



GENETIC PARAMETERS CONTROLLING SOME MAIZE ADAPTIVE TRAITS TO ELEVATED PLANT DENSITIES COMBINED WITH REDUCED N-RATES

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Abstract- Low-N stress is one of the factors most frequently occurring under high-plant density. There are common adaptive traits for both high-density (HD) and low-N (LN) stress. Breeding maize for tolerance to high plant density is suggested as an alternative strategy to improve tolerance to low-N. To start an efficient breeding program in Egypt to develop tolerant maize hybrids to high plant density that are able to maximize productivity from land unit area, the present investigation aimed at determining types of gene action and heterosis for some common adaptive traits to HD and LN stress. Diallel crosses (except reciprocals) were made among six maize inbreds differing in their adaptive traits of maize to both HD and LN. Nine field experiments were conducted in 2012 and 2013 seasons using a randomized complete blocks design in 3 replications, for each experiment which is one of nine combinations among 3 plant densities [20,000 (LD), 30,000 (medium-density ;MD) and 40,000 (HD) Plants/fed (one fed = 4200 m²) and 3 N-rates (0 (LN), 120 (MN) and 240 (HN) kg N/fed), i.e., 9 environments, namely E1 (HN-LD), E2 (HN-MD), E3 (HN-HD), E4 (MN-LD), E5(MN-MD), E6 (MN-HD), E7 (LN-LD), E8 (LN-MD) and E9 (LN-HD). Under all the 9 environments, the highest average heterobeltiosis was exhibited by percent barren stalks (BS), followed by grain yield/plant (GYPP) and anthesis-silking interval (ASI), while the lowest was observed in days to silking (DTS). In general, E9 (HD-LN) showed the largest number of crosses exhibiting significant favorable heterobeltiosis and the largest average favorable heterobeltiosis for GYPP and harvest index (HI) (49.5 and 20.0%, respectively). The cross L29 × L55 showed the largest heterobeltiosis for GYPP in E6 (133.6%), E3 (133.3%), E5 (132.1%), E2 (132.0%), E4 (131.2%) and E1 (117.0%) followed by L17 × L54 cross (in 6 environments), L 17 × L18 (in 4 environments) L53 × L54, L29 × L54 and L54 × L55 crosses (in 3 environments). The three inbreds L53, L17 and L18 were the best general combiners for GYPP and other studied traits under all 9 environments, while the inbreds L29, L54 and L55 were the worst. The best crosses in specific combining ability effects for GYPP were L29 × L55 in 7 environments (E1 through E7), L17 × L54, L53 × L54 and L17 × L18 crosses in 6 environments (E1 through E6) and L18 × L53 cross in E7, E8 and E9. Performance of a given inbred was an indication of its general combining ability for GYPP, HI and BS in 6 environments (from E1 to E6). The estimates of dominance were much higher, in magnitude, than additive variance for all studied traits under all nine environments. The degree of dominance in all cases was over-dominance. Broad-sense heritability was of medium magnitude (~50 %) for all studied traits under all nine environments. Narrow-sense heritability was generally of small magnitude, but reached about 27% in leaf angle (LANG) under E9. Expected genetic advance from selection in the nine environments was generally of small magnitude, especially under E7 and E9, but was very high for chlorophyll concentration index under E6 and GYPP under E4. ASI, BS and HI of both inbreds and hybrids, ears per plant of inbreds and LANG of hybrids could be considered good selection criteria for tolerance to HD-LN stress combination of genotypes.

Keywords- High density-low N stress, Maize, Gene action, Heterobeltiosis, Heritability, Selection criteria.

Introduction

Trying to grow hybrid maize varieties newly released by the National Maize Breeding Program in Egypt at high plant densities causes a drastic reduction in grain yield per unit area. The reason is probably due to the fact that these varieties are not tolerant to high plant densities, because of their tallness, one-eared, decumbent leaf and large-size type plants. On the contrary, modern maize hybrids in developed countries are characterized with high yielding ability from unit area under high plant density up to 100,000 plants ha⁻¹ (ca. 40,000 plants fed⁻¹), due to their morphological and phenological adaptability traits, such as early silking, short anthesis silking interval (ASI), less barren stalks and prolificacy [1,2] 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 unit area in Egypt, breeding programs should be directed towards the development of inbreds and hybrids that

characterize with adaptive traits to high plant density and low-N stresses.

Although high plant density results in interplant competition (especially for light, water and nutrients), which affects vegetative and reproductive growth of maize [3,4], the use of high-density and low-nitrogen tolerant hybrids and improving the fertilization management practices would overcome the negative impacts of such competition and lead to maximizing maize productivity from the same unit area. Tolerance to high plant population density was suggested as an alternative breeding strategy to improve tolerance to diverse abiotic stresses including drought and low N [5]. Low N stress is one of the factors most frequently occurring under high plant density and limits maize production. Low-N availability in soils is an important yield-limiting factor frequently found in farmers' fields where fertilization is not commonly used and organic matter is rapidly mineralized [6]. Ears/plant and anthesis-silking interval are considered

as the most important low-N adaptive traits [7]. Under these circumstances, since the smallholder farmers cannot afford additional inputs, it would be desirable to increase the tolerance of the crop to stresses that occur in their fields [8].

An integrated breeding program was initiated by the Dept. of Agronomy, Fac. of Agric., Cairo Univ. in collaboration with Maize Breeding Program of the Toshka Seed Co., Egypt [9], to develop maize inbred lines and hybrids showing adaptive traits for high-density tolerance from exotic and local materials with an ultimate goal of increasing grain yield per land unit area *via* increasing plant density much higher than that presently used by farmers in Egypt. After evaluation of newly-developed inbreds for their *per se* and hybrid performance, a set of inbreds with obvious diversity in their adaptive traits to high-density tolerance was chosen as parents of a diallel cross mating design to study the inheritance of such traits for the purpose of planning proper breeding program for improving tolerant hybrids to high density. In the mean time, the tolerant inbreds to high density were considered tolerant to low-N and the sensitive ones to high density were also considered sensitive to low-N as per our expectations, so that inheritance of adaptive traits to low-N could also be studied. The diallel analysis proposed by Griffing [10] was adopted, to study the main effects.

And interactions of plant densities, N-rates and genotypes on maize performance. The necessary biometrical and genetic analyses were performed to achieve the objectives.

Objectives of the Present Study

- To determine heterosis and the type of gene action controlling inheritance of some adaptive traits for tolerance to stress combinations between high plant density and low-N stresses.
- To recognize the maize traits of strong associations with grain yield under nine environments, to be used as selection criteria for improving tolerance to these stresses.

Materials and Methods

This study was carried out in 2011, 2012 and 2013 summer seasons 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 meter above sea level). Six maize (*Zea mays* L.) inbred lines [Table-1] in the 6th selfed generation, showing clear differences in performance and general combining ability for grain yield/feddan (fed) under high plant density were chosen as parents of diallel crosses.

Table 1- Designation, parental source, origin and most important traits of 6 inbred lines (L) used for making diallel mating design of this study.

Entry designation	Origin	Institution (country)	Prolificacy	Productivity under high-D or low-N	ASI under high-D or low-N	BS under high-D or low-N
L17-Y	SC 30N11	Pion. Int.Co.	Prolific	High	Short	Low
L18-Y	SC 30N11	Pion. Int.Co.	Prolific	High	Short	Low
L53-W	SC 30K8	Pion. Int.Co.	Prolific	High	Short	Low
L29-Y	Pop 59	ARC-Thailand	Non prolific	Low	Long	High
L54-W	SC 30K8	Pion. Int.Co.	Non prolific	Low	Long	High
L55-W	SC 30K8	Pion. Int.Co.	Non prolific	Low	Long	High

ARC: Agricultural Research Center, PION: Pioneer International Company in Egypt, SC: Single Cross, W: White grains and Y: Yellow grains.

In 2011 season, all possible diallel crosses (except reciprocals) were made among the six parents, so seeds of 15 direct F₁ crosses were obtained. Nine field evaluation experiments were carried out in 2012 and repeated in 2013 season. Each experiment included 15 F₁ crosses and their 6 parents and represents one of nine environments. Evaluation in each season was carried out in 9 environments (from E1 to E9), *i.e.*, three nitrogen (N) levels, namely, high-(HN), medium- (MN) and low-N (LN) by adding 240, 120 and 0 kg N/fed, respectively in two equal doses in the form of urea before 1st and 2nd irrigations and three plant density (D), namely, high- (HD), medium- (MD) and low- (LD) plant density (40,000, 30,000 and 20,000 plant/fed) as follows: E1: HN-LD, E2: HN-MD, E3: HN-HD, E4: MN-LD, E5: MN-MD, E6: MN-HD, E7: LN-LD, E8: LN-MD and E9: LN-HD. Available soil nitrogen in 30 cm depth was analyzed immediately prior to sowing. The available nitrogen to each plant (including soil N and added N) was calculated for each environment and found to be 15.72, 10.48, 7.86, 9.72, 6.48, 4.86, 3.72, 2.48 and 1.86 g N/plant in 2012 season and 15.42, 10.28, 7.71, 9.42, 6.28, 4.71, 3.42, 2.28 and 1.71 g N/plant in 2013 season, with an average across the two seasons of 15.57, 10.38, 7.79, 9.57, 6.38, 4.79, 3.57, 2.38, and 1.79 g N/plant for the nine environments (E1 through E9), respectively. Available soil nitrogen in 30 cm depth was analyzed immediately prior to sowing at the laboratories of Water and Environment Unit, ARC, Egypt and found to be 74.38 and 68.43 Kg N/fed in 2012 and 2013 seasons, respectively. A randomized complete blocks design (RCBD) with three replications was used. Each experimental consisted of one ridge of 4 m long

and 0.7 m width. Seeds were sown in hills at 15, 20 and 30 cm apart, thereafter (before the 1st irrigation) were thinned to one plant/hill to achieve the three plant densities, *i.e.*, 40,000, 30,000 and 20,000 plant/fed, respectively. The soil of the experimental site was clayey loam. All other agricultural practices were followed according to the recommendations of ARC, Egypt.

Data were collected on days to 50% silking (DTS), anthesis-silking interval (ASI), barren stalks (BS), leaf angle (LANG) measured as the angle between stem and blade of the leaf just above ear leaf and chlorophyll concentration index (CCI) measured by chlorophyll concentration meter, Model CCM 200 as the ratio of transmission at 931 nm and 653 nm through the leaf of top-most ear (<http://www.apogeeinstruments.co.uk/apogee-instruments-chlorophyll-content-meter-technical-information/>). At harvest, number of ears per plant (EPP), grain yield per plant (GYPP) and harvest index (HI) were measured.

Combined analysis of variance of the RCBD for each environment (from E1 to E9) across the two seasons was performed if the homogeneity test was non-significant. Diallel crosses were analyzed to determine general combining ability (GCA) and specific combining ability (SCA) variances and effects for studied traits according to Griffing [10] Model I (fixed effect) Method 2. Hayman's approach [11,12] (that assumes random model) was used to estimate genetic components and ratios. The conclusions obtained from Hayman's analyses will not be generalized, but will help us to characterize our genetic material for its proper use in the future breeding programs.

Heterobeltiosis was calculated as a percentage of F_1 relative to the better-parent (BP) values, as follows:

$$\text{Heterobeltiosis (\%)} = 100[(F_1 - BP') / BP']$$

where: F_1' : mean of an F_1 cross, and BP' : mean of the better parent of this cross.

Expected Genetic Advance (GA): from direct selection as a percentage of the mean (\bar{x}) was calculated according to Singh & Chaudhary [13] based on a 10% selection intensity as follows:

$$GA = 100 k h^2 d_{ph} / \bar{x}$$

where: $k = 1.76$ = the standard selection differential for 10% selection intensity, and d_{ph} = the square root of the denominator of the narrow-sense heritability equation. Genetic correlation coefficients were calculated between grain yield per plant and other studied traits under each environment according to Singh & Chaudhary [13] using the following formula:

$$r_g = \delta^2_{gy} / (\delta^2_{gx} \cdot \delta^2_{gy})^{1/2}$$

where: δ^2_{gy} = the genotypic covariance between traits, X and Y and δ^2_{gx} and δ^2_{gy} = the genotypic variance of the two traits, X and Y, respectively.

Rank correlation coefficients were calculated using SPSS 17 computer software between pairs of *per se* performance of inbred lines and their GCA effects; between *per se* performance of F_1 crosses and their SCA effects and between SCA effects and heterobeltiosis of F_1 crosses for studied traits under studied 9 environments. The significance of the rank correlation coefficient was tested according to Steel, et al [14].

Results and Discussion

Heterobeltiosis

Estimates of heterobeltiosis across all F_1 crosses, maximum values and number of crosses showing significant favorable heterobeltiosis for all studied traits under the nine environments across 2011 and 2012 years are presented in [Table-2]. Favorable heterobeltiosis in the studied crosses was considered negative for DTS, ASI, BS and LANG and positive for the remaining studied traits under all combinations between plant densities and N levels. In general, the highest average significant favorable heterobeltiosis was observed in BS (-97.9, -100, -99.6, -97.3, -96.2, -94.3, -40.7, -44.9 and -39.9%) under E1 through E9, respectively, followed by GYPP and ASI traits [Table-2]. However, the lowest average significant (favorable) heterobeltiosis was shown by DTS (-1.9, -4.6, -3.6, -0.9, -1.9, -1.4, -2.9, -3.0 and -3.3%) in E1 through E9, respectively. The traits LANG and CCI, showed on average unfavorable heterobeltiosis under all environments. However, some crosses showed significant favorable heterobeltiosis (reaching to 118.1% under E9 for CCI). In general, E9 environment (low-N and high-D), where both stresses existed, showed the largest number of crosses showing significant favorable heterosis and the largest average favorable heterobeltiosis for GYPP and HI traits (49.5 and 20.0%, respectively). The reason for getting the highest average heterobeltiosis estimates under E9 environment could be attributed to the large reduction in grain yield and its components of the parental inbreds compared to that of F_1 crosses due to severe stresses of both plant density and available soil nitrogen existed in this environment.

Table 2- Estimates (%) of average (Aver.) and maximum (Max.) heterobeltiosis and number (No.) of crosses showing significant favorable heterobeltiosis for studied traits under 9 environments across two years.

Parameter	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
Days to 50% silking (DTS)									
Aver.	-1.9	-4.6	-3.4	-0.9	-1.9	-1.4	-2.9	-3	-3.3
Max.	-7	-13.5	-12	-4.9	-7.5	-9.3	-11.2	-10	-9.4
No.	7	12	9	5	7	8	10	9	9
Anthesis-silking interval (ASI)									
Aver.	-10.6	-34.1	-39.8	-17.1	-27.2	-45.1	-17.4	-19.6	-17.1
Max.	-80	-83.3	-84.6	-83.3	-81.8	-88.9	-36.7	-48.6	-57.1
No.	7	12	14	8	11	14	12	13	12
Barren stalks (BS)									
Aver.	-97.9	-100	-99.6	-97.3	-96.2	-94.3	-40.7	-44.9	-39.9
Max.	-100	-100	-100	-100	-100	-100	-73.1	-76.1	-83.4
No.	15	15	15	15	15	15	13	13	13
Leaf angle (LANG)									
Aver.	34.1	20.3	23.6	32.6	24.6	26.3	32.9	24.3	22.7
Max.	-8.3	-12.3	-8.8	-11.7	-11.1	-4.3	-10.4	-9.7	-5
No.	1	3	2	2	3	1	2	3	1
Chlorophyll concentration index (CCI)									
Aver.	5.4	14.9	-6.8	-0.3	21.6	-10.9	8.6	2	-1.2
Max.	36.3	46.4	67.6	37.5	72.2	40.8	53.4	87.7	118.1
No.	5	11	3	5	13	6	8	6	6
Number of ears per plant (EPP)									
Aver.	5.3	-5.6	-1.8	5.7	9.4	-2.1	6.7	14.8	10
Max.	69.5	45	28.8	30.8	29.3	28.8	26.3	38	40.6
No.	7	4	6	9	11	7	11	12	10
Grain yield per plant (GYPP)									
Aver.	23.7	26.1	29	23.8	20.5	26.8	29.8	33.3	49.5
Max.	117	132	133.3	131.2	132.1	135.5	52.3	73.9	100.1
No.	10	10	10	7	8	9	13	13	14
Harvest index (HI)									
Aver.	6.9	9.2	10.1	5	5	9.7	9.3	11.8	20
Max.	39.4	51.5	49.6	47.3	55.7	55.1	20.3	31.3	34.1
No.	10	10	10	8	8	10	13	13	14

H: high, M: medium, L: low, N: nitrogen, D: density.

These results are in agreement with those of Liu & Tollenaar [15] who reported that increasing plant density from 4 to 12 plants m⁻² resulted in increased heterosis for grain yield of maize. In general, maize hybrids typically yield two to three times as much as their parental inbred lines. However, since a cross of two extremely low yielding lines can give a hybrid with high heterosis, a superior hybrid is not necessarily associated with high heterosis [16]. This author suggested that a cross of two high yielding inbreds might exhibit less heterosis but nevertheless produce a high yielding hybrid. Besides, a hybrid is superior not only due to heterosis but also due to other heritable factors that are not influenced by heterosis. On the contrary, the E5 environment (medium-N and medium-D)

showed the lowest average favorable heterobeltiosis for two traits, i.e., GYPP (20.5%) and HI (5.0%). The largest significant and positive heterobeltiosis for GYPP (135.5%) was shown by the cross L29 × L55 under E6 (medium-N high-D) [Table-3] followed by 133.3, 132.1, 132.0, 131.2 and 117.0% shown by the same cross under E3, E5, E2, E4 and E1, respectively. The second best cross in favorable GYPP heterobeltiosis was L17 × L54 (in 6 environments) followed by L17 × L18 (in 4 environments) and L53 × L54, L29 × L54 and L54 × L55 (in 3 environments). Under the most stressed environment (E9), the highest favorable GYPP heterobeltiosis (100.1%) was shown in L18 × L53 followed by L18 × L55 (91.3%).

Table 3- Estimates of heterobeltiosis (%) for grain yield/plant of F₁ diallel crosses under 9 environments combined across two seasons.

Crosses	E1	E2	E3	E4	E5	E6	E7	E8	E9
	HN-LD	HN-MD	HN-HD	MN-LD	MN-MD	MN-HD	LN-LD	LN-MD	LN-HD
L17XL18	31.0**	41.6**	46.6**	25.4**	28.6**	49.4**	33.8**	54.6**	29.3**
L17XL53	0.1	-5.3	2.5	-2.8	-11.2*	-2.9	32.9**	21.3**	65.5**
L17XL29	-9.3	1.3	-2.5	-7.8*	-7.8	-0.5	35.2**	73.9**	19.5**
L17XL54	55.4**	75.9**	80.0**	54.5**	45.9**	78.6**	34.1**	31.3**	40.4**
L17XL55	-6.8	-0.5	-5.7*	-2.4	-7.9	-4.2	20.7**	44.2**	36.3**
L18XL53	21.3**	14.3**	16.6**	3.4	-13.8**	-8.7**	44.2**	34.0**	100.1**
L18XL29	-2.4	6.8*	-0.9	2.8	4.9	-3.1	30.7**	48.1**	79.1**
L18XL54	16.3**	-10.4**	-15.9**	10.4	-6.7	4.7	44.8**	38.9**	46.9**
L18XL55	29.9**	26.6**	23.8**	8.3	14.6**	13.0**	29.0**	39.9**	91.3**
L53XL29	0.1	2.9	8.9**	9.3	2.6	9.6**	46.9**	11.4**	65.2**
L53XL54	35.7**	31.2**	49.2**	33.6**	29.2**	38.7**	-10.8	-34.1**	-3.3
L53XL55	19.1**	20.3**	45.6**	20.1**	16.6**	35.8**	-23.1**	-3.5	16.9**
L29XL54	22.6**	22.6**	22.5**	42.4**	39.6**	30.1**	48.5**	42.7**	69.4**
L29XL55	117.0**	132.0**	133.3**	131.2**	132.1**	135.5**	52.3**	36.6**	46.6**
L54XL55	25.5**	31.6**	30.9**	29.2**	40.8**	26.3**	28.2**	59.7**	39.0**

H: high, M: medium, L: low, N: nitrogen, D: density and * & ** significant at 0.05 and 0.01 probability levels, respectively.

The superiority of L29 × L55, L54 × L55, L17 × L54 and L18 × L55 in heterobeltiosis estimates for GYPP and/or per feddan under high as well as low plant densities was confirmed by Al-Naggar, et al [17] in a previous work. The two crosses L29 × L55 and L17 × L54 showed the highest *per se* grain yield/fed and are therefore recommended for commercial application under high plant density and high nitrogen conditions and as good genetic material for maize breeding programs.

Combining Ability Variances

Variances estimates for GCA and SCA of the diallel crosses of maize for combined data across two years under 9 environments are presented in [Table-4]. Mean squares due to GCA and SCA indicated significance at P ≤ 0.01 for all studied traits under all 9 environments, suggesting that both additive and non-additive gene effects play important roles in controlling the inheritance of these traits under all environments. A similar conclusion was reported by Al-Naggar, et al [9], Mason & Zuber [18] and Khalil & Khattab [19]. In this study, the magnitude of SCA mean squares was higher than that of GCA mean squares (the ratio of GCA/SCA mean squares was less than unity) for three traits (GYPP, HI and BS) under all environments, ASI in all environments, except E4, suggesting the existence of a greater portion of non-additive than that of additive variance in controlling the inheritance of these traits. A similar conclusion was reported by Mostafa, et al [20], Ahsan, et al [21] and Singh & Shahi [22].

On the contrary, the magnitude of GCA mean squares was higher than that of SCA mean squares (the GCA/SCA ratio exceeded unity) for EPP in 6 environments (E1, E2, E3, E5, E6 and E9), DTS in five environments (E4 through E9) and LANG in 4 environments

(E3, E6, E8 and E9), suggesting the existence of a greater portion of additive and additive × additive than that of non-additive genetic variance in controlling the inheritance of these traits under the respective environments. These results are in agreement with those reported by Al-Naggar, et al [9], Khalil & Khattab [19], El-Shouny, et al [23] and Sultan, et al [24].

Results indicated that mean squares due to the SCA × year interaction were highly significant for LANG and GYPP in most studied environments, indicating that non-additive variance for these cases was affected by years. However, the GCA × year interaction was highly significant for LANG in E1, E2, E3 and E5 and GYPP in E2, E3, E4 and E9 indicating that the additive genetic variance for these cases was affected by years. The mean squares due to SCA × year was higher than those due to GCA × year for LANG and CCI under all environments, BS in all environments, except E3 and GYPP in all environments, except E3, E5 and E9 suggesting that SCA (non-additive variance) is more affected by years than GCA for these cases.

On the contrary, mean squares due to GCA × year was higher than those due to SCA × year for ASI in E3, E4 and E5, EPP in E1, E4, E5 and E7 and HI in E2, E3, E6 and E9, indicating that GCA (additive) variance is more affected than SCA (non-additive) by years for these traits under the respective environments.

GCA Effects of Inbreds

Estimates of GCA effects of parental inbreds for studied traits under the nine environments across two seasons are presented in [Table-5]. The best parental inbreds were those showing negative and significant GCA effects for, DTS, ASI, BS and LANG and those of positive and significant GCA effects for GYPP, HI, CCI and EPP.

For GYPP the best inbred in GCA effects was L53 in 4 environments (E1, E2, E3 and E5) followed by L18 in 3 environments (E7, E8 and E9) and L17 in two environments (E4 and E5). These best

general combiners for grain yield (L53, L18 and L17) were also the best ones in *per se* performance for the grain yield under the respective environments.

Table 4- Mean squares due to GCA and SCA and their interactions with years (Y) for studied characters under 9 environments combined across two seasons.

SOV	Mean squares								
	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
Days to 50 % silking (DTS)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	ns	ns	ns	ns	ns	ns	**	ns
SCA×Y	ns	ns	ns	**	ns	ns	**	*	ns
GCA/SCA	0.8	0.9	0.8	1.8	1.8	2.5	2.5	2	3
GCA×Y/SCA×Y	0.3	0.6	2.8	0.3	1.2	0.4	0.4	2	1.1
Anthesis-silking interval (ASI)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	ns	ns	*	ns	ns	ns	ns	ns
SCA×Y	ns	**	ns	ns	ns	ns	ns	ns	ns
GCA/SCA	0.7	0.5	0.3	1.2	0.5	0.2	0.5	0.2	0.7
GCA×Y/SCA×Y	0.9	0.4	1.4	1.5	1.3	0.6	0.5	0.4	0.1
Barren stalks (BS)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	*	ns	ns	ns	ns	ns	ns	ns
SCA×Y	**	**	ns	*	ns	ns	ns	ns	ns
GCA/SCA	0.2	0.1	0.4	0.1	0.1	0.3	0.2	0.2	0.3
GCA×Y/SCA×Y	0.2	0.9	1.7	0.6	1	0.4	2.2	0.5	0.8
Leaf angle (LANG)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	**	**	*		*	ns	ns	ns	ns
SCA×Y	**	**	**	**	**	**	**	**	**
GCA/SCA	0.7	0.9	1.3	0.7	1	1.2	0.7	1.1	1.9
GCA×Y/SCA×Y	0.9	0.6	0.6	0.6	0.4	0.7	0.5	0.3	0.4
Chlorophyll concentration index (CCI)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	ns	ns	ns	ns	ns	ns	ns	ns
SCA×Y	ns	ns	ns	ns	ns	ns	ns	ns	ns
GCA/SCA	1.2	0.1	2	1.4	0.5	3.3	0.7	1	0.5
GCA×Y/SCA×Y	0.5	0.8	1.2	0.2	0.4	0.3	0.2	0.1	0.3
Number of ears per plant (EPP)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	ns	ns	ns	ns	ns	ns	ns	ns
SCA×Y	**	*	ns	ns	ns	ns	ns	ns	ns
GCA/SCA	1.1	1.9	1.8	0.5	1.1	5.4	0.7	0.4	2.1
GCA×Y/SCA×Y	1.1	1	0.8	3	2.3	0.2	1.3	0.9	0.3
Grain yield per plant (GYPP)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	**	**	**	ns	ns	ns	ns	**
SCA×Y	ns	**	**	**	ns	**	**	ns	**
GCA/SCA	0.5	0.4	0.4	0.4	0.4	0.4	0.4	0.3	0.3
GCA×Y/SCA×Y	0.3	1	1.7	1	1.3	0.4	0.2	0.3	1.2
Harvest index (HI)									
GCA	**	**	**	**	**	**	**	**	**
SCA	**	**	**	**	**	**	**	**	**
GCA×Y	ns	ns	**	**	ns	ns	**	ns	**
SCA×Y	ns	ns	ns	ns	ns	ns	ns	ns	ns
GCA/SCA	0.8	0.6	0.6	0.5	0.6	0.4	0.5	0.2	0.2
GCA×Y/SCA×Y	0.8	1.6	2.2	1	0.6	1.1	0.2	1	1.7

* and ** indicate significance at 0.05 and 0.01 probability levels, respectively and ns: non-significance.

Table 5- Estimates of GCA effects of parents for studied characters under 9 environments combined across two seasons.

Parents	\bar{g}_i								
	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
Days to 50 % silking (DTS)									
L17	-0.64**	-0.85**	-1.38**	-0.72**	-0.43**	-1.78**	-1.30**	-2.05**	-3.04**
L18	-0.03	0.09	0.03	0.06	-0.08	0.64**	-0.28**	0.35**	0.69**
L53	-0.60**	-0.66**	-0.05	0.1	-0.31**	0.22*	0.89**	1.24**	1.15**
L29	-0.16	-0.72**	-0.01	-0.47**	-0.66**	-0.99**	-1.09**	-0.69**	0.04
L54	0.55**	2.13**	1.10**	1.49**	1.65**	2.20**	2.08**	1.76**	2.13**
L55	0.88**	0.01	0.31**	-0.47**	-0.18*	-0.30**	-0.30**	-0.61**	-0.96**
SE g-g _i	0.13	0.13	0.1	0.11	0.12	0.13	0.13	0.1	0.11
Anthesis-silking interval (ASI)									
L17	-0.10*	-0.08	-0.08*	-0.10*	0.02	-0.14**	-0.11	-0.15*	-0.70**
L18	-0.19**	0.22**	-0.16**	0.03	-0.02	-0.14**	-0.22**	0.04	-0.31**
L53	-0.04	-0.31**	-0.22**	-0.49**	-0.38**	-0.08	0.1	0.04	-0.35**
L29	0.13**	0.24**	0.28**	0.44**	0.33**	0.15**	-0.24**	-0.35**	0.24**
L54	-0.25**	-0.12*	0.09*	-0.03	-0.10*	-0.06	0.03	0.27**	0.30**
L55	0.46**	0.05	0.09*	0.15**	0.15**	0.26**	0.43**	0.15*	0.82**
SE g-g _i	0.07	0.07	0.06	0.06	0.06	0.07	0.09	0.11	0.09
Barren stalks (BS)									
L17	-0.17	-0.02	-0.68**	0.02	-0.66**	-1.20**	-1.36**	-2.88**	1.76**
L18	-0.13	-0.13	-0.74**	-0.27**	-0.47**	-0.85**	-2.89**	-1.99**	-3.71**
L53	-0.39**	-0.75**	-1.49**	-0.92**	-0.68**	-1.18**	1.70**	-0.52	-3.58**
L29	-0.09	0.14	0.71**	0.35**	0.95**	0.33	1.01**	0.32	-0.34
L54	0.11	0.29**	0.75**	0.38**	0.91**	1.58**	0.21	3.24**	3.40**
L55	0.67**	0.46**	1.45**	0.43**	-0.05	1.32**	1.32**	1.83**	2.48**
SE g-g _i	0.15	0.13	0.17	0.15	0.19	0.39	0.45	0.48	0.41
Leaf angle (LANG)									
L17	0.1	-0.65**	-0.37**	-0.08	-0.79**	-0.42**	-0.33**	-0.81**	-0.24**
L18	-1.42**	-1.44**	-1.20**	-1.41**	-1.58**	-1.07**	-1.45**	-1.43**	-1.16**
L53	2.56**	2.27**	2.32**	2.51**	2.23**	2.37**	2.36**	2.28**	2.65**
L29	-1.29**	-1.40**	-1.49**	-1.22**	-1.31**	-1.51**	-1.01**	-1.49**	-1.64**
L54	-0.67**	0.54**	0.13	-0.70**	0.65**	-0.09	-0.31**	0.78**	-0.14
L55	0.71**	0.67**	0.61**	0.90**	0.81**	0.72**	0.74**	0.67**	0.53**
SE g-g _i	0.14	0.14	0.13	0.15	0.13	0.12	0.13	0.13	0.11
Chlorophyll concentration index (CCI)									
L17	0.74*	2.13**	2.83**	-4.57**	-0.98**	-5.42**	1.53**	1.74**	-1.78**
L18	2.81**	1.28**	-0.24	1.55**	-0.61*	-0.73**	-1.59**	-0.70**	1.64**
L53	-6.27**	-0.71**	-7.29**	1.01**	-2.48**	-4.75**	-1.86**	-1.24**	-1.57**
L29	0.95**	-0.14	11.34**	4.10**	1.37**	12.68**	0.84**	3.83**	2.12**
L54	2.79**	-1.02**	-2.49**	-5.25**	-1.51**	0.19	2.09**	-1.82**	-0.88**
L55	-1.03**	-1.54**	-4.15**	3.17**	4.20**	-1.97**	-1.01**	-1.82**	0.47**
SE g-g _i	0.5	0.34	0.26	0.55	0.39	0.24	0.54	0.41	0.26
Number of ears per plant (EPP)									
L17	-0.06**	-0.05**	0.01	0.03**	0.05**	-0.07**	0.01	0.01	-0.02
L18	0.05**	0.01	0.02*	0.02*	0.04**	0.14**	0.05**	0.04**	0.10**
L53	0.12**	0.12**	0.09**	0.02*	0.02*	0.01	0.01	0.01	0.03**
L29	-0.04**	0.05**	-0.03**	-0.01	-0.03**	0.01	-0.02**	-0.01	-0.01
L54	-0.03**	-0.01	-0.05**	-0.01	-0.06**	-0.01	0.01	-0.04**	-0.06**
L55	-0.05**	-0.13**	-0.03**	-0.05**	-0.02*	-0.08**	-0.04**	0.01	-0.05**
SE g-g _i	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Grain yield per plant (GYPP)									
L17	9.80**	5.63**	5.81**	14.72**	9.00**	9.37**	-0.3	0.66	-2.86**
L18	9.23**	6.26**	7.10**	1.03	-2.59**	2.38**	7.21**	4.65**	5.91**
L53	12.00**	13.46**	10.98**	10.09**	12.79**	9.29**	-1.57**	2.60**	1.39**
L29	-21.87**	-12.94**	-14.91**	-12.03**	-8.91**	-11.91**	2.79**	-0.51	0.94**
L54	0.47	-5.58**	-4.35**	-3.36**	-4.49**	-2.96**	-0.07	-3.69**	-3.13**
L55	-9.63**	-6.83**	-4.64**	-10.45**	-5.79**	-6.15**	-8.06**	-3.72**	-2.25**
SE g-g _i	0.87	0.54	0.49	0.83	0.69	0.46	0.82	0.58	0.44
Harvest index (HI)									
L17	1.31**	0.75**	1.09**	2.13**	1.82**	1.56**	-0.21	-0.22	-0.46**
L18	0.90**	1.31**	1.36**	0.21**	-0.40**	0.62**	1.07**	0.50**	1.10**
L53	0.73**	1.46**	1.16**	0.72**	1.50**	1.07**	-0.67**	0.88**	0.24*
L29	-2.67**	-2.11**	-2.57**	-1.75**	-1.72**	-2.09**	0.59**	-0.28**	0.01
L54	0.54**	-0.70**	-0.57**	-0.57**	-0.91**	-0.51**	0.53**	-0.52**	-0.79**
L55	-0.80**	-0.71**	-0.47**	-0.75**	-0.30**	-0.64**	-1.31**	-0.36**	-0.1
SE g-g _i	0.11	0.11	0.11	0.11	0.14	0.12	0.19	0.17	0.16

H: high, M: medium, L: low, N: nitrogen, D: density and * and ** significant at 0.05 and 0.01 probability levels, respectively.

On the contrary, the inbred lines L29, L54 and L55 were the worst in GCA effects for GYPP and the worst in *per se* performance for the same trait under the nine environments. Superiority of the inbreds L17, L18 and L53 in GCA effects for GYPP was associated with their superiority in GCA effects for other studied traits. The inbred L53 was also the best general combiner for low BS in 5 environments (E1 through E5) followed by L18 (E7 and E9) and L17 (E8) and short ASI (E2 through E5) followed by L17 (E6 and E9) and L29 (E7 and E8). Inbred L17, the best inbred for GCA effects for GYPP under E4 and E6 conditions was also the best general combiner, *i.e.*, the best in producing good hybrid combinations for early DTS under 8 environments followed by L29 in E5 and high HI in 4 environments (E1, E4, E5 and E6) followed by L18 in 3 environments (E3, E7 and E9) and L53 in E2 and E8. Inbred L18, the best inbred for GCA effects for grain yield under E7, E8 and E9 (the lowest in soil available nitrogen) was also the best general combiner for high EPP in 4 environments (E6, E7, E8 and E9) followed by L53 in E1, E2 and E3 and L17 in E4 and E5 and narrow LANG in E1, E2, E4, E5 and E7 followed by L29 in E3, E6, E8 and E9. The inbred L29 was the best general combiner for CCI in 5 environments (E3, E4, E6, E8 and E9) followed by L17 (E2), L18 (E1), L54

(E7) and L55 (E5). In a previous study [9], the inbred lines L17, L18 and L53 were also the best general combiners for EPP and GYPP under high and low plant densities. Previous studies proved that positive GCA effects for EPP are a good indicator of stress tolerance [6,25].

SCA Effects of Diallel Crosses

Estimates of SCA of F_1 diallel crosses for studied traits under the nine environments are presented in [Table-6]. The best crosses in SCA effects were considered those exhibiting significant negative SCA effects for DTS, ASI, LANG and BS and the worst ones were those showing significant positive SCA effects for the rest of studied traits. For GYPP the largest positive (favorable) and significant SCA effects were recorded by the cross L29 \times L55 followed by L17 \times L54, L53 \times L54 and L17 \times L18 crosses under 6 environments (from E1 to E6), the cross L18 \times L53 followed by L29 \times L54 under the most stressed environments (E7, E8 and E9), the cross L53 \times L29 under E7 and L54 \times L55 under E8 [Table-6]. The above crosses may be recommended for maize breeding programs for the improvement of tolerance to high plant density, as well as tolerance to low-nitrogen and drought tolerance [5,25].

Table 6- Estimates of SCA effects for GYPP under 9 environments combined across two seasons.

Crosses	\hat{S}_{ij}								
	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
L17XL18	33.63**	38.38**	45.93**	30.05**	32.83**	38.88**	8.06**	12.04**	-5.58**
L17XL53	-29.61**	-26.84**	-25.15**	-30.63**	-28.73**	-24.24**	19.37**	13.80**	18.28**
L17XL29	-15.30**	-11.81**	-12.90**	-17.57**	-11.35**	-8.85**	4.59**	17.98**	-5.37**
L17XL54	90.75**	85.15**	80.17**	87.75**	58.68**	71.95**	10.90**	4.29**	8.89**
L17XL55	-22.51**	-20.41**	-27.17**	-9.41**	-14.61**	-18.71**	2.89	3.95*	6.00**
L18XL53	13.28**	4.14**	-0.87	-10.41**	-21.04**	-24.32**	22.71**	20.20**	26.75**
L18XL29	-11.07**	5.07**	0.84	0.74	4.58*	-1.3	2.03	9.01**	13.13**
L18XL54	1.9	-27.80**	-30.63**	5.04*	-14.40**	-1.14	18.09**	6.28**	2.81*
L18XL55	37.44**	28.62**	24.69**	8.53**	13.74**	11.80**	11.36**	6.94**	22.19**
L53XL29	2.12	4.85**	3.97**	13.27**	9.59**	12.31**	29.71**	6.87**	14.37**
L53XL54	50.57**	43.22**	46.91**	47.91**	44.70**	38.95**	-22.96**	-27.37**	-15.70**
L53XL55	27.63**	26.98**	42.48**	30.92**	27.28**	38.51**	-26.76**	-2.23	-6.52**
L29XL54	-6.11**	-10.18**	-7.44**	-1.76	-1.98	-9.24**	20.82**	12.70**	18.66**
L29XL55	101.65**	86.09**	74.13**	99.31**	72.14**	64.83**	21.47**	0.74	2.75*
L54XL55	-14.06**	-6.63**	-9.72**	-18.83**	-4.08*	-17.89**	13.34**	26.78**	7.13**
SE $S_{ij} - S_{ik}$	3.26	2.03	1.81	3.09	2.6	1.72	3.08	2.18	1.65
SE $S_{ij} - S_{kl}$	1.23	0.77	0.68	1.17	0.99	0.65	1.16	0.83	0.62

H: high, M: medium, L: low, N: nitrogen, D: density and * and ** significant at 0.05 and 0.01 probability levels, respectively.

It is worthy to note that for the studied traits, most of the best crosses in SCA effects for a given trait included at least one of the best parental inbred lines in GCA effects for the same trait. The same conclusion was confirmed previously by some investigators [9]. In this study, besides the superiority of crosses in SCA effects for GYPP the cross (L29 \times L55) was also superior in SCA effects for EPP under E4, E5 and E8, BS under E1, E3 and E4, LANG under E6 and ASI under E1, E2 and E3, the cross (L17 \times L54) was superior in SCA effects for EPP under E2, E3 and E6 and LANG under E4, E7 and E8 and the cross (L17 \times L18) was also superior in SCA effects for LANG under E1, DTS under E1, E2, E4 and E5 and ASI under E4 and E5 and the cross (L53 \times L54) was also superior in SCA effects for ASI under E6.

Correlations between *per se* Performance, GCA, SCA and Heterosis

Rank correlation coefficients calculated between mean performance of inbreds parents (\bar{x}_p) and their GCA effects for some selected

characters are presented in [Table-7]. In general, the environment E2 showed significant correlations between \bar{x}_p and GCA effects for 5 out of 6 characters, followed by E3, E4 and E6 (for seven characters), E1 (6 characters) and E5 (5 characters). On the contrary, the most stressed environments (E9 and E7) didn't show any significant correlation coefficient between \bar{x}_p and GCA effects followed by E8 (also severe stress) which showed a significant correlation for one trait (EPP). Out of nine environments, maximum number of significant correlations between \bar{x}_p and GCA effects were shown by GYPP and BS in 6 environments and HI trait in 5 environments. The strongest correlations (highest in magnitude) between \bar{x}_p and GCA effects were shown by BS trait. Under no stress, light and medium stresses, the best performing lines are also the best general combiners and *vice versa* for grain yield and barren stalk percentage traits. This conclusion is not valid in the most stressed environments (especially E9 and E7). A similar conclusion was reported by Meseka, et al [27,28]. For F_1 crosses, there was no significant correlation coefficient between mean performance (\bar{x}_c) and SCA ef-

fects, except in 3 out of 60 cases [Table-7]. The exceptions (that showed significant correlation coefficients between \bar{x}_c and SCA effects) were GYPF (in E4), EPP (in E9), ASI and BS (in E7) and PH (E5). In general, the mean performance of a given cross is not an indication of its specific combining ability. This conclusion was previously reported by Srdić, et al [29] and Fan, et al [30]. Significant correlations between mean performance of crosses (\bar{x}_c) and

heterobeltiosis [Table-7] were exhibited only in 15 out of 60 cases, most of them are shown by BS trait (E1, E2, E3, E4, E5 and E6), ASI (E1, E2, E3 and E7) and LANG (E2, E8 and E9). For these traits, the mean performance of a cross could be used as an indicator of its useful heterosis under the corresponding environments. The trait EPP did not exhibit any correlation between \bar{x}_c and heterobeltiosis under all (nine) environments.

Table 7- Rank correlation coefficients among mean performance of inbreds (\bar{x}_p) and their GCA effects and between pairs of mean performance of F_1 's (\bar{x}_c), SCA effects and heterobeltiosis (Hetero.) parameters under nine environments combined across two seasons.

Correlation	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
Anthesis-silking interval (ASI)									
\bar{x}_p vs. GCA	0.49	0.77*	0.83*	0.03	0.49	0.43	0.43	0.54	0.26
\bar{x}_c vs. SCA	-0.31	-0.09	0.18	-0.15	0.37	-0.36	0.75**	0.43	-0.24
\bar{x}_c vs. Hetero.	0.49*	0.91**	0.60**	0.05	0.21	0.17	0.77**	0.18	0.05
SCA vs. Hetero.	-0.46*	-0.05	0.35	0.64**	0.09	0.17	0.92**	0.1	0.3
Barren stalks (BS)									
\bar{x}_p vs. GCA	1.00**	1.00**	0.94**	0.83*	0.94**	0.77*	-0.14	-0.09	-0.09
\bar{x}_c vs. SCA	0.17	0.35	-0.12	-0.25	0.39	-0.38	-0.53*	0.17	0.13
\bar{x}_c vs. Hetero.	1.00**	0.99**	1.00**	1.00**	0.58*	0.98**	-0.32	0.34	-0.05
SCA vs. Hetero.	0.17	0.37	-0.12	-0.25	0.12	-0.42	-0.02	0.12	0.13
Leaf angle (LANG)									
\bar{x}_p vs. GCA	-0.31	-0.14	0.09	-0.09	-0.2	-0.43	-0.09	-0.2	-0.2
\bar{x}_c vs. SCA	0.07	0	-0.21	0.1	0.28	0.13	-0.22	-0.1	0.38
\bar{x}_c vs. Hetero.	0.15	0.71**	0.18	0.21	0.3	-0.37	0.23	0.75**	0.45*
SCA vs. Hetero.	0.24	0.09	0.37	0.18	-0.09	0.17	0.22	-0.09	0.2
Number of ears per plant (EPP)									
\bar{x}_p vs. GCA	-0.31	0.77*	0.21	0.79*	0.43	1.00**	0.26	0.88*	-0.14
\bar{x}_c vs. SCA	-0.13	-0.04	-0.31	0.35	-0.16	0.21	-0.16	-0.09	0.53*
\bar{x}_c vs. Hetero.	-0.14	0.14	-0.15	0.23	-0.23	-0.32	0.34	0.14	-0.03
SCA vs. Hetero.	-0.03	0.04	0.4	-0.01	0.55*	0.28	-0.1	0.46*	-0.28
Grain yield per plant (GYPP)									
\bar{x}_p vs. GCA	0.77*	0.77*	0.71*	0.77*	0.77*	0.83*	0.49	0.03	0.09
\bar{x}_c vs. SCA	-0.2	0.12	0.11	-0.25	-0.07	-0.25	0.21	0.37	0.23
\bar{x}_c vs. Hetero.	-0.11	-0.16	-0.05	-0.28	-0.34	0.01	0.43	0.70**	0.26
SCA vs. Hetero.	0.22	0.26	0.16	0.12	0.33	-0.36	0.09	0.09	0.31
Harvest index (HI)									
\bar{x}_p vs. GCA	0.94**	0.83*	0.77*	0.94**	0.26	0.89**	-0.43	0.03	-0.09
\bar{x}_c vs. SCA	-0.04	0.03	-0.18	0.15	-0.13	-0.23	-0.11	0.04	0.43
\bar{x}_c vs. Hetero.	-0.25	0	-0.11	0.15	0.11	0.15	0.08	-0.01	0.47*
SCA vs. Hetero.	0.16	0.3	0.21	0.4	0.53*	0.49*	0.13	-0.19	0.09

H: high, M: medium, L: low, N: nitrogen, D: density and * and ** significant at 0.05 and 0.01 probability levels, respectively.

The rank correlations between SCA effects of crosses and their heterobeltiosis percentages [Table-7] were non significant under all (nine) environments for 3 out of 6 traits, namely GYPF, BS and LANG, but were significant under two environments for EPP (E5 and E8) and HI (E6 and E7) and ASI (E4 and E7). In general, results of the present study concluded that the SCA effects of crosses could not be expected from their heterobeltiosis values in most cases for six selected characters under nine environments. Results in [Table-7] indicates that the environment E2 followed by E1 (the lowest stress) exhibited the strongest correlation between \bar{x}_p and GCA effects and between \bar{x}_c and heterobeltiosis, while the environment E7, E8 and E9 (the most severe ones) exhibited the weakest correlation.

Genetic Variances and Ratios, Heritability and Expected Selection Gain

Estimates of genetic variances and ratios for studied traits under 9 environments across two years are presented in [Table-8]. The

dominance genetic component of variation (H_1) was highly significant for all studied traits under all nine environments, except for EPP under E7, indicating that heterosis breeding is the method of choice for the genetic improvement of the most studied traits, *i.e.*, grain yield and adaptive traits to both high plant density and low-nitrogen stress under all environments. The additive component of variation (D) was also highly significant for all studied characters under all environments, except for GYPF and DTS under E7, E8 and E9, EPP in E7, HI under E7 and E9, ASI under E4, E5, E6, E8 and E9, CCI in E2, E5 and E9 and DTS under E2 and E3, where additive was non significant. This indicated that selection may be used in maize heterogeneous populations for improving such traits, where significant additive variance exists under respective environments [9,31]. The estimates of dominance were much higher, in magnitude, than additive variance for all studied traits under all nine environments, suggesting that dominance variance plays the major role in the inheritance of these traits in all cases and that heterosis breeding would be more efficient than selection for improving all studied traits under 9 environments.

The overall dominance effects of heterozygous loci (h^2) controlling all studied traits under all environments, except LANG in E3, E5, E8 and E9 and CCI in E3, E4, E6, E8 and E9, were highly significant, that could be due to the presence of a considerable amount of dominance effects in the parental genotypes. Average degree of dominance ($(H_1/D)^{1/2}$) was greater than unity for all studied traits under all environments, indicating that the degree of dominance in all cases was over dominance. The highest $(H_1/D)^{1/2}$ value was recorded in E9 (GYPP and HI), E7 (BS and CCI), E8 (EPP), E1 (DTS) and E5 (ASI). The ratio ($H_2/4H_1$) indicated a symmetrical distribution of positive and negative dominant genes in parents in most studied

characters under 9 environments. The exceptions were DTS and EPP traits under all environments, 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 traits under all environments. The exceptions were ASI and BS traits under all environments, where the ratio (K_D/K_R) was less than unity, indicating minority of dominant alleles and the excess of recessive alleles ($p > q$) and DTS trait where K_D/K_R was about unity, indicating nearly equal proportion of dominance and recessive alleles in parents, i.e., symmetrical distribution ($p = q = 0.5$).

Table 8- Estimates of genetic parameters and ratios for studied traits under 9 environments across two seasons.

Variance components	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
Days to 50 % silking (DTS)									
D	0.25**	1.28	0.56	2.87**	2.40**	6.06**	2.24	3.12	8.08**
H ₁	12.82**	35.41**	25.10**	8.30**	9.41**	22.32**	16.17**	26.36**	30.27**
h^2	10.07**	46.37**	24.80**	7.92**	13.39**	17.38**	25.05**	28.81**	44.68**
E	0.56	0.59	0.36	0.58	0.47	0.52	0.58	0.59	0.47
$(H_1/D)^{1/2}$	7.16	5.26	6.68	1.7	1.98	1.92	2.69	2.91	1.94
$H_2/4H_1$	5.36	1.68	2.5	8.32	7.09	2.73	3.87	2.25	1.89
K_D/K_R	0.68	0.62	1.79	1.16	1	1.16	0.5	0.71	0.94
h^2/H_2	0.04	0.19	0.1	0.03	0.05	0.07	0.1	0.12	0.2
$h^2_b\%$	43.02	47.2	47.15	40.93	43.18	46.37	45.3	46.63	47.71
$h^2_n\%$	0.52	1.02	0.76	7.5	5.86	7.02	3.02	2.98	6.54
GA%	0.02	0.12	0.08	0.06	0.14	0.52	0.18	0.28	0.24
Anthesis-silking interval (ASI)									
D	0.13**	0.10**	1.00**	0.07	0.07	0.1	0.50**	0.5	0.86
H ₁	2.31**	1.67**	2.60**	1.69**	2.64**	2.84**	2.07**	5.36**	11.19**
h^2	1.13**	2.14**	4.05**	1.17**	2.42**	5.24**	2.34**	7.15**	13.58**
E	0.3	0.21	0.18	0.27	0.21	0.3	0.51	0.93	0.74
$(H_1/D)^{1/2}$	4.2	4.08	1.61	4.97	6.21	5.33	2.03	3.27	3.61
$H_2/4H_1$	0.49	0.63	0.39	0.66	0.41	0.29	1.78	0.73	0.37
K_D/K_R	1.73	0.43	0.89	0.46	0.63	0.67	0.53	0.9	1.3
h^2/H_2	0.25	0.51	1.01	0.26	0.56	1.59	0.16	0.46	0.83
$h^2_b\%$	32.06	35.9	42.01	32.43	38.95	36.27	30.49	30.87	39.55
$h^2_n\%$	1.3	1.14	7.4	0.74	0.62	0.76	3.2	1.7	2.02
GA%	0.22	0.1	0.82	0.1	0.12	0.16	0.3	0.44	0.48
Barren stalks (BS)									
D	0.70**	2.02**	17.78**	1.96**	7.39**	8.68**	5.49**	38.38**	57.26**
H ₁	10.66**	22.94**	72.77**	54.32**	117.57**	94.61**	342.36**	784.06**	906.52**
h^2	48.76**	94.04**	250.53**	224.64**	467.79**	421.47**	528.06**	1281.98**	1246.55**
E	0.83	0.87	1.3	0.64	1.18	8.05	5.24	7.14	4.56
$(H_1/D)^{1/2}$	3.89	3.37	2.02	5.26	3.99	3.3	7.89	4.52	3.98
$H_2/4H_1$	0.19	0.2	0.21	0.22	0.22	0.23	0.18	0.2	0.21
K_D/K_R	1.24	1.49	1.93	1.18	1.39	1.27	2.01	1.89	1.65
h^2/H_2	6.17	5.04	4.07	4.7	4.44	4.78	2.15	2.04	1.66
$h^2_b\%$	38.24	43.25	46.43	47.75	48.04	37.48	46.91	48.08	48.95
$h^2_n\%$	1.66	2.62	8.12	1.14	2.06	2.24	0.54	1.72	2.2
GA%	0.92	2.74	18.96	0.8	2.8	4.1	0.92	7.04	7.28
Leaf angle (LANG)									
D	43.77**	32.89**	33.69**	46.03**	32.35**	32.08**	38.84**	29.13**	29.35**
H ₁	109.84**	81.34**	57.25**	108.41**	84.34**	58.15**	97.83**	76.04**	44.03**
h^2	50.23**	3.64**	7.96	36.93**	12.16	13.71**	33.05**	9.48	6.17
E	0.62	0.59	0.5	0.75	0.51	0.51	0.41	0.46	0.4
$(H_1/D)^{1/2}$	1.58	1.57	1.3	1.53	1.61	1.35	1.59	1.62	1.22
$H_2/4H_1$	0.13	0.2	0.36	0.14	0.18	0.33	0.15	0.18	0.44
K_D/K_R	3.2	3.17	3.94	3.52	3.11	3.6	3.54	2.88	3.35
h^2/H_2	0.86	0.06	0.1	0.61	0.2	0.18	0.56	0.17	0.08
$h^2_b\%$	48.52	48.13	47.53	48.1	48.43	47.67	48.83	48.49	47.77
$h^2_n\%$	17.48	17.48	27.62	19.5	16.56	24.6	18.7	15.8	27.06
GA%	10.14	9.42	11.68	11.26	9.82	11.56	10.86	9.46	10.12

Table 8- Continue...

Variance components	E1 HN-LD	E2 HN-MD	E3 HN-HD	E4 MN-LD	E5 MN-MD	E6 MN-HD	E7 LN-LD	E8 LN-MD	E9 LN-HD
Chlorophyll concentration index (CCI)									
D	79.37**	22.15	183.57**	70.83**	20.58	393.89**	13.11**	41.42**	11.21
H ₁	280.34**	494.81**	779.27**	376.98**	335.53**	473.76**	114.05**	164.77**	177.68**
h ²	181.02**	331.23**	17.68	54.12	460.64**	0.76	61.69**	13.2	7.58
E	4.42	1.77	0.78	5.06	2.96	0.96	4.84	2.89	0.97
(H ₁ /D) ^{1/2}	1.88	4.73	2.06	2.31	4.04	1.1	2.95	1.99	3.98
H ₂ /4H ₁	0.04	0.12	0.17	0.09	0.09	0.16	0.03	0.12	0.16
K _D /K _R	1.58	1.29	1.64	1.47	1.21	2.51	1.29	1.66	1.39
h ² /H ₂	4.34	1.34	0.03	0.38	3.88	0.01	4.9	0.16	0.07
h ² _b %	47.16	49.29	49.8	47.5	48.32	49.61	42.91	46.73	48.92
h ² _n %	8.52	1.48	7.82	5.82	1.94	26.24	3.2	7.82	2.1
GA%	6.14	2.2	19.36	7.18	3.06	54.24	2.06	19.3	5.12
Number of ears per plant (EPP)									
D	0.06**	0.06**	0.02**	0.02**	0.02**	0.03**	0.01	0.01	0.01**
H ₁	0.14**	0.12**	0.05**	0.06**	0.04**	0.04**	0.03	0.05**	0.05**
h ²	0.07**	0.01	0.01**	0.05**	0.09**	0.02**	0.02	0.05**	0.04**
E	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
(H ₁ /D) ^{1/2}	1.53	1.44	1.41	1.86	1.48	1.09	4.87	22.65	2.5
H ₂ /4H ₁	9.44	10.07	22.4	22.22	24.67	26.58	29.41	17.06	13.19
K _D /K _R	2.39	1.89	2.1	3.21	2.1	1.43	1.21	0.91	0.93
h ² /H ₂	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.02	0.01
h ² _b %	43.88	45.63	46.44	38.32	41.16	46.34	41.72	44.76	46.69
h ² _n %	14	13.92	15.54	10.22	12.82	17.14	1.16	0.06	4.2
GA%	0.48	0.48	0.1	0.12	0.06	0.16	0.02	0.02	0.04
Grain yield per plant (GYPP)									
D	1235.1**	870.8**	610.3**	1254.5**	899.9**	579.2**	29.2	81.9	0.6
H ₁	8830.4**	7005.2**	6687.6**	7993.9**	4949.8**	5116.8**	1828.3**	1162.9**	1064.2**
h ²	10233.9**	7236.3**	6363.5**	8335.9**	4229.9**	4446.2**	2770.2**	1891.8**	1754.6**
E	24.7	10.1	12.6	18	10.3	8.4	22.3	8.7	3.8
(H ₁ /D) ^{1/2}	2.7	2.8	3.3	2.5	2.4	2.9	7.9	3.8	42.1
H ₂ /4H ₁	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
K _D /K _R	1.4	1.4	1.3	1.6	1.7	1.4	1.4	1.6	1.1
h ² /H ₂	1.3	1.1	1	1.2	1	0.9	2.1	2.5	2.2
h ² _b %	49.5	49.7	49.6	49.5	49.6	49.7	47.6	48.5	49.3
h ² _n %	4.5	4.1	2.9	5.3	6.3	3.7	0.5	2.4	0.1
GA%	21.9	19.8	12.4	31.7	22	14.6	1.4	4.6	0.1
Harvest index (HI)									
D	18.35**	18.21**	18.78**	28.50**	30.47**	23.07**	0.3	4.97**	0.1
H ₁	78.05**	89.47**	112.23**	101.90**	104.96**	123.50**	41.40**	43.40**	43.12**
h ²	84.64**	98.60**	108.36**	69.88**	62.79**	103.14**	43.67**	65.23**	89.05**
E	0.35	0.22	0.28	0.19	0.55	0.3	1.56	1.01	0.33
(H ₁ /D) ^{1/2}	2.06	2.22	2.44	1.89	1.86	2.31	11.75	2.95	20.77
H ₂ /4H ₁	0.36	0.22	0.12	0.22	0.17	0.08	0.68	0.56	0.47
K _D /K _R	1.68	1.59	1.5	2.15	2.34	1.74	1.05	1.95	1.05
h ² /H ₂	0.76	1.23	2.1	0.77	0.9	2.75	0.39	0.68	1.09
h ² _b %	49.1	49.52	49.5	49.58	48.8	49.5	43.46	45.3	48.52
h ² _n %	7.78	6.74	5.5	10.36	11	6.48	0.2	3.86	0.08
GA%	2.04	2.32	1.92	4.84	5.8	2.96	0.06	0.78	0.01

H: high, M: medium, L: low, N: nitrogen, D: density and * and ** significant at 0.05 and 0.01 probability levels, respectively.

Number of genes or gene groups controlling the inheritance of a given trait (h²/H₂) was one in 4 traits (DTS, ASI, LANG and EPP) and ranged from 1 (E6) to 3 (E8) (GYPP), from 2 (E7 through E9) to 6 (E1) (BS), from 1 (in E7) to 5 (in E1) (CCI) and from 1 to 3 (E6) (HI). Broad-sense heritability (h²_b) was of medium magnitude (close to 50%) for all studied traits under all environments, indicating that the environment and genotype × environment interaction had considerable effects on the phenotype in this experiment. Narrow-sense heritability (h²_n) was generally of small magnitude, but

reached about 27% in LANG under E9. The big difference between broad and narrow sense heritability in this experiment could be attributed to the high estimates of dominance, dominance × dominance and dominance × additive components. Expected genetic advance (GA) from selection (based on 10% selection intensity) across years for studied traits in the nine environments [Table-8] was generally of small magnitude, especially under E9 and E7 environments, but reached its maximum for CCI (54.24% under E6) and GYPP (31.68% for under E4).

On the contrary, the traits DTS, ASI, and EPP showed very low GA < 1% under all environments. 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 [6,32,33]. 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 GA [34-36].

Trait Interrelationships

Estimates of genetic correlation coefficients between GYPP and other studied traits across two years under the nine studied environments (E1 to E9) were calculated across all inbred lines and across all F₁ crosses and presented in [Table-9]. In general, grain yield of

inbreds and hybrids showed very strong positive genetic association with HI trait under all combinations of plant density and N levels. Since nitrogen translocation efficiency (NTRE) proved to be strongly correlated with HI [37], grain yield of inbreds and hybrids in the present study could therefore be considered of a strong association with NTRE. Significant and negative genetic correlation coefficients were observed between grain yield/plant of inbreds and hybrids and each of BS in all environments and ASI in all environments. Less barren stalks and short ASI could, therefore, be used as important selection criteria for high grain yield of maize under different combinations of plant densities and N levels, especially if heritability of BS and ASI is high. Similar conclusions were reported by Bänziger & Lafitte [6], Al-Naggar, et al [17], Miller, et al [38], Edmeades, et al [39] and Gebre [40]. Grain yield showed also a significant and positive genetic correlation with EPP under all environments in inbreds and in E1, E2, E7 and E9 in hybrids.

Table 9- Genetic correlation coefficients between GYPP and other studied traits for parental inbred lines and their diallel cross hybrids under 9 environments combined across two seasons.

Trait	E1	E2	E3	E4	E5	E6	E7	E8	E9
	HN-LD	HN-MD	HN-HD	MN-LD	MN-MD	MN-HD	LN-LD	LN-MD	LN-HD
Inbreds									
DTS	-0.78**	0.01	0.84**	-0.08	-0.11	0.45*	0.92**	0.98**	0.54*
ASI	-1.00**	-0.65**	-1.00**	-0.84**	-0.75**	-0.65**	-0.75**	-0.43*	-0.73**
BS	-0.90**	-1.00**	-0.95**	-0.83**	-0.89**	-0.96**	-0.67**	-0.96**	-0.63**
LANG	0.45*	0.27*	0.21	0.45*	0.41*	0.35	0.29*	0.41*	0.33*
CCI	-0.52*	0.32	-0.88**	0.33	0.05	-0.66*	-0.56*	0.31	-0.51*
EPP	0.47*	0.66**	0.50*	0.78**	0.63**	0.58*	0.87**	0.45*	0.82**
HI	0.94**	0.96**	0.93**	0.94**	0.95**	0.94**	0.80**	0.98**	0.84**
Hybrids									
DTS	0.18	0.28*	0.06	0.13	-0.17	0.16	-0.25	-0.04	-0.03
ASI	-0.55**	-0.85**	-0.98**	-0.79**	-0.80**	-0.62**	-0.44*	-0.77**	-0.74**
BS	-0.84**	-0.91**	-0.93**	-0.70**	-0.87**	-0.28	-0.68**	-0.77**	-1.00**
LANG	-0.29*	-0.33*	-0.43*	-0.43*	-0.22	-0.53**	-0.02	-0.53**	0.33*
CCI	-0.45*	0.28	0.17	0.11	0.25	0.02	0.01	0.31	0.28
EPP	0.53**	0.40*	0.26	0.18	0.31	0.04	0.62**	0.3	0.89**
HI	0.94**	0.98**	0.99**	0.93**	0.96**	0.97**	0.96**	0.93**	0.96**

H: high, M: medium, L: low, N: nitrogen, D: density and *and ** indicate that r_g estimate exceeds once and twice its standard error, respectively.

The positive correlations between grain yield and number of ears/plant are in harmony with other reports [17,41,42]. Grain yield per plant of crosses showed also significant and negative genetic correlations with LANG in most (six) environments, but with less magnitude. This indicated the importance of LANG for tolerance to high plant density. These results are in agreement with those reported by other investigators [25,43]. Traits showing a strong correlation with grain yield and moderate or high heritability may be recommended to plant breeder as selection criteria for improving productivity in addition to grain yield itself. In the present study, selection criteria that could be used in F₂ populations of the 15 studied diallel crosses are ASI, BS and HI in both inbreds and hybrids, EPP in inbreds and LANG in hybrids under severe stress of combination between high density and low-nitrogen conditions. In this aspect, the secondary traits proposed for high productivity were also EPP and ASI under high-population density [44-46] and EPP, ASI and BS under low nitrogen stress [6,7,38,47-49]. In the present study, the correlation values were high or very high, but the heritability values in narrow-sense were generally low, which might be attributed to the large component of non-additive genetic variance for most studied traits under all environments. Further investigations needed to be undertaken using more appropriate maize germplasm of clear

divergence in adaptive traits to both high density and low-N for better identification of the best selection criteria and/or the most effective morphological, phenological and physiological adaptive traits to high-plant density and/or low-soil N stress.

Conclusions

The present investigation indicated that increasing plant density from 20,000 to 40,000 plant per fed together with reducing N-fertilizer rate resulted in increased useful heterosis (heterobeltiosis) for GYPP and HI traits. The crosses L29 × L55 and L17 × L54 showed the highest heterobeltiosis for GYPP (above 133%) under high density and showed the highest *per se* grain yield/fed and are therefore recommended for commercial application under high plant density conditions and as good genetic material for maize breeding programs. Under no stress, light and medium stresses, the best performing lines are also the best general combiners and *vice versa* for grain yield and barren stalk percentage traits. This conclusion is not valid in the most stressed environments (especially E9 and E7). Moreover, in general, the mean performance of a given cross is not an indication of its specific combining ability. Both additive and dominance components of variation were highly significant for all studied traits under all 9 environments. This indicated that selection

may be used in maize heterogeneous populations for improving grain yield and adaptive traits to both high plant density and low nitrogen stress. The estimates of dominance were much higher, in magnitude, than additive variance for all studied traits under all nine environments, suggesting that dominance variance plays the major role in the inheritance of these traits in all cases and that heterosis breeding is the method of choice for the genetic improvement of the most studied traits under HD and LN stresses. Results of the present study also indicated that less barren stalks and short ASI could be used as important selection criteria for high grain yield of maize under different combinations of plant densities and N levels, but the heritability values in narrow-sense were generally low, for most studied traits under all environments.

Conflicts of Interest: None declared.

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