Combining Ability and Heritability of Maize (*Zea mays* L.) Morphologic Traits under Water Stress and Non-stress at Flowering Stage

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Authors' contributions

This work was carried out in collaboration between both authors. Author AMMAN designed the study, wrote the protocol, managed the literature searches and wrote the first draft of the manuscript. Author MMMA managed the experimental process and performed data analysis. Both authors read and approved the final manuscript.

Original Research Article

ABSTRACT

The main objective of the present investigation was to estimate combining ability, genetic variance components and heritability of 12 morphologic traits of maize under water stress (WS) and well watering (WW) at flowering stage. Fifteen F_1 genotypes of incomplete diallel crosses among 6 diverse inbred lines were evaluated under WS and WW at two seasons using a split plot design with three replications. The magnitude of general combining ability (GCA) was higher than specific combining ability (SCA) variance for all studied traits. The best general combiners for grain yield/plant (GYPP) (Sd-7 and IL-92) were also the best combiners for one or more yield traits, under WW and WS. The best cross in SCA effects for GYPP was IL171 × Sd7 followed by IL171 × IL17 under WS and IL24 × CML104 and IL171 × IL17 under WW. The magnitude of additive was much higher than dominance variance for all studied traits, except for ears/row (EPP) under WW and WS. Narrow-sense heritability (h^2_n) was generally of high magnitude (>60%) in most studied traits under both environments. Expected genetic advance (GA) from selection for studied traits in the two environments was generally of moderate magnitude (10-20%) for 11 out of 20 cases,

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namely plant height (PH), ear height (EH), leaf angle, kernels/row (KPR) and EPP, under WW and WS and GYPP under WS. The GA estimate for days to silking, rows/ear, KPP and 100-kernel weight under WW and WS and GYPP under WW, was of low magnitude (<10%). Under WS, heritability and expected genetic gain from selection were higher than WW for all studied traits, except PH and EH, where the opposite was true.

1. INTRODUCTION

Maize (*Zea mays* L.) is the third important cereal crop in Egypt after wheat and rice. According to FAOSTAT [1], harvested area of maize in Egypt in 2014 was 1,039,241 hectares (ca. 2.47 million feddan; one fed=4200 m^2) and produced 8,059,906 tonnes of grains, with an average yield of 7.76 tonnes ha^{-1} (ca. 23.28 ardab/ feddan; one ard=140 kg). According to the same report, Egypt ranks the sixth in the world with respect of average productivity after USA, Germany, Italy, France and Canada. However, Egypt imports every year about six million tons of maize grains to satisfy the local consumption. To reach self-sufficiency of maize production in Egypt, efforts are devoted to extend the acreage of maize; in the desert and to improve the maize productivity from unit area. Growing maize in the desert sandy soils of low water-holding capacity would expose maize plants to water stress, which could result in obtaining low grain yields under such conditions. Loss in grain yield is particularly severe when water stress occurs at flowering stage [2-4].

Maize breeders should pay great attention to develop drought tolerant maize cultivars that could give high grain yield under water-stress conditions. During the last few decades, considerable efforts have been devoted to improve yield performance of maize under water stress conditions through breeding [5]. Several investigators emphasized the role of maize genotypes in drought tolerance. Tolerant genotypes of maize were characterized by having shorter anthesis-silking interval (ASI) [6], more ears/plant [5,7] and greater number of kernels/ear [7,8].

Type of gene action, heritability and expected genetic advance from selection are prerequisites for starting a breeding program for developing a drought tolerant variety of maize. Literature review reveals that little research has been directly focused on studying the mode of gene action controlling yield under drought. Some researchers found that additive genetic effects play a major role in conditioning grain yield under water stress in tropical [9-12] and temperate [13] maize germplasm. Response to selection for yield in populations under water stress conditions has also been reported [14-16], suggesting that additive gene action might be important in controlling yield. Derera et al. [11] also found non-additive gene action playing important roles in controlling grain yield under both water stress and favorable growing environments. Agrama and Moussa [17] reported QTLs with both additive and dominance effects for yield and associated flowering traits. Significance of anthesis-silking interval, silk emergence, anthesis date and number of ears plant^{-1} in breeding drought tolerance in maize has been reported [6,13,18,19]. Many investigators reported a decline in heritability for grain yield under stress [20,21]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [22,23].

A wide array of biometrical tools is available to breeders for characterizing genetic control of economically important traits as a guide to decide the appropriate breeding methodology for hybrid breeding. Diallel analysis is one of the best biometrical tools to achieve that. The main objective of the present investigation was to estimate combining ability, genetic variance components, heritability and expected genetic advance from selection for maize agronomic and yield component traits under water stress (WS) at flowering as compared to well watering (WW).

2. MATERIALS AND METHODS

This study was carried out at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza, Egypt (30° 02'N latitude and 31° 13'E longitude with an altitude of 22.50 meters above sea level), in 2012, 2013 and 2014 seasons.

2.1 Plant Material

Six diverse maize (*Zea mays* L.) inbred lines (Table 1) in some agronomic and yield traits related to drought tolerance were chosen as parents of diallel crosses in this study. These inbreds were provided by Maize Research Department, Agricultural Research Center, Egypt and were used for making diallel crosses.

2.2 Producing F_1 Diallel Crosses

In 2012 summer season, all possible diallel crosses (except reciprocals) were made among the six parents, so seeds of 15 direct F_1 crosses were obtained for evaluation trials.

2.3 Evaluation of F_1`s

2.3.1 Experimental design and treatments

Two field evaluation experiments were carried out in 2013 and 2014 summer seasons. Evaluation in each season was carried out under two irrigation treatments, *i.e.* well-watering (WW) by giving all recommended irrigations and water stress (WS) by withholding the fourth and fifth irrigations to match water stress at flowering stage, *i.e.* 24-day stress period at flowering stage (during silking). A split- plot design in randomized complete blocks (RCB) arrangement with three replications was used. Main plots were devoted to water treatments (WW and WS). Sub-plots were devoted to 15 maize genotypes (15 F_1 diallel crosses). Each sub-plot consisted of one ridge of 4 m long and 0.70 m width, *i.e.* the experimental plot area was 2.8 m^2. Seeds were sown in hills at 25 cm apart, thereafter (before the 1st irrigation) were thinned to one plant/hill to achieve a plant density of about 24,000 plants/fed. Each main plot was surrounded with a wide alley (2.5 m width) to avoid interference of the two water treatments. Sowing date was on May 5 and May 8 in 2013 and 2014 seasons, respectively. All other agricultural practices were followed according to the recommendations of ARC, Egypt. Nitrogen fertilization at the rate of 120 kg N/fed was added in two equal doses of Urea before the first and second irrigation. Fertilization with calcium superphosphate was performed with soil preparation and before sowing. Weed control was performed chemically with Stomp herbicide before the first irrigation and just after sowing and manually by hoeing twice, the first before the second irrigation and the second before the third irrigation. Irrigation was applied by flooding after three weeks for the second irrigation and every 12 days for subsequent irrigations for well watering treatment, but the 4th and 5th irrigations were skipped for water stress treatment. Pest control was performed when required by spraying plants with Lannate (Methomyl) 90% (manufactured by DuPont, USA) against corn borers.

2.3.2 Soil analysis

The analysis of the experimental soil, as an average of the two growing seasons 2013 and 2014, indicated that the soil is clay loam (4.00% coarse sand, 30.90% fine sand, 31.20% silt, and 33.90% clay), the pH (paste extract) is 7.73, the EC is 1.91 dSm^{-1}, soil bulk density is 1.2 g cm-3, calcium carbonate is 3.47%, organic matter is 2.09%, the available nutrients in mg kg^{-1}were Nitrogen (34.20), Phosphorous (8.86), Potassium (242), hot water extractable B (0.49), DTPA - extractable Zn (0.52), DTPA - extractable Mn (0.75) and DTPA - extractable Fe (3.17).

2.3.3 Meteorological data

Meteorological variables in the 2013 and 2014 growing seasons of maize were obtained from Agro-meteorological Station at Giza, Egypt. For May, June, July and August, mean temperature was 27.87, 29.49, 28.47 and 30.33°C, maximum

Table 1. Designation, origin and place bred of six inbred lines used for making the diallel of this study

Inbred designation	Origin*	Institution (country)
IL-171(Y)	Rg-37 G.S. [(PI221866×307A)(SC.14)]	ARC-Egypt
IL-92(W)	Rg-49 G.S. (Beida × 307) (SC.14)	ARC-Egypt
IL-24(W)	G 336 Loc. Bred (H-309 1969, Mexico)	Mexico
Sd-7(W)	A.E.D.	ARC-Egypt
CML-104(Y)	CIMMYT population	CIMMYT- Mexico
IL-17(W)	G 268 Jellicarse (*via* recurrent selection)	ARC-Egypt

Source of information: Maize Research Department, Agricultural Research Center, Egypt.
ARC = Agricultural Research Center, A.E.D. = American Early Dent; an old open-pollinated variety,
W = White grains and Y = Yellow grains

temperature was 35.7, 35.97, 34.93 and 37.07℃ and relative humidity was 47.0, 53.0, 60.33 and 60.67%, respectively, in 2013 season. In 2014 season, mean temperature was 26.1, 28.5, 29.1 and 29.9℃, maximum temperature was 38.8, 35.2, 35.6 and 36.4℃ and relative humidity was 32.8, 35.2, 35.6 and 36.4%, respectively. Precipitation was nil in all months of maize growing season for both seasons.

2.4 Data Recorded

1- Days to 50% anthesis (DTA) (as number of days from planting to anthesis of 50% of all plants/plot).
2- Anthesis-silking interval (ASI) (as number of days between 50% silking and 50% anthesis of all plants/plot). 3- Plant height (PH) (cm) (measured from ground surface to the point of flag leaf insertion for five plants per plot).
4- Ear height (EH) (cm) measured from ground surface to the base of the top most ear relative to the plant height for five plants per plot.
5- Barren stalks (BS) (%) measured as percentage of plants bearing no ears relative to the total number of plants in the plot (an ear was considered fertile if it had one or more grains on the rachis).
6- Leaf angle (LANG) (o) measured as the angle between stem and blade of the leaf just above ear leaf for five plants per plot, according to Zadoks et al. [24].
7- Ears per plant (EPP) calculated by dividing number of ears per plot on number of plants per plot.
8- Rows per ear (RPE) using 10 random ears/plot at harvest.
9- Kernels per row (KPR) using the same 10 random ears/plot.
10- Kernels per plant (KPP) calculated as number of ears per plant × number of rows per ear × number of kernels per row.
11- 100-kernel weight (100-KW) (g) adjusted at 15.5% grain moisture, using shelled grains of each plot.
12- Grain yield/plant (GYPP) (g) estimated by dividing the grain yield per plot (adjusted at 15.5% grain moisture) on number of plants/plot at harvest.

2.5 Biometrical and Genetic Analyses

Analysis of variance of the split-plot design in RCB arrangement was performed on the basis of individual plot observation using the MIXED procedure of SAS ® [25]. Combined analysis of variance across the two seasons was also performed if the homogeneity test was non-significant. Moreover, combined analysis across seasons for each environment (WW or WS) separately was performed as randomized complete block design for the purpose of determining genetic parameters using GENSTAT 10th addition windows software. Least significant difference (LSD) values were calculated to test the significance of differences between means according to Steel et al. [26]. Diallel crosses were analyzed to estimate general (GCA) and specific (SCA) combining ability variances and effects and genetic parameters for studied traits according to Griffing [27] Model I (fixed effect) Method 4. Although Griffing's analysis was based on Model I (fixed effect) since parents of the diallel in this study were selected in purpose for the validity of diallel analysis, Model 2 (that assumes random model) of Method 4 was used to estimate genetic components (additive and dominance variances and their interactions with years), heritability and expected genetic advance from selection as described by Nadaraian and Gunasekaran [28]. The conclusions obtained will not be generalized, but will help us to characterize our genetic material for its proper use in the future breeding programs. Heritability in the broad (h^2_b) and narrow (h^2_n) sense in F_1s were estimated from the following formulae:

$$h^2_b = 100 \ (\delta^2_G/\delta^2_{ph})$$

$$h^2_n = 100 \ (\delta^2_A/\delta^2_{ph})$$

Where δ^2_G and δ^2_{ph} are genetic and phenotypic variance, respectively. The expected genetic advance from selection (GA) as a percent from the mean was calculated, from the following formula:

$$GA\% = 100 \ h^2_n \ k \ \delta_{ph} \ / \ x$$

Where: δ_{ph} = Phenotypic standard deviation, k = Selection differential (the k value for 10% selection intensity) equals (1.76), x = Mean of the trait in respective environment.

3. RESULTS AND DISCUSSION

3.1 Analysis of Variance

Combined analysis of variance across years (Y) of the split-split plot design for the studied genotypes (G) of maize (15 F_1's) under two irrigation (I) regimes is presented in Table 2.

Mean squares due to years were significant (P ≤ 0.05 or 0.01) for DTS (days to silking), LANG (leaf angle), KPR (kernels/row), 100KW (100-kernel weight) and GYPF (grain yield/plant), indicating significant effect of climatic conditions on these traits.

Mean squares due to irrigation regimes were significant (P ≤ 0.05 or 0.01) for all studied traits, except ASI (anthesis-silking interval), PH (plant height), EH (ear height) and LANG, indicating that irrigation regime has a significant effect on most studied traits. Non significance of variance due to irrigation for ASI, PH, EH and LANG might be due to water stress was not severe enough to affect on such traits. Mean squares due to genotypes were significant (P ≤ 0.01) for all studied traits, except ASI and BS, indicating that genotype had a significant effect on most studied traits.

Mean squares due to the 1st order interaction were significant (P ≤ 0.05 or 0.01) for G×Y in seven traits (DTS, PH, EH, LANG, rows/ear; RPE, KPR and 100KW), for G×I in three traits (DTS, LANG and 100KW) and for I×Y, in three traits (PH, EH and 100KW).

Mean squares due to the 2nd order interaction G×I×Y were significant (P ≤ 0.05 or 0.01) for

only three traits, *i.e.* DTS, LANG and 100KW. These results indicated that the rank of maize genotypes differed from irrigation regime to another for seven traits, and the possibility of selection for improved performance of such traits under a specific water stress as proposed by Al-Naggar et al. [29-31].

Combined analysis of variance of a randomized complete blocks design for 12 traits of 15 maize genotypes under each environment (WW and WS) across two seasons (data not presented) showed that mean squares due to genotypes, under both environments were highly significant for all studied traits, except ASI and BS under both environments, indicating the significance of differences among studied F_1 diallel crosses in the majority of cases.

3.2 Effect of Water Stress

The effects of drought at flowering stage on the means of studied traits and across all genotypes in two years expressed as change percentage from well watering (WS) to water stress (WS) are presented in Table 3 and Fig. 1. Mean grain yield/plant (GYPP) was significantly decreased due to water stress at flowering stage by 22.46%. Consistent to these results, several

Table 2. Analysis of variance of split plot for studied traits of 15 maize crosses (G) under two watering treatments (I) across two seasons (Y)

SOV	df	Mean squares					
		DTS	ASI	PH	EH	LANG	BS%
Year (Y)	1	278.83**	0.28	34.4	49	238.33**	0.18
Irrigation (I)	1	86.06**	1.86**	349.5	169.6	26.48	1.25**
Y x I	1	1.03	0.65	7696.1**	1472.1**	0.1	0.49
Error	8	0.69	0.43	98.7	127.2	21.37	0.36
Genotype(G)	16	20.80**	1.28**	5369.6**	1700.5**	209.60**	0.19
Y x G	16	5.06**	0.83	239.0**	91.8**	26.34**	0.27
I x G	16	1.41**	0.91	136.4	42.8	13.29**	0.18
Y x I x G	16	1.50**	0.79	115.2	31.2	9.85*	0.15
Error	128	0.53	0.55	84.4	36.2	5.07	0.20
R^2		0.93	0.42	0.90	0.88	0.88	0.47
		EPP	RPE	KPR	KPP	100-KW	GYPP
Year (Y)	1	0.001	0.001	25.34*	13397	298.7**	88485**
Irrigation (I)	1	1.40**	11.60**	239.06**	1548742**	475.8**	66869**
Y x I	1	0.04	0.19	0.11	26560	64.66**	1486.8
Error	8	0.01	0.31	3.97	5925	3.62	1022.5
Genotype(G)	16	0.08**	11.80**	154.45**	78693**	87.64**	4351**
Y x G	16	0.02	0.60**	9.63**	11824	10.47**	707.9
I x G	16	0.01	0.23	3.03	8391	4.66*	631.3
Y x I x G	16	0.02	0.2	1.64	9967	4.37*	827
Error	128	0.02	0.22	2.04	11090	2.56	561.9
R^2		0.59	0.89	0.92	0.70	0.89	0.79

*and** indicate significant at 0.05 and 0.01 probability levels, respectively*

Table 3. Change (Ch%) in studied traits of maize crosses due to water stress (WS) at flowering as compared to well watering (WW) across two seasons

Trait	Ch%	Trait	Ch%	Trait	Ch%
DTS	-4.51**	ASI	-7.64	PH	-0.13
EH	-0.67	LANG	-2.94	BS	-421.4**
EPP	16.13**	RPE	5.09**	KPR	7.27**
KPP	26.19**	100-KW	18.00**	GYPP	22.46**

*** indicates significant at 0.01 level. Ch%=100(WW-WS)/WW*

investigators reported reductions due to drought stress in grain yield [30-32]. Denmead and Shaw [33] noted that water stress during the vegetative stage of corn production reduced grain yield by 25%, water stress during silking reduced grain yield by 50%, while water stress during grain fill reduced grain yield by 21%. The lower reduction in grain yield recorded in this study due to drought at silking stage as compared with some previous reports might be due to differences in soil and climate conditions prevailed during the seasons and locations of different studies.

Reductions in grain yield of maize due to water stress at flowering was accompanied with significant reductions in ears/plant (16.13%), rows/ear (5.09%), 100-kernel weight (18.00%), kernels/row (7.27%) and kernels/plant (26.19%). On the contrary, withholding irrigation at

flowering stage caused significant increases in days to silking (4.51%) and percentage of barren stalks (421.4%) and non-significant increases in anthesis-silking interval (21.17%) plant height (0.13%), ear height (0.67%) and leaf angle (2.94%). Elongation of anthesis-silking interval due to water stress in this study was in full agreement with Monneveux et al. [34] and Al-Naggar et al. [14,30,31].

3.3 Effect of Genotype

Averages and ranges (minimum and maximum values) of studied traits across the 15 F_1 crosses and across the two years are illustrated in Fig. 1. The F_1 crosses varied greatly in most studied traits. The difference between the highest and lowest genotype (range) was wider under water stress than well watering for DTS, ASI, BS, KPR,
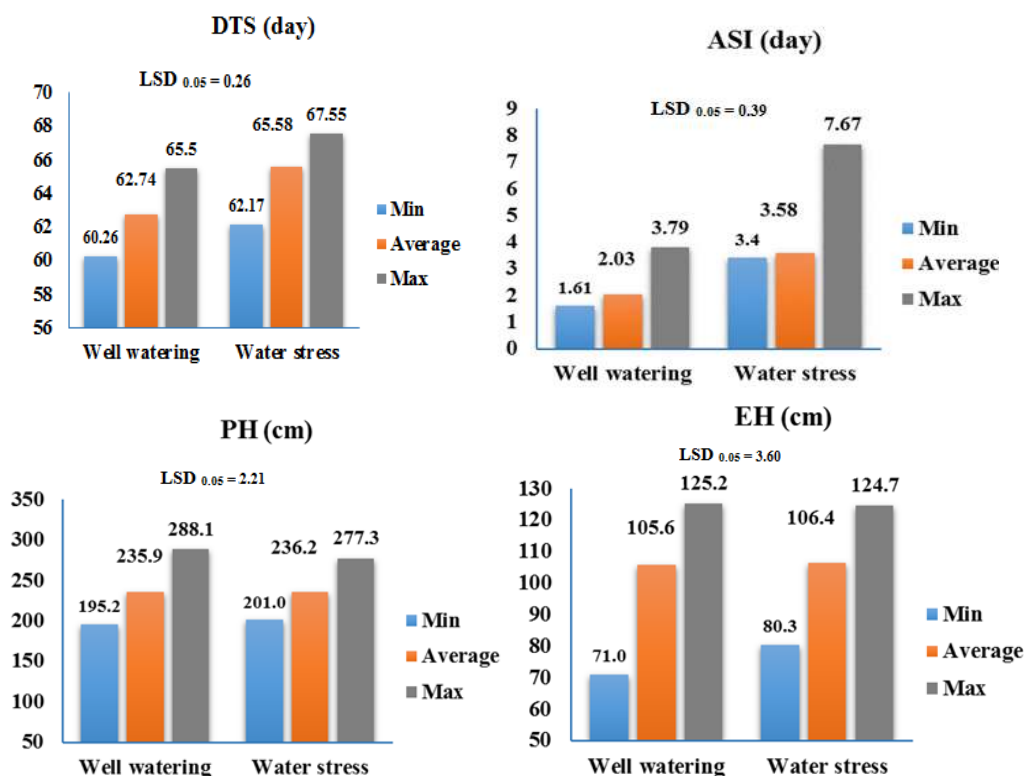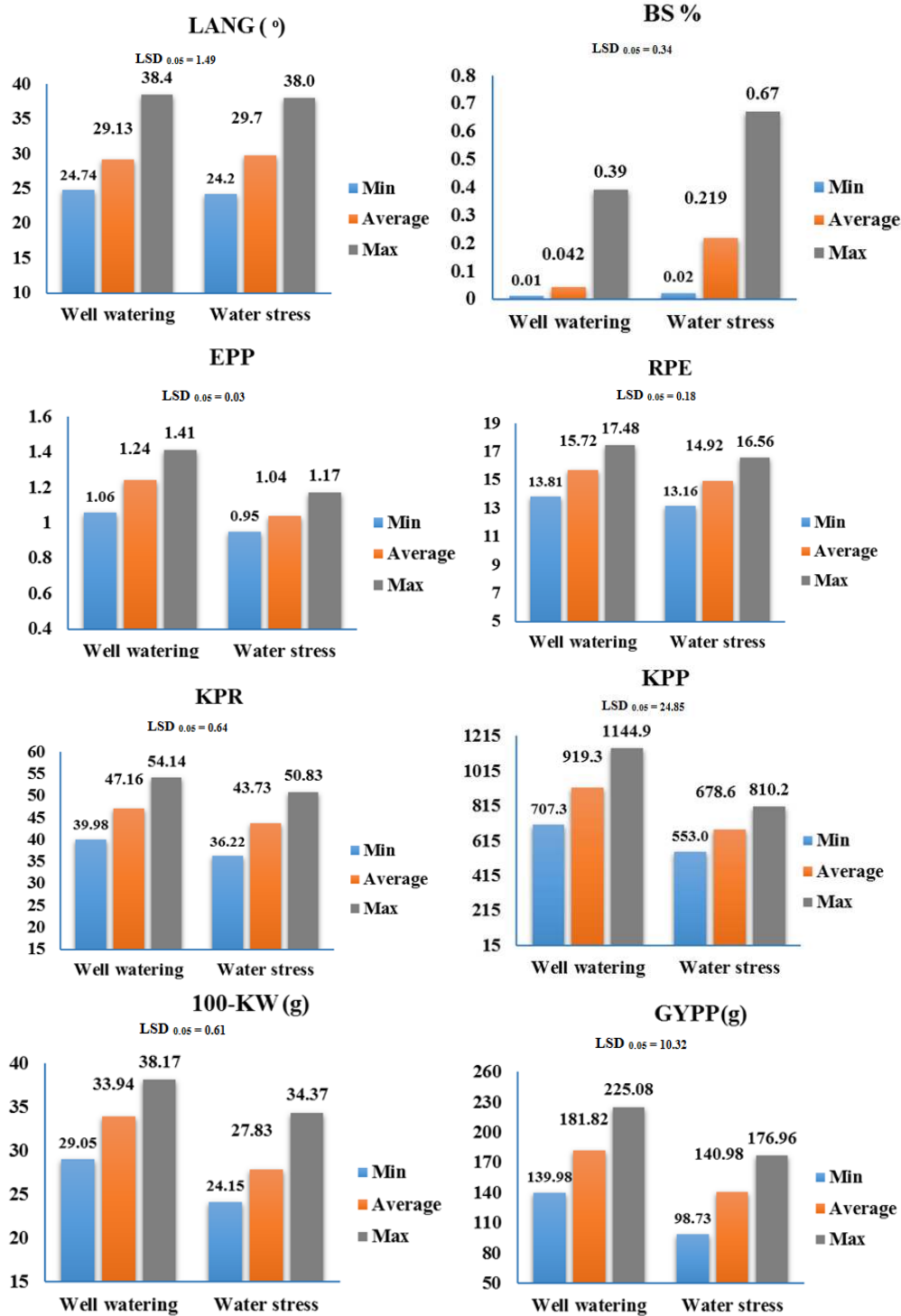
Fig. 1. Average (Aver), minimum (Min) and maximum (Max) values of studied traits across all hybrids under well watering and water stress at flowering across years

100KW and GYPP traits. On the contrary, the range was wider under WW than WS for PH, EPP, RPE and KPP traits. For grain yield/plant, the highest yielding F_1 hybrid was IL 92 x Sd 7 (176.96 g under WS and 225.08 g under WW) followed by Sd 7 x IL 24 (162.57 g under WS and

191.25 g under WW); they were considered the most drought tolerant in this experiment. On the contrary, the cross IL 171 x CML 104 was the lowest yielding (98.73 g under WS and 139.98 g under WW) and showed maximum reduction (29.47%) due to drought; it was considered the most drought sensitive in this experiment.

3.4 Combining Ability Variances

Estimates of variances due to general combining ability (GCA) and specific combining ability (SCA) of the diallel crosses of maize for combined data across two seasons under two environments (WW and WS) are presented in Table 4. Because genotype mean squares were not significant for ASI and BS traits (Table 2), they were not included in combining ability analysis. Mean squares due to GCA and SCA were significant (P≤ 0.01 or 0.05) for all studied traits under both environments, except EPP for GCA and SCA under WW, PH for SCA under WS, RPE, KPP and GYPP for SCA under WW and GYPP for SCA under WS, suggesting that both additive and non-additive gene effects play important roles in controlling the inheritance of most studied traits. A similar conclusion was reported by Mason and Zuber [35], Khalil and Khattab [36] and Al-Naggar et al. [31, 37-39].

In the present study under both environments, the magnitude of GCA mean squares was higher than that of SCA mean squares (the ratio of GCA/SCA mean squares was higher than unity) for all studied traits (Table 4), suggesting the existence of a greater portion of additive and additive × additive than non-additive variance (dominance and epistasis) in controlling the inheritance of these traits under water stress and non-stress environments. These results are in agreement with those reported by Khalil and Khattab [36], and Al-Naggar et al. [31, 38,39].

Results in Table 4 indicate that mean squares due to the GCA × year interaction were significant for DTS, EH, LANG, RPE, KPR, 100-KW and GYPP under WW environment, and PH, LANG, RPE, KPR, 100KW and GYPP under water stress environment, indicating that GCA (additive) variances for these traits under the two environments were affected by years. Mean squares due to SCA × year interaction were

significant for DTS and PH under WW and DTS and 100KW under WS, indicating that SCA (non-additive) variances for these traits under the respective environments were affected by years. This was not true for the rest of cases, suggesting that additive and non-additive variances for these cases were not affected by years. The means squares due to GCA × year was higher than those due to SCA × year for PH, LANG, RPE, KPR, 100KW and GYPP under both environments, PH and KPP under WS, suggesting that GCA was more affected by years than SCA for these cases. On the contrary, mean squares due to SCA × year was higher than those due to GCA × year for the rest of cases, indicating that SCA variance was more affected by years than GCA variance for these cases under the respective environments.

3.5 GCA Effects

Estimates of general combining ability (GCA) effects of parental inbreds for studied traits under the two environments (WW and WS) across two seasons are presented in Table 5. The best parental inbred lines were those showing negative and significant GCA effects for DTS, ASI, PH, EH, BS and LANG and those of positive and significant GCA effects for EPP, RPE, KPR, KPP, 100-KW and GYPP traits.

For GYPF, the best inbred in GCA effects was Sd-7 in both environments (WW and WS) followed by IL-92. These best general combiners for grain yield (Sd-7 and IL-92) were also the best combiners for 100KW, KPR and KPP traits, IL-92 for RPE and Sd-7 for EPP under the two environments. On the contrary, the inbred lines CML-104 and IL-171 were the worst in GCA effects for GYPP under the two environments (Table 5). However, the inbreds IL-24 and CML-104 for DTS, PH and EH, IL-171 for DTS, EH, LANG and RPE and IL-17 for PH and LANG under the two environments were also the best general combiners for producing good hybrid combinations for earliness, short plant stature and/or narrow leaf angles under WW and WS environments.

Previous studies proved that positive GCA effects for EPP and kernels/plant and negative GCA effects for DTA, DTS, BS, and LANG traits are a good indicator of drought stress and/or high density tolerance [13,40].

Table 4. Mean squares due to general (GCA) and specific (SCA) combining ability and their interaction with years for studied traits under well watering (WW) and water stress (WS) conditions

SOV	df	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
		DTS		PH		EH		LANG		EPP	
Year (Y)	1	93.03	131	4358	2022	1054	317.40	87.91	126.03	0.02	0.01
Crosses (C)	14	9.43	16.42**	3492**	2771**	1179**	765.6**	109.8**	110.60**	0.04	0.03**
GCA	5	24.48**	40.28**	9223**	7362**	2521**	1714.0**	223.2**	235.85**	0.05	0.04**
SCA	9	1.06*	3.16**	309**	221	434**	238.7**	46.79**	41.02**	0.04	0.03**
GCA/SCA		23.1	12.7	29.8	33.3	5.8	7.2	4.8	5.7	1.3	1.3
C × Y	14	4.22**	2.39**	89.09	235**	60.06**	68.10	24.83**	13.68**	0.02	0.00
GCA × Y	5	3.79**	0.67	41.44	397**	140.62**	91.50	59.00**	29.84**	0.02	0.01
SCA × Y	9	4.46**	3.34**	116*	145	15.31	55.10	5.85	4.70	0.02	0.00
GCA × Y/SCA × Y		0.8	0.2	0.4	2.7	9.2	1.7	10.1	6.3	1.0	0.0
Error	56	0.51	0.50	53.00	114	18.96	55.50	4.55	5.35	0.03	0.01
		RPE		KPR		KPP		100-KW		GYPP	
Year (Y)	1	0.00	0.14	20.36	15.23	34514	0.11	44.73	308.03	30702	46058
Crosses (C)	14	6.52**	7.02**	77.92**	88.85**	35750*	26860**	49.35**	43.20**	2851*	2002**
GCA	5	17.64**	18.14**	203.35**	229.16**	65740**	48037**	113.81**	93.11**	5765**	5028**
SCA	9	0.34	0.84**	8.23**	10.90**	19089	15095**	13.54**	15.48**	1232	320
GCA/SCA		51.9	21.6	24.7	21.0	3.4	3.2	8.4	6.0	4.7	15.7
C × Y	14	0.36	0.52**	6.59**	4.38**	14749	3222	9.00*	6.77**	963	546
GCA × Y	5	0.69**	0.82**	10.05**	8.62**	5480	5641	16.60**	8.03**	1922*	660
SCA × Y	9	0.19	0.35	4.67	2.02	19899	1879	4.78	6.07**	430	482
GCA × Y/SCA × Y		3.6	2.3	2.2	4.3	0.3	3.0	3.5	1.3	4.5	1.4
Error	56	0.23	0.23	2.84	1.49	19387	4407	3.83	1.62	757	501

*and** indicate significant at 0.05 and 0.01 probability levels, respectively

Table 5. Estimates of general combining ability effects of inbred lines for studied traits under WW and WS

Inbred	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
	DTS		PH		EH		LANG		EPP	
IL-171	-0.49**	-0.40**	1.02	2.54	-13.45**	-12.43**	-1.10**	-2.51**	-0.07*	-0.02
IL-92	1.60**	1.54**	20.94**	12.20**	11.85**	7.53**	2.74**	3.14**	-0.03	-0.03
IL-24	-1.78**	-1.86**	-12.21**	-5.88**	-8.44**	-4.68**	2.99**	1.95**	0.00	-0.06**
Sd-7	1.14**	1.00**	25.69**	25.68**	11.10**	10.41**	2.24**	3.37**	0.06*	0.04*
CML-104	-0.57**	-0.56**	-22.46**	-23.91**	-2.65**	-3.18*	-3.01**	-2.72**	0.01	0.03
IL-17	0.1	0.27*	-12.98**	-10.63**	1.60*	2.36*	-3.85**	-3.24**	0.03	0.04*
SE (ĝi)	0.13	0.14	1.36	1.99	0.81	1.39	0.4	0.43	0.03	0.02
SE (ĝi-ĝj)	0.19	0.21	2.1	3.08	1.26	2.15	0.62	0.67	0.05	0.03
	RPE		KPR		KPP		100-KW		GYPP	
IL-171	1.00**	1.11**	-0.45	-1.02**	-3.69	25.58*	-2.72**	-3.01**	-13.08**	-15.07**
IL-92	0.22**	0.21*	2.30**	2.67**	36.02	32.22**	1.43**	1.74**	9.40*	12.21**
IL-24	0.79**	0.81**	-0.58**	-0.74**	31.56	-14.14	-0.36	-0.68**	-6.91	-1.88
Sd-7	-1.33**	-1.17**	3.50**	3.69**	29.77	29.96**	3.36**	2.09**	25.81**	16.73**
CML-104	-0.39**	-0.50**	-4.93**	-5.02**	-102.13**	-84.28**	-1.69**	-1.19**	-15.09**	-18.57**
IL-17	-0.29**	-0.46**	0.16	0.41*	8.47	10.66	-0.03	1.05**	-0.13	6.58
SE (ĝi)	0.09	0.09	0.31	0.23	25.94	12.37	0.36	0.24	5.13	4.17
SE (ĝi-ĝj)	0.14	0.14	0.49	0.35	40.2	19.16	0.56	0.37	7.94	6.46

*and** indicate significant at 0.05 and 0.01 probability levels, respectively

Table 6. Estimates of specific combining ability effects of F₁ crosses for studied traits under well watering (WW) and water stress (WS) conditions across two seasons

Cross	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
	DTS		PH		EH		LANG		EPP	
IL171 × IL92	-0.42*	0.40*	0.32	1.16	2.74*	2.59	-1.49**	0.53	-0.01	-0.01
IL171 × IL24	-0.27	0.47*	0.81	-4.43	1.37	0.63	-0.57	0.89	-0.03	. -0.01
IL171× Sd7	-0.10	-0.56**	3.91*	6.68*	1.99	-1.12	-2.65**	-2.04**	-0.04*	-0.01
IL171 × CML104	0.67**	0.01	-10.61**	-7.74*	-16.59**	-10.87**	3.27**	-0.12	-0.06*	-0.08*
IL171 × IL 17	0.13	-0.32	5.57**	4.32	10.49**	8.76**	1.43*	0.74	0.13**	0.10**
IL92 × IL24	0.19	-0.30	-1.44	-1.10	2.91*	1.01	0.94	2.24**	0.04*	0.00
IL92 × Sd7	-0.65**	-0.74**	6.32**	3.35	-0.64	-0.07	5.02**	1.99**	0.09**	0.09**

Cross	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
	DTS		PH		EH		LANG		EPP	
IL92 × CML104	0.46*	0.74**	-0.19	3.60	0.95	-0.83	-2.74**	-2.10**	-0.09**	-0.03**
IL92 × IL17	0.42*	-0.10	-5.01*	-7.01*	-5.97**	-2.70	-1.73**	-2.66**	-0.02	-0.05**
IL24 × Sd7	0.08	0.24	-3.20	-1.24	-3.51**	-1.53	0.60	0.01	-0.06**	-0.05**
IL24 × CML104	0.11	0.30	-0.64	1.02	0.57	0.55	-1.49*	-3.58**	0.09**	0.03**
IL24 × IL17	-0.11	-0.70**	4.47*	5.74	-1.34	-0.66	0.51	0.45	-0.04*	0.03**
Sd7 × CML104	-0.06	-0.55*	4.72*	-1.31	10.2**	9.63**	-0.90	2.18**	0.07**	0.07**
Sd7 × IL24	0.73**	1.61**	-11.76**	-7.49*	-8.05**	-6.91**	-2.07**	-2.14**	-0.07**	-0.09**
CML104 × IL17	-1.17**	-0.49*	6.73**	4.43	4.86**	1.51	1.85**	3.61**	0.00	0.02*
SE (ŝij)	0.21	0.23	2.30	3.38	1.38	2.36	0.67	0.73	0.02	0.01
SE (ŝij-ŝik)	0.34	0.37	3.64	5.34	2.18	3.72	1.07	1.16	0.03	0.02
SE (ŝij-ŝkl)	0.27	0.30	2.97	4.36	1.78	3.04	0.87	0.94	0.02	0.01
	RPE		KPR		KPP		100-KW		GYPP	
IL171 × IL92	0.09	0.14	-0.76	-0.85*	-19.12	-12.51	1.65**	1.45**	0.61	-1.41
IL171 × IL24	0.11	-0.23	-1.08*	-0.06	-42.56**	-14.00*	-1.38*	-0.29	-16.12**	-2.47*
IL171× Sd7	0.06	0.17	2.14**	2.10**	21.80	39.48**	1.19*	0.75*	10.31**	9.00**
IL171 × CML104	-0.11	0.27*	0.24	-1.26**	-37.63**	-59.9**	-0.15	-1.32**	-10.11**	-11.87**
IL171 × IL 17	-0.15	-0.35*	-0.55	0.07	77.51**	46.93**	-1.31*	-0.60	15.31**	6.75**
IL92 × IL24	0.23	0.19	-0.48	-0.88*	35.88**	-8.49	-1.13*	-0.91*	4.63	1.43
IL92 × Sd7	-0.28*	-0.51**	0.10	0.94**	46.44**	46.89**	-0.36	0.27	10.18**	3.79**
IL92 × CML104	-0.08	-0.37**	0.13	0.68*	-64.54**	-22.09**	-0.13	0.34	-15.47**	3.79**
IL92 × IL17	0.04	0.56**	1.01*	0.11	1.35	-3.80	-0.03	-1.15**	0.04	-7.60**
IL24 × Sd7	0.15	0.36*	0.13	-0.06	-22.69*	-17.80*	-1.28*	-2.36**	-7.02*	-4.75**
IL24 × CML104	-0.13	-0.06	1.10*	0.21	69.70**	21.24**	1.85**	2.28**	22.78**	5.04**
IL24 × IL17	-0.36*	-0.25	0.34	0.80*	-40.33**	19.06*	1.94**	1.27**	-4.27	0.75
Sd7 × CML104	-0.04	0.06	-1.52**	-0.82*	12.73	27.19**	-0.26	-0.22	0.21	-2.55*
Sd7 × IL24	0.11	-0.07	-0.85	-2.17**	-58.28**	-95.76**	0.71	1.56**	-13.68**	-5.49**
CML104 × IL17	0.36*	0.11	0.05	1.19**	19.75	33.57**	-1.31**	-1.08**	2.59	5.58**
SE (ŝij)	0.15	0.15	0.54	0.39	11.34	7.00	0.62	0.40	2.90	1.16
SE (ŝij-ŝik)	0.24	0.24	0.84	0.61	19.87	11.06	0.98	0.64	4.59	3.06
SE (ŝij-ŝkl)	0.20	0.20	0.69	0.50	15.61	9.03	0.80	0.52	3.74	2.38

*and** indicate significant at 0.05 and 0.01 probability levels, respectively

3.6 SCA Effects

Estimates of specific combining ability effects (SCA) of F_1 diallel crosses for studied traits under the two environments across years are presented in Table 6. The best F1 crosses were those showing negative and significant SCA effects for DTS, ASI, PH, EH, BS and LANG and those of positive and significant SCA effects for EPP, RPE, KPR, KPP, 100-KW and GYPP traits. For GYPP, the largest positive (favorable) and significant SCA effects were recorded by the cross IL 171 × Sd 7 followed by IL 171 × IL 17 under WS and IL 24 × CML104 followed by IL 171 × IL 17 under WW (Table 6). These crosses showed significant and positive SCA effects for one or more yield attributes. The above crosses may be recommended for maize breeding programs for the improvement of tolerance to drought [41,42].

For EPP, RPE, KPR, KPP and 100-KW, the largest positive and significant SCA effects were exhibited by the crosses IL171 × IL17, IL92 × IL17, IL171 × Sd7, IL171 × IL17 and IL24 × CML104, respectively under water stress environment. For LANG, the lowest negative (favorable) and significant SCA effects were exhibited by the crosses IL171 × Sd7, IL92 × CML104, Sd7 × IL24, IL92 × IL17 and IL24 × CML104 . For PH and EH, the lowest negative (favorable) and significant SCA effects were recorded by the crosses IL171 × CML104, and Sd7 × IL24 under both environments. For days to 50% silking, the lowest negative (favorable) and significant SCA effects were shown by the cross CML104 × IL17 and IL92 x Sd7 under both environments. It is worthy to note that for the studied traits, most of the best crosses in SCA effects for a given trait included at least one of the best parental inbred lines in GCA effects for the same trait. The same conclusion for other genetic material was reported previously by Al-Naggar et al. [31,37-39].

3.7 Genetic Variance Components, Heritability and Expected Selection Gain

Estimates of genetic variances, heritability and genetic advance from selection for studied traits under WW and WS environments across two years are presented in Table 7. The estimates of additive genetic component of variation (δ^2_A) were much higher, in magnitude, than dominance (δ^2_D) variance (where the ratio δ^2_A / δ^2_D is > 1) for all studied traits, except EPP, suggesting that additive variance plays the major role in the inheritance of these traits in most cases and that selection breeding would be very efficient for improving studied traits under both environments (WW and WS). This conclusion is in agreement with that reported by Derera et al. [11] and Al-Naggar et al. [31,37-39].

The ratio (δ^2_{AY} / δ^2_{DY}) was greater than unity for EH and RPE under WW and WS, PH, LANG, KPR and GYPP under WS and KPP and 100KW under WW, indicating that additive variance was more affected by seasonal variation than dominance variance. On the contrary, for the rest of cases, the ratio (δ^2_{AY} / δ^2_{DY}) was less than unity, indicating that dominance variance was more affected by seasonal variation than additive variance.

Broad-sense heritability (h^2_b) was generally of high magnitude (>60%) under both environments for most studied traits (16 out of 20 cases) and reached 95.37% under well watering for PH. The remaining cases showed moderate estimates of h^2_b (from 36.00 to 58.61%).The lowest estimate of h^2_b was shown by KPP (36.00%) and EPP (46.67%) under WW, indicating that the environment and genotype × environment interaction had considerable effects on the phenotype for these traits under well watering environment.

Narrow-sense heritability (h^2_n) was generally of high magnitude (>60%) in most studied traits under both environments (13 out of 20 cases) and reached 91.53% under well watering for PH. The lowest estimate of h^2_n (20.00 and 27.27%) was recorded by EPP under WW and WS, respectively. The estimates of h^2_n under WW were higher than those under WS for four out of ten characters, *i.e.* PH (91.53 *vs* 84.93%), LANG (60.92 *vs* 58.32%), RPE (87.68 *vs* 83.88%) and KPR (88.15 *vs* 84.86 %). On the contrary, the estimate of h^2_n under WS was higher than that under WW conditions for six traits, namely DTS (44.22 *vs* 67.66%), EH (66.89 *vs* 70.96%), EPP (20.00 *vs* 27.27%), KPP (35.38 *vs* 40.73%), 100KW (61.81 *vs* 64.48%) and GYPP (39.28 *vs* 61.28%). The small difference between broad and narrow sense heritability in many cases of this experiment could be attributed to the high estimates of additive and additive × additive components.

Table 7. Estimates of additive (δ^2_A), dominance (δ^2_D), genetic (δ^2_g) and phenotypic (δ^2_{ph}) variances, heritability (%) in broad (h^2_b) and narrow (h^2_n) sense and genetic advance (GA%) from selection for studied traits under well watering (WW) and water stress (WS) conditions across seasons

Parameter	WW	WS	WW	WS	WW	WS	WW	WS	WW	WS
	DTS		PH		EH		LANG		EPP	
δ^2_A	0.86	1.66	383	290	99.18	67.60	6.84	8.58	0.001	0.001
δ^2_D	0.28	0.02	16.08	6.33	34.89	15.30	3.41	3.03	0.002	0.003
δ^2_A / δ^2_D	3.07	83	23.79	45.85	2.84	4.42	2.01	2.83	0.75	0.500
δ^2_{AY}	0.06	0.22	0.00	21.00	10.44	3.04	0.00	2.1	0.000	0.001
δ^2_{DY}	0.66	0.47	10.50	5.17	0.61	0.07	0.22	0.11	0.002	0.002
$\delta^2_{AY} / \delta^2_{DY}$	0.09	0.47	0.00	4.06	17.11	43.43	0.00	19.09	0.000	0.500
δ^2_e	0.09	0.08	8.83	19	3.16	9.25	0.76	0.89	0.005	0.002
δ^2_G	1.14	1.68	399	297	134.07	82.90	10.25	11.61	0.003	0.004
δ^2_{Ph}	1.95	2.45	418	342	148.28	95.26	11.23	14.71	0.006	0.005
h^2_b	58.61	68.48	95.37	86.78	90.42	87.02	91.29	78.92	46.67	81.82
h^2_n	44.22	67.66	91.53	84.93	66.89	70.96	60.92	58.32	20.00	27.27
GA%	1.72	2.89	14.13	11.7	13.65	11.41	12.53	13.34	2.33	3.12
	RPE		KPR		KPP		100-KW		GYPP	
δ^2_A	0.7	0.72	8.06	9.18	2511	1767	4.06	3.54	160	182
δ^2_D	0.01	0.04	0.3	0.74	67.5	1101.33	0.73	0.78	66.83	13.5
δ^2_A / δ^2_D	70	18	26.87	12.41	37.2	1.6	5.56	4.54	2.4	13.48
δ^2_{AY}	0.04	0.04	0	0.56	1202	314	0.98	0.16	0	14.84
δ^2_{DY}	0.01	0.02	0.31	0.09	85.33	421.33	0.16	0.74	54.5	3.17
$\delta^2_{AY} / \delta^2_{DY}$	4.00	2.00	0.00	6.22	14.09	0.75	6.13	0.22	0.00	4.68
δ^2_e	0.04	0.04	0.47	0.25	3231	735	0.64	0.27	126	84
δ^2_G	0.71	0.76	8.36	9.92	2578	2868	4.79	4.32	227	196
δ^2_{Ph}	0.8	0.86	9.14	10.82	7096	4337	6.57	5.49	408	297
h^2_b	88.94	88.54	91.43	91.7	36.00	66.00	72.93	78.69	56.00	66.00
h^2_n	87.68	83.88	88.15	84.86	35.38	40.73	61.81	64.48	39.28	61.28
GA%	8.98	9.2	10.3	11.29	6.28	7.03	8.51	8.96	7.81	12.89

Expected genetic advance (GA) from selection (based on 10% selection intensity) across years for studied traits in the two environments (Table 7 above) was generally of moderate magnitude (10-20%) for 11 out of 20 cases, namely PH, EH, LANG, EPP, KPR under WW and WS and GYPP under WS. For DTS, RPE, KPP, 100KW under WW and WS and GYPP under WW, the GA estimate was of low magnitude (<10%) and the lowest was for DTS (1.72% under WW and 2.89% under WS).

The stressed environment (WS) in this experiment, showed higher expected genetic gain from selection than the non-stressed environment (WW) for all studied traits, except PH and EH, where the opposite was true.

In the literature, there are two contrasting conclusions, based on results regarding heritability and predicted genetic advance (GA) from selection under stress and non-stress environments. The first group of researchers concluded that heritability and expected gain from selection is higher under non-stress than those under stress [21,40,43,44]. However, the second group of investigators concluded that heritability and expected GA is higher under stress than non-stress, and that selection should be practiced in the target environment to obtain higher genetic advance [20,37-39,45,46]. Our results confirm the conclusion of the second group of researchers for GYPP, EPP, RPE, KPR, KPP, 100KW, DTS and LANG and the conclusion of the second group of researchers for PH and EH traits.

It is therefore expected that to improve GYPP, EPP, RPE, KPR, KPP, 100KW, DTS and LANG in the present germplasm, it is better to practice selection under water stress conditions, but to improve PH and EH, it is better to practice selection for these traits under no stress conditions to obtain higher values of selection gain.

4. CONCLUSIONS

The present study concluded that both additive and non-additive gene effects were significant for the most studied traits. Concerning the magnitude, additive variance was revealed more pronounced than non-additive effect in the inheritance of these traits and therefore selection breeding would be very efficient for improving studied traits under water stress as well as non-stress conditions. On the other hand, additive variance was more affected by seasonal variation than dominance variance for EH and RPE under WW and WS, PH, LANG, KPR and GYPP under WS and KPP and 100KW under WW. Therefore, for the rest of cases, dominance variance was more affected by seasonal variation than additive variance. Under WS, heritability and expected genetic gain from selection were higher than under WW for all studied traits, except PH and EH, where the opposite was true. This experiment expected that to improve GYPP, EPP, RPE, KPR, KPP, 100KW, DTS and LANG traits in the present germplasm, it is better to practice selection under water stress conditions, but to improve PH and EH, it is better to practice selection for these traits under no stress conditions to obtain higher values of selection gain. For GYPP and one or more yield traits under WS, the best inbred lines for GCA effects were Sd-7 and IL-92 and the best crosses for SCA effects were IL171 × Sd7 and IL171 × IL17. These inbred lines and F_1 crosses could be offered to future maize breeding programs for improving drought tolerance at flowering.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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