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Genetic control for some traits using generation mean analysis in bread wheat (*Triticum aestivum* L.).

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ABSTRACT

In order to study the inheritance and genetic analysis of drought tolerance indicators a six generations of P₁, P₂, F₁, F₂, Bc₁ and Bc₂ of two wheat crosses i.e., Sakha 94 x Tokwie (C₁) and Giza 168 x Tokwie (C₂) 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 over dominance 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 (C₁&C₂) ranged from 0.18 for CC (D) to 0.37 for RWC (D) in C₁. The genetic advance (C₁&C₂) 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 C₁), indicated dominance and additive x additive gene effects. Both additive x additive and dominance x dominance effects were significant for all studied characters (N&D) in two crosses except RWC (D in C₁), 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.

1. 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

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42 inheritance, the magnitude of gene effects and their mode of action [1,2,3]. The plant
43 breeder is interested in the estimation of gene effects in order to formulate the most
44 advantageous breeding procedures for improvement of the attribute in question. Therefore,
45 breeders need information about nature of gene action, heterosis, inbreeding depression,
46 heritability and predicted genetic gain from selection for yield and yield components. [4]
47 Listed three major factors that must be considered and which may limit progress in the
48 analysis of quantitative genetic variation: the number of genes involved the type of gene
49 action, and the genotype- environment interaction.

50 The genetical studies based on the means and variances of basic generations, is a simple
51 method for estimating the gene effects for a polygenic trait and has been reviewed in many
52 crop species. The greatest merit of generation means analysis lies in its ability to estimate
53 the epistatic effects [5]. The possibility of epistasis accounting for a significant proportion of
54 genetic variance of quantitative trait has been investigated extensively in previous studies in
55 crop plants. Amount and type of epistasis can have a major consequence on both the
56 reliability of predictions and the design of breeding program. Statistically, detection of
57 epistasis using generation means analysis is more reliable and efficient than by the analysis
58 of variance approach [6]. However, it has its own limitations and several assumptions. Triple
59 test cross is a powerful method of genetic analysis, which provides unbiased estimates for
60 epistasis. In addition, it also estimates the additive and dominance components of variation
61 with high accuracy when epistasis is absent [7]. The variance estimates attributed to
62 environment, total genetic, additive and dominance deviation effects were obtained from the
63 phenotypic variances for populations P1, P2, F1, F2, BC1 and BC2. These estimates
64 allowed the determination of heritabilities in the broad and narrow sense, mean degree of
65 dominance and minimum number of genes that control each character, by using Burton's
66 expression [8]. The objective of the present investigation was to investigate the genetic
67 analysis of quantitative indicators of drought tolerance in wheat under drought condition
68 using generation mean analysis.

69

70 **2. MATERIAL AND METHODS**

71 **2.1 PLANT MATERIAL AND EXPERIMENTS**

72 The two Egyptian cultivars, Sakha 94 and Giza 168 were more adapted in Egypt and proved
73 high yielding. However, the introduced line (Tokwie) is characterized as a drought tolerant.
74 Therefore, the line introduced was crossed with the Egyptian cultivars in order to enlarge the
75 variability for selection in the breeding program for these characters.

76 The experiments reported herein were carried out during the three successive growing
77 seasons of 2010/2011, 2011/2012 and 2012/2013. In 2010/2011, the parent genotypes of

78 hexaploid wheat (*Triticum aestivum* L.) were sown to secure enough hybrid seed (Table 1).
79 Two crosses namely Sakha 94 x Tokwie (Cross 1) and Giza 168 x Tokwie (Cross 2) were
80 developed at Faculty of Agriculture, Sohag University, Egypt.

81 In 2011/2012 season, F₁ plants were selfed to produce F₂ seeds and backcrossed to the
82 parents to produce BC₁ and BC₂ seeds. In 2012/2013 season, The parents (P₁ and P₂), the
83 first (F₁) and second (F₂) generation hybrids and the first (P₁ x F₁ = BC₁) and second (P₂ x F₁
84 = BC₂) backcrosses were grown in two experiments in a randomized complete blocks design
85 with two replicates for each one. Each replicate consisted of 20 grains in one row for each of
86 the parents and F₁, 40 grains in two rows of each of back cross and 80 grains in four rows
87 for the F₂ population. Rows were 2.0 m long and 30 cm apart and 10 cm between plants.
88 The first experiment was under normal irrigation (N) (gave irrigation when ever required), the
89 second experiment was under drought stress (D) (after the emergence of 50% of the spikes,
90 the water stress treatment received no more water until harvesting). The soil was fertilized at
91 the rate of 20 kg/fed (15% P₂O₅) and 80 kg/fed (33.5% ammonium nitrate) and weeds were
92 controlled by hand.

93 Data were recorded on 5 competitive individual plants for non-segregate basis as (P₁, P₂ and
94 F₁) and 10 plants for BC₁ and BC₂ and 60 plants for F₂ population for each replicate follows:

95 1-No. of spikes/plant (NS).

96 2-100-seed weight (SW) in grams.

97 3-Grain yield/plant (GY) in grams.

98 4-Biological yield/plant (BY) in grams.

99 5-Relative water content (RWC): A 4 cm segment of the youngest leaf was taken and cut
100 into 2 cm segments and weighed (fresh weight = FW). Then the segments were placed in
101 distilled water for 4 hours and reweighed to obtain turgor weight (TW). Thereafter the leaf
102 segments were oven dried and weighed (dried weight = DW). RWC was calculated using the
103 formula of [9], $RWC \% = [(FW - DW) / (TW - DW)] \times 100$.

104 6-Chlorophyll content (CC). Chlorophyll content was measured using a SPAD-502
105 chlorophyll meter (Minolta, Japan). For this measurement the average of three leaves per
106 plant per replication per treatment was taken.

107 2.2. STATISTICAL ANALYSIS

108 Analysis of variance and mean comparison of the characters was done using SAS Software.
109 Generation mean analysis was performed using Mather and Jinks method [5]. In this method
110 the mean of each character is indicated as follows:

111

$$112 Y = m + \alpha [d] + \beta [h] + \alpha^2 [i] + 2\alpha \beta [j] + \beta^2 [1]$$

113

114 Where:

115 Y = The mean of one generation

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116 m = The mean of all generation
117 d = The sum of additive effects
118 h = The sum of dominance effects
119 i = The sum of additive x additive interaction (complementary)
120 1 = The sum of dominance x dominance interaction (duplicate)
121 j = Sum of additive x dominance and α , 2α β and β^2 are the coefficients of genetic
122 parameters.

123 The genetic parameters (m, [d], [h], [i], [j], [1]) were tested for significance using a t-test.
124 To estimate the parameters and to select the most suitable model the least squares method
125 and the joint scaling test of Mather and Jinks [5] were employed.

126 Potence ratio, was estimated by using the formula of Smith [10].

127 Stress Tolerance index (STI) for grain yield were computed as formula using by [1]. STI =
128 $(GY_N)(GY_D)/(GY_N)^2$

129 Where GY_N is grain yield under normal irrigation and GY_D is grain yield under drought.

130 Broad-sense (H_b^2) and narrow-sense (H_n^2) heritability were estimated by [11]. Formulas:

131 $H_b^2 = [V_{F2} - (V_{P1} + V_{P2} + V_{F1})/3] / V_{F2}$ $H_n^2 = [2V_{F2} - (V_{BC1} + V_{BC2})] / V_{F2}$

132 Genetic advance was calculated [12] with a selection intensity of $i=5\%$ for all the characters
133 as:

$$G_A = i.H_b.\sqrt{V_{F2}}$$

134 The components of variation for six generations were calculated by the formulae of F2
135 variance were obtained by the following formula of Mather and Jinks [5] as:

136 $E = 1/3 (V_{P1} + V_{P2} + V_{F1})$

137 $D = 4V_{F2} - 2 (V_{BC1} + V_{BC2})$

138 $H = 4(V_{F2} - 1/2V_D - V_E)$

139 $F = V_{BC1} - V_{BC2}$

140 Where:

141 D - Additive genetic variance

142 H - Dominance variance

143 E - Environmental component of variance

144 F - Correlation between D and H over all loci

145

146 3. RESULTS AND DISCUSSION

147 The analysis of variance (Table 2) revealed significant differences for two environments and
148 generations for No. of spikes/plant (NS), 100-seed weight (SW), grain yield (GY), biological
149 yield (BY), relative water content (RWC) and chlorophyll content (CC) in two crosses,
150 indicating the existence of genetic variation and possibility of selection for drought tolerance.

151 The genotypes x environments interaction was also significant for all studied characters in
152 C₂, except for GY, displaying their similar response and different responses of other traits.

153 While, the genotypes x environments interaction was non-significant for all studied

154 characters in C_1 . Genetic variation was found in wheat for NS, SW, BY and GY by [12, 13,
155 14] and for RWC by [1,16].
156 The data six generations means (Table 3) showed that F_1 hybrids were higher than mid-
157 parent and or best parent for all studied characters under both conditions in two crosses
158 except CC. These results showed the presence of heterotic effects for these characters.
159 In fact the development of any plant breeding program is dependent upon the existence of
160 genetic variability. The efficiency of selection and expression of heterosis also largely upon
161 the magnitude of genetic variability present in the plant population [1,2,15,17,18]. The
162 potence ratio presented in table (3), its values ranged from less than one (0.11) for CC (D in
163 C_2) to more than one (36.91) for RWC (D in C_2), indicating the presence of over dominance
164 for all studied characters in two Crosses under normal (N) and drought stress (D) except CC
165 (D in C_1) was partial dominance. These results are in line with those obtained by
166 [13,15,19,20].
167 The highest stress tolerance index (Table 4) was revealed by the F_1 hybrid (STI=0.85 in C_1
168 and 0.83 in C_2), displaying the presence of heterobeltiosis for drought resistance in the F_1
169 hybrid, followed by P_2 (0.81) in C_1 and P_2 (0.81) and P_1 (0.80) in C_2 .
170 The degree of dominance (h/d), broad-sense (H_b) and narrow-sense (H_n) heritabilities,
171 genetic advance (GA) and genetic components of variation are presented in Tables (5&6),
172 which shows that the degree of dominance (h/d) for all studied characters was greater than
173 one in two crosses (N&D) except NS (N in C_2), indicating the presence of the
174 overdominance type of gene action in the inheritance of these traits. Selection of these
175 characters must therefore be delayed until the F_3 or F_4 generation. This delay permits a loss
176 of non-additive genetics variance through inbreeding, so that the additive genetics variance
177 can be more clearly evaluated. these results are in harmony with those obtained by [21].
178 Whereas they revealed that, the complex genetic behavior particularly additive and
179 dominance components could be successfully exploited in later generation.
180 NS (N in C_2) was controlled by the additive type of gene action; the pedigree method of
181 selection can be used for improved of this trait, While for characters under control of the non-
182 additive type of gene action, biparental mating offers good prospects for increasing the
183 frequency of genetic recombination, hastening the rate of genetic improvement, through it
184 may be necessary to resort to heterosis breeding [1,13,15,22,23,24,25].
185 Heritability estimate indicates the progress from selection for plant characters is relatively
186 easy or difficult to make in breeding program. Plant breeders, through experience, can
187 perhaps rate a series of their response to selection. Heritability gave a numerical description
188 of this concept. Assessment of heritability of various traits is of considerable important in
189 crop improvement program, for example, to predict response to selection [26]. High to

190 moderate broad-sense heritability estimates for all studied characters in two Crosses (N&D)
191 (Tables 5&6) showed that effective progress can be mad through selection. Moderate
192 narrow-sense heritability (0.2-0.5) was show for all studied characters in two crosses (N&D)
193 except CC (D) in Cross 1 and RWC (D) in Cross 2 indicated low heritability estimate (less
194 than 0.2) [27]. The difference between H_n and H_b exhibits the involvement of the dominance
195 effect in the genetic constitution of these characters.

196 The variation observed between the genotypes for the characters investigated exhibited that
197 selection maybe effective for the improvement of drought tolerance [1,2,28,29], however, the
198 selection efficiency is related to the magnitude of heritability and genetic advance [12,17].
199 Heritability estimates along with genetic advance are important selection parameters and
200 normally more helpful in predicting the gain under selection than heritability estimates alone.
201 However, heritability estimates are influenced by the type of genetic material, sample size,
202 method of sampling, conduct of experiment, method of calculation and effect of linkage.
203 Genetic advance which refers to the improvement in the mean genotypic value of selected
204 individuals over the parental population is influenced by the genetic variability, heritability
205 and selection intensity [30,31].

206 The rate of genetic advance is connected with heritability [5]. The genetic advance (C_1 & C_2)
207 was high (more than 40%) for GY (N&D), while NS, BY, RWC and CC (N&D) were moderate
208 (14-40%), indicating the importance of direct selection for these characters and the
209 significance of indirect selection for SW (N&D) in two crosses with low genetic advance (less
210 than 14%) through correlated response with characters having high heritability and genetic
211 advance [1,14,32,33,34].

212 Degree of dominance and variance components are presented in Tables (5&6), E_w , D and H
213 are environmental, additive and dominance components, respectively. F is an indicator of
214 correlation between D and H over all loci. If F is zero it means that dominant genes are in the
215 parent with high performance, while negative F exhibits that dominant genes are in the low
216 performance parent. If the ratio of $F/\sqrt{D \times H}$ is equal to or near one confirms that the
217 magnitude and sign of dominance for all the genes monitoring the character is equal,
218 therefore, the ratio $\sqrt{H/D}$ is a good estimator of dominance. If $F/\sqrt{D \times H}$ is equal to zero or
219 close to zero, the magnitude and sign of the genes controlling the character is not equal and
220 hence $\sqrt{H/D}$ explains average dominance. The h/d ratio estimates the degree of dominance
221 [1,15,18,35]. The ratio of $\sqrt{H/D}$ for all studied characters (N&D) in two crosses showed
222 average dominance except NS (D), GY (D) and CC (N&D) in C_1 and GY (N), RWC (N) and
223 CC (N&D) in C_2 showed over dominance.

224 The estimates of heterosis and inbreeding depression together provide information about
225 type of gene action involved in the expression of various quantitative traits. The percentage

226 of heterosis with regard to High Parent (HP) and Mid-Parent (MP) and Inbreeding
227 Depression (ID) (Fig. 1 and 2) exhibited that mid-parent and high parent heterosis were
228 positive for NS, SW, BY, GY, RWC and CC in two crosses under both conditions except CC
229 was negative (D) (C_1 & C_2) compared with high parent. Inbreeding depression was positive for
230 all studied characters.

231 The joint scaling test [5] was employed to estimate the mean (m), additive effect (d),
232 dominance effect (h), additive x additive (i), additive x dominance (j) and dominance x
233 dominance (l) values (Tables 7&8). The results of A, B, C and D scaling test for the two
234 wheat crosses under both environments, revealed that significant of any of these tests
235 indicates the presence of non-allelic gene interactions or epistasis on the scale of
236 measurement used. Results of scaling test, showed that additive-dominance model is
237 inadequate for explaining the inheritance of all studied characters, indicating the present of
238 non-allelic gene interaction in two crosses under two environments. [36] studied the
239 generation mean analysis in heat tolerance in wheat; they showed the adequacy of additive-
240 dominance model for grain yield and its components.

241 The mean parameters (m) for all studied attributes of two crosses and environments (Tables
242 7&8) which reflect the contribution due to the over all mean plus the locus effects and
243 interaction of the fixed loci were significant. The estimated of dominance gene action (h) was
244 significant for the all studied characters (N&D) in two crosses, indicating the importance
245 gene effects in inheritance of these characters. The significant [d] and [h] in the inheritance
246 of RWC (D in C_2) revealed that both types of additive and dominance effects are involved in
247 the genetics of RWC [1,2,13,15,37].

248 The genetic models fitted (Tables 7&8) for all studied characters (N&D) in two crosses
249 except RWC (D in C_1), indicated dominance and additive x additive gene effects. indicated
250 dominance and additive x additive gene effects. It is there fore suggested that selection
251 should be carried out in late generation and the interaction should be fixed by selection
252 under selfing conditions. The epistatic effect (dominance x dominance [l]) was significant for
253 all studied characters (N&D) in two crosses, which confirm the important role of dominance x
254 dominance gene interaction in the genetic system controlling, these result were reported by
255 [13,15,24,38]. Both additive x additive [i] and dominance x dominance [l] effects were
256 significant for all studied characters (N&D) in two crosses except RWC (D in C_1), supporting
257 the presence of duplicate type of epistasis. This complementary interaction increases the
258 variation between the generation and in the segregating population. The cross, which
259 showed most promising in terms of narrow sense heritability and genetic gain, also showed
260 highest means under both conditions, chance to find stress tolerant breeding material in
261 segregating populations of this cross are promising. these finding are in line with [39], they

262 studied genetic analysis of salt tolerance, and refer to High narrow sense heritability may be
 263 used as a useful indicator index for the selection of salt tolerant genotypes at the vegetative
 264 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

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Table 2. Pedigree and origin of the genotypes used in the two bread wheat crosses

SOV	df	Mean square					
		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

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Ns: No. of spikes/plant; sw: 100-seed weight in grams; BY: Biological yield/plant in grams;
 GY: Grain yield/plant in grams; RWC: Relative water content %; CC: Chlorophyll content
 * and ** significant at 5% and 1% levels of probability, respectively.

283 **Table 3. Mean comparison of the characters studied.**

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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

285 Ns: No. of spikes/plant; sw: 100-seed weight in grams; BY: Biological yield/plant in grams;

286 GY: Grain yield/plant in grams; RWC: Relative water content %; CC: Chlorophyll content

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289 **Table 4. : Grain yield/plant under normal (GY_N) and drought stress (GY_D), and stress**

290 **tolerance index (STI) for each generation.**

Generations	GY _N	GY _D	STI	Generations	GY _N	GY _D	STI
<u>Cross 1</u>				<u>Cross 2</u>			
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	P ₁ x F ₁ (BC ₁)	35.41	26.40	0.75
P ₂ X F ₁ (BC ₂)	36.93	28.18	0.76	P ₂ X F ₁ (BC ₂)	39.72	28.80	0.73

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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

303 Ns: No. of spikes/plant; sw: 100-seed weight in grams; BY: Biological yield/plant in grams;
304 GY: Grain yield/plant in grams; RWC: Relative water content %; CC: Chlorophyll content

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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

311 Ns: No. of spikes/plant; sw: 100-seed weight in grams; BY: Biological yield/plant in grams;
312 GY: Grain yield/plant in grams; RWC: Relative water content %; CC: Chlorophyll content.

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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**

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Ns: No. of spikes/plant; sw: 100-seed weight in grams; BY: Biological yield/plant in grams;
GY: Grain yield/plant in grams; RWC: Relative water content %; CC: Chlorophyll content
* 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.

Character s		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**

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Ns: No. of spikes/plant; sw: 100-seed weight in grams; BY: Biological yield/plant in grams;
GY: Grain yield/plant in grams; RWC: Relative water content %; CC: Chlorophyll content
* and ** significant at 5% and 1% levels of probability, respectively.

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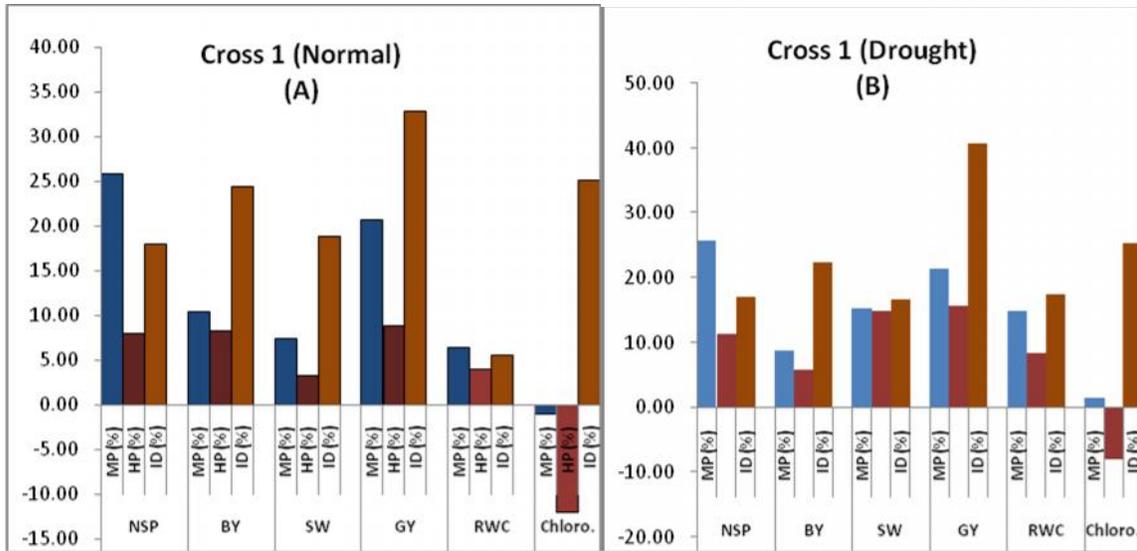


Fig.1. (A&B): Percentage of heterosis and inbreeding depression under two environments in Cross 1 for characters investigated.

HP: High Parent; MP: Mid-Parent;ID: Inbreeding Depression

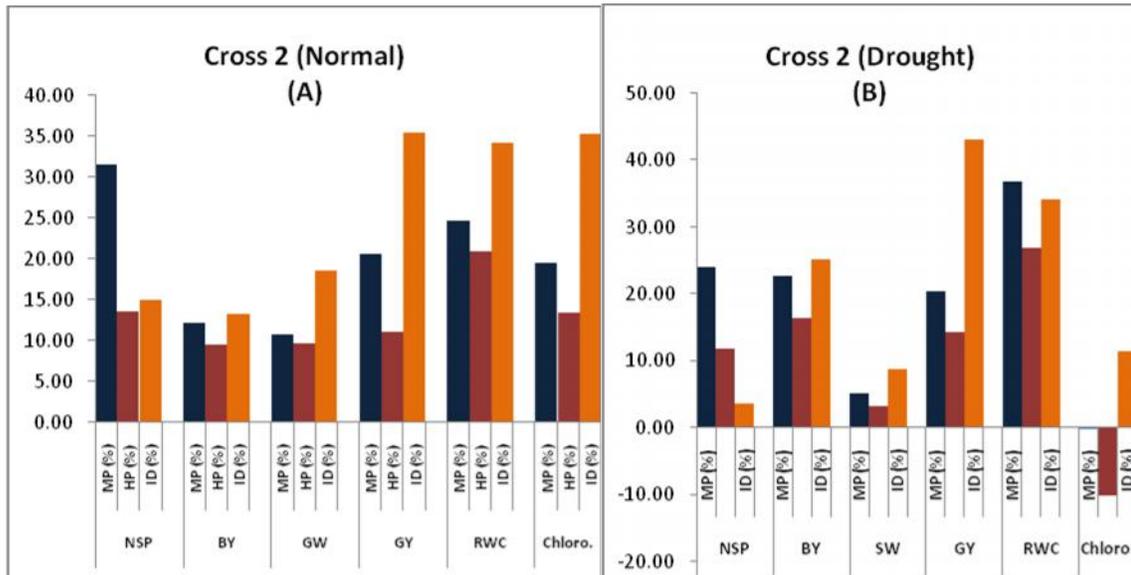


Fig.2. (A&B): Percentage of heterosis and inbreeding depression under two environments in Cross 2 for characters investigated.

HP: High Parent; MP: Mid-Parent;ID: Inbreeding Depression

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404 **4. CONCLUSION**

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406 Genetic analysis showed overdominance in the inheritance of all studied characters under
407 normal and drought conditions in two crosses. The genetic advance in both of tow crosses
408 was high for grain yield under normal and drought conditions; meanwhile it was moderate in
409 number of spikes, RWC and chlorophyll content. The complex genetic behavior especially
410 both of additive x additive and dominance x dominance effects were significant for all studied
411 characters (N&D) in two crosses except RWC under drought in cross 1, whereas several
412 important characters are influenced by dominance and non-allelic gene interaction. It is
413 recommended that selection for improvement of studied traits should be delayed to later
414 generation of segregation population in wheat

415

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422

423 **COMPETING INTERESTS**

424 Author has declared that no competing interests exist.

425

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