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INHERITANCE OF ADAPTIVE CHARACTERISTICS WITH HIGH-PLANT DENSITY AND LOW-N IN MAIZE (*ZEA MAYS* L.)

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SUMMARY

Information on the inheritance of adaptive traits to high plant density (HD) and low N (LN) in maize is a prerequisite for breeders to develop tolerant varieties to these stresses. The objective of the presented study was to estimate additive and dominance variances, heritability, and genetic advancement of the adaptive traits of tolerance to HD and LN stresses. Eight diverse maize inbred lines tolerant to HD and LN were options for diallel crosses. Parents and F₁ crosses sustained evaluation in two seasons under nine environments, viz., three plant densities (high = HD, medium = MD, and low = LD) × three N levels (high = HN, medium = MN, and low = LN). A randomized complete block design with three replications functioned in each environment. Both additive and dominance variances were significant; dominance was appreciably higher than the additive variance in most cases. The degree of dominance was more in the over-dominance range. The highest heritability, along with the highest genetic advance, succeeded from the environment stressed for both HD and LN for leaf angle, penetrated light at the bottom of the plant, and leaf area produced 1g grain, and from the environment stressed for HD for plant height and 100-kernel weight. Moreover, the results suggested that heterosis breeding is the method of choice for the genetic improvement of most studied traits.

Keywords: Plant density, Low N, combining ability, additive, dominance, heritability

Key findings: The results of this study will help maize breeders plan a proper breeding program for improving hybrids tolerant to high plant density and low N stresses in Egypt.

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INTRODUCTION

Available hybrid maize (*Zea mays* L.) cultivars in Egypt currently have breeding and planting at low plant density (about 50,000 plants ha⁻¹). Growing maize cultivars that can tolerate high plant densities of up to 100,000 plants ha⁻¹ is one way to fully maximize the overall amount of maize produced (Huseyin *et al.*, 2003). Over the second half of the 20th century, maize's average grain yield per unit area grew significantly in the USA due to the enhanced tolerance of modern hybrids to high plant densities (Duvick and Cassman, 1999). The Egyptian variety's towering stature, one-eared, decumbent leaves, and large-sized type plants likely contribute to their intolerance of high plant densities. Conversely, due to their morphological and phenological adaptability traits, such as early silking, short anthesis silking interval (ASI), fewer barren stalks, and prolificacy, modern maize hybrids in the United States are characteristic of high-yielding ability from land unit areas under high plant densities (Duvick *et al.*, 2004). Radenovic *et al.* (2007) pointed out that a high preference for cultivars of maize with erect leaves is prevalent to increase population density due to their superior light interception. Breeding programs should focus on creating hybrids with high plant density tolerance and adaptable features to boost maize grain yield per unit area in Egypt (Al-Naggar *et al.*, 2023; Khaled *et al.*, 2023).

According to Khaliq *et al.* (2009), nitrogen is a crucial ingredient for the growth of maize crops. It is the chief raw material needed for plant growth, having an early discovery to be a necessary component of several chemicals involved in metabolism, including proteins, amino acids, enzymes, coenzymes, and some non-proteinase substances (Brady and Weil, 2002). The low N stress is one of the most common issues limiting maize yield at high plant density. In farmer's fields where fertilization is not a routine application and organic matter rapidly mineralizes, low N availability in the soils is a significant yield-limiting factor that regularly persists (Banziger and Lafitte, 1997). The two most significant low-N adaptation features

appeared to be ears/plant and the anthesis-silking interval (Banziger *et al.*, 2000). In these conditions, it is preferable to raise the crop's tolerance to stresses that arise in their fields because smallholder farmers cannot afford additional inputs (Banziger *et al.*, 1999). As an alternative breeding approach, proposing tolerance to high plant population density has remained to improve resistance to various abiotic stresses, such as low N (Vasal *et al.*, 1997; Azzam *et al.*, 2022). Breeding programs should focus on creating hybrids with high plant density and low N tolerance to boost Egypt's maize grain output per unit of land. It is crucial to research how these characteristics attained inheriting.

Particularly in Egypt, such information is difficult to come by. Recessive genes with significant additive gene effects control the inheritance of anthesis silking interval (ASI), according to studies on the inheritance of ASI utilizing generation mean analysis employing maize inbred lines (Hefiny, 2010). Epistatic interactions and dominance gene action significantly influenced how to inherit ASI (Gonzalo *et al.*, 2010; Al-Naggar *et al.*, 2012b; and Hassan *et al.*, 2012). General (GCA) and specific (SCA) combining ability effects seemed to have an equal role in the expression of leaf angle, according to Mason and Zuber (1976). Al-Naggar *et al.* (2012a) found that both additive and dominance variance were highly significant for leaf angle (LANG) and plant height (PH) under both low and high plant densities; the magnitude of additive was higher than the dominance variance for LANG and PH only under low densities. They added that narrow-sense heritability (h^2_n) and expected genetic advance (GA %) estimates were lower in magnitude under high plant density than with low plant density for these traits.

After evaluating a group of newly developed inbred lines *per se* and for hybrid performance (Al-Naggar *et al.*, 2017), a set of eight inbred lines with apparent diversity in their adaptive traits to high-density and low-N tolerance became selected as parents of a diallel cross-mating design. The selection will study the inheritance of such traits to plan a proper breeding program for improving tolerant hybrids to high density and low N. The

objective of the presented study was to estimate general and specific combining ability, additive and dominance variances, heritability, and genetic advancement of the adaptive traits of tolerance to high plant density and low N stresses.

MATERIALS AND METHODS

This study commenced 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 masl). Eight maize inbred lines, four of which are tolerant to low N and high density (D), and four are sensitive (IL51, IL53, IL-80, and IL84), were choices for parental use for diallel crosses in this study based on the findings of a prior study (Al-Naggar *et al.*, 2017). In the 2020 season, creating all possible diallel crosses (except reciprocals) among the eight parents transpired, obtaining seeds of 28 direct F₁ crosses. Field evaluation experiments materialized in the 2021 and 2022 seasons. Each experiment included 28 F₁ crosses and their 8 parents. Evaluation in each season proceeded under nine environments (from E1 to E9), i.e., three nitrogen levels (high-, medium-, and low-N, by adding 476, 285, and 95 kg N/ha, respectively), in two equal doses as urea before the first and second irrigations, and three plant densities, (high-, medium-, and low-plant density [95,200, 71,400, and 47,600 plants/ha]), as follows: E1: High nitrogen-low plant density (HN-LD), E2: High nitrogen-medium plant density (HN-MD), E3: High nitrogen-high plant density (HN-HD), E4: Medium nitrogen-low plant density (MN-LD), E5: Medium nitrogen-medium plant density (MN-MD), E6: Medium nitrogen-high plant density (MN-HD), E7: Low nitrogen-low plant density (LN-LD), E8: Low nitrogen-medium plant density (LN-MD), and E9: Low nitrogen-high plant density (LN-HD).

A randomized complete block design (RCBD) with three replications was operational in each environment. Each experimental plot consisted of one ridge 4 m long and 0.7 m wide, i.e., the plot area was 2.8 m². Seeds

sown in hills had distances at 15, 20, and 30 cm; afterward (before the 1st irrigation), they reached thinning to one plant per hill to achieve the three plant densities, i.e., 95,200, 71,400, and 47,600 plants per ha, respectively. The sowing dates for all environments per season were April 29 and May 13 in the 2021 and 2022 seasons, respectively. All other agricultural practices continued following the recommendations of the ARC Egypt.

As per the recommendation of the Ministry of Agriculture, fertilization with calcium superphosphate at the rate of 70 kg P₂O₅/ha (30 kg P₂O₅/fed) progressed with soil preparation and before sowing. Weed control chemically proceeded with Stomp Extra 45.5 CS (Pendimethyline) (an herbicide manufactured by BASF, USA) before the first irrigation and just after sowing (pre-emergence), and manually by hoeing twice, the first before the second irrigation and the second before the third irrigation. Application of surface irrigation ensued after three weeks for the second irrigation and every 12 days for subsequent irrigations. Pest control occurred when required by spraying plants with Lannate (Methomyl) 90% (manufactured by DuPont, USA) against corn borers.

Data collection for 10 traits included 1) day to 50% anthesis (DTA), 2) anthesis-silking interval (ASI) as the number of days between 50% silking and 50% anthesis, 3) plant height in cm (PH), 4) leaf angle (LANG) measured as leaf angle between blade and stem for the leaf just above the ear using a protractor on 10 guarded plants per plot according to Zadoks *et al.* (1974), 5) leaf area to produce 1 g of grain (LA/1gG), measured as leaf area per plot / grams of grains per plot, 6) penetrated light at the bottom of the plant (PLB) as follows: PLB = 100 (light intensity in lux at the bottom of the plant/light intensity at the top of the plant), 7) chlorophyll concentration index (CCI), measured by the Chlorophyll Concentration Meter, as the ratio of transmission at 931 nm to 653 nm through the leaf of the top-most ear (<http://www.apogeeinstruments.co.uk/apogeeinstruments-chlorophyll-content-meter-technical-information/>), 8) number of kernels plant⁻¹ (KPP), 9) 100-kernel weight (100KW), and

10) grain yield plant⁻¹ (GYPP), adjusted at 15.5% grain moisture at harvest.

Statistical analysis

The data collected from each of the nine environments underwent the standard analysis of variance of randomized complete block design across seasons using GENSTAT 10th addition Windows software.

Genetic analysis of diallel crosses

Diallel cross analysis obtained general (GCA) and specific (SCA) combining ability variances for studied traits according to Griffing's (1956) Model I (fixed effect) Method 2. Although, Griffing's analysis depended on Model I (fixed effect). Since selecting parents of the diallel in this study was for the validity of the diallel analysis, Hayman's approach (that assumes a random model) also helped estimate genetic components. The conclusions obtained from Hayman's analyses will not undergo generalization but will help to characterize the genetic material for its proper use in future breeding programs. The genetic parameters and ratios calculation was according to methods developed by Jinks and Hayman (1953) and Hayman (1954 a, b), as described by Sharma (2003).

Heritability in the broad sense (h^2_b %) for a trait in a separate environment had estimations according to the following formula: $h^2_b \text{ \%} = 100 \times (\delta^2_g / \delta^2_{ph})$, Where: σ^2_g = genetic variance, and δ^2_{ph} = phenotypic variance. The range of the h^2_b reached classification as low (<30%), moderate (30%–60%), and high (>60%), as suggested by Johnson *et al.* (1955).

Narrow-sense heritability (h^2_n) estimation used the following equation: $h^2_n = (1/2D + 1/2H1 - 1/2H2 - 1/2F) / (1/2D + 1/2H1 - 1/4H2 - 1/2F + \hat{E})$. The classification range of the h^2_n was low (<15%), moderate (15%–30%), and high (>30%), as suggested by Johnson *et al.* (1955).

Expected genetic advance (GA) from selection for all studied traits as a percent of the mean proceeded to calculate according to Singh and Narayanan (2000), as follows: GA

(%) = $100 [(K h^2_n \sigma_{ph}) / \bar{x}]$, Where: \bar{x} = General mean, σ_{ph} = Square root of the denominator of the appropriate heritability, h^2_n = The applied heritability, K = Selection differential (K = 1.76, for 10 % selection intensity, used in this study). The range of GA as a percent of mean attained low (<10%), moderate (10%–20%), and high (>20%) classification, as suggested by Johnson *et al.* (1955).

RESULTS AND DISCUSSION

Combining ability variances

Variance estimates due to general (GCA) and specific (SCA) combining ability of the maize diallel crosses for combined data across two seasons under nine environments (combinations of three plant densities × three N-levels) are in Tables 1 and 2. Mean squares due to GCA and SCA indicated significant ($P \leq 0.01$ or $P \leq 0.05$) for all studied traits under nine environments, except mean squares due to GCA for ASI under E3, E5, E7, and E9, leaf angle under E2, E3, E4, and E9, PLB under E7, LA/gG under E4, E5, E7, and E9, and mean squares due to SCA for PLB under E3, LA/gG under E2. These suggest that additive and non-additive gene effects play vital roles in controlling the inheritance of most studied traits under most studied environments. A similar conclusion came from Mason and Zuber (1976), Khalil and Khattab (1998), and Al-Naggar *et al.* (2014).

In the latest study, the magnitude of GCA mean squares was higher than that of SCA (the ratio of GCA/SCA mean squares was higher than unity) for DTA under E9, ASI under E1, E2, E3, E4, E6, and E9, LANG under E1, E4, E5, E6, and E7, CCI under E2, E5, E6, E8, and E9, ELA under E2, E3, E4, E5, E6, E7, and E9, LA/gG under E1, and 100-KW under E6, E7, and E8, suggesting the existence of a higher portion of additive than non-additive variance in controlling the inheritance of these traits under the respective environments.

On the contrary, the magnitude of GCA mean squares was less than that of SCA mean squares (the GCA/SCA ratio was less than

unity) for the remaining traits in most studied environments, especially grain yield plant⁻¹, and all yield attributes, DTA, PH, LA/gG (except E1), and KPP. These indicate the existence of a superior portion of non-additive (dominance and over dominance) than that of additive variance in controlling the inheritance of these traits (majority of cases in the presented study). Such outcomes align with reports from Mostafa *et al.* (1996), Nawar *et*

al. (2002), Ahsan *et al.* (2007), Singh and Shahi (2010), and Al-Naggar *et al.* (2014, 2017). In the promising study, the magnitude of GCA mean squares was higher than that of SCA (the ratio of GCA/SCA mean squares was higher than unity) for DTA under E9, ASI under E1, E2, E3, E4, E6, and E9, LANG under E1, E4, E5, E6, and E7, CCI under E2, E5, E6, E8, and E9, and PLB under E1, E2, E3, E4, E7, and E8.

Table 1. Mean squares due to general (GCA) and specific (SCA) combining ability for days to anthesis, anthesis silking interval, plant height, leaf angle, and chlorophyll concentration index under nine environments combined across 2021 and 2022 seasons.

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 anthesis									
GCA	6.18*	9.03**	7.56**	14.74**	9.79**	8.17**	12.47**	13.36**	14.74**
SCA	16.61**	15.45**	14.86**	13.81**	18.49**	8.50**	13.04**	22.27**	13.24**
GCA×Y	14.20**	25.14**	15.35**	13.76**	15.59**	16.07**	12.07**	24.90**	21.93**
SCA×Y	11.06**	9.38**	12.95**	11.40**	10.80**	10.75**	8.44**	15.86**	9.92**
GCA/SCA	0.37	0.58	0.51	1.07	0.53	0.96	0.96	0.6	1.11
GCA×Y/SCA×Y	1.28	2.68	1.19	1.21	1.44	1.49	1.43	1.57	2.21
Anthesis silking interval									
GCA	2.45**	1.63**	1.17	1.67**	0.62	2.60**	0.65	0.38	3.24**
SCA	1.23*	1.05**	1.01*	1.71**	1.94**	1.63**	1.14*	2.66**	1.68**
GCA×Y	1.86*	0.8	0.37	1.04*	0.44	0.91	0.93	1.82**	2.78**
SCA×Y	0.93	0.96**	0.57	1.25**	0.89	1.14*	1.09*	0.74	1.93**
GCA/SCA	1.99	1.55	1.16	0.98	0.32	1.6	0.57	0.14	1.93
GCA×Y/SCA×Y	2	0.83	0.65	0.83	0.49	0.8	0.85	2.46	1.44
Plant height									
GCA	611.40**	330.05*	248.8*	407.5**	218.5*	328.5**	583.6**	369.4**	601.29**
SCA	4277**	4640**	6252**	4633**	5608.2**	6223**	4853**	6222.5**	8042.7**
GCA×Y	245.99*	193.3	208.29*	411.61**	268.49**	283.59*	699.73**	351.27**	24.71
SCA×Y	444.23**	281.48**	224.15**	342.41**	217.28**	178.92*	309.38**	226.14**	56.77
GCA/SCA	0.14	0.07	0.04	0.09	0.04	0.05	0.12	0.06	0.07
GCA×Y/SCA×Y	0.55	0.69	0.93	1.2	1.24	1.59	2.26	1.55	0.44
Leaf angle									
GCA	43.80**	14.96	14.48	19.83	39.25**	29.32**	25.21*	369.49**	17.57
SCA	18.99	22.03**	15.01**	15.86	16.58*	21.24**	21.04*	6222**	32.51**
GCA×Y	4.83	16.94	27.05**	10.96	20.94*	31.05**	28.67*	351.27**	5.56
SCA×Y	22.57*	24.83**	24.35**	24.79**	18.66**	11.22	21.57*	226.14**	6.01
GCA/SCA	2.31	0.68	0.96	1.25	2.37	1.38	1.2	0.06	0.54
GCA×Y/SCA×Y	0.21	0.68	1.11	0.44	1.12	2.77	1.33	1.55	0.93
Chlorophyll concentration index									
GCA	67.44*	96.05**	49.48**	91.11**	65.06**	112.91**	79.73**	66.05**	171.06**
SCA	79.58**	86.94**	74.77**	95.32**	64.29**	86.88**	85.57**	61.87**	105.55**
GCA×Y	12.19	49.49**	42.83**	37.74*	40.46**	55.29**	26.46*	21.66*	14.42
SCA×Y	34.61	38.06**	26.03**	28.27*	45.48**	32.64**	37.36**	37.13*	11.5
GCA/SCA	0.85	1.1	0.66	0.96	1.01	1.3	0.93	1.07	1.62
GCA×Y/SCA×Y	0.35	1.3	1.65	1.33	0.89	1.69	0.71	0.58	1.25

* and ** indicate significance at 0.05 and 0.01 probability levels, respectively, Y= Years, GCA = general combining ability, and SCA = specific combining ability.

Table 2. Mean squares due to general (GCA) and specific (SCA) combining ability for penetrated light at bottom of plant, leaf area producing one gram of grain, kernels/plant, 100-kernel weight, and grain yield/plant under nine environments combined across 2021 and 2022 seasons.

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
Penetrated light at bottom of plant									
GCA	21.84*	9.63*	5.45*	7.78*	3.4	5.47**	6.29	4.01*	4.70**
SCA	12.18	9.26*	4.98**	5.2*	5.42**	5.72**	5.58	3.24*	5.46**
GCA×Y	9.71	11.08*	3.53	7.04*	8.24**	3.99*	11.01*	5.50*	0.37
SCA×Y	7.24	7.12*	2.31	3.14	5.16*	2.34	4.74	2.55	0.65
GCA/SCA	1.79	1.04	1.09	1.34	0.63	0.96	1.13	1.24	0.86
GCA×Y/SCA×Y	1.34	1.56	1.53	2.24	1.6	1.71	2.32	2.16	0.57
Leaf area producing 1 gram of grain									
GCA	220.9**	237.5**	550.4*	150.6	91.1	1244**	278	647*	325
SCA	72.87*	266.7	1618.5**	236.3**	546.0**	1642**	646**	1067**	2136**
GCA×Y	17	84.75	164.1	152.5	364.1*	586*	226	196	122
SCA×Y	58.75	134.19*	388.1*	108.6	148.8	480*	230	333	189
GCA/SCA	3.03	0.89	0.34	0.64	0.17	0.76	0.43	0.61	0.15
GCA×Y/SCA×Y	0.29	0.63	0.42	1.4	2.45	1.22	0.98	0.59	0.65
Kernels/plant									
GCA	31488**	11124**	18700**	94117**	6692*	17157**	152098**	14436*	18157**
SCA	107122**	111936**	101360**	138995**	83594**	115596**	199646**	90454**	109383**
GCA×Y	6125	3194	11818**	47661**	19755**	17617**	180836**	29463**	1557
SCA×Y	14662**	7947**	8845**	31151**	10146**	6600**	67917**	12899**	2088
GCA/SCA	0.29	0.1	0.18	0.68	0.08	0.15	0.76	0.16	0.17
GCA×Y/SCA×Y	0.42	0.4	1.34	1.53	1.95	2.67	2.66	2.28	0.75
100-Kernel weight									
GCA	6.25*	9.97**	11.09**	12.40**	3.14	17.68**	32.66**	7.72**	9.93**
SCA	7.24**	16.57**	23.92**	8.05**	5.71**	15.01**	11.87*	4.02*	12.39**
GCA×Y	7.30**	3.94	9.01*	2.65	9.29**	7.62**	8.06	3.53*	1.86
SCA×Y	6.09**	4.69*	3.57	6.23**	3.67*	4.15**	16.26**	4.28*	2.91
GCA/SCA	0.86	0.6	0.46	1.54	0.55	1.18	2.75	1.92	0.8
GCA×Y/SCA×Y	1.2	0.84	2.52	0.43	2.53	1.84	0.5	0.82	0.64
Grain yield/plant									
GCA	2095.7**	566.0**	558.8**	3671.2**	985**	1313.4**	3836.1**	2398**	1487**
SCA	6081.3**	3471.2**	2801.2**	8655.1**	8131**	5353.3**	7592.1**	7206**	6740**
GCA×Y	315.6	179.2	290.8*	992.3*	663*	1392.3**	2265.6**	1749**	143.4
SCA×Y	981.1**	504.2**	481.8**	2459.0**	1201**	1381.3**	2417.7**	768.7	293
GCA/SCA	0.34	0.16	0.2	0.42	0.12	0.25	0.51	0.33	0.22
GCA×Y/SCA×Y	0.32	0.36	0.6	0.4	0.55	1.01	0.94	2.28	0.49

* and ** indicate significance at 0.05 and 0.01 probability levels, respectively, Y= Years, GCA = general combining ability, and SCA = specific combining ability.

Results in Tables 1 and 2 indicate that mean squares due to the SCA × year and GCA × year interactions were significant ($P \leq 0.01$) for DTA, PH, LANG, CCI, KPP, and GYPP under all studied environments, with the remaining traits under some environments. It implies that additive and non-additive variances for these traits under the respective environments had years affecting them. However, for the remaining cases, results suggest that years did

not influence additive and non-additive variances.

The mean squares due to SCA × year were higher than those due to GCA × year in all environments for ASI (except under E1, E8, and E9), GYPP (except under E6 and E8), as well as some other cases (Tables 1 and 2). It suggests that SCA (non-additive variance) gained more influences from years than GCA for these cases. Contrastingly, mean squares

due to GCA \times year were higher than those due to SCA \times year in all environments for DTA, PLB (except under E1), KPP (except under E1 and E2), as well as some other cases (Tables 1 and 2), indicative of years influencing GCA (additive) variance more than SCA (non-additive) variance for these traits under the respective environments.

Gene action, heritability and genetic advance

Estimates of genetic variances and ratios for studied traits under nine environments across two years are available in Tables 3 and 4. The dominance genetic component of variation (H_1) was significant ($P \leq 0.05$ or 0.01) for all studied traits under all nine environments, except for ASI under E9 and leaf area produced 1g grain under E9. It indicates that heterosis breeding is the method of choice for the genetic improvement of most studied traits, i.e., grain yield and adaptive traits to high density and adaptive traits to low N stress under all environments.

The additive component of variation (D) was also significant ($P \leq 0.05$ or 0.01) for all studied traits under all environments, except for days to anthesis under E2, E3, E7, and E9, ASI under E6, and grain yield/plant under E8, where additive was not significant. It signifies that selection may be proficient effectively in maize populations for improving such traits where significant additive variance exists under respective environments (Mariani and Desiderio, 1975; Shehata *et al.*, 1982; Ismaeili *et al.*, 2005; Al-Naggar *et al.*, 2011).

The estimates of dominance were much higher in magnitude than additive variance (where the ratio D/H_1 is < 1) for most studied cases, suggesting that dominance variance plays a prime role in the inheritance of most studied traits in most cases. Thus, heterosis breeding would be more efficient than selection for improving studied traits under all environments (all combinations between three plant densities \times three N levels). This conclusion is in agreement with reports by El-Shouny *et al.* (2003), Ahsan *et al.* (2007), and Al-Naggar *et al.* (2011, 2014 and 2015).

The average degree of dominance ($(H_1/D)^{1/2}$) was higher than unity for all studied traits under all environments (except for DTA under E1 and E6, ASI under all environments except E3 and E6, Leaf angle under E3 through E6, and E9, CCI under E1, E2, E4, E5, and E8, penetrated light at the bottom of the plant under E1, E2, E3, E8, and E9, leaf area produced 1g grain under E9, 100-kernel weight under E2, E3, E4, and E6. It indicates that the degree of dominance in most cases was over-dominance. The highest $(H_1/D)^{1/2}$ value was evident in E1 (KPP), E8 (GYPP), and E2 (DTA).

Broad-sense heritability (h^2_b) was of high magnitude ($>60\%$) for plant height, leaf angle, penetrated light at the bottom of the plant, kernels/plant, and grain yield/plant, indicating that the environment had a lesser effect on the phenotype for these traits under all environments. For other studied traits, h^2_b was between low and moderate. The minimum estimates of h^2_b resulted in CCI (7.61% under E9) and 100-kernel weight (5.31% under E8), implying that the environment and genotype \times environment interaction had considerable effects on the phenotype for these traits.

Narrow-sense heritability (h^2_n) was low ($<15\%$) or moderate (15%–30%) in magnitude under all environments for DTA, ASI, PH, CCI, KPP, 100-KW, and GYPP, and of high magnitude ($>30\%$) for remaining traits under all environments. The highest h^2_n appeared for leaf area produced 1g grain under E9 (67.17%), penetrated light at the bottom of the plant under E1 (79.86%), and leaf angle under E9 (79.54%). The lowest h^2_n was notable for DTA under E2 (1.29%), ASI under E9 (1.61%), and CCI under E9 (1.10%). Overall, the traits that showed very high h^2_n were leaf angle, penetrated light at the bottom of the plant, kernels/plant, and grain yield/plant. The big difference between broad and narrow sense heritability in many cases of this experiment could refer to the high estimates of dominance, dominance \times dominance, and dominance \times additive components.

The expected genetic advance (GA) from selection (based on 10% selection intensity) across years for studied traits in the nine environments (Tables 3 and 4) was

Table 3. Estimates of genetic parameters for days to anthesis, anthesis silking interval, plant height, leaf angle, and chlorophyll concentration index traits under nine environments across two years (2021-2022).

Parameter	HN-LD	HN-MD	HN-HD	MN-LD	MN-MD	MN-HD	LN-LD	LN-MD	LN-HD
	E1	E2	E3	E4	E5	E6	E7	E8	E9
Days to anthesis									
D	4.32**	0.13	0.24	0.39*	0.78*	3.36**	0.1	0.68*	0.16
H1	1.31**	4.59**	1.47**	0.86**	3.68**	1.07**	1.54**	2.78**	4.92**
D/H1	3.3	0.03	0.16	0.46	0.21	3.13	0.06	0.24	0.03
(H1/D) ^{1/2}	0.55	5.91	2.5	1.48	2.17	0.57	3.99	2.02	5.51
h ² _b %	44.58	38.07	18.78	14.68	34.97	29.7	13.65	29.71	21.94
h ² _n %	6.39	1.29	9.7	15.98	19.07	5.8	2.02	19.56	5.91
GA%	0.34	0.06	0.45	0.78	0.99	0.24	0.1	1.04	0.27
Anthesis-silking interval									
D	0.72**	0.27*	0.41*	0.77**	0.54*	0.06	0.97**	0.57**	1.12*
H1	0.34*	0.15*	0.99**	0.35*	0.42*	0.28**	0.08	0.17*	0.03
D/H1	2.12	1.83	0.41	2.18	1.3	0.23	11.83	3.23	35.34
(H1/D) ^{1/2}	0.69	0.74	1.56	0.68	0.88	2.11	0.29	0.56	0.17
h ² _b %	34.39	38.22	22.11	32.71	28.64	30.45	16.5	27.6	20.53
h ² _n %	2.14	16.47	19.76	7.83	13.49	9.22	14.34	19.65	1.61
GA%	1.35	6.07	9.78	21.2	12.83	4.07	9.87	13.91	0.7
Plant height									
D	132.8*	88.6*	120.6*	89.2*	82.9*	93.9*	99.4*	112.7*	102.4*
H1	2811**	2119**	1558**	2104**	1914**	1507**	2177**	1423**	1321**
D/H1	0.05	0.04	0.08	0.04	0.04	0.06	0.05	0.08	0.08
(H1/D) ^{1/2}	4.6	4.89	3.59	4.86	4.8	4.01	4.68	3.55	3.59
h ² _b %	82.23	83.27	75.45	81.74	82.47	76.25	83.35	73.05	72.43
h ² _n %	14.68	12.42	19.89	12.02	12.19	15.97	13.24	17.33	17.94
GA%	2.72	2.26	3.77	2.17	2.24	2.95	2.42	3.32	3.74
Leaf angle									
D	9.59*	11.95*	20.88**	8.01**	12.44**	24.66**	6.98*	9.22*	30.43**
H1	12.48**	31.89**	9.88*	5.43**	8.80*	10.98**	11.71**	15.18**	10.86
D/H1	0.77	0.37	2.11	1.48	1.41	2.25	0.6	0.61	2.8
(H1/D) ^{1/2}	1.14	1.63	0.69	0.82	0.84	0.67	1.29	1.28	0.6
h ² _b %	67.59	93.13	99.33	75.64	86.19	73.21	81.04	77.1	91.13
h ² _n %	64.66	81.72	76.16	64.19	75.7	79.3	73.97	72.83	79.54
GA%	10.3	14.98	13.85	10.54	14.9	18.29	13.75	20.09	24.45
Chlorophyll concentration index									
D	25.14**	9.15*	14.03**	28.29**	18.26**	10.31**	10.05**	1.93*	14.91**
H1	13.22**	7.89*	23.81**	22.95**	12.38**	13.56**	23.43**	1.18*	32.60**
D/H1	1.9	1.16	0.59	1.23	1.47	0.76	0.43	1.63	0.46
(H1/D) ^{1/2}	0.73	0.93	1.3	0.9	0.82	1.15	1.53	0.78	1.48
h ² _b %	27.79	11.52	25.1	22.43	20.08	11.09	23	9.04	7.61
h ² _n %	8.66	0.64	2.15	5.03	2.43	0.19	1.11	4.35	1.1
GA%	1.88	0.12	0.28	0.93	0.33	0.03	0.17	1.14	1.19

* and ** indicate significance at 0.05 and 0.01 probability levels, respectively, D = Additive, H1= Dominance, (H1/D)^{1/2}= Degree of dominance, h²_b% = Heritability in broad sense, h²_n% = Heritability in narrow sense, GA%= Genetic advance as a percent of the mean.

Table 4. Estimates of genetic parameters for penetrated light at bottom of plant, leaf area producing 1 gram of grain, kernels/plant, 100-kernel weight, and grain yield/plant traits under nine environments across two years.

Parameter	HN-LD E1	HN-MD E2	HN-HD E3	MN-LD E4	MN-MD E5	MN-HD E6	LN-LD E7	LN-MD E8	LN-HD E9
Penetrated light at bottom of plant									
D	1.23*	2.92*	7.33**	1.12*	2.44*	2.27*	1.98*	6.88**	15.72**
H1	0.14	1.47*	3.51*	1.55*	4.38**	5.34**	3.68*	3.15*	5.74**
D/H1	8.52	1.98	2.09	0.72	0.56	0.43	0.54	2.18	2.74
(H1/D) ^{1/2}	0.34	0.71	0.69	1.18	1.34	1.53	1.36	0.68	0.6
h ² _b %	82.48	92.06	87.48	83.97	90.12	94.02	83.14	88.46	89.53
h ² _n %	79.86	75.45	78.64	59.99	75.11	74.84	73.9	73.15	78.03
GA%	12.11	15.63	15.66	11.62	15.34	16.92	14.7	15.5	20.11
Leaf area produced 1g grain									
D	73.8**	72.8**	86.7**	123.2**	35.6**	30.8**	11.1**	23.2**	60.0**
H1	533**	123.9**	100.6**	326.3**	38.5**	103.2**	305.2**	33.3**	2.3
D/H1	0.14	0.59	0.86	0.38	0.92	0.3	0.04	0.7	26.57
(H1/D) ^{1/2}	2.69	1.3	1.08	1.63	1.04	1.83	5.23	1.2	0.19
h ² _b %	16.54	42.39	50.87	14.46	40.38	68.1	18.11	72.77	79.29
h ² _n %	10.06	30.83	54.14	6.83	30.9	61.69	5.04	25.74	67.17
GA%	3.11	14.99	24	2.29	11.2	26.73	1.99	11.29	28.5
Kernels/plant									
D	188**	4528**	11045**	569**	1187**	4801**	1845**	1112**	3213**
H1	40348**	24857**	67935**	42030**	29115**	40795**	36557**	36699**	24252**
D/H1	0	0.18	0.16	0.01	0.04	0.12	0.05	0.03	0.13
(H1/D) ^{1/2}	14.66	2.34	2.48	8.6	4.95	2.92	4.45	5.75	2.75
h ² _b %	72.05	69.43	64.73	80.04	71.68	44.62	73.58	77.79	52.02
h ² _n %	3.7	25.1	2.62	5.14	11.75	2.74	14.28	8.74	20.63
GA%	1.17	10.96	1.4	1.67	3.45	1.1	4.61	2.61	7.43
100-kernel weight									
D	0.68**	3.45**	12.51**	3.49**	0.63*	1.84**	1.19**	0.52*	0.18*
H1	1.95**	0.64*	5.17**	1.56**	2.17**	0.35	2.51**	1.19**	0.64**
D/H1	0.35	5.36	2.42	2.24	0.29	5.21	0.47	0.44	0.28
(H1/D) ^{1/2}	1.69	0.43	0.64	0.67	1.85	0.44	1.45	1.52	1.88
h ² _b %	21.11	69.35	36.15	34.52	57.16	45.07	19.61	5.31	22.87
h ² _n %	8.47	15	10	9.19	16	14	11.03	2.18	3
GA%	1.69	8.18	11.34	0.8	4.34	4.73	2.38	0.38	2.45
Grain yield/plant									
D	180**	101**	91**	198**	154**	63**	75*	15	190**
H1	2677**	1846**	2005**	1584**	2537**	2731**	893**	1074**	1715**
D/H1	0.07	0.05	0.05	0.12	0.06	0.02	0.08	0.01	0.11
(H1/D) ^{1/2}	3.85	4.28	4.68	2.83	4.06	6.56	3.45	8.46	3
h ² _b %	71.43	45.4	46.76	61.37	65.74	59.55	65.64	68.95	55.78
h ² _n %	4.81	4.6	11.59	24.08	13.06	9.94	19.47	3.59	3.38
GA%	1.5	0.18	3.51	8.7	4.89	3.59	6.22	1.26	0.14

* and ** indicate significance at 0.05 and 0.01 probability levels, respectively, D = Additive, H1= Dominance, (H1/D)^{1/2}= Degree of dominance, h²_b% = Heritability in broad sense, h²_n% = Heritability in narrow sense, GA%= Genetic advance as a percent of the mean.

generally of low magnitude (<10%), especially for DTA (from 0.10% under E7 to 0.99% under E5), CCI (0.12% under E2 to 1.88% under E1) but reached its maximum for leaf angle under E9 (24.45%) and penetrated light at the bottom of the plant under E9 (20.11%).

The environment E9 (stressed for both high density and low N) for the traits leaf angle, penetrated light at the bottom of the plant, and leaf area produced 1g grain, showed the highest heritability and expected genetic gain from the selection. The environment E3 (stressed for high density) showed the maximum heritability and expected genetic gain from selection for plant height and 100-kernel weight.

Based on findings related to heritability and expected genetic advance (GA) from the selection in stressful and non-stressful environments, two opposing conclusions have been apparent in the literature. Heritability and GA from the selection for grain yield are higher in non-stressful environments than in stressful ones, according to the findings of numerous researchers (Shabana *et al.*, 1980; Rosielle and Hamblin, 1981; Banziger and Laffite, 1997; Banziger *et al.*, 1997; and Worku *et al.*, 2007). Nevertheless, according to other researchers (Blum, 1988; Hefny, 2007; and Al-Naggar *et al.*, 2009 and 2010), selection should proceed in the target environment to achieve higher genetic advancement. Heritability and expected GA for the same trait are higher under stress than under non-stress.

Therefore, expectantly, to improve plant height and 100-kernel weight, it is better to practice selection under high-density stress to obtain higher values of selection gain. Similarly, it is more practical to select in a stressed environment for both high density and low N to expand leaf angle, the penetrated light at the bottom of the plant, and the leaf area produced 1 g of grain traits.

CONCLUSIONS

This study found that both additive and dominance gene effects are significant; however, in regulating the inheritance of most studied maize traits across all combinations of

plant densities (LD, MD, and HD) and N levels (LN, MN, and HN), dominance played a more significant role than the additive variance. Therefore, heterosis breeding would be the preferred technique for enhancing maize with a high plant density and a low N tolerance. The best environment for selection differed according to the trait of interest. The study found that it is preferable to practice selection in a stressed environment with high density and low N to improve leaf angle, the penetrated light at the bottom of the plant, and the leaf area that produced 1 g of grain. It is also advisable to practice selection under high-density stress to obtain higher values of selection gain to enhance plant height, rows/ear, kernels/row, and 100-kernel weight. Overall, the results of this study could benefit researchers who need to develop plant density and low-N-tolerant varieties of maize in Egypt.

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