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Heritability and Genetic Parameters of Some Antioxidant Enzyme Activities in Barley (*Hordeum vulgare* L.) Cultivars under Salinity Stress

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ABSTRACT

In order to study the heritability and genetic parameters of antioxidant activity in barely (*Hordeum vulgare* L.) under salinity stress, a seven-parent half diallel (F_1 crosses + parents) was conducted in the non-stress and salt stress (8 and 12 dS m^{-1}) conditions in the greenhouse, during 2016-17, Ardabil, Iran. In this experiment, antioxidant enzymes ascorbate peroxidase (APX), catalase (CAT) and superoxide dismutase (SOD) were measured. The results showed that the salinity had increased the expression of all of the three enzymes and the activity of enzymes were differed under different salinity levels. The average degree of dominance was higher than unity for all cases, suggesting the control of traits by over-dominance. Under saline condition heritability in narrow sense (h^2n) was found low to medium (0.11-0.41) but their broad-sense heritability (h^2b) was estimated relatively high (0.74-0.90). The results suggested the lack of heterosis in control of these traits except for APX activity in 8 dS m^{-1} salinity. Results showed that in APX activity recessive alleles were favorable, in CAT activity, under non-stress condition, dominant alleles, and under 12 dS m^{-1} salinity, recessive alleles were desirable; although, such relations were not clearly revealed in SOD activity. Due to the importance of dominance, it was indicated that the evaluation of genotypes must be done at progressive breeding program. Based on general combining ability effects, it was concluded that under salinity, Rihane and Nosrat had favorable alleles for APX activity. In CAT activity, Nosrat had favorable alleles. In case of SOD, Afzal and Valfajr had favourable alleles. In spite of the importance of physiological traits as selection criteria in breeding of salinity tolerance, presence of large dominance effects should not be neglected and selection for these traits should be delayed until after some inbreeding.

Keywords: Heritability; Ascorbate peroxidase; Catalase; Superoxide dismutase, Salinity

1. Introduction

Soil salinity is considered as a substantial factor persuading crop production and agricultural sustainability in the arid and semi-arid regions, reducing soil value and its productivity (Schleiff 2008; Ashraf 2010) and is considered as a serious abiotic stress in agriculture (Mahajan & Tuteja 2005). It is reported that over 6.5% of the total worldwide land area and 19.5% of irrigated land area salt-affected (FAO 2018). The salinity limits the economic exploitation of land for crop production and reduces the growth and fertility of plants (Frary et al. 2010). Despite the low diversity in plants salinity tolerance, some levels of tolerance and genetic diversity have been presented in some crops such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) (Flower & Yeo 1995; Flower 2004). Barley is the most salt tolerant cereal crop with a tolerance value of 8 dS m^{-1} (Katerji et al. 2006). The salt tolerance of plant genotype expresses its ability to grow and produce appropriate yield in a saline environment (Munns et al. 2002). Similar to other agronomic traits, breeding to tolerate salt stress, requires economic justification, genetic diversity, fast and reliable methods for selection, as well as genetic control of traits (Genec et al. 2010). The effects of salinity stress on plant physiology are well documented. High salinity can cause oxidative stress, leading to lipid peroxidation, protein oxidation and production of reactive oxygen species (ROS) such as superoxide radicals, hydrogen peroxide, hydroxyl radicals and singlet oxygen (Tanou et al. 2009). Plants have extensive defense systems that destroys or neutralize these ROS. These defense systems includes enzymatic and non-enzymatic mechanisms (Loggini et al. 1999). The enzymes of this defense system include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), and glutathione reductase (GR). The non-enzymatic system contains ascorbic acid (ASA), glutathione, alfatucophorol (Vitamin E) and carotenoids (Blokhin et al. 2003). The superoxide dismutase enzyme converts free oxygen radical (O_2^-) into hydrogen peroxide (H_2O_2) and oxygen (O_2), which is the first reaction of ROS detoxification. In the next step, hydrogen peroxide can be detoxified by the catalase and ascorbate peroxidase (DaCosta & Huang 2007). APX has a major role in detoxification of hydrogen peroxide. Therefore, the damage caused by oxidative stress is minimized (Arora et al. 2002; Kocsy et al. 2005). There are many

reports about increasing the APX activity under the salinity stress (Roychoudhury et al. 2010). The role of the SOD enzyme is very important for eliminating O_2^- because the phospholipid membrane is impermeable to superoxide radicals (Alscher et al. 2002). Catalase is one of the enzymes with the maximum output in removing H_2O_2 (Garratt et al. 2002). Most results have shown that antioxidant enzymes activity in barely acts to reduce the oxidative stress damage caused by salinity (Kim et al. 2005) and antioxidant activity in the salt tolerant barely varieties was higher than the sensitive varieties (Xiaoli et al. 2009). The activities of antioxidant enzymes were increased in both roots and shoots under salinity in barley, But the increase was more significant and consistent in the roots. Among the antioxidant enzymes, activity of CAT was increased the most drastically (Kim et al. 2005). Determining the heritability and genetic variance components of traits, is one of the most important parts of each breeding program and helps to breeders in choosing suitable selection methods for identification of superior genotypes. Combining ability analysis also helps to identify superior parents with favorable alleles in construction of breeding populations through hybridization. This experiment was conducted to determine the heritability of some antioxidant enzymes activities in barley under salinity stress.

2. Material and Methods

In this research, 7 salt tolerant and sensitive barley cultivars were selected based on published data in research area, then were evaluated in a pot experiment under non-stress and 12 dS m^{-1} salinity (data not shown), and stress tolerance index (STI) of the cultivars was determined based on grain yield (Table1). In a half diallel, parents were crossed to make hybrids. The F_1 hybrids and their parental lines were grown under three salinity stress (non-stress, 8 and 12 dS m^{-1}) in completely randomized design with three replications at greenhouse of Islamic Azad University, Ardabil, Iran during 2016-17. Five seeds were sown in 25×30 cm plastic pots filled with sterilized sand, garden soil and compost in a 1:1:1 ratio. Salinity stress was exposed by irrigating the pots with the above mentioned saline water in the four-leaf stage. To control the salinity level, electric conductivity of the drained water from pots was measured. Applying salinity gradually completed within two weeks. After reaching to the desired EC, subsequent irrigations done with tap water and saucers were used to return extra water to the pot to prevent salt washing. Pots in non-stress condition were irrigated by the fresh water. After flowering and exposure of plants to salinity, samples were taken from flag leaves and were immediately transferred to the -80 °C freezer. Then, the samples were powdered in liquid nitrogen and enzymes was extracted by Sairam et al. (1998) method. Fresh leaf (0.5 g) were ground in a mortar with pestle in 5mL of 50 mM phosphate buffer (pH 7.8) at 4 °C. The homogenate was centrifuged at 13,000×g for 15 min. The activity of SOD was measured according to the method of Giannopolities & Ries (1977). The 3-mL reaction mixture contained 13 mM methionine, 75 µM nitro blue tetrazolium chloride, 2 µM riboflavin, 50 mM phosphate buffer (pH 7.8), and 0-50 µL enzyme extract. The reaction mixture was incubated for 10 min below two 15-watt fluorescent bulbs. Then the reaction solution was wrapped through the black cloth to measure absorption. Absorbance were measured at a wavelength of 560 nm with a Spectrophotometric. One unit of SOD activity were considered as the amount of enzyme required for 50% preventing of photochemical revival of Nitro Blue tetrazolium Chloride and was calculated according to the equation: Unit SOD=(V/v)-1 where V and v represent the rate of the absorption in absence and in presence of enzyme, respectively. Catalase was assayed by measuring the initial rate of disappearance of hydrogen peroxide by the method of Chance & Maehly (1955). For measurement of CAT activity assay solution (3 mL) contained 50 mM phosphate buffer (pH 7.0), 15 mM H_2O_2 and 100 µL enzyme extract. The reaction was initiated by adding the enzyme extract. Decrease in absorbance of the reaction solution at 240 nm was recorded. Absorbance converted to H_2O_2 concentration following this formula: (H_2O_2(*Mmol*)=0.024×Absorbtion+0.011). One unit of CAT activity was defined as the amount of enzyme required to oxidize 1 mM of H_2O_2 per minute. APX activity were assayed using modified method of Nakano & Asada (1981). The 3-mL reaction solution of APX contained 50 mM phosphate buffer (pH 7.0), 0.5 mM Acid ascorbic, 0.1 mM H_2O_2, and 100 µL enzyme extracts. APX activity was measured by its absorbance at 290 nm. One unit of APX activity was defined as the oxidation of 1 mM of ascorbate per minute. Absorbance converted to acid ascorbic concentration following this formula: (Ascorbat (*Mmol*) =1.255×Absorbtion+0.097). Its absorbance was measured at 560 nm with a spectrophotometer (SHIMADZU, Model UV-120-02, Japan). Enzyme activity expressed in per unit (mg) protein basis.

Table 1- Source / Pedigree of studied barley cultivars

Parent	*cultivar*	*STI**	*Tolerance*	*Pedigree,Origin*
1	Afzal	0.529	tolerant	Chahafzal
2	Nosrat	0.544	tolerant	Karoon/Kavir, Iran
3	Valfajr	0.373	Semi-tolerant	CI-108985, Egypt
4	Kavir	0.416	Semi-tolerant	Arivat, USA
5	Rihane	0.247	sensitive	Atlas 46 /Arivat //Athenais ICB76-2L-1AP-0AP, ICARDA
6	Sahra	0.242	sensitive	L.B. LRAN/ Una8271// Giorias "s" Com, CIMMYT
7	Yusef	0.272	sensitive	Ligne527/chn-01//Gustoe/4/Rhn-08/3/DeirAlla 106//DI71/strain 205

*, determined based on previous work (unpublished data)

2.2. Statistical analysis

Diallel was analyzed by Hayman (1954) graphical method and Griffing (1956) fixed model. The goodness of fit of the additive-dominant model was evaluated by linear regression of Wr on Vr (H_0: b = 1 vs. H_1: b ≠1) (Hayman 1954). The genetic parameters:

D, H_1, H_2 and F were estimated by method of Singh & Singh (1984). Average degree of dominance, broad-sense heritability and narrow-sense heritability were estimated using method proposed by Mather & Jinks (1971). The diallel analysis was done based on the method of Hayman (1954) and calculated by DIAL98 software (Ukai 1989). Genetic components were estimated by electronic spread sheets in the Excel 2010 program.

3. Results and Discussion

The result analysis of variance revealed significant differences among 28 genotypes (7 parents +21 F_1's) for all the studied traits, suggesting the presence of adequate genetic variability to proceed to diallel analysis (Table 2). Significant Salinity×Genotype interaction mean squares indicates the different expression of traits under different salinity levels (Table 2). Salinity had significantly increased the expression of all of the three enzymes activity (Table 2). The results of the goodness of fit of the additive-dominant model are presented in Table 3. The slope of linear regression of W_r on V_r was significantly greater than 0 and had not significant difference with 1 in all cases except for SOD activity under non-stress condition (Table 3), indicating the adequacy of additive-dominance model for traits (Mather & Jinks 1971). Rohman et al. (2006) reported that epistasis effects significantly play a role in controlling wheat morphological traits, and additive-dominance model aren't sufficient for traits fitting. The significance of "a" component in table 4 (except SOD in non-stress) was in accordance with the significance of additive effects (D component) in table 5 except for CAT activity. Singh et al. (2006) showed that the additive and non-additive effects in both F_1 and F_2 generations are important in barley. The dominance genetic effects (b source of variation) was significant for all traits, indicating the presence of dominance effects in the control of traits (Table 4). Non-corrected and corrected dominance variances (H_1 and H_2 components) were also significant confirming the effects of dominance in controlling of the traits (Table 5). The "b_1" component, was non-significant in all studied traits (except APX in 8 ds m^{-1}). The "b_1" item measures the mean deviations of the F_1's from the mid-parental values and becomes significant when the dominance effects at various loci are predominantly in dominance effect. That is, there is a directional dominance effect and measures the average heterosis (Singh & Singh 1984). The "b_2" component was significant in all of the traits, except for APX activity in 8 ds m^{-1} salinity. The significance of the "b_2" item indicated that the mean dominance deviations of the F_1's from their mid parental values differed significantly over the F_1 arrays; this implies the presence of asymmetry in the distribution of alleles among the parents (Hayman 1954). This also means that some parents had a significantly better performance than others (Ramalho et al. 1993). Similar results were reported by Singh & Singh (1992) and Sharma (1998). Since "b_2" is significant for most cases, the "a" item will not measure additive variance unambiguously, but it will be contaminated with non-additive variance also (Singh & Singh 1984). The "b_3" component which is equivalent to specific combining ability variance was significant in all of cases except for APX activity in 8 ds m^{-1} salinity. Significant "b_3" exhibited residual dominance effect (b_3) resulted from additive× additive, additive× dominance and dominance×dominance interaction effects (Chaudhry et al. 1977). The proportion of positive and negative genes was estimated by calculating ($H_2/4H_1$) in table 5. This ratio was found to be less than 0.25 in all of the traits, indicating unequal proportions of positive and negative alleles in loci with asymmetrical distribution of genes in the parents. This is also substantiated by "H_1" being greater than "H_2"in these traits. Similar results were reported in other studies (Bouzerzour & Djakoune 1998; Roy 2000). The estimate of the genetic component "F" was significant in APX activity which is an indication of asymmetry in the distribution of dominant and recessive alleles in the parents. Positive and significant values for this indicator indicate a higher prevalence of dominance alleles among parents (Table 5). The ratio of the total number of dominant and recessive alleles in the parents (KD/KR) was higher than one in all of traits, indicated that parents carry more dominant alleles. Positive values for F substantiated by (KD/KR) being greater than one (Table 5). This finding is in agreement with earlier reports (Ciulca et al. 2000; Bhatnagar et al. 2001; Dharam & Sanjay 2009). According to the results, the average degree of dominance was higher than unity for all traits, indicating the presence of over-dominance in controlling the traits under study (Table 5). The regression line intersected below the point of origin suggesting over dominance for controlling the trait (Figure 1). Similar conclusion was reported by Rebetzke et al. (2003) and Shahbazi et al. (2013) in the genetic control of physiological traits in wheat and barley (Chowdhry et al. 2002; Singh et al. 2006). The narrow-sense heritability of traits was low to moderate (0.11 to 0.41), however, their broad-sense heritability was high (Table 5). Tuberosa (2012) estimated the heritability of most the traits of crops under drought conditions low (0.3-0.4) or intermediate (0.4-0.7). The high broad-sense heritability can be attributed to the low environmental effects in the appearance of these traits. The low narrow-sense heritability of these traits indicated that non-additive effects were primarily responsible for the genetic variation in these hybrids and also the traits were highly influenced by the growing environment. Similar results reported in *brassica napus* (Khan & Khan 2005). For almost all the traits, the parental array points were scattered all along the regression line in the Wr/Vr graphs. The parents with most dominant genes are nearest to the origin and with most recessive genes, farthest from the origin and with equal frequencies of dominant and recessive genes, fall in the middle. Parents along the regression line show genetic interactions or epistasis, more distance more interaction. Parents above regression line, show duplicate epistasis and below regression line, show complementary epistasis (Figure 1). According to parents distance from the origin of the regression line W_r (parent offspring co-variance) on V_r (parental variance), it can be concluded that for APX in non-stress and 8 ds m^{-1}, cultivar Sahra has more dominant alleles, cultivars Kavir and Rihane have more recessive alleles, in 12 ds m^{-1}, Yoosef had more dominant alleles and Nosrat had more recessive alleles. In CAT activity under non-stress condition, Valfajr had more dominant and Kavir had recessive alleles respectively. In 8 and 12 ds m^{-1}, Rihane and Yoosef had more dominant alleles. Moreover, in SOD under 8 ds m^{-1}, Kavir had more dominant alleles and Sahra had more recessive alleles; in 12 ds m^{-1}, cultivar Sahra had more recessive alleles (Figure 1). The correlation coefficients between the parental means and order of dominance "rYr (Wr + Vr)" which indicates the relation between the favorability of alleles and dominance, were significantly positive in APX activity indicating that recessive alleles are favorable. For CAT activity, under

non-stress condition dominant alleles were favorable but under stress (12 ds m^{-1}) recessive alleles were favorable (table 5). Result of combining ability analysis showed that the general combining ability variance is significant (except APX in 8 ds m^{-1}, CAT in non-stress and SOD in 12 ds m^{-1}). The specific combining of traits was significant in all cases except SOD in 12 ds m^{-1} salinity, showing the higher importance of dominance variance than additive variance (Table 6). Joshi et al. (2004) reported that the heterotic effect in the wheat autogamous plant has a negligible effect in breeding the traits based on the specific combining ability. Based on GCA effects (Table 7) it was concluded that in APX activity: Afzal, under non-stress; Rihane, under 8 ds m^{-1} and Nosrat in 12 ds m^{-1} had favorable alleles. In CAT activity; Afzal, under non-stress; Nosrat, under 8 and 12 ds m^{-1} had favorable alleles. In case of SOD: Afzal, under 8 ds m^{-1} and Valfajr, under 12 ds m^{-1} have favorable alleles because of high GCA values. Parents with good general combining ability can be used in hybridization program for varietal improvement.

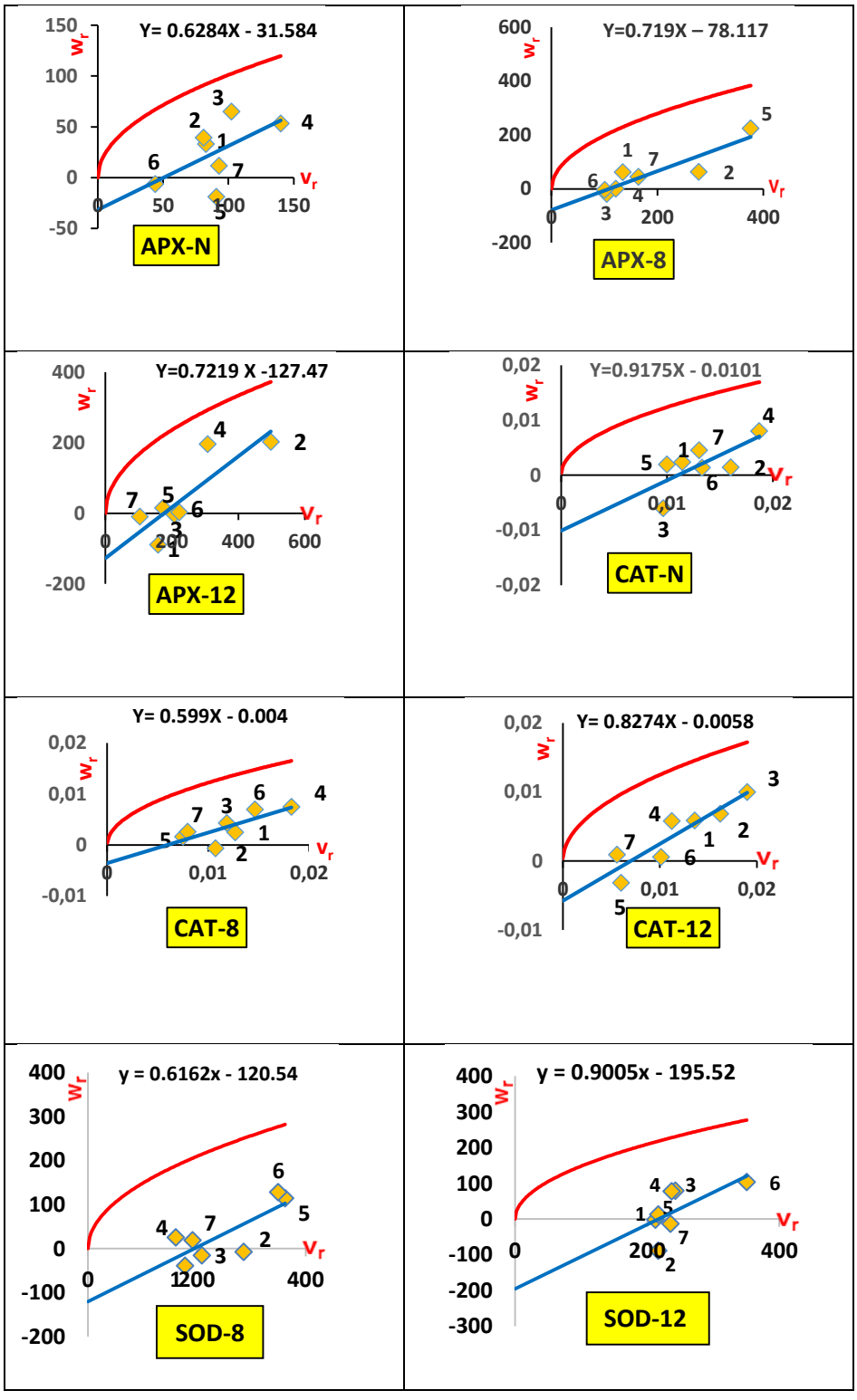

Figure 1- Regression line W_r/V_r

Table 2- Analysis of variance of studied traits under different salinity stress levels

Source of variation	*Degrees of freedom*	*Mean squares*		
		Ascorbate peroxidase	*Catalase*	*Superoxide dismutase*
Genotype	27	486.94**	0.036**	418.72**
Salinity	2	1006.11**	0.080**	696.32*
Salinity× Genotype	54	301.32**	0.019**	333.10**
Error	168	88.21	0.007	150.65
CV%		13.81	1.81	26.81

** and *, significant at P<0.01 and P<0.05

Table 3- Analysis of additive -dominant model by regression of w_r on v_r for traits

Null Hypothesis	*Ascorbate peroxidase*			*Catalase*			*Superoxide dismutase*		
	0	*8*	*12*	*0*	*8*	*12*	*0*	*8*	*12*
b = 0	0.63* ±0.24	0.72** ±0.14	0.722* ±0.21	0.92* ±0.33	0.6* ±0.22	0.83** ±0.16	0.18 *±0.05	0.62* ±0.21	0.90* ±0.37
b = 1	0.63^{NS} ±0.24	0.72^{NS} ±0.14	0.722^{NS} ±0.21	0.92^{NS} ±0.33	0.6^{NS} ±0.22	0.83^{NS} ±0.16	0.18** ±0.05	0.62^{NS} ±0.21	0.90^{NS} ±0.37

NS, Non-significant; ** and *, significant at P<0.01 and P<0.05; b- regression coefficient; 0, 8 and 12 ds m^{-1}- salinity stresses

Table 4- Gene interactions' ANOVA results

Source of variation		*Degrees of freedom*	*Mean Squares*							
			Ascorbate peroxidase			*Catalase*			*Superoxide dismutase*	
			0	*8*	*12*	*0*	*8*	*12*	*8*	*12*
rep		2	8.4^{NS}	55.7^{NS}	3.2^{NS}	0.008^{NS}	0.005^{NS}	0.004^{NS}	0.07^{NS}	0.98^{NS}
a		6	236.1**	468.3**	712.3**	0.016*	0.036**	0.031**	0.16**	0.86**
b		21	235.6**	275.5*	485**	0.025**	0.023**	0.026**	1.4**	0.72**
	b_1	1	25^{NS}	964.3**	137^{NS}	0.01^{NS}	0.008^{NS}	0.063^{NS}	0.24^{NS}	1.94^{NS}
	b_2	6	258.5**	277.1^{NS}	388.8**	0.033**	0.018**	0.022**	0.29**	0.33**
	b_3	14	240.8**	225.7^{NS}	551.1**	0.023**	0.025**	0.025**	1.9**	0.81**
Error		54	34.1	148	89.8	0.007	0.006	0.007	0.11	0.96

NS, Non-significant; ** and *, significant at P<0.01 and P<0.05; a: additive effect; b: non- additive effect; b_1: direct of dominance; b_2- gene frequency balance; b_3- particular dominance; 0, 8 and 12 ds m^{-1}- salinity stresses

Table 5- Estimates of genetic components and related statistics in half- diallel design

Parameters	*Ascorbate peroxidase*			*Catalase*			*Superoxide dismutase*	
	0	*8*	*12*	*0*	*8*	*12*	*8*	*12*
D	91**±4.7	342**±6	249**±7.5	0.01^{NS}±0.1	0.01^{NS}±0.04	0.01^{NS}±0.04	97**±6.4	352**±6.5
H_1	313**±11.3	691**±14.4	921**±18	0.046^{NS}±0.2	0.04^{NS}±0.1	0.04^{NS}±0.1	701**±15.4	1025**±15.5
H_2	224**±10	492**±12.7	758**±15.8	0.037^{NS}±0.1	0.03^{NS}±0.04	0.03^{NS}±0.1	540**±13.6	654**±13.7
F	87**±11.3	499**±14.4	334**±18	0.018^{NS}±0.2	0.01^{NS}±0.1	0.01^{NS}±0.1	105**±15.3	639**±15.5
$\overline{D}$	1.86	1.42	1.93	1.94	1.75	1.67	2.68	1.7
$H_2/4H_1$	0.18	0.18	0.21	0.2	0.21	0.18	0.192	0.159
KD/KR	1.7	3.1	2.1	2.4	1.9	1.8	1.51	3.27
h_n	0.41	0.11	0.15	0.12	0.27	0.37	0.27	0.16
h_b	0.9	0.74	0.88	0.78	0.85	0.85	0.74	0.77
$rY_r(w_r+v_r)$	0.89**	0.79*	0.66^{NS}	-0.73*	-0.59^{NS}	0.73*	0.40^{NS}	0.48^{NS}

NS- Non-significant; ** and * - Significant at P<0.01 and P<0.05; D- additive genotypic variance; H_1- in-corrected dominance variance; H_2- corrected dominance variance; F- average covariance between additive and dominance effects; $\overline{D}$ - average degree of dominance; $H_2/4H_1$- relative distribution of positive and negative alleles between parents; KD/KR- relative distribution of dominant and recessive alleles among parents; h_n- narrow-sense heritability; h_b- broad-sense heritability; $rY_r(w_r+v_r)$- correlation between Y_r and (w_r+v_r); 0, 8 and 12 ds m^{-1}- Salinity stresses

Table 6 - Result of analysis of variance

Source of variation	*Degrees of freedom*	*Ascorbate peroxidase*			*Catalase*			*Superoxide dismutase*	
		0	*8*	*12*	*0*	*8*	*12*	*8*	*12*
GCA	6	493**	269^{NS}	526**	0.015^{NS}	0.05**	0.05**	1.21**	1.58^{NS}
SCA	21	162**	333*	538**	0.023**	0.02**	0.02**	1.05**	0.52^{NS}
Error	54	34.1	148	89.8	0.009	0.01	0.01	0.11	0.96

NS - Non-significant; ** and * - Significant at P<0.01 and P<0.05; 0, 8 and 12 ds m^{-1}- Salinity stresses GCA- General Combining Ability; SCA- Specific Combining Ability

Table 7- General combining ability estimates of parents

Parents	*General combining ability*							
	Ascorbate peroxidase			*Catalase*			*Superoxide dismutase*	
	0	*8*	*12*	*0*	*8*	*12*	*8*	*12*
Afzal	4.58	-0.52	0.74	0.03	0.02	0.03	0.28	0.12
Nosrat	-0.22	0.86	8.08	0.02	0.08	0.06	0.18	-0.2
Valfajr	3.8	3.2	2.19	0.01	0.003	0.05	0.14	0.5
Kavir	3.58	0.04	0.22	-0.04	-0.02	-0.01	-0.04	-0.12
Rihane	-4.96	3.89	-5.42	0.01	-0.01	-0.06	-0.13	-0.15
Sahra	-6.02	-5.39	-2.61	-0.02	-0.03	-0.04	-0.33	-0.11
Yoosef	-0.77	-2.08	-3.19	-0.01	-0.05	-0.03	-0.11	-0.04

0, 8 and 12 ds m^{-1}- Salinity stresses

4. Conclusions

The results suggested that most of the traits adequately can be described by additive-dominance model. Results showed that additive effects and dominant effects were significant in most of traits. In general, all of traits had high broad-sense heritability, indicating the accuracy and precision of the data measured. The degree of dominance was greater than one for all traits, indicated that these traits under the influence of over dominance gene action evidence of the decline in narrow sense heritability. Importance of dominant gene effects was suggested by Dashti et al. (2010) in wheat under salinity stress. We found that dominance was more important, hence, more generations need to be generated and evaluated. In spite of the importance of physiological traits as selection criteria in breeding programs, presence of large dominance effects should not be neglected and selection for these traits should be delayed until after some inbreeding. However, the potential exists for these dominance effects to be exploited in development of F_1 hybrids in cross pollination crops.

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