



Genetic Parameters Controlling Inheritance of Agronomic and Yield Traits of Maize (*Zea mays* L.) under Elevated Plant Density

A. M. M. Al-Naggar^{1*}, M. M. M. Atta¹, M. A. Ahmed² and A. S. M. Younis²

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

²*Department of Field Crops Research, National Research Centre (NRC), Dokki, Giza, Egypt.*

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 high plant density (HD) stress and low density (non-stress) and to identify the parents that carry favorable genes for adaptive traits to HD tolerance. Plants of diallel crosses among 6 parents differing in HD tolerance were grown in the field along with their parents for two seasons using a randomized complete block design with three replications in two separate experiments; the first under HD (95,200 plants/ha) and the second under low density (LD) (47,600 plants/ha). 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 12 studied traits under HD and LD, except for ears/plant (EPP) and rows/ear (RPE), suggesting that heterosis breeding would be more efficient than selection for improving such traits. Narrow-sense heritability (h^2_n) was of small or medium magnitude, but reached to 67.02% for RPE under HD. The degree of dominance in most

*Corresponding author: E-mail: medhatalnaggar@gmail.com;

cases was over dominance. In general, seven traits (anthesis silking interval; ASI, plant height; PH, ear height; EH, barren stalks; BS, RPE, kernels/ear; KPR and 100 kernel weight; 100 KW) showed higher h^2_n and expected selection gain (GA%) under HD than LD environment, while the remaining five traits (days to anthesis; DTA, leaf angle; LANG, EPP, KPP and grain yield/plant; GYPP) showed opposite trend. The inbreds L20, L53 and Sk5 carry genes of high yield and most of its contributing attributes. Genes of low BS are found in L20 and genes of narrow LANG in L53, Sk5 and Sd7. Genes of low PH and EH are found in L18 and L28. Genes of high RPE and short ASI are found in Sd7. Genes for earliness (DTA) exist in L18 and Sd7.

Keywords: Heritability; high density stress; adaptive traits; diallel analysis; gene action.

1. INTRODUCTION

Maximum maize (*Zea mays* L.) grain yield per land unit area could be obtained under high plant density by using hybrids that can withstand high plant density up to 100,000 plants/ha [1]. Egyptian maize hybrids selected under low plant density are not tolerant to high 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.

Average maize grain yield per land unit area in the USA 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. Such information, especially in Egypt is scarce. Elsworth [7] postulated one major gene and two minor genes to explain the segregation for ear number observed in F_2 and backcross populations of two prolific inbreds, two non-prolific inbreds and one semi-prolific inbred. The demonstration that prolificacy may be rapidly transferred from a prolific to a non-prolific inbred by backcrossing indicates that relatively few genes affect ear

number. 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 [8]. Hassan et al. [9] 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 [10]. Mason and Zuber [11] 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.

A wide array of biometrical tools is available to breeders for characterizing genetic control of economically important traits as a guide to decide the appropriate breeding methodology for hybrid breeding. Diallel analysis is one of the best biometrical tools to achieve that. The objectives of the present investigation were: (i) to determine the genetic variance components and ratios, heritability and expected genetic advance from selection for adaptive traits to high density tolerance in maize and (ii) to characterize the parental genotypes with respect to the favorable genes for such traits to be utilized in future breeding programs.

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 [12] six maize (*Zea mays* L.) inbred lines in the

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

Inbred designation	Origin	Institution (country)	Prolificacy	Productivity under high density	Leaf angle
L20-Y	SC 30N11	Pion. Int.Co.	Prolific	High	Erect
L53-W	SC 30K8	Pion. Int.Co.	Prolific	High	Erect
Sk 5-W	Teplacinco # 5	ARC-Egypt	Prolific	High	Erect
L18-Y	SC 30N11	Pion. Int.Co.	Prolific	Low	Wide
L28-Y	Pop 59	ARC-Thailand	Non-Prolific	Low	Wide
Sd 7-W	A.E.D.	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 (Old local open pollinated variety)

8th selfed generation (S_8), showing clear differences in tolerance to high density 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 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 low plant density (LD); *i.e.* 47,600 plants/ha, but the second experiment was done under high plant density (HD); *i.e.* 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 in the 1st and 2nd experiment, respectively, thereafter (before the 1st irrigation) were thinned to one plant/hill to achieve the two plant densities, *i.e.*, 95,200 and 47,600 plants/ha, respectively. Sowing date of the experiments was on May 5 and May 8 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

above ear leaf, according to Zadoks et al. [13]. 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 (LD and 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. [14].

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 [15], Jinks [16] and Hayman [17,18] and described by Sharma [19]. 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 [19]: $t^2 = \frac{(n-2)/4 \{ [MSS(Vr) - (MSS(Wr))^2 / \{MSS(Vr) \times [MSS(Wr) - MSP(Wr.Vr)^2] \}]}{0.05^2}$. 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 "F" value with 4 and (n-2) degrees of freedom. Significant value indicates failure of the assumptions [17,18]. Another test was done by estimating the regression coefficient "bWr.Vr" $b_{Wr.Vr} = \frac{cov(Wr.Vr)}{var Vr} = \frac{MSP(Wr.Vr)}{MSS(Vr)}$. The standard error (SE) for the regression coefficient (b) value was estimated as follows: $SE_b = \frac{[MSS(Wr) - bMSP(Wr.Vr)]^{1/2}}{(n-2)}$ 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 [15]. If all the assumptions were valid, the regression coefficient would be significantly different from zero but not from unity. Hayman [17,18] 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 [20] are used and described as follows: V_{0L0} (V_p) (variance of the parents) = D + Ê, V_{1L1}(V_r)(mean of all the V_r values) = ¼ D - ¼ F + ¼ H₁ + ¼ H₂ + [Ê + Ê (n-2)/2n2], Vr (variance of all the progenies in each parental array) = ¼ D + ¼ H₁ - ¼ H₂ - ¼ F + (n+1)/2n2 Ê, W_{0L01}(Wr) (mean of all the Wr. values) = ½ D - ¼ F + Ê/n, (M_{L1} - M_{L0})² = dominance relationship = ¼ h² + [(n - 1) Ê/n²]. The components of Ê, D, H₁, H₂, h² and F were estimated in F₁ as follows: Ê = [(Errors S.S. + Repls S.S.)/r]/[(r-1) + (c-1) (r-1)]. D = V_{0L0} - Ê. F = 2 V_{0L0} - 4W_{0L01} - [2Ê (n-2)/n]. H₁ = V_{0L0} + 4 V_{0L1} - 4W_{0L01} - [Ê (3n-2)/n]. H₂ = 4 V_{1L1} - 4 V_{0L1} - 2Ê. h² = 4(M_{L1} - M_{L0})² - [4Ê (n-1)/n²]. Where n = number of parents. Ê = 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. H₁ = variance component due to dominance deviation. H₁ = [1 - (u-v)²], where, u and v are the proportions of positive and negative genes, respectively in the parents. h² = 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 (H₁/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 = [(4DH₁)^{1/2} + F]/[(4 DH₁)^{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 indicates 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 (H₂/4H₁) 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 $\neq 0.25$, 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 (\bar{x}) was calculated according to Singh and Narayanan [21] based on 10% selection intensity as follows: $GA = 100[(k.h^2_n \bar{\delta}_{ph})/\bar{x}]$ 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 [15] and later refined by Hayman [17,18]. 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 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: $a = \bar{W}_r - b\bar{V}_r$.

3. RESULTS AND DISCUSSION

3.1 Genetic Variances, Heritability and Expected Selection Gain

Genetic parameters estimated by using the numerical approach of Hayman (1954 a and b) for studied traits under the two environments (LD and 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 LD and HD environments, except for ASI under HD, BS and EPP under LD, 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 tolerance under both environments [21-24].

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

maize populations for improving most studied traits, under LD and HD environments [22-25].

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 LD and HD, except for EPP and RPE, suggesting that dominance variance plays the major role in the inheritance of these traits and that heterosis breeding would be more efficient than selection for improving most studied traits under LD and HD environments. For adaptive traits to abiotic stress tolerance such as drought and high density stress, many investigators reported more importance of dominance than additive variance [26-32].

The overall dominance effects of heterozygous loci in Hayman's model (h^2) controlling all studied traits under LD and HD environments, except BS and EPP under both environments and LANG under LD, were significant ($P \leq 0.01$), 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 EPP under LD and HD and RPE under HD), indicating that the degree of dominance in most cases was over dominance. The highest (H_1/D)^{1/2} value was recorded in LD (ASI and RPE) and HD (GYPP).

The ratio ($H_2/4H_1$) indicated a symmetrical distribution of positive and negative dominant genes in parents in all studied characters under both environments, except RPE under 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 most studied cases. The exceptions were RPE under LD, KPR and KPP under HD, 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 these traits. The lowest estimates of h^2 were shown by ASI under HD (43.48%), BS under LD (48.48%), indicating that the environment and genotype \times environment interaction had considerable effects on the phenotype for these traits.

Table 2. Estimates of genetic parameters for studied traits under low (LD) and high (HD) plant density across two seasons

Genetic parameter	LD	HD	LD	HD	LD	HD	LD	HD
	Days to 50% anthesis		Anthesis-silking interval		Plant height		Ear height	
D	4.42**	3.65**	0.01	0.05	465.70*	777*	227.59*	414.16**
H ₁	7.95**	11.57**	0.22*	0.05	3096.5**	3588**	1395.34**	1248.11**
H ₂	6.44**	10.10**	0.18*	0.03	2527.5**	2780**	1066.2**	838.11**
h ²	18.55**	31.75**	0.64**	1.20**	6887.95**	7248**	2458.41**	1384.84**
E	0.20	0.21	0.06**	0.13**	11.59	9.34	6.86	3.63
F	4.52	3.95	0.03	-0.08	946.94	1545*	504.32	793.09**
D/H ₁	0.56	0.32	0.05	1.00	0.15	0.22	0.16	0.33
(H ₁ /D) ^{1/2}	1.34	1.78	3.97**	1.03	2.58	2.15	2.48	1.74
H ₂ /4H ₁	0.20	0.22	0.21	0.12	0.20	0.19	0.19	0.17
K _D /K _R	2.23	1.87	48.53	16.52	2.30	2.72	2.62	3.46
h ² _b %	93.22	94.68	79.31	43.48	97.50	98.75	97.95	98.48
h ² _n %	35.16	23.66	3.45	21.74	13.03	17.76	13.96	24.86
GA%	3.63	2.59	1.39	4.35	5.94	8.56	10.16	16.36
	Barren stalks		Leaf angle		Ears per plant		Rows per ear	
D	0.23	29.47**	30.90**	13.01**	0.01**	0.006**	1.711**	1.89**
H ₁	2.80	62.87**	32.62**	21.97**	0.00	0.005*	0.763*	0.78*
H ₂	0.60	35.06	21.55**	19.98**	0.00	0.005*	0.805*	0.85*
h ²	0.00	8.59	6.89	20.02**	0.00	0.00	0.804**	0.64**
E	3.22**	8.57**	0.96	0.85**	0.003**	0.00	0.163**	0.15**
F	1.32	51.98**	18.34*	1.94	-0.01	0.00	-0.03	0.20
D/H ₁	0.08	0.47	0.95	0.59	5.00	1.20	2.24	2.42
(H ₁ /D) ^{1/2}	3.49	1.46	1.03	1.30	0.43	0.91	5.22	0.64
H ₂ /4H ₁	0.05	0.14	0.19	0.23	0.00	0.25	0.15	0.27
K _D /K _R	10.12	4.05	1.81	1.12	15.70	1.16	0.98	1.18
h ² _b %	48.48	91.51	91.77	90.44	80.00	97.35	93.82	94.68

Genetic parameter	LD	HD	LD	HD	LD	HD	LD	HD
h_n^2 %	3.68	29.20	47.92	36.31	66.67	53.10	64.88	67.02
GA%	1.62	40.30	24.42	14.21	11.68	9.29	12.76	14.59
	Kernels per row		Kernels per plant		100-kernel weight		Grain yield per plant	
D	28.75**	467.30**	11792**	7489**	16.41**	17.14**	1274*	488.54*
H ₁	113.04**	2045.91**	41828**	36555**	29.66**	39.45**	15757**	9602.99**
H ₂	111.62**	1599.79**	42376**	36435**	28.44**	37.76**	15658**	9584.13**
h^2	413.06**	172.67**	164438**	124730**	94.47**	131.66**	60876**	36753.99**
E	0.84	504.67**	1517*	0.67	0.67	0.55	0.06	0.02
F	11.12	-655.19**	827.00	-450.20	8.76	11.00	418.00	89.92
D/H ₁	0.25	0.23	0.28	0.20	0.55	0.43	0.08	0.05
(H ₁ /D) ^{1/2}	1.98	2.09	1.88	2.21	1.30	1.50	3.52	4.43
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	0.97	1.50	1.54	1.10	1.04
h_b^2 %	99.41	83.28	96.53	97.86	98.57	99.04	99.22	99.19
h_n^2 %	20.16	15.48	21.39	17.00	35.11	30.00	7.48	4.84
GA%	9.89	38.47	11.55	11.10	12.31	13.34	9.22	6.56

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

Narrow-sense heritability (h^2_n) was of small magnitude (< 10%) in GYPP, of high magnitude (> 50%) for EPP and RPE under both environments and of medium magnitude (>10-50%) for the remaining characters. The highest h^2_n was recorded by RPE under HD (67.02%) followed by EPP under LD (66.67%). It is observed that 7 out of 12 characters, namely DTA, EPP, RPE, KPR, KPP, 100KW and GYPP showed higher h^2_n under LD than that HD environment, but five traits, namely ASI, PH, EH and BS exhibited higher estimates of h^2_n under high density stressed environment. The results of the first group of traits (7 traits) are in agreement with those reported by some investigators [33-37], who support the idea that heritability is higher under good (non-stressed) environment than stressed environment. The results of the second group of traits (5 traits) are in agreement with those reported by some researchers [32,38-44], who support the idea that heritability is higher under stressed than non-stressed environment. 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

Expected genetic advance (GA) from selection (based on 10% selection intensity) across years for studied traits in the six environments (Table 2) was generally of small magnitude for DTA (2.59% under HD to 3.63% under LD), ASI (1.39% under LD to 4.35% under HD) and BS (1.62% under LD), but reached its maximum for BS and KPR under HD (40.30 and 38.47%, respectively). In general, seven traits (ASI, PH, EH, BS, RPE, KPR and 100 KW) showed higher GA% under HD than LD environment, while the remaining five traits (DTA, LANG, EPP, KPP and GYPP) showed opposite trend. Thus, based on the present results, it is recommended to practice selection for improving ASI, PH, EH, BS, RPE, KPR and 100 KW traits under high density stressed environment, but for the remaining studied traits, it is better to practice selection under LD environment 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 environment. Many researchers found that heritability and GA from selection for grain yield is higher under non-stress than those under

stress [33-37]. 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 [38-42]. Our results for grain are in the same line with the first group of investigators and concluded that choice of the best selection environment depends also on the trait of interest and its interaction with environment.

3.2 Graphical Approach of Diallel Analysis

The graphical analysis of diallel crosses proposed by Hayman [17,18] will be illustrated on the following bases according to Singh and Narayanan [21]: (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 Figs. (1 to 12) for 12 studied traits under LD (non-stressed) and HD (high-density stressed) environments, 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 LD. For RPE under

both environments, EPP under LD and HD, 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-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 high-density, dispersion of parents around the regression line, for DTA trait (Fig. 1-HD) showed that parent No.1 (L20) is very close to the origin, indicating that it contains more than 75% dominant genes, the parents 4 and 6 are very far from the origin, indicating that they mostly contain recessive genes, while dominant and recessive genes are located in the parents 3, 5 and 2 for such trait.

For anthesis- silking interval (ASI) trait under no stress (Fig. 2-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 high-density for ASI (Fig. 2-HD), the dispersion of parents around the regression line showed that parent 5, 4 and 6 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, parents 3 and 1 have 50-75% of dominant genes, while parent 2 is far from the origin, therefore it has < 25% of dominant genes.

For plant height (PH) trait under non-stressed environment (Fig. 3-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 high-density for PH (Fig. 3-HD), the dispersion of parents around the regression line showed that parents 1, 2, 3 and 6 are close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parent 4 has 50-75% of dominant genes, while parent 5 is far from the origin, therefore it has < 25% of dominant genes.

For ear height (EH) trait under non-stressed environment (Fig. 4-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 high-density for EH (Fig. 4-HD), the dispersion of parents around the regression line showed that parents 1, 3 and 6 are close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 2 and 4 have 50-75% of dominant genes, while parent 5 is far from the origin, therefore it has mostly recessive genes.

For barren stalks (BS) trait under non-stressed environment (Fig. 5-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 high-density for BS (Fig. 5-HD), the dispersion of parents around the regression line showed that parents 2, 5 and 6 are close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parents 3 and 4 have 50-75% of dominant genes, while parent 1 is far from the origin, therefore it has mostly recessive genes.

For leaf angle (LANG) trait under non-stressed environment (Fig. 6-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 high-density for LANG (Fig. 6-HD), the dispersion of parents around the regression line showed that parent 6 is close to the origin of the coordinate, and accordingly has > 75% of dominant genes, parent 1 has 50-75% of dominant genes, while parents 3, 4, 2 and 5 are far from the origin, therefore they have 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.

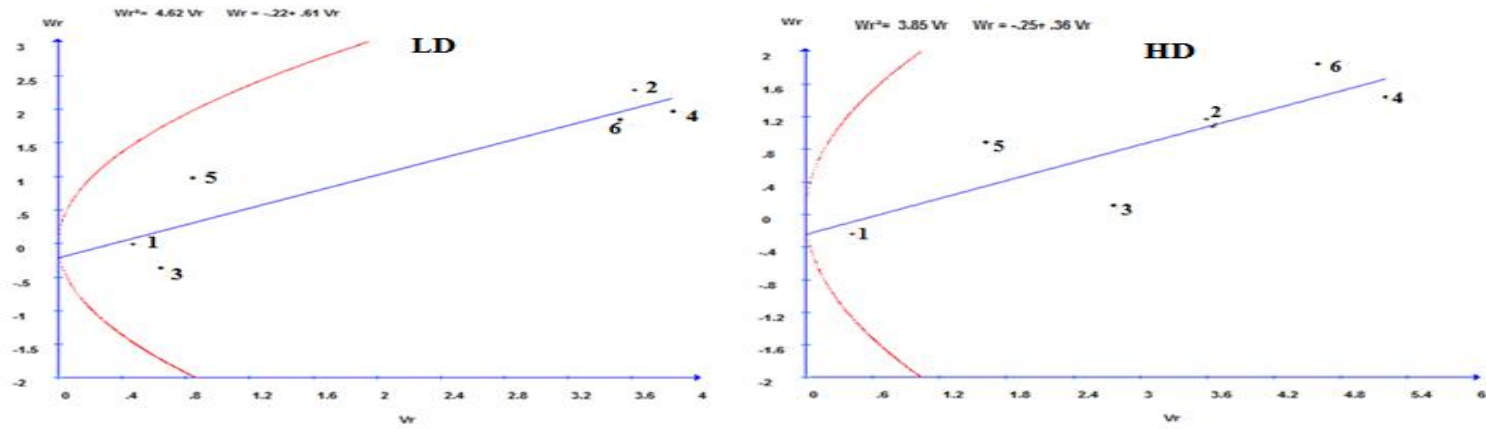


Fig. 1. W_v - V_r graph of days to anthesis (DTA) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

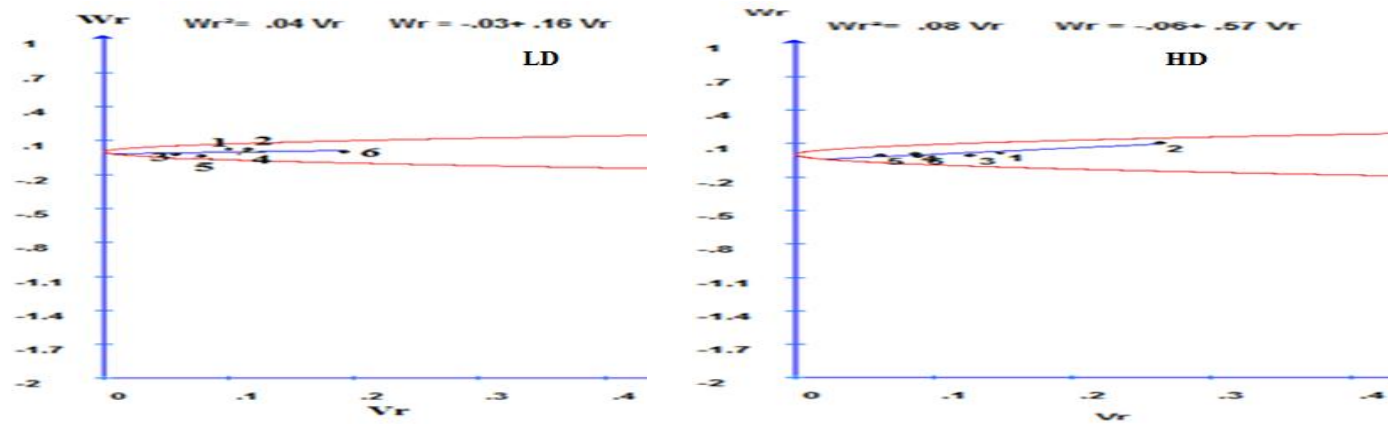


Fig. 2. W_v - V_r graph of anthesis silking interval (ASI) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

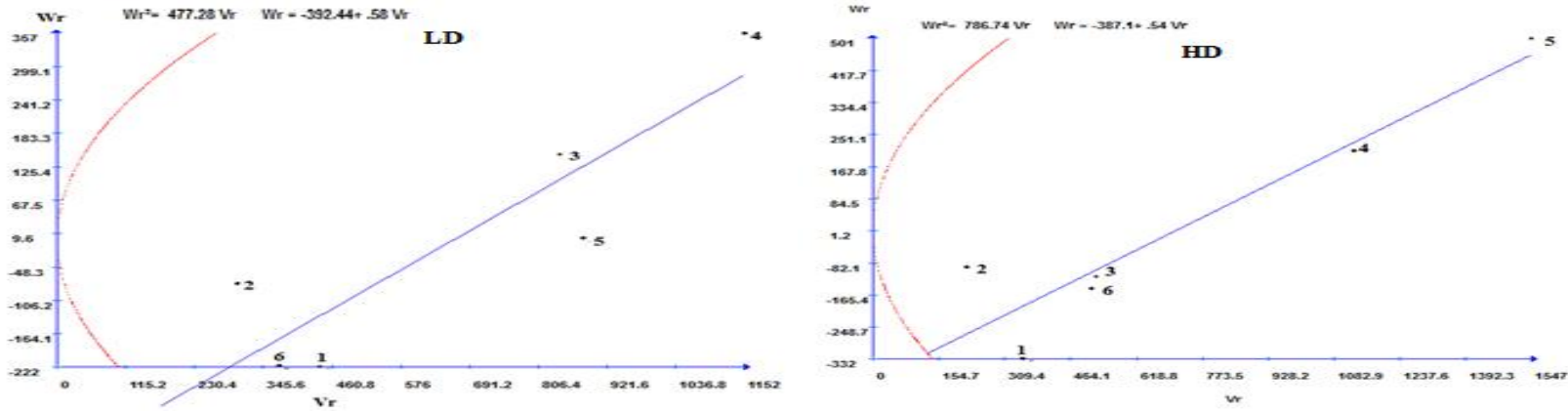


Fig. 3. W_r - V_r graph of plant height (PH) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

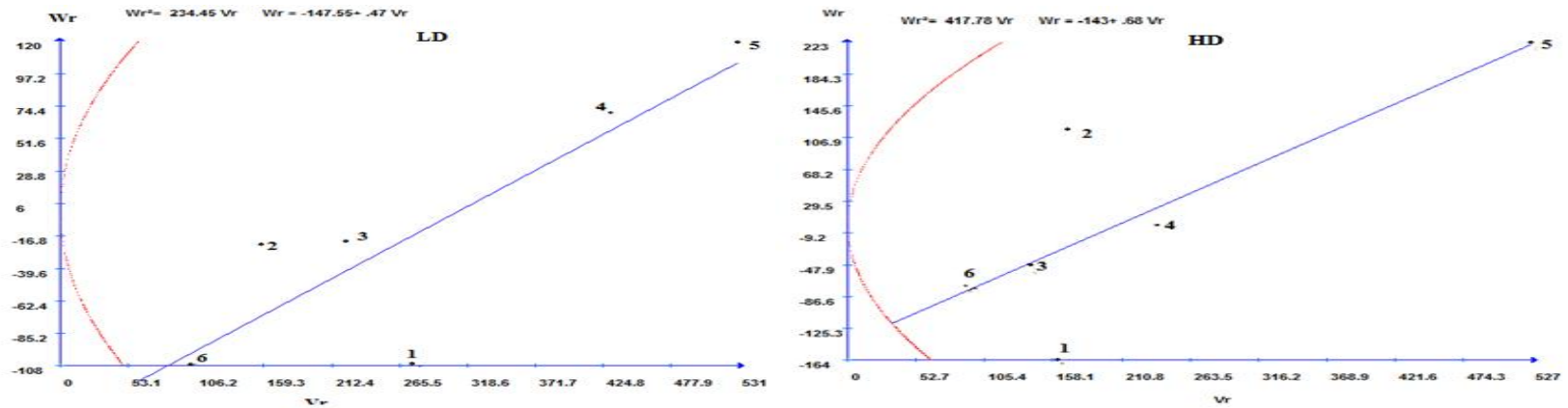


Fig. 4. W_r - V_r graph of ear height (EH) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

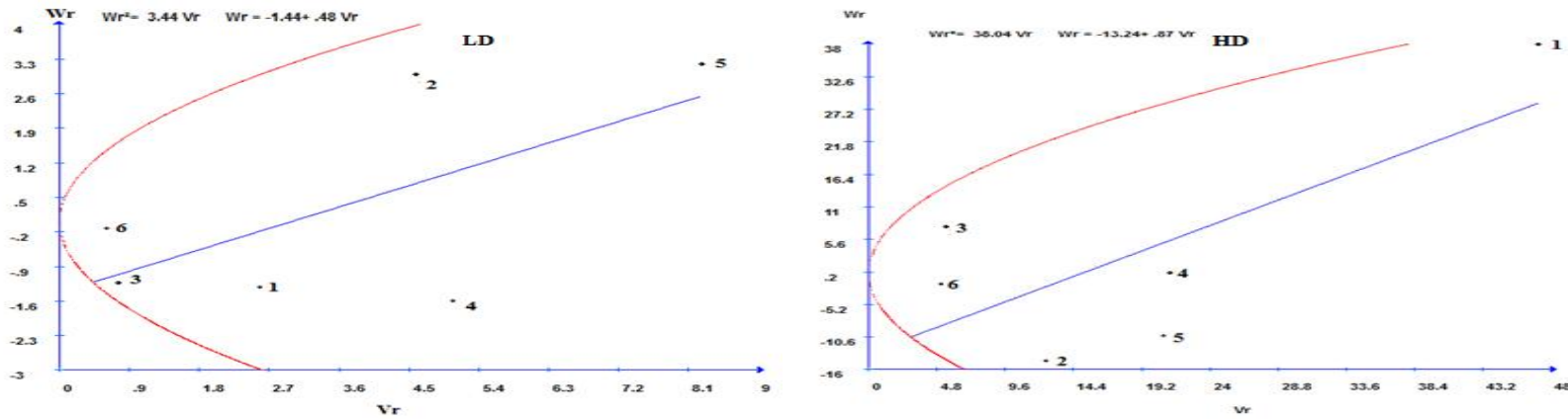


Fig. 5. W_r - V_r graph of barren stalks (BS) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

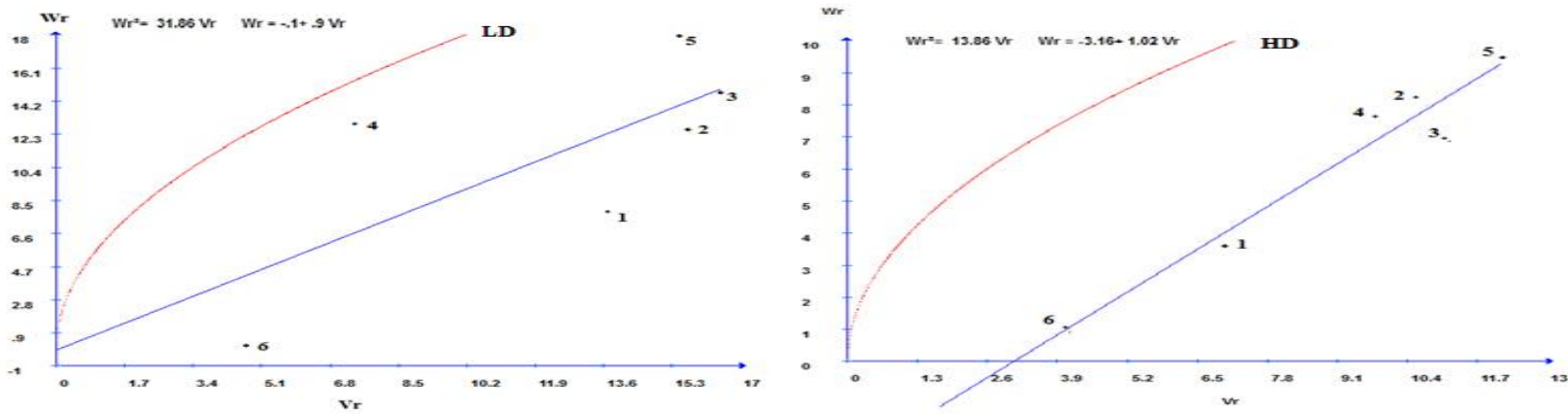


Fig. 6. W_r - V_r graph of leaf angle (LANG) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

For rows per ear (RPE) trait under non-stressed environment (Fig. 8-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 high-density for RPE (Fig. 8-HD), the dispersion of parents around the regression line showed that parents 3 and 6 have 50-75% of dominant genes with parent 3 is the closest to the origin, while parents 1, 4, 2 and 5 are far from the origin, therefore they have mostly recessive genes.

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

For kernels per plant (KPP) trait under non-stressed environment (Fig. 10-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 high-density for KPP (Fig. 10-HD), the dispersion of parents around the regression line showed that parents 1, 2 and 3 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, parent 6 has 50-75% of dominant genes, while parents 5 and 4 are far from the origin, therefore they have mostly recessive genes.

For 100-kernel weight (100 KW) trait under non-stressed environment (Fig. 11-LD), the 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 high-density for 100 KW (Fig. 11-HD), the dispersion of parents around the regression line showed that parents 1, 2 and 3 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, parents 6 and 5 have 50-75% of dominant genes, while parent 4 is far from the origin, therefore it has mostly recessive genes.

For grain yield per plant (GYPP) trait under non-stressed environment (Fig. 12-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 high-density for GYPP (Fig. 12-HD), the dispersion of parents around the regression line showed that parents 1, 2 and 3 are close to the origin of the coordinate, and accordingly have > 75% of dominant genes, while parents 6, 5 and 4 are far from the origin, therefore 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 F₁ hybrids is based on Hayman's graphical approach [17,18], and on the suggestion that genes cause favorable increase in the performance of the trait, such as grain yield and yield 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 [45].

3.3.1 Inbred line L20

Line L20 contains 75-100% dominant genes (favorable) conferring high values for all yield traits (except RPE) under both environments, especially under high density (HD), 50-75% dominant genes for most studied yield traits under the non-stressed (LD). But, this line has mostly dominant genes (unfavorable) for DTA (lateness) under both stressed and non-stressed environments. It contains 50% recessive genes of LANG (favorable) under LD and HD. It contains mostly recessive genes for BS (favorable) under high-D stressed environment. It carries mostly dominant genes for PH and EH traits (unfavorable in our case) under LD and HD environments.

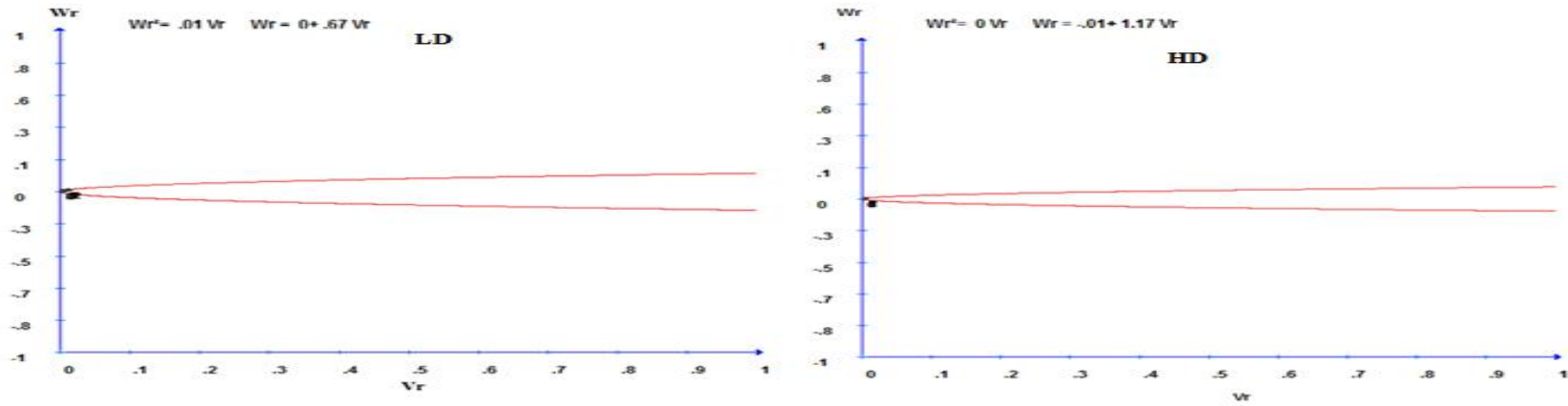


Fig. 7. W_r - V_r graph of ears per plant (EPP) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

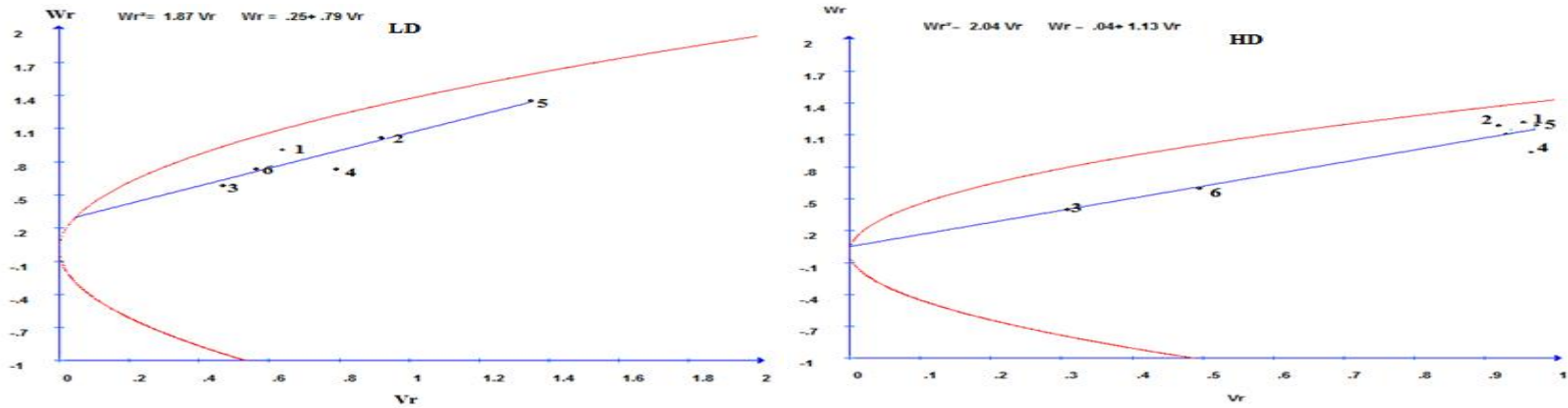


Fig. 8. W_r - V_r graph of rows per ear (RPE) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

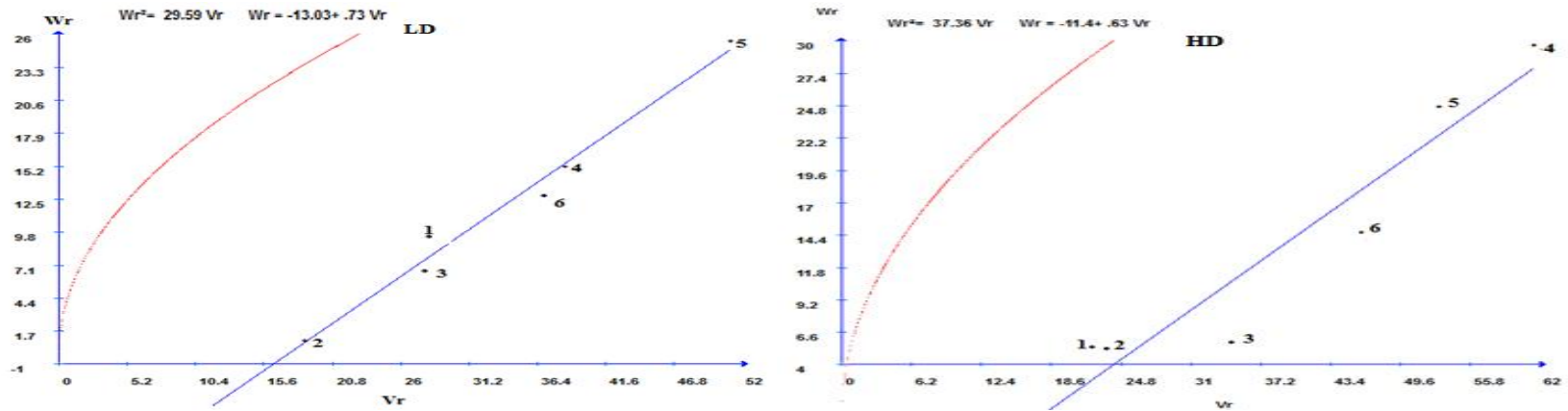


Fig. 9. W_r - V_r graph of kernels per row (KPR) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

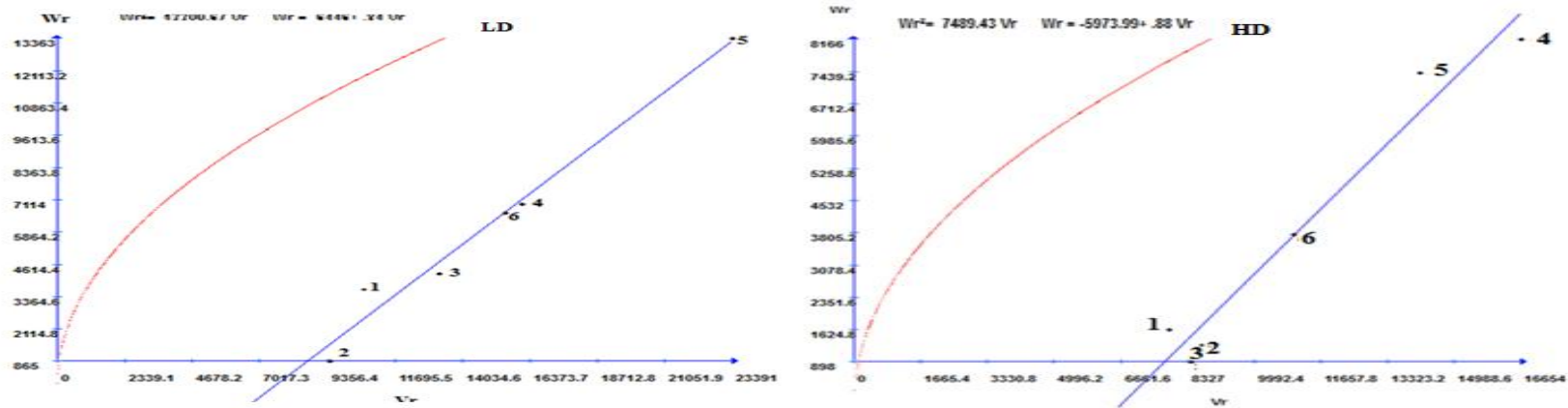


Fig. 10. W_r - V_r graph of kernels per plant (KPP) of F_1 's for combined data across two under low (LD) and high (HD) plant density across two seasons

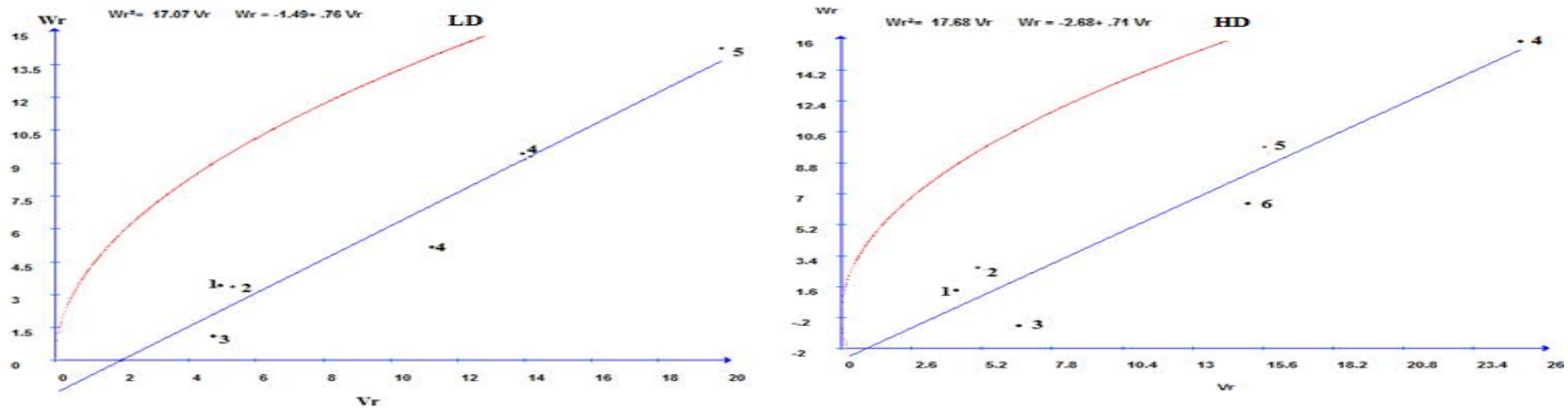


Fig. 11. W_r - V_r graph of 100-kernel weight (100-KW) of F_1 's for combined data across two seasons under low (LD) and high (HD) plant density across two seasons

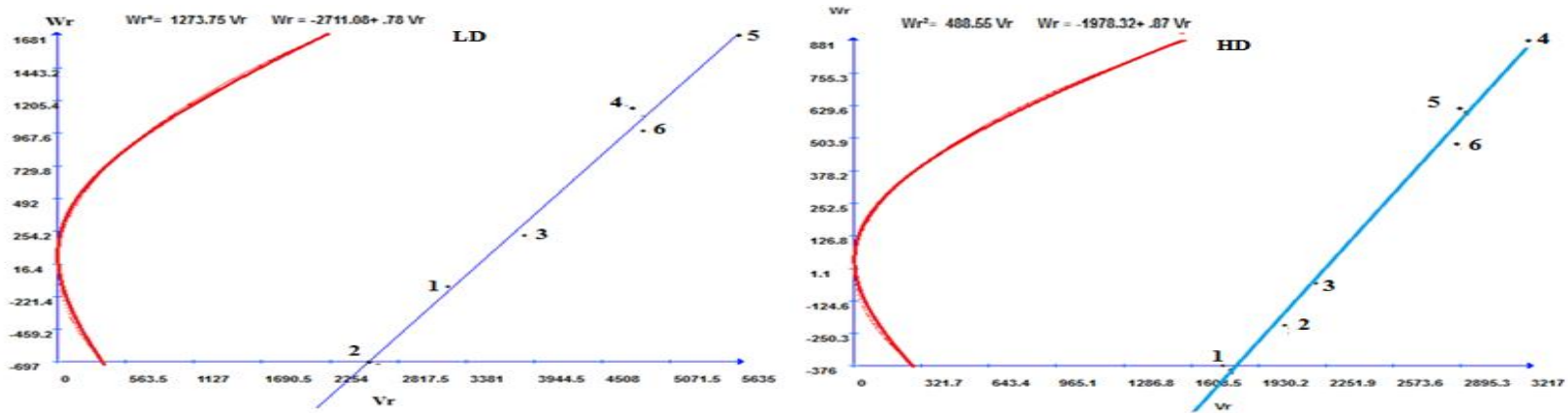


Fig. 12. W_r - V_r graph of grain yield per plant (GYPP) of F_1 's for combined data across two under low (LD) and high (HD) plant density across two seasons

3.3.2 Inbred line L53

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 LANG under both environments. It carries mostly dominant genes for PH trait (unfavorable in our case) under both environments.

3.3.3 Inbred line Sk5

Inbred line Sk5 contains 75-100% dominant genes (favorable) conferring high values for all yield traits (including RPE) under LD and HD environments. 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, especially LD and ASI under LD environment. It has mostly dominant genes for BS (unfavorable) under LD. It carries mostly dominant genes for EH trait (unfavorable in our case) under both environments.

3.3.4 Inbred line L18

Inbred line L18 carries 75-100% recessive genes for yield and its components (unfavorable), especially under HD. It contains 75-100% recessive genes (favorable) for DTA under LD and HD environments. It contains 75-100% recessive genes for plant (PH) and ear (EH) height (favorable in our case) in both environments.

3.3.5 Inbred line L28

Inbred line L28 contains mostly recessive genes for all yield traits (unfavorable) under LD and HD environments. It contains mostly recessive genes for LANG (favorable) under LD and HD environments and BS under LD. It contains 75-100% recessive genes for plant (PH) and ear (EH) height (favorable in our case) in both environments.

3.3.6 Inbred line Sd7

Inbred line Sd7 contains mostly recessive genes for all yield traits (unfavorable) in most cases under all environments, but contains 75-100% dominant genes for RPE (favorable) under LD and HD environments. It contains 75-100% dominant genes for LANG and BS traits

(unfavorable) under both environments. It carries mostly recessive genes (favorable) for ASI under LD and DTA under LD and HD. It contains 75-100% positive genes for plant (PH) and ear (EH) height (unfavorable in our case) in both environments.

Summarizing the above mentioned results, it could be concluded that genes conferring the adaptive traits to HD tolerance are distributed in the parental inbreds as follows: L20, L53 and Sk5 carry genes of high yield and all of its contributing attributes (except RPE in L20 and L53). Genes of low BS are found L20 and genes of narrow LANG in L53, Sk5 and Sd7. Genes of low PH and low EH are found in L18 and L28. Genes of high RPE and short ASI are found in Sd7. Genes for earliness (DTA) are existed in L18 and Sd7. Superiority of the inbreds L20, L53 and Sk5 in grain productivity under high plant density and low-N stresses was reported in previous works [12,28-32,41].

4. CONCLUSION

The present study suggested that heterosis breeding would be more efficient than selection for improving most studied traits under LD and HD environments. Based on the present results, it is recommended to practice selection for improving ASI, BS, KPR and KPP traits under HD stressed environment, but for the remaining studied traits, it is better to practice selection under LD environment in order to obtain higher genetic advance from selection. It seems that the choice of the best selection environment depends also on the trait of interest and its interaction with the environment. This study characterized the six inbred parents with respect of favorable genes for adaptive traits to drought tolerance. The inbred parents L20, L53 and Sk5 carry genes of high yield and all of its contributing attributes (except RPE in L20 and L53). Genes of low BS are found L20 and genes of narrow LANG in L53, Sk5 and Sd7. Genes of low PH and low EH are found in L18 and L28. Genes of high RPE and short ASI are found in Sd7. Genes for earliness (DTA) are existed in L18 and Sd7. This characterization would be fruitful for future plant breeding programs aiming at improving high density tolerance in maize.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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