



Genetic Variance, Heritability and Selection Gain of Maize (*Zea mays* L.) Adaptive Traits to High Plant Density Combined with Water Stress

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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 analyses. All authors read and approved the final manuscript.

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ABSTRACT

The objectives of the present investigation were to determine genetic variance components, heritability and expected genetic advance from selection for agronomic traits of maize under water stress at flowering combined with high plant density; 95,200 plants/ha (WS-HD) as compared with well watering combined with low density; 47,600 plants/ha (WW-LD). Diallel crosses among 6 inbred lines differing in tolerance to both stresses were grown in the field for two seasons using a RCBD design with three replications in two separate experiments; the first under WW-LD and the second under WS-HD. Results across seasons showed that variances due to both additive and dominance were significant, but the magnitude of dominance was much higher than additive variance for all studied traits under WW-LD and WS-HD, except for ears/plant (EPP) and rows/ear (RPE). Narrow-sense heritability (h^2_n) was the lowest in barren stalks (BS) (3.68 and 4.09%), and the highest in EPP (66.67 and 68.75%) under WW-LD and WS-HD, respectively. The degree of dominance in most cases was over dominance. The estimate of h^2_n was higher under WW-LD than WS-HD for days to anthesis (DTA), plant height (PH), ear height (EH), RPE, kernels/plant (KPP)

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and grain yield/plant (GYPP), but were higher under WS-HD than WW-LD for the remaining traits. The non-stressed environment showed higher estimates of genetic advance from selection (GA%) than the stressed one for DTA, PH, EH, BS, KPP and GYPP, but the opposite was true for the remaining traits. The inbreds L20 and L53 carries 75-100% of genes of high yield and its components (except RPE) and genes of short ASI and narrow LANG. Genes of the adaptive traits to stresses (for low PH and low EH) existed in the inbreds L18 and L28. Genes conferring earliness (DTA) existed in L18 and those conferring low BS existed in L28.

Keywords: Inheritance; drought; high density; diallel analysis.

1. INTRODUCTION

Maize (*Zea mays* L.) grain yield per land unit area could be maximized via growing hybrids that can withstand high plant density up to 100,000 plants/ha under elevated plant density [1]. Egyptian maize hybrids selected under low plant density (ca 50,000 plants/ha) are not tolerant to elevated density and therefore are subject to yield losses when grown under high plant density. Thus, grain yield from unit area cannot be increased by increasing plant density using the present Egyptian cultivars.

In the USA, average maize grain yield per land unit area increased dramatically during the second half of the 20th century, due to improvement in crop management practices and greater tolerance of modern hybrids to high plant densities [2-4]. Modern maize hybrids in developed countries are characterized with high yielding ability from land unit area under high plant densities, due to their morphological and phenological adaptability traits, such as early silking, short anthesis silking interval (ASI), less barren stalks (BS) and prolificacy [5]. Radenovic et al. [6] pointed out that maize genotypes with erect leaves are very desirable for increasing the population density due to better light interception.

To increase maize grain yield per land unit area in Egypt, breeding programs should be directed towards the development of inbreds and hybrids characterized with adaptive traits to high plant density tolerance. The nature of inheritance of such traits should be studied. Literature on inheritance of adaptive traits to high density tolerance is scarce. Studies of the inheritance of anthesis-silking interval (ASI) through generation mean analysis using maize inbreds, found that recessive genes control the inheritance of ASI with prominent additive gene effects [5]. Radenovic et al. [6] reported that both dominance gene action and epistatic interactions play major roles in governing the inheritance of

ASI. Anthesis-to-silking interval showed evidence for epistatic interactions and locus by density interaction [7]. Mason and Zuber [8] reported that general (GCA) and specific (SCA) combining ability effects appeared to be equally important in the expression of leaf angle. They also found that crosses of upright-leafed parents tend to produce upright leaf progeny, and vice versa.

Maize is considered more susceptible than most other cereals to drought stress at flowering, when yield losses can be severe through barrenness or reductions in kernels per ear [9]. Thus, developing maize varieties that are tolerant to drought is, considered critical for increasing the maize production [10,11]. Type of gene action, heritability and genetic advance from selection are prerequisites for starting a breeding program for developing 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. Several researchers found that additive genetic effects play a major role in conditioning grain yield under drought stress in tropical [12-15] and temperate [16,17] maize germplasm. Response to selection for yield in populations under drought has also been reported [18-21] suggesting that additive gene action might be important in controlling yield. Derera et al. [14] also found non-additive gene action playing important roles in controlling grain yield under both drought stress and favorable growing environments. Agrama and Moussa [22] 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 [9,10,11,16,17]. Many investigators reported a decline in heritability for grain yield under stress [23-26]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [27-29]. 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.

The objectives of the present investigation were: (i) to determine the type of gene action, heritability and expected genetic advance from selection for maize adaptive traits to high density combined with drought tolerance as compared to optimum conditions 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 [30] six maize (*Zea mays* L.) 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 Making 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 separate 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 well watering (WW) by giving all required irrigations combined with low plant density (47,600 plants/ha), but the second experiment was done under water stress (WS) at flowering by skipping the fourth and fifth irrigations combined with high plant density (95,200 plants/ha). 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 m². Seeds were sown in hills at 15 and 30 cm apart (for the second and first experiment, respectively), thereafter (before the 1st irrigation) were thinned to one plant/hill. Sowing date of the experiments was on May5 and May8 in 2013 and 2014 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 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 nutrient in mg kg⁻¹ are 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 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 temperature was 35.7, 35.97, 34.93 and 37.07°C 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°C, maximum temperature was 38.8, 35.2, 35.6 and 36.4°C 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) (°) measured as the angle between stem and blade of the leaf just

Table 1. Designation, origin and most important traits of six inbred lines used for making diallel crosses of this study

Inbred lines	Origin	Institution/ Country	Prolificacy	Productivity under high density	Leaf angle
L20-Y	SC 30N11	Pion. Int.Co.-Egypt	Prolific	High	Erect
L53-W	SC 30K8	Pion. Int.Co.-Egypt	Prolific	High	Erect
Sk 5-W	Teplacinco # 5 (Tep-5)	ARC-Egypt	Prolific	High	Erect
L18-Y	SC 30N11	Pion. Int.Co.-Egypt	Prolific	Low	Wide
L28-Y	Pop 59	ARC-Thailand	Non-Prolific	Low	Wide
Sd 7-W	A.E.D. (OPV)	ARC-Egypt	Non-Prolific	Low	Erect

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

above ear leaf, according to Zadoks et al. [31]. 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 x number of rows per ear x 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 (well water-low density; WW-LD and water stress-high density; WS-HD) was analyzed separately across seasons as RCBD using GENSTAT 10th addition windows software. Least significant differences (LSD) values were calculated to test the significance of differences between means according to Steel et al. [32].

2.6 Genetic Analyses of F₁ Diallel Crosses

2.6.1 Hayman's numerical approach

The genetic parameters and ratios were calculated according to methods developed by Jinks and Hayman [33], Jinks [34] and Hayman [35,36] and described by Sharma [37]. 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 [37]:

$$t^2 = \frac{(n-2)/4 \{ [MSS(V_r) - (MSS(Wr))^2 / (MSS(V_r) \times [MSS(Wr) - MSP(Wr.Vr)]^2)] \}}{MSS(Wr) - MSP(Wr.Vr)}$$

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 value indicates failure of the assumptions [35,36]. Another test was done by estimating the regression coefficient "bWr.Vr" of Wr on Vr as follows:

$$b_{Wr.Vr} = [cov(Wr.Vr) / varVr] = [MSP(Wr.Vr) / MSS(Vr)]$$

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 (t₁) and from unity (=1) (t₂) can be tested by t-test as under: t₁ = (b-0)/SEb and t₂ = (1-b)/SEb. The foregoing values were tested against the "t" tabulated value for (n-2) degrees of freedom according to Jinks and Hayman [33]. If all the assumptions were valid, the regression coefficient would be significantly different from zero but not from unity. Hayman [35, 36] derived the expectations for the statistics calculated from the F₁ diallel table and the expected values of the component variations using least squares. The notations of Mather and Jinks [38] are used and described as follows:

$$V_{OLO} (V_p) \text{ (variance of the parents)} \\ = D + \hat{E}, V_{1L1}(V_r) \text{ (mean of all the } V_r \text{ values)} \\ = \frac{1}{4} D - \frac{1}{4} F + \frac{1}{4} H_1 + \frac{1}{4} H_2 + [\hat{E} + \hat{E} (n-2)/2n^2]$$

Vr (variance of all the progenies in each parental array) = $\frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} H_2 - \frac{1}{4} F + (n+1)/2n_2 \hat{E}$, $W_{OLO1}(Wr)$ (mean of all the Wr. values) = $\frac{1}{2} D - \frac{1}{4} F + \hat{E}/n$, $(M_{L1} - M_{L0})^2$ = dominance relationship = $\frac{1}{4} h^2 + [(n-1) \hat{E}/n^2]$. The components of \hat{E} , D, H₁, H₂, h² and F were estimated in F₁ as follows:

$$\begin{aligned} \hat{E} &= [(Errors\ S.S. + Repls\ S.S.)/r]/[(r-1) + (c-1)(r-1)]. \\ D &= V_{OL0} - \hat{E}. \quad F = 2 V_{OL0} - 4W_{OL01} - [2\hat{E} (n-2)/n]. \\ H_1 &= V_{OL0} + 4 V_{OL1} - 4W_{OL01} - [\hat{E} (3n-2)/n]. \\ H_2 &= 4 V_{1L1} - 4 V_{0L1} - 2\hat{E}. \quad h^2 \\ F &= 4(M_{L1} - M_{L0})^2 - [4\hat{E} (n-1)/n^2]. \end{aligned}$$

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 is estimated as $(H_1/D)^{1/2}$. 1. If the of 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) is estimated as follows:

$$K_D/K_R = [(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$$

If $K_D/K_R \approx 1.0$, 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 indicates asymmetry of distribution ($p \neq q$). 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 $p \neq q$. Thus: if this ratio ≈ 0.25 , it means symmetrical distribution of positive and negative dominant genes in parents, while if this ratio $\neq 0.25$, it means asymmetry of distribution. Narrow-sense heritability (h^2_n) 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 [39] based on 10% selection intensity as follows:

$$GA = 100[(k.h^2_n \bar{\delta}_{ph})/x]$$

Where: k = 1.76 (selection differential for 10% selection intensity), and $\bar{\delta}_{ph}$ = 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 [33] and later refined by Hayman [35]. 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:

$$W_{rei} = W_r - b\bar{V}_r + b\bar{V}_{ri}$$

Where: W_r = covariance between parents and their off-spring, 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:

$$a = \bar{W}_r - b\bar{V}_r$$

3. RESULTS AND DISCUSSION

3.1 Genetic Variances, Heritability and Expected Selection Gain

Estimates of genetic variances and ratios for studied traits under the two environments (WW-LD and WS-HD) across two years are presented in Table (2). The dominance genetic component of variation (H_1) was significant ($P \leq 0.05$ or 0.01) for all studied traits under both, except for ASI under WS-HD, BS under WW-LD and EPP under both WW-LD and WS-HD environments, indicating that heterosis breeding could be used for the genetic improvement of the most studied traits, *i.e.* grain yield and adaptive traits to high density combined with water stress under both environments [40-43].

The additive component of variation (D) was also significant ($P \leq 0.05$ or 0.01) for all studied characters under both environments, except for PH under WS-HD, and ASI and BS under both WW-LD and WS-HD environments, where additive was not significant. This indicates that selection could also be used in maize

populations for improving most studied traits, where significant additive variance exists under respective environments [40,41,43-46].

The estimates of dominance were much higher, in magnitude, than additive variance (where the ratio D/H_1 is < 1) for all studied traits, except for

EPP and RPE under both WW-LD and WS-HD environments, suggesting that dominance variance plays the major role in the inheritance of most studied traits and that heterosis breeding would be more efficient than selection for improving studied traits under both environments [45-47].

Table 2. Estimates of genetic parameters for studied traits under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD) environments across two seasons

Genetic parameter	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD
	Days to 50% anthesis		Anthesis-silking interval		Plant height		Ear height	
D	4.42**	5.98	0.01	0.03	465.70*	181.80	227.59*	143.20
H ₁	7.95**	37.58**	0.22*	0.30	3096.5**	2448.6**	1395.34**	1044.8**
H ₂	6.44**	28.15**	0.18*	0.26	2527.5**	2195.34**	1066.2**	812.30**
h ²	18.55**	12.53*	0.64**	0.41**	6887.95**	7573.27**	2458.41**	2027**
E	0.20	0.31	0.06**	0.12**	11.59	18.03	6.86	10.60
F	4.52	9.84	0.03	0.07	946.94	417.82	504.32	326.50
D/H ₁	0.56	0.16	0.05	0.10	0.15	0.07	0.16	0.14
(H ₁ /D) ^{1/2}	1.34	2.51	3.97**	3.37	2.58	3.67	2.48	2.70
H ₂ /4H ₁	0.20	0.19	0.21	0.21	0.20	0.22	0.19	0.19
K _D /K _R	2.23	1.98	48.53	1.67	2.30	1.91	2.62	2.46
h ² _b %	93.22	95.52	79.31	73.33	97.50	96.88	97.95	94.75
h ² _n %	35.16	13.63	3.45	6.67	13.03	6.86	13.96	11.95
GA%	3.63	2.41	1.39	1.64	5.94	2.58	10.16	6.74
	Barren stalks		Leaf angle		Ears per plant		Rows per ear	
D	0.23	2.14	30.90**	21.66**	0.01**	0.011**	1.711**	2.62**
H ₁	2.80	39.43**	32.62**	22.26**	0.00	0.00	0.763*	1.62**
H ₂	0.60	20.69**	21.55**	17.99**	0.00	0.004*	0.805*	1.50**
h ²	0.00	5.87	6.89	6.56	0.00	0.035**	0.804**	3.16**
E	3.22**	10.74**	0.96	0.90	0.003**	0.003**	0.163**	0.17*
F	1.32	18.70**	18.34*	8.39	-0.01	0.00	-0.03	1.36*
D/H ₁	0.08	0.05	0.95	0.97	5.00	5.50	2.24	1.62
(H ₁ /D) ^{1/2}	3.49	4.30	1.03	1.01	0.43	0.44	5.22	0.79
H ₂ /4H ₁	0.05	0.13	0.19	0.20	0.00	0.47	0.15	0.23
K _D /K _R	10.12	107.68	1.81	1.47	15.70	1.70	0.98	1.98
h ² _b %	48.48	79.47	91.77	93.90	80.00	81.25	93.82	96.15
h ² _n %	3.68	4.09	47.92	48.33	66.67	68.75	64.88	59.41
GA%	1.62	3.39	24.42	19.34	11.68	15.89	12.76	17.07
	Kernels per row		Kernels per plant		100-kernel weight		Grain yield per plant	
D	28.75**	874.59**	11792**	5652**	16.41**	11.36**	1274*	301.17*
H ₁	113.04**	3688.79**	41828**	48254**	29.66**	19.02**	15757**	6453.80**
H ₂	111.62**	2894.23**	42376**	47794**	28.44**	18.50**	15658**	6379.57**
h ²	413.06**	129.37**	164438**	180620**	94.47**	37.82**	60876**	23113.90**
E	0.84	894.67**	1517*	1.74	0.67	0.81	0.06	0.10
F	11.12	1191.72**	827.00	950.00	8.76	1.85	418.00	-88.41
D/H ₁	0.25	0.24	0.28	0.12	0.55	0.60	0.08	0.05
(H ₁ /D) ^{1/2}	1.98	2.05	1.88	2.92	1.30	1.29	3.52	4.63
H ₂ /4H ₁	0.25	0.20	0.25	0.25	0.24	0.24	0.25	0.25
K _D /K _R	1.22	0.50	1.04	1.06	1.50	1.13	1.10	0.94
h ² _b %	99.41	83.61	96.53	97.23	98.57	97.40	99.22	99.11
h ² _n %	20.16	16.02	21.39	10.48	35.11	36.42	7.48	4.46
GA%	9.89	59.99	11.55	9.76	12.31	13.29	9.22	6.89

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

The overall dominance effects of heterozygous loci in Hayman's model (h^2) controlling all studied traits under both environments, except BS under both environments, LANG under both WW-LD and WS-HD environments, EPP under WW-LD were 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 both environments, except for EPP under both WW-LD and WS-HD environments and RPE under WS-HD, indicating that the degree of dominance in most cases was over dominance.

The ratio ($H_2/4H_1$) indicated a symmetrical distribution of positive and negative dominant genes in parents in all studied characters under both WW-LD and WS-HD environments. The exception was EPP under WS-HD, where $H_2/4H_1$ was greater than 0.25, indicating asymmetry of distribution.

The ratio (K_D/K_R) was more than unity, indicating excess of dominant alleles and minority of recessive alleles ($p > q$) for all studied traits under both WW-LD and WS-HD environments. The exceptions were KPR and GYPP under WS-HD and RPE under WW-LD, where the ratio (K_D/K_R) was less than unity, indicating minority of dominant alleles and the excess of recessive alleles ($p < q$).

Broad-sense heritability (h^2_b) was of high magnitude (greater than 90%) for most studied traits under both environments, indicating that the environment had small effect on the phenotype for studied traits. The lowest estimates of h^2_b were shown by BS (48.48%) under WW-LD environments, indicating that the environment and genotype \times environment interaction had considerable effects on the phenotype for this trait.

Narrow-sense heritability (h^2_n) was generally of small magnitude in BS (3.68 and 4.09%), and of high magnitude for EPP (66.67 and 68.75%) and RPE (64.88 and 59.41%) under WW-LD and WS-HD environments, respectively. The estimate of h^2_n was higher under WW-LD than WS-HD for six characters, namely DTA, PH, EH, RPE, KPP and GYPP, but were higher under WS-HD than WW-LD for the remaining traits (ASI, BS, LANG, EPP, KPR and 100 KW). The marked difference between broad- and narrow-sense heritability in this experiment could be attributed to the high

estimates of dominance, dominance \times dominance and dominance \times additive components.

Our results for ASI, BS, LANG, EPP, KPR and 100KW traits are in agreement with a group of researchers [23,24,47-52], who support the idea that heritability is higher under stressed than non-stressed environment. On the contrary, our results for DTA, PH, EH, RPE, KPP and GYPP traits are in agreement with another group of investigators [25,53-56], who reported that heritability is higher under good (non-stressed) environment than stressed one.

Expected genetic advance (GA) from selection (based on 10% selection intensity) across years for studied traits in the two studied environments (Table 2) was generally of small magnitude especially for ASI (1.39% and 1.64%) and BS (1.62 and 3.39%) under WW-LD and WS-HD environments, respectively, but reached its maximum for KPR (59.99%) under WS-HD. The non-stressed environment (WW-LD) showed higher estimates of GA than the stressed one (WS-HD) for DTA, PH, EH, BS, KPP and GYPP, but the opposite was true for ASI, LANG, EPP, RPE, KPR and 100KW, where GA estimate was higher under stressed environment than non-stressed one.

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 environment. Many researchers found that heritability and GA from selection for grain yield is higher under non-stress than those under stress [25,52-56]. 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 [23,34,47-52]. The present results for grain yield confirm the conclusion of the first group of researchers and that choice of the best selection environment depends also on the trait of interest and its interaction with environment.

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

3.2 Graphical Approach of Diallel Analysis

The graphical analysis of diallel crosses proposed by Hayman [35,36] will be illustrated on the following bases according to Singh and Narayanan [39]: (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 reduces the covariance (W_r) disproportionately 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 Figures (1 to 12) for 12 studied traits under studied

environments, namely WW-LD (well watering combined with low plant density); i.e. non-stressed and WS-HD (water stressed combined with high plant density), that the regression line intercepted the W_r -axis below the origin, i.e. cutting the W_r -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 and WS. For BS under WS, RPE under WW and WS, EPP under WW, the regression line intercepted the W_r -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-LD) showed that, the parents 3, 1 and 5 (Sk5, L20 and L28) are close to the origin of the coordinate, and accordingly have more dominant genes; with L20 is the nearest parent to the origin (contains more than 75% dominant genes), while parents 2,4 and 6 (L53, L18 and Sd7) have mostly recessive genes. Under both stresses (WS-HD), for DTA trait (Fig. 1-WS-HD), the parent 1 (L20) is the closest one to the origin, indicating that it contains more than 75% dominant genes, the parents 3, 6 and 4 contain 50-75% dominant genes and the parents 2 and 5 are very far from the origin, indicating that they mostly contain recessive genes.

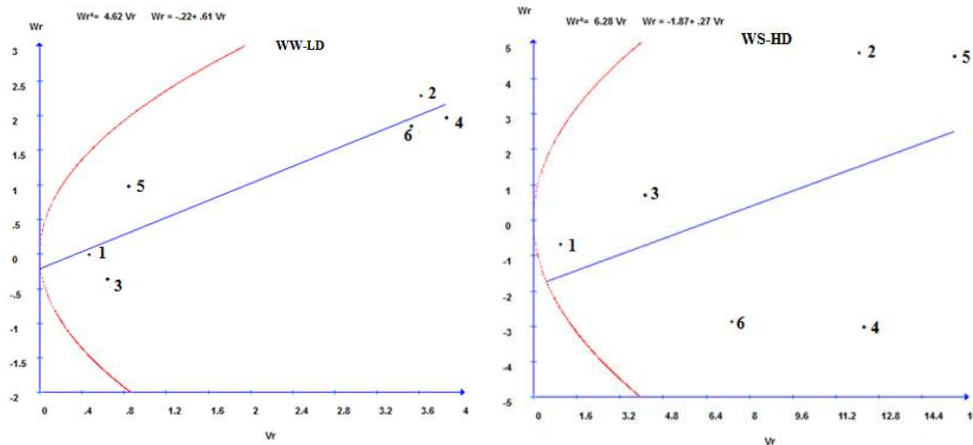


Fig. 1. W_r - V_r graph of days to anthesis (DTA) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

For anthesis-silking interval (ASI) trait under no stress (Fig. 2-WW-LD), the dispersion of parents around the regression line reveals that parents 3 and 5 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 2, 3 and 4 have 50% dominant genes, while parent 6 is far from the origin and therefore has < 25% of dominant genes. Under a combination of high density and water stress for ASI (Fig. 2-WS-HD), the dispersion of parents around the regression line indicated that the parents 2 and 4 contain > 75% dominant genes, parents 3 and 5 contains 50-70% dominant genes, parent 6 has around 50% dominant genes and the parent 1 contains mostly recessive genes.

For plant height (PH) trait under non-stressed environment (Fig. 3-WW-LD), the dispersion of parents around the regression line reveals that parents 2, 6 and 1 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 3 and 5 have 50% dominant genes, while parent 4 is far from the origin and therefore has < 25% of dominant genes. Under a combination of high density and water stress for PH (Fig. 3-WS-HD), the dispersion of parents around the regression line indicated that the parents 2 and 6 contain > 75% dominant genes, parents 1, 3 and 5 contain 50-70% dominant genes, parent 4 contains mostly recessive genes.

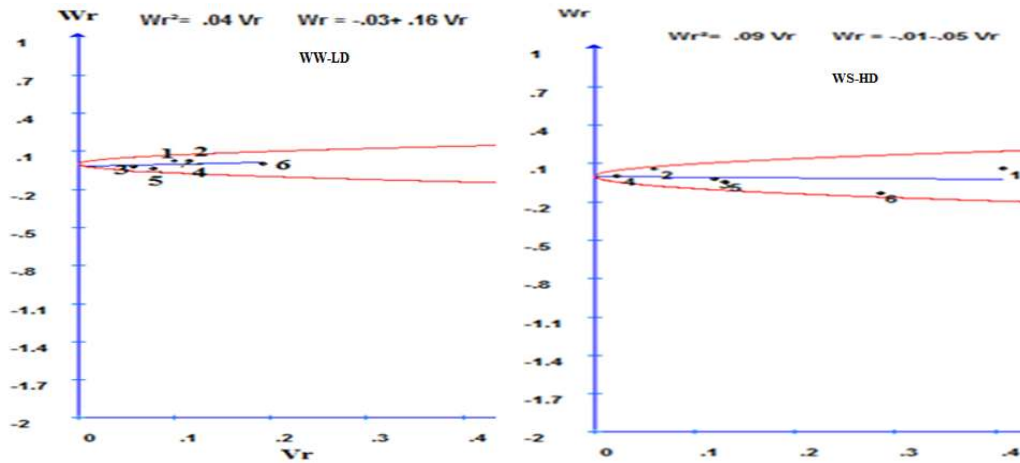


Fig. 2. W_r - V_r graph of anthesis silking interval (ASI) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

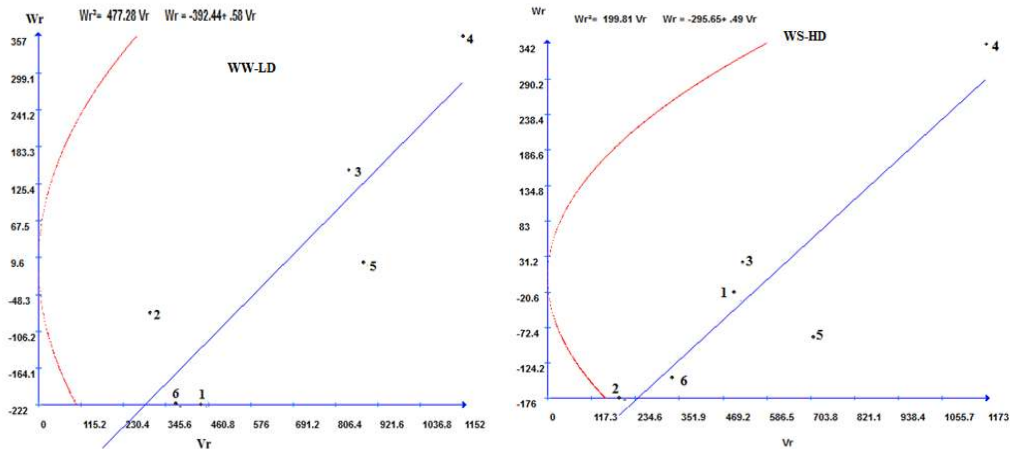


Fig. 3. W_r - V_r graph of plant height (PH) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

For ear height (EH) trait under non-stressed environment (Fig. 4-WW-LD), the dispersion of parents around the regression line reveals that parents 6 and 1 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 2 and 3 have 50% dominant genes, while parents 4 and 5 are far from the origin and therefore have mostly recessive genes. Under a combination of high density and water stress for EH (Fig. 4-WS-HD), the dispersion of parents around the regression line indicated that the parents 3, 2 and 6 contain > 75% dominant genes, parents 1 and 4 contain 50-70% dominant genes, parent 5 contains mostly recessive genes.

For barren stalks (BS) trait under non-stressed environment (Fig. 5-WW-LD), the dispersion of parents around the regression line reveals that parents 3, 6, 1 and 4 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parent 2 has 50% dominant genes, while parent 5 is far from the origin and therefore has mostly recessive genes. Under a combination of high density and water stress for BS (Fig. 5-WS-HD), the dispersion of parents around the regression line indicated that the parents 3, 6 and 1 contain > 75% dominant genes, parents 2 and 4 contain 50-70% dominant genes, but parent 5 contains mostly recessive genes.

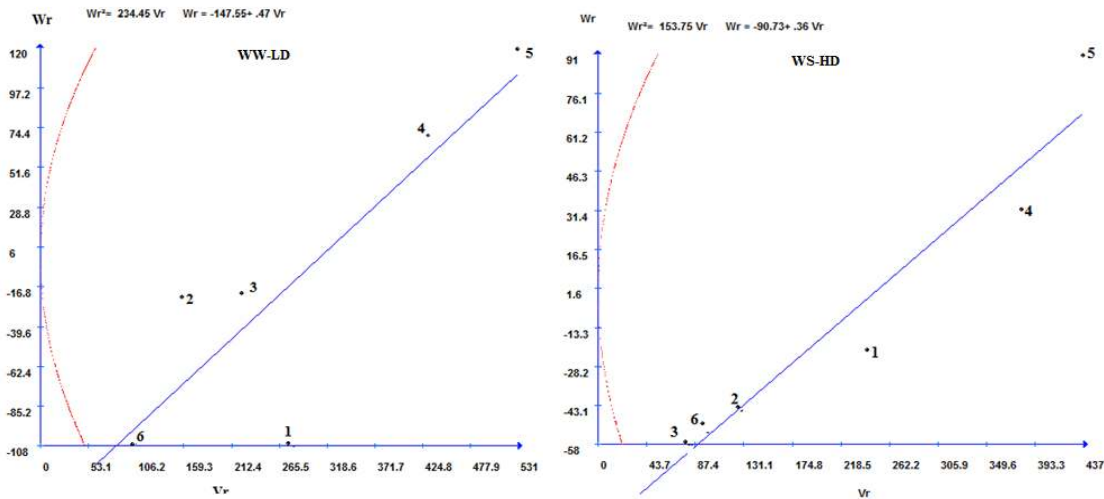


Fig. 4. Wr-Vr graph of ear height (EH) of F₁'s for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

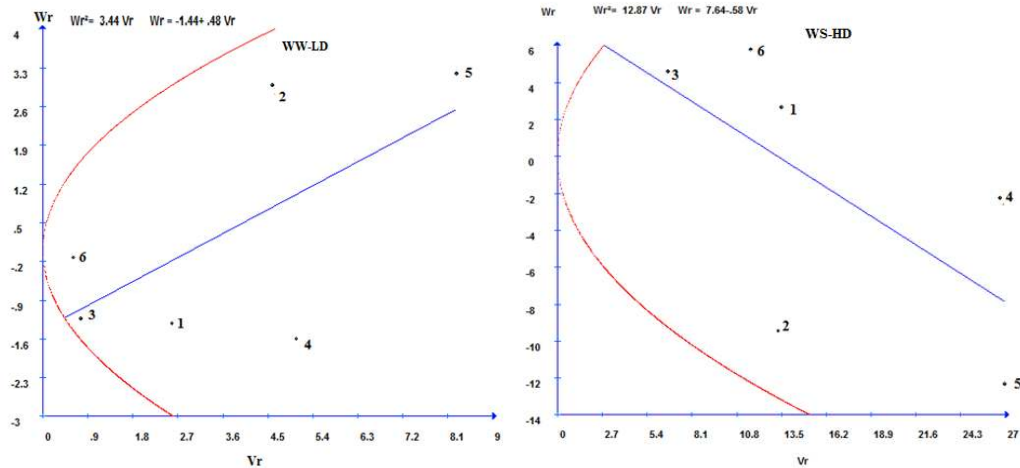


Fig. 5. Wr-Vr graph of barren stalks (BS) of F₁'s for combined data across two seasons with well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

For leaf angle (LANG) trait under non-stressed environment (Fig. 6-WW-LD), the dispersion of parents around the regression line reveals that parent 6 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, the parents 1 and 4 have 50% dominant genes, while parents 2, 3 and 5 are far from the origin and therefore has mostly recessive genes. Under a combination of high density and water stress for LANG (Fig. 6-WS-HD), the dispersion of parents around the regression line indicated that the parent 6 contains >75% dominant genes,

parents 1,4, 5 and 2 contain 50-70% dominant genes, but parent 3 contains mostly recessive genes.

For ears/plant (EPP) trait under all studied 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.

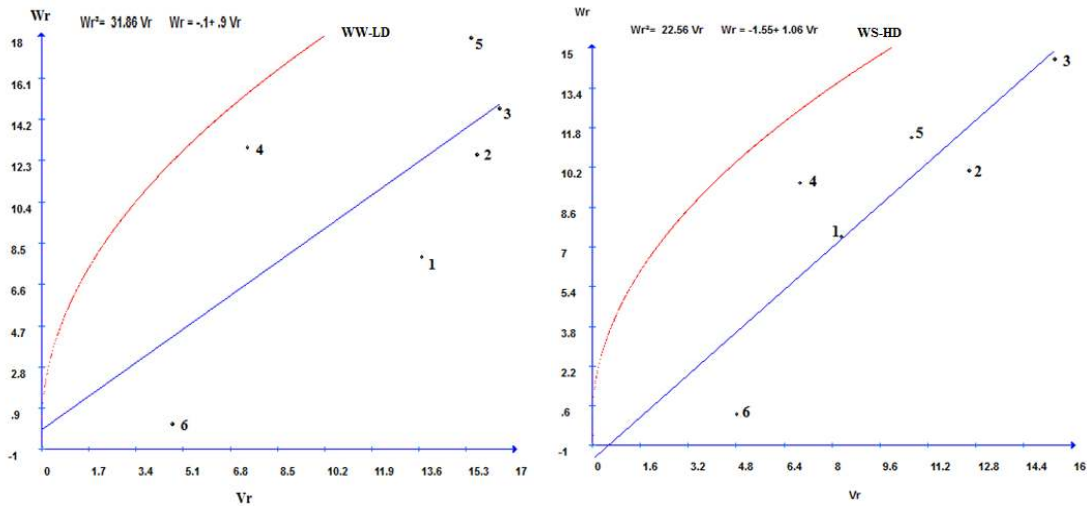


Fig. 6. W_r - V_r graph of leaf angle (LANG) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

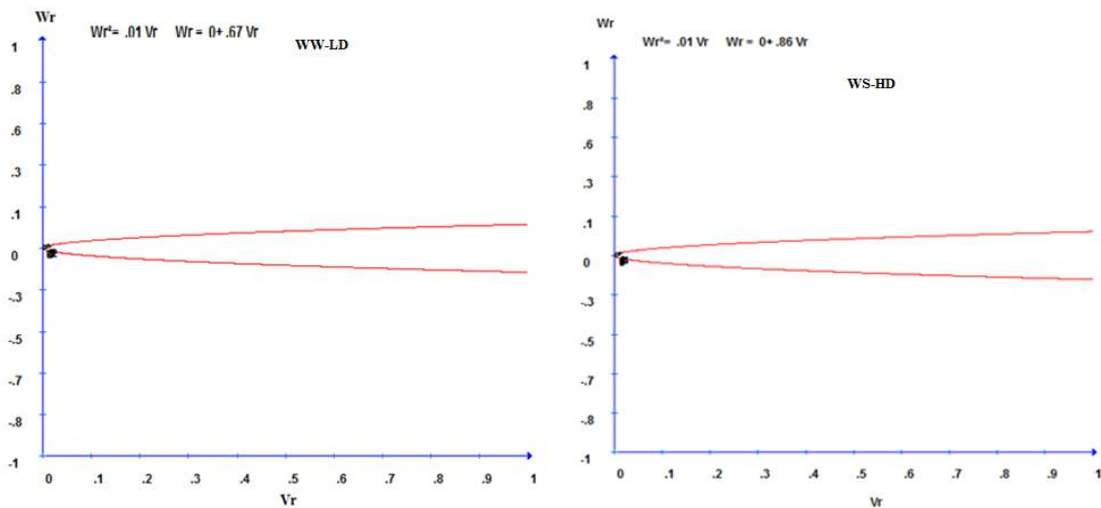


Fig. 7. W_r - V_r graph of ears per plant (EPP) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

For rows per ear (RPE) trait under non-stressed environment (Fig. 8-WW-LD), the dispersion of parents around the regression line reveals that parents 3 and 6 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 1, 4 and 2 have 50% dominant genes, while parent 5 is far from the origin and therefore has mostly recessive genes. Under a combination of high density and water stress for RPE (Fig. 8-WS-HD), the dispersion of parents around the regression line indicated that the parent 3 contains >75% dominant genes, parents 1, 5, 6 and 2 contain 50-70% dominant genes, but parent 4 contains mostly recessive genes.

For kernels per row (KPR) trait under non-stressed environment (Fig. 9-WW-LD), the dispersion of parents around the regression line reveals that parent 6 2 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, the parents 1, 3, 4 and 6 have 50% dominant genes, while parent 5 is far from the origin and therefore has mostly recessive genes. Under a combination of high density and water stress for KPR (Fig. 9-WS-HD), the dispersion of parents around the regression line indicated that the parents 2, 1 and 3 contain > 75% dominant genes, parents 5, 6 and 4 contain mostly recessive genes.

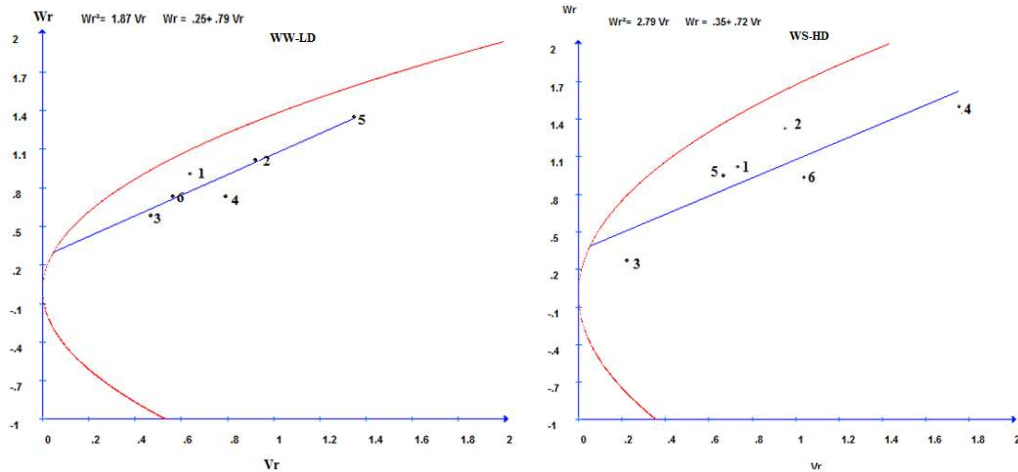


Fig. 8. W_r - V_r graph of rows per ear (RPE) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

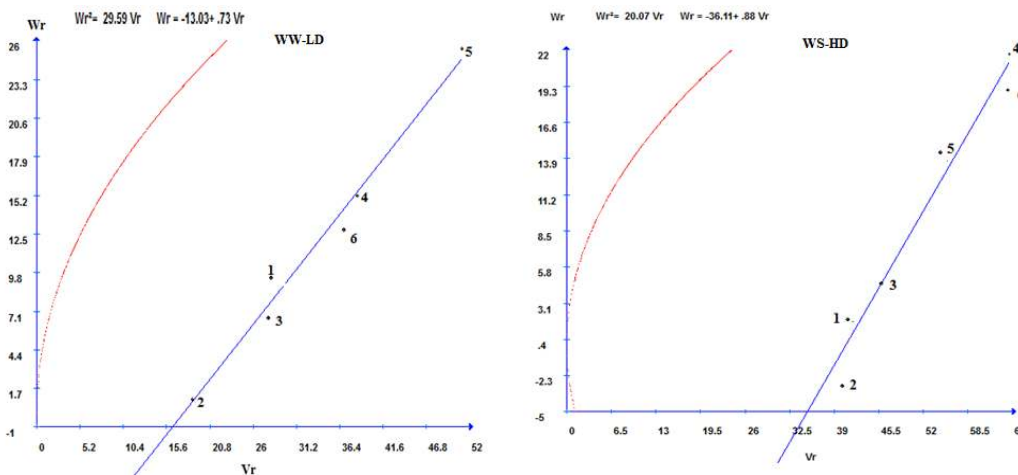


Fig. 9. W_r - V_r graph of kernels per row (KPR) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

For kernels per plant (KPP) trait under non-stressed environment (Fig. 10-WW-LD), the dispersion of parents around the regression line reveals that parents 2, 1 and 3 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 4 and 6 have 50% dominant genes, while parent 5 is far from the origin and therefore has mostly recessive genes. Under a combination of high density and water stress for KPP (Fig. 10-WS-HD), the dispersion of parents around the regression line indicated that the parent 3 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 4, 5, 2 and 1 contain > 75% dominant genes, but parent 6 contains mostly recessive genes.

dispersion of parents around the regression line reveals that parents 3, 1 and 2 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 4 and 6 have 50% dominant genes, while parent 5 is far from the origin and therefore has mostly recessive genes. Under a combination of high density and water stress for 100KW (Fig. 11-WS-HD), the dispersion of parents around the regression line indicated that the parent 3 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 4, 5, 2 and 1 contain > 75% dominant genes, but parent 6 contains mostly recessive genes.

For 100-kernel weight (100KW) trait under non-stressed environment (Fig. 11-WW-LD), the

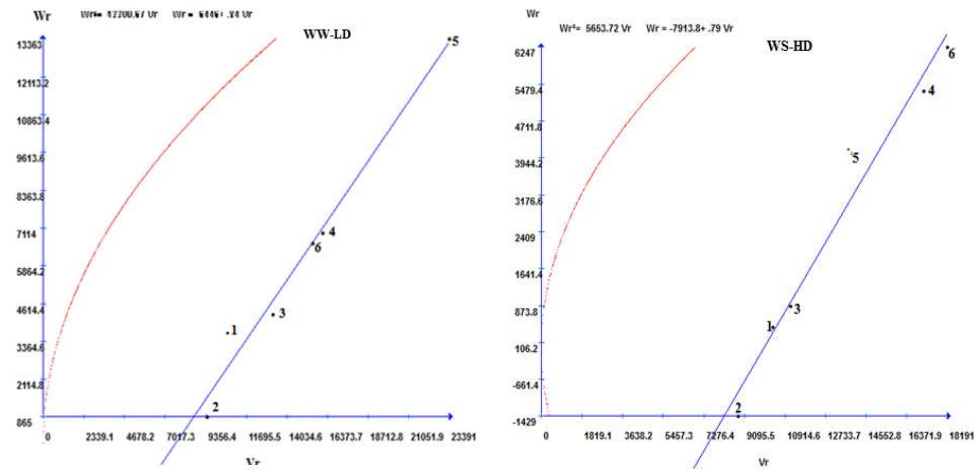


Fig. 10. W_r - V_r graph of kernels per plant (KPP) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

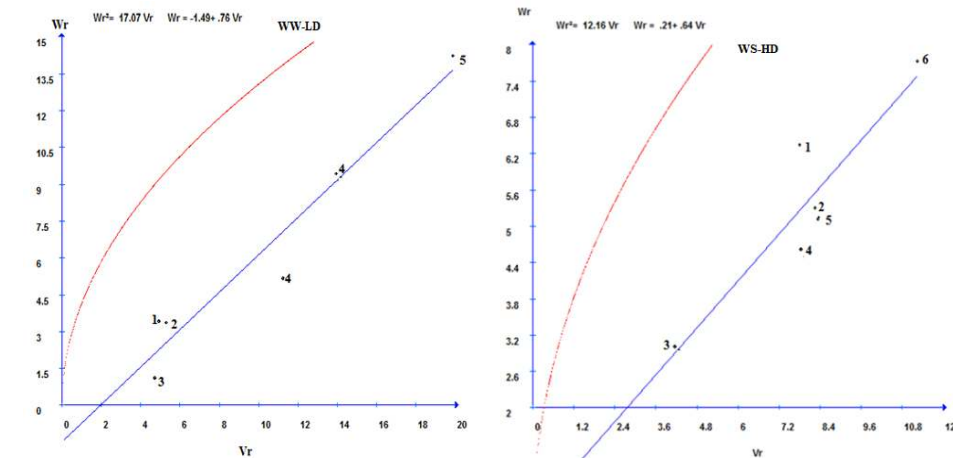


Fig. 11. W_r - V_r graph of 100-kernel weight (100-KW) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

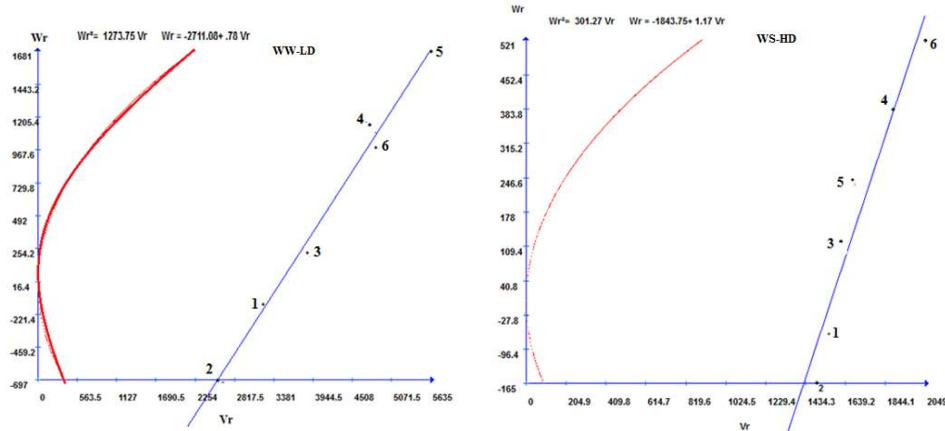


Fig. 12. W_r - V_r graph of grain yield per plant (GYPP) of F_1 's for combined data across two seasons under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD)

For grain yield per plant (GYPP) trait under non-stressed environment (Fig. 12-WW-LD), the dispersion of parents around the regression line reveals that parents 2, 1 and 3 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, the parents 4, 5 and 6 are far from the origin and therefore have mostly recessive genes. Under a combination of high density and water stress for GYPP (Fig. 12-WS-HD), the dispersion of parents around the regression line indicated that the parents 2, 1 and 3 contain > 75% dominant genes, parents 3 and 5 contain 50-75% dominant genes, but parents 4 and 6 are far from the origin, i.e. they have mostly recessive genes.

3.3 Dominance vs. Recessive Genes in Studied Inbreds

The following description of genes (dominant vs. recessive) controlling the studied characters present in the parental inbreds of the F_1 hybrids is based on Hayman's graphical approach [35,36], and on the suggestion that genes cause favorable increase in the performance of the trait, such as grain yield and and its components are dominant, and those cause favorable decrease in the trait performance, such as DTA, ASI, PH, EH, BS and LANG are recessive in nature [57]. Line L20 contains 75-100% dominant genes (favorable) conferring high values for all yield traits (except RPE) under both environments, especially under high-density combined with water stress (WS-HD), 50-75% dominant genes for most studied yield traits under the non-stressed (WW-LD). It also contains recessive genes (favorable) conferring short ASI under the

combined two stresses together. But, this line has mostly dominant genes (unfavorable) for DTA traits (lateness) under both stressed and non-stressed environments. It contains 50% recessive genes of LANG (favorable) under WW-LD and WS-HD. It carries mostly dominant genes for PH and EH traits (unfavorable in our case) under WW-LD environments. Line L53 contains 75-100% dominant genes (favorable) conferring high values for all yield traits (except RPE) under both environments. It also contains recessive genes (favorable) conferring small ASI trait under the combined two stresses together and small LANG under both environments. It carries mostly dominant genes for PH trait (unfavorable in our case) under both environments.

Inbred line Sk5 contains 75-100% dominant genes (favorable) conferring high values for all yield traits (including RPE) under WW-LD environment. It also contains mostly recessive genes (favorable) conferring small LANG under both stressed and non-stressed environments. It contains mostly dominant genes for increasing DTA (unfavorable) under both environments. It has mostly dominant genes for BS (unfavorable) under both environments. It carries mostly dominant genes for EH trait (unfavorable) under both environments. Inbred line L18 contains 75-100% recessive genes (favorable) for DTA under WW-LD environment. It contains 75-100% recessive genes for plant (PH) and ear (EH) height (favorable) in both environments. Inbred line L28 contains mostly recessive genes for all yield traits (unfavorable) in most cases, especially under WW-LD environment. It contains mostly recessive genes for LANG

(favorable) under WW-LD environment and BS under both environments. It contains 75-100% recessive genes for plant (PH) and ear (EH) height (favorable) in both environments. Inbred line Sd7 contains mostly recessive genes for all yield traits (unfavorable) in most cases under both environments, but contains 75-100% dominant genes for RPE (favorable) under WW-LD environment. It contains 75-100% dominant genes for LANG and BS traits (unfavorable) under both environments. It carries mostly recessive genes (favorable) for ASI and DTA under WW-LD. It contains 75-100% positive genes for plant (PH) and ear (EH) height (unfavorable) in both environments.

It could be concluded that favorable genes for high grain yield and its components are carried by L20 and L53 under both environments. These two lines also carry favorable genes for short ASI and narrow LANG under both environments; *i.e.* adaptive traits to high density and drought stresses. Genes of the adaptive traits to stresses low plant height and low ear height existed in the inbreds L18 and L28 under both environments. Genes conferring earliness (DTA) existed in L18 and those conferring low barrenness existed in L28 under both environments. The inbred line Sd7 carries genes of high RPE, short ASI and low DTA but only under non-stressed environment. Superiority of the inbreds L20, L53 and Sk5 in grain productivity under high plant density and low-N stresses was reported in previous works [19-21,30,50-52].

4. CONCLUSIONS

The present study suggested that heterosis breeding would be more efficient than selection for improving most adaptive traits to high density combined with drought stress. Based on the present results, it is recommended that to improve DTA, PH, EH, BS, KPP and GYPP in the present germplasm, it is better to practice selection for these traits under non stressed environment (WW-LD), but to improve ASI, LANG, EPP, RPE, KPR and 100KW, it is better to practice selection under the stressed one (WS-HD) to obtain higher values of selection gain. This study characterized the six inbred parents with respect of favorable genes for adaptive traits to high density combined with drought stress. The inbred parents L20 and L53 carry favorable genes for high grain yield and all of its components (except RPE), short ASI and narrow leaf angle (LANG) under WS-HD. The inbreds L18 and L28 carry genes of short PH,

low EH and low BS under both WW-LD and WS-HD environments. The inbred Sd7 carries favorable genes for high number of RPE and low ASI and DTA, but only under WW-LD conditions. This characterization would be fruitful for future plant breeding programs aiming at improving high density and drought tolerance in maize.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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