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Genetic Analysis of Agronomic Traits in Bread Wheat Using Six Parameters Model under Heat Stress

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INHERITANCE of yield and yield contributing characters were investigated using generation mean analysis, utilizing the means of six populations in parents, F1, F2 and backcross generations of three crosses of bread wheat using six parameters model under favorable and heat stress conditions. This study was carried out during the three successive seasons of 2009/2010, 2010/2011 and 2011/2012 at the Experimental Farm of Faculty of Agriculture, Sohag University, Egypt. The objective of this study was to determine nature of gene action controlling yield and its components. Additive (d) and additive x additive were highly significant and positive for most traits in all the three crosses under favorable sown and heat stress, suggesting the possibility of obtaining further improvements of these traits using a pedigree selection method. Dominance and dominance x dominance gene actions were also found, though the significance and direction was specific for each environment and genotypic cross, indicating the importance of dominance gene effects. Heritability estimates in narrow sense in F_2 were relatively high to moderate more than 34.26% and 42.22% under favorable and heat stress, respectively. The promising crosses were the first cross (Giza164 x Qimma 4) and third cross (Gemmeiza 9 x Johara14), were found to high in magnitude which had high genetic advance associated with high heritability and would be interest in breeding programs for heat tolerance.

Keywords: Wheat, Gene action, Gene effects, Epistasis, Additive, Dominance, Heritability, Six parameters model, Heat stress.

Wheat (Triticum aestivum L.) was considered as important cereal crop not only in Egypt but also all over world. There was an increasing demand in wheat-world wide. The annual world production of wheat amounts to 670,875,110 tones. After maize and rice, wheat ranks as the third most important crop in the world (FAO, 2012). In the world, there was an urgent need to increase the productivity of wheat to reduce the food gap resulting from population increase.

Generation mean analysis, which provide the estimates of main gene effects (additive and dominance) along with their digenic interactions (additive x additive, additive x dominance and dominance x dominance) helps in understanding the nature of gene effects involved in different traits concern and

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accordingly the breeding procedure could be applied in developing superior populations. The study of the genotype by environment interaction and the estimation of genetic parameters were needed, once it provides information about the nature of genes involved in the inheritance of traits under investigation and help in choosing the most satisfactory breeding method, what helps breeders to make decisions. Bayoumi *et al.* (2008) found that additive dominance model were adequate for revealing the inheritance of grain yield and its components. Yap (1993) studied the inheritance pattern of long bean through diallel cross, which does not provide the estimates of different non-allelic gene interactions operating in the inheritance. Epistasis, which was known to play an important role in the expression of heterotic potential, has been demonstrated by Rebetzke *et al.* (2003). Sharma *et al.* (2003), indicated that both additive and non-additive gene effects were predominant for most studied traits, though the non-additive gene effects were also important.

The Upper Egypt region presents an inconvenient high temperatures occurrence during the wheat cycle special. Heat stress, due to increased temperature, was an agricultural problem in many areas in the world (Wahid *et al.,* 2007). Many studies have confirmed the damaging effect of heat on wheat (Rane & Nagarajan, 2004 and Cargnin *et al.,* 2006), as well as the presence of genotype by environment interaction under contrasting temperature conditions (Cargnin *et al.*, 2006), Haj *et al.* (2007), El-Marakby *et al.* (2007) and Khan *et al.* (2007) found reduction of days to heading, plant height, no. of spikes/m^2, no. of kernels/spike, 1000-kernel weight and final grain yield with delayed sowing date. The major yield components in wheat were tillers/plant, kernels/spike and 1000-kernel weight (Maloo *et al.*, 1993). Hu & Rajaram (1994) also reported that kernels/spike could be considered a potential selection criterion under late sown condition. High temperature has been used as a screening tool for predicting high wheat yield in rainfed environments (Olivares-Villegas *et al.,* 2007). The potential of high temperature for screening wheat genotypes was based on its significant correlations with grain yield (Reynolds *et al.*, 2001) and the genotype differences observed between cultivars (Araus *et al.,* 2003).

The objectives of this study were to determine: i) The nature of gene action controlling yield and its component in three wheat crosses grown under favorable and heat stress conditions, ii) Estimate heterosis, inbreeding effect, potence ratio, broad and narrow sense heritability, genetic advance and as selection parameters in bread wheat.

Material and Methods

Six bread wheat cultivars representing a wide range of diversity were chosen as parents in this study under heat stress to obtain the following three crosses. Three of these cultivars were adapted and heat tolerant (Giza164, Giza168 and Gemmeiza 9) in Egypt. While the others were introduced (Qimma 4, Cham 6 and Johara14) from ICARDA-Syria. The parental genotypes were used to obtaine the following crosses; cross 1 (Giza164 x Qimma 4); cross 2 (Giza168 x

Cham 6) and cross 3 (Gemmeiza 9 x Johara14). The present study was carried out at the experimental farm of Faculty of Agriculture, Sohag University, Sohag, Egypt during the three successive seasons 2009/2010 to 2011/2012. In the first season 2009/2010, the parental genotypes were crossed to obtain F_1 kernels. In the second season 2010/2011, the hybrid kernels of the three crosses were sown to give F_1 plants, at the same time, these plants were selfed to produce F_2 and some of F_1 plants of each cross were backcrossed to each of the both parents to produce the backcrosses (BC_1 and BC_2). In 2011/2012, the six populations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of the three crosses were sown in a randomized complete block design with three replications under two different sowing dates, favorable sown date as "Favorable", 15 November; (D1) and late sowing date as "Heat stress", 20 December; (D2) in two separate experiments (Table 1). Experimental unit consisted of four rows for each genotype of the two parents and F1 and five rows for each of the two backcrosses and 10 rows for the F2 population. Row was 3.5m in length, 30 cm apart and 10 cm between kernels within a row. Data were recorded on 20, 20, 20 and 200 plants which were selected at random for both parents, F1, backcrosses and F2 of each cross, receptively. The type of soil in which the plants were grown surface layer of experiment soil was clay compared with subsurface layer which transported layer as results of reclamations.

TABLE 1. Maximum and minimum air temperatures (ºC) in Sohag during wheat growth stages in favorable (November) and heat stress conditions (December).

Months	Years					
	2009/2010		2010/2011		2011/2012	
	Max.	Min.	Max.	Min.	Max.	Min.
November	26.16	13.43	29.23	13.52	22.03	8.57
December	22.54	8.67	24.41	10.18	21.37	7.55
January	23.29	8.03	19.05	7.51	18.93	4.22
February	26.51	8.03	27.64	9.42	20.81	7.09
March	28.76	13.35	28.02	10.83	23.20	8.00
April	33.81	12.00	33.49	20.53	31.58	15.75
May	36.81	22.96	36.00	25.6	39.55	26.41

Statistical and genetic analysis

Tests for scale effects were computed following the methods explained by Mather (1949) and Hayman & Mather (1955). Estimation of different gene effects in the interacting crosses were done using six parameters (Hayman, 1958) and three parameters (Jinks & Jones, 1958) models. The quantities A, B and C

and their variances were calculated to test adequacy of the additive-dominance model in each case where: $A = 2\overline{BC1} - \overline{P1} - \overline{F1}$, $B = 2\overline{BC2} - \overline{P2} - \overline{F1}$, $C = 4\overline{F2} - 2\overline{F1} - \overline{P1} - \overline{P2}$. The variances of these estimates were calculated as follows:-

$$V_A = 4V(\overline{BC1}) + V(\overline{P1}) + V(\overline{F1}) , V_B = 4V(\overline{BC2}) + V(\overline{P2}) + V(\overline{F1}) \text{ and}$$

$$V_C = 16V(\overline{F2}) + 4V(\overline{F1}) + V(\overline{P1}) + V(\overline{P2}),$$ the standard error of A, B, C and D were obtained by taking the square root of their respective variance. *T–test* values were calculated by dividing the effects of h, d, i, j and L on their respective standard errors. Generation means were analysed using the procedure of Gamble (1962) for estimation and separation of gene effects involved in the inheritance of yield and its component into six parameters. Hayman (1958) and Jinks & Jones (1958) gave six-parameter model for estimations of various genetic components. According to Hayman (1958);

$$m = Mean = \overline{F2} , d = Additive.effect = \overline{BC1} - \overline{BC2} ,$$

$$h = Do\min ance.effect = \overline{F1} - \overline{F2} - 0.5(\overline{P1}) - 0.5(\overline{P2}) + 2(\overline{BC1}) + 2(\overline{BC2})$$

$$i == Additive * Additive.type.of.gene.\operatorname{int} eraction = 2(\overline{BC1}) + 2(\overline{BC2}) - 4\overline{F2}$$

$$j = Additive * Do\min ance.type.of.gene.\operatorname{int} eraction = \overline{BC1} - 0.5(\overline{P1}) - (\overline{BC2}) + 0.5(\overline{P2})$$

$$L = Do\min ance * Do\min ance.type.of.gene.\operatorname{int} eraction = \overline{P1} + \overline{P2} + 2\overline{F1} + 4\overline{F2} - 4(\overline{BC1}) - 4(\overline{BC2})$$

The variance values in this concern were obtained as follows:- $V_m = V(\overline{F2})$,

$$V_d = V(\overline{BC1}) - V(\overline{BC2})$$

$$V_h = V(\overline{F1}) - 16V(\overline{F2}) - 0.25V(\overline{P1}) - 0.25V(\overline{P2}) + 4V(\overline{BC1}) + 4V(\overline{BC2})$$

$$V_i = 4V(\overline{BC1}) + 4V(\overline{BC2}) - 16V(\overline{F2})$$

$$V_j = V(\overline{BC1}) - 0.25V(\overline{P1}) - V(\overline{BC2}) + 0.25V(\overline{P2}) .$$

$$V_l = V(\overline{P1}) + V(\overline{P2}) + 4V(\overline{F1}) + 16V(\overline{F2}) - 16V(\overline{BC1}) - 16V(\overline{BC2}) .$$

The standard error of h, d, i, j and L was obtained by taking the square root of their respective variance. The predicted genetic advance (GA) calculated using the procedure of Allard (1960) as follow: (GA) = h^2 *x* (σP) *x* K, where: σP = standard deviation, h^2 = heritability in narrow sense, K = constant value that reflects the selection intensity. The value for K (2.06) in this study was used in 5% selection intensity. Heterosis was determined as the percent of the deviation of F_1 hybrid from its better parent (BP) or its mid-parent (MP) values as this formula for better-parent (BP) = [(F_1 – B.P.)/ B.P. X 100] where; F_1 is the mean of F_1 hybrid. B.P. is the mean of the better parent. Or for mid-parent (MP) = [(F_1 – M.P.)/ M.P. X 100] where; M.P. is the mean of the (P_1 + P_2)/ 2. Inbreeding depression was estimated as the average percentage decrease of the F_2 from the F_1, potence ratio (P) was also calculated according to Peter & Frey (1966). Heritability in broad and narrow sense were estimated according to the formulae provided by Mather (1949).

Results and Discussion

Mean performance

Mean and standard error of the studied traits in the three crosses for six populations P_1, P_2, F_1, F_2, BC_1 and BC_2 under favorable and heat stress treatments presented in Table 2. Analysis of variance indicted that there were significant differences among generations in all traits under this study. The results revealed that generation means were significantly different for all studied traits in all crosses. The F_1 mean values exceeded the mid values of the two parental means for most of studied traits in the three crosses under favorable sown and heat stress treatments, indicating the prevalence of heterotic effects and presence of dominance effects controlling these traits. For heading date the cross 3 was earlier than the mid parent indicating the presence of partial dominance. F_1 means were larger than the high performing parent for; 1000- kernel weight and grain yield/plant under favorable sown and heat treatments in all crosses, while for heading date the cross 1, spike length in crosses 1 and 2, number of spikes/plant in crosses 1 and 3 and number of kernels/spike in crosses 1 and 2 under favorable sown and heat stress treatments indicating that increasing allels were more frequent than decreasing one under stress condition.

The F_2 populations mean performance values were intermediate between the two parents and less than F_1 mean performance values for all most traits confirming the importance of non-additive gene action for the studied traits. While, the mean performance of F_2 population recorded high values for most studied traits under favorable sown. However, the two populations (BC_1 and BC_2) mean performance values varied under the two levels of favorable sown and heat stress treatment and each trait tended toward the mean of its recurrent parent, reflecting the effect of epistasis. These results were in line with those obtained by Farag (2009) and Amin (2013).

Estimation of type of gene action

Scaling and joint scaling test

The values of A, B and C should be equal zero within the limits of their standard error. The significant of any one of those scales was taken to indicate the presence of non- allelic interaction. Estimation of gene effects using six parameter model revealed the interaction components to be significant. Hence the six parameter model was employed to allow estimation of the additional parameters that were necessary to specify the effects of interaction of non-allelic genes. Testing for non- allelic interaction with the six parameter model and type of epistasis under favorable sown and heat stress treatments given in Table 3. The A, B and C scaling test almost all crosses and traits were found significant. However, the scaling test A some crosses for few traits like cross 1 for days to heading, crosses 1 and 3 for spike length and cross 3 for grain yield were not significant under favorable and heat stress treatments (Table 3).

TABLE 2. Mean performance ± standard error of P_1, P_2, F_1, F_2, BC_1 and BC_2 of three crosses combinations for various quantitative traits in bread wheat under favorable and heat stress conditions.

Sowing date	Crosses	Generations					
		P_1	P_2	F_1	F_2	BC_1	BC_2
		Days to heading					
Favorable	Cross 1	81.62±0.25	79.30±0.19	84.14±0.62	80.64±0.32	83.08±0.56	74.86±0.47
Heat stress	Cross 1	62.85±0.28	63.44±0.21	65.63±0.72	59.67±0.38	65.63±0.67	60.64±0.54
Favorable	Cross 2	98.33±0.15	89.30±0.14	95.84±0.36	92.94±0.24	91.86±0.32	87.08±0.46
Heat stress	Cross 2	80.63±0.17	72.33±0.16	78.59±0.41	73.42±0.28	76.24±0.36	71.41±0.46
Favorable	Cross 3	98.68±0.13	91.68±0.14	94.63±0.40	91.68±0.45	89.08±0.42	86.86±0.35
Heat stress	Cross 3	73.02±0.15	68.76±0.16	68.13±0.47	64.18±0.54	65.47±0.48	63.84±0.41
		Spike length (cm)					
Favorable	Cross 1	11.88±0.13	10.00±0.15	12.56±0.30	11.11±0.22	11.62±0.33	10.38±0.26
Heat stress	Cross 1	10.34±0.15	8.40±0.17	10.93±0.35	9.11±0.25	10.23±0.38	8.93±0.30
Favorable	Cross 2	10.0±0.14	9.98±0.15	11.56±0.46	11.18±0.29	12.42±0.47	10.28±0.39
Heat stress	Cross 2	8.98±0.16	8.68±0.17	9.94±0.52	9.50±0.33	10.81±0.53	8.94±0.44
Favorable	Cross 3	11.50±0.13	9.40±0.19	10.80±0.21	10.60±0.14	11.20±0.32	9.40±0.23
Heat stress	Cross 3	9.66±0.14	7.99±0.22	8.86±0.25	8.27±0.17	9.07±0.37	7.71±0.27
		Number of spikes/plant					
Favorable	Cross 1	10.80±0.09	9.00±0.10	12.60±0.32	11.01±0.24	10.24±0.26	9.16±0.31
Heat stress	Cross 1	7.78±0.12	6.39±0.13	9.20±0.40	8.81±0.29	7.48±0.32	6.46±0.39
Favorable	Cross 2	11.80±0.13	7.54±0.13	8.98±0.42	8.44±0.37	9.46±0.32	8.32±0.42
Heat stress	Cross 2	8.61±0.16	5.43±0.16	6.38±0.52	6.37±0.25	7.10±0.40	5.74±0.52
Favorable	Cross 3	15.64±0.14	14.78±0.13	16.46±0.33	15.89±0.26	17.12±0.32	15.05±0.29
Heat stress	Cross 3	11.89±0.16	11.38±0.14	12.35±0.37	11.92±0.29	13.18±0.36	11.44±0.33
		Number of kernels/spike					
Favorable	Cross 1	55.68±0.26	44.00±0.27	64.12±0.40	58.66±0.31	65.88±0.48	63.66±0.48
Heat stress	Cross 1	37.86±0.34	29.48±0.34	42.96±0.51	36.37±0.40	45.46±0.58	43.29±0.60
Favorable	Cross 2	53.57±0.26	48.42±0.27	58.24±0.73	54.38±0.39	57.77±0.66	54.54±0.58
Heat stress	Cross 2	36.96±0.34	32.93±0.33	39.02±0.91	35.35±0.50	39.28±0.82	36.27±0.72
Favorable	Cross 3	73.66±0.15	64.88±0.12	69.22±0.38	67.46±0.22	72.12±0.26	67.89±0.34
Heat stress	Cross 3	52.30±0.17	46.71±0.15	46.38±0.49	42.50±0.29	49.04±0.34	45.49±0.44
		1000-Kernel weight (g)					
Favorable	Cross 1	48.12±0.25	40.00±0.23	52.70±0.49	49.22±0.32	52.80±0.45	50.44±0.39
Heat stress	Cross 1	37.53±0.33	30.80±0.31	41.11±0.64	37.41±0.43	41.71±0.58	39.34±0.50
Favorable	Cross 2	49.00±0.25	42.00±0.27	56.00±0.79	53.20±0.42	56.0±0.65	53.30±0.77
Heat stress	Cross 2	39.20±0.32	33.18±0.35	43.68±1.03	40.96±0.56	45.36±0.83	42.05±0.98
Favorable	Cross 3	50.00±0.17	47.80±0.19	52.60±0.63	48.80±0.26	52.80±0.32	49.80±0.52
Heat stress	Cross 3	38.00±0.23	35.85±0.25	38.40±0.84	34.65±0.36	38.54±0.43	36.35±0.70
		Grain yield/plant (g)					
Favorable	Cross 1	30.78±0.24	27.04±0.22	34.24±0.63	29.20±0.35	33.98±0.38	29.88±0.67
Heat stress	Cross 1	19.39±0.30	17.31±0.27	20.89±0.78	17.52±0.44	21.07±0.46	18.82±0.82
Favorable	Cross 2	36.26±0.16	34.56±0.19	43.28±0.62	39.36±0.33	42.88±0.49	40.24±0.62
Heat stress	Cross 2	24.29±0.20	22.81±0.23	28.13±0.74	24.80±0.41	28.30±0.59	26.16±0.75
Favorable	Cross 3	37.78±0.25	36.64±0.29	40.87±0.74	38.08±0.39	40.24±0.42	36.46±0.77
Heat stress	Cross 3	23.42±0.31	23.08±0.37	24.52±0.94	21.71±0.50	25.35±0.53	22.24±0.98

Cross 1 = (Giza 164 x Qimma 4), Cross 2 = (Giza168 x Cham 6), Cross 3 = (Gemmeiza 9 x Johara14)

TABLE 3. Scaling and joint scaling test of generation mean for various quantitative traits in the three crosses of bread wheat under favorable and heat stress conditions.

Sowing date	cross	Scaling and joint scaling test		
		A	B	C
Days to heading				
Favorable	Cross 1	0.40	-13.72**	-6.64**
Heat stress	Cross 1	2.79	-7.80**	-18.85**
Favorable	Cross 2	-10.45**	-10.98**	-7.55**
Heat stress	Cross 2	-6.73**	-8.11**	-16.45**
Favorable	Cross 3	-15.15**	-12.59**	-12.90**
Heat stress	Cross 3	-10.21**	-9.21**	-21.35**
Spike length				
Favorable	Cross 1	-1.20	-1.80**	-2.56*
Heat stress	Cross 1	-0.81	-1.47*	-4.15**
Favorable	Cross 2	3.08**	-0.98	1.42
Heat stress	Cross 2	2.69*	-0.74	0.47
Favorable	Cross 3	0.10	-1.40*	-0.10
Heat stress	Cross 3	-0.37	-1.43*	-2.29**
Number of spikes/plant				
Favorable	Cross 1	-2.92**	-3.28**	-0.96
Heat stress	Cross 1	-2.02**	-2.67**	2.67
Favorable	Cross 2	-1.86*	0.12	-3.54*
Heat stress	Cross 2	-0.80	-0.32	-1.31
Favorable	Cross 3	2.14**	-1.14	0.22
Heat stress	Cross 3	2.13**	-0.85	-0.29
Number of kernels/spike				
Favorable	Cross 1	11.96**	19.20**	6.72**
Heat stress	Cross 1	10.09**	14.14**	-7.79**
Favorable	Cross 2	3.73*	2.42	-0.95
Heat stress	Cross 2	2.58	0.59	-6.54*
Favorable	Cross 3	1.36*	1.68*	-7.14**
Heat stress	Cross 3	-0.59	-2.12*	-21.77**
1000-grain weight				
Favorable	Cross 1	4.78**	8.18**	3.36**
Heat stress	Cross 1	4.78**	6.78**	-0.92
Favorable	Cross 2	8.40**	8.60**	9.80**
Heat stress	Cross 2	7.84**	7.25**	4.12
Favorable	Cross 3	3.00**	-0.80	-7.80**
Heat stress	Cross 3	0.69	-1.54	-12.05**
Grain yield/plant				
Favorable	Cross 1	2.94**	-1.52	-9.50**
Heat stress	Cross 1	1.86	-0.54	-8.39**
Favorable	Cross 2	6.22**	2.64	0.06
Heat stress	Cross 2	4.18**	1.37	-4.18
Favorable	Cross 3	1.83	-4.59**	-3.84
Heat stress	Cross 3	2.76	-3.12	-8.73**

$* p < 0.05$, $**p < 0.01$.

While, the scaling test B in cross 2 for spike length, in crosses 2 and 3 for number of spikes/plant, in cross 2 for number of kernels/spike, in cross 3 for 1000-kernel weight and in crosses 1 and 2 for grain yield under favorable sown and heat stress treatments were found not significant. As well as, the scaling test C in cross 2 for spike length, in crosses 1 and 3 for number of spikes/plant and in cross 2 for grain yield under favorable sown and heat stress treatments showed not significant. These results, in general indicated that the presence of non-allelic interaction for all studied traits in all crosses under study except number of spikes/plant in cross 2 under heat stress. It was worthy to mention that if scaling test A, B and C were significant this indicate to the inadequacy of the simple model in interpreting the differences between population means. Also, the scaling test estimates for the excepted traits indicated the absence of non-allelic interactions and additive-dominance mode was adequate. These results were in agreement with El-Aref *et al.* (2011) and Amin (2013).

Gene action and epistasis

The estimate of mean parameter (m) for all studied traits which reflected the contribution due to the overall mean plus the locus effects and interactions of the fixed loci was found to be highly significant of the three crosses under favorable and heat stress treatments (Table 4). It was suggested that the additive (d) effect was significantly positive for all traits under favorable sown and heat stress. This clearly indicated the significant contribution of additive gene effects in the inheritance of these traits in respective crosses. Additive (d) gene effect was more important than dominance (h) in the genetic control of spike length, indicating that this character was relatively simply inherited (Sharma *et al.,* 2003). Additive gene effect (a) was quiet small in magnitude relative to the dominance gene effects. Additive gene effect was found for number days to heading, spike length, number of spikes/ plant, number of kernels/ spike, 1000-kernel weight and grain yield/ plant (Farag, 2009 and Hamam, 2013).

However, the dominance effects were reported for days to heading under heat stress (El-Sayed & El-Shaarawy, 2006). The dominance effects (h) for number of kernels/spike, 1000-kernel weight and grain yield/plant in all crosses under favorable sown and heat stress was significant and positive. As well as for; days to heading and spike length in cross 1 were significant and positive under heat stress, indicating the importance of dominance gene effects in the inheritance of these traits; and their magnitude was also higher than that of additive effects, suggesting greater important of dominance effects in the expression of these traits. While days to heading in crosses 1 and 3 and number of spikes/plant in cross 1 were significant and negative under favorable sown indicate diminishing effect could occur in the expression of these traits. On the other hand, significant of (d) and (h) components indicated that both additive and dominance gene effects were important in the inheritance of these traits and selecting desirable traits would be effective in the late generations. The epistatic gene effects with higher estimate of (h) effects could contribute a sizeable part of variation for these traits (Hendawy, 2003 and El-Aref *et al.,* 2011).

TABLE 4. Estimates of gene effects and components of variance for quantitative traits in the three crosses of bread wheat under favorable and heat stress conditions.

Sowing date	cross	Gene effects						Epistasis
		Mean (m)	Additive (d)	Dominance (h)	Additive x Additive (i)	Additive x Dominance (j)	Diminance x Dominance (L)	
				Days to heading				
Favorable	Cross 1	80.64**	8.22**	-3.00	-6.68**	7.06**	20.00**	D
Heat stress	Cross 1	59.67**	5.00**	16.33**	13.85**	5.29**	-8.84*	D
Favorable	Cross 2	92.94**	4.78**	-11.86**	-13.88**	0.27	35.31**	D
Heat stress	Cross 2	73.42**	4.84**	3.72*	1.61	0.69	13.23**	C
Favorable	Cross 3	91.68**	2.22**	-15.39**	-14.84**	-1.28*	42.58**	D
Heat stress	Cross 3	64.18**	1.63**	-0.83	1.93	-0.50	17.49**	D
				Spike length				
Favorable	Cross 1	11.11**	1.24**	1.18	-0.44	0.30	3.44	C
Heat stress	Cross 1	9.11**	1.30**	3.42*	1.86	0.33	0.42	C
Favorable	Cross 2	11.18**	2.14**	2.15	0.68	2.03**	-2.78	D
Heat stress	Cross 2	9.50**	1.86**	2.60	1.49	1.72**	-3.44	D
Favorable	Cross 3	10.60**	1.80**	-0.85	-1.20	0.75	2.50	D
Heat stress	Cross 3	8.27**	1.36**	0.52	0.49	0.53	1.31	C
				Number of spikes/plant				
Favorable	Cross 1	11.01**	1.08**	-2.54*	-5.24**	0.18	11.44**	D
Heat stress	Cross 1	8.81**	1.02*	-5.25**	-7.37**	0.32	12.06**	D
Favorable	Cross 2	8.44**	1.14*	1.11	1.80	-0.99	-0.06	D
Heat stress	Cross 2	6.37**	1.35*	-0.46	0.18	-0.24	0.94	D
Favorable	Cross 3	15.89**	2.07**	2.03	0.78	1.64**	-1.78	D
Heat stress	Cross 3	11.92**	1.74**	2.28	1.57	1.49**	-2.85	D
				Number of kernels/spike				
Favorable	Cross 1	58.66**	2.22**	38.72**	24.44**	-3.62**	-55.60**	D
Heat stress	Cross 1	36.37**	0.87**	41.26**	31.97**	-3.32*	-56.16**	D
Favorable	Cross 2	54.38**	3.23**	14.35**	7.10**	0.66	-13.25**	D
Heat stress	Cross 2	35.35**	3.01**	13.79**	9.72**	1.00	-12.89**	D
Favorable	Cross 3	67.46**	4.23**	10.13**	10.18**	-0.16	-13.22**	D
Heat stress	Cross 3	42.50**	3.56**	15.93**	19.06**	0.76	-16.35**	D
				1000-Kernel/spike				
Favorable	Cross 1	49.22**	2.36**	18.24**	9.60**	-1.70**	-22.56**	D
Heat stress	Cross 1	37.41**	2.37**	19.42**	12.48**	-1.00	-24.05**	D
Favorable	Cross 2	53.20**	3.40**	17.70**	7.20**	-0.10	-24.20**	D
Heat stress	Cross 2	40.96**	3.31**	18.46**	10.97**	0.30	-26.06**	D
Favorable	Cross 3	48.80**	3.00**	13.70**	10.00**	1.90**	-12.20**	D
Heat stress	Cross 3	34.65**	2.19**	12.68**	11.20**	1.11	-10.35**	D
				Grain yield/plant				
Favorable	Cross 1	29.20**	4.10**	16.25**	10.92**	2.23**	-12.34**	D
Heat stress	Cross 1	17.52**	2.24*	12.24**	9.70**	1.20	-11.02*	D
Favorable	Cross 2	39.36**	2.64**	16.67**	8.80**	1.79*	-17.66**	D
Heat stress	Cross 2	24.80**	2.14*	14.31**	9.73**	1.40	-15.27**	D
Favorable	Cross 3	38.08**	3.78**	4.74*	1.08	3.21**	1.68	C
Heat stress	Cross 3	21.71**	3.11**	9.63**	8.36**	2.94**	-7.99	D

* $p < 0.05$, ** $p < 0.01$. C = Complementary, D= Duplicate

Considering the contribution of epistatic gene effects, additive x additive (i) interaction had enhancing effect in the expression for; number of kernels/spike, 1000-kernel weight and grain yield/plant in all crosses under favorable sown and heat stress treatments except grain yield/plant in cross 3 under favorable sown treatment were highly significant and positive. As well as for; days to heading in cross 1 was positive and significant under heat stress. While days to heading in all crosses and number of spikes/plant in cross 1 were negative and significant under favorable sown treatment (Table 4).

On the other hand, highly positive and significant additive × dominance (j) types of epistasis was found for; days to heading in cross 1; spike length in the cross 2; number of spikes/plant in the cross 3 and grain yield/plant in the cross 3 under favorable sown and heat stress treatments. As well as, 1000-kernel weight in cross 3 and grain yield/plant in the crosses 1 and 2 under favorable sown treatment were positive and significant. However, highly negative and significant were found for number of kernels/spike under favorable sown and heat stress treatments, days to heading in cross 3 and 1000-kernel weight in the cross 1 under favorable sown treatment.

The dominance × dominance (L) interactions with higher magnitude were significant or highly significant positive for; days to heading in the two crosses 2 and 3 and number of spikes/plant in the cross 1 under favorable sown and heat stress treatments, days to heading in cross 1 only under favorable sown date. On the other hand, number of kernels/spike in all crosses; 1000-kernel weight in all crosses and grain yield/plant in the two crosses 1 and 2 under favorable sown and heat stress treatments were highly negative and significant. The negative (L) interactions indicating their reducing effect in the expression of some of the traits in the present study. These results confirm the importance role of dominance x dominance gene action in the genetic system. The same results were reported by El-Sayed & El-Shaarawy (2006) and Hamam (2013).

All the three types of epistatic gene interactions (i, j and L) were significant and were associated significant and negative dominance effect for days to heading; with significant and positive dominance effect for number of kernels/spike all crosses, suggesting that materials could be selected for earliness with high grains intensity in wheat.

Complementary epistasis was revealed by similar signs of (h) and (L), while differences, in signs of (h) and (L) indicate duplicate epistasis. The contribution of the traits was not unidirectional and in some cases, it had reducing (−) effects, whereas, in other increasing (+) effects. The results in Table 4 showed that duplicate epistasis was prevailing for all traits studied except; days to heading in cross 2 and spike length in crosses 1 and 3 under heat stress and spike length in cross1 and grain yield/plant in cross 3 only under favorable sown showed complementary epistasis effects. This indicated that duplicate epitasis was of greater importance than complementary epitasis for most studied traits. These

results were in agreement with those of Sharma *et al.* (2003), Abd-El-Aty & Katta (2007), Saint Pierre *et al.* (2010) and Yadav & Singh (2011).

The three parameter models was applied for number of spikes/plant in cross 2 under heat stress as the scaling test indicated absence of non-allelic interaction (Table 5). The mean effect [m] was highly significant; the additive gene effect [d] was highly significant positive while the dominance [h] gene effect was negative and not significant for number of spikes/plant in cross 2 under heat stress. This would indicate the additive gene effect play the major role in controlling the genetic system of the number of spikes/plant in cross 2 under heat stress. The character was governed by additive gene effects, although the effect of contributions was reducing. Similar results were obtained by Rahman & Saad (2000).

TABLE 5. Estimates of m, d and h for number of spikes/plant for the non-interacting cross 2, Giza168 x Cham 6 of bread wheat using three parameter models of Jinks and Jones under heat stress.

Character	Gene effects		
	[m]	**[d]**	**[h]**
Number of spikes/plant	Cross 2 = (Giza168 x Cham 6)		
	6.8**±1.65	1.59**±0.11	-1.40±4.4

m = mean, d = additive effect, h = dominance effect.
* $p < 0.05$, **$p < 0.01$.

The relative magnitude of additive and dominance effects for the traits in each cross varied, leading to the variation in the inheritance. Those traits were controlled by additive (d) and additive x additive (i) gene effects, can be improved by pedigree selection whereas those were under the control of dominance (h) and dominance x dominance (L), heterosis breeding might be effective for the development of superior populations (Rahman & Saad, 2000).

Heterosis, inbreeding depression, heritability and genetic advance
    Heterosis and inbreeding effect (%)
Heterosis was expressed as the percentage deviation of F_1 mean performance from the better or mid parent of different traits. In this concern, percentages of heterosis over better and mid-parent values under favorable sown and heat stress treatments were presented in Table 6. Positive highly significant heterosis over mid and better parent values were obtained for; days to heading in two crosses 1 and 2, spike length in two crosses 1 and 2, number of spikes/plant in two crosses 1 and 3, number of kernels/spike in two crosses 1 and 2, 1000-kernel weight in two crosses 1 and 2 and grain yield/plant in all crosses under favorable sown and heat stress treatments. As well as for; spike length, number of spikes/plant, number of kernels/spike and 1000-kernel weight in cross 3 were found positive highly significant heterosis over mid and better parents values only under favorable sown. Moreover, spike length and number of spikes/plant in cross 3 were found positive highly significant

heterosis over better parent values only under heat stress. While negative highly significant heterosis for mid-parent were obtained for, days to heading in cross 3; number of spikes/plant in cross 2 and number of kernels/spike in cross 3 under heat stress treatment. As well as, days to heading in cross 3 and number of kernels/spike in cross 3 were found negative insignificant heterosis over better parent values only under heat stress. A significant and negative heterotic effect for earliness in some crosses was previously detected by Abd El-Aty & Katta (2007) and Yadav & Singh (2011). On the other hand, significant positive heterotic effects relative to the higher parents were found for spike length by Sharma *et al.* (2003) and for 1000-kernel/weight and grain yield/plant by Farag (2009) and Hamam (2013).

Inbreeding depression

Measured as reduction in performance of F_2 generation due to inbreeding presented in Table 6. Results showed that significant positive values for all traits studied under favorable sown and heat stress treatments except; spike length in cross 2 and number of spikes/plant in two crosses 2 and 3 under favorable sown and heat stress treatments were not significant positive values. As well as, Inbreeding depression recorded not significant positive values for spike length in cross 3 only under favorable sown and number of spikes/plant in crosses 1 under heat stress. While number of spikes/plant in cross 1 under heat stress treatment was not significant positive value. These results were in close agreements with those of Abd El-Aty & Katta (2007), Yadav & Singh (2011) and Hamam (2013).

Potence ratio

The level of degree of dominance of six various traits computed using generation means and presented as potence ratio in Table 6. It could be summarized that, concerning days to heading, spike length, number of spikes/plant, number of kernels/spike, 1000-kernel weight and grain yield/plant results of potence ratio for most cases in F_1 and F_2 exceeded unity, either with positive or negative sign indicating that the over dominance existed in the heredity found for all the traits studied with some exceptions. The results showed partial dominance were found for days to heading in cross 2 in F_1 under favorable sown and heat and for F_1 only in the cross 3 under favorable sown and for F_2 in crosses 1 and 2 only under favorable sown. Spike length in cross 3 in F_1 under favorable sown and heat stress treatments, for F_2 in crosses 1 and 3 under favorable sown and in cross 1 also under heat stress were found partial dominance. Number of spikes/plant in cross 2 in F_1, for number of kernels/spike in cross 3 (for F_1 and F_2) only under favorable sown and in cross 2 for F_2 under heat stress revealed partial dominance. As well as partial dominance was indicated for 1000-kernel weight for F_2 only in cross 3 under favorable sown and for grain yield/plant in cross 1 in F_2 under favorable sown. These results were harmony with those obtained by Darwish & Ashoush (2003), Abd El-Aty & Katta (2007) and Yadav & Singh (2011).

TABLE 6. Genetic advance, heterosis relative to mid-parent (M.P) and better parent (B.P), inbreeding depression in F_2, potence ratio in F_1 and F_2 and heritability in F_2 for studied characters in bread wheat under favorable and heat stress conditions.

Sowing date	Cross	Genetic advance %	Heterosis (%)		Inbreeding depression (%) F_2	Potence ratio		Heritability (%) F_2	
			M.P	B.P		F_1	F_2	Broad sense	Narrow sense
Days to heading									
Favorable	Cross 1	10.50	4.57**	6.10**	4.16**	3.17	0.31	90.81	68.05
Heat stress	Cross 1	17.02	3.94**	3.45**	9.07**	-8.39	23.42	91.57	70.68
Favorable	Cross 2	7.02	2.16**	7.32**	3.03**	0.45	-0.39	93.25	63.33
Heat stress	Cross 2	10.25	2.75**	8.65**	6.57**	0.51	-1.47	93.60	64.82
Favorable	Cross 3	14.03	-0.58	3.22**	3.12**	-0.16	-2.00	98.14	92.69
Heat stress	Cross 3	24.29	-3.89**	-0.91	5.81**	-1.29	-6.30	98.28	93.45
Spike length									
Favorable	Cross 1	53.66	14.81**	25.60**	11.54**	1.72	0.36	93.01	78.41
Heat stress	Cross 1	75.45	16.65**	30.09**	16.63**	1.61	-0.53	93.26	79.00
Favorable	Cross 2	71.42	14.57**	15.83**	3.29	13.36	19.82	94.51	73.76
Heat stress	Cross 2	96.07	12.60**	14.50**	4.41	7.58	9.18	94.79	74.61
Favorable	Cross 3	32.76	3.35**	14.89**	1.85	0.33	0.29	85.15	34.26
Heat stress	Cross 3	51.50	0.35	10.84**	6.64*	0.04	-1.33	86.28	42.22
Number of spikes/plant									
Favorable	Cross 1	61.16	27.27**	40.00**	12.62**	3.00	2.47	96.31	84.90
Heat stress	Cross 1	88.91	29.86**	43.94**	4.24	3.05	4.89	92.57	84.04
Favorable	Cross 2	88.52	-7.14**	19.10**	6.01	-0.32	-1.15	94.98	78.34
Heat stress	Cross 2	94.15	-9.19**	17.44**	0.06	-0.41	-0.82	82.90	50.10
Favorable	Cross 3	45.36	8.22**	5.24**	3.46	2.91	3.16	95.17	85.16
Heat stress	Cross 3	68.37	6.12**	3.86**	3.46	2.81	2.25	95.19	85.13
Number of kernels/spike									
Favorable	Cross 1	13.87	28.65**	15.16**	8.52**	2.45	3.02	90.11	68.80
Heat stress	Cross 1	28.98	27.59**	13.46**	15.34**	2.22	1.29	90.47	72.45
Favorable	Cross 2	18.96	14.21**	20.28**	6.63**	2.81	2.63	90.74	68.46
Heat stress	Cross 2	37.16	11.67**	18.51**	9.41**	2.02	0.40	91.03	70.22
Favorable	Cross 3	8.78	-0.07	6.69**	2.54**	-0.01	-0.82	92.43	78.91
Heat stress	Cross 3	18.53	-6.32**	-0.72	8.36**	-1.12	-5.02	93.07	79.95
1000-Kernel/spike									
Favorable	Cross 1	17.23	19.61**	31.75**	6.60**	2.13	2.54	90.96	80.39
Heat stress	Cross 1	30.44	20.31**	33.46**	9.00**	2.06	1.92	91.14	81.96
Favorable	Cross 2	21.15	23.08**	33.33**	5.00**	3.00	4.40	91.96	62.52
Heat stress	Cross 2	36.74	20.70**	31.65**	6.22*	2.49	3.17	92.48	66.97
Favorable	Cross 3	13.82	7.57**	5.20**	7.22**	3.36	-0.18	89.03	67.72
Heat stress	Cross 3	27.05	3.99**	1.05	9.77**	1.37	-4.24	89.66	69.60
Grain yield/plant									
Favorable	Cross 1	31.91	18.44**	26.63**	14.72**	2.85	0.31	91.39	70.22
Heat stress	Cross 1	66.68	13.83**	20.69**	16.12**	2.43	-1.59	91.66	72.39
Favorable	Cross 2	22.80	22.23**	25.23**	9.06**	9.26	9.29	93.34	63.26
Heat stress	Cross 2	45.49	19.45**	23.33**	11.86**	6.17	3.35	93.86	66.07
Favorable	Cross 3	27.05	9.84**	11.54**	6.83**	6.42	3.05	90.65	68.85
Heat stress	Cross 3	61.50	5.46**	6.23**	11.49**	7.45	-18.19	91.08	70.36

$p < 0.05$, **$p < 0.01$.

The broad and narrow sense heritability

 Heritability estimates in broad sense were relatively high for all studied traits in all crosses, ranged from 85.15% and 86.28% for spike length in cross 3 to 98.14% and 98.28% for days to heading in cross 3 under favorable sown and heat stress treatments, respectively (Table 6). While, heritability estimates in narrow sense were moderate to low for all studied traits in all crosses, ranged from 34.26% and 42.22% for spike length in cross 3 to 92.69% and 93.45% for days to heading in cross 3 under favorable sown and heat stress treatments respectively, indicating that these traits greatly affected by non-additive and environmental effects. These results were coincident with those reported by El-Sayed & El-Shaarawy (2006) and Khaled (2007). Talebi & Fayyaz (2012) reported that broad sense heritability estimates was very high under both control and stress conditions, for number of kernels/spike, while broad sense heritability significantly decreased under stress conditions for 1000-grain weight. The degree of improving studied traits were based on the high heritability and genetic advance shown by the different characters, especially; spike length, number of spikes/plant, number of kernels/spike, 1000-kernel weight and grain yield/plant. Determinant genetic effects of the phenotypic expression of these characters were fundamentally of the additive type. For this reason, a high response should be achievable after several selection cycles. The development of crosses adapted to the heat stress conditions depends on improvement of potential yield and yield evaluation under high temperature. Breeding strategies like diallel selective mating in early segregating generation followed by recurrent selection might be appropriate approach toward genetic improvement of bread wheat.

The expected genetic advance

The gain from selection as % of F_2 means (Table 6) was highest for all crosses for number of spikes/plant followed by spike length, number of kernels/spike, 1000-kernel weight and grain yield/plant and lower for days to heading. The expected genetic advance as percent of F_2 ranged from (7.02%) for days to heading in cross 2 to (10.25%) for days to heading in cross 2 under favorable sown and heat stress treatments, respectively and ranged from (88.52%) for number of spikes/plant in cross 2 to (96.07%) for spike length in cross 2 under favorable sown and heat stress treatments, respectively (Table 6). These results indicated the possibility of practicing selection in early generations and obtain high yielding genotypes. Therefore, selection in those particular populations should be effective and satisfactory for successful breeding purposes. Substantial progress to obtain desirable segregants for yield and its components in the F3 generation could be achieved by selection of the most desirable 10% plants in the F_2 generation. El-Sherbeny *et al.* (2000) reported that gain for selection was high for 100-kernel weight followed by number of spikes/pant and grain yield/plant.

Conclusion

These results suggested that selection in F_2 population would be effective to improve these characters in early generations of wheat breeding under favorable and heat stress condition. It can be concluded that the degree of improving studied traits based on the high heritability and positive additive genetic advance shown by the different traits, especially; number of spikes/plant, number of kernels/spike, 1000-kernel weight and grain yield/plant. Determinant genetic effects of the phenotypic expression of these traits were fundamentally of the additive type. For this reason, a high response should be achievable after several selection cycles. The development of varieties adapted to the heat conditions depends on improvement of potential yield and yield evaluation in different environments. Generally, the most promising crosses were the cross 1 (Giza164 x Qimma 4) and cross 3 (Gemmeiza 9 x Johara14) were found to higher in magnitude which had high genetic advance associated with high heritability and would be interest in breeding programs for evolving better wheat yield and yield component traits in bread wheat under normal and heat stress.

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التحليل الوراثي لبعض الصفات المحصولية فى قمح الخبز باستخدام موديل العشائر الست تحت ظروف الاجهاد الحراري

خـلـف علــى همام

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وراثة صفة المحصول والصفات المساهمة فيه تمت بواسطة التحقق من تحليل متوسطات الاجيال، والاستفادة من متوسطات الست عشائرفى إجيال :الاباء، الجيل الاول، الجيل الثانى ، والهجن الرجعية، لثلاثة هجن من قمح الخبز مستخدما موديل العشائر الست تحت ظروف الزراعة فى الميعاد الأمثل و الزراعة فى وقت متأخر (معاملة الاجهاد الحرارى). أُجريت هذه الدراسة خلال ثلاث مواسم ٢٠١٠/٢٠٠٩ ، ٢٠١١/٢٠١٠ و ٢٠١٢/٢٠١١ م فى المزرعة البحثية لكلية الزراعة – جامعة سوهاج ـ مصر. كان الهدف من هذه الدراسة هو تحديد طريقة فعل الجين المتحكم في وراثة صفات المحصول و مكوناته. كان تأثير الفعل الجيني الإضافي (d) و التفاعل المضيف X المضيف (i) عالى المعنوية وإيجابياً في توريث معظم الصفات المدروسة في الهجن الثلاثة تحت ظروف الميعاد الأمثل للزراعة و الإجهاد الحرارى، مما يؤدى إلى إمكانية زيادة تحسين هذه الصفات باستخدام برنامج سجل النسب. كان تقدير تأثير الفعل الجيني السيادي (h) والسيادي X السيادي (L) معا إيجابياً في توريث معظم الصفات المدروسة في الهجن الثلاثة تحت ظروف الميعاد الأمثل للزراعة و الإجهاد الحرارى ، مما يدل على أهمية دور فعل الجيني السيادي في وراثة هذه الصفات. كما أظهرت الدراسة قيم معامل التوريث بالمعنى الضيق في عائلات الجيل الثاني(F₂) بلغت أكثر من ٣٤,٢٦% و ٤٢,٢٢٪ تحت ظروف ميعاد الزراعة الأمثل والإجهاد الحراري، على التوالى. كما أوضحت نتائج الدراسة ان افضل الهجن المبشرة هو الهجين الأول (Giza164 x Qimma 4) والهجين الثالث (Gemmeiza 9 x Johara14)، نظرا لارتفاع كلا من قيم النسب المئوية للتحسين الوراثي المتوقع مع قيم معامل التوريث العالية، وذلك سوف يكون مهم لبرامج تربية النبات لتحمل الاجهاد الحرارى.