Genetic control of drought stress using generation mean analysis in bread wheat (*Triticum aestivum* L.).

ABSTRACT

In order to study the inheritance and genetic analysis of drought tolerance indicators a six generations of P_1, P_2, F_1, F_2, Bc_1 and Bc_2 of two wheat crosses i.e., Sakha 94 x Tokwie (C_1) and Giza 168 x Tokwie (C_2) under normal irrigation (N) and drought stress (D) were studied using generation mean analysis at Faculty of Agriculture, Sohag University, Egypt. Genetic variation was found for No. of spikes/plant (NS), 100-seed weight (SW), grain yield (GY), biological yield (BY), relative water content (RWC) and chlorophyll content (CC) (N&D) in two crosses. High heterosis was observed for all studied characters (N&D) except CC in two crosses. Genetic analysis showed overdominance in the inheritance of all studied characters (N&D) in two crosses. High to moderate heritability values in broad sense were detected for all characters in both crosses. Narrow-sense heritability (C_1&C_2) ranged from 0.18 for CC (D) to 0.37 for RWC (D) in C_1. The genetic advance (C_1&C_2) was high (more than 40%) for GY (N&D), while NS, BY, RWC and CC (N&D) were moderate (14-40%), indicating the importance of direct selection for these characters. The genetic models fitted for all studied characters (N&D) in two crosses except RWC (D in C_1), indicated dominance and additive x additive gene effects. Both additive x additive [i] and dominance x dominance [1] effects were significant for all studied characters (N&D) in two crosses except RWC (D in C_1), supporting the presence of duplicate type of epistasis. Since several important characters are influenced by dominance and non-allelic gene interaction, it is advisable to delay selection to later generation with increased homozygosity.

Key words: Wheat (*Triticum aestivum* L.), drought stress, generation mean analysis, gene action.

Introduction

In Egypt, wheat production is far below what is needed to meet the local consumption of the growing population resulting in increasing wheat imports. To formulate an efficient breeding program for developing drought-tolerance varieties, it is essential to understand the mode of inheritance, the magnitude of gene effects and their mode of action (Farshadfar et at., 2001, 2008; Iqbal et at., 2007).

The plant breeder is interested in the estimation of gene effects in order to formulate the most advantageous breeding procedures for improvement of the attribute in question. Therefore, breeders need information about nature of gene action, heterosis, inbreeding depression, heritability and predicted genetic gain from selection for yield and yield components. Sprague (1963) listed three major factors that must be considered and which may limit progress in the analysis of quantitative genetic variation: the number of genes involved, the type of gene action, and the genotype- environment interaction.

The genetical studies based on the means and variances of basic generations, is a simple method for estimating the gene effects for a polygenic trait and has been reviewed in many crop species. The greatest merit of generation means analysis lies in its ability to estimate the epistatic effects (Mather and Jinks, 1982).

The possibility of epistasis accounting for a significant proportion of genetic variance of quantitative trait has been investigated extensively in previous studies in crop plants. Amount and type of epistasis can have a major consequence on both the reliability of predictions and the design of breeding program. Statistically, detection of epistasis using generation means analysis is more reliable and efficient than by the analysis of variance approach (Lamkey and Lee, 1993).

However, it has its own limitations and several assumptions. Triple test cross is a powerful method of genetic analysis, which provides unbiased estimates for epistasis. In addition, it also estimates the additive and dominance components of variation with high accuracy when epistasis is absent (Kearsey and Jinks, 1968).

The variance estimates attributed to environment, total genetic, additive and dominance deviation effects were obtained from the phenotypic variances for populations P1, P2, F1, F2, BC1 and BC2. These estimates allowed the determination of heritabilities in the

broad and narrow sense, mean degree of dominance and minimum number of genes that control each character, by using Burton's (1951) expression.

The objective of the present investigation was to investigate the genetic analysis of quantitative indicators of drought tolerance in wheat under drought condition using generation mean analysis.

Material and methods

The two Egyptian cultivars, Sakha 94 and Giza 168 were more adapted in Egypt and proved high yielding. However, the introduced line (Tokwie) is characterized as a drought tolerant. Therefore, the line introduced was crossed with the Egyptian cultivars in order to enlarge the variability for selection in the breeding program for these characters. The experiments reported herein were carried out during the three successive growing seasons of 2010/2011, 2011/2012 and 2012/2013. In 2010/2011, the parent genotypes of hexaploid wheat (*Triticum aestivum* L.) were sown to secure enough hybrid seed (Table 1). Two crosses namely Sakha 94 x Tokwie (Cross 1) and Giza 168 x Tokwie (Cross 2) were developed at Faculty of Agriculture, Sohag University, Egypt.

In 2011/2012 season, F_1 plants were selfed to produce F_2 seeds and backcrossed to the parents to produce BC_1 and BC_2 seeds. In 2012/2013 season, The parents (P_1 and P_2), the first (F_1) and second (F_2) generation hybrids and the first (P_1 x F_1 = BC_1) and second (P_2 x F_1 = BC_2) backcrosses were grown in two experiments in a randomized complete blocks design with two replicates for each one. Each replicate consisted of 20 grains in one row for each of the parents and F_1, 40 grains in two rows of each of back cross and 80 grains in four rows for the F_2 population. Rows were 2.0 m long and 30 cm apart and 10 cm between plants. The first experiment was under normal irrigation (N) (gave irrigation when ever required), the second experiment was under drought stress (D) (after the emergence of 50% of the spikes, the water stress treatment received no more water until harvesting). The soil was fertilized at the rate of 20 kg/fed (15% P2O5) and 80 kg/fed (33.5% ammonium nitrate) and weeds were controlled by hand.

Data were recorded on 5 competitive individual plants for non-segregate basis as (P_1,P_2 and F_1) and 10 plants for BC_1 and BC_2 and 60 plants for F_2 population for each replicate follows:

1-No. of spikes/plant (NS).

2-100-seed weight (SW) in grams.

3-Grain yield/plant (GY) in grams.

4-Biological yield/plant (BY) in grams.

5-Relative water content (RWC): A 4 cm segment of the youngest leaf was taken and cut into 2 cm segments and weighed (fresh weight = FW). Then the segments were placed in distilled water for 4 hours and reweighed to obtain turgor weight (TW). Thereafter the leaf segments were oven dried and weighed (dried weight = DW). RWC was calculated using the formula of Ritchie et al. (1990), RWC % = [(FW – DW) / (TW – DW)] x 100.

6-Chlorophyll content (CC). Chlorophyll content was measured using a SPAD-502 chlorophyll meter (Minolta, Japan). For this measurement the average of three leaves per plant per replication per treatment was taken.

Statistical analysis:

Analysis of variance and mean comparison of the characters was done using SAS Software. Generation mean analysis was performed using Mather and Jinks method (1982). In this method the mean of each character is indicated as follows:

$$Y= m + \alpha [d] + \beta [h] + \alpha^2 [i] + 2\alpha \beta [j] + \beta^2 [1]$$

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 x additive interaction (complementary)
1 = The sum of dominance x dominance interaction (duplicate)
j = Sum of additive x dominance and α, 2α β and β^2 are the coefficients of genetic parameters.

The genetic parameters (m, [d], [h], [I], [j], [1]) were tested for significance using a t-test.

To estimate the parameters and to select the most suitable model the least squares method and the joint scaling test of Mather and Jinks (1982) were employed.

Potence ratio, was estimated by using the formula of Smith (1952).

Stress Tolerance index (STI) for grain yield were computed as formula using by Farshadfar, et al. (2001), $STI = (GY_N)(GY_D)/(GY_N)^2$

where GY_N is grain yield under normal irrigation and GY_D is grain yield under drought.

Broad-sense (H_b^2) and narrow-sense (H_n^2) heritability were estimated by Warner (1952)

formulas:

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

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

Genetic advance was calculated (Johanson, 1955) with a selection intensity of i=5% for all the characters as: $G_A = i.H_b.\sqrt{V_{F2}}$

The components of variation for six generations were calculated by the formulae of F2 variance were obtained by the following formula of Mather and Jinks (1982) as:

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

$D = 4V_{F2} - 2 (V_{Bc1} + V_{BC2})$

$H= 4(V_{F2}-1/2V_D -V_E)$

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

Where:

D - Additive genetic variance

H - Dominance variance

E - Environmental component of variance

F - Correlation between D and H over all loci

Results and discussion

The analysis of variance (Table 2) revealed significant differences for two environments and generations for No. of spikes/plant (NS), 100-seed weight (SW), grain yield (GY), biological yield (BY), relative water content (RWC) and chlorophyll content (CC) in two crosses, indicating the existence of genetic variation and possibility of selection for drought tolerance. The genotypes x environments interaction was also significant for all studied characters in C_2, except for GY, displaying their similar response and different responses of other traits. While, the genotypes x environments interaction was non-significant for all studied characters in C_1. Genetic variation was found in wheat for NS, SW, BY and GY by Tammam, 2005; Farshadfar et al., 2008; Amin, 2013 and for RWC by Manette et al., 1988; Farshadfar et al., 2001.

The data six generations means (Table 3) showed that F1 hybrids were higher than mid-parent and or best parent for all studied characters under both conditions in two crosses except CC. These results showed the presence of heterotic effects for these characters.

In fact the development of any plant breeding program is dependent upon the existence of

genetic variability. The efficiency of selection and expression of heterosis also largely upon the magnitude of genetic variability present in the plant population (Singh and Narayanan, 1993; Singh and Chaudhary, 1999; Farshadfar et al., 2001, 2008; Amin, 2013). The potence ratio presented in table (3), its values ranged from less than one (0.11) for CC (D in C_2) to more than one (36.91) for RWC (D in C_2), indicating the presence of over dominance for all studied characters in two Crosses under normal (N) and drought stress (D) except CC (D in C_1) was partial dominance. These results are in line with those obtained by Ketata et al., 1976, Moshref, 1996,Tammam, 2005 and Amin, 2013.

The highest stress tolerance index (Table 4) was revealed by the F_1 hybrid (STI=0.85 in C_1 and 0.83 in C_2), displaying the presence of heterobeltiosis for drought resistance in the F_1 hybrid, followed by P_2 (0.81) in C_1 and P_2 (0.81) and P_1 (0.80) in C_2.

The degree of dominance (h/d), broad-sense (Hb) and narrow-sense (Hn) heritabilities, genetic advance (GA) and genetic components of variation are presented in Tables (5&6), which shows that the degree of dominance (h/d) for all studied characters was greater than one in two crosses (N&D) except NS (N in C_2), indicating the presence of the overdominance type of gene action in the inheritance of these traits. Selection of these characters must therefore be delayed until the F_3 or F_4 generation. This delay permits a loss of non-additive genetics variance through inbreeding, so that the additive genetics variance can be more clearly evaluated. these results are in harmony with those obtained by Zaazaa et al., (2012), whereas they revealed that, the complex genetic behavior particularly additive and dominance components could be successfully exploited in later generation.

NS (N in C_2) was controlled by the additive type of gene action; the pedigree method of selection can be used for improved of this trait, While for characters under control of the non-additive type of gene action, biparental mating offers good prospects for increasing the frequency of genetic recombination, hastening the rate of genetic improvement, through it may be necessary to resort to heterosis breeding (Gill et al., 1972; Sharma and Singh, 1976; Srivastava et al., 1980; Farshadfar et al., 2001; Tammam, 2005; Kheiralla et al., 1993; Amin, 2013).

Heritability estimate indicates the progress from selection for plant characters is

199 relatively easy or difficult to make in breeding program. Plant breeders, through
200 experience, can perhaps rate a series of their response to selection. Heritability gave a
201 numerical description of this concept. Assessment of heritability of various traits is of
202 considerable important in crop improvement program, for example, to predict response to
203 selection, Nyguist, 1991. High to moderate broad-sense heritability estimates for all
204 studied characters in two Crosses (N&D) (Tables 5&6) showed that effective progress
205 can be mad through selection. Moderate narrow-sense heritability (0.2-0.5) was show for
206 all studied characters in two crosses (N&D) except CC (D) in Cross 1 and RWC (D) in
207 Cross 2 indicated low heritability estimate (less than 0.2) (Tefra and Peat, 1997).The
208 difference between H_n and H_b exhibits the involvement of the dominance effect in the
209 genetic constitution of these characters.
210 The variation observed between the genotypes for the characters investigated exhibited
211 that selection maybe effective for the improvement of drought tolerance (Umarahan et al.,
212 1997; Farshadfar et al., 2001; Farshadfar et al., 2008), however, the selection efficiency is
213 related to the magnitude of heritability and genetic advance (Johnson et al., 1955; Singh
214 and Narayanan, 1993). Heritability estimates along with genetic advance are important
215 selection parameters and normally more helpful in predicting the gain under selection
216 than heritability estimates alone. However, heritability estimates are influenced by the
217 type of genetic material, sample size, method of sampling, conduct of experiment,
218 method of calculation and effect of linkage. Genetic advance which refers to the
219 improvement in the mean genotypic value of selected individuals over the parental
220 population is influenced by the genetic variability, heritability and selection intensity
221 (Alza and Martinez, 1997; Sharma, 2003).
222 The rate of genetic advance is connected with heritability (Mather and links, 1982). The
223 genetic advance (C_1&C_2) was high (more than 40%) for GY (N&D), while NS, BY,
224 RWC and CC (N&D) were moderate (14-40%), indicating the importance of direct
225 selection for these characters and the significance of indirect selection for SW (N&D) in
226 two crosses with low genetic advance (less than 14%) through correlated response with
227 characters having high heritability and genetic advance (Sharma et al., 1991; Farshadfar
228 et al., 2001 and 2008; Golparvar 2012).
229 Degree of dominance and variance components are presented in Tables (5&6), Ew, D and

H are environmental, additive and dominance components, respectively. F is an indicator of correlation between D and H over all loci. If F is zero it means that dominant genes are in the parent with high performance, while negative F exhibits that dominant genes are in the low performance parent. If the ratio of F/√DxH is equal to or near one confirms that the magnitude and sign of dominance for all the genes monitoring the character is equal, therefore, the ratio √H/D is a good estimator of dominance. If F/√DxH is equal to zero or close to zero, the magnitude and sign of the genes controlling the character is not equal and hence √H/D explains average dominance. The h/d ratio estimates the degree of dominance (Kearsey and Farshadfar, 1998; Sharma, 1998; Singh and Chaudhary, 1999; Farshadfar et al., 2001, 2008). The ratio of √H/D for all studied characters (N&D) in two crosses showed average dominance except NS (D), GY (D) and CC (N&D) in C_1 and GY (N), RWC (N) and CC (N&D) in C_2 showed over dominance.

The estimates of heterosis and inbreeding depression together provide information about type of gene action involved in the expression of various quantitative traits. The percentage of heterosis with regard to High Parent (HP) and Mid-Parent (MP) and Inbreeding Depression (ID) (Fig. 1,2,3 and4) exhibited that mid-parent and high parent heterosis were positive for NS, SW, BY, GY, RWC and CC in two crosses under both conditions except CC was negative (D) (C_1&C_2) compared with high parent. Inbreeding depression was positive for all studied characters.

The joint scaling test (Mather and Jinks, 1982) was employed to estimate the mean (m), additive effect (d), dominance effect (h), additive x additive (i), additive x dominance (j) and dominance x dominance (1) values (Tables 7&8). The results of A, B, C and D scaling test for the two wheat crosses under both environments, revealed that significant of any of these tests indicates the presence of non-allelic gene interactions or epistasis on the scale of measurement used. Results of scaling test, showed that additive-dominance model is inadequate for explaining the inheritance of all studied characters, indicating the present of non-allelic gene interaction in two crosses under two environments. Lal et al., (2013) studied the generation mean analysis in heat tolerance in wheat; they showed the adequacy of additive-dominance model for grain yield and its components.

The mean parameters (m) for all studied attributes of two crosses and environments (Tables 7&8) which reflect the contribution due to the over all mean plus the locus

effects and interaction of the fixed loci were significant. The estimated of dominance gene action (h) was significant for the all studied characters (N&D) in two crosses, indicating the importance gene effects in inheritance of these characters. The significant [d] and [h] in the inheritance of RWC (D in C_2) revealed that both types of additive and dominance effects are involved in the genetics of RWC (Farshadfar et al., 2001; 2003; 2008; Tammam, 2005; Amin, 2013).

The genetic models fitted (Tables 7&8) for all studied characters (N&D) in two crosses except RWC (D in C_1), indicated dominance and additive x additive gene effects. indicated dominance and additive x additive gene effects. It is there fore suggested that selection should be carried out in late generation and the interaction should be fixed by selection under selfing conditions. The epistatic effect (dominance x dominance [1]) was significant for all studied characters (N&D) in two crosses, which confirm the important role of dominance x dominance gene interaction in the genetic system controlling, these result were reported by Srivastava et al., 1992; Kearsey and Pooni, 2004; Tammam, 2005; Amin, 2013. Both additive x additive [i] and dominance x dominance [1] effects were significant for all studied characters (N&D) in two crosses except RWC (D in C_1), supporting the presence of duplicate type of epistasis. This complementary interaction increases the variation between the generation and in the segregating population. The cross, which showed most promising in terms of narrow sense heritability and genetic gain, also showed highest means under both conditions, chance to find stress tolerant breeding material in segregating populations of this cross are promising.these finding are in line with Dashti et al., (2012), they studied genetic analysis of salt tolerance, and refer to High narrow sense heritability may be used as a useful indicator index for the selection of salt tolerant genotypes at the vegetative growth stage in wheat.

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Table 1: Pedigree and origin of the genotypes used in the two bread wheat crosses.

Cross	Parental name	Pedigree	Origin
Cross 1	Sakha 94 (P1)	Opata/Rayon//Kauz	Egypt
	Tokwie (P2)	-------	South Africa
Cross 2	Giza 168 (P1)	Mill/Buc//Seri	Egypt
	Tokwie (P2)	-------	South Africa

Table 2: Analysis of variance for various characters investigated.

		Mean square					
SOV	**df**	**NS**	**SW**	**BY**	**GY**	**RWC**	**CC**
Cross 1							
Environments (A)	**1**	**9.61****	**5.58****	**10859.21****	**715.70****	**1234.65****	**659.63****
Error	**2**	**0.05**	**0.08**	**7.02**	**45.63**	**3.33**	**2.41**
Generations (B)	**5**	**8.94****	**0.82****	**283.17***	**191.21****	**120.94****	**227.39****
A x B	**5**	**0.35^{ns}**	**0.13^{ns}**	**25.55^{ns}**	**7.54^{ns}**	**12.54^{ns}**	**11.98^{ns}**
Error	**20**	**0.25**	**0.07**	**84.49**	**14.90**	**15.23**	**1.05**
Cross 2							
Environments (A)	**1**	**14.06****	**9.06****	**11600****	**620.63****	**1441.29****	**1416.27****
Error	**2**	**0.05**	**0.001**	**149.70**	**0.08**	**11.95**	**2.94**
Generations (B)	**5**	**18.49****	**0.53**	**269.52****	**207.59****	**532.92****	**179.34****
A x B	**5**	**1.03****	**0.10****	**20.87****	**5.71^{ns}**	**53.83****	**58.96****
Error	**20**	**0.17**	**0.02**	**48.62**	**4.13**	**10.39**	**4.26**

*** and ** significant at 5% and 1% levels of probability, respectively.**

Table 3: Mean comparison of the characters studied.

Generations	Characters											
	NS		SW		BY		GY		RWC		CC	
	N	D	N	D	N	D	N	D	N	D	N	D
Cross 1												
Gemmeiza 9 (P_1)	14.87	13.17	6.10	4.84	100.97	64.60	44.49	33.76	67.97	54.67	46.47	40.17
Inbred line 1 (P_2)	10.67	10.17	5.63	4.80	96.98	60.91	37.70	30.58	71.21	61.73	59.70	49.37
F_1 (P_1 x P_2)	16.07	14.67	6.30	5.56	109.32	68.29	48.41	41.03	74.02	66.91	52.57	45.40
F_2	13.17	12.17	5.11	4.63	82.69	52.95	32.52	23.16	69.85	55.21	39.37	33.93
P_1 x F_1 (BC_1)	14.67	13.67	5.74	4.91	96.16	65.05	40.66	30.49	67.14	53.35	46.20	37.43
P_2 X F_1 (BC_2)	12.67	12.07	5.36	4.78	95.70	61.61	36.93	28.18	68.50	56.55	54.30	40.93
$LSD_{0.05}$	1.88	1.01	0.45	0.42	4.25	5.19	4.31	3.85	2.01	1.36	3.08	3.94
Potence ratio	-1.57	-2.00	1.83	4.27	5.19	3.00	1.89	4.32	-2.73	14.97	-1.10	1.41
Cross 2												
Sids 1 (P_1)	14.67	12.67	5.75	4.62	101.76	67.85	42.40	34.07	66.97	52.73	53.70	39.33
Inbred line 2 (P_2)	10.67	10.17	5.63	4.80	96.98	60.91	37.70	30.58	71.21	61.73	59.70	49.37
F_1 (P_1 x P_2)	16.67	14.17	6.30	4.95	111.44	79.03	47.11	38.91	86.14	78.36	67.73	44.40
F_2	14.17	13.67	5.13	4.52	96.58	59.19	30.39	22.14	56.74	51.66	43.87	39.33
P_1 x F_1 (BC_1)	14.17	13.17	6.09	5.00	100.03	62.42	35.41	26.40	74.97	55.87	52.53	40.43
P_2 X F_1 (BC_2)	12.67	11.67	5.75	4.73	98.63	60.62	39.72	28.80	81.87	61.60	55.37	44.77
$LSD_{0.05}$	1.90	1.20	0.51	0.46	3.52	2.59	2.52	2.32	1.49	2.41	2.93	2.89
Potence ratio	-2.00	-2.20	-10.22	2.70	5.05	4.22	-2.40	-3.78	8.04	36.91	19.46	0.11

Table 4: Grain yield/plant under normal (GY_N) and drought stress (GY_D), and stress tolerance index (STI) for each generation.

Generations	GY_N	GY_D	STI	Generations	GY_N	GY_D	STI
Cross 1				**Cross 2**			
Gemmeiza 9 (P_1)	44.49	33.76	0.76	Sids 1 (P_1)	42.40	34.07	0.80
Inbred line 1 (P_2)	37.70	30.58	0.81	Inbred line 2 (P_2)	37.70	30.58	0.81
F_1 (P_1 x P_2)	48.41	41.03	0.85	F_1 (P_1 x P_2)	47.11	38.91	0.83
F_2	32.52	23.16	0.71	F_2	30.39	22.14	0.73
P_1 x F_1 (BC_1)	40.66	30.49	0.75	P1 x F1 (BC1)	35.41	26.40	0.75
P_2 X F_1 (BC_2)	36.93	28.18	0.76	P2 X F1 (BC2)	39.72	28.80	0.73

Table 5: Genetic parameters and components of variation for all studied characters in the cross 1 under normal (N) and drought stress (D) conditions.

Characters		h/d	H_b	H_n	G_A	D	H	F	E_w	√H/D	F/√HxD
NS	N	+2.65	0.69	0.28	25.06	19.80	9.07	+1.40	5.42	0.68	0.11
	D	+3.63	0.67	0.20	22.83	13.40	17.53	-0.80	5.50	1.14	-0.05
SW	N	+5.79	0.78	0.33	8.87	7.21	2.80	-0.11	1.19	0.62	-0.03
	D	+12.31	0.83	0.32	12.55	9.30	5.76	+0.60	1.27	0.79	-0.08
BY	N	+134.72	0.79	0.36	20.29	17.82	3.75	-1.60	2.56	0.46	-0.20
	D	+13.69	0.74	0.33	25.05	21.56	5.51	-1.55	4.34	0.51	0.14
GY	N	+8.94	0.79	0.29	56.63	40.35	29.26	-2.36	7.49	0.85	-0.07
	D	+13.67	0.74	0.24	46.60	28.68	33.12	+0.99	7.90	1.08	0.03
RWC	N	+2.70	0.74	0.32	21.36	18.03	5.42	-1.88	3.73	0.55	-0.19
	D	-2.40	0.76	0.37	23.76	22.37	1.39	-1.16	3.74	0.25	-0.21
CC	N	-5.31	0.73	0.21	23.43	13.25	19.00	-1.20	4.13	1.20	-0.08
	D	-6.18	0.74	0.18	19.92	9.20	20.27	2.24	3.36	1.48	0.16

Table 6: Genetic parameters and components of variation for all studied characters in the cross 2 under normal (N) and drought stress (D) conditions.

Characters		h/d	H_b	H_n	G_A	D	H	F	E_w	√H/D	F/√HxD
NS	N	+0.67	0.73	0.30	27.98	22.50	9.33	-0.75	5.00	0.64	-0.05
	D	-1.50	0.70	0.29	25.06	20.70	7.27	-0.35	5.17	0.59	-0.03
SW	N	+11.06	0.81	0.32	10.66	8.09	4.51	+0.03	1.21	0.75	0.005
	D	+6.07	0.75	0.29	6.71	5.01	3.01	+0.50	1.08	0.78	0.13
BY	N	+16.48	0.66	0.31	17.92	16.21	2.37	-0.32	2.91	0.63	-0.02
	D	+13.32	0.77	0.26	22.80	14.91	13.45	-1.67	4.50	0.38	-0.27
GY	N	-8.51	0.71	0.24	47.64	30.87	30.76	-2.37	9.52	1.00	-0.08
	D	-11.79	0.75	0.30	53.60	41.71	20.66	+0.75	8.47	0.70	-0.03
RWC	N	-15.04	0.79	0.25	23.83	14.53	17.22	+2.08	3.16	1.09	0.11
	D	-8.63	0.77	0.19	19.62	20.62	8.74	+1.30	2.81	0.65	0.10
CC	N	-18.15	0.69	0.20	19.73	11.20	15.91	+0.88	4.25	1.19	0.07
	D	-3.03	0.80	0.26	20.01	12.34	14.16	+0.03	2.41	1.07	0.002

Table 7: Estimates of scaling test and types of gene action using generation means for all studied characters cross 1 under normal (N) and drought stress (D) conditions.

Characters		Scaling test				Genetic parameters					
		A	B	C	D	m	[d]	[h]	[i]	[j]	[l]
NS	N	-1.60**	-1.40**	-5.00**	-1.00**	13.17**	2.00	5.30**	2.00**	-0.10	1.00**
	D	-0.50**	-0.70**	-4.00**	-1.40**	12.17**	1.60	5.80**	2.80**	0.10	-1.60**
SW	N	-0.91**	1.20**	-3.88**	-0.88**	5.11**	0.38	2.20**	1.77**	0.14	0.45**
	D	-0.57**	-0.80**	-2.23**	-0.43**	4.63**	-0.13	1.60**	0.86*	0.12	0.52**
BY	N	-17.97**	-14.91**	-85.85**	-26.49**	82.69**	0.47	63.32**	52.97**	-1.53	-20.09**
	D	-2.79**	-5.97**	-50.30**	-20.77**	52.95**	3.44	47.08**	41.54**	1.60	-32.78**
GY	N	-11.58**	-10.26**	-46.95**	-12.56**	32.52**	3.74	33.43**	25.11**	-0.66	-3.28**
	D	-11.81**	-13.25**	-49.78**	-12.36**	23.16**	2.31	31.58**	24.72**	0.72	-0.34**
RWC	N	-7.71**	-8.23**	-7.84**	4.05**	69.85**	-1.36	-3.67*	-8.10**	0.26	24.04**
	D	-14.89**	-15.54**	-29.40**	0.51**	55.21**	-3.21	7.69**	-1.03	0.32	31.46**
CC	N	-6.63**	-3.67**	-53.83**	-21.77**	39.37**	-8.10	43.02**	43.53**	-1.48	-33.23**
	D	-10.70**	-12.90**	-44.60**	-10.50**	33.93**	-3.50	21.63**	21.00**	1.10	2.60**

* and ** significant at 5% and 1% levels of probability, respectively.

Table 8: Estimates of scaling test and types of gene action using generation means for all studied characters in the cross 2 under normal (N) and drought stress (D) conditions

Characters		Scaling test				Genetic parameters					
		A	B	C	D	m	[d]	[h]	[i]	[j]	[l]
NS	N	-3.00**	-2.00**	-2.00**	1.50**	14.17**	1.50	1.00*	-3.00**	-0.50	8.00**
	D	-0.50**	-1.00**	3.50**	2.50**	13.67**	1.50	-2.25**	-5.00**	-0.25	6.50**
SW	N	0.13**	-0.43**	-3.88**	-1.57**	5.13**	0.34	3.76**	3.15**	0.28	-2.85**
	D	0.43**	-0.29**	-2.23**	-0.70**	4.52**	0.27	1.64**	1.40**	0.36	-1.54**
BY	N	-13.14**	-11.16**	-35.30**	-5.50**	96.58**	1.40	23.07**	11.00**	-0.99	13.30**
	D	-22.04**	-18.70**	-50.05**	-4.66**	59.19**	1.80	23.98**	9.32**	-1.67	31.41**
GY	N	-18.70**	-3.37**	-50.77**	-14.36**	30.39**	-4.32	36.77**	28.71**	-7.67	-6.65**
	D	-20.19**	-11.89**	-53.91**	-10.92**	22.14**	-2.41	28.42**	21.83**	-4.15	10.25**
RWC	N	-3.18**	6.39**	-83.50**	-43.36**	56.74**	-6.90	103.7**	86.71**	-4.78	-89.92**
	D	-19.35**	-16.88**	-64.55**	-14.16**	51.66**	-5.73**	49.44**	28.31**	-1.23	-7.91**
CC	N	-16.37**	-16.70**	-73.40**	-20.17**	43.87**	-2.83	51.37**	40.33**	0.16	-7.27**
	D	-2.87**	-4.23**	-20.17**	-6.53**	39.33**	-4.33	13.12**	13.07**	0.68	-5.97**

* and ** significant at 5% and 1% levels of probability, respectively

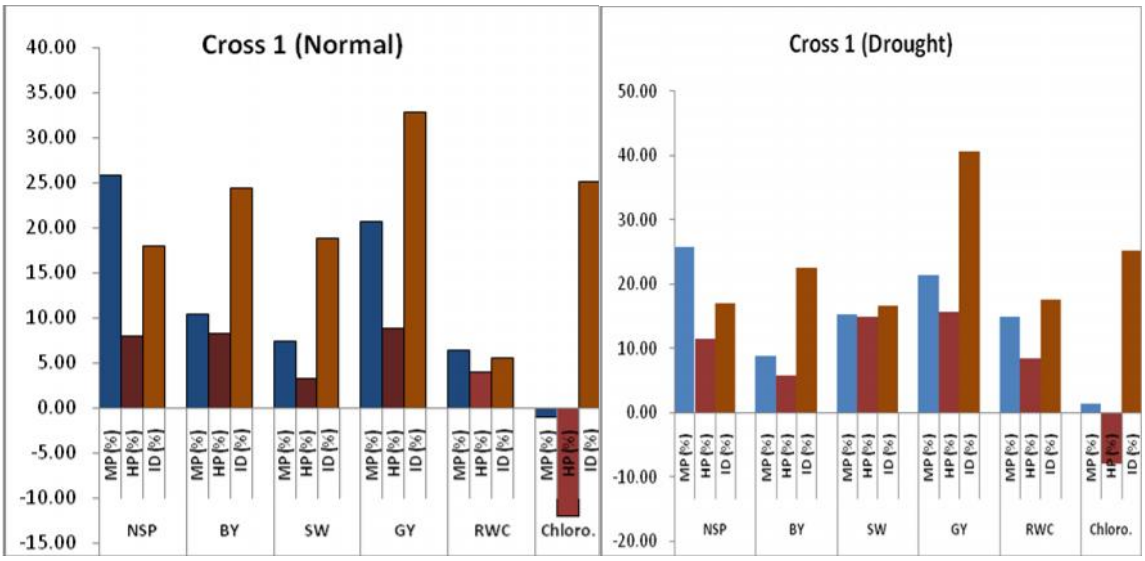

Fig 1&2: Percentage of heterosis and inbreeding depression under two environments in Cross 1 for characters investigated.

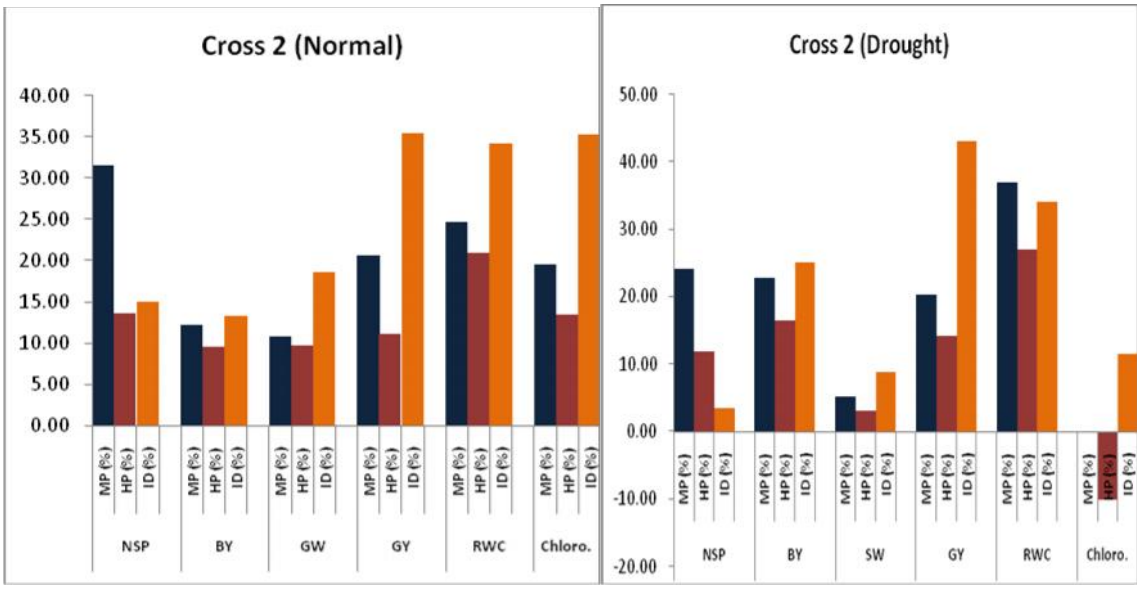

Fig 3&4: Percentage of heterosis and inbreeding depression under two environments in Cross 2 for characters investigated.