Journal of Applied Life Sciences International
7(4): 1-17, 2016; Article no.JALSI.28582
ISSN: 2394-1103

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Direct *vs* Indirect Selection for Maize (*Zea mays* L.) Tolerance to High Plant Density Combined with Water Stress at Flowering

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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 analyses. All authors read and approved the final manuscript.

Article Information

DOI: 10.9734/JALSI/2016/28582
Editor(s):
(1) Muhammad Kasib Khan, Department of Parasitology, University of Agriculture, Pakistan.
Reviewers:
(1) Kurşad Demirel, Canakkale Onsekiz Mart University, Turkey.
(2) B. K. Baruah, GIMT-Tezpur, Assam, India.
(3) Aysun Cavusoglu, Kocaeli University, Arslanbey Agricultural Vocational School, Turkey.
(4) Anonymous, Cadi Ayyad University, Morocco.
Complete Peer review History: http://www.sciencedomain.org/review-history/16024

Original Research Article

Received 27th July 2016
Accepted 27th August 2016
Published 2nd September 2016

ABSTRACT

Aim: The objectives of this investigation were to identify secondary trait(s) for selection of high maize grain yield under high plant density combined with drought stress at flowering and to identify whether the best selection environment is the optimum or stressed one.
Study Design: Randomized complete blocks design (RCBD) in 3 replications.
Place and Duration of Study: This study was carried out at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza, Egypt in 2012, 2013 and 2014 seasons.
Methodology: Six maize inbred lines differing in tolerance to high density and drought at flowering [three tolerant (T); L-20, L-53, Sk-5, and three sensitive (S); L-18 , L-28, Sd-7] were chosen for diallel crosses. Parents and hybrids were evaluated in the field in two seasons under two contrasting environments; well watered and low density of 47,600 plants ha^{-1} (WW-LD) and water

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stress and high density of 95,200 plants ha^{-1} (WS-HD).
Results: Strong favorable and significant genetic correlations were detected between grain yield/plant (GYPP) or stress tolerance index and all yield components for inbreds and hybrids and days to anthesis (DTA), plant height (PH), ear height (EH), barren stalks (BS) and leaf angle (LANG) for hybrids. The traits DTA, EH, LANG, ears/plant (EPP), rows/ear (RPE), kernels/row (KPR), kernels/plant (KPP) and 100- kernel weight (100 KW) under both WW-LD and WS-HD environments had high narrow sense heritability (h^2_n).
Conclusion: Low DTA, EH and LANG and high rows/ear (RPE), EPP, 100KW, KPR and KPP could be considered secondary traits to drought and high density tolerance**.** The optimum selection environment for GYPP is the WS-HD environment for hybrids and WW-LD environment for inbreds.

Keywords: Selection environment; secondary traits; relative efficiency; high density; drought.

1. INTRODUCTION

Egyptian maize cultivars exhibit yield loss per plant as well as per unit area when grown under high population density, because they are bred under low population density. Thus, grain yield ha^{-1} cannot be increased by increasing plant density using the present Egyptian cultivars [1]. Developing new Egyptian maize cultivars of adaptive traits to high plant density is the first step to enhance their productivity from land unit area. Maximization of maize productivity per land unit area could be attained by using high plant density, optimum fertilization and irrigation as well as hybrids that can withstand high plant density up to 100,000 plants/ha [2]. Average maize grain yield per land unit area in the USA increased dramatically during the second half of the 20th century, due to improvement in crop management practices and greater tolerance of modern hybrids to high plant densities [3,4]. Modern maize hybrids in developed countries are characterized with high yielding ability from land unit area under high plant densities, due to their morphological and phenological adaptability traits, such as early silking, short anthesis silking interval (ASI), less barren stalks (BS) and prolificacy [5]. Radenovic et al. [6] pointed out that maize genotypes with erect leaves are very desirable for increasing the population density due to better light interception.

Maize is considered more susceptible than most other cereals to drought stresses at flowering, when yield losses can be severe through barrenness or reductions in kernels per ear [7-9]. Tolerant genotypes of maize were characterized by having shorter anthesis-silking interval (ASI) [10], more ears/plant [11,12] (and greater number of kernels/ear [12,13].

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 [14]. Similarly, Rosielle and Hamblin [15] also indicated that magnitudes of selection responses and correlated responses will depend on heritabilities and phenotypic standard deviations as well as genetic correlations. Other studies that computed phenotypic correlation found positive correlations between grain yield and yield components, ear height and plant height [16]. Hallauer and Miranda [17] summarized available estimates of genetic correlations in literature among 13 traits of maize of different populations under normal environmental conditions. They reported that average genetic correlations with yield were larger for ear traits than for plant and ear height, days to flowering, and tiller number. Plant height and ear height had the highest association (r = 0.81), and some of the ear traits showed moderate correlations. Unlike the results mentioned for groups of populations, days to flowering were negatively correlated (r = - 0.52) with yield for Iowa Stiff Stalk Synthetic.

The main criteria for drought tolerant or high plant density tolerant trait selection is the association of each trait with grain yield under stress conditions [18,19]. Based on evaluation of S1 to S3 progenies from six elite tropical maize populations, Bolaños and Edmeades [7] reported high correlations (rg= 0.7 to 0.8) between GY and kernels ear-1, ears plant-1, and kernels plant-1 under drought and across all moisture regimes. These associations increased when the stress levels intensified. A strong phenotypic association between grain yield and grain number m-2in both water- stressed and well-watered environments (r = 0.96; r = 0.87) was reported by Chapman and

Edmeades [20]. Bolaños and Edmeades [7] also indicated that variation in grain number has a more pronounced effect on yield rather than grain weight. Similar results were reported in two of these populations by Guei and Wassom [21], who found high associations between grain yield and days to 50% silking, ASI, and EPP under drought stress. Chapman and Edmeades [20] reported a strong phenotypic association between grain yield and grain number m_{-2} (GNA) in both water-stressed and well-watered environments (r=0 .96; r=0.87). Under drought and low N stress conditions, yield increases were strongly associated with reduced ASI, reduced barrenness and increased harvest index [18,19,22].

Hallauer and Miranda [17] 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 as demonstrated earlier. 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 [23]. Falconer, [14] indicated that a trait measured in two different environments is to be regarded not as one trait but as two. If the genetic correlation between the trait in the two environments is high, then performance in two different environments represents very nearly the same trait, determined by very nearly the same set of genes, but If it is low, then the traits are to a great extent different, and high performance requires a different set of genes [14]. The objectives of the present investigation were: (i) to identify secondary trait(s) for tolerance to drought at flowering stage combined with high plant density 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 (drought combined with 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 (30º 02'N latitude and 31º 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 [24], six maize (*Zea mays* L.) inbred lines in the 8^{th} selfed generation (S_8), showing clear differences in performance and general combining ability for grain yield under drought stress and high plant density, were chosen in this study to be used as parents of diallel crosses (Table 1).

2.2 Making F_1 Diallel Crosses

In 2012 season, all possible diallel crosses (except reciprocals) were made among the six parents, so seeds of 15 direct F_1 crosses were obtained. Seeds of the 6 parents were also increased by selfing in the same season (2012) to obtain enough seeds of the inbreds in the 9^{th} selfed generation (S_9 seed).

2.3 Evaluation of Parents, F_1's and Checks

Two field evaluation experiments were carried out in 2013 and 2014 seasons at the agricultural experiment and research station of the faculty of

Table 1. Designation, origin and most important traits of 6 inbred lines (L) used for making diallel crosses of this study

Inbred designation	Origin	Institution (country)	Prolificacy	Productivity under high density and water stress	Grain color
L20	SC 30N11	Pion. Int.Co.	Prolific	High	Yellow
L53	SC 30K8	Pion. Int.Co.	Prolific	High	White
Sk 5	Teplacinco #5	ARC-Egypt	Prolific	High	White
L18	SC 30N11	Pion. Int.Co.	Prolific	Low	Yellow
L28	Pop 59	ARC-Thailand	Non-Prolific	Low	Yellow
Sd 7	A.E.D.	ARC-Egypt	Non-Prolific	Low	White

ARC = Agricultural Research Center, Pion. Int. Co. = Pioneer International Company in Egypt, SC = Single cross, A.E.D. = American Early Dent (Old open pollinated variety) agriculture, Cairo University. Each experiment included 15 F_1 crosses, their 6 parents. Evaluation in each season was carried out under two environments; The 1st experiment under well watering by giving all recommended irrigations combined with plant density; 47,600 plants/ha (WW-LD) and the 2nd under water stress by withholding two irrigations (the 4th and 5th) at flowering combined with high density ; 95,200 plants/ha (WS-HD). 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 plot area was 2.8 m^2. Seeds were sown in hills at 25 cm apart, thereafter (before the 1st irrigation) were thinned to one plant/hill to achieve a plant density of 47,600 plants/ha. Each experiment was surrounded with a wide alley (3.5 m width) to avoid interference of the two water treatments. Sowing date of both environments each season was on May 5 and May 8 in 2013 and 2014 seasons, respectively.

The soil analysis of the experimental soil at the Agricultural Experiment and Research Station of the Faculty of Agriculture, Cairo University, Giza, Egypt, 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) was 7.73, the EC was 1.91 dSm^{-1}, soil bulk density was 1.2 g cm^{-3}, calcium carbonate was 3.47%, organic matter was 2.09%, the available nutrient in mg kg^{-1} are Nitrogen (34.20), Phosphorous (8.86), Potassium (242), hot water extractable B (0.49), DTPA - extractable Zn (0.52), DTPA - extractable Mn (0.75) and DTPA - extractable Fe (3.17). Meteorological variables in the 2013 and 2014 growing seasons of maize were obtained from Agro-meteorological Station at Giza, Egypt. For May, June, July and August, mean temperature was 27.87, 29.49, 28.47 and 30.33ºC, maximum temperature was 35.7, 35.97, 34.93 and 37.07ºC 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 29.9ºC, maximum temperature was 38.8, 35.2, 35.6 and 36.4ºC 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. All other agricultural practices were followed according to the recommendations of ARC, Egypt.

2.4 Data Recorded

Days to 50% anthesis (DTA) (as number of days from planting to anthesis of 50% of plants per plot). Anthesis-silking interval (ASI) (as number of days between 50% silking and 50% anthesis of plants per plot). Plant height (PH) (cm) (measured from ground surface to the point of flag leaf insertion for five plants per plots). Ear height (EH) (cm) measured from ground surface to the base of the top most ear relative to the plant height for five plants per plots. Barren stalks (BS) (%) measured as percentage of plants bearing no ears relative to the total number of plants in the plot (an ear was considered fertile if it had one or more grains on the rachis). Leaf angle (LANG) (º) measured as the angle between stem and blade of the leaf just above ear leaf, according to Zadoks et al. [25]. Ears per plant (EPP) calculated by dividing number of ears per plot on number of plants per plot. Rows per ear (RPE) using 10 random ears/plot at harvest. Kernels per row (KPR) using the same 10 random ears/plot. Kernels per plant (KPP) calculated as: Number of ears per plant × number of rows per ear × number of kernels per row. 100-kernel weight (100-KW) (g) adjusted at 15.5% grain moisture, using shelled grains of each plot. Grain yield/plant (GYPP) (g) estimated by dividing the grain yield per plot (adjusted at 15.5% grain moisture) on number of plants/plot at harvest. Stress tolerance index (STI): Stress tolerance index (DTI) modified from equation suggested by Fageria [26] was used to classify genotypes for tolerance to water stress. The formula used is as follows: STI= (Y_1/AY_1) X (Y_2/AY_2), Where, Y_1 = grain yield mean of a genotype at non-stress. AY_1 = average yield of all genotypes at non-stress. Y_2 = grain yield mean of a genotype at stress. AY_2 = average yield of all genotypes at stress.

2.5 Biometrical Analysis

Each environment (WW-LD and WS-HD) was analyzed separately across seasons as RCBD using GENSTAT 10th addition windows software. Least significant differences (LSD) values were calculated to test the significance of differences between means according to Steel et al. [27]. The genetic parameters were calculated according to methods developed by Hayman [28] and described by Sharma [29]. Narrow-sense heritability (h^2_n) was estimated using the following equation: $h^2_n = [1/4D / (1/4D + 1/4H_1 – 1/4F + \hat{E}]$.

Expected genetic advance (GA) from direct selection, for each studied trait under each environment (WW-LD or WS-HD) was calculated according to Singh and Chaudhary [30] s follows GA = 100 k h^2_n δ_p/x where x = general mean of the appropriate irrigation, δ_p = square root of the denominator of the appropriate heritability under WW or WS, h^2 = the applied heritability and 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: $r_g = \delta^2_{jk}/(\delta_j \, . \, \delta_k)$, were, where δ^2_{jk} 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 [14] as follows: CRj = 100 i $H^{½}$j $H^{½}$k r_{gjk} $\delta p/x_j$, where, CRj = correlated response in environment j (or in GYPP), $H^{½}$j and $H^{½}$k = square roots of heritabilities 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 (WW-LD and WS-HD), is presented in Table 2. Mean squares due to years were significant (P≤0.05 or 0.01) for DTA, BS and 100 KW under both WW-LD or WS-HD, PH, BS and KPR under WW-LD and LANG, EPP, KPP and GYPP under WS-HD. Mean squares due to parents and F_1 crosses under both environments were significant (P≤ 0.01 or 0.05) for all studied traits, except ASI under both environments and PH, BS and EPP under WS-HD for parents and ASI under WW-LD and EPP and KPR under WS-HD for hybrids, indicating the significance of differences among studied parents and among F_1 diallel crosses in the majority of cases. Genotypic variation under elevated plant density and/or drought was reported by several investigators [31-40].

Mean squares due to parents *vs.* F_1 crosses were significant (P≤ 0.05 or 0.01) for all studied traits under all environments, except for ASI under both environments, BS under WW-LD, suggesting the presence of significant heterosis for most studied cases. Mean squares due to the interactions parents × years (P×Y) and crosses × years (F_1×Y) were significant (P≤ 0.05 or 0.01) for 12 and 18 out of 24 cases, respectively. Mean squares due to parents *vs.* crosses × years were significant (P≤ 0.05 or 0.01) in 13 out of 24 cases, indicating that heterosis differed from season to season in these cases.

3.2 Mean Performance

Means of studied 12 traits across years under the two environments (WW-LD and WS-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 (WW-LD and WS-HD). The highest GYPP of all inbreds was achieved under WW-LD environment due to optimum irrigation and low competition between plants. 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 Sd7 exhibited the lowest mean for GYPP under WW-LD and WS-HD environments, 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 both environments.

Under WW-LD and WS-HD environment, the highest GYPP was recorded by the cross L20 × L53 followed by the crosses L53 x Sk5 and L53 × Sd7. These crosses could therefore be considered responsive to well watering coupled with low plant density and tolerant to water stress coupled with high density. The superiority of these crosses in GYPP to other studied F_1'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 WW-LD and WS-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 placement, the widest leaf angle and the latest in anthesis. Several investigators emphasized the role of maize genotypes in drought and/or high density tolerance. Tolerant genotypes of maize were characterized by their morphological and phenological adaptability traits, such as early silking, short anthesis silking interval (ASI) [10], less barren stalks and prolificacy [1,5,6,35-40], more ears/plant [11,12] and greater number of kernels/ear[12,13,20].

3.3 Genetic Correlations

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

3.3.1 Across inbreds

Grain yield/plant of inbreds showed perfect positive genetic association with STI (r_g= 0.99) under WS-HD environment; that is why the estimates of genetic correlation coefficients between GYPP and other traits are very close to those between STI and the same traits (Table 4).

In general, grain yield per plant of inbreds showed very strong, significant 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 non-stressed. The strong relationships between grain yield and all yield components are in harmony with other reports [1,24,41-44].

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 (STI) under WS-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 STI of crosses showed significant and negative genetic correlations with DTA, PH, EH, BS, and LANG in both environments (Table 5). This indicates the importance of these traits in tolerance to both drought and high density. These results are in agreement with those reported by other investigators [19,40,45].

Significant and negative r_g values detected between GYPP or STI of hybrids and DTA, PH, EH, BS, and LANG traits in both environments, indicating that early anthesis, shorter plant, lower ear placement, lower barrenness and narrower leaf angle of F_1 crosses are of high yielding, under high density combined with drought conditions, i.e. high density and drought tolerance. This conclusion is in agreement with others [40,46].

3.4 Heritability

Broad-sense heritability (h^2_b) was of high magnitude (> 91%) for eight out of 12 studied traits (DTA, PH, EH, LANG, RPE, KPP, 100KW and GYPP) under WW-LD and WS-HD environments (Table 6), indicating that the environment had small effect on the phenotype of these traits. The lowest estimates of h^2_b were shown by BS (48.48%) under WW-LD. In general, the magnitude of h^2_b was higher under WS-HD than LD in six out of 12 studied traits (50% of cases). Bänziger et al. [47] 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. According to Dabholkar [48], 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 [15,49]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [17,48,50,51]

Narrow-sense heritability (h^2_n) was generally of medium magnitude, but ranged from 3.45 to 66.67% under WW-LD and 4.46 to 68.75% under WS-HD. The lowest h^2_n estimates were recorded by ASI (3.45 and 6.67), BS (3.68 and 4.09%) and GYPP (7.48 and 4.46%) under WW-LD and WS-HD, respectively. The highest h^2_n was recorded by EPP (66.67 and 68.75%) and RPE (64.88 and 59.41%) under WW-LD and WS-HD, respectively. It is observed that 7 out of 12 characters, showed higher h^2_n under WW-LD than under WS-HD environment, namely DTA, PH, EH, RPE, KPR, KPP and GYPP, but the remaining traits, exhibited higher estimates of h^2_n under 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 × dominance and dominance × additive components. The results of the first group of traits (7 traits) are in agreement with those reported by some investigators [33-37,52,53], 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 [36,49, 54-56], who support the idea that heritability is higher under stressed than non-stressed environment.

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, EH, LANG, EPP, RPE, 100KW, KPR and KPP. These traits could be considered secondary traits to WS and HD tolerance.

3.5 Predicted Selection Gain

The expected genetic advance for studied traits under the two studied environments (WW-LD and WS-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 WW-LD than WS-HD for six traits, namely DTA, PH, EH, LANG, KPP and GYPP, but showed higher value under WS-HD than WW-LD for six traits, namely ASI, BS, EPP, RPE, KPR, and 100 KW. Thus, based on the present results, it is recommended to practice selection for improving ASI, BS, EPP, RPE, KPR, and 100KW traits under high density stressed environment , but for the remaining studied traits DTA, PH, EH, LANG, KPP and GYPP, it is better to practice selection under non-stressed environment in order to obtain higher genetic advance from selection. In the literature, there are two contrasting conclusions, based on results regarding heritability and predicted genetic advance (GA) from selection under stress and non-stress environment. Many researchers found that heritability and GA from selection for grain yield is higher under non-stress than those under stress [15,19,47]. 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 [49,54-56]. Our results agree with the first group of investigators.

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, 100KW and GYPP. Selection for the secondary traits KPP under WW-LD and WS-HD and PH under WS-HD were 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 281.1% under WW-LD and WS-HD, respectively) and for low PH (RE = -180.4% under WS-HD) was significantly superior to direct selection for grain yield itself. We therefore conclude that KPP and PH trait are valuable adjunct in increasing the efficiency of selection for grain yield under water stress combined with high density conditions. This character is related to genotypic stress tolerance. Tolerant genotypes of maize were characterized by greater number of kernels/ear [12,13].

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 [17] 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 [23].

Table 2. Mean squares of 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 environments (WW-LD and WS-HD)

SOV	df	Mean squares											
		WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD
		DTA		ASI		PH		EH		BS		LANG	
Years (Y)	1	**	**	ns	ns	*	ns	ns	ns	*	**	ns	*
P	5	**	**	ns	ns	**	ns	**	**	*	ns	**	**
F_1	14	*	**	ns	*	**	**	**	**	**	**	**	**
P vs F_1	1	**	**	ns	ns	**	**	**	**	ns	**	**	**
P × Y	5	**	**	ns	ns	ns	**	ns	**	*	ns	**	**
F_1 × Y	14	ns	*	*	**	*	ns	**	**	**	ns	**	**
P vs F_1 × Y	1	ns	**	ns	ns	ns	**	ns	**	ns	**	*	**
		EPP		RPE		KPP		KPR		100-KW		GYPP	
Years (Y)	1	ns	**	ns	ns	ns	**	*	ns	**	**	ns	**
P	5	**	ns	**	**	**	**	**	**	**	**	**	**
F_1	14	**	ns	**	**	**	ns	**	**	**	**	**	**
P vs F_1	1	**	**	**	**	**	**	**	**	**	**	**	**
P × Y	5	ns	ns	**	ns	ns	ns	*	ns	**	*	**	ns
F_1 × Y	14	*	**	*	ns	**	ns	**	ns	**	**	**	**
P vs F_1 × Y	1	*	**	ns	ns	ns	**	**	**	**	**	ns	ns

** and ** significant at 0.05 and 0.01 probability levels, respectively, ns = not significant, WW = Well watering, WS = Water stress, LD= low density, HD= high density, DTA = Days to 50% anthesis, ASI = Anthesis silking interval, PH = 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*

Table 3. Means of studied agronomic and yield traits of each inbred and hybrid under well watering combined with low density (WW-LD) and water stress combined with high density (WS-HD) across two seasons

Genotype	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD	WW-LD	WS-HD
	DTA		ASI		PH		EH		LANG		BS	
Parents												
L20	59.7	65.2	2.3	4.0	194.2	197.7	72.3	79.5	23.3	26.7	9.2	19.5
L53	63.3	69.5	2.8	4.9	233.7	222.3	99.3	102.1	23.8	25.3	12.2	16.2
Sk5	61.0	68.7	2.7	4.4	174.7	198.5	72.3	97.8	19.7	21.7	9.4	17.6
L18	64.6	68.8	2.7	4.7	178.3	181.0	66.3	78.3	31.3	32.2	12.1	11.8
L28	60.0	63.3	2.7	4.5	182.8	198.2	56.7	72.0	35.0	34.7	7.5	14.0
Sd7	64.1	68.8	3.0	4.6	202.3	212.0	87.8	95.2	26.5	29.7	9.2	21.6
Average	62.1	67.4	2.7	4.5	194.3	201.6	75.8	87.5	26.6	28.4	9.9	16.8
Crosses												
L20 X L53	58.0	62.3	2.0	4.4	216.0	239.2	78.2	92.1	20.2	23.7	6.1	8.1
L20 XSK5	59.0	64.2	2.3	5.0	243.3	256.0	105.1	110.2	28.3	29.0	10.5	14.5
L20 X L18	60.0	64.7	2.0	4.8	247.2	254.3	110.7	118.1	29.8	31.7	10.4	15.5
L20 X L28	59.0	63.5	2.5	5.3	240.2	250.3	104.4	113.9	27.5	29.8	9.6	13.5
L20 X Sd7	59.2	63.7	2.8	5.8	242.2	252.2	107.3	115.5	28.3	30.2	9.8	14.1
L 53 X Sk5	59.0	63.0	2.0	4.6	224.0	243.3	93.8	101.8	24.7	25.7	8.5	10.5
L53 X L18	60.5	70.0	2.0	5.0	267.0	265.5	117.3	125.3	32.3	33.8	11.0	17.9
L53 X L28	59.0	63.5	2.0	5.0	238.0	245.8	99.5	110.8	25.8	27.8	8.7	12.5
L53 X Sd7	59.0	63.5	2.0	4.7	234.0	244.5	96.7	108.8	25.3	26.7	8.7	11.6
Sk5 X L18	59.0	63.5	2.1	5.0	238.7	249.2	103.1	112.5	27.0	28.5	9.4	13.2
Sk5 X L28	59.8	64.3	2.3	5.3	245.2	253.5	109.1	116.4	29.5	30.7	10.3	14.6
Sk5 X Sd7	60.0	65.2	2.2	5.3	255.2	260.7	113.8	121.3	31.0	32.8	10.8	16.9
L18 X L28	61.5	72.3	2.7	4.8	273.0	278.7	125.3	135.3	35.2	36.5	15.8	26.4
L18 X Sd7	60.0	65.0	2.0	4.7	251.2	257.3	113.1	119.7	30.3	32.3	10.6	16.2
L28 X Sd7	59.8	69.9	2.2	4.4	247.3	257.5	105.8	116.5	28.5	30.3	9.7	14.2
Average	59.5	65.2	2.2	4.9	244.2	253.9	105.5	114.6	28.3	30.0	10.0	14.6
LSD 0.05	1.2	1.1	0.5	0.5	5.6	6.6	4.2	3.6	1.5	1.7	1.5	1.7

	KPR		**KPP**		**EPP**		**RPE**		**100-KW**		**GYPP**	
Parents												
L20	37.4	27.2	681.1	312.4	1.3	1.0	15.3	13.6	34.1	27.2	106.6	41.6
L53	42.4	29.0	755.1	356.3	1.4	1.0	16.0	13.9	35.4	28.8	132.1	50.9
Sk5	33.7	23.3	575.1	260.4	1.3	0.9	14.2	12.6	31.7	24.8	77.6	26.1
L18	29.1	17.4	492.1	167.9	1.2	0.7	12.9	9.6	26.4	20.6	46.7	10.6
L28	28.2	21.4	458.1	228.9	1.1	0.8	12.6	11.6	25.6	22.6	44.4	16.9
Sd7	30.9	19.3	524.6	173.9	1.2	0.9	13.3	10.7	28.1	20.4	55.1	8.0
Average	33.6	22.9	581.0	250.0	1.2	0.9	14.0	12.0	30.2	24.1	77.1	25.7
Crosses												
L20 X L53	54.0	47.2	1001.4	628.7	1.5	1.2	16.6	15.1	40.6	34.0	277.4	161.1
L20 XSK5	46.5	38.7	851.2	509.1	1.3	1.0	14.8	13.0	35.8	26.9	221.7	115.8
L20 X L18	44.6	37.3	800.6	493.2	1.2	1.0	14.2	12.9	35.4	26.7	219.2	129.7
L20 X L28	45.7	39.2	829.1	512.3	1.2	1.0	14.9	13.2	36.3	28.0	232.8	113.8
L20 X Sd7	45.5	38.7	818.5	504.1	1.2	1.0	14.8	13.0	35.9	27.5	226.7	121.5
L 53 X Sk5	48.5	42.5	903.1	553.8	1.3	1.0	15.8	13.8	38.1	30.5	245.5	137.0
L53 X L18	42.5	35.3	743.2	456.7	1.1	0.9	13.8	12.1	33.9	25.2	197.5	95.3
L53 X L28	46.9	40.7	862.1	533.0	1.3	1.0	15.0	13.4	37.2	28.9	237.5	106.9
L53 X Sd7	47.7	41.3	885.4	543.5	1.3	1.0	15.4	13.7	37.6	29.9	241.0	132.5
Sk5 X L18	46.3	39.6	844.8	520.7	1.3	1.0	14.9	13.2	36.7	28.4	234.8	123.2
Sk5 X L28	45.1	38.3	806.2	498.3	1.2	1.0	14.5	13.0	35.6	27.1	223.2	124.0
Sk5 X Sd7	43.4	36.0	773.0	471.6	1.2	1.0	13.8	12.5	34.6	25.6	207.2	99.7
L18 X L28	40.6	32.6	668.0	376.2	1.1	0.9	12.4	11.6	31.8	23.0	171.1	73.6
L18 X Sd7	43.8	36.5	777.9	479.2	1.2	1.0	13.9	12.7	34.8	26.1	213.3	101.7
L28 X Sd7	46.0	39.5	811.3	493.7	1.2	1.0	14.4	13.1	36.3	28.9	227.6	118.0
Average	45.8	38.9	825.1	505.0	1.2	1.0	14.6	13.1	36.0	27.8	225.1	116.9
LSD 0.05	0.09	0.13	0.5	0.9	64.5	85.1	2.1	3.0	1.6	1.7	13.8	8.6

Table 4. Genetic correlation coefficients between stress tolerance index (STI), GYPP with other studied traits for parental inbred lines under two environments (WW-LD and WS-HD) across 2013 and 2014 seasons

Trait	WW-LD	WS-HD	WS-HD
	GYPP		STI
DTA	-0.15	0.05	0.17
ASI	-0.21	-0.06	0.07
PH	0.74	0.51	0.64
EH	0.68	0.37	0.45
BS	0.42	0.15	0.17
LANG	-0.67	-0.6	-0.58
EPP	0.98**	0.89*	0.90*
RPE	0.99**	0.93**	0.89*
KPR	0.99**	0.97**	0.96**
KPP	0.99**	0.98**	0.97**
100-KW	0.97**	0.99**	0.97**
GYPP	–	–	0.99**

*WW-LD = well watering low density, WS-HD= water stress high density, *and ** indicate that r_g estimate exceeds once and twice its standard error, respectively.*

Table 5. Genetic correlation coefficients between GYPP and/or GYPF with other studied traits for 15 F_1 under two environments (WW-LD and WS-HD) across 2013 and 2014 seasons

Trait	WW-LD	WS-HD	WW-HD
	GYPP		STI
DTA	-0.96**	-0.71**	-0.71**
ASI	-0.42	-0.31	-0.36
PH	-0.98**	-0.87**	-0.90**
EH	-0.98**	-0.91**	-0.95**
BS	-0.98**	-0.95**	-0.97**
LANG	-0.99**	-0.88**	-0.93**
EPP	0.94**	0.88**	0.94**
RPE	0.98**	0.92**	0.98**
KPR	0.96**	0.90**	0.96**
KPP	0.98**	0.92**	0.96**
100-KW	1.00**	0.90**	0.96**
GYPP	–	–	0.98**

*H = high, M = medium, L = low, WW = well watering, WS= water stress, D = density and *and ** indicate that r_g estimate exceeds once and twice its standard error, respectively.*

Table 6. Heritability (%) estimates in broad-sense (h^2_b) and narrow-sense (h^2_n) under two environments (WW-LD and WS-HD) across 2013 and 2014 seasons

Trait	h^2_b%		h^2_n%	
	WW-LD	WS-HD	WW-LD	WS-HD
DTA	93.22	95.52	35.16	13.63
ASI	79.31	73.33	3.45	6.67
PH	97.50	96.88	13.03	6.86
EH	97.95	94.75	13.96	11.95
BS	48.48	79.47	3.68	4.09
LANG	91.77	93.90	47.92	48.33
EPP	80.00	81.25	66.67	68.75
RPE	93.82	96.15	64.88	59.41
KPR	99.41	83.61	20.16	16.02
KPP	96.53	97.23	21.39	10.48
100-KW	98.57	97.40	35.11	36.42
GYPP	99.22	99.11	7.48	4.46

Choosing the optimal environment in which to achieve maximum genetic gain is important factor for crop breeders. Falconer [14] and Allen et al*.* [57] 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 WW-LD and WS-HD 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 two traits of inbreds ASI and BS under both environments, DTA, PH, EH, LANG under WW-LD, and EPP, RPE, KPP and 100 KW under WS-HD, 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.

On the contrary, the traits KPR and GYPP of inbreds under both environments, EPP RPE, 100KW and KPP traits of inbreds under WW-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 is therefore concluded that for these traits of inbreds under respective environments, the predicted gain from indirect selection under WW-LD or WS-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 (RE = 540.5%) followed by KPP (RE = 192.0%) from indirect selection under WW-LD for the use under WS-HD environment.

Table 7. Estimates of genetic gain from direct and indirect (Secondary traits vs. yield) selection in maize under two environments (WW-LD and WS-HD) across 2013 and 2014 seasons

Traits	Direct selection gain (%)		Indirect selection gain (%), *i.e.* secondary traits vs. yield and relative efficiency (RE%)	
	WW-LD	**WS-HD**	**WW-LD**	**WS-HD**
DTA	3.6	2.4	-0.5 (-14.4)	-0.7(-28.6)
ASI	1.4	1.6	0.0 (-0.8)	0.0(-1.3)
PH	5.9	2.6	-5.5 (-92.0)	-4.7(-180.4)
EH	10.2	6.7	-3.8 (-37.6)	-4.3(-64.1)
BS%	1.6	3.4	-0.1 (-7.5)	-0.6(-16.3)
LANG	24.4	19.3	-1.4 (-5.77)	-1.6(-8.31)
EPP	11.7	15.9	0.0 (0.2)	0.0(0.2)
RPE	12.8	17.1	0.3 (2.6)	0.6(3.5)
KPR	9.9	60.0	1.3 (13.45)	10.6(17.60)
KPP	11.6	9.8	27.5 (238.1)	27.4(281.1)
100-KW	12.3	13.3	1.0 (8.5)	1.2(9.1)
GYPP	10.0	6.4	1.3 (13.4)	1.8(28.7)

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

Table 8. Genetic advance from indirect selection i.e. selection environment vs. target environment for traits in inbreds across two seasons

Selection environment vs. target environment	DTA	ASI	PH	EH	BS	LANG
WW-LD vs.WS-HD	1.6	0.8	4.2	8.9	-0.3	23.5
RE%	(44.2)	(55.9)	(71.5)	(88.0)	(-20.6)	(96.1)
WS-HD vs. WW-LD	3.3	1.6	3.8	8.9	-1.6	20.8
RE%	(135.0)	(98.9)	(147.0)	(131.4)	(-48.2)	(107.8)
	EPP	**RPE**	**KPR**	**KPP**	**100-KW**	**GYPP**
WW-LD vs.WS-HD	13.5	12.8	15.2	22.2	16.4	49.8
RE%	(115.6)	(100.7)	(153.4)	(192.0)	(133.2)	(540.5)
WS-HD vs. WW-LD	10.0	14.2	64.0	9.4	10.7	10.5
RE%	(63.1)	(83.2)	(106.7)	(96.7)	(80.3)	(151.9)

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 traits in F_1 hybrids across two seasons

Selection environment vs. target environment	DTA	ASI	PH	EH	BS%	LANG
WW-LD vs.WS-HD	1.8	0.6	3.8	7.9	1.2	22.3
RE%	(49.1)	(42.7)	(63.3)	(77.4)	(70.9)	(91.4)
WS-HD vs. WW-LD	3.7	1.7	3.4	7.3	4.9	19.7
RE%	(151.5)	(101.1)	(130.4)	(108.6)	(143.8)	(102.1)
	EPP	**RPE**	**KPR**	**KPP**	**100-KW**	**GYPP**
WW-LD vs.WS-HD	12.8	13.0	9.6	12.1	15.3	10.4
RE%	(109.4)	(102.1)	(97.2)	(105.0)	(124.4)	(112.6)
WS-HD vs. WW-LD	10.7	15.1	50.5	7.3	9.7	3.4
RE%	(67.3)	(88.3)	(84.2)	(75.2)	(72.6)	(49.3)

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

3.5.2.4 Across hybrids

For the studied traits of F_1 crosses KPR under both environments, DTA, ASI, PH, EH, BS and LANG, under WW-LD, and EPP, RPE, KPP,100KW and GYPP under WS-HD, i.e. in 13 out of 24 cases (54.2%), 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 WS-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 and drought stresses would ensure the preservation of alleles for stresses [58] and the direct selection under optimal environment would take advantage of the high heritability [49,57,59,60].

On the contrary, the hybrid traits DTA, ASI, PH, EH, BS and LANG under WS-HD environment and EPP, RPE, KPP, 100 KW and GYPP under WW-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 WS-HD or WW-LD environment would improve the trait of interest in a way better than the direct selection. Maximum expected gain in hybrids was obtained for DTA trait from indirect selection under WS-HD for the use under WW-LD environment (RE = 1521.5%) followed by BS from indirect selection under WS-HD for the use under WW-LD environment (RE = 143.8%) and then 100 KW and GYPP from indirect selection under WW-LD for the use under WS-HD environment (RE = 124.4 and 112.6, respectively %).

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 in WS-HD environment 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 WS-HD is WW-LD environment and *vise 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 be produced, namely a certain type of stress environment, to minimize genotype x environment interaction. Ceccarelli [61] has argued for this approach, but it may result in 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. [60] has argued for this approach, citing results from 17 years of the CIMMYT winter performance nursery.

Our results 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 near-optimum and stress conditions, with selection of those genotypes that perform well in both environments [62]. 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 plant, lower ear placement, lower barrenness and narrower leaf angle of F_1 crosses are of high yielding, under high density combined with drought conditions, i.e. of high tolerance to density and drought. The results concluded 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, EH, LANG, EPP, RPE, 100KW, KPR and KPP. These traits are qualified to be considered secondary traits to HD tolerance. Results also concluded that KPP and PH traits are valuable adjunct in increasing the efficiency of selection for grain yield under high water stress combined with high density stress conditions. These characters are related to genotypic high density stress and water 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 in WS-HD environment 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 WS-HD is WW-LD environment and *vise versa*. Further investigations should be conducted on identification of the best secondary trait(s) and the optimum selection environment for high density and drought tolerance of maize using a variety of germplasm and stressed environments with drought and high plant density.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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