Numerical and Graphical Diallel Analyses of Maize (*Zea mays* L.) Agronomic and Yield Traits under Well Watering and Water Deficit at Silking

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Authors' contributions

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

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ABSTRACT

The objectives of the present investigation were to determine the type of gene action, heritability and expected genetic advance from selection for agronomic and yield traits of maize under water stress and optimum irrigation and to identify the parents that contain favorable genes for adaptive traits to drought tolerance. Plants from a six-parental diallel cross were grown in the field for two seasons using a randomized complete block design with three replications in two separate experiments; the first under well-watered (WW) conditions and the second under water stress (WS) at silking. Results across seasons showed that variances due to both additive and dominance effects were significant, but the magnitude of dominance was much higher than additive variance for all studied traits under WW and WS, except for ears/plant (EPP) and rows/ear (RPE) under WW. Narrow-sense heritability (h^2_n) was of small magnitude, but ranged from 0.86% (EPP under WS) to 66.67% (EPP under WW). It was observed that 10 out of 12 characters, showed higher h^2_n under WW than that under the WS environment, but only two traits, namely anthesis-silking interval

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(ASI) and barren stalks (BS) exhibited higher estimates of h^2_n under the water stressed environment. The traits ASI, BS, kernels/row (KPR) and kernels/plant (KPP) showed higher expected selection gain under water-stressed than the non-stressed environment, but the remaining traits showed an opposite trend. The inbred parents L20, L53 and Sk5 carried favorable genes for high grain yield and all of its components (except RPE), short ASI and narrow leaf angle (LANG) under WS. These inbreds would be of great value for future plant breeding programs aiming at improving drought tolerance in maize.

1. INTRODUCTION

Water is a basic requirement for plant growth and development. Without water, the plant goes under drought conditions, which severely affects its growth, and ultimately the yield of crops is reduced. Maize (*Zea mays* L.) is considered more susceptible than most other cereals to drought stresses at flowering, when yield losses can be severe through barrenness or reductions in kernels per ear [1]. Thus, developing maize varieties that are tolerant to drought is, considered critical for increasing maize production [2,3]. Knowledge of gene action, heritability and genetic advance from selection is a prerequisite for starting a breeding program for developing drought tolerant varieties of maize.

The manner in which target traits are inherited has, of course, major consequences for the whole breeding strategy. Success of breeders in improving the characteristics of a population depends on the degree of correspondence between phenotypic and genotypic values [4]. A quantitative measure, which provides information about the correspondence between genotypic variance and phenotypic variance, is heritability [5]. The term heritability has been further divided into broad sense and narrow sense, depending whether it refers to the genotypic value or breeding value, respectively [6]. The ratio of genetic variance to phenotypic variance is called heritability in the broad sense or genetic determination. On the other hand, the ratio of additive variance to phenotypic variance is called heritability in the narrow sense. However, the type of gene action involved in the expression of a character has a significant role in determining heritability values. Characters that are controlled largely by genes acting in an additive fashion have higher values of heritability than characters governed by genes with large non- additive effects [5-7]. According to Dabholkar [5], it is important to note that heritability is a property not only of the character being studied, but also the population being sampled and the environmental circumstances to which individuals have been subjected. More variable environmental conditions also reduce the magnitude of heritability while more uniform conditions increase it [8-10].

In addition to predicting response to selection, heritability estimates are used to identify optimum environments for selection [11]. Whether direct or indirect selection is superior depends upon the heritability of the selected trait in stress and non-stress environments and the genetic correlation between stress and non-stress environments [12-14]. However, many investigators reported a decline in heritability for grain yield under stress [8-10]. A number of reports on heritability are available for different traits of maize under drought stress and low N conditions [1,15,16]. They suggested ASI as a highly heritable trait. Bänziger et al. [17] found that broad sense heritability for grain yield under low N was on average 29% smaller than under high N because of lower genotypic variance under low N. In general, standard errors of heritability, genetic correlations, variances, and covariances increase with decreasing heritability [6].

Bänziger and Lafitte [16] concluded that secondary traits are valuable adjuncts in increasing the efficiency of selection for grain yield when broad-sense heritability of grain yield is low. Similarly under three moisture regimes, studies based on S_1 to S_3 progenies in six tropical maize populations indicated increased broad sense heritability with decreased stress for most traits except EPP [1]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [5,7,18,19]. Thus, when planning to improve an adaptive trait to a given stress, priority should be given to estimation of heritability of this trait under targeted environmental conditions. Hallauer and Miranda [19] noted that heritability coefficients, as well as additive genetic correlation, depend on the population under

selection and on environmental conditions. This indicates that the advantage of direct and indirect selection must be investigated for each particular situation as demonstrated earlier. Productivity of the plants in the selection environments and/or a high correlation between yield in the test and the target environments have been used to identify the most appropriate selection environments [14].

Literature review reveals that little research has been directly focused on studying the mode of gene action controlling yield under drought. Several researchers found that additive genetic effects play a major role in conditioning grain yield under drought stress in tropical [20-23] and temperate [24,25] maize germplasm. Response to selection for yield in populations under drought has also been reported [20,21,26-29], suggesting that additive gene action might be important in controlling yield. Derera et al. [22] also found non-additive gene action playing important roles in controlling grain yield under both drought stress and favorable growing environments. Agrama and Moussa [30] 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 for drought tolerance in maize has been reported [1,24,25,31].

The objectives of the present investigation were: (*i*) to determine the type of gene action, heritability and expected genetic advance from selection for drought tolerance adaptive traits of maize under water deficit and optimum watering at flowering and (*ii*) to identify the parents that contain favorable genes for such traits.

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

Based on the results of previous experiments [32] six maize inbred lines in the 8th selfed generation (S_8), showing clear differences in tolerance to water stress, were chosen in this study to be used as parents of diallel crosses (Table 1).

2.2 Generation of F_1 Diallel Crosses

In 2012 season, all possible diallel crosses (except reciprocals) were made among the six parents, so seeds of 15 direct F_1 crosses were obtained. Seeds of the six parents were also increased by selfing in the same season (2012) to obtain enough seeds of the inbreds in the 9th selfed generation (S_9).

2.3 Evaluation of Parents and F_1`s

Two field experiments were carried out in each season of 2013 and 2014. Each experiment included 21 genotypes (15 F_1 crosses and their six parents). The first experiment was done under optimum irrigation by giving all required irrigations, but the second experiment was done under deficit irrigation at flowering by skipping the fourth and fifth irrigations, *i.e.* from age of 57 to 81 days (24 days of drought stress). A randomized complete blocks design with three replications was used in each experiment.

Each experimental plot consisted of one ridge of 4 m long and 0.7 m width, *i.e.* the experimental plot area was 2.8 m^2. Seeds were sown in hills at 20 cm apart, thereafter (before the 1st irrigation, *i.e.* after 21 days from sowing) were thinned to one plant/hill. Sowing date of the experiments was on May5 and May8 in 2013 and 2014

Table 1. Designation, origin and drought tolerance of six inbred lines used for making diallel crosses of this study

Inbred designation	Origin	Institution (country)	Drought tolerance
1. L20-Y	SC 30N11	Pion. Int.Co.- Egypt	Tolerant
2. L53-W	SC 30K8	Pion. Int.Co.- Egypt	Tolerant
3. Sk 5-W	Teplacinco - 5	ARC-Egypt	Tolerant
4. L18-Y	SC 30N11	Pion. Int.Co.- Egypt	Sensitive
5. L28-Y	Pop 59	ARC-Thailand	Sensitive
6. Sd 7-W	A.E.D.	ARC-Egypt	Sensitive

ARC = Agricultural Research Center, Pion. Int. Co. = Pioneer International Company in Egypt, SC = Single cross, A.E.D. = American Early Dent; an old open-pollinated variety, W = White grains and Y = Yellow grains

seasons, respectively. The soil of the experimental site was clayey loam. All other agricultural practices were followed according to the recommendations of ARC, Egypt. The analysis of the experimental soil, as an average of the two growing seasons 2013 and 2014, indicated that the soil was clay loam (4.00% coarse sand, 30.90% fine sand, 31.20% silt, and 33.90% clay), the pH (paste extract) was 7.73, the EC is 1.91 dSm^{-1}, soil bulk density was 1.2 g cm^{-3}, calcium carbonate was 3.47%, organic matter was 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). Meteorological variables in the 2013 and 2014 growing seasons of maize were obtained from the Agro-meteorological Station at Giza, Egypt. For May, June, July and August, mean temperature was 27.87, 29.49, 28.47 and 30.33℃, maximum 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

Days to 50% anthesis (DTA) (as number of days from planting to anthesis of 50% of plants per plot). Anthesis-silking interval (ASI) (as number of days between 50% silking and 50% anthesis of plants per plot). Plant height (PH) (cm) (measured from ground surface to the point of flag leaf insertion for five plants per plots). 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 plots. 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). Leaf angle (LANG) (^{o}) measured as the angle between stem and blade of the leaf just above ear leaf, according to Zadoks et al. [33]. Ears per plant (EPP) calculated by dividing number of ears per plot on number of plants per plot. Rows per ear (RPE) using 10 random ears/plot at harvest. Kernels per row (KPR) using the same 10 random ears/plot. Kernels per plant (KPP) calculated as: number of ears per plant ×

number of rows per ear × number of kernels per row. 100-kernel weight (100-KW) (g) adjusted at 15.5% grain moisture, using shelled grains of each plot. 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 Statistical Analysis

Each environment (WW and WS) was analyzed separately across seasons as RCBD 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. [34].

2.6 Genetic Analyses of F_1 Diallel Crosses

2.6.1 Hayman's numerical approach

The genetic parameters and ratios were calculated according to methods developed by Jinks and Hayman [35], Jinks [36] and Hayman [37,38] and described by Sharma [39]. The variance and covariance statistics across replications were used to obtain estimates of the components of variation and their respective standard errors. The validity of the assumptions of diallel analysis was tested by the following formula [39]: $t^2=\{(n-2)/4[(MSS(Vr)-(MSS(Wr)]^2/\{MSS(Vr)x[MSS(Wr)-MSP(Wr.Vr)^2]\}$ Where: Wr = covariance between parents and their off-spring and Vr = variance of each array in which a particular parent is involved. Significance of calculated ''t'' value was tested against the tabulated "t" value with 4 and (n-2) degrees of freedom. Significant values indicated failure of the assumptions [37,38]. Another test was done by estimating the regression coefficient ''bWr.Vr'' of Wr on Vr as follows: $b_{Wr.Vr=}[cov(Wr.Vr)/var Vr]=[MSP(Wr.Vr)/MSS(Vr)]$. The standard error (SE) for the regression coefficient (b) value was estimated as follows: $SE_b=[MSS(Wr)-bMSP(Wr.Vr)(n-2)]^{1/2}$ Where: n = number of parents. The significance of (b) different from zero (t_1) and from unity (=1) (t_2) was tested by t-test as follows: $t_1 = (b-0)/SEb$ and $t_2 = (1-b)/SEb$. The foregoing values were tested against the ''t'' tabulated value for (n-2) degrees of freedom according to Jinks and Hayman [35]. If all the assumptions were valid, the regression coefficient would be significantly different from zero but not from unity. Hayman [37,38] derived the expectations for the statistics calculated from the F_1 diallel table and the expected values of the

component variations using least squares. The notations of Mather and Jinks [40] were used and described as follows: V_{0L0} (V_p) (variance of the parents) = $D + \hat{E}$, $V_{1L1}(V_r)$(mean of all the V_r values) = ¼ D - ¼ F + ¼ H_1 + ¼ H_2 + [$\hat{E} + \hat{E}$ (n-2)/2n2], Vr (variance of all the progenies in each parental array) = ¼ D + ¼ H_1- ¼ H_2 - ¼ F + (n+1)/2n_2 $\hat{E}$,W_{0L01}(Wr) (mean of all the Wr. values)= ½ D - ¼ F + $\hat{E}$/n, $(M_{L1} - M_{L0})^2$ = dominance relationship = ¼ h^2 + [(n -1) $\hat{E}/n^2$)]. The components of $\hat{E}$, D, H_1, H_2, h^2 and F were estimated in F_1 as follows: $\hat{E}$ = [(Errors S.S. + Reps S.S.)/r]/[(r-1) + (c-1) (r-1)]. D = $V_{0L0} - \hat{E}$. F = 2 V_{0L0} - 4W_{0L01} - [2$\hat{E}$ (n-2)/n]. H_1 = V_{0L0} + 4 V_{0L1} - 4W_{0L01} - [$\hat{E}$ (3n-2)/n]. H_2 = 4 V_{1L1} - 4 $V0_{L1}$ - 2$\hat{E}$. h^2 = 4$(M_{L1} - M_{L0})^2$ - [4$\hat{E}$ (n-1)/n^2]. Where n = number of parents. $\hat{E}$ = expected environmental component of variance. D = variance due to additive effects of the genes. F = mean of the covariance of additive and dominance effects across all arrays. H_1= variance component due to dominance deviation. $H_{1=}[1-(u-v)^2]$, where, u and v are the proportions of positive and negative genes, respectively in the parents. h^2= algebraic sum of dominance effects across all loci in heterozygous phase in all crosses. The following genetic parameters were also calculated: Average degree of dominance was estimated as $(H_1/D)^{1/2}$. 1. If this ratio is zero, there is no dominance. 2. If it is greater than zero, but less than one, there is partial dominance. 3. If it is equal to 1, there is complete dominance. 4. If it is greater than 1, it indicates over dominance. Ratio of dominant and recessive genes in the parents (K_D/K_R) was estimated as follows: K_D/K_R = [$(4DH_1)^{1/2}$+ F]/[(4 $DH_1)^{1/2}$ - F] If K_D/K_R ≈1.0, it means nearly equal proportion of dominance and recessive alleles in parents, *i.e.* symmetrical distribution; p = q = 0.5. Any deviation from 1.0 indicated asymmetry of distribution (p # q). Thus: Ratio > 1 refers to excess of dominant alleles and minority of recessive alleles (p > q). Ratio < 1 means minority of dominant alleles and excess of recessive alleles (p < q). The ratio of dominant genes with positive or negative effects in parents $(H_2/4H_1)$ was determined. The maximum theoretical value of 0.25 for this ratio arises when, p = q = 0.5 at all loci. A deviation from 0.25 would stem when p ≠ q. Thus: if this ratio ≈ 0.25, it means symmetrical distribution of positive and negative dominant genes in parents, while if this ratio ≠ 0.25, it means asymmetry of distribution. Narrow-sense heritability (h^2n) was estimated using the following equation: h^2_n = [1/4D / (1/4D + 1/4H_1– 1/4F + $\hat{E}$]. The expected genetic advance (GA) from direct selection as a percentage of the mean (x) was calculated

according to Singh and Narayanan [41] based on 10% selection intensity as follows: GA = 100[(k.h^2_n δ_{ph})/x] Where: k = 1.76 (selection differential for 10% selection intensity), and δ_{ph}= square root of the dominator of the narrow sense heritability.

2.6.2 V_r-W_r graphs

Based on parental variance (V_r) and parent-offspring co-variance (W_r) relationships diallel cross progenies, a two-way representation of parental arrays along a regression line of W_r on V_r was first suggested by Jinks and Hayman [35] and later refined by Hayman [37]. This two directional depiction is widely known as the W_r - V_r graph. For drawing the regression line, the expected W_{rei} values were calculated as follows: $W_{rei} = W_r - b\overline{V}_r + b \overline{V}_{ri}$, where: W_r is array mean of variances, V_r= array mean of covariance and b= regression coefficient. The regression line was drawn by plotting W_{rei} against V_r values. The point of interception of the regression line with W_r ordinate, *i.e.*, (a) was obtained by the following equation: a = $\overline{W}_r$ - b $\overline{V}$r.

3. RESULTS AND DISCUSSION

3.1 Genetic Variances and Ratios, Heritability and Selection Gain

Estimates of genetic variances and ratios for studied traits under the two environments across two years are presented in Table (2). The dominance genetic component of variation (H_1) was significant (P ≥0.05 or 0.01) for all studied traits under both environments, except for BS and EPP under WW. The additive component of variation (D) was also significant (P ≥0.05 or 0.01) for all studied characters under WW and WS environments, except for BS, PH, EH and EPP under WS and ASI and BS under WW, where additive variance was not significant. This indicated that selection may be used in maize populations for improving such traits, where significant additive variance existed under respective environments [42-45].

The estimates of dominance were much higher, in magnitude, than additive variance (where the ratio D/H_1 is < 1) for all studied traits under WW and WS, except for EPP and RPE under WW (22 out of 24 cases), suggesting that dominance variance played a major role in the inheritance of these traits in most cases and that heterosis breeding would be more efficient than selection

for improving studied traits under all environments. Derera et al. [22] also found non-additive gene action playing important roles in controlling grain yield under both drought stress and favorable growing environments. For adaptive traits to abiotic stress tolerance, many investigators reported greater importance of dominance than additive variance [45-50].

The overall dominance effects of heterozygous loci in Hayman's model (h^2) controlling all studied traits under all environments, except BS under both environments, ASI under WS, LANG under WW, EPP under WW and WS were highly significant, that could be due to the presence of a considerable amount of dominant genes in the parental genotypes.

Average degree of dominance $(H_1/D)^{1/2}$ was greater than unity for all studied traits under all environments (except for EPP under WW), indicating that the degree of dominance in most cases was over dominance. The highest $(H_1/D)^{1/2}$ value was recorded in WW (EPP) and WS (GYPP and RPE).

The ratio $(H_2/4H_1)$ indicated a symmetrical distribution of positive and negative dominant genes in parents in all studied characters under WW and WS environments, where $H_2/4H_1$ was ≤ 0.25.

The ratio (K_D/K_R) was more than unity, indicating excess of dominant alleles and minority of recessive alleles (p > q) for most studied cases (74 out of 120 cases). The exceptions were KPR and LANG under WS, and RPE under WW, where the ratio (K_D/K_R) was less than unity, indicating minority of dominant alleles and the excess of recessive alleles (p < q) and GYPP trait under WS, where K_D/K_R was unity, indicating equal proportion of dominance and recessive alleles in parents, *i.e.,* symmetrical distribution (p = q = 0.5).

Broad-sense heritability (h^2_b) was of high magnitude (greater than 90%) for eight traits (DTA, PH, EH, LANG, RPE, KPP, 100 KW and GYPP) out of 12 studied traits under WW and WS environments, indicating that the environment had small effect on the phenotype of these traits. The lowest estimates of h^2_b were shown by BS (48.48% under WW) and ASI (69.23% under WS), indicating that the environment and genotype × environment interaction had considerable effects on the phenotype for these traits.

Narrow-sense heritability (h^2_n) was generally of small magnitude and ranged from 0.86% to 66.67%. The lowest h^2_n was recorded for EPP under WS and ASI (3.45%) under WW. The highest h^2_n was recorded for EPP (66.67%) under WW followed by RPE (64.88%) under WW. It was observed that 10 out of 12 characters, showed higher h^2_n under WW than that under WS environment, but only two traits, namely ASI and BS exhibited higher estimates of h^2_n under the water stressed environment. The big difference between broad and narrow sense heritability in this experiment could be attributed to the high estimates of dominance, dominance × dominance and dominance × additive components.

In general, our results are in agreement with those reported by some researchers [10,12,16,17,51] who suggested that heritability is higher under good (non-stressed) environments. But these results are in disagreement with other investigators [8,9,50,52-54], who suggested the idea that heritability is higher under stressed than non-stressed environments.

Expected genetic advance (GA) from selection (based on 10% selection intensity) across years for studied traits in WW and WS environments (Table 2) was generally of small magnitude and ranged from 0.19 to 77.33%. The highest expected genetic gain from selection was recorded for KPR under WS followed by LANG under WW (24.42%). In general, four traits (ASI, BS, KPR and KPP) showed higher GA% under water-stressed than non-stressed environment, while the remaining eight traits showed opposite trend. Thus, based on the present results, it is recommended to practice selection for improving ASI, BS, KPR and KPP traits under a water stressed environment, but for the remaining studied traits, it is better to practice selection under optimum irrigation in order to obtain higher genetic advance from selection.

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. Many researchers found that heritability and GA from selection for grain yield is higher under non-stress than those under stress [10,12,16,17,51]. However, other investigators reported that heritability and expected GA for the same trait is higher under stress than non-stress, and that selection should be practiced in the target environment to obtain higher genetic advance [8,9,50,52-54].

Table 2. Estimates of genetic parameters and ratios for studied traits under well watering (WW) and water stress (WS) conditions across two seasons

Genetic parameter	WW	WS	WW	WS	WW	WS	WW	WS
	Days to 50% anthesis		Anthesis-silking interval		Plant height		Ear height	
D	4.42**	4.37**	0.01	0.04**	465.70*	132.90	227.59*	131.30
H_1	7.95**	12.20**	0.22*	0.14**	3096.5**	3021**	1395.34**	1214.6**
H_2	6.44**	9.43**	0.18*	0.10**	2527.5**	2843**	1066.2**	1018.3**
h^2	18.55**	26.13**	0.64**	0.01	6887.95**	10774 **	2458.41**	3028.8**
E	0.20	0.14	0.06**	0.08**	11.59	9.02	6.86	5.38
F	4.52	6.11*	0.03	0.00	946.94	288.80	504.32	288.30
D/H_1	0.56	0.36	0.05	0.29	0.15	0.04	0.16	0.11
$(H_1/D)^{1/2}$	1.34	1.67	3.97**	1.91	2.58	4.77	2.48	3.04
$H_2/4H_1$	0.20	0.19	0.21	0.18	0.20	0.24	0.19	0.21
K_D/K_R	2.23	2.44	48.53	2.57	2.30	1.59	2.62	2.13
$h^2_b\%$	93.22	96.95	79.31	69.23	97.50	95.36	97.95	98.01
$h^2_n\%$	35.16	26.15	3.45	15.38	13.03	4.20	13.96	9.72
GA%	3.63	3.03	1.39	4.83	5.94	1.88	10.16	6.69
	Barren stalks		Leaf angle		Ears per plant		Rows per ear	
D	0.23	2.93	30.90**	11.40**	0.01**	0.00	1.711**	1.27**
H_1	2.80	23.10**	32.62**	32.55**	0.001	0.02*	0.763*	1.56**
H_2	0.60	15.99**	21.55**	28.63**	0.00	0.01	0.805*	1.30**
h^2	0.00	0.00	6.89	45.26**	0.00	0.01	0.804**	1.35**
E	3.22**	6.18**	0.96	0.82**	0.003**	0.003*	0.163**	0.18**
F	1.32	-0.32	18.34*	-2.42*	-0.01	0.01	-0.03	0.35
D/H1	0.08	0.13	0.95	0.35	5.00	0.01	2.24	0.81
$(H_1/D)^{1/2}$	3.49	2.81	1.03	1.69	0.43	9.75	5.22	1.11
$H_2/4H_1$	0.05	0.17	0.19	0.22	0.00	0.18	0.15	0.21
K_D/K_R	10.12	0.96	1.81	0.88	15.70	7.03	0.98	1.29
$h^2_b\%$	48.48	80.81	91.77	92.85	80.00	87.07	93.82	94.02
$h^2_n\%$	3.68	9.10	47.92	25.46	66.67	0.86	64.88	42.19
GA%	1.62	7.20	24.42	9.88	11.68	0.19	12.76	9.26

Genetic parameter	WW	WS	WW	WS	WW	WS	WW	WS
	Days to 50% anthesis		**Anthesis-silking interval**		**Plant height**		**Ear height**	
	Kernels per row		**Kernels per plant**		**100-kernel wt**		**Grain yield per plant**	
D	28.75**	1950.72**	11792**	13438**	16.41**	10.05**	1274*	694**
H_1	113.04**	8434.18**	41828**	64702**	29.66**	24.21**	15757**	13385**
H_2	111.62**	6681.15**	42376**	61508**	28.44**	21.83**	15658**	13184**
h^2	413.06**	818.42**	164438**	203012**	94.47**	48.40**	60876**	47901**
E	0.84	1978.00**	1517*	1.07	0.67	0.66	0.06	0.05
F	11.12	2621.69**	827.00	3526.33	8.76	5.58	418.00	14.29
D/H_1	0.25	0.23	0.28	0.21	0.55	0.42	0.08	0.05
$(H_1/D)^{1/2}$	1.98	2.08	1.88	2.19	1.30	1.55	3.52	4.39
$H_2/4H_1$	0.25	0.20	0.25	0.24	0.24	0.23	0.25	0.25
K_D/K_R	1.22	0.51	1.04	1.13	1.50	1.44	1.10	1.00
$h^2_b\%$	99.41	84.00	96.53	97.37	98.57	98.11	99.22	99.31
$h^2_n\%$	20.16	15.78	21.39	17.20	35.11	28.78	7.48	4.93
GA%	9.89	77.33	11.55	12.65	12.31	9.53	9.22	7.42

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

3.2 Graphical Diallel Analysis

The graphical analysis of diallel crosses proposed by Hayman [37,38] will be illustrated on the following bases according to Singh and Narayanan [41]: (1) The parabola marks the limits within which the variance-covariance points (V_r, W_r) should lie, (2) If the regression coefficient (b) of (V_r, W_r) is not different from unity, the genetic control system may be deduced to be additive without the complications of gene interactions, (3) Complementary gene effects (epistasis) generally reduce the covariance (W_r) disproportionally more than the variance (V_r) causing the slope of the regression line (b) to be less than unity, (4) When dominance is complete, the regression line with b = 1 would pass through the origin, (5) Over dominance causes the regression line to intercept the (W_r) axis below the origin, while partial dominance causes the regression line to intercept the (W_r) axis above the origin point, (6) The closeness of the regression line or (V_r, W_r) points to the limiting parabola indicates little dominance and (7) The order of the array points on the regression line is a good indicator of the dominance order of parents. The parents with more dominant genes are located nearer to the origin, while those with more recessive genes fall farther from the origin. The parents with equal frequencies of dominant and recessive genes occupy an intermediate position.

Based on the above information, in the F_1 diallel Hayman's approach, it is clear from (Figs. 1 to 12) for 12 studied traits under non-stressed and water stressed environments, that the regression line intercepted the Wr-axis below the origin, *i.e.* cutting the Wr-axis in the negative region (intercept= a < 0 (negative) or D (additive variance) < H_1 (dominance variance), indicating the presence of over-dominance for most studied cases. The regression line passed through the origin (D=H_1), indicating complete dominance for ASI under WW (Fig. 2), EPP under WS (Fig. 7). For ASI under WS (Fig. 2), BS under WS (Fig. 5), RPE under WS (Fig. 8), EPP under WW and WS (Fig. 7), the regression line intercepted the Wr-axis above the origin (D> H_1), indicating partial dominance and the predominance of additive variance in these cases.

The dispersion of parents (1 = L20, 2 = L53, 3 = Sk5, 4 = L18, 5 = L28 and 6 = Sd7) around the regression line for days to anthesis (DTA) under no stress (Fig. 1-WW) showed that, parents 3, 1 and 5 were close to the origin of the coordinate, and accordingly had more dominant genes; with L20 was the nearest parent to the origin (contained more than 75% dominant genes), while parents 2, 4 and 6 had mostly recessive genes. For DTA under WS environment (water stressed) (Fig. 1-WS), parents 1 and 5 were very close to the origin, indicating that they contained > 75% dominant genes, parents 3, 4 and 6 contain 50-75% dominant genes and parent 2 mostly contained recessive genes.

For anthesis- silking interval (ASI) under no stress (Fig. 2-WW), the dispersion of parents
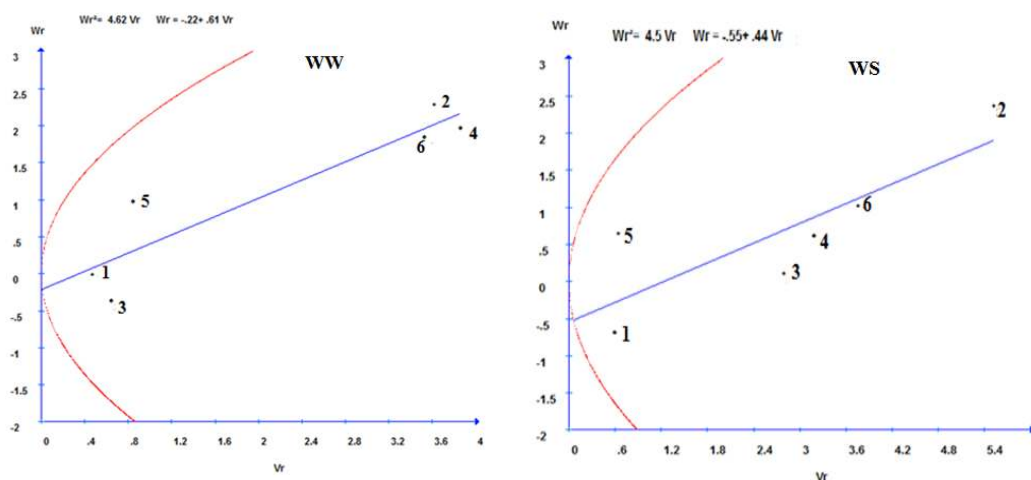

Fig. 1. Wr-Vr graph of days to anthesis (DTA) of F_1's for combined data across two seasons under well watering (WW) and water stress (WS) conditions
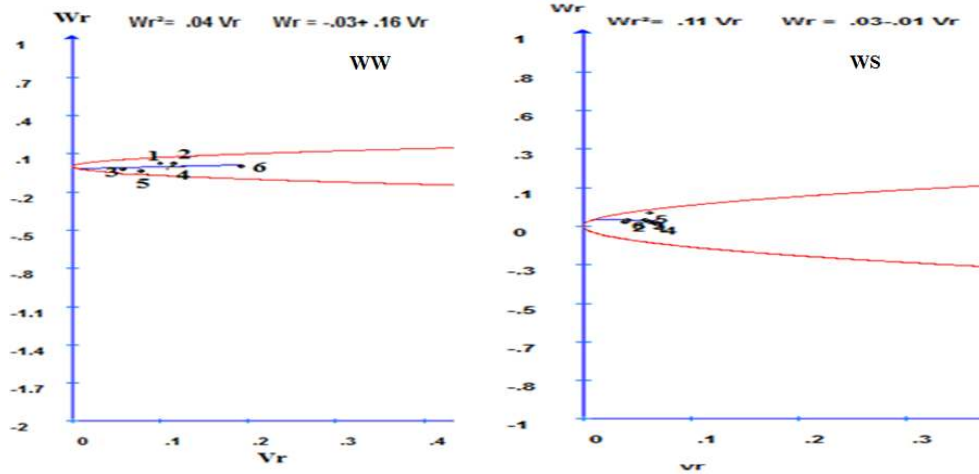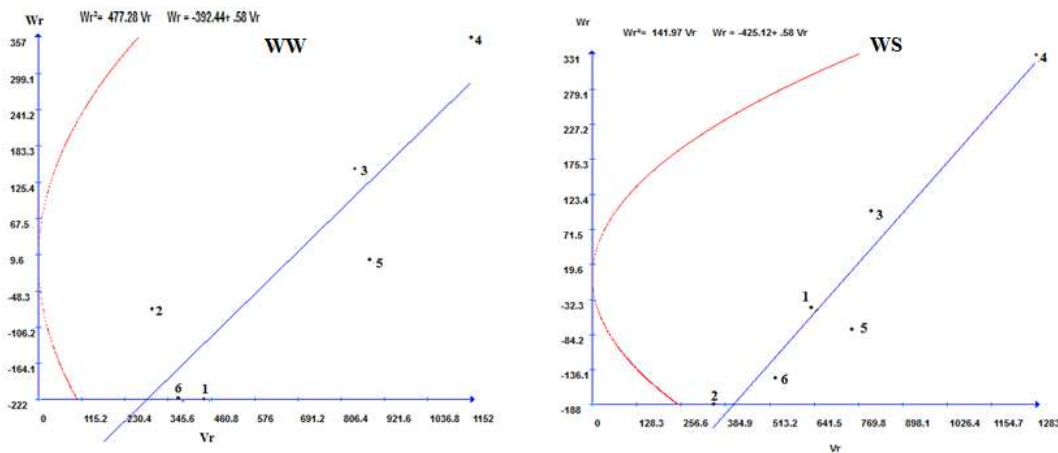
Fig. 2. Wr-Vr graph of anthesis silking interval (ASI) of F_1's for combined data across two seasons under well watering (WW) and water stress (WS) conditions

around the regression line revealed that parents 3 and 5 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 2, 3 and 4 had 50% dominant genes, while parent 6 is far from the origin and therefore has < 25% of dominant genes. Under the water stressed environment (Fig. 2-WS), all the parents were close to each other, with parent 2 being the closest to the origin (had the highest percentage of dominant genes) and parent 4 was the farthest (had the lowest percentage of dominant genes).

For plant height (PH) under non-stressed environment (Fig. 3-WW), the dispersion of

parents around the regression line revealed that parents 2, 6 and 1 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, the parents 3 and 5 have 50% dominant genes, while parent 4 was far from the origin and therefore had < 25% of dominant genes. Under the water stressed environment (Fig. 3-WS), parents 2 and 6 were close to the origin, i.e. contained >75% dominant genes, parents 1, 5 and 3 had 50-75% dominant genes, but parent 4 was far from the origin, i.e. contained mostly recessive genes for PH.

For ear height (EH) under the non-stressed environment (Fig. 4-WW), the dispersion of

Fig. 3. Wr-Vr graph of plant height (PH) of F_1's for combined data across two seasons under well watering (WW) and water stress (WS) conditions
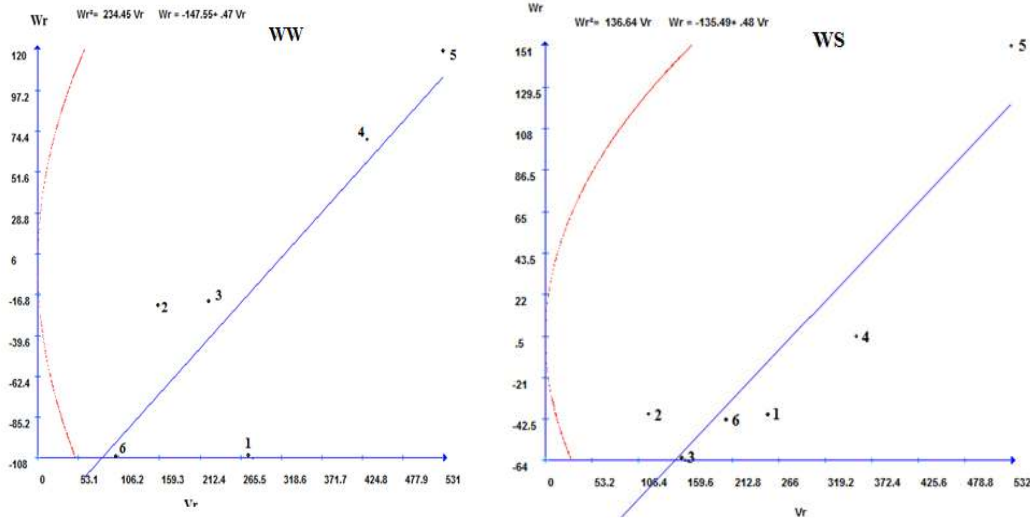
10

Fig. 4. Wr-Vr graph of ear height (EH) of F$_1$'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions

parents around the regression line revealed that parents 6 and 1 were close to the origin of the coordinate, and accordingly had > 75% of the dominant genes, parents 2 and 3 had 50% dominant genes, while parents 4 and 5 were far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 4-WS), parents 2, 3, 1 and 6 were close to the origin, i.e. contained >75% dominant genes, parent 4 had 50-75% dominant genes, and parent 5 was far from the origin, *i.e.*it contained mostly recessive genes for EH.

For barren stalks (BS) under the non-stressed environment (Fig. 5-WW), the dispersion of parents around the regression line revealed that parents 3, 6, 1 and 4 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parent 2 had 50% dominant genes, while parent 5 was far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 5-WS), parents 3 and 6 were close to the origin, *i.e.* contained >75% dominant genes, parents 1 and 2 had 50-75% dominant genes, and parents 4 and 5 were far from the origin, *i.e.* contained mostly recessive genes for BS.
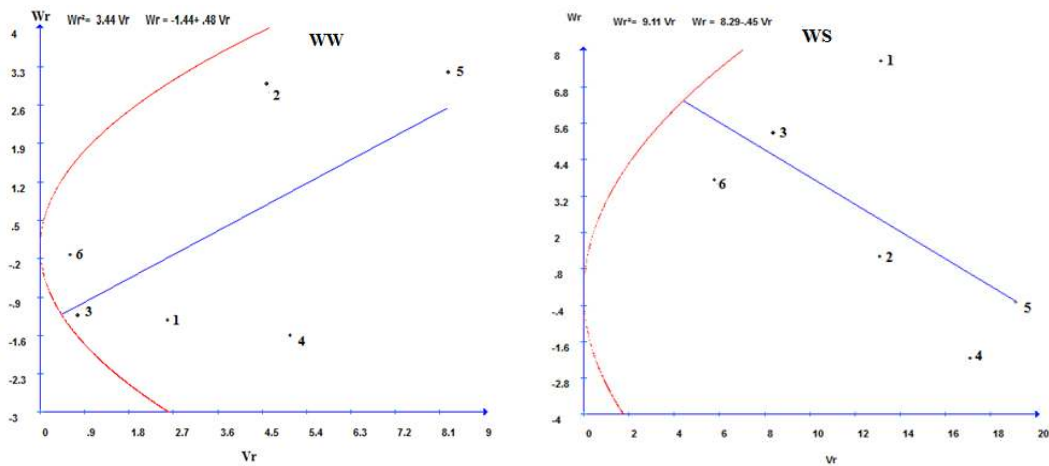

Fig. 5. Wr-Vr graph of barren stalks (BS) of F$_1$'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions
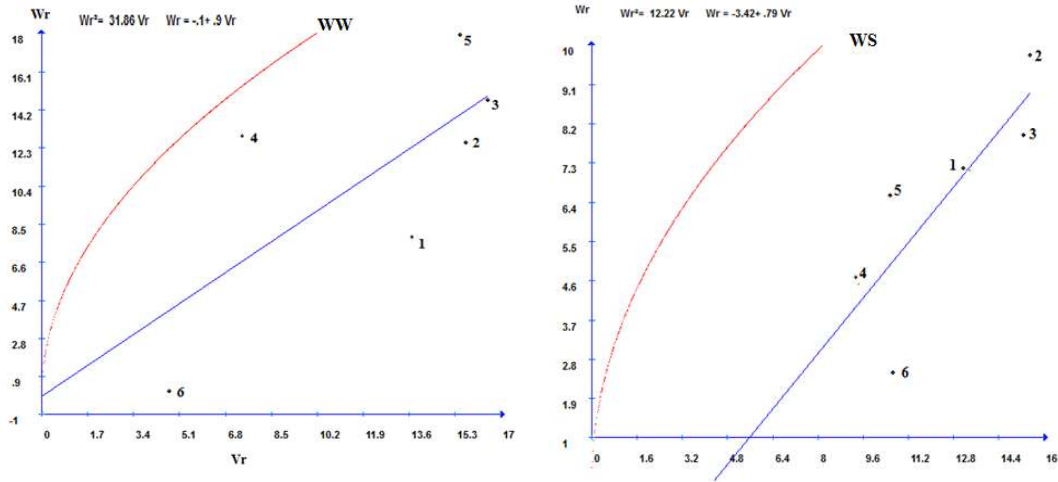
Fig. 6. Wr-Vr graph of leaf angle (LANG) of F_1's for combined data across two seasons under well watering (WW) and water stress (WS) conditions

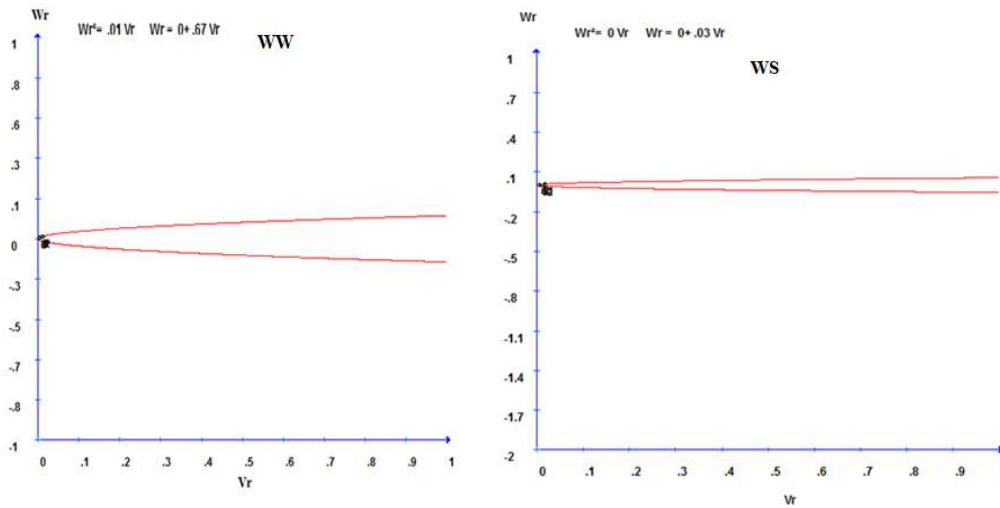**Fig. 7. Wr-Vr graph of ears per plant (EPP) of F_1's for combined data across two seasons under well watering (WW) and water stress (WS) conditions**

For leaf angle (LANG) under the non-stressed environment (Fig. 6-WW), the dispersion of parents around the regression line revealed that parent 6 was close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 1 and 4 had 50% dominant genes, while parents 2, 3 and 5 were far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 6-WS), parent 6 was close to the origin, *i.e.* contained >75% dominant genes, parents 4 and 5 had 50-75% dominant genes, and parents 1, 3 and 2 were far from the origin, *i.e.* contained mostly recessive genes for LANG.

For ears/plant (EPP) under both environments (Fig. 7), there was no dispersion of parents around the regression line. They were assembled in one point very close to the origin of the coordinate. The partial dominance (additive) and complementary gene effects (epistasis) may play roles in inheritance of this trait.

For rows per ear (RPE) under the non-stressed environment (Fig. 8-WW), the dispersion of parents around the regression line revealed that parents 3 and 6 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 1, 4 and 2 had 50%
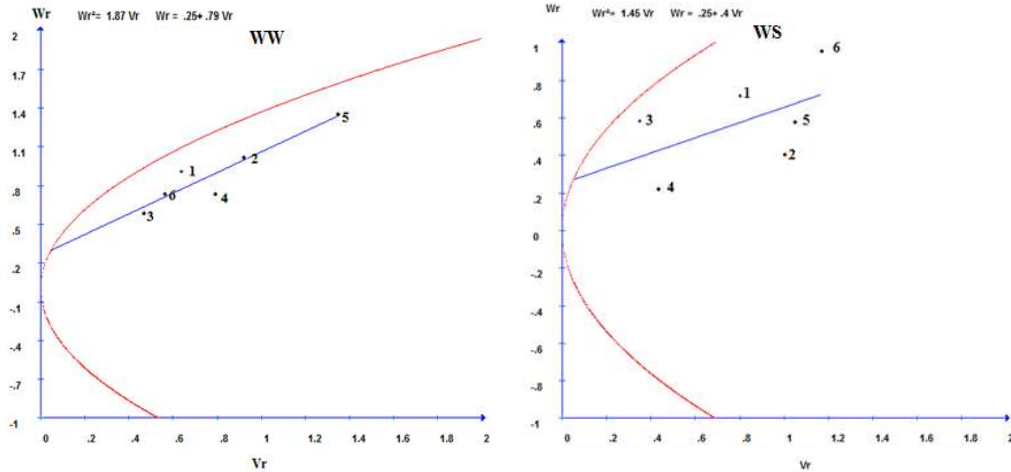
Fig. 8. Wr-Vr graph of rows per ear (RPE) of F₁'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions

dominant genes, while parent 5 was far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 8-WS), parents 3 and 4 were close to the origin, *i.e.* contained >75% dominant genes, parents 1, 2 and 5 had 50-75% dominant genes, and parent 6 was far from the origin, *i.e.* contained mostly recessive genes for RPE.

For kernels per row (KPR) under the non-stressed environment (Fig. 9-WW), the dispersion of parents around the regression line revealed that parent 6 2 was close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 1, 3, 4 and 6 had 50%

dominant genes, while parent 5 was far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 9-WS), parent 2 was close to the origin, *i.e.* contained >75% dominant genes, parents 1, 3 and 4 had 50-75% dominant genes, and parents 5 and 6 were far from the origin, *i.e.* contained mostly recessive genes for KPR.

For kernels per plant (KPP) under the non-stressed environment (Fig. 10-WW), the dispersion of parents around the regression line revealed that parents 2, 1 and 3 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents
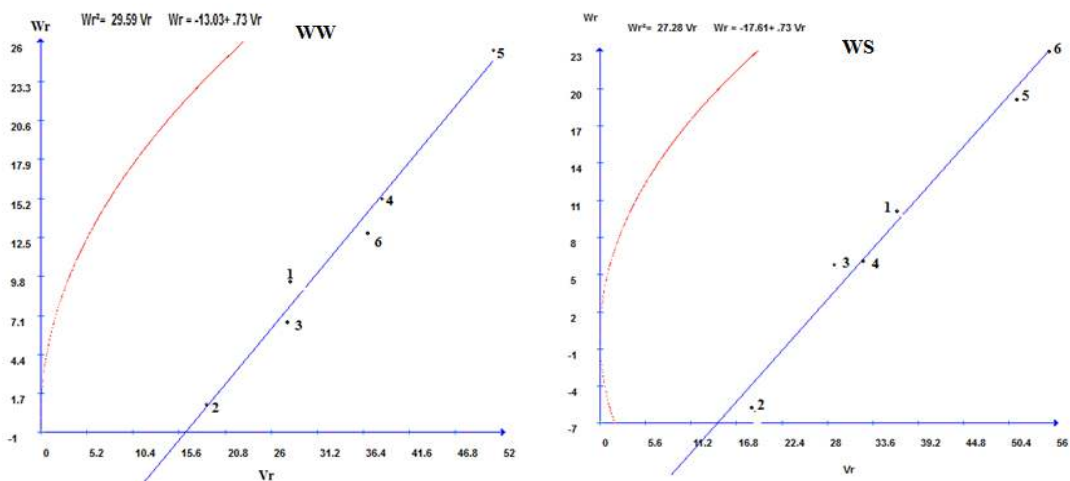

Fig. 9. Wr-Vr graph of kernels per row (KPR) of F₁'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions
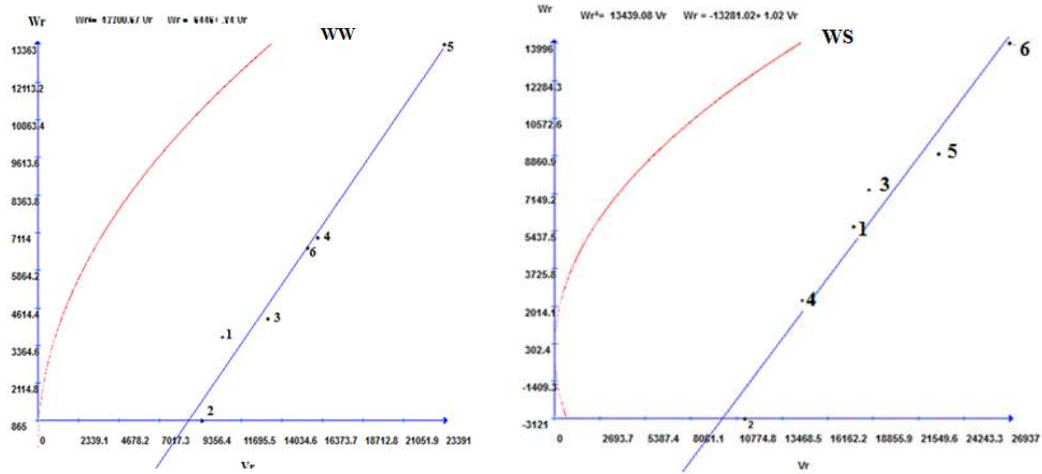
13

Fig. 10. Wr-Vr graph of kernels per plant (KPP) of F$_1$'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions

4 and 6 had 50% dominant genes, while parent 5 was far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 10-WS), parent 2 was close to the origin, *i.e.* contained >75% dominant genes, parents 1, 3 and 4 had 50-75% dominant genes, and parents 5 and 6 were far from the origin *i.e.* contained mostly recessive genes for KPP.

For 100-kernel weight (100 KW) under the non-stressed environment (Fig. 11-WW), the dispersion of parents around the regression line revealed that parents 3, 1 and 2 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 4 and 6 had

50% dominant genes, while parent 5 was far from the origin and therefore had mostly recessive genes. Under the water stressed environment (Fig. 11-WS), parents 2,4, 3 and 1 were close to the origin, *i.e.* contained >75% dominant genes, and parents 5 and 6 were far from the origin, *i.e.* contained mostly recessive genes for 100 KW.

For grain yield per plant (GYPP) under the non-stressed environment (Fig. 12-WW), the dispersion of parents around the regression line revealed that parents 2, 1 and 3 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 4, 5 and 6 were far from the origin and therefore had mostly
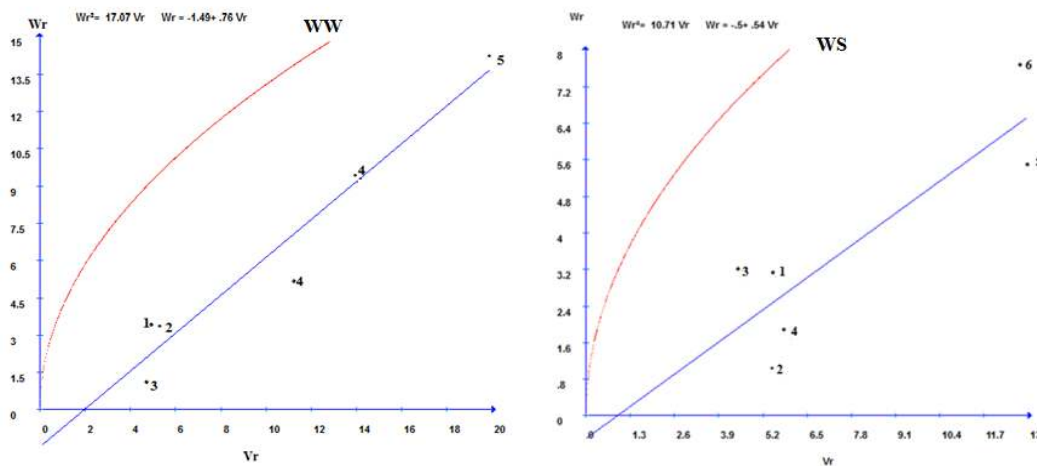

Fig. 11. Wr-Vr graph of 100-kernel weight (100-KW) of F$_1$'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions
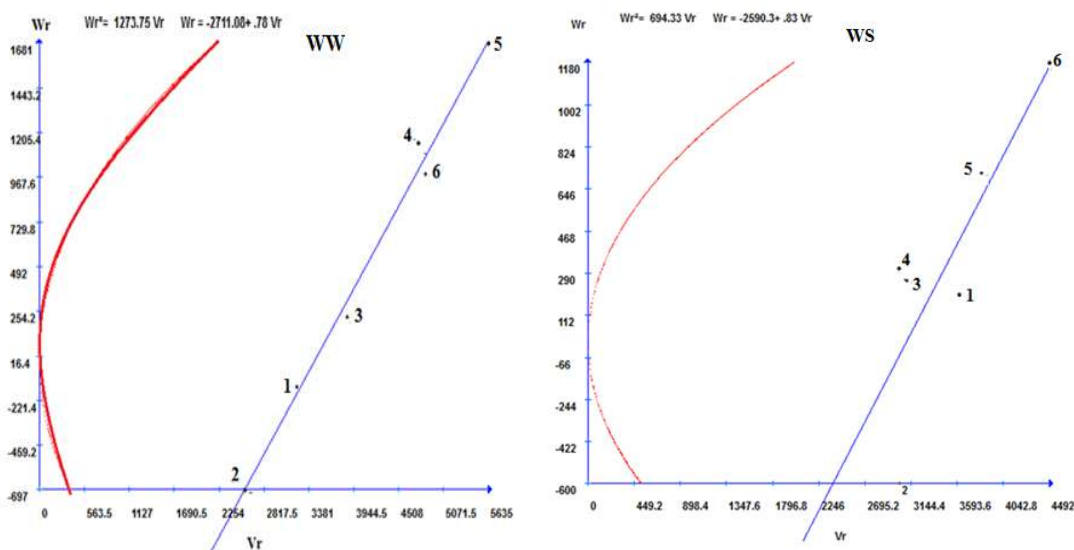
14

Fig. 12. Wr-Vr graph of grain yield per plant (GYPP) of F₁'s for combined data across two seasons under well watering (WW) and water stress (WS) conditions

recessive genes. Under the water stressed environment (Fig. 12-WS), parent 2 was close to the origin, *i.e.* contained >75% dominant genes, parents 1, 3 and 4 had 50-75% dominant genes, and parents 5 and 6 were far from the origin, *i.e.* contained mostly recessive genes for GYPP.

3.2.1 Characterization of parental inbreds for favorable genes

The following description of genes (dominant *vs*. recessive) controlling the studied characters present in the parental inbreds of the F₁ hybrids is based on Hayman's graphical approach [37,38], and on the suggestion that genes that cause favorable increases in the performance of the trait, such as grain yield and yield components are dominant, and those that cause favorable decreases in the trait performance, such as DTA, ASI, PH, EH, BS and LANG are recessive in nature [55].

3.2.1.1 Inbred line L20

Inbred line L20 contained 75-100% dominant genes (favorable) conferring high values for all yield traits (except RPE) under both environments, 50-75% dominant genes for most studied yield traits under the non-stressed (WW) and water stressed environments (WS). It also contained recessive genes (favorable) conferring short ASI under water stress. It contained 50% recessive genes of LANG (favorable) under WW.

3.2.1.2 Inbred line L53

Inbred line L53 contained 75-100% dominant genes (favorable) conferring high values for all yield traits (except RPE) under both WW and WS environments. It also contained recessive genes (favorable) conferring small ASI trait under water stress and non-stress.

3.2.1.3 Inbred line Sk5

Inbred line Sk5 contained 75-100% dominant genes (favorable) conferring high values for all yield traits (including RPE) under WW and WS environments. It also contained mostly recessive genes (favorable) conferring small LANG under stressed and non-stressed environments.

3.2.1.4 Inbred line L18

Inbred line L18 contained 75-100% recessive genes (favorable) for DTA under WW environment. It contained 75-100% recessive genes for plant (PH) and ear (EH) height (favorable in our case) in both environments.

3.2.1.5 Inbred line L28

Inbred line L28 contained mostly recessive genes for LANG (favorable) under the WW environment and BS under both environments. It contained 75-100% recessive genes for plant (PH) and ear (EH) height (favorable in our case) in both environments.

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3.2.1.6 Inbred line Sd7

Inbred line Sd7 contained 75-100% dominant genes for RPE (favorable) under WW and WS environments. It contained mostly recessive genes (favorable) for ASI and DTA under WW and WS.

4. CONCLUSIONS

The present study suggested that heterosis breeding would be more efficient than selection for improving most studied traits under WW and WS environments. Based on the present results, it is recommended to practice selection for improving ASI, BS, KPR and KPP traits under water stressed environment, but for the remaining studied traits, it is better to practice selection under optimum irrigation in order to obtain higher genetic advance from selection. This study managed to characterize the six inbred parents with respect of favorable genes for adaptive traits to drought tolerance. The inbred parents L20, L53 and Sk5 carried favorable genes for high grain yield and all of its components (except RPE), short ASI and narrow leaf angle (LANG) under WS. The inbreds L18 and L28 carried genes of short PH, low EH and low BS under WW and WS. The inbred Sd7 carried favorable genes for high number of RPE and low ASI and DTA under WW and WS. This characterization would be fruitful for future plant breeding programs aiming at improving drought tolerance in maize.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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