ANALYSIS OF DIALLEL CROSSES AMONG TEN MAIZE POPULATIONS DIFFERING IN DROUGHT TOLERANCE

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ABSTRACT

All possible crosses (excluding reciprocals) were made between ten maize open-pollinated populations (differing in drought tolerance) in 1999 season. In 2000 season, the parental populations and their 45 F_1's were evaluated in two sowing dates under water-stress and non-stress conditions (at flowering stage) at the Exp. Sta. of Fac. of Agric., Cairo Univ., Giza. The objectives were to study performance, combining ability, type of gene action, heterosis, heritability and expected selection gain for drought tolerance in populations and their F_1 crosses. Estimates of heterobeltiosis were higher in magnitude under water stress than under control. Maximum heterobeltiosis for grain yield (38.61 %) was reached under stress by the cross Cairo-1 X BS-11. General (GCA) was greater in magnitude than specific (SCA) combining ability variance for all studied traits under both control and water-stress conditions. GCA variance was more affected by sowing dates than SCA variance under both stress treatments. Giza-2 and C-87 populations were the best general combiners for increasing grain yield of hybrids under stress and control treatments. The crosses Giza-2 x Tuxpeno, Cairo-1 x BS-11 and Giza-2 x Cairo-1 are superior in SCA effects, *per se* performance and estimates of heterobeltiosis for grain yield under stress and non-stress conditions and therefore were recommended for use in maize drought tolerance breeding programs. Variance components estimates were several times larger for additive (δ^2_A) than for dominance for all studied traits, except ears/plant under control and rows/ear and grain yield under stress. Degree of dominance was partial in most cases. Overdominance was manifested by ears/plant under control and rows/ear under stress. Complete dominance was shown by grain yield, kernels/row and 100-kernel weight under stress. No dominance was exhibited by ASI under control and stress and ears/plant under stress conditions. Heritability in the narrow sense (h_n) under stress ranged from 20.8 % for ASI to 47.5 % for kernels/row. Estimates of h_n under control were higher than those under stress for all traits except ASI and ears/plant. Genetic advance estimates from direct selection under control were higher than those under water stress for grain yield and 100-kernel weight. The opposite was true for the rest of studied traits. Predicted gain from direct selection in one environment was greater than from indirect selection at another environment for all studied traits. In none of the studied cases was selection for a secondary trait predicted to be more effective in improving grain yield than direct selection for grain yield. Under water stress, responses of grain yield to selection for ASI was predicted to be larger than responses of grain yield to selection for any other studied trait, suggesting that ASI is a valuable adjunct in increasing the efficiency of selection for grain yield under stress.

Key words: *Maize, Zea mays, Populations, Diallel crosses, Drought tolerance, Combining ability, Heterosis, Heritability, Selection gain.*

INTRODUCTION

Developing drought tolerant varieties of maize (*Zea mays* L.) is of important for the successful production of this crop in the newly reclaimed lands of Egypt, where irrigation water is limited and soils have low water-holding capacity.

Information about combining ability and type of gene action of traits related to drought tolerance are necessary for maize breeder to design an appropriate breeding programme for improving drought tolerance. If the estimate of general combining ability (GCA) or additive genetic variance is of major importance the most effective breeding procedure would be the intrapopulation selection, whereas a hybrid program may be appropriate if specific combining ability (SCA) or non-additive variance is the major component (Cockerham 1961). Diallel analysis provides information on (i) the nature and amount of genetic parameters and (ii) general and specific combining ability of parents and their crosses, respectively (Singh and Chaudhary 1999)

Published work on the combining ability, heterosis and type of gene action of maize traits under water-stress conditions is generally lacking. Some reports indicate that estimates of additive genetic variance, heterosis, heritability and expected gain from selection are higher under stressful environments (Mashingaidze 1984, Younis *et al* 1988, Sharma and Bhalla 1991 and El-Sayed 1998). Others showed that these genetic parameters increased under optimum environments (Allen *et al* 1978, Blum 1988 and Bolanos and Edmeades 1996).

Open–pollinated populations of maize are an important source of extracting elite inbred lines to be used under water stress to develop improved drought tolerant single and three-way cross hybrids. All possible crosses (except reciprocals) were made in this study among ten local and exotic open–pollinated populations of maize differing in drought tolerance. Populations and their F_1's were evaluated under water-stress and non-stress conditions at flowering stage. The objectives were: (i) to evaluate the *per se* performance of populations and their F_1's under two irrigation regimes, (ii) to determine combining ability, heterosis, type of gene action, heritability and predicted selection gain under water-stress and non-stress conditions and (iii) to identify the best populations, and F_1's which could be recommended for breeding drought tolerant maize hybrids.

MATERIALS AND METHODS

In 1999 season, ten maize open-pollinated populations viz., Giza-2, C-87, DTP-1, DTP-2, Cairo-1, BS-10, BS-11, BS-26, Tuxpeno and Pool 27

(DTP-1, DTP-2, Tuxpeno and Pool 27 were obtained from CIMMYT-Mexico, BS-10, BS-11 and BS-26 from Dr. A.R. Hallauer, Iowa State Univ., Ames, USA, Cairo-1 and C-87 from Agronomy Dept., Fac. of Agric., Cairo Univ., and Giza-2 from ARC, Giza, Egypt) were grown and all possible crosses (excluding reciprocals) were made between them at the experimental farm of the Faculty of Agriculture, Cairo Univ., Giza. To insure good sampling, a minimum of 40 plants were used as male parents and 40 plants as female parents for each cross. Seeds from female plants of each cross were then mixed, and 45 inter-population crosses were produced.

In 2000 season, the parental populations and 45 population crosses (a total of 55 genotypes) were field evaluated at the Experimental Station of Fac. of Agric., Cairo Univ., Giza under drought stress and non-stress environments in two sowing dates. The first date was on May 14 and the second was on June 3. The experimental design used in each sowing date was a split-plot design with three replications. The two soil moisture regimes (control and stress) at flowering stage were alloted to main plots and genotypes to the sub-plots. Each sub-plot consisted of one row 6 m long 70 cm wide. The recommended practices for maize production were used. The trials were harvested after black layer development.

The data recorded were: anthesis-silking interval (ASI), number of ears/plant, number of rows/ear, number of kernels/row, 100-grain weight and grain yield/plant adjusted at 15.5 % grain moisture. All yield components were measured on 5 guarded plants/plot, while ASI was measured on a plot basis as the number of days between 50 % anthesis and 50 % silking.

The ordinary analysis of variance of a split plot design at each separate sowing date and the combined analysis of variance over the two sowing dates were done according to Steel and Torrie (1980). Heterobeltiosis (%) was computed as a percentage of F_1 superiority over the better parent. General (GCA) and specific (SCA) combining abilities were estimated according to method 2, model I (fixed model) of Griffing (1956) over two sowing dates for each soil moisture regime.

Variance components (additive and dominance variances) were estimated according to Cockerham (1961). Heritabilities in the narrow (h^2_n) sense were estimated according to Hallauer and Miranda (1988). Genetic advance (GA) from direct selection was calculated according to Becker (1984) and GA from indirect selection was estimated according to Falconer (1989). Genetic correlation (r_g) used for GA calculation was estimated from two variances (σ^2_j and σ^2_k) and the covariance (σ^2_{jk}), i.e $r_g=\sigma^2_{jk}/(\sigma^2_j\sigma^2_k)$. Average degree of dominance "a" was calculated from the following equation: $a = (\sigma^2_D / \sigma^2_A)^{1/2}$. The estimates of "a" were used to determine the type of dominance, as follows: a = 0 indicates no dominance, a < ± 1 indicates positive or negative partial dominance, a = ± 1 indicates positive or negative complete dominance and a > ± 1 indicates positive or negative over-dominance.

RESULTS AND DISCUSSIONS

Analysis of variance

Combined analysis of variance over two sowing dates (Table 1) showed that highly significant differences existed among studied genotypes for all traits. Significant or highly significant differences were also noted among parents, crosses and the comparison parents vs. crosses for all traits except ASI and ears/plant for parents vs. crosses. Highly significant differences were shown among moisture regimes for only four traits, namely: rows/ear, kernels/row, 100-kernel weight and grain yield/plant. Significant or highly significant differences also existed among sowing dates for ears/plant, kernels/row and 100-kernel weight.

Mean squares due to sowing dates x moisture regimes interaction were significant for only rows/ear and 100-kernel weight. Significant or highly significant mean squares were observed for sowing dates x genotypes, sowing dates x parents and sowing dates X crosses interactions for all traits except for ears/plant. On the other hand, variances due to sowing dates x parents vs. crosses interaction were not significant for all traits except grain yield/plant.

All variances due to moisture regimes x genotypes, moisture regimes x parents, and moisture regimes x crosses interactions were significant or highly significant for only four traits, namely, rows/ear, kernels/row, 100-kernel weight and grain yield/plant. In addition, mean squares due to moisture regimes X parents vs. crosses were significant only for 100-kernel weight.

All variances due to moisture regimes x sowing dates X genotypes, moisture regimes X sowing dates X parents, and moisture regimes X sowing dates X crosses interactions were significant or highly significant only for three traits, namely, rows/ear, 100-kernel weight and grain yield/plant except moisture regimes x sowing dates X parents interaction for grain yield/plant. Thus, the performance of genotypes varies with water supply and sowing dates, confirming previous results (Denmand and Shaw 1960, Moss and Downey 1971 and El-Sayed 1998).

Table 1. Mean squares for combined analysis of variance of studied traits for maize parental populations and population crosses evaluated under two moisture regimes in 2000 season.

S.O.V.	M.S.					
	ASI	Ears/ plant	Rows/ ear	Kernels/ Row	100-kernel wt.	Grain yield/plant
Sowing dates (D)	86.55	0.550*	3.550	1850.04**	1285.79**	8860.87
Moisture regimes (M)	3.64	0.150	51.630**	2659.23**	2055.31**	165189.28**
D x M	0.12	0.210	3.350*	5.60	233.41**	6631.64
Error $_{(a)}$	16.31	0.090	0.440	10.06	17.54	2315.22
Genotypes (G)	4.47**	0.080**	7.670**	115.77**	91.73**	3722.08**
Parents (P)	7.37**	0.050*	13.150**	190.09**	144.69**	5975.25**
Crosses (C)	3.97**	0.080**	6.290**	89.34**	81.24**	2846.87**
P vs. C	0.01	0.002	18.920**	610.01**	76.65**	21952.85**
G x D	4.68**	0.030	1.240**	18.21**	10.11**	876.77**
D x P	11.67**	0.030	1.240*	18.53**	8.53*	512.57*
D x C	3.35**	0.030	1.250**	18.03**	10.60**	942.51**
D x P vs. C	0.12	0.050	0.510	23.38	2.63	1262.05*
G x M	1.53	0.020	1.200**	13.98**	13.49**	659.33**
M x P	0.96	0.020	1.290*	27.82**	22.57**	1182.05**
M x C	1.65	0.020	1.170**	11.26**	11.63**	554.34**
M x P vs. C	1.21	0.050	0.290	9.00	13.83*	574.24
G x D x M	1.99	0.040	0.940*	8.18	8.04**	374.42*
D x M x P	0.94	0.010	1.280*	7.86	11.01**	298.34
D x M x C	2.20	0.040	0.89*	8.42	7.48**	386.56*
D x M x P vs. C	1.89	0.050	0.003	0.39	5.99	525.38
Error$_{(b)}$	2.06	0.025	0.61	6.42	3.79	264.68

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

Mean performance

Mean performance of parental populations and their diallel crosses subjected to water stress and non-stress (control) conditions is presented in Table (2). For grain yield/plant trait, the yield value under stress as a percentage of yield under control, the relative yield, is considered here as an expression of the relative drought tolerance or drought index (TI). In this respect, mean grain yield was significantly reduced due to soil moisture stress at flowering stage by 24 % over all parental populations and by 20 % overall crosses.

Claasen and Shaw (1970), Kaul *et al* (1972), Nesmith (1991) and El-Sayed (1998) also found that water stress at flowering stage is very critical and causes significant reductions in maize grain yield. Nesmith (1991) reported that yield loss due to water stress during anthesis was 90 %. El-Sayed (1998) reported a yield loss of 33.0 % as a result of drought stress at flowering stage. Differences among results might be attributed to differences in the genetic material used and/or differences in the environmental conditions prevailing during stress in different experiments.

Table 2. Average performance, highest and lowest values, as well as drought tolerance index (TI) for parental populations, and their diallel crosses under stress and control conditions in 2000 season (Data are combined over two sowing dates).

Trait		Control		Stress		TI (%)	
		Parents	Crosses	Parents	Crosses	Parents	Crosses
ASI (days)	Highest	6.0	6.7	6.2	6.5	128	130
	Lowest	4.2	3.5	3.5	3.7	84	71
	Average	5.03	5.14	5.07	4.94	101	97
Ears/ plant	Highest	1.4	1.5	1.2	1.3	109	120
	Lowest	1.0	1.0	1.0	1.0	79	85
	Average	1.16	1.14	1.10	1.13	95	100
Rows/ ear	Highest	15.5	16.3	15.8	16.0	102	106
	Lowest	13.0	13.0	12.5	12.4	88	82
	Average	14.08	14.46	13.42	13.92	95	96
Kernels/ row	Highest	38.1	42.5	34.5	39.8	100	97
	Lowest	24.1	29.9	21.5	26.4	72	77
	Average	34.08	36.27	29.58	32.36	87	89
100-kernel wt. (g)	Highest	36.5	37.7	33.5	32.9	95	104
	Lowest	25.6	26.2	22.8	21.9	68	78
	Average	31.8	32.3	27.68	28.91	87	90
Grain yield/ plant (g)	Highest	191.0	205.5	131.0	154.0	90	97
	Lowest	87.3	117.3	70.8	92.0	61	61
	Average	141.0	153.6	105.0	123.0	76	80

Grain yield reductions due to drought imposed at flowering stage were accompanied by significant losses in number of rows/ear, kernels/row and 100-kernel weight, i.e. in yield components (Table 2). Reduction in each yield component, separately, was not as high as reduction in grain yield. For yield components, maximum reduction due to water stress was shown by kernels/row and 100-kernel weight. Mean number of kernels/row decreased by 13 and 11 % and mean kernel weight reduced 13 and 10 % due to water stress as compared to control, for parental populations and their diallel crosses, respectively.

Minimum reductions of 5 and 4 % occurred in number of rows/ear for populations and their crosses, respectively. Our results are consistent with those of El-Sayed 1998, who reported that reduction of maize grain yield due to drought stress at flowering stage was only associated with reduction in grain number and size. In maize, reduction in grain number has been found to be a result of abortion of the fertilized ovules after a period of water stress at flowering stage (Moss and Downey, 1971).

When both absolute grain yield under stress and relative yield were taken as an index of drought tolerance in an agronomic sense, the parental populations BS-26, C-87, DTP-1 and Giza-2 would be regarded as the most drought resistant parental populations under the present study. Moreover, the crosses Giza-2 X Tuxpeno, Giza-2 X C-87, Giza-2 X Cairo-1, Giza-2 X BS-10, C-87 X BS-11, C-87 X BS-10, Giza-2 X BS-26 and Cairo-1 X BS-11 could be considered the most drought resistant population crosses under the conditions of the present study. On the other hand, the parental populations Pool-27, Cairo-1 and Tuxpeno and the crosses DTP-1 X Cairo-1, DTP-1 X Pool-27, DTP-2 X Cairo-1, DTP-2 X Pool-27, BS-26 X Pool-27 and Tuxpeno X Pool-27 could be regarded as the most susceptible genotypes under the present study. It is worthy to note that Giza-2, C-87 and DTP-1 populations excelled in absolute yields under stress and excelled also in their potential yield (under control), i.e. in their yield under full irrigation. Moreover, the crosses Giza-2 X Tuxpeno, Giza-2 X C-87, Giza-2 X Cairo-1 excelled in absolute yield under stress as well as under control. Superiority of Giza-2 and DTP-1 under both stress and control conditions was also reported by El-Sayed (1998). He also found that Cairo-1 was inferior in drought tolerance in absolute and relative terms.

It is interesting that most superior population crosses in drought tolerance include at least one of their parental populations showing superiority in drought tolerance, using both criteria.

Overall genotypes, characters most related to grain yield under both stress and control conditions were ASI, kernels/row and 100-kernel weight. In general, the magnitude of correlation coefficients between grain yield and other traits under stress was lower than that under control. Yield under stress conditions was significantly negatively correlated with ASI ($r = -0.32^*$) and significantly positively correlated with kernels/row ($r = 0.70^{**}$) and 100-kernel weight ($r = 0.50^{**}$). The negative correlation between grain yield and ASI (or asynchrony of pollen and silk) has been reported by several investigators (Claassen and Shaw 1970, Moss and Downey 1971, Hall *et al* 1982, Edmeades *et al* 1993, Bolanos and Edmeades 1996 and El-Sayed 1998). Claassen and Shaw (1970) indicated that the establishment of final kernel number occurs in a 2-week period following flowering. El-Sayed (1998) suggested that ASI could be used as an indicator of drought tolerance.

Heterosis

The contrast mean squares of the parents *vs.* crosses was significant for grain yield, rows/ear, kernels/row and 100-kernel weight (Table 1) indicating the existence of significant heterosis for these traits. The expression of useful heterosis (the degree of superiority of the F_1 over the better parent) averaged over sowing dates differed according to the studied trait, the soil moisture regime and the population cross (Table 3). Average heterobeltiosis estimates over all crosses were generally low in magnitude; with the highest average heterobeltiosis (6.41 %) shown by grain yield trait under water stress.

For rows/ear significant positive heterobeltiosis was observed for only two crosses i.e BS-26 X Tuxpeno (11.3 %) and DTP-2 X BS-10 (6.77 %) under control. While under water stress, the number of significant positive heterobeltiosis estimates for rows/ear was eleven, the highest estimate was shown by DTP-2 X BS-10 (12.60 %), Giza-2 X BS-11 (11.40 %) and BS-26 X Tuxpeno (11.0 %).

With respect to kernels/row, heterobeltiosis ranged from –20.0 % (BS-11 x Pool-27) to 16.1 % (Cairo-1 x BS-11) under control and from –19.3 % (DTP-1 x Pool-27) to 28.03 % (Giza-2 x Cairo-1) under water stress. Significant positive heterobeltiosis estimates were observed for 7 crosses under control and 9 crosses under stress conditions. The best 5 crosses in heterobeltiosis for kernels/row under stress were Giza-2 x Cairo-1 (28.03 %), Cairo-1 X Pool-27 (24.02%), Cairo-1 x BS-11 (15.75 %), BS-26 x Tuxpeno (15.36 %) and DTP-2 x BS-11 (15.41 %).

Heterobeltiosis for100-kernel weight ranged from –18.5 % (BS-26 x Tuxpeno) to 7.4 % (C-87 x Cairo-1) under control and from –23.0 % (DTP-2 x Pool-27) to 30.4 % (BS-10 x Tuxpeno) under water stress. Significant positive heterobeltiosis under stress was observed in six crosses: BS-10 x Tuxpeno (30.4 %), BS-10 x Pool-27 (14.2 %), Tuxpeno x Pool-27 (13.1 %), DTP-1 x Tuxpeno (10.2 %), BS-10 x BS-26 (9.27 %) and BS-10 x BS-11 (8.66 %).

For grain yield/plant, heterobeltiosis ranged from –25.03 % (Giza-2 x Pool-27) to 31.5 % (Cairo-1 x BS-11) under control and from –25.2 % (BS-26 x Pool-27) to 38.61 % (Cairo-1 x BS-11) under water stress. The number of crosses showing significant positive heterobeltiosis for grain yield was six under control and ten under stress. Under both stress and non-stress conditions, the highest significant positive heterobeltiosis estimates were exhibited by the crosses Cairo-1 X BS-11, Cairo-1 X BS-10 and BS-10 X BS-11. Moreover, under water stress conditions, the crosses Giza-2 X Tuxpeno and Giza-2 X BS-10 were also amongst the best 5 crosses in heterobeltiosis estimates for grain yield (Table 3).

Table 3. Summary of heterobeltiosis estimates (%) for studied traits of maize population crosses under stress and non-stress environments (Data are combined over two sowing dates, 2000 season.

Trait		Control	Stress
Rows/ ear	Range (%)	(-10.3)** - 11.3**	(-17.6)** - 12.6**
	Average (%)	-1.13 %	-0.25 %
	Best 5 crosses	BS-26 x Tuxpeno, DTP-2 x BS-10, C-87 x BS-10, BS-10 x BS-26, C-87 x BS-26	DTP-2 x BS-10, Giza-2 x BS-11, BS-26 x Tuxpeno, DTP-1 x Cairo-1, Giza-2 x Tuxpeno
Kernels/ row	Range (%)	(-20.00)** - 16.10**	(-19.30)** - 28.03**
	Average (%)	0.28	0.84
	Best 5 crosses	Cairo-1 x BS-11, Giza-2 x BS-26, Cairo-1 BS-26, DTP-1 x Cairo-1, BS-26 x Tuxpeno	Giza-2 x Cairo-1, Cairo-1 x Pool-27, Cairo-1 x BS-11, BS-26 x Tuxpeno, DTP-2 x BS-11,
100-kernel wt.	Range (%)	(-18.50)** - 7.40*	(-23.00)** - 30.40**
	Average (%)	-4.59	-3.11
	Best 5 crosses	C-87 x Cairo-1, DTP-2 x Cairo-1, Cairo-1 x BS-26, Cairo-2 x C-87, DTP-1 x Tuxpeno	BS-10 x Tuxpeno, BS-10 x Pool-27, Tuxpeno x Pool-27, DTP-1 x Tuxpeno, BS-10 x BS-26
Grain yield/ plant	Range (%)	(-25.03)** - 31.50**	(-25.20)** - 38.61**
	Average (%)	-1.49	6.41
	Best 5 crosses	Cairo-1 x BS-11, DTP-2 x Cairo-1, Cairo-1 x BS-10, BS-10 x BS-11, Cairo-1 x BS-26	Cairo-1 x BS-11, Giza-2 x Tuxpeno, Cairo-1 x BS-10, BS-10 x BS-11, Giza-2 x BS-10

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

It is interesting that the number of crosses showing significant positive heterosis estimates for grain yield and its components increased under stress than that under control. Moreover, in most cases for grain yield and yield components the estimates of heterobeltiosis were higher in magnitude under water stress than the respective estimates under control. Similar to our results, Younis *et al* (1988) found that heterosis increased under water stress than under full irrigation.

Falconer (1960) pointed out that if crossed populations do not differ in gene frequencies there will be no heterosis. Hallauer and Miranda (1988), also stated that abundant heterosis manifested in a cross of two populations leads to conclusion that the parental varieties are more genetically diverse than varieties manifest little or no heterosis. Results of this work suggest wide genetic diversity among some of the populations studied, particularly between local (G-2 and C-87) and exotic germplasm (Pool-27 and BS-11). A detailed study of genetic relationships between these populations will be dealt with in a future publication.

Combining ability variances

Analysis of variance of combining ability for parental populations and their diallel crosses under control and water stress is presented in Table (4). Highly significant differences due to general (GCA) combining ability mean squares were observed for all studied traits under both stress and control conditions with the exception of ears/plant under control. Highly significant differences due to specific (SCA) combining ability variances were also observed for all traits under both control and stress conditions, except for ASI under control and ASI and ears/plant under water stress. This indicated the importance of both additive and non-additive types of genetic variances in the inheritance of most studied characters under control and water-stress conditions.

Interaction mean squares due to GCA x sowing dates (D) and SCA x sowing dates under control were significant or highly significant for all traits except GCA x sowing dates for ears/plant and SCA x sowing dates for ears/plant and rows/ear. Under water stress GCA x sowing dates variances showed significant or highly significant mean squares for four traits (ASI, kernels/row, 100-kernel weight and grain yield/plant) and SCA x sowing dates interaction showed highly significant variances for all traits except ears/plant and rows/ear.

Contribution of the variation due to GCA to the total variation was greater than the contribution of the variation due to SCA for all studied traits under both control and water stress conditions as shown by GCA/SCA ratio (Table 4). The ratio of mean squares due to GCA to mean squares due to SCA ranged from 2.6 (ears/plant) to 16.29 (100-kernel-weight) under control and from 2.69 (ASI) to 7.10 (kernels/row) under water stress. Mashingaidze (1984), also found that both general (GCA) and specific (SCA) combining ability variances were important for drought resistance traits; with greater GCA variance, indicating a preponderance of additive gene effects. He suggested that simple selection technique should be effective in increasing drought resistance in the material studied by him. This conclusion is applicable in the genetic material used in the present study.

Mean squares due to GCA x sowing dates interaction were greater than those due to SCA x sowing dates for all studied traits under control and water stress treatments, where the GCA x D/SCA x D ratio exceeded the unity except for ears/plant and 100-kernel weight under stress and non-stress conditions and rows/ear under stress conditions. This suggested that GCA variance is more affected by sowing dates than SCA variance for most traits.

Table 4. Analysis of variance of combining ability computed according to Griffing (1956) method 2 model 1 for studied traits on maize populations and their F_1 crosses evaluated under control and drought stress over two sowing dates in 2000 season

S.O.V.	ASI	Ears/ plant	Rows/ ear	M.S. Kernels/ Row	100-kernel wt.	Grain yield/plant
				Control		
Sowing dates (D)	40.08**	0.04	0.001	826.03**	211.78**	80.61
Genotypes (G)	2.86**	0.06**	4.405**	54.24**	54.46**	2592.84**
GCA	7.53**	0.13	15.948**	198.05**	250.00**	10803.41**
SCA	1.93	0.05**	2.097**	25.48**	15.35**	950.73**
GCA x D	6.95**	0.03	1.921**	24.48**	7.17*	966.47**
SCA x D	3.08*	0.03	0.775	11.43*	8.11**	578.27**
GCA/SCA	3.90	2.60	7.61	7.77	16.29	11.36
GCA x D/SCA x D	2.26	1.00	2.48	2.14	0.88	1.67
				Drought stress		
Sowing dates (D)	46.59**	0.72**	6.89**	1029.61**	1307.43**	15411.90**
Genotypes (G)	3.13**	0.04**	4.44**	75.51**	50.76**	1788.57**
GCA	6.56**	0.09**	12.62**	265.27**	166.49**	5296.49**
SCA	2.44	0.03	2.81**	37.56**	27.62**	1086.98**
GCA x D	4.82*	0.03	0.86	20.24**	8.94*	771.30**
SCA x D	2.56	0.04*	1.28**	11.31**	10.44**	575.62**
GCA/SCA	2.69	3.00	4.49	7.10	6.03	4.87
GCA x D/SCA x D	1.88	0.75	0.67	3.65	0.86	1.34

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

General combining ability effects

Estimates of GCA effects of parental populations under control and water stress are presented in Table (5). Significant positive GCA effects would be of interest for all studied traits except ASI, where negative GCA effects would be more agronomically useful. In this sense, with respect to ASI, although insignificant GCA effects were obtained, DTP-1, was the most favorable general combiner under both stress and control conditions. Insignificant GCA effects for ears/plant under both soil-moisture regimes could not differentiate among parental populations.

Regarding rows/ear, BS-11 and Pool-27 showed highly significant positive GCA effects under both irrigation treatments. It is concluded that these two populations were the best general combiners for increased number of rows/ear. For kernels/row the best general combiner was BS-26 (followed by Giza-2) under both control and stress conditions. The best general combiners for 100-kernel weight were Giza-2, C-87, Cairo-1 and DTP-2 under both control and water stress treatments.

Table 5. General combining ability effects for parental populations evaluated under *control and drought stress conditions over two sowing dates in 2000* season.

Parents	ASI		Ears/plant		Rows/ear		Kernels/row		100-kernel wt.		Grain yield	
	Cont.	Stress	Cont.	Stress	Cont.	Stress	Cont.	Stress	Cont.	Stress	Cont.	Stress
1. Giza 2	-0.09	-0.24	0.02	0.03	0.01	-0.24	1.49*	1.04	2.71**	2.18**	21.72**	9.94*
2. C 87	-0.25	-0.26	-0.04	-0.02	-0.14	-0.16	0.23	0.71	1.76**	1.78**	14.24**	11.84**
3. DTP-1	-0.48	-0.54	0.04	0.03	-0.34	-0.13	-0.19	0.21	-0.15	-0.13	-2.57	-0.84
4. DTP-2	-0.18	-0.09	0.04	0.01	-0.53*	-0.28	-0.65	-1.41*	1.01	1.29*	-3.51	-4.43
5. Cairo 1	0.21	0.29	0.02	0.05	-0.24	-0.45*	0.47	-1.17	1.85**	1.17*	5.45	-5.18
6. BS 10	-0.14	0.07	0.03	0.03	-0.29	-0.12	-0.19	0.98	-0.59	-0.33	-5.36	5.08
7. BS 11	-0.11	0.07	-0.01	0.00	0.93**	0.89**	-0.21	0.66	-1.93**	-0.89	-5.45	3.15
8. BS 26	0.21	0.06	-0.07	-0.06	-0.20	0.00	1.99**	2.77**	-2.63**	-2.04**	-5.51	0.86
9. Tuxpeno	0.14	0.13	0.03	-0.01	0.08	-0.12	1.11	0.55	0.27	-1.19*	3.86	-2.11
10. Pool 27	0.68	0.53	-0.06	-0.05	0.72**	0.61**	-4.06**	-4.34**	-2.29**	-1.84**	-22.88**	-18.30**
S.E. g_i	0.39	0.40	0.04	0.04	0.22	0.21	0.74	0.64	0.53	0.53	4.67	4.22
S.E. g_i-g_j	0.58	0.59	0.07	0.06	0.33	0.31	1.10	0.96	0.79	0.79	6.97	6.29

*, ** indicate significance differences from zero at 0.05 and 0.01 levels of probability, respectively.

With respect to grain yield/plant, Giza-2 and C-87 populations showed significant or highly significant positive GCA effects and therefore were considered in this study the best general combiners for increasing grain yield of the hybrids under both control and water stress conditions. It is very interesting that these two populations (Giza-2 and C-87) are also the best general combiners for 100-kernel weight. In addition, Giza-2 was best general combiner for kernels/row under both control and water stress. On the other hand, Pool-27 population was the worst general combiner for grain yield, 100-kernel weight and kernels/row.

It is worthy to note that the superiority of the local populations Giza-2 and C-87 in their GCA effects for grain yield was also associated with superiority of these genotypes in their absolute and relative yield under water-stress as compared to control conditions. Inbred lines may be derived from these populations characterized by high yielding *per se* performance and high yielding potential in hybrid combinations under water stress conditions.

Specific combining ability effects

The best five population crosses in specific combining ability (SCA) effects under control and water stress are presented in Table (6). The most desirable crosses were those showing the highest positive SCA effects for any of the studied traits, except ASI trait, where favorable SCA effects should be the lowest negative ones.

Table 6. The best five crosses in specific combining ability effects (arranged in descending order) under control and water-stress conditions over two sowing dates in 2000 season.

Trait	Control	Stress
ASI	BS-10 x BS-11, Cairo-1 x BS-26, DTP-1 x Cairo-1, DTP-2 x Cairo-1, DTP-1 x Tuxpeno	BS-10 x BS-11, Giza-2 x BS-10, C-87 x Pool-27, BS-11 x Tuxpeno, DTP-2 x BS-11
Ears/plant	Giza-2 x DTP-1, Giza-2 x Cairo-1 DTP-1 x BS-10, C-87 x DTP-2 Tuxpeno x Pool-27	C-87 x DTP-2, C-87 x Cairo-1, Tuxpeno x Pool-27, Giza-2 x DTP-1, DTP-1 x BS-10
Rows/ear	BS-26 x Tuxpeno, DTP-1 x Pool-27, Giza-2 x Cairo-1, C-87 x BS-10, DTP-2 x Pool-27	DTP-1 x Pool-27, BS-26 x Tuxpeno C-87 x Cairo-1, DTP-2 x BS-10, BS-10 x BS-26
Kernels/row	Cairo-1 x BS-11, Cairo-1 x BS-26, Giza-2 x BS-26, Tuxpeno x Pool-27, BS-26 x Tuxpeno	Giza-2 x Cairo-1, BS-26 x Tuxpeno, Cairo-1 x BS-10, DTP-2 x BS-10, Giza-2 x BS-26
100-kernel wt.	DTP-1 x Tuxpeno, Tuxpeno x Pool-27, Giza-2 x BS-11, DTP-2 x Cairo-1, BS-10 x Pool-27	BS-10 x Tuxpeno, DTP-1 x Tuxpeno, Cairo-1 x Pool-27, C-87 x Tuxpeno, Giza-2 x Pool-27
Grain yield	Giza-2 x Tuxpeno, DTP-1 x BS-11, DTP-2 x Cairo-1, Cairo-1 x BS-11, BS-26 x Tuxpeno	Giza-2 x Tuxpeno, Cairo-1 x BS-11, Giza-2 x Cairo-1, Cairo-1 x BS-10, Giza-2 x BS-26

Under stress, crosses exhibiting the highest SCA effect for yield and its components involved one parent from BS-10, C-87, DTP-1, G-2, whereas under no-stress, the parents are BS-10, DTP-1, Giza 2, Cairo-1 and BS-26.

It is interesting that the F_1 crosses Giza-2 x Tuxpeno, Giza-2 X Cairo-1, Giza-2 X BS-26 and Cairo-1 X BS-11 are superior to all crosses in SCA effects, *per se* performance and heterobeltiosis estimates for grain yield under stress and control conditions. These crosses would be considered of value in maize drought tolerance breeding.

Components of genetic variance:

Variance components estimates (Table 7) were many times larger for additive (σ^2_A) than for dominance (σ^2_D) for most traits under control and water stress treatments as estimated by the σ^2_A/σ^2_D ratio. This ratio ranged from 1.18 (rows/ear) to 4.10 (100-kernel weight) under control and from 1.02 (kernels/row) to 20.52 (plant height) under water stress. In contrast, the σ^2_D was larger than σ^2_A i.e the σ^2_A/σ^2_D was less than unity for ears/plant under control and rows/ear and grain yield/plant under stress conditions.

Table 7. Estimates of variance components and heritability of all traits for parental populations and their crosses evaluated under control and *drought stress over two sowing dates in 2000 season.*

Trait	σ^2_A	σ^2_D	σ^2_A/σ^2_D	«a»	σ^2_{Ad}	σ^2_{Dd}	$\sigma^2_{Ad}/\sigma^2_{Dd}$	h^2_n
					Control			
ASI	**0.16**	**(-0.25*)**	**α**	**0.00**	**0.64**	**0.36**	**1.78**	**19.3**
Ears/plant	**0.008**	**0.012**	**0.67**	**1.22**	**0.00**	**0.00**	**0.00**	**26.7**
Rows/ear	**1.04**	**0.88**	**1.18**	**0.92**	**0.20**	**0.04**	**5.00**	**48.4**
Kernels/row	**13.28**	**9.36**	**1.42**	**0.84**	**2.16**	**1.38**	**1.57**	**51.8**
100-Kernels wt.	**19.64**	**4.84**	**4.10**	**0.50**	**(-0.16)**	**1.45**	**0.00**	**76.0**
Grain yield/plant	**788.72**	**248.40**	**3.18**	**0.56**	**64.72**	**95.62**	**0.68**	**67.7**
					Water stress			
ASI	**0.16**	**(-0.08)**	**α**	**0.00**	**0.36**	**0.14**	**2.57**	**20.8**
Ears/plant	**0.004**	**(-0.01)**	**α**	**0.00**	**0.00**	**0.007**	**0.00**	**36.4**
Rows/ear	**0.84**	**1.04**	**0.81**	**1.11**	**(-0.08)**	**0.24**	**0.00**	**40.0**
Kernels/row	**18.24**	**17.52**	**1.04**	**0.98**	**1.48**	**1.92**	**0.77**	**47.5**
100-Kernels wt.	**11.68**	**11.44**	**1.02**	**0.99**	**(-0.24)**	**2.21**	**0.00**	**46.9**
Grain yield/plant	**334.48**	**340.92**	**0.98**	**1.00**	**32.6**	**112.55**	**0.29**	**42.5**

*** any variance estimate preceded by negative sign was considered zero.**

Moreover, the magnitude of interaction variance due to additive x sowing dates (σ^2_{Ad}) was markedly higher than dominance x sowing dates (σ^2_{Dd}) for ASI, rows/ear and kernels/row under control and ASI under stress, indicating that additive type of gene action was more affected by environment than dominance gene action for these traits. In contrast, the $\sigma^2_{Ad}/\sigma^2_{Dd}$ was lower than unity for ears/plant, 100-kernel weight and grain yield /plant under control and ears/plant, rows /ear, kernels/row, 100-kernel weight and grain yield under stress, indicating that dominance types of gene action was more affected by environment than additive types of gene action for these traits.

Degree of dominance "a" (Table 7) was partial in most cases ($a < 1$). Overdominance ($a > 1$) was manifested by ears/plant under control and rows/ear under stress. Complete dominance of the higher parent was shown for grain yield, kernels/row and 100-kernel weight under stress. No dominance ($a = 0$) was manifested by ASI under control, and ASI and ears/plant under water stress.

Heritability

Heritability estimates in the narrow sense are presented in Table (7). They ranged from 19.3 % for ASI to 76.0 % for 100-kernel weight under control and from 20.8 % for ASI to 47.5 % for kernels/row under stress.

Estimates of h_n for grain yield/plant were of higher magnitude (67.7 %) under control than under stress (42.5 %). Moreover, h_n of medium magnitudes were also detected for rows/ear (48.4 and 40.0 %), kernels/row (51.8 and 47.5 %) and 100-kernel weight (76.0 and 46.9 %) under both control and water stress, respectively. Under control h_n was higher than under stress conditions for all traits except ASI and ears/plant.

Literature includes two contrasting opinions regarding the best environment for maximizing heritability. Some researchers (Russell 1969, Stuber and Moll 1977 and Troyer and Rosenbrook 1983 and El-Sayed 1998) found that heritability for some traits were increased in stressful environments. In contrast, other investigators reported decreases in heritability under stress environments (Frey 1964, Subandi and Compton 1974 and Blum 1988). Our results agree with the second opinion for all studied traits except ASI and ears/plant.

Predicted selection gain

Direct selection

Genetic advance estimates from direct selection under control treatment (Table 8) were higher than those under water stress for 100-kernel weight and grain yield/plant. On the other hand, under water stress treatment, estimates of genetic advance from direct selection were higher the remaining studied traits. The largest genetic advance was predicted for grain yield, while the lowest expected genetic advance was shown by ASI.

Indirect selection

Predicted gain from indirect selection are used to compare the response to selection in one environment with performance in another environment (Table 8). The predicted gain from direct selection in both stress and non-stress environments was greater than the predicted correlated gain from indirect selection in the other environment, as indicated by the relative efficiency values < 100 % for all single environments. It is therefore concluded that for all studied traits, greater improvement would occur from direct selection carried out under the target environment than would be obtained from indirect selection at another environment. Our results are consistent with those reported by El-Sayed (1998).

There are two contrasting strategies for identifying genotypes that will be high yielding under drought. The first is to evaluate genotypes under specified drought conditions, namely, a certain type of drought, to minimize

Table 8. Genetic advance from direct selection (R) and indirect selection (CR) for parental populations and population crosses evaluated in 2000 season.

Treatment	ASI	Ears/ plant	Rows/ ear	Kernels /row	100-kernel wt.	Grain yield/plant
			Direct selection (C)			
Control	13.9	15.4	16.3	17.7	24.5	33.2
Stress	14.6	18.2	17.5	23.1	20.3	26.3
			Indirect selection (CR)			
			a. selection environment vs. response environment.			
Control vs. Stress	1.9	12.3	8.4	11.1	14.7	18.12
R. E (%)	(13.0)	(67.6)	(48.0)	(48.1)	(72.4)	(68.9)
Stress vs. Control	1.9	14.6	10.7	15.1	15.6	18.1
R. E (%)	(13.6)	(94.8)	(61.1)	(85.3)	(63.7)	(54.6)
			b. secondary traits vs. yield			
Control	-12.1	14.3	9.7	18.2	21.9	-
R. E (%)	(-36.4)	(43.1)	29.2	(54.8)	(65.9)	-
Stress	-19.7	16.6	8.1	14.5	9.7	-
R. E (%)	(-74.9)	(63.1)	(30.8)	(55.1)	(36.9)	-

Values in parentheses indicate the relative efficiencies (R.E) = CR/R x 100

genotype x environment interaction (Ceccarelli 1989). However, in this approach, lower heritability, particularly across years may result in slow progress from selection. Second, genotypes may be evaluated under conditions maximizing heritability, (Braun *et al* 1992) but progress from selection may be counteracted by problems of genotype x environments interactions. Our results are in favor of the first strategy in all cases. A third strategy, currently used at CIMMYT, uses simultaneous evaluation under near-optimum and drought conditions, and selection of those genotypes that perform will in both environments (Calhoun *et al* 1994 and Byrne *et al* 1995). However, ultimate evaluation must be performed in the target environment prior to recommendation of a cultivar for commercial production.

Indirect selection for grain yield

Response of grain yield to selection for secondary traits was estimated (Table 8) i.e selection for reduced values of ASI, increased ears/plant, rows/ear, kernels/row or 100-kernel weight. Indirect selection for grain yield under no-stress was greatest for 100 kernel weight. Under stress, the greatest indirect response in grain yield was predicted form selection to lower ASI values. However, in no case was selection for a secondary trait predicted to be more effective at improving grain yield than direct selection for grain yield.

It is evident that ASI is a valuable adjunct in increasing the efficiency of selection for grain yield under stress conditions. Other secondary traits which were not considered in this study may deserve further attention regarding their value in a water deficit breeding program.

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تحليل الهجن الدائرية بين عشرة عشائر من الذرة الشامية تختلف فى تحملها للجفاف

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تم فى موسم ١٩٩٩ إجراء التهجينات الدائرية (Diallel) بكل التوافيق الممكنة (ما عدا الهجن العكسية) بين عشرة عشائر ذرة مفتوحة التلقيح تختلف فى تحملها للجفاف. وفى موسم ٢٠٠٠ تم تقييم العشائر الأبوية والهجن تحت ظروف الجفاف (فى مرحلة التزهير) والرى الكامل فى تجربتين منزرعتين فى ميعادين مختلفين بمزرعة كلية الزراعة-جامعة القاهرة بالجيزة بتصميم القطع المنشقة . كانت الأهداف تقدير القدرة على الائتلاف ونوع فعل الجين وقوة الهجين والقدرة على التوريث والعائد المتوقع من الانتخاب لتحمل الجفاف. كانت قيم قوة الهجين للأب الأحسن أعلى تحت ظروف الجفاف عنها تحت ظروف الكنترول. تم الحصول على أعلى قيمة لقوة الهجين للأب الافضل فى صفة محصول الحبوب (٣٨,٦١ %) تحت الجفاف بواسطة الهجين Cairo-1 x BS-11 . كان تباين القدرة العامة على الائتلاف (GCA) اكبر من تباين القدرة الخاصة على الائتلاف (SCA) فى كل الصفات المدروسة تحت ظروف الجفاف وظروف الكنترول. كانت العشيرتين المحليتين جيزة-٢ وC-87 احسن العشائر المدروسة فى القدرة الائتلافية العامة لزيادة محصول الحبوب فى الهجن تحت ظروف الجفاف والكنترول. وتفوقت الهجن Giza-2 x Tuxpeno و Cairo-1 x BS-11 و Giza-2 x Cairo-1 فى تأثيرات الـ SCA وفى أدائها وفى قيم قوة الهجين للأب الأحسن بالنسبة لصفة محصول الحبوب تحت كل من ظروف الجفاف والكنترول ولذلك تمت التوصية باستخدامها فى برامج التربية لتحمل الجفاف فى الذرة. كانت تقديرات التباين التجميعى (δ^2_A) اكبر بشكل ملحوظ من تقديرات تباين السيادة (δ^2_D) فى كل الصفات المدروسة ما عدا عدد الكيزان/النبات تحت ظروف الكنترول وعدد الصفوف/الكوز ومحصول الحبوب تحت ظروف الجفاف. كان التباين التجميعى اكثر تأثرا بالبيئة من تباين السيادة لصفة الفترة بين نثر اللقاح وخروج الحريرة (ASI) تحت ظروف الجفاف بينما كان العكس صحيحا لبقية الصفات المدروسة. كانت السيادة جزئية فى معظم الحالات بينما ظهرت السيادة الفائقة فى صفة عدد الكيزان تحت ظروف الكنترول وعدد صفوف الكوز تحت ظروف الجفاف وظهرت السيادة الكاملة فى صفات محصول لحبوب وعدد الحبوب بالصف ووزن الألف حبة تحت ظروف الجفاف ولم يكن هناك سيادة فى صفة ASI تحت ظروف الجفاف والكنترول وعدد الكيزان تحت ظروف الجفاف. تراوحت قوة التوريث بمعناها الخاص تحت ظروف الجفاف بين ٢٠,٨ % لصفة ASI و ٤٧,٥ % لعدد الحبوب فى الصف. كانت تقديرات قوة التوريث الخاصة تحت ظروف الكنترول أعلى منها تحت ظروف الجفاف لكل الصفات المدروسة ما عدا ASI وعدد كيزان النبات. كانت تقديرات التقدم الوراثى من الانتخاب المباشر تحت ظروف الكنترول أعلى منها تحت ظروف الجفاف لصفتى محصول الحبوب ووزن الـ ١٠٠ حبة وكان

العكس صحيحا بالنسبة لبقية الصفات. كان التحسين المتوقع من الانتخاب المباشر فى كل بيئة أكبر من التحسين من الانتخاب غير المباشر فى بيئة أخرى لكل الصفات المدروسة. لم يلاحظ فى أى من الصفات المدروسة أن تفوق الانتخاب لصفة ثانوية فى تحسين المحصول على الانتخاب المباشر لصفة المحصول نفسه. ومع ذلك فإن الاستجابة لتحسين صفة المحصول عن طريق الانتخاب غير المباشر لصفة ASI كانت أكثر فاعلية من باقى الصفات فى تحسين المحصول بصفة غير مباشرة، مما يقترح أن هذه الصفة (ASI) تعتبر مساعدا قويا فى زيادة كفاءة الانتخاب لمحصول الحبوب تحت ظروف الجفاف.

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