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Screening Criteria and Selection Environment for Tolerance to Elevated Plant Density in Maize (Zea mays L.) Inbreds and Hybrids

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Authors' contributions

This work was carried out in collaboration between all authors. Author AMMAN designed the study, wrote the protocol and wrote the first draft of the manuscript. Authors MMMA and MAA managed the literature searches. Author ASMY managed the experimental process and performed data analysis. All authors read and approved the final manuscript.

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ABSTRACT

Indirect selection would be effective if heritability of the secondary trait is greater than that of the primary trait and genetic correlation between them is strong. The objectives of this investigation were to identify secondary trait(s) for selection of high maize grain yield under high plant density (HPD) and to identify whether the best selection environment is the optimum or stressed one. Diallel crosses among diverse inbreds in tolerance to HPD were evaluated in the field in two seasons under two contrasting environments; low density (LD); 47,600 plants/ha and high density (HD); 95,200 plants/ha, using RCBD with three replications. Strong favorable and significant genetic correlations were detected between grain yield/plant (GYPP) or HPD tolerance and each of yield components and days to anthesis (DTA), anthesis silking interval (ASI), plant height (PH), ear height (EH), barren stalks (BS) and leaf angle (LANG) for hybrids. The traits DTA, PH, EH, BS, LANG, ears/plant (EPP), rows/ear (RPE), 100- kernel weight (100 KW), kernels/row (KPR), kernels/plant (KPP), under both LD and HD environments had much higher narrow sense

heritability (h_n^2) than GYPP (> 3 fold). Thus, these traits could be considered secondary traits to HPD tolerance. Selection for high KPP was more efficient in improving grain yield than selection for yield itself with a relative efficiency (RE) of 238.1 and 203.7% under LD and HD, respectively. It can be concluded that choosing the optimum selection environment to achieve maximum gain is affected by the genotype and the trait of interest. With respect of GYPP of hybrids, the direct selection is the best. The optimum selection environment is the target environment, while for inbreds; the indirect selection is the best. The optimum selection environment for high yield under HD is the optimum environment (LD).

Keywords: Indirect selection; target environment; correlations; high plant density; relative efficiency.

1. INTRODUCTION

Despite increasing grain yield of maize in Egypt due to the use of single and three-way cross hybrids under high inputs and low plant density, there is lack of information on utilization of high density tolerant maize hybrids to increase crop yield per unit area. One of the potential methods to maximize total production of maize in Egypt is through raising productivity per land unit area. Grain yield per land unit area is the product of grain yield per plant and number of plants per unit area [1,2]. Maximum yield per unit area may be obtained by growing maize hybrids that can withstand high plant density up to 100,000 plants ha⁻¹ [3].

Whether direct or indirect selection is superior depends upon the heritability of the selected trait in stress and non-stress environments and the genetic correlation between stress and nonstress environments [4-6]. However, many investigators reported a decline in heritability for grain yield under stress [7,8]. A large number of studies have been conducted on maize to estimate both broad and narrow sense heritability. A number of reports on heritability are available for different traits of maize under high density and drought stress conditions [9-11]. They suggested anthesis silking interval (ASI) as a highly heritable trait. Bänziger et al. [12] found that broad sense heritability for grain yield under low N were on average 29% smaller than under high N because of lower genotypic variance under low N. In general, standard errors of heritability, genetic correlations, variances, and covariances increase with decreasing heritability [13]. Bänziger and Lafitte [11] concluded that secondary traits are valuable adjuncts in increasing the efficiency of selection for grain yield when broad-sense heritability of grain yield is low. Furthermore, it should be kept in mind that the estimate of heritability applies only to sampled environments [14-17]. Thus, when planning to improve an adaptive trait to a given

stress, priority should be given to estimate heritability of this trait under targeted environmental conditions. Hallauer and Miranda [15] noted that heritability coefficients, as well as additive genetic correlation, depend on the population under selection and on environmental conditions. This indicates that the advantage of direct and indirect selection must be investigated for each particular situation. Productivity of the plants in the selection enviroments and/or a high correlation between yield in the test and the taget environments have been used to identify the most appropriate selection environments [6].

Genetic correlation in particular determines the degree of association between traits and how they may enhance selection. It is useful if indirect selection gives greater response to selection for traits than direct selection for the same trait. It is suggested that indirect selection would be effective if heritability of the secondary trait is greater than that of the primary trait and genetic correlation between them is substantial [13]. Similarly, Rosielle and Hamblin [8] also indicated that magnitudes of selection responses and correlated responses will depend on heritability and phenotypic standard deviations as well as genetic correlations. Other studies reported that computed phenotypic correlation found positive correlations between grain yield and yield components, ear height and plant height [18]. The main criterion for high density or low N tolerant trait selection is the association of each trait with grain yield under stress conditions [2].

The objectives of the present investigation were: (i) to identify secondary trait(s) for high plant density tolerance in maize inbreds and hybrids to be used in screening programs for selecting the tolerant genotypes and (ii) to estimate the efficiency of indirect selection relative to direct selection for a given trait in order to identify the best selection environment for use in the target environment (high density stressed).

2. MATERIALS AND METHODS

This study was carried out at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza, Egypt (30° 02'N latitude and 31° 13'E longitude with an altitude of 22.50 meters above sea level), in 2012, 2013 and 2014 seasons.

2.1 Plant Material

Based on the results of previous experiments [19], six maize (*Zea mays* L.) inbred lines in the 8^{th} selfed generation (S₈), showing clear differences in performance and general combining ability for grain yield under high plant density, were selected in this study and used as parents of diallel crosses (Table 1).

2.2 Making F₁ Diallel Crosses

In 2012 season, diallel crosses (except reciprocals) were made among the six parents, and seeds of 15 direct F_1 crosses were obtained. Seeds of the 6 parents were also increased by selfing in the same season (2012) to obtain enough seeds of the inbreds in the 9th selfed generation (S₉).

2.3 Evaluation of Parents and F₁'s

Two field experiments were carried out in each of 2013 and 2014 seasons at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza. Each experiment included 21 genotypes ($15 F_1$ crosses and their 6 parents). The first experiment was done under low plant density (low-D; 47,600 plants/ha) while the second experiment was done under high plant density (high-D; 95,200 plants/ha). A randomized complete blocks design

(RCBD) with three replications was used in each experiment.

Each experimental plot consisted of one ridge of 4 m long and 0.7 m width, *i.e.* the experimental plot area was 2.8 m². Seeds were sown in hills at 15 and 30 cm apart, thereafter (before the 1st irrigation) were thinned to one plant/hill to achieve a plant density of 47,600 and 95,200 plants/ha, for the first and second experiment, respectively. Sowing dates of the two experiments were on May 5 and May 8 in 2013 and 2014 seasons, respectively. The soil of the experimental site was clayey loam. All other agricultural practices were followed according to the recommendations of Agricultural Research Center (ARC), Egypt.

2.4 Physical and Chemical Soil Analysis

The analysis of the experimental soil, as an average of the two growing seasons 2013 and 2014, indicated that the soil is clay loam (4.00% coarse sand, 30.90% fine sand, 31.20% silt, and 33.90% clay), the pH (paste extract) is 7.73, the EC is 1.91 dSm-1, soil bulk density is 1.2 g cm-3, calcium carbonate is 3.47%, organic matter is 2.09%, the available nutrient in mg kg-1are Nitrogen (34.20), Phosphorous (8.86), Potassium (242), hot water extractable B (0.49), DTPA - extractable Zn (0.52), DTPA - extractable Mn (0.75) and DTPA - extractable Fe (3.17).

2.5 Meteorological Data

Meteorological variables in the 2013 and 2014 growing seasons of maize were obtained from Agro-meteorological Station at Giza, Egypt. For May, June, July and August, mean temperature was 27.87, 29.49, 28.47 and 30.33°C, maximum temperature was 35.7, 35.97, 34.93 and 37.07°C

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

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

ARC = Agricultural Research Center, Pion. Int. Co. = Pioneer International Company in Egypt, SC = Single cross, A.E.D. = American Early Dent; an old open-pollinated variety, W = White grains and Y = Yellow grains and relative humidity was 47.0, 53.0, 60.33 and 60.67%, respectively, in 2013 season. In 2014 season, mean temperature was 26.1, 28.5, 29.1 and 29.9°C, maximum temperature was 38.8, 35.2, 35.6 and 36.4°C and relative humidity was 32.8, 35.2, 35.6 and 36.4%, respectively. Precipitation was nil in all months of maize growing season for both seasons.

2.6 Data Collected

- Days to 50% anthesis (DTA) (as number of days from planting to anthesis of 50% of plants per plot).
- 2. Anthesis-silking interval (ASI) (as number of days between 50% silking and 50% anthesis of plants per plot).
- Plant height (PH) (cm) (measured from ground surface to the point of flag leaf insertion for five plants per plots).
- 4. Ear height (EH) (cm) measured from ground surface to the base of the top most ear relative to the plant height for five plants per plots.
- 5. Barren stalks (BS) (%) measured as percentage of plants bearing no ears relative to the total number of plants in the plot (an ear was considered fertile if it had one or more grains on the rachis).
- Leaf angle (LANG) (°) measured as the angle between stem and blade of the leaf just above ear leaf, according to Zadoks et al. [20].
- Ears per plant (EPP) calculated by dividing number of ears/plot on number of plants/plot.
- 8. Rows per ear (RPE) using 10 random ears/plot at harvest.
- 9. Kernels per row (KPR) using the same 10 random ears/plot.
- Kernels per plant (KPP) calculated as: number of ears per plant × number of rows per ear × number of kernels per row.
- **11. 100-kernel weight (100-KW)** (g) adjusted at 15.5% grain moisture, using shelled grains of each plot.
- 12. Grain yield/plant (GYPP) (g) estimated by dividing the grain yield per plot (adjusted at 15.5% grain moisture) on number of plants/plot at harvest.

High density tolerance index (DTI) modified from equation suggested by Fageria [21] was used to classify genotypes for tolerance to water stress. The formula used is as follows:

$$\mathsf{DTI}=(\mathsf{Y}_1/\mathsf{AY}_1)\times(\mathsf{Y}_2/\mathsf{AY}_2)$$

Where,

- Y_1 = mean grain yield of a genotype at nonstress.
- AY₁ = average yield of all genotypes at nonstress.
- Y_2 = mean grain yield of a genotype at stress.
- AY_2 = average yield of all genotypes at stress.

2.7 Biometrical Analysis

Each environment (LD and HD) was analyzed separately across seasons as RCBD using GENSTAT version 10. Least significant differences (LSD) values were calculated to test the significance of differences between means according to Steel et al. [22]. The genetic parameters were calculated according to methods developed by Hayman [23] and described by Sharma [24]. Narrow-sense heritability (h_{n}^2) was estimated using the following equation:

$$h_{n}^{2} = [1/4D / (1/4D + 1/4H_{1} - 1/4F + \hat{E}].$$

Expected genetic advance (GA) from direct selection, for each studied trait under each environment (LD and HD) was calculated according to Singh and Chaudhary [25] as follows:

$$GA = 100 \text{ k} \text{ h}_{n}^{2} \delta_{p} / x$$

where

- x = general mean of the appropriate plant density.
- δp = square root of the denominator of the appropriate heritability under LD or HD.
- h^2 = the applied heritability.
- k = selection differential (k = 1.76, for 10% selection intensity, used in this study).

Genetic correlation coefficients (r_g) among studied environments for each trait (or among traits for each environment) were first calculated from variances and covariances as follows:

$$r_{g} = \delta^{2}_{jk} / (\delta_{j} \cdot \delta_{k}),$$

where δ_{jk}^2 is the genetic covariance between studied environments (or between traits) j and k.

 δ_j and δ_k are the genetic standard deviations of studied environments (or traits)) j and k, respectively. Indirect correlated response (CRj) in environment j (or in GYPP trait) from selection in environment k (or in a secondary trait) was

then estimated according to Falconer [13] as follows:

$$CRj = 100 \text{ i } \text{H}^{\frac{1}{2}} \text{j } \text{H}^{\frac{1}{2}} \text{k } r_{\text{aik}} \delta p/x_{\text{i}}$$

where, CRj = correlated response in environment j (or in GYPP), H^{'z}j and H^{'z}k = square roots of heritability of traits j and k, respectively, r_{gjk} = genetic correlation among environments (or traits) j and k and X_j = general mean of environment (or of GYPP).

3. RESULTS AND DISCUSSION

3.1 Analysis of Variance

Combined analysis of variance across two seasons of a randomized complete blocks design for 12 traits of 21 maize genotypes for each of the two experiments (LD and HD), is presented in Table 2. Mean squares due to years were significant either (p≤0.05) or (p≤0.01) for DTA, PH, KPP and 100 KW under both LD and HD, BS under LD and ASI, EH, EPP and GYPP under HD. Mean squares due to parents and F₁ under both environments crosses were significant either (p≤0.05) or (p≤0.01) for all studied traits, except ASI under LD and high-D, indicating the significance of differences among studied parents and among F1 diallel crosses in the majority of cases. Genotypic variation under elevated plant density has also been reported by several investigators [26-28].

Mean squares due to parents vs. F_1 crosses were significant either (p≤0.05) or (p≤0.01) for all studied traits under both environments, except for ASI under LD and HD, BS under LD, EPP under HD, suggesting the presence of significant heterosis for the studied traits. Mean squares due to the interactions among parents × years (P×Y) and crosses × years (F_1 ×Y) were significant either (p≤0.05) or (p≤0.01) for 13 and 18 out of 24 cases, respectively. Mean squares due to parents vs. crosses × years (P × C) were significant either (p≤0.05) or (p≤0.01) only in 8 out of 24 cases, indicating that heterosis did not differ from season to season in the studied cases.

3.2 Mean Performance

Means of the 12 studied traits across years under the two environments (LD and HD) for each inbred and hybrid is presented in Table 3. In general, GYPP of the three inbreds L53, L20 and Sk5 was higher than that of the other three inbreds (L18, L28 and Sd7) under both environments (LD and HD). The highest GYPP of all inbreds was achieved under LD environment due to low competition between plants.

SOV							Mea	n squa	ires				
	df	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD
		D	TA	ŀ	ASI		PH		EH		BS	L	ANG
Y	1	**	**	ns	*	*	*	ns	**	*	ns	ns	ns
Р	5	**	**	ns	ns	**	**	**	**	*	**	**	**
F₁	14	*	**	ns	ns	**	**	**	**	**	**	**	**
P vs F₁	1	**	**	ns	ns	**	**	**	**	ns	**	**	**
P×Y	5	**	*	ns	ns	ns	ns	ns	**	*	*	**	**
F₁ × Y	14	ns	**	*	ns	*	ns	**	**	**	ns	**	**
P vs F ₁ × Y	1	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	*
· · · ·		EPP		RPE		KPP)	KPR	2	100-	KW	GYP	P
Y	1	ns	*	ns	ns	ns	ns	*	*	**	*	ns	**
Р	5	**	**	**	**	**	**	**	**	**	**	**	**
F₁	14	**	**	**	**	**	**	**	**	**	**	**	**
P vs F₁	1	**	ns	**	**	**	**	**	**	**	**	**	**
P×Y	5	ns	*	**	ns	ns	ns	*	ns	**	ns	**	*
F₁ x Y	14	*	ns	*	*	**	ns	**	*	**	**	**	**
P vs F₁ x Y	1	*	**	ns	ns	ns	ns	**	ns	**	ns	ns	**

Table 2. Combined analysis of variance of RCBD across two years for studied traits of 6 parents (P) and 15 F_1 crosses (F) and their interactions with years (Y) under two plant densities

* and ** significant at 0.05 and 0.01 probability levels, respectively, ns=non-significant, LD= low density, HD = high density, DTA = Days to 50% anthesis, ASI = Anthesis silking interval, RH = Plant height, EH = Ear height, BS = Barren stalks, LANG = Leaf angle, EPP = Ears per plant, RPE = Rows per ear, KPR = Kernels per row, KPP = Kernels per plant, 100-KW = 100 Kernel weight, GYPP = Grain yield per plant The inbred L53 showed the highest mean for GYPP under both environments. The inbred L20 was the second highest for grain yield, while inbred Sk5 came in the third rank. On the contrary, the inbreds L18 and L28 exhibited the lowest mean for GYPP under HD and LD environment, respectively. The superiority in GYPP of L53, L20 and Sk5 over other inbreds was associated with superiority in all studied yield components. Sk5 had the shortest plants and the narrowest LANG. But L53 had the tallest plant and the highest ear position under low and high density conditions.

Under low density (LD) and high density (HD) environment, the highest GYPP was recorded by the cross L20 x L53 followed by the crosses L53 x Sk5 and L53 × Sd7. These crosses could therefore be considered responsive to optimum plant density and tolerant to high density. The superiority of these crosses in GYPP to other studied F1's was also expressed in all studied yield components, namely EPP, RPE, KPR, KPP, and 100-KW as well as in the shortest plant and lowest ear height, narrowest leaf angle, lowest barrenness and the earliest in DTA under both LD and HD conditions. On the contrary, the cross L18 x L28 showed the lowest GYPP, EPP, RPE, KPR, KPP and 100-KW, the tallest plant, the highest ear height, the widest leaf angle and the latest in anthesis. Differential responses of maize genotypes to elevated plant density were reported by several investigators [26-28]. Tolerant genotypes of maize were characterized by their morphological and phenological adaptability traits, such as early silking, short anthesis silking interval (ASI), less barren stalks and prolificacy [29-35].

3.3 Genetic Correlations

Estimates of genetic correlation coefficients between each of GYPP or density tolerance index (DTI) and other studied traits across the two seasons under the two studied environments (LD and HD) were calculated across all inbred lines and across all F_1 crosses and presented in Tables 4 and 5.

3.3.1 Across inbreds

Grain yield/plant of inbreds showed perfect positive genetic association with DTI (r_g = 0.97) under HD environment; that is why the estimates of genetic correlation coefficients between GYPP and other traits are very close to those between DTI and the same traits (Table 4).

In general, grain yield (either per plant or per feddan) of inbreds showed very strong and positive genetic association with all grain yield components, namely ears/plant, rows/ear, kernels/row, kernels/plant and 100-kernel weight under the two environments; stressed and nonstressed. The strong relationships between grain yield and all yield components are in harmony with other researchers [26-28].

The exception in the present study was only the genetic correlation between GYPP and PH, which was not significant under both LD and HD, but was significant under HD between DTI and PH (0.87*). All other correlations, *i.e.* between GYPP or DTI and each of DTA, ASI, EH, BS and LANG traits of inbreds under both environments were not significant.

3.3.2 Across crosses

Grain yield/plant of crosses had perfect positive genetic associations with density tolerance index (DTI) under HD environment (Table 5). Grain yield/plant of crosses showed very strong and positive genetic correlation with all grain yield components, namely ears/plant, rows/ear, kernels/row, kernels/plant and 100-kernel weight under both stressed and non-stressed environments.

On the contrary, GYPP and DTI of crosses showed significant and negative genetic correlations with DTA, ASI, PH, EH, BS, and LANG in both environments (Table 5). This indicates the importance of these traits in tolerance to high density. These results are in agreement with those reported by other investigators [33-38].

Significant and negative r_g values detected between GYPP or DTI of hybrids and DTA, ASI, PH, EH, BS, and LANG traits in both environments, indicating that early anthesis, shorter anthesis silking interval, shorter plant, lower ear placement, lower barrenness and narrower leaf angle of F₁ crosses are of high yielding, under high density conditions, i.e. high density tolerance. This conclusion is in agreement with others [33-35,38,39].

3.4 Heritability

Broad-sense heritability (h_b^2) was of high magnitude (> 90%) for eight out of 12 studied traits (DTA, PH, EH, LANG, RPE, KPP, 100 KW

and GYPP) under LD and HD environments (Table 6), indicating that the environment had small effect on the phenotype of these traits. The lowest estimates of h²_b were shown by BS (48.48%) and ASI (43.48%) under HD, indicating that the environment and genotype × environment interaction had considerable effects on the phenotype for these two traits. In general, the magnitude of h²_b was higher under HD than LD in eight out of 12 studied traits. Bänziger et al [12] found that broad sense heritability for grain vield under low N were on average 29% smaller than under high N because of lower genotypic variance under low N. According to Dabholkar [14], it is important to note that heritability is a property not only of the character being studied, but also the population being sampled and the environmental circumstances to which individuals have been subjected. More variable environmental conditions also reduce the magnitude of heritability while more uniform conditions increase it [7,8]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [14-17].

Narrow-sense heritability (h²_n) was generally of small magnitude and ranged from 3.45 to 67.02%. The lowest h^2_n was recorded by ASI (3.45%) under LD and BS (3.68%) under low density; also GYPP showed very low h²_n (4.84 and 7.48%) under HD and LD, respectively. The highest h²_n was recorded by RPE (67.02%) under HD and EPP (66.67%) followed by RPE (64.88%) under LD. It is observed that 7 out of 12 characters, showed higher h²_n under LD than under HD environment, namely DTA, LANG, EPP, KPR, KPP, 100 KW and GYPP, but the remaining traits, exhibited higher estimates of h_n^2 under high density stressed than non-stressed environment. The big difference between broad and narrow sense heritability in this experiment could be attributed to the high estimates of dominance, dominance x dominance and dominance x additive components. The results of the first group of traits (7 traits) are in agreement with those reported by some investigators [8,11,12,40,41], who support the idea that heritability is higher under good (non-stressed) environment than stressed environment. The results of the second group of traits (5 traits) are in agreement with those reported by some researchers [2,7,42-44], who support the idea that heritability is higher under stressed than non-stressed environment. The marked

difference between broad- and narrow-sense heritability in this experiment could be attributed to the high estimates of dominance, dominance × dominance and dominance × additive components.

It could be concluded from our results on genetic correlations between GYPP or DTI and other traits and on heritability in narrow-sense, that the hybrid traits showing strong correlations with yield or with DTI under HD and at the same time show much higher narrow-sense heritability than GYPP (> 3 fold) are DTA, PH, EH, BS, LANG, EPP, RPE, 100 KW, KPR and KPP. These traits are qualified to be considered secondary traits to HD tolerance.

3.5 Predicted Selection Gain

The expected genetic advance for studied traits under the two studied environments (LD and HD) were calculated for direct and indirect selection for secondary trait vs. yield and for selection environment vs. target environment using 10% selection intensity.

3.5.1 Direct selection

Genetic advance from direct selection (Table 7) showed higher value under LD than HD for five traits, namely DTA, LANG, EPP, KPP and GYPP, but showed higher value under HD than LD for seven traits, namely ASI, BS, PH, EH, RPE, KPR, and 100 KW. Thus, based on the present results, it is recommended to practice selection for improving ASI, BS, PH, EH, RPE, KPR, and 100 KW traits under high density stressed environment, but for the remaining studied traits DTA, LANG, EPP, KPP and GYPP, it is better to practice selection under nonstressed environment in order to obtain higher genetic advance from selection. In the literature, there are two contrasting conclusions, based on results regarding heritability and predicted genetic advance (GA) from selection under stress and non-stress environment. Many researchers found that heritability and GA from selection for grain yield is higher under nonstress than those under stress [8,11,12, 40]. However, other investigators reported that heritability and expected GA for the same trait is higher under stress than non-stress, and that selection should be practiced in the target environment to obtain higher genetic advance [7,42,44,45].

Genotypes	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD
		DTA		ASI		PH		EH	L	ANG		BS
						Parer	nts (P)					
L20	59.7	62.6	2.3	4.7	194.2	212.7	72.3	91.5	23.3	23.0	9.2	26.2
L53	63.3	65.8	2.8	5.2	233.7	250.3	99.3	128.0	23.8	22.2	12.2	10.0
Sk5	61.0	65.7	2.7	4.8	174.7	201.7	72.3	87.9	19.7	20.7	9.4	11.0
L18	64.6	67.5	2.7	4.7	178.3	186.7	66.3	86.7	31.3	28.2	12.1	10.0
L28	60.0	63.5	2.7	4.5	182.8	166.5	56.7	64.8	35.0	30.3	7.5	13.9
Sd7	64.1	67.2	3.0	4.3	202.3	204.7	87.8	95.7	26.5	25.3	9.2	15.4
Average (P)	62.1	65.4	2.7	4.7	194.3	203.8	75.8	92.4	26.6	24.9	9.9	14.4
	Crosses (F ₁)											
L20 X L53	58.0	60.7	2.0	3.8	216.0	227.0	78.2	91.2	20.2	22.3	6.1	5.6
L20 XSK5	59.0	62.0	2.3	4.3	243.3	255.2	105.1	112.4	28.3	28.2	10.5	12.6
L20 X L18	60.0	62.0	2.0	4.2	247.2	258.5	110.7	119.1	29.8	28.5	10.4	12.7
L20 X L28	59.0	61.5	2.5	4.0	240.2	252.5	104.4	114.3	27.5	26.5	9.6	10.7
L20 X Sd7	59.2	62.0	2.8	3.6	242.2	253.5	107.3	116.5	28.3	27.2	9.8	11.5
L 53 X Sk5	59.0	61.0	2.0	3.8	224.0	238.3	93.8	106.2	24.7	24.0	8.5	8.0
L53 X L18	60.5	62.7	2.0	4.3	267.0	271.8	117.3	122.7	32.3	31.0	11.0	16.2
L53 X L28	59.0	61.5	2.0	4.0	238.0	247.8	99.5	110.3	25.8	25.8	8.7	10.0
L53 X Sd7	59.0	61.3	2.0	4.0	234.0	245.5	96.7	109.2	25.3	25.0	8.7	9.5
Sk5 X L18	59.0	61.5	2.1	4.0	238.7	250.2	103.1	112.3	27.0	26.3	9.4	10.4
Sk5 X L28	59.8	62.0	2.3	4.0	245.2	255.3	109.1	118.2	29.5	27.5	10.3	11.9
Sk5 X Sd7	60.0	62.5	2.2	4.2	255.2	266.5	113.8	121.0	31.0	30.0	10.8	14.9
L18 X L28	61.5	64.7	2.7	3.8	273.0	280.7	125.3	131.6	35.2	35.3	15.8	22.4
L18 X Sd7	60.0	62.2	2.0	4.3	251.2	263.0	113.1	120.2	30.3	29.0	10.6	13.6
L28 X Sd7	59.8	62.2	2.2	3.8	247.3	257.0	105.8	116.4	28.5	28.3	9.7	12.1
Average(F ₁)	59.5	62.0	2.2	4.0	244.2	254.9	105.5	114.8	28.3	27.7	10.0	12.1
LSD ₀₅	1.2	1.2	0.5	0.6	5.6	5.0	4.2	3.1	1.5	1.9	1.5	1.9

Table 3. Means of studied agronomic and yield traits of each inbred and hybrid under low (LD) and high (HD) plant densities across two seasons

Genotypes	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD	LD	HD
		EPP		RPE		KPR		KPP	10	00-KW	G	YPP
						Pare	ents (P)					
L20	1.3	1.2	15.3	14.7	37.4	35.8	681.1	492.0	34.1	29.0	106.6	71.5
L53	1.4	1.2	16.0	14.8	42.4	36.5	755.1	508.1	35.4	29.8	132.1	71.7
Sk5	1.3	1.1	14.2	13.6	33.7	28.5	575.1	415.1	31.7	26.4	77.6	53.0
L18	1.2	1.0	12.9	11.4	29.1	21.6	492.1	282.0	26.4	18.7	46.7	20.1
L28	1.1	1.0	12.6	12.0	28.2	24.8	458.1	354.6	25.6	23.0	44.4	30.5
Sd7	1.2	1.0	13.3	12.3	30.9	25.6	524.6	366.3	28.1	22.8	55.1	32.9
Average (P)	1.2	1.1	14.0	13.1	33.6	28.8	581.0	403.0	30.2	24.9	77.1	46.6
						Cros	ses (F₁)					
L20 X L53	1.5	1.2	16.6	15.8	54.0	50.5	1001.4	767.6	40.6	35.2	277.4	191.6
L20 XSK5	1.3	1.1	14.8	13.8	46.5	42.2	851.2	621.2	35.8	31.1	221.7	153.1
L20 X L18	1.2	1.0	14.2	13.1	44.6	41.0	800.6	586.5	35.4	31.1	219.2	178.1
L20 X L28	1.2	1.1	14.9	13.7	45.7	42.5	829.1	626.5	36.3	32.3	232.8	156.3
L20 X Sd7	1.2	1.1	14.8	13.6	45.5	41.9	818.5	614.8	35.9	32.1	226.7	159.9
L 53 X Sk5	1.3	1.1	15.8	14.6	48.5	44.9	903.1	677.7	38.1	33.8	245.5	184.7
L53 X L18	1.1	1.0	13.8	12.9	42.5	39.1	743.2	554.8	33.9	29.7	197.5	138.3
L53 X L28	1.3	1.1	15.0	14.1	46.9	43.2	862.1	657.6	37.2	33.0	237.5	165.7
L53 X Sd7	1.3	1.1	15.4	14.4	47.7	43.9	885.4	667.4	37.6	33.5	241.0	182.0
Sk5 X L18	1.3	1.1	14.9	14.0	46.3	43.0	844.8	638.4	36.7	32.7	234.8	165.1
Sk5 X L28	1.2	1.0	14.5	13.3	45.1	41.6	806.2	597.5	35.6	31.7	223.2	167.1
Sk5 X Sd7	1.2	1.0	13.8	13.0	43.4	40.0	773.0	567.1	34.6	30.4	207.2	145.2
L18 X L28	1.1	1.0	12.4	11.7	40.6	35.8	668.0	456.9	31.8	27.7	171.1	122.9
L18 X Sd7	1.2	1.0	13.9	13.1	43.8	40.4	777.9	575.6	34.8	30.7	213.3	148.6
L28 X Sd7	1.2	1.1	14.4	13.6	46.0	43.1	811.3	614.2	36.3	32.6	227.6	165.8
Average(F ₁)	1.2	1.1	14.6	13.6	45.8	42.2	825.1	614.9	36.0	31.8	225.1	161.6
LSD ₀₅	0.09	0.05	0.5	0.8	64.5	69.5	2.1	2.4	1.6	1.6	13.8	9.4

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Table 4. Genetic correlation coefficients between GYPP or density tolerance index (DTI) with other studied traits for parental inbred lines under low (LD) and high (HD) plant density across 2013 and 2014 seasons

Trait	LD	HD	HD
	GYPP	GYPP	DTI
DTA	-0.15	-0.51	-0.40
ASI	-0.21	0.67	0.76
PH	0.74	0.79	0.87*
EH	0.68	0.63	0.75
BS	0.42	0.41	0.28
LANG	-0.67	-0.78	-0.72
EPP	0.98**	0.97**	0.99**
RPE	0.99**	0.99**	0.97**
KPR	0.99**	0.98**	0.99**
KPP	0.99**	0.98**	0.96**
100-KW	0.97**	0.98**	0.94**
GYPP			0.97**

HD = high density, LD= low density, *and ** indicate that r_g estimate exceeds once and twice its standard error, respectively

3.5.2 Indirect selection

3.5.2.1 Secondary trait vs. grain yield

Responses of grain yield to selection for secondary traits were calculated (Table 7) such that selection was either for a decrease in DTA, ASI, PH, EH, BS and LANG traits or an increase in EPP, RPE, KPR, KPP, 100 KW and GYPP. Selection for the secondary trait KPP under LD and HD was more effective at improving grain yield than direct selection for grain yield itself. This conclusion is based on comparisons between predicted responses of improving grain yield indirectly via a single secondary trait and directly via grain yield trait itself by calculating the value of relative efficiency (RE%). These comparisons showed that indirect selection for high KPP (RE = 238.1 and 203.7% under LD and HD, respectively) was significantly superior to direct selection for grain yield itself. It was concluded that KPP trait is valuable adjunct in increasing the efficiency of selection for grain yield under high density stress and non-stress conditions. This character is related to genotypic drought stress tolerance. Tolerant genotypes of maize were characterized by greater number of kernels/ear [45,46].

3.5.2.2 Selection environment vs. target environment

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. Hallauer and Miranda [15] noted that heritability coefficients, as well as additive genetic correlation, depend on the population under selection and on environmental conditions. This indicates that the advantage of direct and indirect selection must be investigated for each particular situation. Productivity of the plants in the selection environments and/or a high correlation between yield in the test and the target environments have been used to identify the most appropriate selection environments [6].

Table 5. Genetic correlation coefficients between GYPP or density tolerance index (DTI) with other studied traits for 15 F_1 crosses under low (LD) and high (HD) plant density across 2013 and 2014 seasons

Trait	LD	HD	HD
	GYPP	GYPP	DTI
DTA	-0.96**	-0.88**	-0.92**
ASI	-0.42*	-0.50*	-0.56*
PH	-0.98**	-0.91**	-0.98**
EH	-0.98**	-0.84**	-0.94**
BS	-0.98**	-0.92**	-0.96**
LANG	-0.99**	-0.91**	-0.96**
EPP	0.94**	0.80**	0.90**
RPE	0.98**	0.86**	0.95**
KPR	0.96**	0.87**	0.96**
KPP	0.98**	0.88**	0.96**
100-KW	1.00**	0.91**	0.97**
GYPP			0.98**

 $HD = high density, LD = low density, *and ** indicate that <math>r_g$ estimate exceeds once and twice its standard error, respectively

Table 6. Heritability (%) estimates in broadsense (h_b^2) and narrow-sense (h_n^2) under two plant densities (LD and HD) across 2013 and 2014 seasons

Trait	h	² b%	h²	"%
	LD	HD	LD	HD
DTA	93.22	94.68	35.16	23.66
ASI	79.31	43.48	3.45	21.74
PH	97.50	98.75	13.03	17.76
EH	97.95	98.48	13.96	24.86
BS	48.48	91.51	3.68	29.20
LANG	91.77	90.44	47.92	36.31
EPP	80.00	97.35	66.67	53.10
RPE	93.82	94.68	64.88	67.02
KPR	99.41	83.28	20.16	15.48
KPP	96.53	97.86	21.39	17.00
100-KW	98.57	99.04	35.11	30.00
GYPP	99.22	99.19	7.48	4.84

Variance	Direc	t selection gain (%)	%) Indirect selection gain (%) i.e. secondary traits				
components			vs. yield and re	elative efficiency (RE%)			
	LD	HD	LD	HD			
DTA	3.6	2.6	-0.5 (-14.4)	-0.5 (-19.3)			
ASI	1.4	4.4	0.01 (-0.7)	0.035 (-0.8)			
PH	5.9	8.6	-5.5 (-92.0)	-7.5 (-88.0)			
EH	10.2	16.4	-3.8 (-37.6)	-5.1 (-31.0)			
BS%	1.6	40.3	-0.1 (-7.5)	-1.5 (-3.7)			
LANG	24.4	14.2	-1.4 (-5.77)	-1.0 (-6.86)			
EPP	11.7	9.3	0.02 (0.2)	0.02 (0.2)			
RPE	12.8	14.6	0.3 (2.6)	0.4 (2.4)			
KPR	9.9	38.5	1.3 (13.45)	5.6 (14.51)			
KPP	11.6	11.1	27.5 (238.1)	22.6 (203.7)			
100-KW	12.3	13.3	1.0 (8.5)	1.1 (8.4)			
GYPP	10.0	6.9	1.3 (13.4)	1.8 (26.3)			
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Table 7. Estimates of genetic gain from direct and indirect (Secondary traits vs. yield) selection in maize under low (LD) and high (HD) plant density across two seasons

RE % = *Relative efficiency* = (*Predicted gain from indirect selection*/*Predicted gain from direct selection*) × 100

Choosing the optimal environment in which to achieve maximum genetic gain is important factor for crop breeders. Falconer [13] and Allen et al. [47] concluded that the heritability of yield and the genetic correlation between the yield in the selection and target environments could be used to identify the best environment that would optimize correlated response.

The expected genetic advance for studied traits under high density stressed and non-stressed environments were calculated for direct and indirect selection using 10% selection intensity for inbreds (Table 8) and crosses (Table 9).

3.5.2.3 Across inbreds

For the three traits of inbreds ASI, BS and EPP under both environments, PH, RPE and 100 KW under HD and DTA and LANG of inbreds under LD, the predicted gain from direct selection in each environment was greater than the predicted gain from indirect selection at another environment, as indicated by the relative efficiency values < 100% in all single environments for these traits (Table 8). It is therefore concluded that for these traits of inbreds under respective environments. the predicted gain from direct selection under high density stress or non-stress environment would improve the trait under consideration in a way better than the indirect selection.

Ear height, KPR, KPP and GYPP traits of inbreds under both environments, DTA and LANG under HD and PH, RPE and 100 KW traits of inbreds under LD environment, the predicted gain from indirect selection in each environment was greater than the predicted gain from direct selection at another environment, as indicated by the relative efficiency value > 100% in all single environments for these traits (Table 8). It was concluded that for these traits of inbreds under respective environments, the predicted gain from indirect selection under LD or HD environment would improve the trait of interest in a way better than the direct selection. Maximum expected gain for inbreds was obtained for GYPP trait from indirect selection under LD for the use under HD environment (RE = 306.1%) followed by the same trait (GYPP) from indirect selection under LD for the use under HD environment (RE = 200.2%).

3.5.2.4 Across hybrids

For the studied traits of F1 crosses ASI, EPP, KPR, 100 KW, and GYPP under both environments, DTA and LANG, under LD, and PH, EH, BS, RPE and KPP under HD, i.e. in 17 out of 24 cases (70.8%), the predicted gain from direct selection in each environment was greater than the predicted gain from indirect selection at another environment, as indicated by the relative efficiency values less than 100% for these traits in the respective single environments (Table 9). It is therefore concluded that for these traits of maize hybrids under respective environments, the predicted gain from direct selection under HD stress or non-stress environment would improve the trait under consideration in a way better than the indirect selection.

The direct selection under high density stress would ensure the preservation of alleles for stress [48] and the direct selection under optimal environment would take advantage of the high heritability [7,47,49,50].

On the contrary, the hybrid traits DTA and LANG under HD environment and PH, EH, BS, RPE and KPP under LD environment, the predicted gain from indirect selection in each environment was greater than the predicted gain from direct selection at another environment, as indicated by the relative efficiency value > 100% in all single environments for these traits (Table 9). It is therefore concluded that for these traits of hybrids under respective environments, the predicted gain from indirect selection under HD or LD environment would improve the trait of interest in a way better than the direct selection. Maximum expected gain was obtained for BS trait from indirect selection under LD for the use under HD environment (RE = 225.7%) followed by DTA from indirect selection under HD for the use under LD environment (RE = 120.0%) and

then EH from indirect selection under LD for the use under HD environment (RE = 112.7%).

It is observed that choosing the optimum selection environment to achieve maximum gain is affected by the genotype (inbred or hybrid in our case) and the trait of interest as well as the interaction with the environment (stressed or non-stressed). For example, with respect of GYPP of hybrids, the direct selection is better than indirect selection, *i.e.* the optimum selection environment is the target environment, while for inbreds the indirect selection is the best, *i.e.* the optimum selection environment for high yield under HD is LD environment and *vice versa*.

Literature includes two contrasting strategies for identifying genotypes that will be high yielding under stress environments: (1) genotypes may be evaluated under the conditions they will be ultimately produced, namely a certain type of stress environment, to minimize genotype x environment interaction. Ceccarelli [51] has argued for this approach, but it may result in

Table 8.	Genetic advance	from indirect	selection, i	i.e. selection	environment vs	. target
	environment for	studied traits	in maize in	breds across	s two seasons	

Selection environment vs. target environment	DTA	ASI	РН	EH	BS	LANG
Low-D vs. High-D	2.6	-0.2	6.6	13.5	-1.4	23.4
RE%	(70.7)	(-14.1)	(111.4)	(132.7)	(-87.6)	(95.9)
High-D vs. Low-D	3.0	-0.3	7.7	16.6	-8.3	16.4
RE%	(115.6)	(-7.0)	(89.7)	(101.6)	(-20.5)	(115.2)
	EPP	RPE	KPR	KPP	100-KW	GYPP
Low-D vs. High-D	10.3	13.8	12.2	18.0	14.5	28.2
RE%	(87.9)	(108.2)	(123.0)	(155.7)	(118.0)	(306.1)
High-D vs. Low-D	8.2	13.3	48.0	11.1	13.2	13.1
RE%	(88.4)	(91.5)	(124.7)	(100.4)8	(99.3)	(200.2)
	(2) 11 (1				<u> </u>	

RE% = Relative efficiency = (Predicted gain from indirect selection / Predicted gain from direct selection) ×100

Table 9. Genetic advance from indirect selection, *i.e.* selection environment vs. target environment for studied traits in maize F₁'s hybrids across two seasons

Selection environment vs. target environment	DTA	ASI	PH	EH	BS%	LANG
Low-D vs. High-D	2.7	-1.0	6.2	11.5	3.7	20.6
RE%	(-74.2)	(-70.7)	(105.0)	(112.7)	(225.7)	(84.3)
High-D vs. Low-D	3.1	-1.6	7.2	12.6	17.9	15.0
RE%	(120.0)	(-36.8)	(84.1)	(77.0)	(44.4)	(105.7)
	EPP	RPE	KPR	KPP	100-KW	GYPP
Low-D vs. High-D	10.4	13.6	8.7	12.7	12.1	7.7
RE%	(88.6)	(106.6)	(88.2)	(109.9)	(98.0)	(83.2)
High-D vs. Low-D	8.2	13.1	37.0	8.5	11.8	4.2
RE%	(88.4)	(90.0)	(96.1)	(76.2)	(88.2)	(64.6)

RE% = Relative efficiency = (Predicted gain from indirect selection / Predicted gain from direct selection) ×100

lower heritability, particularly across years. (2) genotypes may be evaluated under optimum conditions maximizing heritability, but perhaps encountering problems with genotype x environment. Braun et al. [50] has argued for this approach, citing results from 17 years of the CIMMYT winter performance nursery.

Results of this study are in favor of the first strategy in some traits and/or genotypes and the second strategy in other traits and/or genotypes. A third alternative, currently used at CIMMYT, which is simultaneous evaluation under nearoptimum and stress conditions, with selection of those genotypes that perform well in both environments [52]. However, ultimate evaluation must be performed in the target environment prior to recommendation for a cultivar for commercial production.

4. CONCLUSIONS

This study concluded that early anthesis, shorter anthesis silking interval, shorter plant, lower ear placement, lower barrenness and narrower leaf angle of F₁ crosses are of high yielding, under high density conditions, i.e. high density tolerance. The results on genetic correlations between GYPP or density tolerance index (DTI) and other studied traits and on narrow-sense heritability, concluded that the traits showing strong correlations with yield or DTI under HD and at the same time show much higher narrowsense heritability than GYPP (> 3 fold) are DTA, PH, EH, BS, LANG, EPP, RPE, 100 KW, KPR and KPP. These traits are qualified to be considered secondary traits to HD tolerance. Results also concluded that KPP trait is valuable adjunct in increasing the efficiency of selection for grain yield under high density stress conditions. This character is related to genotypic high density stress tolerance. Results concluded that choosing the optimum selection environment to achieve maximum gain is depend on the maize genotype (inbred or hybrid) and the trait of interest. With respect of GYPP of hybrids, the direct selection is better than indirect selection, i.e. the optimum selection environment is the target environment, while for inbreds the indirect selection is the best, *i.e.* the optimum selection environment for high yield under HD is LD Further environment and vice versa. investigations should be conducted on identification of the best secondary trait(s) and the optimum selection environment for high density tolerance of maize using a variety of germplasm and drought stressed environments.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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