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Nuclear and Cytoplasmic Inheritance of Salt Tolerance in Bread Wheat Plants Based on Ion Contents and Biological Yield

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ABSTRACT- Although inter-variety variability for salt tolerance has been reported in bread wheat plants, little information is available on the genetic control of ion contents and biomass yield under saline conditions. A diallel cross, including reciprocals of two salt tolerant, two moderately tolerant and two sensitive Iranian and exotic bread wheat varieties, was analyzed to investigate the inheritance of ion contents in young leaves at the seedling stage, and biomass yield (BY) and stress tolerance index (STI) at maturity. Specific reciprocal effects were also studied in F_2 populations derived from some F_1 reciprocal crosses. The materials were evaluated in a gravel culture under high salinity (EC=22.5 dSm^{-1}) and non-stress (control) conditions. Dominance gene effects were more important for Na^+, K^+ concentrations, K^+/Na^+ ratio and BY in control, but both additive and non-additive effects were observed for BY, K^+ concentration and STI in salt stress condition. Significant general and specific maternal effects were observed in F_1 generations for all traits, except for BY in the saline condition. Significant general and specific reciprocal effects indicated cytoplasmic and cytoplasmic × nuclear genes interaction in the response to salt tolerance, respectively. The most tolerant parent, 'Roshan' was the best combiner parent for related salt tolerant traits followed by 'Kharchia'. The results obtained from maternal effects in F_1 and F_2 generations indicated that 'Roshan' was more salt tolerant when used as a female parent. Some crosses in the tolerance×sensitive, tolerance×tolerance and moderately tolerant×sensitive groups proved to be the best combinations for obtaining desirable segregants for salt tolerance based on their *per se* performances, specific combining ability and heterotic effects.

Keywords: Bread wheat, Combining ability, Heterosis, Ion content, Salinity tolerance, Stress tolerance index

INTRODUCTION

Salt stress is a serious problem in arid and semi-arid regions and continues to be one of the most complex traits for plant physiologists, geneticists and breeders (9). Wheat physiological processes differ in their response to salt stress from one physiological stage to another (28). Complex physiological-genetic relationships of salt tolerance must be used to select superior genotype(s) with high agronomic performance. Since salt

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tolerance has a complex inheritance, different selection criteria have been reported based on shoot and/or root ion contents (7, 11, 29 and 34) , organic solutes (18, 23) and agronomic traits (1, 14 and 24) to select for salinity tolerance. Breeders must evaluate many lines during selection for salt tolerance because identification of a plant with all the related genes is difficult (23). In large breeding programs with thousands of segregating lines yield selection is difficult. It is therefore important to use physiological parameterswhich show a relationship with yield and its components as selection criteria for salt tolerance (27).

In durum wheat Munns and James (27) found that genotypes with the lowest Na^+ concentrations produced the greatest dry matter. Other works on bread and durum wheat, showed that salt tolerance is associated with low rates of transport of Na^+ to shoots with high selectivity for K^+ over Na^+ and therefore, K^+/Na^+ ratio in young leaves is suggested as an important factor (7, 19, 31). K^+/Na^+ ratio is controlled by a gene (or genes) located on chromosome 4D of bread wheat (10) and has been linked to molecular markers on the distal third of chromosome 4DL (6). The enhanced K^+/Na^+ ratio in *Lophopyrum elongatum* is affected by genes on most of the chromosomes (30). Genetic studies of the populations developed from crosses between wheat genotypes with low and high Na^+ uptake indicated two major gene loci controlling leaf-blade Na^+ accumulation (26).

Stress tolerance index (STI) has also been proposed as a more important indicator of stress tolerance which can be used to identify genotypes that produce high yields under both non-stress and stress environments (8 and 33). STI is estimated based on geometric mean productivity and the stress intensity value.

Genotypic variations for salt tolerance have been reported under saline conditions in bread and durum wheat (14, 24, 25, 31, 32 and 35). For example, differences between bread wheat genotypes with contrasting rates of Na^+ uptake were estimated to be up to 98% by Munns (25). However, less attention has been given to genetic sources of physiological traits such as Na^+ and K^+ concentrations and K^+/Na^+ ratio in leaves, probably because these traits are much more difficult to quantify. Although powerful new molecular tools manipulating genetic resources are available, the applications of the new approaches are not yet fully utilized to introduce new genes for tolerance into current cultivars of wheat (28)

Nuclear or cytoplasmic effects are important factors in the provision of the adaptation of plants to environmental conditions. The role of cytoplasm has been reported in the inheritance of aluminum tolerance (21) and cold resistance (3) in wheat plants. However, its role in the salinity tolerance of wheat has been less investigated. The use of crosses between wheat varieties that were broadly different in salt tolerance, as a source of novel germplasm for improving salinity tolerance, provides an opportunity to investigate genetic diversity and to estimate the genetic parameters for use in breeding programs. Hayman's analysis (16) for full diallel crosses provides appropriate information and tests of significance of genetic components.

In this study we have used Na^+ and K^+ contents, K^+/Na^+ ratio of young leaves at seedling stage, biomass dry yield (BY) and STI at maturity for six bread wheat cultivars (2 exotic and 4 Iranian) and their full set of diallel crosses, to characterize the inheritance of salt tolerance as measured by the above mentioned traits and to investigate general and specific reciprocal effects in F_1 hybrids and specific reciprocal effects in F_2 populations derived from some F_1 hybrids, and to estimate general combining ability

(GCA) effects of parents and specific combining ability (SCA) effects of their crosses.

MATERIALS AND METHODS

Two exotic bread wheat cultivars: Shorawaki (SH) and Kharchia (KH) and four Iranian cultivars: Roshan (RO), Ghods (GH), Alvand (AL) and Niknejad (NI) were intermitted in all combinations, including reciprocals, to form a complete diallel mating design. In order to evaluate specific reciprocal effects in F_2 generations, seeds of some direct and reciprocal F_1 hybrids were sown and harvested at maturity stage. Based on biomass yield (BY) and Fernandez (8) stress tolerance index (STI), RO and KH were rated as salt tolerant, NI and SH as moderately salt tolerant, and AL and GH as salt sensitive genotypes (5). Seeds of each generation were surface-sterilized with 0.5% sodium hypochlorite solution, rinsed with deionised water and germinated for three days. Four uniformly germinated seeds of the parents and their F_1 generations, as one replicate, were planted into a pot (30×30 cm) containing truly washed gravel. The germinated seeds of F_2 populations were planted in trays containing gravel. Seedlings were irrigated on the first day with half strength-Hoagland's solution (17) and raised to full strength after one week. In the salt-stress treatment, when leaf two of each genotype appeared (four to seven days after planting), 25 mM NaCl was added to the irrigation solution daily to obtain a final electrical conductivity of 20-22.5 dSm^{-1}. Furthermore $CaCl_2$ was added to bring up the molar ratio of $Na^+:Ca^{2+}$ to 20:1. The pH was adjusted to seven with HCl. For the non-stress treatment, parents and F_1 generations (but not F_2 populatíons) were planted in the same way as the salinity treatment, but irrigated with Hoagland's solution. Plants were grown in the greenhouse with average day/night temperatures of 28°C /22°C and relative humidity of 60-70 %. The photoperiod was 14 h and the light source was fluorescent-incandescent lamps with PAR of 414 µmol $m^{-2}S^{-1}$. The experimental design of each growing condition for parents and F_1 hybrids was a completely randomized design with three replications. F_2 populations were evaluated only under salinity condition without replication.

When leaf four appeared (15-20 days after salt treatment) the blades of leaves two and three were harvested, washed with distilled water, and dried at 70ºC for two days. The samples were weighed and incinerated at 500ºC for three to four hours and treated with HCl. Sodium and K^+ were analyzed by flame photometry. The measurement of Na^+ and K^+ was adjusted in comparison to a standard sample curve and finally, the ratio of K^+/Na^+ was calculated.

All maturity data were recorded on dry biomass yield (BY). The salt tolerance indices (STI) of F_1 and parents were calculated for BY based on the equation (1) given by Fernandez (8):

$$STI = \left\{ \frac{(Y_P)(Y_S)}{(\bar{Y_P})^2} \right\} \qquad (1)$$

where Y_S and Y_P are the biomass yields of a genotype under salt stress and non stress conditions, respectively and $\bar{Y_P}$ is the mean biomass yield over all genotypes evaluated under non stress conditions. Prior to analysis of variance, data for element contents were subjected to tests of normality using Q-Q plot (20). Genetic analysis was performed using Hayman's (16) analysis. General combining ability (GCA) effects of parents and specific combining ability (SCA) effects of crosses were calculated using Method 1, Model 1 of Griffing (1956). Specific and general reciprocal effects of parents and F_1 generations were determined based on Cockerham and Weir (4). Also specific reciprocal effects of F_2 populations were examined using Student's ***t*** test. Finally, heterosis, measured as the difference of F_1 mean from its high-parental mean, was calculated for each cross.

RESULTS AND DISCUSSION

Hayman's (16) analysis (Table 1) showed both additive (a) and dominance (b) effects to be highly significant for all studied traits in both environments. Based on the components of variance (Table 1) dominance gene effects were more important for Na^+, K^+, K^+/Na^+, and BY in the control, while both additive and dominance gene effects were important for K^+, BY and STI in the saline condition. These results were also confirmed by $2\sigma^2g/(2\sigma^2g + \sigma^2s)$ which are given in Table 1. Singh and Chatrath (36) reported that dominance gene effects were important in the inheritance of yield, but for plant height additive gene effects were relatively more important in some wheat crosses under saline condition. As shown in Table 1, all characters showed directional dominance (b_1), dominance effects common to the progeny of a particular parent (b_2), and dominance effects specific to a particular cross (b_3). The differences between reciprocal crosses (c and d) were clearly significant for all traits except for BY in the saline condition (Table 1).

Salt treatment affected general reciprocal effects (Table 2) of SH, Al, and RO for Na^+ concentration, SH, and AL for K^+ concentration, SH, GH, and RO for K^+/Na^+ ratio, and AL, for BY. SH showed significant maternal effects tending toward higher Na^+ and lower K^+, K^+/Na^+ ratio in the saline condition and STI, and BY in both conditions. However, RO had significant general reciprocal effects tending toward lower Na^+ and higher K^+/Na^+ ratio in the saline condition and high STI and BY in both conditions. KH showed no significant maternal effect for any of the studied traits in either condition, except for STI which was negative and significant. AL had positive and significant maternal effects for Na^+ and K^+ concentrations only in the control condition and a negative and significant effect for BY in the salinity treatment. No significant maternal effect was observed for GH in either condition, except for K^+/Na^+ ratio in the control treatment.

NI showed significant general maternal effects for low Na^+ and high K^+ concentrations and K^+/Na^+ ratio in both conditions. General maternal effects are related to extra-nuclear factors including various sorts of cytoplasmic effects and genes, pre- and postnatal maternal environment, and common external environment of sibs (4). Therefore, based on our results, RO and NI were more useful female parents for improving salt tolerance.

Specific reciprocal effects for F_1 crosses are given in Table 3. There was no clear concordance between specific reciprocal effects in the control with those in the saline condition. Highest reciprocal differences were observed in both control and saline conditions for BY. More than 50% of the crosses showed significant specific reciprocal effects in the control treatment, but no significant specific reciprocal effect was observed in the saline condition. In the saline condition, crosses SH×AL, AL×RO and GH×NI for Na^+, K^+ concentrations and K^+/Na^+ ratio; SH×GH, SH×RO, KH×AL and AL×NI for

Na^+ and K^+/Na^+ ratio; and RO×NI for Na^+ and K^+ had significant specific reciprocal effects. Only crosses AL×RO and KH×AL had positive and significant specific reciprocal effects for STI. Specific reciprocal effects are thought to represent interactions between nuclear and extra-nuclear factors (2). The highest interaction was observed for Na^+ concentration in both conditions and the lowest for BY in the saline condition. In the same line With these results Singh and Singh (37) reported that there was no significant reciprocal effect for biological yield in some crosses of spring wheat grown under saline conditions. In contrast, Salam et al (35) reported no major maternal factors influencing ion accumulation in some F_1 hybrids of wheat plants. In addition, reciprocal effects for salt tolerance have been reported among some rice crosses (12). These results showed that parental selection as male or female for some genotypes is an important factor in hybridization programs to improve salt tolerance.

Table 1. Diallel analysis for ion contents, biomass yield (BY) and stress tolerance index (STI) in control and saline conditions

		Mean Square								
		Na^+		K^+		K^+/Na^+		BY		
Source	df	Control	Salinity	Control	Salinity	Control	Salinity	Control	Salinity	STI
a	5	0.1839**	0.3076**	0.2425**	0.2718**	18.279**	1.1721**	1.8895**	2.0823**	2.0896**
b	15	0.1573**	0.2732**	0.2535**	0.0772**	25.418**	1.4205**	1.2754**	0.6503**	0.6296**
	1	0.7184**	0.8703**	0.2448**	0.0008**	15.641**	4.6106**	7.5095**	1.0728**	1.7317**
b3	9	0.1349**	0.2798**	0.3331**	0.1136**	20.271**	1.5150**	0.9960**	0.7122**	0.6232**
c	5	0.0281**	0.1796**	0.1785**	0.0414**	03.092**	1.3999**	0.6882**	0.0265	0.2964**
d	10	0.0470**	0.2118**	0.5261**	0.0246**	04.048**	1.6831**	0.4318**	0.0301	0.1704**
Error	72	0.0016	0.0058	0.0093	0.0190	0.0819	0.6083	0.0339	0.0831	0.0900
σ^2g		0.0001	0.0012	0.0028	0.0057	0.1020	0.0060	0.0181	0.0362	0.0328
σ^2s		0.0242	0.0517	0.0293	0.0131	3.9470	0.2580	0.2308	0.1009	0.1011
$2\sigma^2g/(2\sigma^2g + \sigma^2s)$		0.0082	0.0444	0.1605	0.4653	0.0491	0.0444	0.1356	0.4178	0.3935

σ^2g and σ^2s are variance components of general and specific combining abilities, respectively.
**** Significant at 0.01 probability level. a, additive effects, b, dominance effects, b1, directional dominance, b2, dominance effects of a particular parent, b3, dominance effects of a particular cross, c, general reciprocal effects and d, specific reciprocal effects**

Table 4 shows the means and significant levels of ***t*** tests in direct and reciprocal crosses of F_2 populations derived from some F_1 hybrids for Na^+, K^+ concentrations, K^+/Na^+ ratio and BY. As shown, F_2 reciprocal crosses of AL × RO differed significantly for Na^+, K^+ concentrations and the K^+/Na^+ ratio. RO × NI cross for K^+/Na^+ ratio; SH ×AL cross for Na^+ and K^+ concentrations; and finally KH × AL for the K^+/Na^+ ratio showed a significant specific reciprocal effect. As with the results of specific reciprocal effect in F_1 generations under salinity condition (Table 3), there were no significant differences between F_2 reciprocal crosses for BY.

Table 2. Estimated general reciprocal effects (C_i) for Na^+, K^+, K^+/Na^+, BY and STI of parents in control and saline conditions

Parents	Na^+(mM/g DW)		K^+(mM/g DW)		K^+/Na^+		BY(g)		STI
	Control	Salinity	Control	Salinity	Control	Salinity	Control	Salinity	
Shorawaki	0.014	0.545**	-0.296	-0.289**	1.142	-1.743**	-1.257**	-0.225**	-0.336*
Kharchia	-0.057	0.157	-0.121	-0.044	0.175	-0.430	-0.597	-0.117	-0.292 *
Alvand	0.150*	0.091	0.424*	-0.092	-0.888	-0.412	-0.055	-0.160*	-0.065
Ghods	0.031	0.216	-0.296	-0.064	-2.673*	-0.086	0.632	0.100	0.130
Roshan	0.071	-0.414*	-0.271	0.169	-1.389	1.365*	1.019*	0.295**	0.476**
Niknejad	-0.208**	-0.593**	0.559**	0.320**	3.633**	1.311*	0.258	0.107	0.087
SE (C_i)	0.035	0.122	0.112	0.062	0.638	0.341	0.240	0.057	0.087
SE ($C_i - C_j$)	0.050	0.173	0.159	0.087	0.902	0.482	0.339	0.081	0.123

*** and ** Significantly different from zero at *P*= 0.05 and *P*= 0.01 probability levels, respectively**

In comparison with F_1 reciprocal crosses (Table 3) most of the F_2 reciprocal crosses showed no significant specific reciprocal effect at least for one of the measured traits under saline conditions. Seeds of F_1 hybrids may prove soft and weakened with a smaller size and their vigor is dependent on the female parent (22). This will diminish their sprouting and germination energy in such a way that the F_1 plants slow down their growth on early developmental stages. Grieve and Francois (15) concluded that initial seed size has a significant role in the salt tolerance of wheat plants; bigger and heavier seeds in their experiment showed more tolerance than smaller seeds. The results of general and specific maternal effects in F_1 hybrids may be affected by these limitations.

The best selected parents and crosses based on their *per se* performances, combining abilities and high parental heterosis are given in Table 5. RO proved to be the best combiner for K^+/Na^+, BY and STI and had the second or third rank order for K^+ and Na^+ concentrations based on its GCA effects. KH was a good combining parent for all traits except K^+. AL showed positive and significant GCA effects for K^+ concentration, BY and STI. SH was a good combining parent only for Na^+ concentration.

GH had no positive and significant GCA effect for any traits. So in comparison with per se performance, RO was the most salt tolerant parent to be used for the breeding program followed by KH. AL×RO had the highest SCA effects for all the traits except for K^+ concentration. Also this cross showed high per se performances for all the traits, and its high-parent heterosis for Na^+, K^+ concentrations, K^+/Na^+, BY and STI were -31.05%, 9.42%, 9.22%, 18.32% and 9.55%, respectively. Therefore, this cross was the best combination for all traits and could be used to obtain desirable segregates for salt tolerance. Furthermore, significant and negative SCA effects were present in crosses of SH ♂×NI♀, SH ♂×RO♀ and SH♂×GH♀ for Na^+ concentration with high-parent heterosis of -8.62%, -38.7% and -75.8%, respectively. Nonetheless, the latter two crosses also had low and significant Na^+ concentration and positive and significant performances and high parent heterosis (38.34% and 6.6%, respectively) for K^+/Na^+ ratio. These crosses had a low rank order for BY and STI, indicating that they were salt tolerant at the seedling stage. For BY, crosses KH♂×Al♀ and Al♂×KH♀ had high SCA effects (Table 5) and positive heterosis; RO♂×KH♀, KH♂×AL♀ and GH♂×NI♀ had high SCA effects but negative heterosis. SH♂×GH♀ had high SCA and positive heterosis (57.34%) for STI but

GH♂×NI♀ showed negative heterosis for this trait and its rank order was low based on its performance.

Table 3. Estimated specific reciprocal effects (d_{ij}) for Na^+, K^+, K^+/Na^+, BY of crosses in control and the saline conditions and ST

	Na^+(mM/g DW)		K^+(mM/g DW)		K^+/Na^+		BY(g)		
Crosses	Control	Salinity	Control	Salinity	Control	Salinity	Control	Salinity	STI
SH×KH	0.001	0.035	-0.020	0.047	-0.075	-0.034	0.370**	-0.025	0.055
SH×AL	-0.025	-0.324**	0.038	0.114*	0.592	0.442**	0.353**	-0.035	0.053
SH×GH	0.039*	-0.166**	-0.137	0.016	-1.651**	0.700**	0.123	0.115	0.078
SH×RO	-0.006	-0.096**	0.019	0.024	0.115	0.500**	0.045	0.125	0.071
SH×NI	-0.022	0.008	0.396*	0.089*	-0.123	0.139	0.365**	0.045	0.079
KH×AL	0.025	-0.170**	0.060	-0.035	-0.149	0.371**	0.428**	-0.040	0.188**
KH×GH	0.112**	0.107**	0.060	0.059	-0.849*	-0.195	-0.047	0.102	0.013
KH×RO	-0.130**	-0.026	0.110	0.080	1.120**	0.204	0.235	-0.023	0.076
KH×NI	0.050*	-0.032	-0.130	-0.014	-0.372	0.017	0.350*	0.053	0.069
AL×GH	-0.083**	-0.119**	-0.155	0.032	0.313	0.184	0.442**	0.005	0.073
AL×RO	-0.007	-0.071*	-0.027	0.118*	-0.167	0.596**	0.287*	0.043	0.197**
AL×NI	-0.060**	-0.396**	-0.145	0.021	1.185**	0.446**	0.108	0.037	0.035
GH×RO	-0.027	-0.059	-0.491**	0.045	-0.588	0.038	0.242	0.062	0.073
GH×NI	0.064**	-0.335**	0.555**	0.126**	1.073**	0.736**	-0.355**	0.060	-0.038
RO×NI	-0.239**	0.162**	-0.118	0.098*	1.870**	-0.027	-0.210	-0.088	-0.059
SE (d_{ij})	0.018	0.032	0.152	0.040	0.334	0.118	0.118	0.064	0.054
SE ($d_{ij}-d_{kl}$)	0.026	0.045	0.216	0.056	0.472	0.167	0.166	0.091	0.076

***,** Significantly different from zero at P= 0.05 and P= 0.01 probability levels, respectively**
SH = Shorawaki; KH = Kharchia; AL = Alvand; GH = Ghods; RO = Roshan; NI = Niknejad

Our results revealed the importance of exploiting both additive and non-additive effects with dominance superiority for improvement of wheat plants for saline conditions. Since both additive and non-additive components of genetic variance were involved in governing the inheritance of these salinity tolerance traits, the most suitable breeding procedure would be one which emphasizes the additive genetic variance and at the same time maintains heterozygosity. Therefore, it is desirable to conduct bi-parental mating, inter-mate desirable segregates, and to practice selection to accumulate favorable additive genes and simultaneously exploit the dominance variance. Also the use of tolerant female parent and susceptible male parent is an important factor in improving salt tolerance of wheat plants.

Table 4. Means of direct and reciprocal F_2 generations and probability of significant levels (*P*) of t tests for Na^+, K^+, K^+/Na^+ ratios and BY

	Na^+(mM/g DW)			K^+(mM/g DW)			K^+/Na^+			BY(g)		
	Direct	Recip-rocal	*P*	Direct	Recip-rocal	*P*	Direct	Recip-rocal	*P*	Direct	Recip-rocal	*P*
SH×KH	0.215	0.265	0.120	0.566	0.662	0.254	2.590	2.500	0.412	3.250	2.980	0.140
SH×AL	0.324	0.552	0.031	0.756	0.578	0.042	2.330	1.040	0.055	2.950	2.550	0.345
SH×GH	0.298	0.301	0.180	0.621	0.563	0.421	2.080	1.870	0.154	2.260	1.980	0235
SH×NI	0.238	0.205	0.120	0.320	0.304	0.110	1.818	1.418	0.236	1.739	1.645	0.125
KH×AL	0.354	0.256	0.072	0.554	0.742	0.035	1.560	2.900	0.041	1.980	2.250	0.405
KH×NI	0.231	0.251	0.320	0.398	0.404	0.095	3.457	3.333	0.320	2.930	2.789	0.410
AL×GH	0.452	0.363	0.072	0.662	0.604	0.364	1.460	1.660	0.124	1.950	2.220	0.120
AL×RO	0.102	0.204	0.003	0.820	0.735	0.041	8.040	3.650	0.000	4.220	3.910	0.085
AL×NI	0.322	0.378	0.256	0.654	0.666	0.523	2.030	1.760	0.074	2.420	1.980	0.068
GH×RO	0.221	0.335	0.058	0.578	0.498	0.095	2.620	1.490	0.231	3.330	0.278	0.201
RO×NI	0.354	0.225	0.120	0.742	0.701	0.125	2.100	3.120	0.024	2.980	3.330	0.150

SH=Shorawaki, KH = Kharchia; AL, = Alvand; GH = Ghods; RO = Roshan; NI = Niknejad

Table 5. The best selected parents and crosses for different traits under high salt stress condition

Character	Best parents based on				Best crosses based on			
	Gca		Performance		Sca		Performance	
Na^+	SH	-0.115	RO	0.365	AL × RO	-0.266	SH × GH	0.302
mM/g DW	KH	-0.058	NI	0.413	SH × NI	-0.228	SH × RO	0.354
	RO	-0.035	KH	0.450	SH × GH	-0.077	AL × RO	0.409
					SH × RO	-0.073		
Range		*-0.115-0.114*		*0.365-0.536*		*-0.266-0.367*		*0.302-1.492*
K^+	AL	0.129	AL	1.057	KH × AL	0.1959	KH × AL	1.216
mM/g DW	RO	0.061	KH	0.988	AL × NI	0.153	AL × RO	1.167
			RO	0.943	SH × RO	0.082	AL × NI	1.150
					RO × NI	0.077		
K^+/Na^+	RO	0.224	RO	2.590	AL × RO	0.537	AL × RO	2.853
	SH	0.131	KH	2.200	SH × RO	0.378	SH × RO	2.773
	KH	0.069	NI	1.988	SH × GH	0.366	SH × GH	2.569
					SH × NI	0.240		
Range		*-0.240-0.224*		*1.552-2.590*		*-0.684-0.537*		*0.457-2.853*
BY	RO	0.314	RO	1.56	AL × RO	0.533	AL × RO	1.910
Na^+	SH	-0.115	RO	0.365	AL × RO	-0.266	SH × GH	0.302
	AL	0.128	KH	1.11	KH × AL	0.310	RO × KH	1.520
	KH	0.090	SH	1.00	KH × RO	0.204	AL × KH	1.430
					GH × NI	0.166		
Range		*-0.243-0.314*		*0.83-1.56*		*-0.373-0.533*		*0.33-1.91*
STI	RO	0.371	RO	1.61	AL × RO	0.613	AL × RO	1.780
	AL	0.090	KH	0.94	SH × GH	0.133	KH × RO	1.130
	KH	0.046	NI	0.72	GH × NI	0.111	KH × AL	0.740
Range		*-0.201-0.371*		*0.46-1.61*		*-0.409-0.613*		*0.13-1.78*

SH = Shorawaki; KH = Kharchia; AL = Alvand; GH = Ghods; RO = Roshan; NI = Niknejad

REFERENCES

1. Bastianpillai, V. A., C. Stark, and J. Unger. 1982. Growth, organogenesis, and yield formation in wheat under NaCl stress in greenhouse trails. Beitr. Trop. Landwirtsch. Veterinaermed 20:359-363.
2. Borges, O. L. 1987. Diallel analysis of maize resistance to sorghum downy mildew. Crop Sci. 27:178-180.
3. Calahan, C. and C. N. Low. 1979. The genetic control of cold resistant and vernalization requirement in wheat. Heredity. 42:125-132.
4. Cockerham, C. C. and B. S. Weir. 1977. Quadratic analyses of reciprocal crosses. Biometrics. 33:187-203.
5. Dehdari, A., A. Rezai, and S. A. M. Maibody. 2005. Salt tolerance of seedling and adult bread wheat plants based on ion contents and agronomic traits. Commun. Soil Sci. Plant Anal. 36:1-15.
6. Dubcovasky, J., G. Santamaria., E. Epstein., M. C. Luo and J. Dvorak. 1996. Mapping of the K^+/Na^+ discrimination locus KNa1 in wheat. Theor. Appl. Genet. 92:448-454.
7. Dvorak, J. and J. Gorham. 1992. Methodology of gene transfer by homoeologous recombination into *Triticum turgidum*: Transfer of K^+/Na^+ discrimination from *Triticum aestivum*. Genome 35:639-646.
8. Fernandez, G. C. J. 1993. Effective selection criteria for assessing plant stress tolerance. ***In:*** Adaptation of Food Crops to Temperature and Water Stress, C. G. Kuo ***(ed.)***, AVRDC, Shanhua, Taiwan. pp. 257 -270.
9. Flowers, T. J. and A. R. Yeo. 1995. Breeding for salinity resistance in crop plants. Where next? Aust. J. Plant Physiol. 22:875-884.
10. Gorham, J., C. Hardy, R. G. Joense, L. R. Joppaz, and C. N. Law. 1987. Chromosomal location of a K/Na discrimination character in the D genome of wheat. Theor. Appl. Genet. 74:584-588.
11. Gorham, J., A. Bristol, E. M. Young, and R.G. Wyn Jones. 1991. The presence of the enhance K/Na discrimination trait in diploid triticum species. Theor. Appl. Genet. 82:729-736.
12. Gregoria, G. B. and D. Senadhira. 1993. Genetic analysis of salinity tolerance in rice (*oryza sativa* L.). Theor. Appl. Genet. 86:333-338.
13. Griffing, B. 1956. Concept of general and specific combing ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9:463-493.
14. Grieve, C. M., S. M. Lesch, L. E. Francois and E. V. Mass. 1992. Analysis of main-spike yield components in salt-stressed wheat. Crop Sci. 32:697-703.
15. Grieve, C. M. and L. E. Francois. 1992. The importance of initial seed size in wheat plant response to salinity. Plant and Soil. 147:197-205.

16. Hayman, B. I. 1954. The theory and analysis of diallel cross. Genetics. 39:789-809.
17. Hoagland, D. R. and D. I. Arnon. 1950. The water-culture method for growing plants without soil. California Agric. Exp. Stn. Circu. 347.
18. Hu, R. C., H. Schnyder and U. Schmidhalter. 2000. Carbohydrate deposition and partitioning in elongating leaves of wheat under saline soil condition. Aust. J. Plant Physiol. 27:363-370.
19. Husain, S., S. Von Caemmere and R. Munns. 2004. Control of salt transport from roots to shoots of wheat in saline soil. Func. Plant Bot. 31:1115-1126.
20. Johnson, R. A. and D. W. Wichern. 1996. Applied Multivariate Statistical Analysis. Sperling Book House, New Delhi.
21. Klimashevski, E. L. 1986. The genetic control of utilising nutrition elements. Vestnik selsko-hozaystvennoy nauki, Bull. Agric. Sci. 7:77-87.
22. Koval, V. S. and B. V. Rigin. 1990. Role of nucleus and cytoplasm in the inheritance of salt tolerance in barley. At: http://www.geocities.com/ CapeCanaveral/Lab/5799/ engl/cytoeng.htm.
23. Mahar, A. R., P. A. Hollington, D. S. Virk and J. R. Witcombe. 2003. Selection for early heading and salt tolerance in bread wheat. Cereal Res. Cummu. 31: 81-88.
24. Mass, E. V. and C. M. Grieve. 1990. Spike and leaf development in salt-stressed wheat. Crop Sci. 30:1309-1313.
25. Munns, R. 2005. Genes and salt tolerance: bringing them together. New Phytol. 167:645-663.
26. Munns, R., G. J. Rebetzke, S. Husain, R. A. James and R. A. Hare. 2003. Genetic control of sodium exclusion in durum wheat. Aust. J. Agric. Res. 54:627-635.
27. Munns, R., and R. A. James. 2003. Screening methods for salt tolerance: a case study with tetraploid wheat. Plant and Soil. 253:201-218.
28. Munns, R., R. A. James and A. Lauchli. 2006. Approaches to increasing the salt tolerance of wheat and other cereals. J. Exp. Bot. 57:1025-1043.
29. Munns, R., R. A. Hare, R. A. James, and G. J. Rebetzke. 2000. Genetic variation for improving salt tolerance of durum wheat. Aust. J. Agric. Res. 51:69-74.
30. Omielan, J. A., E. Epstein, and J. Dvorak. 1991. Salt tolerance and ionic relations of wheat as affected by individual chromosomes of salt tolerant *(Lophopyrum elongatum)*. Genome. 34:961-974.
31. Poustini, K. and A. Siosemardeh. 2004. Ion distribution in wheat cultivars in response to salinity stress. Field Crops Res. 85:125-133.
32. Rashid, A., R. H. Qureshi, P. A. Hollington, and R. G. Wyn Jones. 1999. Comparative responses of wheat (*Triticum aestivum L.*) cultivars to salinity at the seedling stage. J. Agron. Crop. Sci. 182:199-207.
33. Rosielle, A. A. and J. Hamblin. 1981. Theoretical aspects of selection for yield in stress and non stress environments. Crop Sci. 21:943-946.

34. Saha, S. H., J. Gorham, B. P. Foster, and R. G. Wyn Jones. 1987. Salt tolerance in triticeae: The contribution of the D genome to cation selectivity in hexaploid wheat. J. Exp. Bot. 38:254-269.

35. Salam, A., P. A. Hallington, J. Gorham, R. G. Wyn and C. Gliddon. 1999. Physiological genetics of salt tolerance in wheat (*Triticum eastivum* L.): Performance of wheat varieties, inbred lines, and reciprocal F_1 hybrids under salin conditions. J. Agron. Crop Sci. 183:145-150.

36. Singh, K. N. and R. Chatrath. 1997. Combining ability studies in bread wheat (*Triticum aestivum* L.) under salt stress environments. Ind. J. Genet. 57:127-132.

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

وراثت هسته ای و سیتو پلاسمی تحمل به شوری در گندم نان بر اساس محتوای یونی و عملکرد بیولوژیک

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چکیده– با وجود این که تنوع بین واریته ای برای تحمل به شوری در گندم نان گزارش شده است اما، اطلاعات کمی در خصوص کنترل ژنتیکی محتوای یونی و عملکرد بیولوژیک در شرایط شوری وجود دارد. به منظور بررسی نحوه توارث محتوای یونی در مرحله گیاهچه ای و عملکرد بیولوژیکی و شاخص تحمل به تنش در مرحله رسیدگی دو رقم مقاوم، دو رقم نیمه مقاوم و دو رقم حسساس گندم های ایرانی و خارجی به صورت یک طرح تلاقی های دای آلل کامل با هم تلاقی داده شدند. برخی نتاج نسل دوم نیز برای مطالعه آثار معکوس خصوصی تولید شدند. والدین و نتاج آنها تحت دو شرایط شور (هدایت الکتریکی، ۲۲/۵ دسی زیمنس بر متر) و غیر شور (شاهد) در محیط سنگریزه ارزیابی شدند. نتایج نشان داد که برای صفات Na^+ ، K^+ و نسبت K^+/Na^+ و عملکرد بیولوژیک در شرایط غیر شور اثر غالبیت ژن، و برای عملکرد بیولوژیک K^+ و شاخص تحمل به تنش در شرایط شور هر دو اثر غالبیت و افزایشی نقش دارند. آثار معکوس عمومی و خصوصی معنی داری برای تمامی صفات در نسل اول مشاهده شد به جز برای عملکرد بیولوژیک در شرایط شور. این آثار به ترتیب مبین نقش عوامل سیتوپلاسمی و اثر متقابل عوامل سیتوپلاسمی با ژن های هسته ای در واکنش به شوری ارقام بودند. گندم روشن که متحمل ترین رقم بود، بهترین ترکیب شونده برای صفات نیز بود و بعد از آن کارچیا این خصوصیات را داشت. نتایج آثار مادری در نسل های اول و دوم نشان داد که رقم روشن وقتی به عنوان والد ماده به کار رفت تحمل زیادتری نسبت به شوری نشان داد. برخی تلاقی ها در گروه های متحمل × حساس، متحمل × متحمل و نیمه متحمل × حساس بر اساس میانگین صفت ها، قابلیت ترکیب پذیری خصوصی و هتروزیس برای تهیه نسل های در حال تفکیک و انتخاب در آنها به منظور بهبود تحمل به شوری مناسب تشخیص داده شدند.

واژه های کلیدی: **تحمل به شوری، شاخص تحمل به تنش، گندم نان، قابلیت ترکیب پذیری، محتوای یونی، هتروزیس**

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