components of variation are presented in Table 5. The variation observed between the genotypes for the characters investigated exhibited that selection may be effective for the improvement of salt tolerance, however, the selection efficiency is related to the magnitude of heritability (Farshadfar *et al*., 2001).

Low broadsense heritability (less than 0.2) was shown for K^+ and Na^+, but SL, LW, Bio and K^+/Na^+ displayed moderate (0.2-0.5) and root length revealed high (greater than 0.5) heritability (Stanfield, 2002). The low H_b for K^+ and Na^+ suggested that environmental effects constitute a major portion of the total phenotypic variation for these characters (Khaksar, 2006).

D, H and EW (Table 5) are additive, dominance and environmental components, respectively. The ratio $\sqrt{H/D}$ is a suitable estimator of dominance (Kearsey and Pooni, 1996; Farshadfar, 1998; Khaksar, 2006). The ratio of $\sqrt{H/D}$ showed over dominance for SL, Bio K^+, Na^+ and K^+/Na^+, while, partial dominance for RL and LW.

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