

## GENE ACTION OF EARLINESS AND GRAIN FILLING IN BREAD WHEAT UNDER TWO IRRIGATION REGIMES

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### ABSTRACT

*Fifteen diallel crosses among six Egyptian bread wheat cultivars and lines showing clear differences in earliness were made and evaluated under full and stress irrigation regimes. Water stress caused a significant reduction in all studied traits; with grain yield of F<sub>1</sub> showing maximum reduction (22.3%). Genetic differences were found in all earliness and grain filling traits under both irrigation treatments. Line-1 and Sakha-61 X Sids-4 were early heading and maturing as well as having high yielding ability. Line-1 X Line-3 had the best yield under both irrigation regimes and the lowest reduction due to drought besides its intermediate earliness. Some crosses showed significant desirable heterobeltiosis for all studied traits under both irrigation regimes. Both general (GCA) and specific (SCA) combining ability variances were significant for all studied traits under stress and non-stress; with higher magnitude for GCA than SCA. The best general combiners were Sids-4, Line-1 and Line-2 for days to heading (DTH) and to maturity (DTM) and Sakha-61, Line-3 and Gemmeiza-10 for grain filling rate (GFR) and grain yield (GY). Additive and dominance genetic variances were significant under both irrigation regimes, for all studied traits. Additive was more important than dominance for DTH, DTM and grain filling period (GFP), while the opposite was true for grain yield / plant. The degree of dominance was partial for DTH, DTM and GFP, complete for GFR and overdominance for GY. Number of genes (gene groups) controlling the inheritance was one for GFP, GFR, two for DTH under stress and DTM under non-stress, three for DTH and DTM under stress and four for DTM under stress conditions. Narrow-sense heritability estimates were very high for DTH and GFP, high for DTM, moderate for GFR and low for GY. A very strong negative genetic association ( $r_g$ ) was detected between DTH and GFP, suggesting that early heading genotypes showed longer GFP and a strong positive  $r_g$  between GFR and GY, suggesting that GFR was the most important factor for increasing GY.*

Key words: *Wheat, Triticum aestivum, Earliness, Grain filling, Gene action, GCA, SCA, Heritability, Heterobeltiosis, Correlation.*

### INTRODUCTION

Developing new early-maturing cultivars of bread wheat (*Triticum aestivum* L.) without loss of inherent yielding ability is an objective of the Wheat Breeding Program in Egypt. Yield losses due to certain stresses may be minimized in early-maturing cultivars, since they would escape such stresses that might occur late in season (Clarke *et al* 1984 for drought and

Menshawy 2005 for heat stress). In Egypt, the success of wheat to be cultivated in the rainfed area of the Northern Coast and late planting in the North Delta, may depend entirely on the early maturing cultivars. However, many investigators reported that early-maturing cultivars were more drought tolerant than late ones (Fischer and Maurer 1978 and Kheiralla *et al* 1993).

The possibility of double cropping wheat and cotton in Egypt has also heightened interest in high-yielding early-maturing wheats (Menshawy 2007). Early harvest of the wheat crop is critical to allow cotton crop sufficient time to develop and to produce an adequate yield.

A better understanding of the inheritance and type of gene action for earliness and grain filling traits would help wheat breeders to increase and stabilize grain yield. Several scientists found that maturity is controlled by one gene (Johnson *et al* 1966 and Shehab El-Din 1997) with earliness being dominant or partially dominant. Other researchers found that a two-gene model was more likely (Pinthus 1963, Shehab El-Din 1997). Three-gene (Crumpacker and Allard 1962) and four-gene (Wehrhahn and Allard 1965) models have been proposed and some data indicated the presence of another dominant gene for lateness. Modifying factors have been suggested (Klaimi and Qualset 1973 and Pinthus 1963). Polygenic control also has been reported (Edwards *et al* 1976). However information is lacking regarding inheritance of grain filling rate and duration in wheat.

Additive gene action is evidently accounted for a large amount of the variation for days to heading (Bhatt 1972, Avey *et al* 1982, and Menshawy 2000 and 2005) days to maturity (Menshawy 2000, 2005 and 2007), grain filling duration and rate (Rasyad and Van Sanford 1992, Beiquan and Kronstad 1994, Mou and Kronstad 1994 and Menshawy 2004), but dominance also was important (Crumpacker and Allard 1962, Avey *et al* 1982 and Menshawy 2005) for earliness traits, while epistasis was reported in several studies (Amaya *et al* 1972, Ketata *et al* 1976 for earliness and Przulj and Mladenov 1999 for grain filling traits).

To exploit different types of gene action involved in inheritance of earliness and grain filling traits of some Egyptian bread wheat genotypes, information regarding their relative magnitude and estimates of combining ability are essential. Such information will help wheat breeders in their identification of parents and selection strategies. This study was undertaken: (1) to determine the mode of inheritance, combining ability and heritability estimates for the duration to heading and maturity and the duration and rate of grain filling in some Egyptian bread wheat genotypes under different irrigation regimes, (2) to test the relationships between grain yield, earliness and grain filling traits and (3) to identify some early maturing and high-yielding genotypes under drought stress conditions.

## MATERIALS AND METHODS

The experimental field work of this investigation was carried out at Sakha Agricultural Research Station, Agricultural Research Center (ARC) during 2003/2004, 2004/2005 and 2005/2006 seasons.

### Materials

Based on the results of previous experiments conducted by Wheat Research Department of the ARC, six bread wheat cultivars and experimental lines, showing clear differences in earliness were chosen to be used as parents of this study (Table 1).

### The F<sub>1</sub> diallel crosses

All possible crosses (excluding reciprocals) were made among the six parents. So, seeds of 15 direct F<sub>1</sub> crosses were obtained. Since the produced hybrid seed was not enough to start the evaluation experiment, the six parents were repeatedly sown in 2004/2005 season in the same field and seeds of the same 15 F<sub>1</sub>'s were produced in sufficient quantities. Seeds of the 6 parents were also increased by selfing in the same season (2004/2005).

### Evaluation of parents and F<sub>1</sub>'s

One field experiment was carried out in 2005/2006 growing season, for evaluating the 15 F<sub>1</sub> crosses and their 6 parents under drought stress and non-stress conditions. The planting date was on 23<sup>rd</sup> of November, 2005. A split-plot design with three replications was used. Main plots were devoted to the two irrigation regimes, i.e normal irrigation by giving the recommended number (5) of irrigations and stress irrigation by giving only two irrigations (sowing irrigation and the next one after 21 days) after which irrigation was stopped till the end of the season. A border of 30 meters width was left between the two main plots. Besides, a canal in the middle of this border of a 5 m width and 1 m depth was dug. The purpose of making this border was to prevent water interference from the full-irrigated main plot to the stressed one. Moreover, the whole experiment was isolated by a border of at least 14 m width far away from any source of irrigation water. Sub-plots were devoted to the 21 genotypes (6 parents + 15 F<sub>1</sub>'s). Each experimental sub-plot consisted of one row of 2.50 m long and 30 cm wide with a total area of 0.75 m<sup>2</sup>. Individual seeds were sown in hills along the row at 25-cm space between each 2 hills. The mechanical soil analysis of the experimental site showed that the soil texture was clayey and the particle size distribution was about 46% clay, 37% silt and 17% sand. Fertilization, pest control and other cultural practices were applied according to the recommendations of the ARC for the region.

**Table 1. Name, pedigree and expected earliness of the six Egyptian genotypes of bread wheat.**

No	Genotype	Pedigree	Maturity
1	Sakha 61	Linna/RLA220/7c/Yr"S" CM 15430-25-55-0S-0S	Early
2	Sids 4	Maya"S"Mon"S"/CMH74A592/3/sakha8* 2SD10002-140sd-3sd-1sd-0sd	Very early
3	Cemmeiza 10	Maya74"S"/ON//1160-147/3/BB/GII/ 4/ CHAT"S"/S/Crow"S" CGM5820-3GM-1GM-2GM-0GM	Late
4	Line # 1	SAKHA 12 /S/ KVZ // CNO 67 / PJ 62 /3/ YD "S" / BLO "S" /4/ K 134 (60) / VEE S.14665-4S-1S-0SY-0S	Early
5	Line # 2	CNO"s"/ GLL/3/ SON 64/ KLRE// BB/4/ UP 301/5/ TL //FN.TH/2*NAR 59 /6/ (BB* CNO** CNO* TOTA / JAR) 2F5 / 2F2** (IN* TGLR** CNO"s" *PJ 62*JAR"S") 2F1 /7/ BL1133/3/ CMH 79A.955*2/ CNO 79// CMH 79A.955 /BOW"s" S.13299-1S-1S-1S-1S-0S	Early
6	Line # 3	SHI # 4414 / CROW "S" // GIZA 163 S.12601-10S-4S-2S-0S	Late

#### Data recorded

The following earliness and grain filling characters, were recorded on a plot basis, while grain yield / plant was recorded on five guarded plants per plots: (1) Days to heading (DTH) as number of days from sowing date to the date at which 50% of main spike awns/ plot have completely emerged from the flag leaves, (2) Days to maturity (DTM) as number of days from sowing date to the date at which 50% of main peduncles / plot have turned to yellow color (physiological maturity), (3) Grain filling period (GFP) as number of days from 50 % anthesis to 50% physiological maturity,(4) Grain filling rate (GFR) in g / day determined by dividing grain yield / plant on the duration of grain filling period and (5) Grain yield / plant (GY/P) in g recorded as the weight of grains of each individual plant.

#### Biometrical analysis

The collected data were subjected to the normal analysis of variance of the split-plot design according to Snedecor and Cochran (1989). Under each irrigation regime data were subjected to the normal analysis of variance for randomized complete blocks design. Genotypes degrees of freedom were partitioned into parents, crosses and parents vs crosses. Percentages of  $F_1$  relative to the better parent mean (heterobeltiosis) were calculated as follows: Heterobeltiosis (%) =  $(F_1 - BP) / BP \times 100$ , where:  $F_1$  = mean of the  $F_1$  cross and BP = mean of the better parent. General (GCA) and specific (SCA) combining ability variances and effects were estimated according to Griffing's (1956) Method II Model I. The genetic parameters were estimated under each irrigation regime by using Hayman's

approach as developed by Hayman (1954 a and b). The genotypic correlation coefficients were calculated, according to Falconer (1989).

## RESULTS AND DISCUSSION

### Analysis of variance

Analysis of variance of the split-plot experiment (data not presented) indicated that mean squares due to genotypes and irrigation regimes were highly significant for all studied traits. This suggests the presence of significant differences among the studied genotypes and among the irrigation regimes for all studied traits. Genotypic differences in earliness, grain filling and grain yield were previously recorded by many researchers (Gebeyehou *et al* 1982, Ehdaie and Waines 1996 and Menshawy 2007). This suggests that improving of such traits is possible *via* breeding procedures.

Mean squares due to the interaction between irrigation regimes and genotypes were significant or highly significant for 3 traits (DTH, DTM and GFP), suggesting that genotypes responded differently to the different irrigation regimes for these traits and supporting previous results (Fischer and Maurer 1978 and El-Morshidy *et al* 2001).

Separate analysis of variance under each irrigation regime (Table 2) indicated that mean squares due to genotypes (parents, F<sub>1</sub> crosses and parents vs F<sub>1</sub> crosses) were highly significant for all studied traits under both water stress and non-stress, except for grain filling period and rate under normal irrigation. The significant mean squares due to parents vs F<sub>1</sub>s indicated significant heterosis.

**Table 2. Partitioning genotypes degrees of freedom and mean Squares for studied traits under stress and non-stress.**

S.O.V	d.f	Mean squares				
		DTH	DTM	GFP	GFR	GY/P
		Non-stress				
Genotypes	20	260.8**	46.3**	110.1**	0.5**	562.7**
Parents (P)	5	72.0**	6.4**	213.2**	0.9**	412.0**
Crosses (C)	14	342.7**	60.3**	81.0**	0.4*	547.9**
P vs C	1	58.5**	50.3**	2.8	0.1	152.3**
GCA	5	1023.1**	151.7**	418.1**	1.4**	1053.6**
SCA	15	6.5**	11.2**	7.5**	0.2**	399.0**
GCA/SCA		158.1	13.5	55.9	6.8	2.6
		Stress				
Genotypes	20	205.3**	40.6**	78.8**	0.3**	282.3**
Parents (P)	5	75.0**	21.7**	169.3**	0.6**	115.2**
Crosses (C)	14	265.3**	48.6**	51.1**	0.2**	351.2**
PvsC	1	17.2**	23.2**	14.0**	0.1**	152.2**
GCA	5	806.9**	138.0**	291.4**	0.9**	462.4**
SCA	15	4.8**	8.1**	7.9**	0.1**	222.3**
GCA/SCA		168.5	17.0	37.0	6.1	2.1

\*,\*\*= significant at 0.05 and 0.01, probability levels, respectively. DTH= days to heading, DTM= days to maturity, GFP= grain filling period, GFR = grain filling rate and GY/P = grain yield/plant

### **Mean performance**

Means of different studied traits of 6 wheat parental genotypes and their 15 diallel F<sub>1</sub> crosses under water stress and non-stress conditions are presented in Table (3). Water stress caused a significant reduction in all studied traits. The greatest reduction was exhibited by GY (20.0 and 22.3%) followed by GFR (9.1 and 14.3%), while the lowest reduction was shown by DTH (1.4 and 1.1%) for parents and hybrids, respectively. In other words, water stress caused significant earliness in heading (1.4 and 1.0 days) and in maturity (7.1 and 7.2 days), shortness in GFP (3.6 and 4.2 days) as well as reduction in GFR (0.1 and 0.2 g / day) and in grain yield / plant (10.3 and 13.6 g) for parents and F<sub>1</sub> crosses, respectively. Reductions due to water stress were also reported by previous investigators (e.g. El-Ganbehy 2001 and Farhat 2005).

Data in Table (3) indicated great genotypic differences in earliness, grain filling and yield characteristics. The F<sub>1</sub>'s were generally earlier in heading (by 2.0 and 1.6 days) and maturity (by 2.6 and 2.7 days), shorter in GFP (by 0.5 and 1.1 days) and greater in GFR (by 0.3 and 0.2 g/day) and grain yield / plant (by 8.0 and 4.7 g) than parents under normal and water stress conditions, respectively. This indicated the superiority of heterozygotes over homozygotes in wheat performance under both conditions. Similar conclusions were also reported by Ashoush et al (2001).

As indicated from Table (3) Sids-4 was the earliest parent in heading and maturity under normal and stress conditions, respectively. Line-1 and Line-2 showed also earliness in heading and maturity. On the other hand, Line-3 was the latest parent in heading and maturity. Moreover, Gemmeiza-10 showed lateness in heading and maturity. These results agreed with the previous expectations when these genotypes were chosen as parents for the present investigation.

The earliest F<sub>1</sub> cross was Sids-4 X Line-1 followed by Sids-4 X Line-2 in heading and Sids-4 X Line-2 followed by Sids-4 X Line-1 in maturing under normal and stress conditions, respectively. It is worthy to note that all parents of these early maturing F<sub>1</sub> crosses were the earliest ones in both heading and maturity. On the contrary, the F<sub>1</sub> cross Gem.-10 X Line-3 (both parents were the latest maturing ones) was the latest cross in both heading and maturity under stress and non-stress.

The highest parental means were exhibited by Sids-4 for GFP, Line-3 for GFR and grain yield / plant, while the lowest means were recorded by Line-3 for GFP and Sids-4 for GFR and grain yield / plant under both stress and non-stress. It is worth noting that the low grain yield / plant shown by Sids-4 could be attributed to the very low number of tillers / plant (data not presented).

The highest means of F<sub>1</sub> crosses were shown by Sids-4 X Line-1 for GFP, Sakha-61 X Line-3, Gem.-10 X Line-3 and Sids-4 X Line-1 for GFR .

Table 3. Mean performance of studied traits in wheat parents and F<sub>1</sub> crosses evaluated under stress (S) and non-stress (N) conditions at Sakha in 2005/2006.

Genotypes	DTH			DTM			GFP (days)			GFR (g/day)			GY/P (g)		
	N	S	Red.%	S	N	Red.%	S	N	Red.%	S	N	Red.%	S	N	Red.%
Sak. 61(1)	93.3	93.3	0.0	150.0	145.0	3.3	42.7	39.7	7.0	1.3	1.1	15.4	57.1	43.0	24.6
Sids 4(2)	80.7	80.3	0.5	146.7	141.0	3.9	52.0	48.7	6.4	0.4	0.3	25.0	19.0	15.3	19.5
Gem.10(3)	103.3	101.0	2.2	158.3	151.3	4.4	41.0	38.3	6.5	1.5	1.2	20.0	60.6	45.9	24.3
Line 1(4)	82.0	81.3	0.8	147.7	141.0	4.5	51.7	47.7	7.8	1.3	1.0	23.1	64.9	47.1	27.4
Line 2(5)	83.3	83.0	0.4	149.0	140.3	5.8	51.7	45.3	12.3	1.0	1.0	0.0	49.4	45.3	8.3
Line 3(6)	113.3	108.3	4.4	158.3	149.0	5.9	31.0	28.7	7.5	2.1	1.7	19.1	65.8	49.7	12.6
Average	92.6	91.2	1.4	151.7	144.6	4.7	45.0	41.4	8.0	1.1	1.0	9.1	51.3	41.0	20.0
1×2	87.3	86.7	0.7	146.7	139.7	4.8	45.3	41.0	9.6	1.6	1.4	12.4	72.9	57.1	21.7
1×3	97.7	95.0	2.8	154.3	144.7	6.2	42.7	37.7	11.7	1.5	1.2	20.0	63.0	45.4	27.9
1×4	86.3	84.7	1.9	147.3	140.7	4.5	47.0	44.0	6.4	1.2	1.0	16.7	57.9	42.7	26.3
1×5	86.0	85.7	0.4	148.3	141.0	4.9	48.3	43.3	10.4	1.2	1.1	8.3	57.9	45.8	20.9
1×6	100.3	98.0	2.3	152.0	146.7	3.5	37.7	36.7	2.7	1.7	1.4	17.7	63.7	52.4	17.7
2×3	92.3	92.0	0.3	147.0	141.7	3.6	40.7	37.7	7.4	1.7	1.3	23.5	69.4	48.3	30.3
2×4	78.7	78.7	0.0	145.7	137.7	5.5	53.0	47.0	11.3	0.6	0.5	16.7	29.9	23.7	20.8
2×5	79.7	79.7	0.0	144.7	137.3	5.1	51.0	45.7	10.5	0.9	0.9	0.0	47.8	40.2	16.0
2×6	95.0	94.0	1.1	148.3	142.0	4.3	39.3	36.0	8.6	1.6	1.3	18.8	61.0	46.8	23.4
3×4	90.0	90.0	0.0	149.0	142.7	4.2	45.0	40.7	9.6	1.4	1.2	14.3	64.0	48.1	24.8
3×5	90.3	90.0	0.3	149.3	142.7	4.4	45.0	40.7	9.6	1.5	1.1	26.7	67.4	44.9	33.3
3×6	106.0	103.0	2.8	156.7	147.3	6.0	36.7	32.3	11.8	1.7	1.4	17.6	60.1	45.3	24.5
4×5	81.0	80.3	0.9	148.0	137.7	7.0	53.0	45.3	14.5	0.8	0.9	-12.5	43.0	38.7	9.9
4×6	94.3	93.0	1.4	149.7	143.3	4.3	41.3	38.3	7.3	1.5	1.6	-6.7	61.8	60.1	2.7
5×6	94.0	93.0	1.1	150.0	143.7	4.2	42.0	38.7	7.9	1.7	1.2	29.4	69.3	45.6	34.2
Average	90.6	89.6	1.1	149.1	141.9	4.8	44.5	40.3	9.4	1.4	1.2	14.3	59.3	45.7	22.3
L.S.D	I	0.4		1.9			1.8			0.1			5.9		
0.05	G	1.1		2.0			1.5			0.3			10.0		
	I×G	1.5		2.0			2.2			0.4			14.2		

DTH= days to heading, DTM= days to maturity, I = irrigations, G = Genotypes, GFP= grain filling period, GFR = grain filling rate and GY/P= grain yield/plant, I = irrigations; G = Genotypes.

and Sakha-61 X Sids-4 for grain yield / plant, while the lowest ones were exhibited by Gem.-10 X Line-3 for GFP and Sids-4 x Line-1 for GFR and grain yield / plant.

It is worthy to note that the parent Line-1 and F<sub>1</sub> cross Sakha-61 X Sids-4 had two advantages, i.e. earliness in heading and maturity and high-yielding ability. Moreover, the F<sub>1</sub> cross Line-1 X Line-3 had the best drought tolerance (expressed by the highest absolute yield under drought and the lowest yield reduction due to drought) besides its intermediate earliness. These genotypes could be recommended for developing more early maturing, high-yielding and more drought tolerant cultivars.

### **Heterobeltiosis**

Percentages of heterosis relative to better parent (heterobeltiosis or useful heterosis) in F<sub>1</sub>'s for the studied traits are presented in Table (4). It is worthnoting that the most desirable heterotic effects were considered as the lowest negative heterobeltiosis estimates for DTH, DTM and GFP and the largest positive ones for GFR and GY traits. Some crosses showed heterobeltiosis for all studied traits under both irrigation regimes. The F<sub>1</sub> cross Sids-4 X Line-1 showed significant negative (favorable) heterobeltiosis for days to heading under water stress and non-stress and for days to maturity under water stress conditions.

Regarding grain filling rate, a relatively high heterobeltiosis estimate was shown by Sids-4 X Gem.-10 under non-stress and Sakha-61 X Sids-4, Sids-4 X Gem.-10 and Line-1 X Line-3 under stress.

Significant positive heterobeltiosis percentages for grain yield / plant were also recorded by Line-2 X Line-3 (21.9%) under non-stress and Sakha-61 x Sids-4 (32.9%) and Line-1 X Line-3 (21.0%) under water stress conditions.

It is worthy to note that the crosses Sids-4 X Gem.-10 under non-stress and Sakha-61 X Sids-4 and Line-1 X Line-3 under water stress showed the highest positive and significant heterobeltiosis estimates for both GFR and GY traits. The crosses showing the best heterobeltiosis could be recommended to improve the respective traits.

### **Combining ability**

Analysis of variance of general (GCA) and specific (SCA) combining ability is presented in Table (2). Results showed highly significant estimates of GCA mean squares for the five studied traits. Highly significant estimates of SCA variances were also observed for the same traits. These results indicated that both additive and non-additive gene effects played important roles in the inheritance of earliness and grain filling traits as well as grain yield / plant.

**Table 4. Estimates of heterobeltiosis (%) in wheat F<sub>1</sub> crosses under stress and non-stress conditions.**

Crosses	DTH	DTM	GFP	GFR	GY/P
Non-stress					
1x2	8.2**	0.0	6.2**	-9.0**	-2.9
1x3	4.7**	2.8*	4.1**	-17.0**	-16.1
1x4	5.2**	-0.3	10.2**	-29.9**	-22.9*
1x5	3.2**	-0.5	13.3**	-32.2**	-22.9*
1x6	7.5**	1.3	21.3**	-8.7**	-15.2*
2x3	14.4**	0.2	-0.8	14.2**	14.5*
2x4	-2.5**	-0.7	2.6*	-55.6**	-53.9**
2x5	-1.2	-1.4	-1.3	-6.0**	-3.2
2x6	17.7**	1.1	26.9**	-16.2**	7.4
3x4	9.8**	0.9	9.8**	-3.4**	-1.3
3x5	8.4**	0.2	9.8**	1.4**	11.2
3x6	2.6**	-1.0	18.3**	-10.8**	-0.8
4x5	-1.2	0.2	2.6*	-35.7**	-33.8**
4x6	15.0**	1.4	33.3**	-19.5**	-4.8
5x6	12.9**	0.7	35.5**	-10.8**	21.9*
Average	7.0	0.3	12.8	-15.9	-8.2
Stress					
1x2	8.0**	-0.9	3.4**	30.6**	32.9**
1x3	2.2**	-0.2	-1.7	0.8**	-1.1
1x4	4.2**	-0.2	10.9**	-10.2**	-9.3
1x5	3.3**	0.5	9.2**	-1.9**	1.1
1x6	5.0**	1.2	27.9**	-16.8**	5.5
2x3	14.6**	0.5	-1.7	6.7**	5.4
2x4	-2.0**	-2.3*	-1.4	-49.5**	-49.7**
2x5	-0.8	-2.1*	0.8	-12.0**	-11.3*
2x6	17.1**	0.7	25.6**	-5.1**	-5.8
3x4	10.7**	1.2	6.1**	-1.7**	2.3
3x5	8.4**	1.7	6.1**	-8.3**	-2.1
3x6	2.0**	-1.1	12.8**	-18.5**	-8.7
4x5	-1.2	-1.9	0.0	-50.3**	-17.8**
4x6	14.4**	1.6	33.7**	49.5**	21.0**
5x6	12.1**	2.4*	34.9**	-32.4**	-8.3
Average	6.5	0.1	11.1	-7.9	-3.1

\*,\*\*= significant at 0.05 and 0.01, probability levels, respectively. DTH= days to heading, DTM= days to maturity, GFP= grain filling period, GFR = grain filling rate and GY/P = grain yield/plant.

In general, for all studied traits, the magnitude of mean squares due to GCA was much higher than that due to SCA, since the ratio of GCA/SCA exceeded the unity, suggesting that additive was much larger and more important than non-additive gene effects in the inheritance of these traits. This was more pronounced in days to heading followed by grain filling duration than other traits. The higher importance of GCA over SCA variance for studied traits was also reported by Bhatt (1972), Avey *et al* (1982) and Menshawy (2000) for duration to heading, Menshawy (2002, 2005 and 2007) for duration to maturity, Mou and Kronstad (1994) and Beiquan and Kronstad (1994) for GFR and GFP and Larik *et al* (1995) for grain yield. It is interesting to note that breeding procedures that take advantage of additive genetic variance would be recommended to improve earliness and grain filling traits.

*Estimates of GCA effects for studied traits are presented in Table (5). Data showed that the parents Sid-4, Line-1 and Line-2 had the lowest significant and negative GCA effects (favorable) for days to heading and to maturity under both water stress and non-stress conditions. These parents could be considered the best general combiners for the improvement of earliness traits (DTH and DTM) in the breeding programs.*

Results also showed a great concordance between *per se* performances and GCA effects of the parents for earliness traits. Early heading and maturity parents (*per se*) were good general combiners for these traits and the opposite was true.

For grain filling period, Line-1 and Line-2 followed by Sids-4 showed the highest significant and positive GCA effects, while Line-3 followed by Gem.-10 exhibited the lowest significant and negative GCA effects under both water stress and non-stress conditions. Line-3 followed by Sakha-61 (under no stress) and by Gem.-10 (under water stress) had the highest significant and positive GCA effects for grain filling rate.

For grain yield / plant the best general combiners were Sakha-61 followed by Gem.-10 and then Line-3 under no stress and Line-3 followed by Sakha-61 and then Gem.-10 under water stress.

Specific combining ability (SCA) effects of the  $F_1$  crosses for the studied traits are shown in Table (6). The results of earliness revealed that the  $F_1$  crosses showing negative SCA effects (desirable) outnumbered those showing positive SCA effects (undesirable) for days to heading and days to maturity under both water stress and non-stress. The best SCA effect for days to heading was obtained from the crosses Sids-4 X Line-1, Sakha-61 x Line-3 under both stress and non-stress, Line-2 X Line-3 and Gem.-10 X Line-2 under non-stress and Sids-4 X Line-2, Sakha-61 x Gem.-10 and Sakha-61 X Line-1 under water stress conditions. Considering days to heading, the cross Sids-4 X Gem.10 under both stress and non-stress, Gem.-10 X line-2, Gem.-10 X Line-1 under non-stress and Sakha-61 X Gem.-10, Sakha-61 X Sids-4 and Line-1 X Line-2 exhibited the lowest negative (desirable) and significant SCA effects among all tested crosses. It is interesting to note that all these crosses were produced among early X late or early x early maturing parents. Moreover, such good SCA crosses might come from two parents possessing good GCA or from one with good GCA and other with poor GCA effect for earliness traits.

The lowest significant and negative SCA effects for grain filling period was obtained from the cross Sids-4 x Gem.-10 under stress and non-stress and Sakha-61 X Sids-4 and Sids-4 X Line-3 under water stress.

**Table 5. Estimates of general combining ability effects of wheat parents under stress and non-stress conditions.**

Parents	DTH	DTM	GFP	GFR	GY/P
Non-stress					
Sakha 61	0.75*	-0.84	-0.79*	0.17*	7.59*
Sids 4	-5.50*	-2.92*	2.58*	-0.29*	-10.70*
Gemmeiza 10	5.58*	3.00*	-2.58*	0.16*	5.01*
Line 1	-5.50*	-1.75*	3.75*	-0.17*	-2.32
Line 2	-5.08*	-1.33*	3.75*	-0.17*	-2.61
Line 3	9.75*	3.04*	-6.71*	0.29*	3.07
S.E. 0.05 ( $\bar{g}_i$ )	0.23	0.27	0.32	0.05	2.22
S.E. 0.05 ( $\bar{g}_i - \bar{g}_j$ )	0.35	0.42	0.49	0.08	3.43
Stress					
Sakha 61	0.79*	0.49*	-0.31	0.05	2.36
Sids 4	-4.83*	-2.31*	2.53*	-0.24*	-7.97*
Gemmeiza 10	5.21*	2.86*	-2.35*	0.09*	1.68
Line 1	-5.13*	-1.85*	3.28*	-0.10*	-0.37
Line 2	-4.46*	-1.98*	2.49*	-0.10*	-0.59
Line 3	8.48*	2.78*	-5.64*	0.31*	4.89*
S.E. 0.05 ( $\bar{g}_i$ )	0.18	0.27	0.29	0.04	1.62
S.E. 0.05 ( $\bar{g}_i - \bar{g}_j$ )	0.28	0.42	0.45	0.07	2.51

\*= significant at 0.05 probability level DTH= days to heading, DTM=days to maturity, GFP= grain filling period, GFR = grain filling rate and GY/P = grain yield/plant.

Four crosses showed the best SCA effects for both grain filling rate and grain yield / plant: Sakha-61 X Sids-4 and Sids-4 X Gem.-10 under both stress and non-stress conditions, Sids-4 X Line-3 under no stress and Line-1 X Line-3 under water stress. These crosses were also the best ones in *per se* performance for both traits (GFR and GY).

#### Genetic variance components and proportions

Components of genetic variance for the studied traits calculated according to Hayman (1954 a and b) are presented in Table ( 7 ). Additive genetic component of variation (D) for the five studied traits was highly significant under both water-stress and non-stress conditions. Moreover, the dominance component of variation ( $H_1$  and  $H_2$ ) was significant or highly significant for all studied traits under both stress and non-stress. These results indicated the importance of both additive and dominance genetic variances in the inheritance of these traits under both conditions. The magnitude of additive was greater than that of dominance genetic variance for all studied traits except for grain yield, indicating that additive was more important than dominance and played the major role in the inheritance of earliness and grain filling traits under the two irrigation regimes. On the contrary, dominance gene effects were more important than additive ones in the inheritance of grain yield / plant under both irrigation regimes. Similar conclusions were reported by Bhatt (1972), Avey *et al* (1982) and Menshawy (2000, 2004 and 2005) for days to heading and to maturity, Mou and Kronstad (1994), Rasyad and Van Stanford (1992), Beiquan and

**Table 6. Estimates of specific combining ability effects of F<sub>1</sub> crosses for studied characters.**

Crosses	DTH	DTM	GFP	GFR	GY/P
	Non-stress				
1×2	0.89	-0.23	-1.13	0.39*	18.24*
1×3	0.14	1.52*	1.38	-0.20*	-7.44
1×4	-0.11	-0.73	-0.63	-0.11*	-5.18
1×5	-0.86	-0.15	0.71	-0.14*	-4.95
1×6	-1.36*	-0.86	0.50	-0.11*	-4.84
2×3	1.86*	-2.94*	-4.00*	0.48*	17.25*
2×4	-1.52*	0.48	2.00*	-0.33*	-14.89*
2×5	-0.94	-0.94	0.00	0.06*	3.30
2×6	-0.44	-1.65*	-1.28	0.21*	10.85*
3×4	-1.27*	-2.11*	-0.83	0.09*	3.50
3×5	-1.36*	-2.19*	-0.83	0.16*	7.13
3×6	-0.52	0.80	1.29	-0.15*	-5.83
4×5	0.39	1.23	0.83	-0.19*	-9.95*
4×6	-1.11*	-1.48*	-0.38	0.03	3.17
5×6	-1.86*	-1.57*	0.29	0.19*	10.99*
S.E. 0.05 (S <sub>ij</sub> )	0.63	0.75	0.87	0.01	5.09
S.E. 0.05 (S <sub>ij</sub> -S <sub>mi</sub> )	0.93	1.12	1.30	0.02	7.10
S.E. 0.05 (S <sub>ij</sub> -S <sub>mj</sub> )	0.86	1.04	1.20	0.06	6.42
	Stress				
1×2	0.66	-1.20	-1.86*	0.47*	18.37*
1×3	-1.05*	-1.36*	-0.32	-0.05*	-2.99
1×4	-1.05*	-0.66	0.39	-0.10*	-3.94
1×5	-0.71	-0.20	0.52	-0.01	-0.35
1×6	-1.26*	0.72	1.98*	-0.04*	0.81
2×3	1.58*	-1.57*	-3.15*	0.31*	10.28*
2×4	-1.42*	-0.86	0.56	-0.28*	-12.34*
2×5	-1.09*	-1.07	0.02	0.09*	4.39
2×6	0.37	-1.16	-1.52*	0.10*	5.58
3×4	-0.13	-1.03	-0.90	0.07*	2.48
3×5	-0.80	-0.91	-0.11	-0.01	-0.50
3×6	-0.67	-0.99	0.00	-0.11*	-5.58
4×5	-0.13	-1.20	-1.07	-0.06*	-4.68
4×6	-0.34	-0.28	0.06	0.24*	11.24*
5×6	-1.01*	0.18	1.19	-0.16*	-3.07
S.E. 0.05 (S <sub>ij</sub> )	0.49	0.75	0.79	0.01	4.45
S.E. 0.05 (S <sub>ij</sub> -S <sub>mi</sub> )	0.73	1.12	1.18	0.02	6.64
S.E. 0.05 (S <sub>ij</sub> -S <sub>mj</sub> )	0.68	1.04	1.10	0.04	5.14

\*= significant at 0.05 probability level DTH= days to heading , DTM= days to maturity, GFP= grain filling period, GFR = grain filling rate and GY/P = grain yield/plant.

**Table 7. Components of variance for studied traits under stress (S) and non-stress (N) at Sakha in 2005/2006 season.**

Parameter	DTH		DTM		GFP		GFR		GY	
	N	S	N	S	N	S	N	S	N	S
D	176.89**	135.15**	27.07**	21.24**	70.10**	55.79**	0.29**	0.19*	337.24**	43.35**
	± 0.21	± 0.33	± 1.26	± 0.25	± 1.89	± 1.04	± 0.03	± 0.03	± 54.82	± 39.43
F	9.59**	1.67*	3.52	-1.33	2.43	14.30**	0.15	0.09	349.17**	137.02
	± 0.52	± 0.80	± 3.07	± 0.06	± 4.63	± 2.53	± 0.08	± 0.06	± 133.93	± 96.32
H <sub>1</sub>	6.72**	5.05**	10.27**	6.53**	8.55	9.70**	0.26**	0.16*	513.87**	264.39**
	± 0.54	± 0.83	± 3.19	± 0.62	± 4.81	± 2.88	± 0.08	± 0.07	± 139.17	± 100.09
H <sub>2</sub>	5.50**	4.16**	9.35**	5.54**	6.70	2.98*	0.19*	0.13*	359.42**	213.07*
	± 0.49	± 0.75	± 2.85	± 0.56	± 4.30	± 2.58	± 0.07	± 0.06	± 124.33	± 89.41
h <sup>2</sup>	11.66**	7.39**	17.34**	19.94**	0.07	2.01	0.01	0.02	44.05	48.77
	± 0.33	± 0.50	± 1.92	± 0.38	± 2.89	± 1.74	± 0.05	± 0.04	± 83.68	± 60.18
E	0.36**	0.36**	0.88	0.56**	0.96	0.63	0.02	0.01	34.84	20.28
	± 0.08	± 0.08	± 0.47	± 0.09	± 0.72	± 0.43	± 0.01	± 0.01	± 20.72	± 14.90
(H <sub>1</sub> /D) <sup>1/2</sup>	0.19	0.19	0.62	0.55	0.35	0.42	0.95	0.92	1.23	1.36
H <sub>2</sub> /4H <sub>1</sub>	0.20	0.21	0.23	0.21	0.20	0.15	0.18	0.20	0.17	0.20
K <sub>D</sub> /K <sub>N</sub>	1.32	1.07	1.24	0.89	1.10	1.89	1.76	1.75	2.44	2.09
K(h <sup>2</sup> /H <sub>2</sub> )	2.12	1.77	1.85	3.60	0.01	0.34	0.06	0.16	0.12	0.23
h <sup>2</sup> (n.s)	0.98	0.98	0.79	0.86	0.93	0.91	0.62	0.59	0.36	0.28
h <sup>2</sup> (b.s)	0.99	0.99	0.92	0.96	0.97	0.97	0.89	0.88	0.82	0.80
c <sup>2</sup>	0.01	0.01	0.03	0.01	0.01	0.01	0.13	0.17	0.29	0.57
r	0.74	0.01	0.97	0.84	0.60	0.13	-0.89	-0.65	-0.77	-0.71

\*,\*\*= significant at 0.05 and 0.01, probability levels, respectively. DTH= days to heading, DTM= days to maturity, GFP= grain filling period, GFR = grain filling rate and GY/P = grain yield/plant.

Kronstad (1994), Mashiringwani *et al* (1994) and Menshawy (2004 and 2007) for grain yield in bread wheat.

The results suggested that selection in segregating generations would be effective in the improvement of earliness, grain filling traits and grain yield of bread wheat.

The estimates of  $H_1$  were relatively smaller in magnitude than  $H_2$ , indicating that the positive and negative alleles at loci controlling each studied trait were not equal in proportion in the parents. These results agreed with those reported by Abd El-Aty and Katta (2002) and Menshawy (2004 and 2005).

The F estimates were positive and significant for all studied traits except for days to maturity under water stress conditions, suggesting that dominant genes were more frequent than recessive ones among the parental genotypes, in the majority of cases. A similar conclusion was also reported by Menshawy (2005).

The overall dominance effects of heterozygous loci ( $h^2$ ) controlling days to heading and days to maturity under both stress and non-stress in all crosses were highly significant, indicating that the effect of dominance in these traits were unidirectional and due to heterozygosity. On the other hand,  $h^2$  estimates for grain filling period and rate and grain yield were not significant, under the two irrigation regimes in spite of the significance of  $H_1$  and  $H_2$ ; that could be due to the presence of a considerable amount of canceling dominance effects in the parental genotypes. A similar conclusion was reported by Menshawy (2005) for grain filling period and rate.

Average degree of dominance  $(H_1/D)^{1/2}$  was less than unity for days to heading, days to maturity and grain filling period, indicating that partial dominance played the most important role in the inheritance of these traits. In this respect, Przulj and Mladenov (1999), Abd El-Aty and Katta (2002) and Menshawy (2004 and 2005) reported that partial dominance was important in the inheritance of these traits.

Results indicated that the  $(H_1/D)^{1/2}$  was close to unity for GFR and greater than unity for GY, indicating that the degree of dominance was complete for GFR and overdominance for GY under both irrigation regimes. The proportions of the genes with positive and negative effects in the parents ( $H_2 / 4H_1$ ) which estimate the frequencies at non-additive loci controlling the studied traits under both irrigation regimes, were less than 0.25 (Table 7), suggesting some asymmetrical distribution at loci showing dominance. These results confirmed those obtained from  $H_2$  estimates which showed also unequal frequencies of positive and negative genes controlling inheritance of studied traits under the two irrigation regimes. A similar conclusion was reported by Menshawy (2004 and 2005).

The proportion of dominant and recessive genes ( $K_D / K_R$ ) was more than unity for all studied traits under the two irrigation regimes, except for days to maturity under water stress, which was less than unity, indicating the existence of more dominant than recessive alleles in the parents. This conclusion confirmed the previously reported positive estimates of F.

Number of genes or genes groups (K) controlling the inheritance of studied traits was one for each of grain filling period and rate and grain yield / plant, two for days to heading under stress and days to maturity under non-stress, three for days to heading under non-stress and four for days to maturity under water stress conditions. In this regard, conflicting results were reported by different investigators.

Several scientists found that one gene controlled heading and maturity traits (Johnson *et al* 1966, Shehab El-Din 1997 and Menshawy 2004 and 2005). Others proposed two-gene (Pinthus 1963), three-gene (Crumpacker and Allard 1962) and four-gene (Wehrhahn and Allard 1965) models for controlling such traits. Polygenic control has also been reported (Edwards *et al* 1976).

The correlation coefficient ( $r$ ) between the order of dominance ( $V_r, W_r$ ) and parental measurements was positive and high for DTH, DTM and GFP under both irrigation regimes, except DTH and GFP under water stress, indicating that the expression of high parental values for these traits were associated with recessive genes. Therefore, dominance appeared to be unidirectional in the parents, showing complete recessiveness. On the contrary, the  $r$  value was negative and high for grain filling rate and grain yield / plant, under both irrigation regimes, suggesting that the expression of high scores in the parents is associated with dominant genes, showing unidirectional dominance in the parents for these traits, *i.e.* completely dominant. Therefore, data indicated that dominance direction was towards earliness in heading, maturity and GFP traits and towards higher grain filling rate and grain yield / plant. Low  $r$  values were exhibited by days to heading and grain filling period under water stress, indicating that dominance was bidirectional in the parents for these cases.

Narrow sense heritability estimates ( $h_b^2$ ) were very high for days to heading, grain filling period, high for days to maturity, moderate for grain filling rate and low for grain yield / plant under both conditions (Table 7). High values of narrow-sense heritability of all studied traits, except grain yield / plant indicated that the expected gain from selection for these traits would be high and few cycles of selection are needed for the improvement of these traits. This conclusion was supported by many investigators (Shehab El-Din 1997, Abd El-Aty and Katta 2002 and Menshawy 2004 and 2005).

### Trait interrelationships

Estimates of genotypic correlation coefficients ( $r_g$ ) between pairs of studied traits are presented in Table (8). In general,  $r_g$  values were little higher in magnitude under water stress than those under non-stress, but showed similar trends under both irrigation regimes.

A very strong positive genetic association was found between days to heading and days to maturity ( $r_g = 0.93$  under stress and  $0.91$  under non-stress). This means that selection for early heading will simultaneously help in improving early maturity. Days to heading was highly positive correlated with grain filling rate ( $r_g = 0.83$  and  $0.85$  under stress and non-stress, respectively). Moreover, a very strong negative genetic association was exhibited between days to heading and grain filling period ( $r_g = -0.97$  under water stress and  $-0.96$  under non-stress) indicating that selection for earlier heading would be accompanied by longer grain filling duration. Menshawy (2007) also reported that days to heading was significantly and positively correlated with days to maturity and grain filling rate and *vice versa* with grain filling period. It is worthnoting that grain filling period was negatively correlated ( $r_g = -0.91$ ) with grain filling rate under both irrigation regimes.

**Table 8. Estimates of genotypic correlation coefficients( $r_g$ ) Between studied wheat traits under stress (below diagonal) and non-stress (above diagonal) conditions.**

Trait	DTH	DTM	GFP	GFR	GY
DTH		0.91	-0.96	0.83	0.52
DTM	0.93		-0.77	0.60	0.31
GFP	-0.97	-0.82		-0.91	-0.61
GFR	0.85	0.67	-0.91		0.89
GY	0.56	0.40	-0.64	0.89	

DTH= days to heading , DTM= days to maturity, GFP= grain filling, period, GFR = grain filling rate andGY/P= grain yield/plant.

Grain yield / plant exhibited a high positive genetic correlation with grain filling rate, but showed moderate negative genetic correlation with grain filling period and moderate positive genetic correlation with days to heading under both irrigation regimes. This suggested that the high grain filling rate is the most important factor for increasing grain yield / plant. Sofield *et al* (1977) found the rate of grain filling was more important for grain weight than the duration of grain filling. Little genetic association between grain filling rate and grain filling duration has been found in wheat by Gebeyehou *et al* (1982) and Wong and Baker (1986); these authors suggested that yield might be increased by breeding for an increased grain filling rate without altering grain filling period. Menshawy (2007) also reported that grain filling rate was highly significantly and positively correlated with grain yield, reflecting the importance of grain filling rate in grain yield improvement.

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## فعل الجين لصفات التذكير وامتلاء الحبوب في قمح الخبز تحت نظامين من الري

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تم عمل الهجن للتبادلية بين ستة أصناف وسلالات مصرية من قمح الخبز (سغا ٦١، سدس ٤، جيمزة ١٠، سلالة ١، سلالة ٢، سلالة ٣) تختلف في التذكير وتم تقييم الآباء والهجن تحت نظامين من الري (الأول ري كامل والثاني أعطي رية الزراعة ورية المحياة ثم منع الري بعد ذلك). كان الهدف هو تقدير نوع فصل الجين والقدرة على الانتلاف وكفاءة للتورث لصفات التزهير وامتلاء الحبوب. تسبب الإجهاد المائي في حدوث نقص معنوي في متوسطات كل الصفات المدروسة، وحدث أقصى نقص في محصول الحبوب للهجن (٢٢,٣%). أظهرت النتائج وجود اختلافات بين التركيب الوراثية في كل الصفات المدروسة تحت كلا نظامي الري وكانت السلالة-١ والهجين (سغا-٦١ X سدس-٤) هما الأكبر في التزهير والتضخ وفي نفس الوقت الأعلى محصولا. كما كان للهجين (السلالة-١ X السلالة-٢) الأحسن محصولا تحت كلا النظامين والأقل نقصا في المحصول بسبب الجفاف ومتوسط للتذكير في التضخ. أظهرت بعض الهجن قوة هجين معنوية مرغوبة بالنسبة للأب الأحسن في الصفات المختلفة المدروسة تحت كلا نظامي الري. كما كانت كل من تباينات القدرة العامة والقدرة الخاصة على الانتلاف معنوية لكل الصفات المدروسة وكانت قيم تباين القدرة العامة أكبر من قيم القدرة الخاصة على الانتلاف. كانت الآباء الأحسن في تأثيرات القدرة العامة على الانتلاف هي سدس-٤، سلالة-١ وسلالة-٢ بالنسبة لصفتي عدد الأيام حتى طرد السنابل وعدد الأيام حتى التضخ الفسيولوجي وسغا-٦١، سلالة-٣ وجيمزة-١٠ بالنسبة لصفتي معدل امتلاء الحبوب ومحصول الحبوب للنبات. كانت التباينات المضافة وتباينات السيادة لجميع الصفات معنوية تحت كل من نظامي الري. كان التباين المضيف أكثر أهمية من تباين السيادة بالنسبة لكل الصفات ما عدا صفة محصول حبوب النبات حيث كان العكس فيها صحيحا. كانت درجة السيادة جزئية لصفات عدد الأيام للطرد والتضخ وفترة امتلاء الحبوب. وكاملة لصفة معدل امتلاء الحبوب وذات سيادة فائقة لصفة محصول الحبوب. كان عدد الجينات (مجاميع الجينات) التي تتحكم في وراثية الصفات هو واحد بالنسبة لفترة ومعدل امتلاء الحبوب واثنان لعدد الأيام حتى الطرد تحت الإجهاد وعدد الأيام حتى التضخ تحت عدم الإجهاد وثلاثة لعدد الأيام حتى الطرد وحتى التضخ تحت الإجهاد وأربعة لعدد الأيام حتى التضخ تحت ظروف الإجهاد. كانت تقديرات كفاءة للتورث بالمعنى الخاص عالية جدا لصفتي عدد الأيام حتى الطرد وفترة امتلاء الحبوب، وعالية لعدد الأيام حتى التضخ ومتوسطة لمعدل امتلاء الحبوب ومنخفضة لمحصول الحبوب للنبات. وجد أن هناك ارتباطا وراثيا سلبا قويا بين عدد الأيام للتزهير وطول فترة الامتلاء. مما يقترح أن التركيب المبكرة في الطرد أظهرت فترة امتلاء حبوب أطول. وكذلك ارتباطا موجبا قويا بين معدل امتلاء الحبوب ومحصول النبات مما يقترح أن صفة معدل امتلاء الحبوب هي الأهم في زيادة محصول الحبوب.

المجلة المصرية لتربية النبات ١١ (٣): ٢٧٧ - ٢٩٢ (٢٠٠٧)