

## INHERITANCE OF GRAIN OIL CONTENT AND YIELD CHARACTERISTICS IN MAIZE

A.M.M. Al-Naggar<sup>1</sup>, M.A. El-Lakany<sup>1</sup>, H.Y. El-Sherbieny<sup>2</sup>  
and W. M. El-Sayed<sup>2</sup>

1- Department of Agronomy, Faculty of Agriculture, Cairo University, Giza, Egypt.

2- Maize Dept., Field Crops Res. Inst., ARC, Giza, Egypt.

### ABSTRACT

Six maize inbreds with contrasting grain oil content (three of high-oil and three of low-oil) were used to carry out one set of diallel crosses without reciprocals. The diallel crosses and their parents were grown in the field at two locations (Sids and Sakha) to evaluate grain oil content in one experiment, and the same crosses, without their parents were grown at the same locations to evaluate oil yield and grain yield traits in another experiment. The randomized complete block design was used for both experiments. The objectives were to estimate combining ability, type of gene action, heritability and expected selection gain for oil content and yield and grain yield traits. In general, average heterosis relative to high parent (heterobeltiosis) for oil content across locations was in the negative direction (-2.26 %). However, six out of 15  $F_1$ 's showed significant positive heterobeltiosis for oil content, namely L-15×L-13 (76.36%), L-2×L-18 (46.60%), L-1×L-18 (17.74%), L-2×L-13 (16.95%), L-8×L-15 (15.40%) and L-8×L-13 (10.84%). Both general (GCA) and specific (SCA) combining ability mean squares were highly significant for all studied traits. The best GCA effects were shown by the two inbreds L-2 and L-18 for oil content and oil yield. The best SCA effects were exhibited by the  $F_1$  cross L-15×L-13 and L-2×L-18 for oil content, oil yield/ plant and per feddan. Both additive and dominance variances were important, but the magnitude of dominance was several fold greater than that of additive and played the major role in the inheritance of studied oil yield and grain yield traits. The degree of dominance for oil content, 100-kernel weight, kernels/ plant, oil yield and grain yield traits was overdominance. Narrow-sense heritability ranged from 11.34% for kernels/ plant to 53.06% for oil yield/ plant. Expected selection gain ranged from 1.82% for kernels/ plant to 38.95% for oil yield/ feddan. The genetic correlation between protein and oil content was positive but small ( $r_g=0.132$ ) and insignificant, suggesting that simultaneous improvement of both traits might be feasible.

Key words: Oil content, Oil yield, Heterobeltiosis, Gene action, Heritability, Correlations  
*Zea mays*.

### INTRODUCTION

The value of high-oil maize (*Zea mays* L.) (HOM) is reflected in higher oil, amino acid and protein contents than normal maize (Han *et al* 1987 and Song 2001) and good germplasm quality for breeding. Oil content of HOM grain is >6%. Maize oil is characterized by high levels of unsaturated fatty acids and low levels of saturated fatty acids (Weber 1970 and Zai and Gao 2001). Given the high levels of unsaturated fatty acids, especially oleic (18:1) in HOM, including this grain in the diet would have positive health effects. Using HOM grain not only improves the food-energy utilization rate but also reduces the amount of supplemental fats needed in livestock feed (Goldman *et al* 1994).

Using traditional breeding methods across 100 or more years, many HOM populations have been developed (Alexander *et al* 1967, Miller *et al* 1981, Dudley and Lambert 1992 and 2004, Song *et al* 1999, Song and Chen 2004, Lambert *et al* 2004 and Moose *et al* 2004). Despite many years of selective breeding and germplasm isolation, results have been variable and somewhat ambiguous, leaving questions about the mode of HOM inheritance.

The oil content in maize grains was reported as a quantitative trait (Dudley 1977). Berke and Rocheford (1995) detected 31 RFLP loci associated to oil content. The additive genetic variance seems to be the main component in the control of this trait (Dudley 1977). Several workers have proven the efficiency of recurrent selection for the increase of oil content (Misevic and Alexander 1989, Dudley and Lambert 1992 and Song *et al* 1999). Signs of exhaustion of the genetic variability of oil content were not observed at the above mentioned studies. However, non-additive gene effects including dominance and epistasis had the predominant role in the inheritance of grain oil content in maize (Dodiya and Joshi 2003, Amit and Joshi 2007, Dudley 2008 and Dudley and Johnson 2009).

Considering the increasing importance of maize oil production, there is a need to develop HOM hybrids. To start utilizing HOM inbreds and populations in the development of HOM hybrids, genetic control of oil content and yield should be identified. Therefore, the objectives of the present study were: (i) to measure type of gene action, heritability and genetic advance from selection for maize oil content and other grain quality and yield traits and (ii) to identify relationships among those traits in a group of diallel crosses among HOM and low-oil maize (LOM) inbreds.

## MATERIALS AND METHODS

### Materials

Based on the results of a previous experiment, six inbreds (three of them, namely L-1, L-2 and L-18 were HOM inbreds and the other three namely L-8, L-13 and L-15 were low oil maize inbreds; LOM) were chosen for making diallel crosses. These inbred lines, in the S<sub>9</sub> generation, were isolated from different Thailand's HOM populations and CIMMYT's QPM pools.

In 2007 season, seeds of the six inbred lines were grown at Giza Res. Sta. of ARC. All possible crosses (excluding reciprocals) were made among them and 15 F<sub>1</sub> - single cross seeds were produced. Seeds of the six parental lines were also increased in 2007 season. Because of non-sufficient quantities of diallel cross seeds obtained in 2007, diallel crossing was repeated in 2008 season and sufficient seeds were produced.

### **Evaluation of the diallel crosses**

Two field evaluation experiments were carried out at two locations (Sakha and Sids Res. Sta. of the Agric. Res. Center, ARC). The first experiment included the six parental inbreds (differing in oil content) and their 15 diallel crosses, i.e. 21 entries, and conducted to determine grain oil content after artificial sibbing for each entry to prevent pollen effect from other entries on the oil content. The second experiment included the same 15 diallel crosses but did not include their parent inbreds and conducted to evaluate the oil yield and grain yield traits of these diallel crosses. A randomized complete block design (RCBD) was used for each experiment at each location with 2 replicates for the 1<sup>st</sup> experiment and 4 replicates for the 2<sup>nd</sup> experiment. The planting dates were 12<sup>th</sup> and 14<sup>th</sup> of May, 2009 at Sids and Sakha, respectively for both experiments. The experimental plot was one row of 6 m long and 80 cm wide (4.8 m<sup>2</sup>), with a distance of 25 cm between each two hills. In all experiments, all agricultural practices recommended by the ARC were followed.

Data were recorded on: number of kernels/ row; as average of 10 random plants per plot, 100-kernel weight (g), grain yield per plant (g); estimated by dividing grain yield per plot (adjusted at 15.5% grain moisture) on number of plants per plot, grain yield per feddan (ardab); on plot basis, grain protein content and oil content (%); using the Zeltex ZX-800 Near-Infrared (NIR) non-destruction whole grain analyzer manufactured by Zeltex Inc., Maryland, USA, protein yield per plant (g); calculated by multiplying average grain yield per plant by protein percentage of the same entry, protein yield per feddan (kg); calculated by multiplying average grain yield per feddan by protein percentage of the same entry, oil yield/ plant (g); calculated by multiplying average grain yield per plant by oil percentage of the same entry; oil yield/ feddan; calculated by multiplying average grain yield per feddan by oil percentage of the same entry.

### **Biometrical procedures**

The data collected were subjected to the normal analysis of RCBD for separate location and across locations if the homogeneity (Bartlett test) was not significant and estimates of LSD were calculated to test significance of differences between means according to Snedecor and Cochran (1989).

General (GCA) and specific (SCA) combining ability variances and effects were estimated according to Griffing's (1956) Method 2 model I (fixed effect) for grain protein content and Method 4 model I for other studied traits. In this experiment, when parents were not included, although the parental material are fixed samples, they will be considered here as random variable for the purpose of analysis using method 4 model 2 of Griffing (1956). Conclusion will be applied to these base populations and will not be generalized due to sampling effect.

Hayman's analysis was used in the 1<sup>st</sup> experiment conducted for the genetic analysis of only grain protein content. The genetic parameters were estimated by using Hayman's approach developed by Jinks and Hayman (1953); Jinks (1954) and Hayman (1954 a&b). The standard errors for components of variation were estimated according to Singh and Chaudhary (2000). The following genetic parameters and ratios were also calculated: (1) mean degree of dominance =  $(H_1/D)^{1/2}$  (when:  $D > H_1$  and the intercept is positive indicates partial dominance;  $D = H_1$  and line passes through origin indicates complete dominance and  $D < H_1$  and the intercept is negative; means overdominance), (2) proportion of genes with positive and negative effects in the parents estimated by dividing  $H_2/4H_1$ , (3) proportion of dominant and recessive genes in the parents ( $K_D/K_R$ ) and (4) coefficient of correlation (r) between the parental order of dominance ( $W_r+V_r$ ) and parental measurement ( $Y_r$ ).  $V_r/W_r$  graphs were constructed according to Hayman (1954 a&b) for protein content. Heritability in the broad ( $h^2_b$ ) and narrow ( $h^2_n$ ) sense was estimated from the following formulae:  $h^2_b = 100 (\delta^2_G/\delta^2_{ph})$  and  $h^2_n = 100 (\delta^2_A/\delta^2_{ph})$ . The expected genetic advance (GA) from selection was calculated as follows:  $GA = 100 k h^2_n \delta_{ph} / \bar{X}$ , where: k = selection differential = 1.76 using 10% selection intensity,  $h^2_n$  = narrow sense heritability,  $\delta_{ph}$  = square root of the dominator of heritability and  $\bar{X}$  = overall mean. Percentages of heterosis relative to the mid-parent and to the higher-parent (heterobeltiosis) for studied traits were calculated as follows: heterosis =  $100[(F_1-MP)/MP]$  and heterobeltiosis =  $100[(F_1-HP)/HP]$ , where:  $F_1$  = mean of  $F_1$  cross, MP = mean of the two parents and HP = mean of the high parent. Genetic correlation coefficients between pairs of studied traits were estimated across locations according to Falconer (1989).

## RESULTS AND DISCUSSION

### Oil content experiment

#### Analysis of variance of oil content

Analysis of variance for grain oil content of six maize inbred lines and their 15  $F_1$  diallel crosses at Sids and Sakha locations as well as combined analysis across locations is presented in Table (1).

Mean squares due to locations were highly significant, suggesting the presence of significant effect of climate and soil conditions on oil content of maize grain. Mean squares due to genotypes were highly significant for grain oil content under both, and across, locations, suggesting significant differences among studied genotypes for such trait. Partitioning genotypes degrees of freedom to their components indicated highly significant mean squares due to parents and  $F_1$ 's for grain oil content. Such significant differences in oil content among maize genotypes were also recorded by previous researchers (Ruschel 1975, Mittelmann 2003 and Mittelmann *et al.*

**Table 1. Analysis of variance for grain oil content (%) of six maize parental inbred lines and their 15 diallel F<sub>1</sub>'s at Sids, Sakha and across locations in 2009 season.**

SV	df	Mean squares		
		Sids	Sakha	Combined
Locations (L)	1	-	-	3.52 **
Replications (Rep)	1	0.06	2.01 **	-
Rep / L	2	-	-	1.06 **
Genotypes (G)	20	16.80 **	17.19 **	33.91 **
Parents (P)	5	15.67 **	16.24 **	31.90 **
Crosses (C)	14	17.70 **	17.58 **	35.21 **
P vs. C	1	9.75 **	16.48 **	15.76 **
G × L	20	-	-	0.07
P × L	5	-	-	0.01
C × L	14	-	-	0.08
P vs. C × L	1	-	-	0.23
Error	20	0.08	0.14	-
	40	-	-	0.11
CV%		3.59	6.86	4.16

\*\* indicate significance at 0.01 probability level.

2006, Munamava *et al* 2004, Seiam and Khalifa 2007 and Oliveira *et al* 2007).

Mean squares due to parents vs. F<sub>1</sub>'s were highly significant under both locations, indicating the presence of significant heterosis regarding maize grain oil concentration. Mean squares due to genotypes × locations, parents × locations and crosses × locations were not significant for oil content. Mittelman *et al* (2003) also found that for oil content, the genotype × location interaction was not significant. The oil content seems to be less influenced by the effect of environment and genotype × environment interaction than the protein content (Genter *et al* 1956 and Berke and Rocheford 1995).

### Mean oil content

Mean percentage of grain oil of the six maize inbreds and their 15 F<sub>1</sub>'s at Sids and Sakha as well as combined data across locations is presented in Table (2).

In general, mean grain oil content at Sakha was higher than that at Sids location by 0.18% for inbreds and 0.50% for F<sub>1</sub> crosses. The lower oil content at Sids might be attributed to the higher temperature at Sids as compared to Sakha, confirming results of Oikeh *et al* (1998).

The F<sub>1</sub> crosses were generally higher than their parental inbreds in grain oil content by 1.07% at Sids, 1.39% at Sakha and 1.23% for combined data across the two locations. This suggested the superiority of heterozygotes over homozygotes in maize grain oil content. Similar

**Table 2. Mean grain oil content (%) of six maize parental inbred lines and their 15 F<sub>1</sub> diallel crosses at Sids and Sakha locations and their combined data across locations in 2009 season.**

Genotypes	Sids	Sakha	Combined
<u>Parents</u>			
P <sub>1</sub> (L-1)	8.65	8.79	8.72
P <sub>2</sub> (L-2)	10.15	10.29	10.22
P <sub>3</sub> (L-8)	3.75	3.89	3.82
P <sub>4</sub> (L-15)	5.15	5.29	5.22
P <sub>5</sub> (L-18)	9.65	10.05	9.85
P <sub>6</sub> (L-13)	4.65	4.79	4.72
Average (parents)	7.00	7.18	7.09
LSD <sub>0.05</sub>	0.59	0.39	0.31
<u>Crosses</u>			
P <sub>1</sub> × P <sub>2</sub>	9.17	9.50	9.33
P <sub>1</sub> × P <sub>3</sub>	8.63	9.10	8.86
P <sub>1</sub> × P <sub>4</sub>	4.90	5.30	5.10
P <sub>1</sub> × P <sub>5</sub>	11.51	11.69	11.60
P <sub>1</sub> × P <sub>6</sub>	4.37	5.31	4.84
P <sub>2</sub> × P <sub>3</sub>	9.88	10.42	10.15
P <sub>2</sub> × P <sub>4</sub>	7.64	8.43	8.03
P <sub>2</sub> × P <sub>5</sub>	14.53	15.44	14.98
P <sub>2</sub> × P <sub>6</sub>	11.81	12.10	11.95
P <sub>3</sub> × P <sub>4</sub>	5.99	6.06	6.03
P <sub>3</sub> × P <sub>5</sub>	5.15	5.80	5.48
P <sub>3</sub> × P <sub>6</sub>	4.96	5.51	5.23
P <sub>4</sub> × P <sub>5</sub>	6.30	6.77	6.54
P <sub>4</sub> × P <sub>6</sub>	9.10	9.32	9.21
P <sub>5</sub> × P <sub>6</sub>	7.10	7.77	7.43
Average (crosses)	8.07	8.57	8.32
LSD <sub>0.05</sub>	0.55	0.88	0.57
Average (genotypes)	7.67	8.17	7.97
LSD <sub>0.05</sub>	0.58	0.79	0.47

conclusion was reported by previous investigators (Varma *et al* 2002, Umakanth and Kumar 2002, Mittelmann *et al* 2006 and Oliveira *et al* 2007).

The studied inbred parents varied significantly in grain oil content; the highest mean grain oil percentage was shown by P<sub>2</sub> (L-2) (10.15, 10.29) followed by P<sub>5</sub> (L-18) (9.65,10.05) and P<sub>1</sub> (L-1) (8.65, 8.79) in Sids and Sakha locations, respectively. On the contrary, P<sub>3</sub> (L-8), P<sub>6</sub> (L-13) and P<sub>4</sub> (L-15) inbreds exhibited the lowest grain oil percentage. The mean grain oil content of the inbred lines in the present experiment showed a similar trend to that recorded in the line × tester experiment (Al-Naggar *et al* 2010) that was evaluated at Giza, based on which parents for the present investigation were chosen. This ascertains the validity of diallel analysis to estimate the genetic parameters controlling inheritance of grain oil content in this group of genotypes.

The highest  $F_1$  cross for grain oil content combined across locations was  $P_2 \times P_5$  (L-2  $\times$  L-18) (14.98%) followed by  $P_2 \times P_6$  (L-2  $\times$  L-13) (11.95%),  $P_1 \times P_5$  (L-1  $\times$  L-18) (11.60%),  $P_2 \times P_3$  (L-2  $\times$  L-8) (10.15%),  $P_1 \times P_2$  (L-1  $\times$  L-2) (9.33%) and  $P_4 \times P_6$  (L-15  $\times$  L-13) (9.21%). It is worthy to note that most of these high oil crosses included at least one high-oil parent in each hybrid with the exception of  $P_4 \times P_6$  which included two low-oil parents. The superiority of the last  $F_1$  cross in grain oil content might be attributed to epistatic effects, confirming results of Dudley (2008) and Dudley and Johnson (2009). On the contrary,  $P_1 \times P_4$ ,  $P_3 \times P_6$ ,  $P_3 \times P_4$  and  $P_3 \times P_5$  exhibited the lowest  $F_1$ 's for grain oil content, where one or two of their parents are of low oil content.

Combined data across locations indicated that the range in grain oil content for  $F_1$  crosses (4.84 to 14.98%) was wider than that for their parents (3.80 to 10.22%). The overall mean of grain oil content was 7.97% (Table 2), which is higher than the mean values found in the literature for normal maize (between 3.5 and 4.5%, Alexander 1986, Lima 2000 and Tosello 1987). In this study, higher means than those reported in the literature were observed in the parents as well as in the hybrids. The analysis of maize oil content of several studies agrees with the variability we observed, resulting in different concentrations in different inbreds and hybrids. Lima (2000), analyzed some Brazilian hybrids, and found values between 3.6 and 6.9%. In another study on the genetic variation for oil content in maize with normal endosperm, Mittelman (2003) found values between 3.77 and 5.10%. Besides, these results of the literature indicate that the QPM and high-oil inbreds in the present study have the potential to compose new base populations, *per se* or in crosses, aiming at the improvement for high grain oil content. This conclusion was also reported by Oliveira *et al* (2007).

#### **Heterosis for oil content**

Percentages of heterosis relative to mid and high parent for grain oil content at Sids, Sakha and combined across locations are presented in Table (3). In general, average mid-parent heterosis for grain oil content at Sakha (20.51%) was higher than that at Sids (16.45%).

Moreover, average heterosis relative to high-parent (heterobeltiosis) for oil content at Sids, Sakha and across locations was generally in the negative direction (-4.00, -0.57 and -2.26%, respectively). However, out of the 15  $F_1$ 's, six crosses showed significant positive heterobeltiosis for oil content, namely  $P_4 \times P_6$  (76.36%),  $P_2 \times P_5$  (46.60%),  $P_1 \times P_5$  (17.74%),  $P_2 \times P_6$  (16.95%),  $P_3 \times P_4$  (15.40%) and  $P_3 \times P_6$  (10.84%). The magnitude of heterobeltiosis percentage was considerably high in the two crosses  $P_4 \times P_6$  and  $P_2 \times P_5$  (>46%). The *per se* performance of these crosses for mean oil

**Table 3. Estimates of heterosis (%) for grain oil content (%) relative to mid- and high-parent at Sids, Sakha and combined across locations (2009 season).**

Cross	Heterosis (%) relative to					
	Mid-parent			High-parent		
	Sids	Sakha	Comb.	Sids	Sakha	Comb.
P <sub>1</sub> × P <sub>2</sub>	-2.50	-0.42	-1.45	-9.70	-7.68	-8.68
P <sub>1</sub> × P <sub>3</sub>	39.11**	43.51**	41.54**	-0.29	3.53	1.63
P <sub>1</sub> × P <sub>4</sub>	-29.06**	-24.72**	-26.87**	-43.41**	-39.70**	-41.54**
P <sub>1</sub> × P <sub>5</sub>	25.79**	24.04**	24.91**	19.28*	16.27*	17.74*
P <sub>1</sub> × P <sub>6</sub>	-34.29**	-21.88**	-28.02**	-49.48**	-39.65**	-44.52**
P <sub>2</sub> × P <sub>3</sub>	42.09**	46.95**	44.54**	-2.71	1.26	-0.71
P <sub>2</sub> × P <sub>4</sub>	-0.13	8.14	4.04	-24.73**	-18.12*	-21.40**
P <sub>2</sub> × P <sub>5</sub>	46.72**	51.82**	49.30**	43.10**	50.05**	46.60**
P <sub>2</sub> × P <sub>6</sub>	59.60**	60.39**	60.00**	16.36*	17.54*	16.95*
P <sub>3</sub> × P <sub>4</sub>	34.61**	31.98**	33.27**	16.31*	14.52*	15.40*
P <sub>3</sub> × P <sub>5</sub>	-23.10**	-16.80*	-19.90*	-46.63**	-42.29**	-44.42**
P <sub>3</sub> × P <sub>6</sub>	17.98**	26.91**	22.52**	6.56	14.99*	10.84*
P <sub>4</sub> × P <sub>5</sub>	-14.87**	-11.74*	-13.28*	-34.72**	-32.64**	-33.65**
P <sub>4</sub> × P <sub>6</sub>	85.61**	84.86**	85.23**	76.60**	76.13**	76.36**
P <sub>5</sub> × P <sub>6</sub>	-0.77	4.64	1.98	-26.48**	-22.74**	-24.57**
<b>Average</b>	<b>16.45</b>	<b>20.51</b>	<b>18.51</b>	<b>-4.00</b>	<b>-0.57</b>	<b>-2.26</b>

\* and \*\* indicate significance at 0.05 and 0.01 probability levels, respectively.

content was also high (Table 2) and could therefore be recommended for maize breeding programs to improve grain oil content. Heterosis for grain oil content of maize was also reported by several investigators (Varma *et al* 2002, Umakanth and Kumar 2002, Kaushik *et al* 2004, Mittelmann *et al* 2006, Amit and Joshi 2007, Seiam and Khalifa 2007 and Oliveira *et al* 2007).

In this study, despite the significance demonstrates the existence of differences between the hybrids and parents, the heterotic effect acts in the opposite sense to the desired, that is, in many hybrids there is a reduction in the grain oil content, compared to the higher parent mean. This fact shows the mean dominance of the alleles for low oil content. In spite of the negative mean heterobeltiosis, different combinations with total positive heterosis or heterobeltiosis can be observed. This demonstrates the existence of bidirectional dominance for the trait in the different loci, with prevalence of loci with dominance for reduction of the oil content. This conclusion was also reported by Oliveira *et al* (2007). In a program targeting hybrids, the strategy would therefore be to select combinations with positive heterosis. This situation would indicate parent pairs that are divergent precisely in the loci with dominance for high oil content.



### Combining ability for oil content

Analysis of variance for GCA and SCA of grain oil content is presented in Table (4). Results showed highly significant mean squares due to GCA and SCA for grain oil content at Sids, Sakha and across locations, indicating that both additive and non-additive gene effects played important roles in the inheritance of this trait. However, the magnitude of GCA was higher than that of SCA mean squares; the ratio of GCA/SCA exceeded the unity.

**Table 4. Combining ability mean squares (according to Griffing 1956) method 2 model I for grain oil content (%) at Sids and Sakha and their combined data in 2009 season.**

S.O.V.	d.f.	Mean squares		
		Sids	Sakha	Combined
GCA	5	19.13 **	20.26 **	78.76 **
SCA	15	4.82 **	4.70 **	18.96 **
GCA × Loc	5	-	-	0.03
SCA × Loc	15	-	-	0.08
Error	20	0.08	0.14	-
	40	-	-	0.11
GCA/SCA		3.97	4.31	4.15
GCA × Loc / SCA × Loc		-	-	0.38

\*\* indicate significance at 0.01 probability level.

The higher importance of GCA over SCA variance for oil content in maize grains was also reported by Dubey *et al* (2001). On the contrary, Bhatnagar *et al* (2004) reported that GCA gene effects are important for grain oil content of maize.

GCA effects for grain oil content are presented in Table (5). Data showed that the parental inbreds P<sub>2</sub> (L-2) and P<sub>5</sub> (L-18) had positive and highly significant GCA effects (favorable) for grain oil content at both and across locations. Moreover, the inbred P<sub>1</sub> (L-1) showed positive and significant GCA effects at Sids and positive but insignificant GCA effects at Sakha and across locations. It is worthy to note that the inbred P<sub>5</sub> (L-18) showed superiority in GCA effects for oil content in a previous line × tester (Al-Naggar *et al* 2010) and this diallel experiment. On the contrary, P<sub>3</sub>, P<sub>4</sub> and P<sub>6</sub> inbreds showed negative and highly significant GCA effects (unfavorable) for this trait.

The results revealed that the inbred lines P<sub>2</sub>, P<sub>5</sub> followed by P<sub>1</sub> can be considered as the best general combiners for the improvement of grain oil contents of their hybrid combinations. It is worthy to note that the high *per se* performance of these three inbreds is in accordance with their high positive GCA effects for grain oil content, *i.e.* high-oil inbreds were good general combiners for this trait. These three inbreds could be recommended for maize breeding programs for improving grain oil content. Inbreds

**Table 5. Estimates of GCA effects of maize parental inbreds for grain oil content at Sids, Sakha and across locations (season 2009).**

Parents	Sids	Sakha	Combined
P <sub>1</sub> (L-1)	0.19 *	0.16	0.18
P <sub>2</sub> (L-2)	2.37 **	2.41 **	2.39 **
P <sub>3</sub> (L-8)	-1.53 **	-1.57 **	-1.55 **
P <sub>4</sub> (L-15)	-1.26 **	-1.34 **	-1.30 **
P <sub>5</sub> (L-18)	1.19 **	1.30 **	1.24 **
P <sub>6</sub> (L-13)	-0.96 **	-0.95 **	-0.96 **
SE gi	0.09	0.12	0.12
SE gi-gj	0.14	0.19	0.17

\* and \*\* indicate significance at 0.05 and 0.01 probability level, respectively.

showing significant positive GCA effects for oil content would be ideal for initiating a high-oil composite or a segregating generation of single or three-way cross hybrid amenable for selection of high-oil genotypes, as proposed by Miranda and Chaves (1991). On the contrary, the inbreds P<sub>3</sub>, P<sub>4</sub> and P<sub>6</sub> were the lowest in both GCA effects and mean *per se* performance for oil content.

Specific combining ability effects of the F<sub>1</sub> crosses for grain oil content are presented in Table (6). The best SCA effects for oil content were obtained from the crosses P<sub>4</sub> × P<sub>5</sub>, P<sub>2</sub> × P<sub>5</sub>, P<sub>2</sub> × P<sub>6</sub>, P<sub>1</sub> × P<sub>3</sub> and P<sub>1</sub> × P<sub>5</sub>. Such good crosses for SCA effects might come from two parents possessing good GCA effects (such as P<sub>2</sub> × P<sub>5</sub>), from one with good and other with low GCA effects (such as P<sub>2</sub> × P<sub>6</sub>, P<sub>1</sub> × P<sub>3</sub> and P<sub>1</sub> × P<sub>5</sub>) or from two parents possessing low GCA effects (such as P<sub>4</sub> × P<sub>6</sub>) for grain oil content.

**Table 6. Estimates of SCA effects of F<sub>1</sub> crosses for grain oil content at Sids, Sakha and across locations (season 2009).**

Crosses	Sids	Sakha	Combined
P <sub>1</sub> × P <sub>2</sub>	-1.16 **	-1.24 **	-1.20 **
P <sub>1</sub> × P <sub>3</sub>	2.2 **	2.34 **	2.27 **
P <sub>1</sub> × P <sub>4</sub>	-1.79 **	-1.69 **	-1.74 **
P <sub>1</sub> × P <sub>5</sub>	2.36 **	2.06 **	2.21 **
P <sub>1</sub> × P <sub>6</sub>	-2.62 **	-2.07 **	-2.35 **
P <sub>2</sub> × P <sub>3</sub>	1.27 **	1.41 **	1.34 **
P <sub>2</sub> × P <sub>4</sub>	-1.23 **	-0.81 **	-1.02 **
P <sub>2</sub> × P <sub>5</sub>	3.2 **	3.57 **	3.38 **
P <sub>2</sub> × P <sub>6</sub>	2.64 **	2.47 **	2.55 **
P <sub>3</sub> × P <sub>4</sub>	1.02 **	0.80 *	0.91 **
P <sub>3</sub> × P <sub>5</sub>	-2.28 **	-2.10 **	-2.19 **
P <sub>3</sub> × P <sub>6</sub>	-0.31	-0.14	-0.23
P <sub>4</sub> × P <sub>5</sub>	-1.39 **	-1.35 **	-1.37 **
P <sub>4</sub> × P <sub>6</sub>	3.56 **	3.45 **	3.50 **
P <sub>5</sub> × P <sub>6</sub>	-0.9 **	-0.75 *	-0.82 *
SE S <sub>ij</sub>	0.25	0.33	0.29
SE S <sub>ij</sub> -S <sub>ik</sub>	0.37	0.50	0.44
SE S <sub>ij</sub> -S <sub>kl</sub>	0.34	0.46	0.41

\* and \*\* indicate significance at 0.05 and 0.01 probability level, respectively.

It is interesting to note that the crosses  $P_4 \times P_6$ ,  $P_2 \times P_5$ ,  $P_2 \times P_6$  and  $P_1 \times P_5$  showed superiority in SCA effects, mean *per se* performance and heterobeltiosis for grain oil content. These crosses could be recommended for maize breeding programs to improve grain oil content trait. Identifying the best parents in GCA effects and the best hybrid combinations in SCA effects for use in future programs of improving oil content in maize was reported by Sinobas and Monteagudo (1996), Dodiya and Joshi (2003), Bhatnagar *et al* (2004) and Amit and Joshi (2007).

#### Gene action, heritability and selection gain for oil content

Components of genetic variance and heritability for grain oil content calculated according to Hayman (1954 a & b) are presented in Table (7).

**Table 7. Components of variance and heritability for maize grain oil content at Sids, Sakha and across locations (season 2009).**

Parameters	Sids	Sakha	Combined
D	7.796**	8.05*	7.951**
$H_1$	19.503**	18.70*	19.109**
$h^2$	2.317	3.89	3.059
E	0.039	0.07	0.024
$(H_1/D)^{\%}$	1.582	1.52	1.550
$H_2/4H_1$	0.041	0.07	0.056
$K_D/K_R$	0.918	0.90	0.912
$K (h^2/\bar{I}_2)$	0.726	0.73	0.720
$h^2_{\delta}\%$	0.997	0.99	0.998
$h^2_{\alpha}\%$	0.281	0.30	0.294
R	0.699	0.70	0.701
GA%	32.05	31.9	32.37

\*\* indicate significance at 0.01 probability level.

Additive genetic component of variation (D) for grain oil content was highly significant at Sids, Sakha and across locations. Several investigators also reported significant role of additive effect on oil content of maize (Dudley 1977, Miller *et al* 1981, and Mittelman *et al* 2003) suggesting that recurrent selection methods are efficient for improving oil content in maize. Moreover, the dominance component of variation ( $H_1$ ) was highly significant for the same trait under both, and across, locations. The magnitude of dominance was, however, much greater than that of additive genetic variance, indicating that dominance was more important than additive and played the major role in the inheritance of grain oil content. Similar conclusion was reported by Dodiya and Joshi (2003), Mangolin *et al* (2004) and Amit and Joshi (2007). Dudley (2008) and Dudley and Johnson (2009) reported the importance of epistasis in the inheritance of oil content. They noted that epistasis could contribute to the long continued response to selection for high-oil in the Illinois long-term selection strains and also may help explain the continued success of commercial corn breeding. The results

of the present investigation suggested that heterosis breeding could also be considered an efficient method for improving grain oil content in maize.

The overall dominance effects of heterozygous loci ( $h^2$ ) controlling grain oil content were not significant in spite of the significance of  $H_1$ ; that could be due to the presence of a considerable amount of cancelling dominance effects in the parental genotypes. Average degree of dominance  $(H_1/D)^{1/2}$  was greater than unity, indicating that the degree of dominance for this trait was overdominance. The role of overdominance in controlling the inheritance of maize oil content was also reported by Mangolin *et al* (2004) and Amit and Joshi (2007). The proportions of the genes with positive and negative effects in the parents ( $H_2/4H_1$ ) which estimate the frequencies at nonadditive loci were less than 0.25, suggesting asymmetrical distribution at loci showing dominance. The proportion of dominant and recessive genes ( $K_D/K_R$ ) was close to unity, suggesting that dominant and recessive genes controlling grain oil content in the parents were in equal proportion. The correlation coefficient ( $r$ ) values between the order of dominance ( $V_r$ ,  $W_r$ ) and parental measurements was significant and positive for grain oil content, indicating that the expression of high scores in most of the parents is associated with dominant genes.

Broad sense heritability ( $h^2_b$ ) estimates for grain oil content were very high, confirming results of Mangolin *et al* (2004) and Wang *et al* (2009). However, narrow sense heritability for the same trait was below average (28.1, 30.0 and 29.4% at Sids, Sakha and across locations, respectively). The big difference between broad and narrow-sense heritability of this trait could be attributed to the high estimates of non-additive genetic components.

Predicted genetic advance (GA) from selection (based on 10% selection intensity) for grain oil content (Table 7) was reasonably high (32.05, 31.91 and 32.37% at Sids, Sakha and across locations, respectively). These high values of expected GA relative to those reported in the literature may be attributed to the high estimates of phenotypic standard deviation ( $\sigma^2_{ph}$ ) for oil content in this study. This indicates that selection in segregating generations of crosses derived from the best inbreds of this study for high oil content in GCA effects and *per se* performance would be very efficient in improving this trait. Previous selection programs for oil content in maize achieved actual good progress in this trait (Misevic and Alexander 1989, Dudley and Lambert 1992 and Song *et al* 1999).

#### **Graphical analysis of grain oil content**

Graphical analysis proposed by Hayman (1954 a&b) for grain oil content (Figures 1 and 2) showed that the regression line intercepted ( $W_r$ ) axis below the origin at both locations, indicating that overdominance controlled grain oil content trait. The correlation coefficient ( $r$ ) between the parental means and their corresponding values of ( $V_r$ ,  $W_r$ ) for this trait at

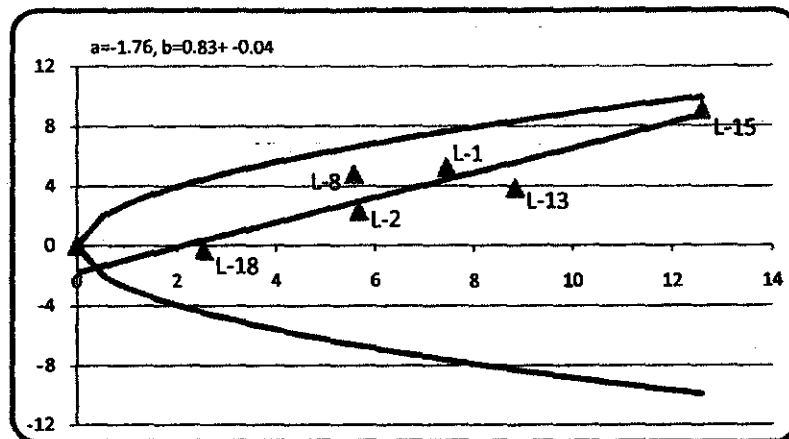


Fig. 1. Vr/Wr graph for grain quality oil content at Sids.

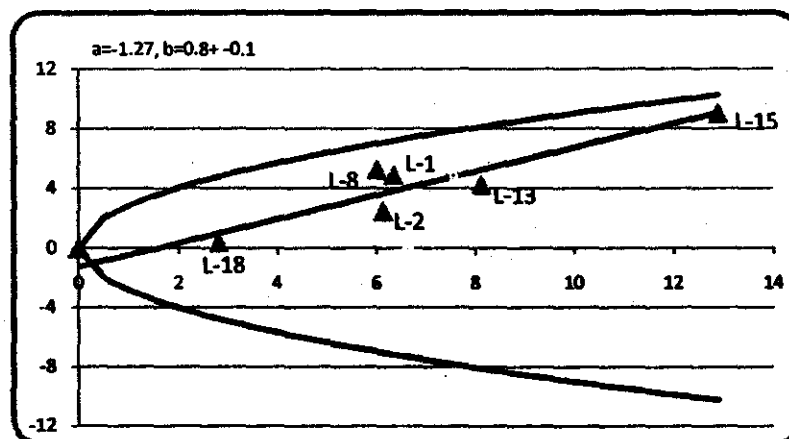


Fig. 2. Vr/Wr graph for grain quality oil content at Sakha.

both and across locations was significant and positive, indicating that dominant genes generally act towards increasing percentage of grain oil. Accumulation of dominant genes in the parents is indicative for increasing grain oil content. The array points on the  $V_r/W_r$  graph for grain protein content (Figures 1 and 2) at both locations may give evidence that the parents  $P_2$  (L-2),  $P_5$  (L-18) and  $P_1$  (L-1) which had the highest grain oil content contained most of the dominance genes, while the parents  $P_4$  (L-15) and  $P_6$  (L-13) which had the lowest grain oil content contained most of recessive genes. A reasonable agreement between mean performance and dominance order of the parents for this trait in both and across locations is a good indicator of accurate reliance on the results

## Oil yield and grain yield experiment

### Analysis of variance for oil yield and grain yield traits

Analysis of variance combined across locations (Table 8) showed that mean squares due to locations were highly significant for all studied traits, indicating that Sids and Sakha locations differ in their climatic and/or soil conditions. Mean squares due to crosses were highly significant, suggesting that the crosses used in this experiment differ significantly for studied oil yield and grain yield characters.

Mean squares due to crosses  $\times$  locations interaction were highly significant for all studied traits, indicating that oil diallel crosses performed differently under different locations for yield and grain yield traits, confirming results of Munamava *et al* (2004).

**Table 8. Analysis of variance of maize oil yield and grain yield traits for the oil diallel crosses evaluated across two locations in 2009 season.**

SV	df	Mean squares					
		100 KW	K/P	GY/P	GY/F	OY/P	OY/F
Locations (L)	1	249.41**	762893.32 **	14608.57 **	288.08 **	288.15 **	109416.41 **
Rep./L	6	2.73	4632.88	287.42	4.39	2.73	1157.06
Crosses (C)	14	27.03 **	22811.46 **	1856.69 **	34.61 **	275.58 **	113035.49 **
C $\times$ L	14	11.52 **	10535.50 **	1177.23 **	22.71 **	16.07 **	6546.73 **
Error	84	4.99	2537.06	170.35	3.56	1.57	754.81
CV%		8.29	7.17	6.97	7.09	8.01	8.82

- \* and \*\* indicate significance at 0.05 and 0.01 probability levels, respectively.

- 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan, OY/P = oil yield per plant and OY/F = oil yield per feddan.

### Mean performance for oil and grain yield traits

Means of the studied oil yield and grain yield traits, combined across locations for the oil diallel crosses are presented in Table (9).

Crosses of the oil diallel showed significant variability in all studied characters expressed by the range. The wider range was exhibited by oil yield/ feddan and oil yield/ plant. Studied diallel crosses showed a significant variability in oil yield and grain yield traits. Oil yield/ feddan across locations ranged from 174.58 ( $P_1 \times P_6$ ) to 608.48 kg ( $P_2 \times P_5$ ). It was the highest for the cross  $P_2 \times P_5$  followed by  $P_2 \times P_6$  (463.97 kg),  $P_2 \times P_3$  (390.17 kg),  $P_1 \times P_5$  (372.81 kg) and  $P_1 \times P_2$  (369.53 kg). The same crosses were also the highest, with the same order, for oil yield/ plant. This superiority in oil yield is mainly due to the superiority of these crosses in grain oil concentrations (Table 2). It is worthnoting that these best crosses in oil yield include two high-oil parents ( $P_2 \times P_5$ ,  $P_1 \times P_5$  and  $P_1 \times P_2$ ) or at least one parent of high-oil content ( $P_2 \times P_6$  and  $P_2 \times P_3$ ), since the best parents in oil content were  $P_1$ ,  $P_2$  and  $P_5$  (Table 2).

**Table 9. Means of studied oil yield and grain yield traits of the oil diallel crosses (data are combined across locations in 2009 season).**

Crosses	100KW (g)	K/P	GY/P (g)	GY/F (ardab)	OY/P (g)	OY/F (kg)
P <sub>1</sub> × P <sub>2</sub>	27.49	729.20	200.59	28.32	18.71	369.53
P <sub>1</sub> × P <sub>3</sub>	25.70	629.90	160.84	22.86	14.34	285.54
P <sub>1</sub> × P <sub>4</sub>	24.57	711.65	173.99	24.58	8.88	175.50
P <sub>1</sub> × P <sub>5</sub>	22.79	714.41	162.72	22.98	18.89	372.81
P <sub>1</sub> × P <sub>6</sub>	26.25	702.59	183.54	25.65	8.91	174.58
P <sub>2</sub> × P <sub>3</sub>	26.46	745.33	195.66	27.42	19.90	390.17
P <sub>2</sub> × P <sub>4</sub>	29.78	681.43	198.16	27.64	15.89	310.68
P <sub>2</sub> × P <sub>5</sub>	26.90	742.06	198.62	28.89	29.88	608.48
P <sub>2</sub> × P <sub>6</sub>	26.29	752.02	194.05	27.72	23.18	463.97
P <sub>3</sub> × P <sub>4</sub>	26.73	820.70	217.29	30.11	13.09	253.63
P <sub>3</sub> × P <sub>5</sub>	26.91	672.09	177.79	25.79	9.72	197.70
P <sub>3</sub> × P <sub>6</sub>	27.29	660.61	178.68	25.85	9.33	189.59
P <sub>4</sub> × P <sub>5</sub>	28.61	687.78	194.98	27.81	12.80	255.41
P <sub>4</sub> × P <sub>6</sub>	29.94	601.34	179.08	25.87	16.47	333.16
P <sub>5</sub> × P <sub>6</sub>	28.26	684.78	192.31	27.94	14.37	292.59
Average	26.93	702.39	187.22	26.63	15.62	311.56
Range High	29.94	820.70	217.29	30.11	29.88	608.48
Low	22.79	601.34	160.84	22.86	8.88	174.58
LSD <sub>0.05</sub>	2.220	50.082	12.977	1.877	1.245	27.317

- 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan, OY/P = oil yield per plant and OY/F = oil yield per feddan.

It is interesting to mention that the cross P<sub>2</sub> × P<sub>5</sub> followed by the cross P<sub>2</sub> × P<sub>6</sub>, P<sub>1</sub> × P<sub>2</sub> and P<sub>2</sub> × P<sub>3</sub> showed very high means for all oil yield and grain yield traits. The lowest oil yield/ feddan was shown by P<sub>1</sub> × P<sub>6</sub> (174.58 kg) followed by P<sub>1</sub> × P<sub>4</sub> (175.50 kg). Grain yield/ feddan of the studied crosses, across locations ranged from 22.86 ard (P<sub>1</sub> × P<sub>3</sub>) to 30.11 ard (P<sub>3</sub> × P<sub>4</sub>). The highest mean grain yield per feddan was shown by the cross P<sub>3</sub> × P<sub>4</sub> (30.11 ard) followed by P<sub>2</sub> × P<sub>5</sub> (28.89 ard) and P<sub>1</sub> × P<sub>2</sub> (28.32 ard). Grain yield/ plant across locations, ranged from 160.84 g (P<sub>1</sub> × P<sub>3</sub>) to 217.29 g (P<sub>3</sub> × P<sub>4</sub>). The cross P<sub>3</sub> × P<sub>4</sub> exhibited the highest mean grain yield/ plant and the highest mean number of kernels/ plant (820.7). In general, the best crosses in mean grain yield were among the best crosses in mean number of kernels/plant and to a less extent to the best crosses in mean weight of 100 kernels. This indicates that number of kernels is more important than kernel weight in determining the final grain yield per plant and per feddan. The previously mentioned superior crosses in oil yield could be recommended to maize breeding programs aiming at improving oil and grain yields.

#### **Combining ability variances for oil yield and grain yield traits**

Results (Table 10) indicated that mean squares due to GCA and SCA were highly significant for all studied oil yield and grain yield traits. The ratio of GCA/SCA was greater than unity for all studied traits, except for

**Table 10. Combining ability variances computed according to Griffing (1956) method 4 model I of oil diallel crosses for oil yield and grain yield traits (data are combined across locations in 2009 season).**

SV	df	Mean Squares					
		100 KW	K/P	GY/P	GY/F	OY/P	OY/F
GCA	5	40.91**	12947.06**	2603.20**	53.12**	514.87**	209930.47**
SCA	9	19.32**	28291.68**	1441.59**	24.32**	142.64**	59204.95**
GCA × L	5	12.90*	5460.41	849.09**	10.18**	18.19**	5287.31**
SCA × L	9	10.75*	13355.00**	1359.53**	29.68**	14.89**	7246.41**
Error	84	4.99	2537.06	170.53	3.56	1.57	754.81
GCA/SCA		2.12	0.46	1.81	2.18	3.61	3.55
GCA×L/SCA×L		1.20	0.41	0.62	0.34	1.22	0.73

- \* and \*\* indicate significance at 0.05 and 0.01 probability levels, respectively.

- 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan, OY/P = oil yield per plant and OY/F = oil yield per feddan.

number of kernels per plant, indicating that GCA was more important than SCA in the inheritance of most studied traits. In this regard, GCA effects for grain yield and quality traits were prevalent in CIMMYT's low land tropical late and subtropical QPM germplasm (Vasal *et al* 1993 a&b) and subtropical and temperate intermediate maturity germplasm (Beck *et al* 1991). On the contrary, San Vicente *et al* (1998) and Bhatnagar *et al* (2004) reported that GCA effects were non-significant for grain yield but highly significant for agronomic and kernel quality traits.

Mean squares due to GCA × locations and SCA × locations were significant and highly significant for all studied traits, except GCA × locations for kernels/plant, indicating that both GCA and SCA are affected by locations for most studied traits. The ratio GCA × L/ SCA × L exceeded unity for 100KW and oil yield/ plant, suggesting that GCA was more affected by locations than SCA for these traits. On the other hand, this ratio was less than unity for the remaining traits, indicating that SCA was more affected by locations than GCA for these traits.

#### **Combining ability effects for oil yield and grain yield traits**

General combining ability (GCA) effects combined across locations are presented in Table (11). Data indicated that the highest positive (favorable) and significant GCA effect was exhibited by the inbred parent P<sub>2</sub> (L-2) for grain yield/ plant, oil yield/ plant and oil yield/ feddan. The parental inbred P<sub>5</sub> (L-18) came in 2<sup>nd</sup> rank in GCA effects for oil yield/ plant and oil yield/ feddan. These inbred parents are also superior in GCA effects of oil content (Table 11) and could therefore be considered good general combiners and could contribute positively in their hybrid combinations for



**Table 11. General Combining ability effects of the inbred parents for studied oil yield and grain yield traits (data are combined across locations in 2009 season).**

Parent	100-KW	K/P	GY/P	GY/F	OY/P	OY/F
P <sub>1</sub> (L-1)	-1.94	-6.05	-13.6 *	-2.19 *	-2.10 *	-44.96 **
P <sub>2</sub> (L-2)	0.60	34.52	12.75 *	1.71 *	7.36 **	146.26 **
P <sub>3</sub> (L-8)	-0.34	4.18	-1.46	-0.28	-2.94 *	-60.29 **
P <sub>4</sub> (L-15)	1.19	-2.27	6.85	0.72	-2.75 *	-57.35 **
P <sub>5</sub> (L-18)	-0.31	-2.71	-2.42	0.07	1.89 *	42.30 **
P <sub>6</sub> (L-13)	0.81	-27.66	-2.11	-0.03	-1.47 *	-25.97 *
SE g <sub>i</sub>	1.73	22.99	5.96	0.86	0.57	12.54
SE g <sub>r</sub> -g <sub>i</sub>	1.58	35.62	9.23	1.34	0.89	19.43

- \* and \*\* indicate significance at 0.05 and 0.01 probability levels, respectively.

- 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan, OY/P = oil yield per plant and OY/F = oil yield per feddan.

the enhancement of oil content and yield and grain yield of maize. Moreover these inbreds (P<sub>2</sub> and P<sub>5</sub>) were the best in mean *per se* for oil content (Table 2).

Specific combining ability (SCA) effects across locations are presented in Table (12). Results indicated that the highest positive and significant SCA effects were shown by the cross P<sub>2</sub> × P<sub>5</sub> followed by P<sub>4</sub> × P<sub>6</sub>, P<sub>1</sub> × P<sub>3</sub>, P<sub>1</sub> × P<sub>5</sub> and P<sub>3</sub> × P<sub>4</sub> for oil yield per plant and per feddan and the cross P<sub>3</sub> × P<sub>4</sub> for grain yield per plant and per feddan and kernels/ plant. The last hybrid showed also high SCA effects for oil yield per plant and per feddan. It is worthnoting that the best crosses in SCA effects and mean *per se* performance were P<sub>2</sub> × P<sub>5</sub> and P<sub>1</sub> × P<sub>5</sub> for oil yield. These crosses could be recommended for maize breeding programs for improving oil and grain yield traits.

#### **Gene action, heritability and selection gain for oil yield and grain yield traits**

Data presented in Table (13) indicated that both additive ( $\delta^2_A$ ) and dominance ( $\delta^2_D$ ) variances played roles in the inheritance of studied oil yield and grain yield traits, confirming results of Dudley (1977), Berke and Rocheford (1995) and Kumar *et al* (1997). The ratio  $\delta^2_A/\delta^2_D$  exceeded unity for all studied traits except for K/P, suggesting that additive was more important than dominance variance in the inheritance of these traits and therefore selection would be effective in their improvement. These results are in agreement with those reported by Dudley (1977), Miller *et al* (1981) Mittelmann *et al* (2003) and Bhatnagar *et al* (2004). On the other hand, the ratio  $\delta^2_A/\delta^2_D$  was less than unity for kernels/ plant, suggesting that dominance was more important than additive variance in the inheritance of this trait. Average degree of dominance “a” exceeded the unity for 100-kernel weight, kernels/ plant, oil yield per plant and per feddan, suggesting

**Table 12. Specific Combining ability effects of the inbred parents of the oil diallel crosses for studied oil yield and grain yield traits (data are combined across locations in 2009 season).**

Crosses	100 KW	K/P	GY/P	GY/F	OY/P	OY/F
P <sub>1</sub> × P <sub>2</sub>	2.04	-1.65	14.23	2.17	-2.18*	-43.34*
P <sub>1</sub> × P <sub>3</sub>	0.98	-70.61	-11.32	-1.31	3.75*	79.22**
P <sub>1</sub> × P <sub>4</sub>	-1.55	17.58	-6.48	-0.57	-1.90	-33.75
P <sub>1</sub> × P <sub>5</sub>	-1.92	20.78	-8.47	-1.53	3.48*	63.91*
P <sub>1</sub> × P <sub>6</sub>	0.45	33.91	12.03	1.24	-3.16*	-66.05*
P <sub>2</sub> × P <sub>3</sub>	-0.55	4.25	-2.85	-0.64	-0.15	-7.36
P <sub>2</sub> × P <sub>4</sub>	1.04	-53.22	-8.66	-1.42	-4.34*	-89.79**
P <sub>2</sub> × P <sub>5</sub>	-0.33	7.86	1.07	0.48	5.01*	108.36**
P <sub>2</sub> × P <sub>6</sub>	-2.21	42.77	-3.80	-0.59	1.66	32.13
P <sub>3</sub> × P <sub>4</sub>	-1.14	116.41**	24.68 *	3.04 *	3.15*	59.72*
P <sub>3</sub> × P <sub>5</sub>	0.73	-31.76	-5.55	-0.62	-4.85*	-95.87**
P <sub>3</sub> × P <sub>6</sub>	-0.02	-18.30	-4.97	-0.47	-1.89	-35.71
P <sub>4</sub> × P <sub>5</sub>	0.70	-9.64	3.33	0.40	-1.96	-41.10
P <sub>4</sub> × P <sub>6</sub>	0.95	-71.13	-12.88	-1.45	5.06*	104.92**
P <sub>5</sub> × P <sub>6</sub>	0.83	12.75	9.62	1.27	-1.67	-36.30
SE S <sub>ij</sub>	1.73	39.02	10.11	1.46	0.97	21.28
SE S <sub>ij</sub> S <sub>ik</sub>	2.74	61.69	15.99	2.31	1.53	33.65
SE S <sub>ij</sub> S <sub>ij</sub>	2.23	50.37	13.05	1.89	1.25	27.47

- \* and \*\* indicate significance at 0.05 and 0.01 probability levels, respectively.

- 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan, OY/P = oil yield per plant and OY/F = oil yield per feddan.

**Table 13. Additive ( $\delta^2_A$ ), dominance ( $\delta^2_D$ ) variances, degree of dominance (a), narrow ( $h^2_n$ ) and broad ( $h^2_b$ ) sense heritability and genetic advance (GA) from selection for oil yield and grain yield traits of the oil diallel crosses (data combined across locations in 2009 season).**

Parameter	100 KW	K/P	GY/P	GY/F	OY/P	OY/F
$\delta^2_A$	1.22	465.63	104.50	3.02	22.18	9093.05
$\delta^2_D$	1.07	1867.09	10.26	0.67	16.55	6742.82
$\delta^2_A / \delta^2_D$	1.13	0.25	10.19	4.51	1.34	1.35
$\delta^2_G$	2.29	1401.46	114.76	3.69	38.73	15835.87
$\delta^2_{A \times L}$	0.27	-986.82	-63.81	-2.44	0.26	-161.07
$\delta^2_{D \times L}$	1.44	2704.49	297.25	6.53	2.81	1500.60
$\delta^2_{Ph}$	4.00	4105.95	412.01	10.22	41.80	17306.47
"a"	1.33	2.83	0.44	0.67	1.22	1.22
$h^2_n$ %	30.50	11.34	25.36	29.55	53.06	52.41
$h^2_b$ %	77.25	34.13	27.85	36.11	92.66	91.50
GA %	3.99	1.82	4.84	6.25	38.68	38.95

- 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan, OY/P = oil yield per plant and OY/F = oil yield per feddan.

that overdominance was controlling the inheritance of these traits and confirming results of Mangolin *et al* (2004). However, partial dominance was acting for grain yield per plant and per feddan in this group of crosses.

Broad-sense heritability ( $h^2_b$ ) estimates were very high for oil yield/ plant (92.66%) and per feddan (91.50%), suggesting that the environment had very low effect on the phenotypic variance of oil yield traits. On the contrary, the  $h^2_b$  estimates were average for 100-kernel weight (57.25%) and below average for remaining traits, ranging from 27.85% for grain yield/ plant to 36.11% for grain yield/ feddan, indicating that the environment had high effect on the phenotype for these traits; this was obvious, since the magnitude of  $\delta^2_{DxI}$  was relatively high for such traits. Mangolin *et al* (2004) obtained also very high estimate of broad-sense heritability (98%) for oil content, but Wang *et al* (2009) reported different estimates of  $h^2_b$  ranging from 38 to 98% depending on the population used.

Narrow-sense heritability ( $h^2_n$ ) estimates were average for oil yield per plant (53.06%) and per feddan (52.41%) and below average for other traits, ranging from 11.34% for kernels/ plant to 30.50% for 100-kernel weight. The difference between  $h^2_b$  and  $h^2_n$  was very small for grain yield per plant and per feddan, suggesting the small effect of non-additive component of variance in the inheritance of these traits. On the contrary, the difference between  $h^2_b$  and  $h^2_n$  was high for the oil yield traits, suggesting that non-additive component of variance is of considerable magnitude in the genetic variance and played important role in their inheritance.

Calculated predicted genetic advance (GA) from selection, based on 10% selection intensity, was the highest for oil yield per plant (38.68%) and per feddan (39.95%) and the lowest for kernels/ plant (1.82%). For the remaining traits, GA percentage ranged from 3.99% (for 100-kernel weight) to 6.25% (for grain yield/ feddan). The high estimate of GA for oil yield traits indicates that few cycles of selection would be sufficient for improving these traits. Actual improvement via selection achieved for oil content and yield (Mittelmann *et al* 2003 and Wang *et al* 2009) confirmed the high predicted GA estimates of the present investigation.

### **Trait interrelationships**

Genetic correlation coefficients ( $r_g$ ) of pairs of studied grain yield and quality traits in the oil diallel crosses calculated across locations are presented in Table (14). A strong positive genetic association was found between oil content and each of oil yield/ plant (0.936) and oil yield/ feddan (0.934). This means that selection for high oil content will simultaneously help in obtaining high oil yield either per plant or per feddan. Moreover, oil yield/ feddan was very strongly and positively correlated with oil yield per plant ( $r_g=0.989$ ) and significantly and positively correlated with grain yield/ feddan ( $r_g=0.416$ ) and grain yield/ plant ( $r_g=0.341$ ). Thus, selection for high

**Table 14. Genetic correlation coefficient ( $r_g$ )  $\pm$  standard error of pairs of studied grain yield and quality traits in the oil diallel crosses across locations (n=120) in 2009 season.**

	PY/P	PY/F	OC%	OY/P	OY/F	100KW	K/P	GY/P	GY/F
PC%	0.777 $\pm 0.061$	0.787 $\pm 0.058$	0.132 $\pm 0.180$	0.139 $\pm 0.178$	0.128 $\pm 0.178$	-0.061 $\pm 0.140$	0.158 $\pm 0.280$	0.062 $\pm 0.256$	0.101 $\pm 0.167$
PY/P		0.953 $\pm 0.013$	0.109 $\pm 0.207$	0.321 $\pm 0.184$	0.288 $\pm 0.186$	0.286 $\pm 0.134$	0.515 $\pm 0.110$	0.710 $\pm 0.082$	0.956 $\pm 0.096$
PY/F			0.133 $\pm 0.209$	0.324 $\pm 0.307$	0.333 $\pm 0.184$	0.263 $\pm 0.137$	0.441 $\pm 0.122$	0.635 $\pm 0.096$	0.688 $\pm 0.086$
OC%				0.936 $\pm 0.026$	0.934 $\pm 0.026$	-0.166 $\pm 0.341$	0.257 $\pm 5.521$	0.049 $\pm 0.180$	0.086 $\pm 0.175$
OY/P					0.989 $\pm 0.004$	0.105 $\pm 0.165$	0.280 $\pm 3.097$	0.376 $\pm 0.158$	0.385 $\pm 0.150$
OY/F						0.094 $\pm 0.164$	0.275 $\pm 0.163$	0.341 $\pm 0.159$	0.416 $\pm 0.149$
100KW							-0.361 $\pm 0.121$	0.535 $\pm 0.097$	0.505 $\pm 0.097$
K/P								0.582 $\pm 0.090$	0.470 $\pm 0.107$
GY/P									0.890 $\pm 0.026$

- PY/P = protein yield per plant, PY/F = protein yield per feddan, OC% = % grain oil content, OY/P = oil yield per plant, OY/F = oil yield per feddan, 100 KW = 100 kernel weight, K/P = number of kernels per plant, GY/P = grain yield per plant, GY/F = Grain yield per feddan and PC% = % grain protein content.

-  $r_g$  estimate was considered significant when it equals or exceeds two fold of its corresponding SE estimate.

oil content (OC), high oil yield /plant (OY/P), high grain yield per plant (GY/P) and per feddan (GY/F) would help in obtaining high oil yield/feddan, *i.e.* OC, OY/P, GY/P and GY/F traits could be considered as secondary traits to oil yield /feddan. The proper secondary traits should exhibit a strong genetic association with the primary trait (oil yield in our case) and high heritability in the narrow sense. In this study  $h^2_n$  estimate was 29.40% for oil content, 53.06% for oil yield/ plant, 4.84% for grain yield/ plant and 6.25% for grain yield/ feddan. The strong genetic association with oil yield/ feddan and the relatively high narrow-sense heritability for oil content and oil yield/ plant, would qualify the last two traits to be considered as good selection criteria for improving oil yield /feddan. It is also interesting to mention that oil yield/plant showed high and significant genetic correlation with oil content and significant but small in magnitude correlation coefficient with grain yield per plant and per feddan.

Grain yield per plant showed significant and positive correlation coefficient with kernels/ plant (0.582) and 100 kernel weight (0.535), oil yield/ plant (0.376) and protein yield/ plant (0.710). Genetic correlation between grain yield/ plant and each of oil content (0.049) and protein content (0.062) were very low and insignificant. Negative correlations between oil content and yield in maize are frequently found in the literature,

suggesting an unlikely simultaneous selection for both traits (Misevic and Alexander 1989, Tatis 1990 and Dudley and Lambert 1992). On the other hand, the ability of the plant to produce carbohydrates and to synthesize oil are physiologically independent in the interval of 4 to 7% of oil (Alexander and Lambert 1968). However, associations found here occurred in a favorable direction, indicating a facility for the simultaneous selection of quality and yield traits, confirming the results of Mittelman *et al* (2003). High grain yield and high oil content were recorded in some maize hybrids (Umakanth and Kumar 2002 and Dudley *et al* 2007). In the present investigation, some high-oil high-protein yield hybrids could be obtained, namely  $P_2 \times P_5$  (L-2  $\times$  L-18),  $P_2 \times P_6$  (L-2  $\times$  L-13) and  $P_2 \times P_3$  (L-2  $\times$  L-8) in the present diallel experiment (data of both traits together are not presented). These crosses could be of great value for maize breeding programs to improve high-protein yield high-oil yield hybrids.

Oil and protein content were insignificantly correlated ( $r_g=0.132$ ). Associations between protein and oil content varied in the literature from not significant (Dorsey-Redding *et al* 1991 and Sene *et al* 2001) to highly positive values (Song *et al* 1999). On the contrary, Seiam and Khalifa (2007) reported a negative phenotypic correlation between oil and protein content. Our results are in agreement with those reported by Mittelman *et al* (2003) regarding the weak positive correlation between oil and protein content. Results of the present study concluded that despite of the weak correlation between oil and protein content, the favorable direction of correlation indicates the possibility of simultaneous selection for both high oil and high protein content.

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### توراث صفات محتوى الزيت ومحصول الحبوب فى الذرة الشامية

أحمد مدحت محمد النجار<sup>١</sup>، محمد على اللقاني<sup>١</sup>، حمدى يوسف الشربيني<sup>٢</sup>،  
وانل محمد النبوى السيد<sup>٢</sup>

١. قسم المحاصيل - كلية الزراعة - جامعة القاهرة - الجيزة - مصر  
٢. قسم بحوث الذرة - معهد بحوث المحاصيل الحقلية - مركز البحوث الزراعية - الجيزة - مصر

استخدمت فى هذه الدراسة ست سلالات تربية داخلية من الذرة الشامية ثلاث منها عالية الزيت وثلاث منخفضة للزيت فى عمل مجموعة كاملة من الهجن التبادلية بدون الهجن العكسية. زرعت الهجن التبادلية مع الآباء فى الحقل فى موقعين (سدس وسخا) لتقدير محتوى زيت الحبة فى التجربة الأولى وزرعت نفس الهجن بدون الآباء فى نفس الموقعين لتقييم محصول الزيت ومحصول الحبوب فى التجربة الثانية، واستخدم تصميم القطاعات الكاملة العشوائية فى كل تجربة وفى كل موقع فى مكررين بالتجربة الأولى وأربع مكررات فى التجربة الثانية. كانت الأهداف هى تقدير القدرة على الأكتلاف ونوع فعل الجين وكفاءة التوريث والتحصين المتوقع بالانتخاب لصفات محتوى الزيت ومحصول الحبوب والزيت. بصفة عامة كانت قوة الهجين بالنسبة للأب الأعلى لصفة محتوى الزيت فى الإتجاه المثلث (-2.26%). ومع ذلك أظهرت ستة هجن - من الـ 10 - هجين قوة هجين بالنسبة للأب الأعلى معنوية وموجبة لهذه الصفة وهم L-15×L-13 (76.36%) وL-2×L-18 (46.60%) وL-1×L-18 (17.74%) وL-2×L-13 (16.90%) وL-8×L-15 (10.40%) وL-8×L-13 (10.84%). كان كلا من متوسطات المربعات للقدرة العامة (GCA) والخاصة (SCA) على الأكتلاف عالية المعنوية لكل الصفات المدروسة. كانت النسبة GCA/SCA تتعدى الوحدة بالنسبة لكل الصفات المدروسة عدا صفتى محتوى الزيت وعدد الحبوب بالنبات فكانت أقل من الواحد. ظهرت أحسن تأثيرات للقدرة العامة على الأكتلاف بواسطة السلالتين L-2 وL-18 لمحتوى ومحصول الزيت. وظهرت أحسن تأثيرات قدرة خاصة على الأكتلاف بواسطة الهجينين L-15×L-13 متنوع بالهجين L-2×L-18 لمحتوى زيت الحبة ومحصول حبوب النبات والقدان. كان كلا من التباين المضيف وتباين السيادة هامين ولكن مقدار تباين السيادة كان أكبر عدة مرات من التباين المضيف ولعب الدور الأهم فى وراثية كل الصفات المدروسة. وكانت درجة السيادة لكل صفات الزيت والمحصول تحت الدراسة من نوع السيادة الفائقة. تراوحت كفاءة التوريث بالمعنى الخاص من 11.34% لعدد حبوب النبات إلى 53.06% لمحصول الزيت للقدان وتراوح التحسين المتوقع بالانتخاب من 1.82% لعدد حبوب

النبات إلى ٣٨.٩٥٪ لصفة محصول الزيت للفدان. وجدت علاقة (إرتباط) وراثية قوية بين محتوى زيت الحبة و محصول زيت النبات ( $r_p=0.936$ ) والفدان ( $r_p=0.934$ ). أما بالنسبة للارتباط الوراثي بين محتوى البروتين ومحتوى الزيت بالحبة فكان صغيراً ( $r_p=0.132$ ) وغير معنوياً ولكنه كان موجباً، مما يقترح بأن التحسين المتزامن لكل من هاتين الصفتين يمكن أن يحدث في نفس الوقت. وتستنتج الدراسة أن إستنباط أصناف الذرة الهجين يمكن أن يكون له دور كبير في زيادة محتوى و محصول الزيت نتيجة لتأثير قوة الهجين كما أن الإنتخاب في العشائر الإعتزالية للهجن بين السلالات ذات التأثيرات العالية للقدرة العامة على الإكتلاف والتي تم التعرف عليها في هذه الدراسة يمكن أن يكون فعالاً في زيادة محتوى و محصول الزيت. وأنه يمكن الحصول على تركيب وراثية ذات محتوى زيت عالي و محتوى بروتين عالي في نفس الوقت.

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