



Inheritance of Drought Tolerance Using Six Populations Model in Two Bread Wheat Crosses

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DROUGHT stress is the primary restricting factor of crop productivity in Egypt. The development of drought-tolerant lines is urgent. However, drought tolerance is a complex trait. So, this work aimed to reveal the genetic background and gene effects controlling of yield parameters and to discover the epistasis in two bread wheat crosses; Sakha 93 × pureline 5 and Gemmeiza 10 × pureline 42 under irrigated and drought conditions, utilizing seven generations *viz.* P1, P2, F1, BC1, BC2, F2 and F3.

Genetic analysis revealed that additive and dominance effects are involved in the genetics for most traits in both crosses and conditions. Both additive × additive and additive × dominance effects were significant in most cases, supporting the presence of duplicate type of epistasis. Therefore, early generation selection would have failed.

F1 hybrids (Drought susceptibility indexes were 0.278 in cross I and 0.295 in cross II), were less affected by drought stress conditions, displaying the presence of heterobeltiosis for drought tolerance. Broad-sense and narrow-sense heritabilities and genetic advance ranged from moderate to high for most of the studied traits and these two crosses could be selected to produce high yielding lines under drought conditions.

Keywords: Drought stress, Gene effects, Genetic advance, Seven populations, *Triticum aestivum*.

Introduction

Wheat is considered the important cereal crop in Egypt. Great efforts by wheat breeders must be continued to increase wheat productivity to meet the demands of a growing Egyptian population, specially with the increased incidences of severe drought and high temperature and as water resources become more limiting. Developing drought-tolerance cultivars is the ultimate goal of plant breeders to comprehend the mode of inheritance, the magnitude of gene impacts and their mode of action. Among the environmental stress's, drought is the second contributor to yield decrease after disease losses (Farshadfar et al., 2001, 2003, 2008a; Milad et al., 2016).

Yield is a quantitative trait and is affected by many genetic and non-genetic variables. To

increase yield, it is important to improve agronomic characteristics which influence grain yield by understanding the inheritance pattern of these traits (Singh et al., 1986). Breeders need information about nature of gene action, heterosis, inbreeding depression, heritability and predicted genetic gain from selection for grain yield and its contributing traits. Therefore, the type of gene effect plays a key role in selection of the breeding method for a given trait.

The scaling tests (A, B, C and D) were applied to identify the presence of epistasis as indicated by Mather & Jinks (1982). Generation mean analysis was applied to estimate genetic parameters of mean, additive effects, dominance deviations and effects attributed to non-allelic genetic interactions (epistatic effects) for each trait, utilizing the joint scaling test according to Mather & Jinks (1982).

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Since genetic information got from multi generation are dependable compared with those based on one generation. Therefore, six populations (P1, P2, F1, F2, BC1 and BC2) are considered the one which might be give detailed genetic information for the utilized genotypes.

Heterosis and inbreeding depression are essential approaches for genetic parameter's interpretation in most crops, including wheat. The nature and degree of heterosis and inbreeding depression may potentially assume an essential role in choosing the appropriate breeding methods. Genetic parameters, like genotypic coefficient of variation (GCV) is helpful in detecting the amount of variability present in the germplasm. In addition, information on heritability is basic for selection as it indicates the extent of transmissibility of a character into next generations and the quality of phenotype data in multilocation trials (Sabesan et al., 2009). High heritability estimates reveal the high genetic advance of traits and offers a better scope for genotype selection for early segregating generations (Singh and Chatrath, 1992 and Memon et al., 2005). Therefore, heritability estimates play an important role for planning the suitable breeding strategy.

This study aims to determine the gene action-type controlling grain yield and its contributing traits and discovery of epistasis in the two bread wheat crosses under normal irrigation and drought stress conditions, using seven generations model. This information is essential for the improvement of drought tolerant wheat varieties.

Materials and Methods

Seven generations (P₁, P₂, F₁, BC₁, BC₂, F₂ and F₃) were made from two crosses, the first cross (cross I) was done between two Egyptian cultivars, Sakha 93 and Gemmeiza 10 which demonstrated high yield. Whereas the second cross (cross II) was implemented between two pure lines F₈ (RL 5 and 42) which were characterized as drought tolerant

in a previous study by Said et al. (2015) (Table 1).

The experiments were conducted at the experimental field of the Agronomy department, faculty of agriculture, Sohag university, Egypt during four growing seasons 2015/2016, 2016/2017, 2017/2018 and 2018/2019. The two crosses were produced in 2015/2016 season. The F₁ crosses and four parents were grown in 2016/2017 season to produce F₂, BC₁ and BC₂ and more grains of F₁. In the third season 2017/2018 produced F₃ and more grains of BC₁ and BC₂. In the fourth season of 2018/2019 the obtained grains of seven populations (P₁, P₂, F₁, BC₁, BC₂, F₂ and F₃) of the two crosses were evaluated using randomized complete blocks design with two replicates.

Two irrigation treatments were applied: the first treatment was under full irrigated (irrigation at all stages of plant growth) and the second treatment was under drought stress during grain filling period (water stress was started after anthesis till maturity). Homogenous generations (P₁, P₂ and F₁) were grown in two rows and heterogeneous generations (BC₁, BC₂) in four rows and (F₂, F₃), in six rows, with 10 and 30 cm intra and inter row spacings. The cultural practices were carried out as recommended for wheat production.

Ten competitive individual plants for homogenous generations (P₁, P₂ and F₁) and 40 plants for BC₁ and BC₂, while 60 plants for F₂ and F₃ were phenotyped and the following traits were measured: (i) No. of spikes/plant, (ii) 100-grain weight (gm), (iii) Grain yield/plant (gm), (iv) Biological yield/plant (gm), (v) Relative water content (%) was determined according to Bars and Weatherly (1962), (vi) Chlorophyll concentration (mg cm⁻²) was determined as chlorophyll index using Chlorophyll Meter (SPAD-502), and (vii) Harvest index = (Grain yield)/(Grain + straw yield). Average of meteorological data were computed using ETo_Calculator_V3.2. FAO 2018 (Table 2).

TABLE 1. Pedigree and origin of the genotypes used in bread wheat crosses

Crosses	Parental name	Pedigree	Origin
Cross I	Sakha 93 (P1)	Sakha 92/TR 810328	Egypt
	Pure line 5 (P2)	May'S'/Mon'S'/CMH74A.592/3/Giza 157*2// Tokwie	Egypt//South Africa
	Gemmeiza 10 (P1)	Maya74"s"/On//1160-147/3/Bb/4/ Chat"s"/5/Ctow	Egypt
Cross II	Pure line 42 (P2)	May'S'/Mon'S'/CMH74A.592/3/Giza157*2//Kasyon/glennson-81	Egypt//ICARDA

TABLE 2. Average of meteorological data of the growing season 2018/2019

Measurement	2018 / 2019						
	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Mean
Max. Temp. (C°)	28.7	24.1	22.5	24.7	29.1	34	27.18
Min. Temp. (C°)	13.4	8.4	6.7	8.3	11.6	16.4	10.80
RH (%)	48	52	50	56	30	28	44.00
WS (m/sec.)	1.7	1.5	1.3	1.6	1.8	1.9	1.63
DS (hours/days)	9.4	9.2	9	9.8	10	10.6	9.67

Statistical analysis

Analysis of variance and mean comparison of the characters was done using SAS Software. Generation mean analysis was performed using Mather & Jinks (1982). To estimate the parameters and to select the most suitable model, we used the least squares method and the joint scaling test.

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

$$P = (F_1 - MP) / 1/2 (P_2 - P_1) \text{ where: MP: the mid-parent values} = 1/2(P_1 + P_2).$$

Drought susceptibility index (DSI) values for grain yield was computed as described by Fisher & Maurer (1978). Heterosis (mid parent (MP) and best parent (BP)), inbreeding depression (%) (I.D.%) and genetic coefficient of variation (%) (G.C.V. %) were estimated according to Mather & Jinks (1982).

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

$$H_b^2 = [V_{F_2} - (V_{P_1} + V_{P_2} + V_{F_1})/3] / V_{F_2}$$

$$H_n^2 = [2V_{F_2} - (V_{BC1} + V_{BC2})] / V_{F_2}$$

Expected genetic advance (G_A) from selection was calculated by Johanson et. al. (1955) using 5% selection intensity :

$$G_A = i.H_b.\sqrt{V_{F_2}}$$

The components of F_2 variation were calculated by the formula of Farshadfar (1998):

$$D = 4V_{F_2} - 2(V_{BC1} + V_{BC2})$$

$$H = 4(V_{F_2} - 1/2V_D - V_E)$$

$$E = 1/3 (V_{P_1} + V_{P_2} + V_{F_1})$$

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

where, V is the variance.

Results

The results of the ANOVA and LSD means comparison test revealed significant or highly significant differences between parents and among the other generations for all studied traits in the two crosses under two irrigation treatments. However, the interaction between genotypes and environments was also significant (Table 3).

Data of means of seven generations (Table 4) showed that mean of values of the F1 hybrid in grain yield/plant was more than the mid-parents in the cross I under drought stress conditions. Meanwhile, in cross II, mean of values of the F1 hybrid showed a significant difference between the mid-parents and best-parent under two treatments. Therefore, the F1 hybrids were higher than mid-parent and or best parent in 100-kernel weight in two crosses under two conditions, biological yield/plant in cross I under two treatments, relative water content under normal for two crosses and under drought in cross II and chlorophyll concentration under drought for two crosses and under normal in cross II. The values of potence ratio presented in Table 4, ranged from 0.22 for grain yield to 2.76 for 100 kernel weight under drought stress in the cross I. Meanwhile, potence ratio ranged from 0.02 for relative water content to 6.75 for grain yield under drought conditions in the cross II.

The variation of drought susceptibility indexes (DSI_{GY}) (Table 4) for cross I ranges from 0.278 to 0.596 and for cross II, from 0.295 to 0.503. F1 hybrids ($DSI=0.278$ in cross 1 and 0.295 in cross 2), were less affected by drought stress conditions. The percentage of heterosis with regard to high Parent (HP) and Mid-Parent (MP), Inbreeding Depression (ID) and genotypic

coefficient of variations (GCV) (Fig. 1, 2) exhibited that mid-parent heterosis were positive for all studied traits in two crosses under full irrigated and drought stress, except the number of spikes/plant under irrigated in cross II. Grain yield/plant under full irrigated in cross I and harvest index under two crosses and environments were negative compared with mid-parent. Meanwhile, high-parent heterosis were positive for all studied traits in two crosses under full irrigated and drought stress, except the number of spikes/plant and the harvest index under both crosses and environments, biological yield/plant and grain yield/plant under two conditions in cross I and relative water content under drought in cross II were negative compared with high-parent. Inbreeding depression was positive for all studied characters in two crosses under full irrigated and drought stress conditions. The highest values of genotypic coefficient of variations were obtained for most studied traits in both crosses in two environments.

The results of scaling test for all studied traits in the two crosses under both conditions (Table 5) were significant. The dominance-additive model was suitable and fitted for all the studied traits in two crosses under full irrigated and drought stress conditions. All the genetic components of the mean (m), additive (a), dominance (d), additive x additive (aa) and additive x dominance (ad) gene effects were significant or highly significant for all the characters investigated under two crosses and environments. This indicates that besides

additive and dominance gene effects, epistasis gene effects is also involved in the inheritance of these characters except number of spikes/plant under drought stress in two crosses was under the control of additive type of gene action and epistasis.

Additive gene effect (d) was highly significant for biological yield/plant, relative water content and chlorophyll concentration under full irrigated in cross I and relative water content under drought condition in cross II. Meanwhile, the assessment of dominance gene action (h) was significant for the rest traits in two crosses and environments. The additive and dominance gene effects in two crosses under both environments (Table 6) were important in the inheritance of all studied traits except for the number of spikes/plants under drought stress was under the control of additive type of gene action. But dominant component was more effective than the additive one in cross II under two conditions. Meanwhile, additive variance was more effective than the dominance in cross I for the most traits under drought condition. Both additive x additive (aa) and additive x dominance (ad) effects (Table 5) were significant for all studied characters in two crosses under two environments, supporting the presence of duplicate type of epistasis except number of spikes/plant under drought stress in cross I. However, dominance x dominance (dd) gene effects were also significant for most of the studied traits in cross I, meanwhile in cross II were of minor importance in general for most of the studied traits.

TABLE 3. Analysis of variance for all studied traits

SOV	df	Mean square						
		Number of spikes/plant	100 kernel weight	Biological yield/plant	Grain yield/plant	Harvest index	Relative water content	Chlorophyll concentration
Cross I								
Environments (A)	1	17.36**	7.07**	26810.71**	1271.33**	16.79**	4014.75**	620.70**
A (rep.)	4	4.36	0.27	15.12	12.06	3.47	12.84	7.05
Generations (B)	6	5.47**	0.29**	834.83**	82.17**	96.31**	222.38**	103.27**
A x B	6	0.80**	0.34**	266.97**	64.16**	15.67**	98.03**	22.48**
Error	24	0.22	0.01	2.17	0.59	2.42	1.37	2.11
Cross II								
Environments (A)	1	3.43*	4.91**	5268.82**	916.58**	21.80**	1535.61**	269.04**
A (rep.)	4	2.66	0.20	14.77	4.69	9.69	6.15	5.88
Generations (B)	6	13.35**	0.59**	246.58**	36.87**	80.03**	32.39**	95.82**
A x B	6	1.68*	0.19**	27.78**	7.57**	40.08**	5.12**	17.08**
Error	24	0.74	0.02	1.54	1.72	2.80	1.85	3.63

* and ** significant at 0.05 and 0.01 levels of probability, respectively.

The estimates of genetics of variation in grain yield and its contributing traits are given in Table 6, which show that the estimate of dominance (h/d) for all studied traits was less than one in both crosses under irrigated and drought stress conditions except relative water content under drought in cross II. Meanwhile, for relative water content under drought in cross

II under control of the over dominance type of gene action. Degree of dominance and variance components are presented in Table 5, Ew, D and H are environmental, additive and dominance components, respectively. The ratio of $\sqrt{H/D}$ for all studied characters in two crosses under both environments showed partial dominance except relative water content under stress in cross II.

TABLE 4. Mean comparison of the traits studied under full irrigated (FI) and drought stress (DS) and drought susceptibility index (DSI)

Generations	Number of spikes/ plant		100 kernel weight		Relative water content		Chlorophyll concentration	
	FI	DS	FI	DS	FI	DS	FI	DS
Cross I								
P ₁	14.67±0.29	13.67±0.50	5.70±0.09	4.86±0.12	72.97±1.13	59.70±0.64	49.80±1.01	41.33±0.96
P ₂	12.33±0.28	11.67±0.51	4.99±0.07	4.61±0.13	66.25±0.89	41.67±0.71	43.97±0.75	35.30±0.18
F ₁	14.33±0.25	13.33±0.58	5.92±0.06	5.07±0.11	76.48±1.15	64.98±0.62	52.30±1.09	45.37±0.63
F ₂	12.67±0.29	11.67±0.50	5.01±0.11	4.59±0.10	67.33±0.59	46.13±0.79	43.07±1.06	40.73±0.43
F ₃	13.33±0.28	12.33±0.58	5.23±0.07	4.70±0.11	67.65±1.10	50.30±0.70	46.90±0.55	43.71±0.81
BC ₁	12.67±0.58	12.67±0.50	5.75±0.06	4.52±0.09	68.30±0.79	49.31±0.97	59.11±1.30	44.60±0.53
BC ₂	13.00±0.29	11.33±0.55	5.30±0.11	4.41±0.13	66.05±1.06	42.08±0.68	50.00±0.61	42.30±1.08
LSD _{0.05}	0.92	0.73	0.21	0.89	2.48	1.58	2.32	1.52
Potence ratio	0.71	0.67	1.63	2.76	2.04	1.58	1.86	2.34
Cross II								
P ₁	15.83±0.44	13.83±0.43	5.10±0.07	4.34±0.08	72.10±0.36	60.29±0.49	47.20±0.45	38.80±0.38
P ₂	10.83±0.43	9.83±0.43	5.89±0.08	4.88±0.07	76.13±0.80	64.87±0.45	51.50±0.51	47.00±0.21
F ₁	13.00±0.34	12.83±0.44	6.02±0.07	4.97±0.07	78.36±0.34	62.61±0.16	52.83±0.28	47.43±0.27
F ₂	11.16±1.09	11.67±1.33	4.84±0.31	4.67±0.17	70.04±1.29	58.15±1.45	42.67±1.87	40.07±2.06
F ₃	12.00±0.73	12.67±0.67	5.06±0.11	4.84±0.11	71.92±0.95	61.85±0.78	46.50±0.95	43.67±1.46
BC ₁	14.17±0.73	13.00±0.72	5.51±0.10	4.83±0.10	72.73±0.69	61.84±1.41	44.40±0.64	33.83±1.39
BC ₂	12.17±0.88	11.17±1.09	5.80±0.13	4.91±0.11	75.04±0.79	62.06±1.35	45.80±1.46	44.67±1.37
LSD _{0.05}	1.44	1.61	0.36	0.15	1.87	2.86	2.38	2.40
Potence ratio	0.13	0.50	1.32	1.33	2.11	0.02	1.62	1.11

TABLE 4. Cont.

Generations	Biological yield/plant		Harvest index		Grain yield/plant		DSI
	FI	DS	FI	DS	FI	DS	
Cross I							
P ₁	113.97±0.75	74.60±1.30	36.84±0.38	41.01±0.39	41.99±0.93	30.59±0.73	0.376
P ₂	74.72±0.87	52.95±0.80	46.58±0.98	49.97±0.34	34.30±0.61	26.46±0.88	0.296
F ₁	103.04±1.28	69.79±0.84	38.46±0.72	41.12±0.55	37.03±0.58	28.98±0.68	0.278
F ₂	91.57±0.91	63.07±0.99	38.82±1.90	39.79±1.60	35.54±0.67	25.10±0.62	0.416
F ₃	93.48±0.75	64.99±0.97	33.43±0.78	42.48±0.40	36.75±0.58	25.55±0.67	0.438
BC ₁	95.63±1.42	75.13±1.07	39.31±1.79	39.32±1.78	39.77±0.70	24.92±1.09	0.596
BC ₂	85.30±0.89	53.80±0.93	41.59±1.80	33.17±1.74	29.91±0.74	22.85±0.86	0.309
LSD _{0.05}	3.15	1.95	2.87	2.47	1.30	1.44	
Potence ratio	0.44	0.56	0.67	0.97	0.29	0.22	
Cross II							
P ₁	80.77±0.34	55.90±0.61	43.53±0.18	43.15±0.39	35.16±0.38	24.12±0.42	0.463
P ₂	64.52±0.36	50.82±0.34	51.99±0.66	51.74±0.72	33.54±0.50	25.30±0.63	0.326
F ₁	85.32±0.41	60.79±0.38	43.51±0.14	45.52±0.55	37.12±0.49	28.67±0.38	0.295
F ₂	67.43±1.84	48.50±1.73	43.24±1.50	45.38±1.91	29.16±1.44	22.11±1.35	0.319
F ₃	77.16±1.12	54.16±0.67	45.33±0.78	53.32±0.42	33.61±0.67	23.61±0.38	0.424
BC ₁	84.99±1.12	59.08±0.73	43.56±0.84	43.60±1.43	34.62±0.91	23.03±0.97	0.503
BC ₂	73.26±1.36	47.37±1.09	40.73±0.84	38.98±0.65	33.21±1.02	25.26±1.17	0.315
LSD _{0.05}	2.29	2.12	2.47	3.04	2.15	2.50	
Potence ratio	1.56	2.92	1.00	0.45	3.43	6.75	

The broad-sense heritability estimates were high for all studied characters in the cross II under both conditions and ranged between 81.74% for 100 kernel weight to 97.94% for chlorophyll concentration under drought (Table 6). Meanwhile, in cross I, broad-sense heritability values were varied from a low 34.04% for chlorophyll concentration under full irrigated to moderate 49.87% for relative water content under drought, while it was high 82.87% for harvest index under well-watered. High narrow-sense heritability (greater than 50%) was demonstrated for all studied traits in two crosses under irrigated and drought conditions except grain yield and harvest index under drought, relative water

content and chlorophyll concentration under two conditions in cross I. Meanwhile, in cross II indicated moderate narrow-sense heritability values (20-50%) for number of spikes and relative water content under well-watered, grain yield under well-watered and drought, harvest index under drought conditions. The expected genetic advance (Table 6) ranged from low (4.36) for chlorophyll concentration under drought to high (53.76) for number of spike/plant under drought in the first cross and from low (8.35) for relative water content under well-watered to high (47.85) for number of spike/plant under drought in the second cross. Meanwhile, grain yield/plant was moderate in two crosses under both conditions.

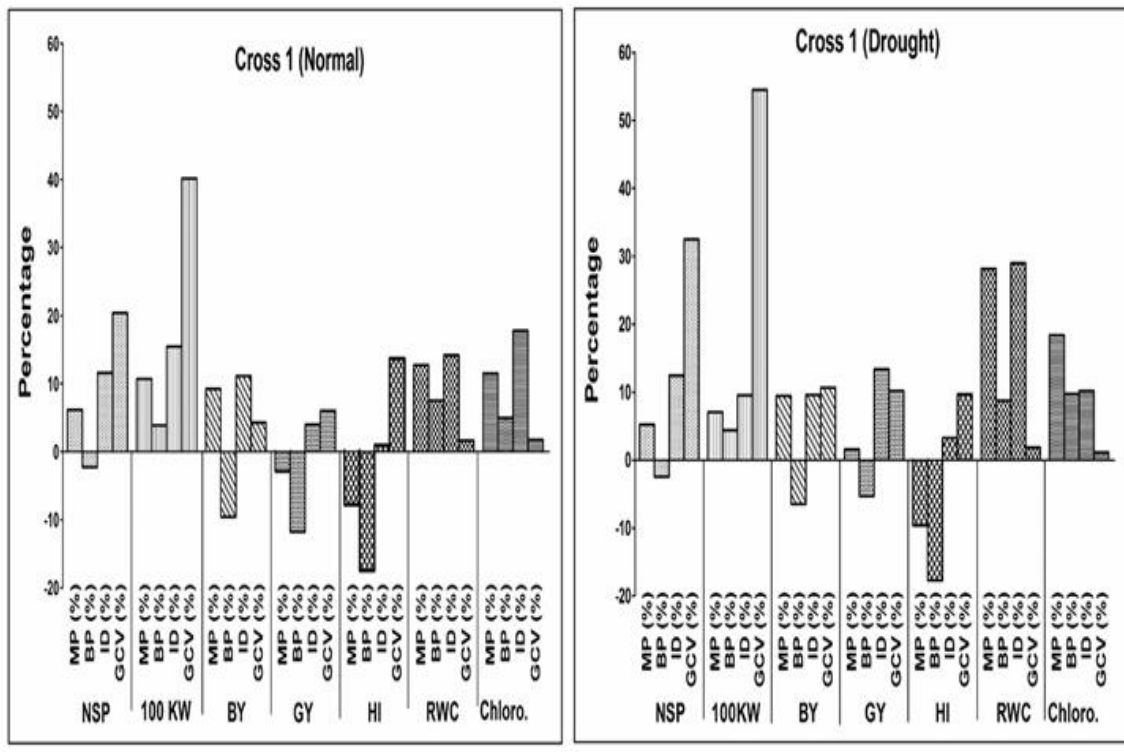


Fig. 1. Heterosis, inbreeding depression (I.D%) and genetic coefficient of variation (G.C.V%) in cross I under normal irrigation and drought stress for all characters investigated

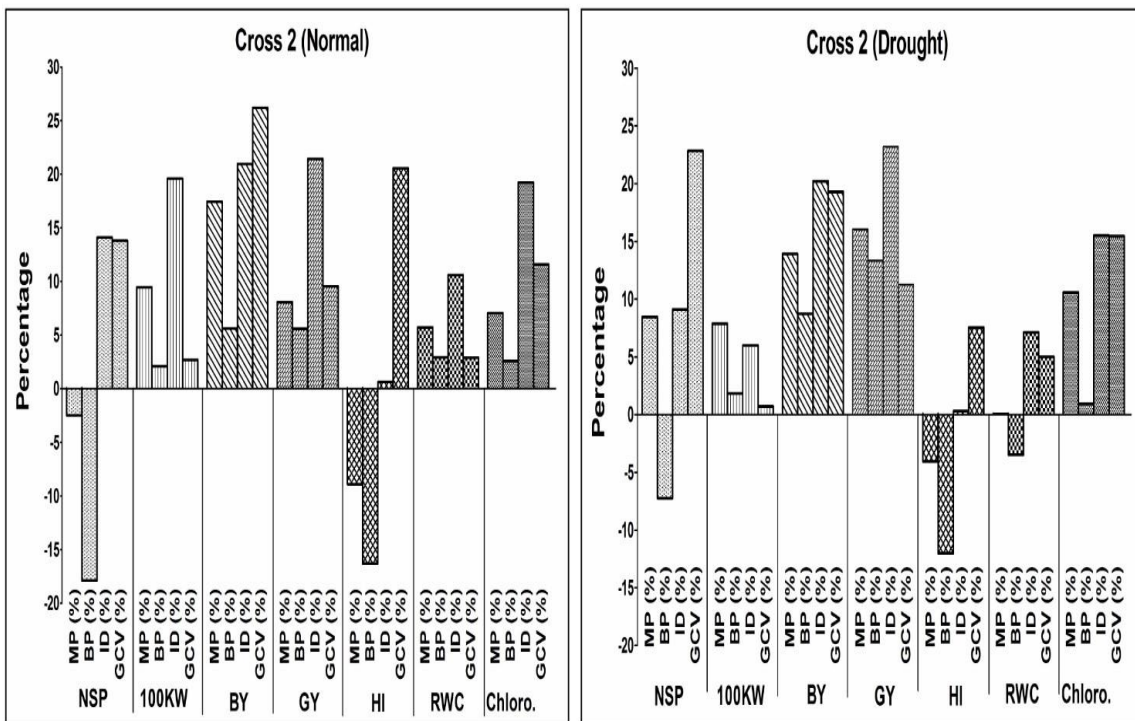


Fig. 2. Heterosis, inbreeding depression (I.D%) and genetic coefficient of variation (G.C.V%) in cross II under normal irrigation and drought stress for all characters investigated

TABLE 5. Estimates of scaling test and types of gene action using generation means for all studied traits in two crosses under full irrigated (FI) and drought stress (DS) conditions based on six parameters model

Characters		Scaling test				Genetic parameters					
		A	B	C	D	m	[a]	[d]	[aa]	[ad]	[dd]
Cross I											
Number of spikes/plant	FI	-1.67**	-0.67**	-5.00**	-1.33**	13.42**	0.67**	3.50*	2.67*	-0.50**	0.33
	DS	-1.66**	-2.33**	-5.33**	-0.67**	23.38**	1.33**	2.00	1.33	0.33**	2.67
100 kernel weight	FI	-0.12*	-0.32**	-2.52**	-1.04**	5.41**	0.45**	2.65**	2.08**	0.10**	-1.64**
	DS	-0.90**	-0.87**	-1.27**	0.25*	4.68**	0.11**	-0.16**	-0.50**	-0.01**	2.27**
Biological yield/plant	FI	-15.76**	-17.17**	-48.51**	-7.79**	98.82**	20.33**	34.28**	15.58**	0.70**	17.35**
	DS	5.88**	-15.15**	-14.84**	-2.79**	64.90**	21.34**	11.59**	5.57**	10.51**	3.70
Grain yield/plant	FI	0.53*	-11.51**	-8.19**	6.24**	35.54**	9.86**	-3.92**	-2.92**	2.80**	13.79
	DS	-9.73**	-9.74**	-14.62**	4.24**	25.10**	2.07**	-4.38*	-4.84**	0.01**	24.30**
Harvest index	FI	7.88**	-18.19**	-5.08**	4.61**	38.82**	8.16**	-8.47**	-5.23**	13.03**	15.53
	DS	-15.79**	-6.14**	-14.06**	2.04*	39.79**	-9.31**	-12.23**	-7.87**	-4.83**	29.80**
Relative water content	FI	-13.85**	-12.64**	-26.86**	-0.19*	69.65**	2.75**	9.23**	0.37**	-0.61**	26.12**
	DS	-26.04**	-22.47**	-46.79**	0.86**	50.59**	7.23**	12.55**	-1.72**	-1.78**	50.23**
Chlorophyll concentration	FI	12.90**	5.13**	-26.37**	-22.20**	49.16**	6.80**	49.82**	44.40**	3.88**	-62.43**
	DS	2.50*	3.93**	-4.43**	-5.43**	41.91**	2.30**	17.92**	10.87**	-0.72**	-17.30**
Cross II											
Number of spikes/plant	FI	-0.50**	0.50**	-8.00**	-0.67**	11.16**	2.00**	2.00*	4.00**	-0.50**	-7.33
	DS	-0.33*	-0.33*	-2.67**	-1.00**	11.67**	2.00**	3.00	2.00*	0.01**	-1.33
100 kernel weight	FI	-0.09*	-0.31**	-3.67**	-0.75**	4.84**	-0.29**	3.79**	3.27**	0.11**	-2.86*
	DS	0.35**	-0.04*	-0.47**	-0.39**	4.67**	-0.07**	1.14**	0.78**	0.19**	-1.09
Biological yield/plant	FI	3.88**	-3.32**	-46.23**	-23.40**	67.43**	11.73**	59.46**	46.79**	3.60**	-47.36*
	DS	1.47**	-16.87**	-34.30**	-9.45**	48.50**	11.71**	26.33**	18.90**	9.17**	-3.50
Grain yield/plant	FI	-3.05**	-4.24**	-26.32**	8.29**	29.16**	1.41**	21.79**	19.03**	0.60**	-11.75
	DS	-6.73**	-3.46**	-18.72**	2.14**	22.01**	-2.22**	12.49**	8.54**	-1.64**	1.64
Harvest index	FI	-7.19**	-6.20**	-12.59**	0.40*	44.00**	-4.77**	-2.67**	-0.81**	-0.49**	14.20
	DS	-11.21**	9.12**	-4.10**	-10.90**	46.59**	-14.58**	1.82**	2.10**	-10.21**	-0.11
Relative water content	FI	-4.99**	-4.41**	-24.77**	-7.68**	70.04**	-2.30**	19.61**	15.36**	-0.29**	-5.96
	DS	-0.78**	-3.38**	-17.79**	-7.60**	58.15**	-0.21**	15.23**	15.20**	2.08**	-12.59
Chlorophyll concentration	FI	-11.23**	-12.73**	-33.70**	-4.87**	42.67**	-1.40**	13.22**	9.73**	0.75**	14.23
	DS	-18.57**	-5.10**	-20.40**	1.63**	40.07**	10.83**	1.27**	-3.27**	-6.73**	26.93*

- m, [a], [d], [aa], [ad] and [dd] denote: Mean, additive, dominance effects, additive x additive, additive x dominance and dominance x dominance, respectively.

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

TABLE 6. Genetic parameters and components of variation for all studied characters in the two crosses under full irrigated (FI) and drought stress (DS) conditions

Genetic parameters	Genetic variance				$\sqrt{H/D}$	$F/\sqrt{H*D}$	h/d	Heritabilities		G.S	
	D	H	F	E				H _b	H _n		
Characters	Cross I										
	Number of spikes/plant	FI	9.10	-3.93	-0.60	1.42	-0.65	14.12	-0.43	78.48	69.11
DS		10.85	-4.80	0.35	1.53	-0.67	15.87	-0.44	79.78	71.53	53.76
100 kernel weight	FI	6.50	-2.48	-0.49	1.35	0.62	29.19	-0.32	93.76	69.33	36.41
	DS	7.01	-2.01	-0.10	1.34	-0.54	28.73	-0.36	93.06	72.30	40.58
Biological yield/plant	FI	10.91	-3.06	1.60	2.56	-0.53	3.42	-0.28	75.40	52.41	12.85
	DS	19.78	-6.29	2.55	5.01	-0.57	2.76	-0.32	72.93	53.46	32.45
Grain yield/plant	FI	7.49	-3.20	0.22	2.49	0.66	4.28	-0.43	63.28	55.18	20.26
	DS	3.33	-0.87	-1.84	3.06	0.51	3.05	-0.30	68.20	48.74	28.93
Harvest index	FI	15.28	-4.64	-0.57	2.20	0.15	4.14	-0.30	82.87	59.52	38.97
	DS	6.98	0.16	1.45	1.61	0.44	2.27	0.16	82.76	35.77	17.09
Relative water content	FI	3.57	-1.34	2.05	3.07	0.62	1.30	-0.38	42.03	33.71	5.42
	DS	2.56	-0.84	-0.70	1.73	0.57	2.08	-0.33	49.87	37.03	5.38
Chlorophyll concentration	FI	2.83	-1.29	-3.29	2.99	0.67	1.69	-0.46	81.13	56.53	6.18
	DS	1.65	-0.72	1.44	1.79	0.66	1.30	-0.43	80.28	50.77	4.36
Cross II											
Number of spikes/plant	FI	3.25	-0.17	0.75	0.50	-0.22	4.43	-0.05	86.05	45.35	29.92
	DS	5.50	-0.75	2.00	0.58	0.93	11.44	-0.14	89.06	51.56	47.85
100 kernel weight	FI	0.48	-0.22	0.02	0.01	-0.61	34.27	-0.37	86.37	68.79	34.27
	DS	0.10	-0.03	0.01	0.02	-0.55	29.66	-0.30	81.74	58.15	29.66
Biological yield/plant	FI	46.42	-11.10	-2.66	1.63	-0.49	5.57	-0.24	93.96	49.03	40.29
	DS	23.45	-4.74	-4.88	1.91	-0.40	3.82	-0.20	90.74	56.86	49.70
Grain yield/plant	FI	5.82	-0.23	1.66	0.64	-0.20	4.42	-0.04	89.76	46.76	20.94
	DS	3.96	0.99	1.25	0.47	0.50	4.20	0.25	91.29	36.44	28.93
Harvest index	FI	19.46	-1.67	0.11	1.62	-0.30	3.14	-0.09	91.63	50.11	22.29
	DS	4.41	2.43	-2.07	0.56	0.74	1.62	0.55	92.39	29.77	9.78
Relative water content	FI	6.60	-2.54	0.47	0.89	-0.62	4.20	-0.38	82.02	66.68	8.35
	DS	1.17	4.65	-0.49	0.45	1.99	2.46	3.99	92.76	49.14	10.89
Chlorophyll concentration	FI	11.60	-1.70	3.45	0.55	-0.39	3.03	-0.15	94.75	55.52	13.75
	DS	13.88	-1.49	-0.10	0.26	-0.33	2.40	-0.11	97.94	54.85	19.32

h/d, H_b, H_n, G.S, D, H, E and F denote: The degree of dominance, broad-sense, narrow sense heritabilities, genetic advance, additive, dominance, environmental components and an indicator of correlation between D and H over all loci, respectively.

Discussion

Developing new cultivars that tolerate drought stress is a key objective for wheat breeders in Egypt to increase the cultivated area of wheat in the new reclaimed lands, where drought stress is the main obstacle. But, the Egyptian wheat cultivars have narrow genetic variability under water limitation. So, the selection within these cultivars to improve wheat yield potential under such conditions would not be effective. Therefore, hybridization between the Egyptian wheat cultivars which showed high yielding and the drought tolerant pure lines was carried out to increase genetic variation, which empowered us to reveal the genetic architecture of yield components and the relationships among breeding materials which is essential to plant breeders for improving this crop under drought stress conditions (Abdel-Nour, 2011; Abd El-Rahman, 2013).

Post-anthesis drought stress is the most important problem influencing wheat production in dryland regions and the effect of water stress on grain filling period is to select stress tolerant genotypes (Wahid et al., 2007; El-Nakhlawy et al., 2015; Milad et al., 2016). The existence of genetic variability for these traits in the studied materials showed that selection possibly successful for the improvement of drought tolerance (Manette et al., 1988; Farshadfar et al., 2001; Tammam, 2005; Farshadfar et al., 2008a; Amin, 2013). Therefore, the advancement of any plant breeding program is reliant upon the presence of genetic variability. Whereas, the efficiency of selection and expression of heterosis likewise depend on the magnitude of genetic variability in the plant population (Singh & Narayanan, 1993; Singh & Chaudhary, 1999; Farshadfar et al., 2001, 2008a, b; Amin, 2013; Abd El-Rady, 2018).

Potence ratio refers to over dominance, where its values exceeded the unity. Meanwhile, potence ratio which less than unity, indicates partial dominance in genetic system controlling the characters. Similar findings were obtained by Yadav & Singh (2011), Amin (2013), Hamam (2014) and Kumar et al. (2017). The quantitative traits in wheat are highly influenced by environment conditions, especially wheat yield. So, the improvement of wheat yield is dependent upon a better understanding of the genetic coefficients of variation, heritability estimates

and type of gene action. Variation is partitioned into heritable and non heritable components order to estimate suitable genetic parameters.

D, H, E and F denote (Table 6); additive, dominance, environmental components and an indicator of correlation between D and H over all loci, respectively. If the ratio of $F/\sqrt{D \times H}$ is equal to one or close one affirms that the magnitude and sign of dominance for all the genes controlling trait is equal, therefore, the ratio $\sqrt{H/D}$ is a suitable estimator of dominance. If $F/\sqrt{D \times H}$ is equal to zero or near to zero, the magnitude and sign of the genes monitoring trait is not equal and hence $\sqrt{H/D}$ explains average dominance. The h/d ratio estimates the degree of dominance (Singh & Chaudhary, 1999; Kearsey & Pooni, 2004; Farshadfar et al., 2001, 2008b). The ratio of $\sqrt{H/D}$ showed partial dominance for all studied characters in two crosses under both environments (Table 6) except RWC under stress in cross 2, indicating over dominance.

According to Mather & Jinks (1982) significant results of the scaling test indicates that the additive-dominance model is inadequate to interpret gene effects. To determine the genetic parameters, one of the best methods is the generations mean analysis (Singh & Singh, 1992; Kearsey & Pooni, 1998), Generation mean analysis is a simple and useful technique in plant breeding for estimating the dominance and additive gene effects and their digenic interactions is helpful in deciding breeding procedures to be adopted for the improvement of quantitative characters like yield.

The dominance and additive gene effects and their digenic (additive x additive and additive x dominance) interactions responsible for inheritance of quantitative characters in both crosses except number of spikes/plant under drought stress was only under the control of additive type of gene action and epistasis (Table 4), regarding the existence of additive and non-additive effects in controlling studied traits, the recurrent selection followed by pedigree breeding can prove useful in improving drought tolerance in bread wheat. It helps us in understanding the performance of the parents used in crosses and potential of crosses to be used either for heterosis exploitation or pedigree selection (Sharma & Sain, 2004).

The importance of both additive and dominance gene action in the inheritance of seed yield per hectare has reported by Mote et al. (2007), Romanus et al. (2008), Uperati (2011) and Pallavi et al. (2019). Patel et. al. (2018) revealed that traits are reflecting via both additive and dominance gene action from one generation to others may be because coupling or repulsion linkage. This can be helpful to accumulate desirable genes and facilitate breaking of unwanted linkage in wheat crop. The dominant effect was more effective than the additive one in the second cross under two environments, demonstrating the improvement of the characters needs intensive selection through later generations in cross 2. Meanwhile, additive variance was more effective than the dominance in the first cross for most traits under drought condition, it's advised that selection in early segregating generations would be successful in cross 1, similar results were reported by El-Hosary et al. (1997), Tammam (2005), Amin (2013).

The proposed drought susceptibility index (DSI) of genotypes by Fischer & Maurer (1978) was calculated by determining the changes in grain yield (GY) under irrigated and drought stress. Knowledge of the degree of heterosis and inbreeding depression together provide information about type of gene action involved in the expression of different quantitative characters. F1 hybrids (DSI= 0.278 in cross 1 and 0.295 in cross 2), were less affected by drought stress conditions (Table 4), displaying the presesnce of heterobeltiosis for drought resistance in the F1 hybrid.

The selection efficiency is related to the magnitude of heritability and genetic advance (Johnson et al., 1955; Singh & Narayanan, 1993). Whereas heritability estimates along with genetic advance are important selection parameters and normally more helpful in predicting the gain under selection than heritability estimates alone. However, heritability estimates are impacted with the type of genetic material, sample size, technique of sampling, conduct of experiment, method of calculation and effect of linkage. Genetic advance which refers to the improvement in the mean genotypic value of selected individuals over the parental population is affected with the genetic variability, heritability and selection intensity (Alza & Martinez, 1997; Sharma, 2003).

This integral interaction increases the variation between the generation and in the segregating population. Where, the crosses, which demonstrated high heritability values coupled with high genetic advance, also indicated highest means in the two conditions, opportunity to discover stress tolerant breeding material in segregating populations of these crosses are promising.

Conclusion

The investigated traits in the present study have shown complex genetic behaviour. Additive, dominance and epistatic effects seemed to have played roles in the inheritance of all studied traits in both crosses. Whereas, in the cross combination Sakha 93/ RL 5, additive variance was more effective than the dominance for most traits under drought condition, it is suggested that the selection in early segregating generations could be significant for the improvement of these traits. Meanwhile, in the cross combination Gemmeiza 10/ RL 42, the dominant effect was more effective than the additive one under full irrigated and drought stress, the improvement of the characters needs intensive selection through advanced generations. The epistasis has been expressed through influencing traits and it is recommended that breeders should be aware of this as a source of variation that may influence predicted gain in a selection program. The information on genetics of various contributing traits would help wheat breeders in the selection of breeding programs which can exploit additive as well as non-additive gene effects for improving these traits.

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وراثة تحمل الجفاف باستخدام نموذج الستة عشائر في هجينين من قمح الخبز

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الإجهاد الناتج عن الجفاف هو العامل الأساسي الذي يحد من إنتاجية المحاصيل ، وأصبح تربية السلالات للمقاومة للجفاف أكثر أهمية ، ووراثة تحمل الجفاف سمة معقدة ، لذلك تهدف هذه الدراسة إلى التعرف على وراثة وتأثيرات فعل الجينات وتفاعلاتها التي تتحكم في معاملات الغلة في هجينين من قمح الخبز هما (سحا 93 × سلالة 5) و (جميزا 10 × سلالة 42) تحت ظروف الري الطبيعي والجفاف، باستخدام سبعة أجيال هم الأب الأول، الأب الثاني، الجيل الأول، الجيل الثاني، الجيل الثالث، الهجين الرجعي الأول والهجين الرجعي الثاني، حيث تم إجراء البحث في المزرعة البحثية بالكوثر، كلية الزراعة، جامعة سوهاج، سوهاج، مصر.

أظهر التحليل الجيني أن كل من تأثيرات الجينات المضافة والسيادية هي المتكيفة في معظم الصفات في كل من الهجينين تحت ظروف الري الطبيعي والجفاف، كذلك كانت تأثيرات تفاعلاتها من النوع المضافة x المضافة والسيادية x السيادية هي المتكيفة في معظم الصفات، مما يظهر أن اختيار الأجيال المبكرة للانتخاب قد تؤدي إلى الفشل. كما أظهرت النتائج أن نباتات الجيل الأول كانت أقل تأثرًا بظروف إجهاد الجفاف، حيث كان معامل الحساسية للجفاف له هو 0.278 للهجين الأول وكان 0.295 للهجين الثاني. كما تراوحت قيم درجة التوريث العامة والخاصة والتقدم الوراثي من متوسط إلى مرتفع لمعظم الصفات المدروسة للهجينين، وبناء على هذه النتائج يمكن الاستفادة من هذين الهجينين لإنتاج سلالات عالية الغلة لظروف الجفاف.