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Estimation of Genetic Parameters Controlling Inheritance of Maize Quantitative Traits under Different Plant Densities Using Line × Tester Analysis

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Authors' contributions

This work was carried out in collaboration between all authors. Author AMMA designed the study, wrote the protocol, and wrote the first draft of the manuscript. Authors AMMA, RS, MSH and TAE supervised the study and managed the literature searches. Authors ASMY and AMAM managed the experimental process and performed data analyses. All authors read and approved the final manuscript.

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ABSTRACT

Type of gene action, heritability and genetic advance from selection are prerequisites for starting a breeding program for developing plant density tolerant variety of maize. The objective of the present investigation was to estimate general (GCA) and specific (SCA) combining ability variances, type of gene action, heritability and genetic advance from selection for traits related to high density tolerance in maize. A split plot experiment with three replications was carried out; where plant densities were devoted to main plots, namely low (LD), medium (MD) and high (HD) density (47,600 to 71,400 and 95,200 plants/ha, respectively) and sub-plots to genotypes. A line x tester analysis was used. Both GCA and SCA variances were important in the expression of studied traits under all plant densities, but magnitude of δ^2_{SCA} was much higher than that of δ^2_{GCA}.

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Estimates of dominance (δ^2_D) genetic variance were appreciably larger than additive (δ^2_A) variance estimates for most studied traits under all plant densities, so the breeding method of choice for improving maize plant density tolerance would be heterosis breeding. The degree of dominance "a" was in the over-dominance range (a > 1) for most studied cases. The highest estimate of narrow sense heritability (88.15%) was shown by upper stem diameter (SDU) under MD followed by ears/plant (EPP) (83.85%) under LD, while the lowest estimate (0.00%) was shown by anthesis-silking interval (ASI) under LD and MD. The best environment in achieving the highest predicted gain from selection (GA%) was the HD environment for most studied traits followed by the LD environment for grain yield and its components. The highest GA under each environment was achieved by penetrated light at ear (PL-E) under low density (32.13%) and SDU under medium (31.73%) and high density (36.95%).

Keywords: Heritability; genetic advance; plant density tolerance; gene action.

1. INTRODUCTION

Maize (*Zea mays* L.) hybrids in Egypt are selected and grown under low plant density (ca 50,000 plants/ha) and are subject to yield losses when grown under high plant density (ca 100,000 plants/ha) [1]. Thus, grain yield from unit land area in Egypt cannot be increased by increasing plant density until new hybrids of plant density tolerance can be developed and released for commercial use. Maximum yield per unit area may be obtained by growing maize hybrids that can tolerate high plant density up to 100,000 plants ha^{-1} [2]. Average maize grain yield per unit land area in the USA increased dramatically during the second half of the 20th century, due to greater tolerance of modern hybrids to high plant densities [3]. Modern maize hybrids in USA 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 [4]. Maize genotypes with erect leaves are very desirable for increasing the population density due to better light interception [5]. In US maize germplasm evaluated for plant density tolerance, a subset of traits including leaf angle, upper stem diameter, leaf area required to produce one gram of grain, kernel rows per ear, days to canopy closure, barrenness, kernels $plant^{-1}$, kernel length, leaf number, upper leaf area, stay green, zipper effect, kernels per row, and anthesis-to-silking interval were associated with grain yield across plant densities ranging from 47,000 to 133,000 plants ha^{-} [6].

To increase maize grain yield per land unit area, breeding programs in Egypt should be directed towards the development of inbreds and hybrids characterized with adaptive traits to high plant density tolerance [7]. Combining ability of available germplasm and nature of inheritance of such traits should be studied to start such a program. These information, especially in Egypt are scarce. Combining ability has been defined as the performance of a line in hybrid combinations [8]. Since the final evaluation of inbred lines can be best determined by hybrid performance, it plays an important role in selecting superior parents for hybrid combinations and in studying the nature of genetic variation [9]. Sprague and Tatum [10] introduced the concepts of general (GCA) and specific (SCA) combining ability. For random individuals, the authors reported that GCA is associated with additive effects of the genes, while SCA is related to dominance and epistatic effects (non-additive effects) of the genes. Investigators reported more proportional and significant GCA effects for yield, days to silk and plant height in different groups of broad based CIMMYT maize populations and pools across locations [11]. Shewangizaw et al. [12] also reported significant GCA and SCA for most traits, but predominance of non-additive genetic variance in the case of yield. Estimates of combining abilities across environments have indicated that both GCA and SCA for most characters interacted with environmental change, but GCA was found to be more sensitive to environmental change than SCA [13].

Type of gene action, heritability and genetic advance from selection are prerequisites for starting a breeding program for developing plant density tolerant variety of maize. Literature review reveals that little research has been directly focused on studying the mode of gene action controlling yield under high plant density. Several researchers found that additive genetic effects play a major role in conditioning grain yield under plant density stress in tropical [14,15]

and temperate [16] maize germplasm. Response to selection for yield in populations under plant density has also been reported [17-19] suggesting that additive gene action might be important in controlling yield. Derera et al. [14] also found non-additive gene action playing important roles in controlling grain yield under both plant density stress and favorable growing environments. Agrama and Moussa [20] reported QTLs with both additive and dominance effects for yield and associated traits. Many investigators reported a decline in heritability for grain yield under stress [21,22]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [9,23]. Thus, when planning to improve an adaptive trait to a given stress, priority should be given to estimation of heritability of this trait under targeted environmental conditions.

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. Line × tester analysis proposed by Kempthorne [24] is one of the biometrical tools to achieve that. The objective of the present investigation was to estimate general and specific combining ability variances, type of gene action, heritability and genetic advance from selection for traits related to high density tolerance in maize.

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 2015 and 2016 seasons.

2.1 Genetic Materials

Twenty three maize inbred lines, of different origins were chosen on the basis of their adaptive traits to high plant density and/or drought, to be used as females in this study. Sixteen of them (IL15, IL17, IL24, IL51, IL53, IL80, IL84, IL151, IL171, Sk9, CML67, CML104, Inb174, Inb176, Inb208 and Inb213) were obtained from Agricultural Research Center, Ministry of Agriculture, Egypt and seven (L14, L17, L18, L20, L21, L28 and L53) were obtained from Agronomy Department, Faculty of Agriculture, Cairo University, Egypt. Three testers of different genetic backgrounds were used as males to make all possible testcrosses with the 23 inbred females, namely the commercial inbred line Sd7, the commercial single cross hybrid SC 10 and the commercial synthetic Giza 2 (open-pollinated variety).

2.2 Making the Testcrosses

In 2015 summer season, the 23 inbred lines (females) and the three testers (males) were crossed to the three testers and consequently, seeds of 69 F_1 testcrosses were obtained. Parental inbred lines and the inbred tester Sd7 were also self-pollinated at the same season to obtain enough quantities of seeds for the evaluation experiment in the next season.

2.3 Experimental Design and Treatments

In 2016 season, a field experiment was carried out during the early summer. The experiment was conducted to evaluate 100 genotypes, namely 23 inbred lines, three testers, 69 testcrosses and five high-yielding commercial hybrids as checks (the single crosses SC 168, SC 2031, SC 30K9, SC30N11 and the three-way cross TWC 1100). A split-plot design in randomized complete blocks arrangement with three replications was used. The main plots were allotted to three plant densities and the sub-plots were devoted to genotypes (100 genotypes). The inbred lines were separated from other studied material in each block, because of their differences in plant height and vigor. The date of planting was the 20th of May. Sub-plots were single rows 4.0 m long and 0.70 m wide, with hills spaced at a distance of 15 cm for the high density (HD), 20 cm for the medium density (MD) and 25 cm for the low plant density (LD) with two plants hill^{-1} and plants were thinned to one plant hill^{-1} before the first irrigation to achieve the plant densities 95,200, 71,400 and 47,600 plants/ha, respectively. Nitrogen fertilization at the rate of 285.6 kg N/ha was added in two equal doses of Urea before the first and second irrigation. Fertilization with calcium superphosphate was performed with soil preparation and before sowing. Weed control was performed chemically with Stomp (Pendimethalin) herbicide before the first irrigation and just after sowing and manually by hoeing twice, the first before the second irrigation and the second before the third irrigation. Irrigation was applied by flooding after three weeks for the second irrigation and every 12 days for subsequent irrigations. Pest control was performed when required by spraying plants

with Lannate (Methomyl) 90% (manufactured by DuPont, USA) against corn borers.

2.4 Soil Analysis and Meteorological Data

The analysis of the experimental soil, indicated that the soil is clay loam (5.50% coarse sand, 22.80% fine sand, 36.40% silt, and 35.30% clay), the pH (paste extract) is 7.92, the EC is 1.66 dSm^{-1}, soil bulk density is 1.2 g cm^{-3}, calcium carbonate is 7.7%, the available nutrients in mg kg^{-1}were Nitrogen (371.0), Phosphorous (0.4), Potassium (398), DTPA-extractable Zn (4.34), DTPA-extractable Mn (9.08) and DTPA-extractable Fe (10.14). Meteorological variables in the 2016 growing season 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.

2.5 Parameters Recorded

1. **Days to 50% anthesis (DTA)**: (Number of days from planting to anthesis of 50% of plants), it was measured on all plants $plot^{-1}$.
2. **Anthesis-silking interval (ASI)** (day): (Number of days between 50% silking and 50% anthesis), it was measured on all plants $plot^{-1}$.
3. **Plant height (PH)** (cm): It was measured on 10 guarded plants $plot^{-1}$ from ground to the point of flag leaf insertion.
4. **Leaf angle** (LANG) (^{o}): It was measured as leaf angle between blade and stem for the leaf just above ear using a protractor on 10 guarded plants $plot^{-1}$ according to Zadoks et al. [25].
5. **Lower stem diameter (SDL)** (mm)**:** It was measured with caliper from 10 guarded plants/plot as the stem diameter above second node; two measurements were taken; the first measurement was used as a base line with the second measurement recorded after a 90 degree turn of the caliper.
6. **Upper stem diameter (SDU)** (mm)**:** It was measured with caliper from 10 guarded plants/plot as the stem diameter on third internode below flag leaf.
7. **Leaf area to produce 1 g of grain (LA/1Gg)** (cm^{2})**:** It was measured as leaf area per plot /grams of grains per plot. At 70 days from sowing date light intensity was measured and then penetrated light inside the canopy was calculated for each genotype. The Lux-meter apparatus was used. The light intensity in (lux) was measured at 12 am (noon time) at the top of the plant and at the base of top-most ear. Penetrated light inside the canopy was measured as a percentage of light penetrated from the top of the plant to the base of top-most ear as follows:
8. **Penetrated light at the base of top-most ear (PL-E)** (%): It was calculated from 10 guarded plants/plot as follows: PLE =100 (light intensity at the base of top-most ear/light intensity at the top of the plant).
9. **Chlorophyll concentration index (CCI)** (%): It was measured by Chlorophyll Concentration Meter, Model CCM-200, USA, as the ratio of transmission a 931 nm to 653nm through the leaf of top-most ear. It was measured on 5 guarded plants/plot.
10. **Tassel fresh weight (TFW)** (g): IT was measured on 5 guarded plants $plot^{-1}$.
11. **Tassel dry weight (TDW)** (g)**:** It was measured on 5 guarded plants $plot^{-1}$.
12. **Tassel branch number (TBN):** It was measured as number of branches on 5 guarded plants $plot^{-1}$. Traits No. 10, 11 and 12 were measured according to Mansfield and Mumm [6].
13. **Number of ears $plant^{-1}$ (EPP)**: It was estimated by dividing number of ears $plot^{-1}$ on number of plants $plot^{-1}$.
14. **Number of rows ear^{-1} (RPE)**: Using 10 random ears $plot^{-1}$ at harvest.
15. **Number of kernels $plant^{-1}$ (KPP)**: Calculated by multiplying number of ears $plant^{-1}$ by number of rows ear^{-1} by number of kernels row^{-1}.
16. **Hundred kernel weight (100KW)** (g): Adjusted at 155g water kg^{-1} grain.
17. **Grain yield $plant^{-1}$ (GYPP)** (g): It was estimated by dividing the grain yield $plot^{-1}$ (adjusted at 15.5% grain moisture) on number of plants $plot^{-1}$ at harvest.
18. **Grain yield ha^{-1} (GYPH)** (ton): It was estimated by adjusting grain yield $plot^{-1}$ at 15.5% grain moisture to grain yield ha^{-1}.

2.6 Biometrical Analyses

Analysis of variance of the split-plot design was performed on the basis of individual plot observation using the MIXED procedure of SAS ® [26]. The data collected from each plant density were subjected to the standard analysis

of variance of randomized complete blocks design according to Steel et al. [27] using GENSTAT 10th addition windows software. Data of the testcrosses were further subjected to line × tester analysis according to Kempthorne [24]. The sum of squares for F_1 hybrids was partitioned into their components, *i.e.* males (testers), females (inbred lines) and females (lines) × males (testers) interaction. The model used to estimate general (GCA) and specific (SCA) combining ability effects of the X_{ijk}^{th} observation is as follows: $X_{ijk} = \mu + g_i + g_j + s_{ij} + e_{ijk}$ Where: μ = overall population mean. g_i = GCA effect of the i^{th} male parent. g_j= GCA effect of the j^{th} female parent. s_{ij}= SCA effect of the ij cross combination. e_{ijk} = the error associated with the x_{ijk} observation. i= number of male parents. j= number of female parents. k= number of replications. The expectations of mean squares due to males, females and male x female are equivalent to the general combining ability for males ($\delta^2_{GCA(m)}$), general combining ability for females ($\delta^2_{GCA(f)}$) and specific combining ability (δ^2_{SCA}), respectively. Estimates of additive (δ^2_A) and dominance (δ^2_D) variances, heritability and genetic advance from selection were calculated according to Sharma [28]. Average degree of dominance "a" was calculated by the following equation:"a" = $[2\ \delta^2_D/\ \delta^2_A]^{1/2}$. The estimates of the average degree of dominance "a" were used to indicate the type of dominance, as follows: "a" = 0 indicates no dominance, "a" < 1 indicates partial dominance, "a" = 1 indicates complete dominance and "a" > 1 indicates over dominance. Heritability in the narrow (h^2_n) sense in testcrosses was estimated from the following formulae: $h^2_n = 100\ (\delta^2_A/\delta^2_{ph})$. The expected genetic advance from selection was calculated as follows: $GA = 100\ h^2_n\ k\ \delta_{ph} / \bar{x}$, Where δ_{ph} = phenotypic standard deviation, k = selection differential (the k value for 10% selection intensity used in this study equals 1.76), $\bar{x}$ = mean of the crosses for the respective trait.

3. RESULTS AND DISCUSSION

3.1 Analysis of Variance of Line × Tester

Analysis of variance of line × tester under low- , medium- and high-density conditions in 2016 season is presented in Table 1. Mean squares due to testcrosses and their components, *i.e.* lines, testers and lines × testers were significant ($p \leq 0.05$ or $p \leq 0.01$) under all plant densities for all studied traits, except DTA for lines under MD and testers under HD, ASI for testers under LD, MD and HD and EPP for testers under HD, indicating significant GCA for lines, GCA for testers and SCA for line x tester crosses in most cases (Table 1).

3.2 Contribution of Lines, Testers and Lines x Testers to Total Variation

Relative contribution (%) of variances due to lines (L), testers (T) and L x T to total variation for studied traits under low (LD), medium (MD) and high (HD) plant densities is presented in Table (2). Inbred lines (females) were the biggest contributor to the total variation; since they showed the highest percentage of contribution in 27 cases out of total 54 cases (8 traits under HD, 9 traits under MD and 10 traits under LD). It is worthy to note that lines were the highest contributor to the total variation under all densities (HD, MD and LD) for three traits, namely GYPP, GYPF and LANG. It could be concluded that inbred lines used in this study showed big variation for most studied traits under density stressed and non-stressed environments.

In the second place comes lines x testers; they showed the highest contributor to total variation in 26 cases out of 54 cases (9 traits under HD, 9 traits under MD and 8 traits under LD). Testers were the highest contributor to total variation in one case only (SDL under HD).

3.3 Combining Ability Variances of Testcrosses

Estimates of variances due to general (δ^2_{GCA}) and specific (δ^2_{SCA}) combining ability calculated according to the line × tester analysis proposed by Kempthorne [24] are presented in Table (3). Significant δ^2_{GCA} variances were shown for most studied traits under low, medium and high density. However, significant δ^2_{SCA} variances were exhibited for all studied traits under all plant densities. This indicates that both GCA and SCA variances are important in the expression of studied traits under low, medium and high plant densities, 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 several investigators [17-19,29-32].

The magnitude of δ^2_{SCA} is much higher than that of δ^2_{GCA}, expressed in the ratio $\delta^2_{GCA}/\ \delta^2_{SCA}$, which was less than unity for all studied traits under all plant densities, except for LANG under

HD, SDU under all densities and EPP under LD. This indicates that non-additive genetic variance (dominance and epistasis) is predominating over additive variance in the inheritance of all studied traits under all plant densities (LD, MD and HD), except the above mentioned cases. A similar conclusion was reported by several investigators [31-34]. On the contrary, other investigators [35-38] suggested the existence of a greater portion of additive and additive × additive than non-additive variance in controlling the inheritance of studied traits under elevated plant density environments. Different conclusions reported by different investigators might be due to different genotypes and genotype x environment interaction.

It is observed that δ^2_{GCA} increased by increasing the stress of plant density, except for LANG, SDU, PL-E, EPP, RPE, KPP, 100-KW and GYPP traits, where δ^2_{GCA} decreased by increasing plant density. However, δ^2_{SCA} generally decreased by increasing the stress of plant density, except for LA/1gG, CCI, EPP, RPE, 100-KW and GYPF, where where δ^2_{GCA} increased by increasing plant density.

Table 1. Significance of mean squares of line × tester analysis of variance for studied traits of 69 testcrosses partitioned into lines (L), testers (T) and L × T under low (LD), medium (MD) and high (HD) plant density in 2016 season

SOV	df	LD	MD	HD	LD	MD	HD	LD	MD	HD
		Days to 50% anthesis			Anthesis-silking interval			Plant height		
Crosses (C)	68	**	**	**	**	**	**	**	**	**
Lines (L)	22	**	ns	**	**	**	*	**	**	**
Testers (T)	2	**	**	ns	ns	ns	ns	**	**	**
L × T	44	**	**	**	**	**	*	**	**	**
		Leaf angle			Lower stem diameter			Upper stem diameter		
Crosses (C)	68	**	**	**	**	**	**	**	**	**
Lines (L)	22	**	**	**	**	**	**	**	**	**
Testers (T)	2	**	**	**	**	**	**	**	**	**
L × T	44	**	**	**	**	**	**	**	**	**
		Leaf area to produce 1 g of grain			Penetrated light at ear			Chlorophyll concentration index		
Crosses (C)	68	**	**	**	**	**	**	**	**	**
Lines (L)	22	**	**	**	**	*	*	**	**	**
Testers (T)	2	*	*	**	**	**	**	**	*	*
L × T	44	**	**	**	**	**	**	**	**	**
		Tassel fresh weight			Tassel dry weight			Tassel branch number		
Crosses (C)	68	**	**	**	**	**	**	**	**	**
Lines (L)	22	**	**	**	*	*	**	**	**	*
Testers (T)	2	ns	**	*	**	**	**	*	*	*
L × T	44	**	**	**	**	**	**	**	**	**
		Ears per plant			Rows per ear			Kernels per plant		
Crosses (C)	68	**	**	**	**	**	**	**	**	**
Lines (L)	22	**	**	**	**	**	*	**	**	**
Testers (T)	2	**	**	ns	**	*	*	**	**	**
L × T	44	**	**	**	**	**	**	**	**	**
		100-kernel weight			Grain yield per plant			Grain yield per hectare		
Crosses (C)	68	**	**	**	**	**	**	**	**	**
Lines (L)	22	**	**	*	**	**	**	**	**	**
Testers (T)	2	**	**	**	**	**	**	**	**	**
L × T	44	**	**	**	**	**	**	**	**	**

*ns, * and ** indicate non-significant, significant at 0.05 and 0.01 probability levels, respectively*

Table 2. Relative contribution (%) of variances due to lines (L), testers (T) and L x T to total variation for studied traits under low (LD), medium (MD) and high (HD) plant densities

	LD	MD	HD	LD	MD	HD	LD	MD	HD
	Days to 50% anthesis			**Anthesis-silking interval**			**Plant height**		
Lines (L)	35.58	48.19	58.07	18.72	29.44	44.98	32.02	38.14	45.97
Tester (T)	2.38	2.81	0.25	1.24	1.48	3.91	7.17	10.51	17.38
L x T	62.04	49.00	41.68	80.05	69.09	51.11	60.81	51.35	36.65
	Leaf angle			**Lower stem diameter**			**Upper stem diameter**		
Lines (L)	49.55	56.09	58.26	48.98	48.58	33.21	42.32	51.07	51.22
Tester (T)	18.63	17.39	17.21	29.92	33.01	40.95	40.35	39.85	38.32
L x T	31.83	26.52	24.53	21.1	18.41	25.84	17.33	9.08	10.46
	Leaf area to produce 1 g of grain			**Penetrated light at ear**			**Chlorophyll concentration index**		
Lines (L)	37.75	38.17	42.76	54.2	37.83	32.08	47.36	49.68	40.36
Tester (T)	1.23	0.84	3.67	1.21	22.99	31.76	9.14	7.00	9.38
L x T	61.02	60.99	53.56	44.59	39.19	36.17	43.5	43.32	50.26
	Tassel fresh weight			**Tassel dry weight**			**Tassel branch number**		
Lines (L)	34.88	32.17	40.67	42.24	40.13	48.5	48.23	51.07	43.92
Tester (T)	0.24	4.13	7.49	9.85	20.84	23.59	7.42	5.18	7.13
L x T	64.88	63.7	51.84	47.91	39.03	27.91	44.35	43.75	48.94
	Ears per plant			**Rows per ear**			**kernels per plant**		
Lines (L)	29.7	29.15	36.83	39.13	32.69	48.11	51.79	45.17	52.09
Tester (T)	5.86	3.24	0.68	5.3	8.43	2.86	4.35	2.45	1.36
L x T	64.43	67.64	62.41	55.56	58.88	49.02	43.87	52.39	46.55
	100-kernel weight			**Grain yield per plant**			**Grain yield per hectare**		
Lines (L)	58.1	50.6	48.2	60.85	57.95	59.61	60.9	57.98	59.6
Tester (T)	1.54	0.68	2.51	4.26	1.84	0.59	4.25	1.84	0.6
L x T	40.37	48.72	49.29	34.89	40.2	39.8	34.85	40.18	39.8

Estimates of dominance (δ^2_D) genetic variance calculated from the line x tester analysis (Table 4) were appreciably larger than additive (δ^2_A) variance estimates for all studied traits under all plant densities, except LANG and SDU under all plant densities, PH, PL-E and TDW under HD and GYPP and GYPF under LD. δ^2_D equaled δ^2_A for EPP under high density. The predominance of dominance genetic variance for most studied traits under elevated plant density was also reported by Singh and Shahi [34] and Al-Naggar et al. [31,32]. Thus, heterosis breeding is the best choice for improving such traits under plant density stress conditions.

The measure of the degree of dominance "a" was in the over-dominance range (a> 1) for 42 out of 54 cases (77.8%), i.e. in most studied traits. However, partial dominance (0< a >1) controlled the inheritance of SDU under all plant densities, and EPP under LD; *i.e.* 4 cases (7.4%). No dominance (a= 0) was observed for the inheritance of ASI under LD and MD, TFW under LD, EPP under MD; i.e. in 7.4% of studied cases. Additive was only the genetic component controlling inheritance of the later cases.

Estimates of broad-sense heritability (h^2_b) were generally higher under low-density for only one trait (ASI), under high density for five traits (DTA, LA/1gG, PL-E, EPP and RPE) and under medium density for 13 traits (the rest of studied traits). This may be due to the greater genetic variance under elevated density than under the low density. The h^2_b estimate ranged from 51.89% for ASI under HD to 99.66% for EPP under HD.

The highest environment in narrow-sense heritability (h^2_n) was high density for 9 traits (DTA, ASI, PH, LANG, LA/18G, PL-E, TFW, TDW and RPE), medium density for 4 traits (SDL, SDU, CCI, and TBN) and low density for five traits (EPP, KPP, 100-KW, GYPP and GYPF). The highest estimate of h^2_n (88.15%) was shown by SDU under MD followed by (83.85%) which was shown by EPP under LD, while the lowest estimate (0.00%) was shown by

ASI under LD and MD due to the absence of additive genetic variance.

The results of this investigation (Table 4) indicated that the best environment in achieving the highest predicted gain from selection (GA%) was the high plant density environment for 9 traits (DTA, ASI, PH, LANG, SDU, LA/1gG, TFW, TDW and RPE), followed by the low plant density environment for seven traits (GYPP, GYPF, 100-KW, KPP, EPP, TBN and PL-E) and the medium density environment for two traits (SDL and CCI). The highest GA under each environment was achieved by PL-E under low density (32.13%) and SDU under medium (31.73%) and high density (36.95%). On the contrary, the lowest GA estimate was shown by ASI (0.00%) under low and medium density and by DTA (1.53%) under high density.

Table 3. Variance components due to general (GCA) and specific (SCA) combining ability estimated from the line x tester analysis of variance for studied traits of 69 testcrosses under low (LD), medium (MD) and high (HD) plant density

Components	LD	MD	HD	LD	MD	HD	LD	MD	HD
	Days to 50% anthesis			Anthesis-silking interval			Plant height		
$\delta^2_{GCA\ (L)}$	0.08**	0.37*	0.70**	-0.06	-0.01	0.05*	2.40**	12.63**	41.07**
$\delta^2_{GCA(\ T)}$	-0.01	0.01**	-0.04	-0.01	-0.01	0.01	9.42**	11.88**	33.49**
$\delta^2_{GCA\ (Aver)}$	0.05**	0.22**	0.39**	-0.04	-0.01	0.03*	5.28**	12.32**	37.96**
δ^2_{SCA}	1.56**	0.97**	1.00**	0.27**	0.16**	0.07*	74.09**	55.82**	39.61**
$\delta^2_{GCA/\ SCA}$	0.03	0.23	0.39	0	0	0.44	0.07	0.22	0.96
	Leaf angle			Lower stem diameter			Upper stem diameter		
$\delta^2_{GCA\ (L)}$	6.41**	5.37**	5.71**	2.45**	1.72**	0.87**	2.30**	2.51**	2.47**
$\delta^2_{GCA(\ T)}$	4.69**	2.91**	2.87**	2.65**	2.02**	2.45**	3.88**	3.05**	2.91**
$\delta^2_{GCA\ (Aver)}$	5.7**	4.36**	4.55**	2.53**	1.84**	1.52**	2.95**	2.73**	2.65**
δ^2_{SCA}	7.25**	4.44**	3.87**	1.47**	1.07**	1.26**	1.44**	0.64**	0.71**
$\delta^2_{GCA/\ SCA}$	0.79	0.98	1.17	1.73	1.73	1.21	2.05	4.24	3.74
	Leaf area to produce 1 g of grain			Penetrated light ear			Chlorophyll concentration index		
$\delta^2_{GCA\ (L)}$	2.71**	3.14**	9.85**	22.5**	1.26*	0.38*	2.72**	3.80**	2.90**
$\delta^2_{GCA(\ T)}$	-0.83	-1.14	1.10**	-0.83	2.10**	1.16**	1.09**	0.98*	1.94*
$\delta^2_{GCA\ (Aver)}$	1.26**	1.39**	6.26**	12.9**	1.6**	0.7**	2.05**	2.64**	2.51**
δ^2_{SCA}	29.78**	34.78**	45.51**	37.2**	3.25**	1.22**	5.82**	8.43**	13.41**
$\delta^2_{GCA/\ SCA}$	0.04	0.04	0.14	0.35	0.49	0.57	0.35	0.31	0.19
	Tassel fresh weight			Tassel dry weight			Tassel branch number		
$\delta^2_{GCA\ (L)}$	1.18**	0.10**	3.95**	1.60*	1.50*	2.30**	1.44**	1.00**	0.96*
$\delta^2_{GCA(\ T)}$	-1.87	0.54**	1.97*	0.96**	1.99**	2.13**	0.43**	0.16**	0.35*
$\delta^2_{GCA\ (Aver)}$	-0.08	0.28**	3.14**	1.34**	1.7**	2.23**	1.02**	0.65**	0.71**
δ^2_{SCA}	44.2**	28.5**	19.9**	5.79**	4.15**	2.63**	3.37**	2.14**	3.37**
$\delta^2_{GCA/\ SCA}$	0.00	0.01	0.16	0.23	0.41	0.85	0.3	0.3	0.21
	Ears per plant			Rows per ear			kernels per plant		
$\delta^2_{GCA\ (L)}$	-0.009**	-0.003	0.011**	0.07**	0.02**	0.17*	1206**	384**	668**
$\delta^2_{GCA(\ T)}$	0.002**	0.002**	-0.006	0.02**	0.06*	0.01*	136.3**	1.898**	-25.07
$\delta^2_{GCA\ (Aver)}$	0.009**	-0.002	0.004**	0.05**	0.04**	0.1**	766.7**	227.1**	383.2**
δ^2_{SCA}	0.003**	0.006**	0.012**	0.44**	0.55**	0.49**	2295**	1478**	1492**
$\delta^2_{GCA/\ SCA}$	3.21	0.00	0.34	0.11	0.07	0.21	0.33	0.15	0.26
	100-kernel weight			Grain yield per plant			Grain yield per hectare		
$\delta^2_{GCA\ (L)}$	2.17**	1.77**	1.79*	372.3**	172.8**	175.1**	7.59**	7.95**	14.29**
$\delta^2_{GCA(\ T)}$	-0.02	-0.15	0.03**	32.87**	0.10**	-7.68	0.67**	0.001**	-0.63*
$\delta^2_{GCA\ (Aver)}$	1.27**	0.98**	1.07**	232.9**	101.84**	100.02**	4.75**	4.69**	8.16**
δ^2_{SCA}	3.16**	4.82**	5.44**	401.91	263.5**	250.1**	8.18**	12.09**	20.42**
$\delta^2_{GCA/\ SCA}$	0.4	0.2	0.2	0.58	0.39	0.4	0.58	0.39	0.4

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

In the literature, there are two contrasting strategies for identifying genotypes that will be high yielding under abiotic stress: (i) Genotypes may be evaluated under the conditions in which they will ultimately be produced, namely a certain type of stress, to minimize genotype x environment interaction. Ceccarelli [39] has argued for this approach, but it may result in lower heritability. (ii) Genotypes may evaluated under optimum conditions maximizing heritability; but perhaps encountering problems with genotype x environments. Braun et al. [40] has argued for his approach, citing results from 17 years of the CIMMYT winter performing nursery. A third alternative, currently used at CIMMYT, which is simultaneous evaluation under near optimum and stress conditions, with selection of those genotypes that perform well in both environments [41]. However, ultimate evaluation must be performed in the target environment prior to recommendation for a cultivar for commercial production.

Table 4. Estimates of additive (δ^2_A) and dominance (δ^2_D) variance, degree of dominance "a", broad (h^2_b) and narrow (h^2_n) sense heritability and genetic advance from selection (GA%) under low (LD), medium (MD) and high (HD) plant density

Parameter	LD	MD	HD	LD	MD	HD	LD	MD	HD
	Days to 50% anthesis			**Anthesis-silking interval**			**Plant height**		
δ^2_A	0.09	0.44	0.79	-0.08	-0.02	0.06	10.56	24.65	75.91
δ^2_D	1.56	0.97	1.00	0.27	0.16	0.07	74.09	55.82	39.61
"a"	5.89	2.10	1.59	0.00	0.00	1.53	3.75	2.13	1.02
δ^2_{Ph}	1.82	1.58	1.96	0.28	0.25	0.25	146.52	102.71	157.59
δ^2_G	1.65	1.42	1.79	0.18	0.14	0.13	84.65	80.47	115.52
h^2_b (%)	90.49	89.46	91.16	66.20	55.64	51.89	57.78	78.35	73.31
h^2_n (%)	4.97	28.02	40.14	0.00	0.00	24.42	7.21	24.00	48.17
GA (%)	0.20	0.99	1.53	0.00	0.00	7.26	0.70	1.78	4.12
	Leaf area to produce 1 g of grain			**Penetrated light ear**			**Chlorophyll concentration index**		
δ^2_A	11.41	8.72	9.09	5.06	3.68	3.03	5.90	5.46	5.30
δ^2_D	7.25	4.44	3.87	1.47	1.07	1.26	1.44	0.64	0.71
"a"	1.13	1.01	0.92	0.76	0.76	0.91	0.70	0.48	0.52
δ^2_{Ph}	20.50	13.72	13.66	7.07	4.89	4.69	7.68	6.20	6.14
δ^2_G	18.66	13.16	12.96	6.52	4.75	4.29	7.34	6.11	6.01
h^2_b (%)	91.02	95.97	94.88	92.22	97.14	91.41	95.62	98.55	97.83
h^2_n (%)	55.64	63.61	66.54	71.50	75.32	64.62	76.85	88.15	86.30
GA (%)	15.77	18.61	25.00	13.62	13.78	13.40	25.21	31.73	36.95
	LA/1g			**PL-E**			**CCI**		
δ^2_A	2.51	2.77	12.52	25.85	3.20	1.40	4.10	5.29	5.02
δ^2_D	29.78	34.78	45.51	37.20	3.25	1.22	5.82	8.43	13.41
"a"	4.87	5.01	2.70	1.70	1.43	1.32	1.68	1.79	2.31
δ^2_{Ph}	36.72	40.23	62.05	73.04	7.26	2.85	11.02	14.10	19.39
δ^2_G	32.29	37.55	58.03	63.05	6.45	2.62	9.92	13.71	18.42
h^2_b (%)	87.93	93.35	93.52	86.32	88.89	91.71	89.96	97.21	95.03
h^2_n (%)	6.84	6.89	20.17	35.39	44.16	48.93	37.18	37.48	25.88
GA (%)	2.07	1.70	5.10	32.13	22.84	22.04	4.44	5.62	5.17
	Tassel fresh weight			**Tassel dry weight**			**Tassel branch number**		
δ^2_A	-0.15	0.56	6.28	2.68	3.39	4.47	2.05	1.31	1.42
δ^2_D	44.18	28.46	19.85	5.79	4.15	2.63	3.37	2.14	3.37
"a"	0.00	10.08	2.51	2.08	1.56	1.08	1.81	1.81	2.18
δ^2_{Ph}	46.75	29.77	27.10	8.98	7.65	7.26	5.72	3.55	5.07
δ^2_G	44.03	29.02	26.13	8.47	7.55	7.09	5.41	3.45	4.80
h^2_b (%)	94.17	97.48	96.40	94.32	98.69	97.75	94.64	97.09	94.67
h^2_n (%)	0.00	1.88	23.15	29.85	44.40	61.56	35.79	36.78	28.11
GA (%)	0.00	0.80	12.25	10.45	17.58	29.00	6.56	5.99	6.23
	Ears per plant			**Rows per ear**			**kernels per plant**		
δ^2_A	0.02	0.00	0.01	0.10	0.07	0.21	1533	454	766

Parameter	LD	MD	HD	LD	MD	HD	LD	MD	HD
δ^2_D	0.00	0.01	0.01	0.44	0.55	0.49	2295	1478	1492
"a"	0.58	0.00	1.41	2.97	3.96	2.16	1.73	2.55	1.97
δ^2_{Ph}	0.02	0.00	0.02	0.60	0.66	0.73	4192	2045	2385
δ^2_G	0.02	0.00	0.02	0.54	0.62	0.70	3828	1932	2258
h^2_b (%)	96.89	96.05	99.66	90.51	92.97	95.46	91.33	94.51	94.70
h^2_n (%)	83.85	0.00	40.27	16.65	10.73	27.98	36.58	22.22	32.14
GA (%)	20.81	0.00	10.11	1.60	1.16	3.44	7.57	3.88	7.08
	100-kernel weight			**Grain yield per plant**			**Grain yield per hectare**		
δ^2_A	2.53	1.97	2.14	465.8	203.7	200.0	9.49	9.37	16.32
δ^2_D	3.16	4.82	5.44	401.9	263.50	250.1	8.18	12.09	20.42
"a"	1.58	2.21	2.25	1.31	1.61	1.58	1.31	1.61	1.58
δ^2_{Ph}	5.99	6.90	7.76	914.5	478.9	463.2	18.62	22.02	37.81
δ^2_G	5.70	6.78	7.57	867.7	467.10	450.1	17.67	21.46	36.74
h^2_b (%)	95.05	98.31	97.55	94.88	97.54	97.16	94.92	97.46	97.17
h^2_n (%)	42.27	28.49	27.53	50.93	42.53	43.18	50.98	42.57	43.17
GA (%)	6.19	4.86	5.32	16.38	12.97	16.07	16.38	12.99	16.07

Note: Negative estimate of variance was considered zero

Two groups of researchers reported two contrasting conclusions; the first group of investigators reported that heritability and expected genetic advance is higher under stress than non-stress conditions, and that selection should be practiced in the target (stressed) environment to obtain higher genetic advance [7,21,23,]. The second group of researchers found that heritability and GA from selection for grain yield is higher under non-stress than those under stress [42-45]. Our results for grain yield and its components, TBN, TSL and PL-E are in agreement with the second group, but for other studied traits our results are in agreement with the first group.

4. CONCLUSIONS

This study concluded that both additive and dominance gene effects play important roles, but the magnitude of dominance was higher than additive variance in controlling the inheritance of most studied maize traits under all plant densities (LD, MD and HD), so the breeding method of choice for improving maize plant density tolerance (PDT) would be heterosis breeding. The best environment for selection differed according to the trait of interest. The study concluded that to achieve the highest predicted gain from selection for grain yield and its components, it is preferable to practice selection in the LD environment. In general, the results of this study could be useful for researchers who need to develop plant density tolerant varieties of maize in Egypt.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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