Asian Research Journal of Agriculture
1(2): 1-15, 2016, Article no.ARJA.28552

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Secondary Traits and Selection Environment for Drought Tolerance at Flowering in Maize (*Zea mays* L.) Inbreds and Their F_1 Diallel Crosses

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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.

Article Information

DOI: 10.9734/ARJA/2016/28552
Editor(s):
(1) Anita Biesiada, Department of Horticulture, Wroclaw University of Environmental and Life Sciences, Poland.
Reviewers:
(1) Anélia Marais, Western Cape, South Africa.
(2) I. Gazendam, ARC-Vegetable and Ornamental plant institute, South Africa.
(3) Mónica Guadalupe Lozano Contreras, National Institute of Forest Research Agricultural and Livestock (INIFAP), Mexico.
Complete Peer review History: http://www.sciencedomain.org/review-history/15816

Original Research Article

Received 25th July 2016
Accepted 10th August 2016
Published 16th August 2016

ABSTRACT

The objectives of this investigation were to identify secondary trait(s) for selection of high maize grain yield under drought stress conditions and to identify whether the best selection environment is the optimum or stressed one. Diallel crosses among diverse inbreds in tolerance to drought were evaluated in the field in two seasons under two contrasting environments; well watered (WW) and water stressed (WS) at flowering using RCBD in 3 replications. Results across seasons revealed significant differences among inbreds and among hybrids for most studied characters. Strong favorable and significant genetic correlations (> 0.91) were detected between grain yield/plant (GYPP) or drought tolerance index and each of 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, LANG, kernels/row (KPR), kernels/plant (KPP), 100- kernel weight (100 KW) under both WW and WS environments and anthesis silking interval (ASI) under WS had high narrow sense heritability (h^2_n). Thus, low DTA and LANG and high rows/ear (RPE), 100KW, KPR

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and KPP could be considered secondary traits to drought tolerance. Selection for low PH and high KPP was more efficient in improving grain yield than selection for yield itself with a relative efficiency (RE) of -160.6 and 240.1%, respectively. Results 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, *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 is the optimum environment (WW).

Keywords: Selection criteria; target environment; correlations; deficit irrigation; relative efficiency.

1. INTRODUCTION

Maize (*Zea mays* L.) in Egypt is used for human food, animal feed and poultry industry and ranks second to wheat among cereal crops. Maize is a summer season crop in Egypt and depends on flood irrigation from River Nile and its branches and canals. However, the amount of water available for irrigation is reducing, especially at the ends of canals and due to expanding maize cultivation into the deserts and competition with other crops; especially rice. In order to stabilize maize production in Egypt, there is need to develop maize hybrids with drought tolerance. Developing maize varieties that are tolerant to drought is, therefore considered critical for increasing the maize production [1] and ensuring food security [2].

Several investigations have been undertaken over the years to improve drought tolerance in breeding programs. Edmeades et al. [3] demonstrated that germplasm developed from drought tolerant source populations performed significantly better under drought stress compared to conventional populations. 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 [4]. Susceptibility of maize yield to stresses at flowering has been documented in maize germplasm [5-7].

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 [8]. Similarly, Rosielle and Hamblin [9] 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 reported that computed phenotypic correlation found positive correlations between grain yield and yield components, ear height and plant height [10]. The main criteria for drought tolerant or low N tolerant trait selection is the association of each trait with grain yield under stress conditions [11,12]). Based on evaluation of S_1 to S_3 progenies from six elite tropical maize populations, Bolaños and Edmeades [4] reported high correlations (rg= 0.7 to 0.8) between grain yield and kernels/ear, ears/plant, and kernels/plant 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/m2 in both water-stressed and well- watered environments (r = 0.96; r = 0.87) was reported by Chapman and Edmeades [13]. Bolaños and Edmeades [4] 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 [14] who found high associations between grain yield and days to 50% silking, ASI, and EPP under drought stress. Chapman and Edmeades [13] reported a strong phenotypic association between grain yield and grain number/m2 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 [12,15].

Hallauer and Miranda [16] 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 [17].

The objectives of the present investigation were: (i) to identify secondary trait(s) for drought tolerance in maize inbreds and hybrids at flowering stage 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 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 [18], six maize (*Zea mays* L.) inbred lines in the 8th selfed generation (S_8), showing clear differences in performance and general combining ability for grain yield under drought stress at flowering stage, 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 9th 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 Agriculture, Cairo University. Each experiment included 15 F_1 crosses as well as their 6 parents. Evaluation in each season was carried out under two environments; the 1st experiment under well watering (WW) by giving all recommended irrigations and the 2nd under water stress (WS) by withholding two irrigations (the 4th and 5th) at flowering.

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 was 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 nutrients in mg kg-1 were 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 30.33℃, maximum temperature was 35.7, 35.97, 34.93 and 37.07℃ 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℃, maximum temperature was 38.8, 35.2, 35.6 and 36.4℃ 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

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

Entry Designation	Origin	Institution (Country)	Prolificacy	Productivity under 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)

the angle between stem and blade of the leaf just above ear leaf, according to Zadoks et al. [19]. 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. Drought tolerance index (DTI): Drought tolerance index (DTI) modified from equation suggested by Fageria [20] was used to classify genotypes for tolerance to water stress. The formula used is as follows: DTI= (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 and WS) 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. [21]. The genetic parameters were calculated according to methods developed by Hayman [22,23] and described by Sharma [24]. Narrow-sense heritability (h^2_n) was estimated using the following equation: $h^2_n = [1/4D / (1/4D + 1/4H_1 – 1/4F + \hat{E}]$, where $\hat{E}$ = expected environmental component of variance, D = variance due to additive effects of the genes, F = mean of the covariance of additive and dominance effects across all arrays, H_1= variance component due to dominance deviation.

Expected genetic advance (GA) from direct selection, for each studied trait under each environment (WW or WS) was calculated according to Singh and Chaudhary [25] as follows GA = 100 k h^2_n δp / x where x = general mean of the appropriate irrigation, δp = 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 [8] 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 of a randomized complete blocks design for 12 traits of 21 maize genotypes (6 inbreds and 15 F_1 crosses) under two environments (WW and WS) across two seasons is presented in Table 2. Mean squares due to years were significant ($P \leq 0.05$ or 0.01) for DTA, BS and 100 KW under both WW and WS, PH and KPR under WW and LANG and GYPP under WS. Mean squares due to parents and F_1 crosses under both environments were significant ($P \leq$ 0.01) for all studied traits, except ASI of parents and F_1's under WW and parents under WS, indicating the significance of differences among studied parents and among F_1 diallel crosses in most studied characters. Genotypic variation under drought stress was reported by Al-Naggar et al. [26-29].

Mean squares due to parents *vs.* F_1 crosses were significant ($P \leq$ 0.05 or 0.01) for all studied traits under both environments, except for ASI under WW and WS and BS under WW, suggesting the presence of significant average heterosis for most studied cases. Mean squares due to the interactions parents × years (P × Y) and crosses × years (F_1 × Y) were significant ($P \leq$ 0.05 or 0.01) for most studied cases (37 out of 48 cases, *i.e.* 77.1%). Mean squares due to parents *vs.* crosses × years were significant ($P \leq$ 0.05 or 0.01) in 13 out of 24 cases; nine of them were expressed in WS environment for ASI, BS, LANG, EPP, RPE, KPR, KPP, 100-KW, and GYPP traits. This indicates that heterosis differ from season to season in these cases.

3.2 Mean Performance

Means of studied 12 traits across years under the two environments (WW and WS) 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 and WS). The highest GYPP of all inbreds was achieved under WW environment because of the optimum irrigation. 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 inbred Sd7 exhibited the lowest mean for GYPP under both environments. 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. However, L53 had the tallest plant and the highest ear position under water stress and non-stress conditions.

Table 2. Mean squares from 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 water stress (WS) and well watered (WW) conditions

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

** and ** significant at 0.05 and 0.01 probability levels, respectively, WW = Well watering, WS = Water stress, 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*

Table 3. Means of studied agronomic and yield traits of each inbred and hybrid under water stress (WS) and well watering (WW) across two seasons

Genotypes	WW	WS	WW	WS	WW	WS	WW	WS
	DTA		ASI		PH (cm)		EH (cm)	
				Inbreds				
L20	59.7	61.7	2.3	3.3	194.2	174.5	72.3	65.7
L53	63.3	65.8	2.8	2.7	233.7	192.2	99.3	88.2
Sk5	61.0	64.8	2.7	2.7	174.7	168.7	72.3	75.0
L18	64.6	65.8	2.7	3.2	178.3	158.2	66.3	67.1
L28	60.0	61.3	2.7	2.7	182.8	175.8	56.7	52.8
Sd7	64.1	65.7	3.0	3.4	202.3	184.7	87.8	72.1
Average (P)	62.1	64.2	2.7	3.0	194.3	175.7	75.8	70.1
				F_1 crosses				
L20 X L53	58.0	59.5	2.0	2.7	216.0	222.5	78.2	83.1
L20 XSK5	59.0	60.8	2.3	3.0	243.3	236.3	105.1	100.2
L20 X L18	60.0	61.5	2.0	2.6	247.2	240.2	110.7	105.9
L20 X L28	59.0	61.0	2.5	2.7	240.2	235.7	104.4	102.2
L20 X Sd7	59.2	61.0	2.8	2.9	242.2	236.8	107.3	103.9
L 53 X Sk5	59.0	60.0	2.0	3.0	224.0	229.5	93.8	92.8
L53 X L18	60.5	62.0	2.0	2.9	267.0	248.8	117.3	114.6
L53 X L28	59.0	60.8	2.0	2.5	238.0	232.0	99.5	98.5
L53 X Sd7	59.0	60.1	2.0	2.9	234.0	231.0	96.7	96.1
Sk5 X L18	59.0	61.0	2.1	2.6	238.7	233.8	103.1	100.4
Sk5 X L28	59.8	61.5	2.3	2.5	245.2	238.3	109.1	104.6
Sk5 X Sd7	60.0	61.5	2.2	3.0	255.2	246.3	113.8	110.9
L18 X L28	61.5	63.1	2.7	3.1	273.0	254.7	125.3	120.4
L18 X Sd7	60.0	61.5	2.0	3.0	251.2	243.2	113.1	108.8
L28 X Sd7	59.8	61.5	2.2	3.0	247.3	240.3	105.8	105.5
Average (C)	59.5	61.1	2.2	2.8	244.2	238.0	105.5	103.2
LSD 0.05	1.2	1.3	0.5	0.4	5.6	4.6	4.2	5.4
	BS (%)		LANG (^{0})		EPP		RPE	
				Inbreds				
L20	9.2	7.4	23.3	25.5	1.3	1.1	15.3	14.1
L53	12.2	10.0	23.8	25.2	1.4	1.3	16.0	15.0
Sk5	9.4	15.7	19.7	24.0	1.3	1.1	14.2	13.7
L18	12.1	11.2	31.3	31.0	1.2	1.2	12.9	13.0
L28	7.5	11.9	35.0	32.7	1.1	1.1	12.6	12.3
Sd7	9.2	14.5	26.5	26.8	1.2	1.2	13.3	11.7
Average (P)	9.9	11.8	26.6	27.5	1.2	1.2	14.0	13.3
				F_1 crosses				
L20 X L53	6.1	5.5	20.2	24.7	1.5	1.5	16.6	16.1
L20 XSK5	10.5	13.2	28.3	30.7	1.3	1.3	14.8	14.0
L20 X L18	10.4	14.3	29.8	33.7	1.2	1.2	14.2	13.6
L20 X L28	9.6	12.5	27.5	31.0	1.2	1.2	14.9	14.1
L20 X Sd7	9.8	13.2	28.3	31.8	1.2	1.2	14.8	14.0
L 53 X Sk5	8.5	8.0	24.7	26.8	1.3	1.4	15.8	15.0
L53 X L18	11.0	16.4	32.3	35.5	1.1	1.1	13.8	13.0
L53 X L28	8.7	10.6	25.8	29.0	1.3	1.3	15.0	14.6
L53 X Sd7	8.7	9.3	25.3	27.8	1.3	1.3	15.4	14.8
Sk5 X L18	9.4	11.4	27.0	30.3	1.3	1.2	14.9	14.2
Sk5 X L28	10.3	13.7	29.5	32.8	1.2	1.2	14.5	13.9
Sk5 X Sd7	10.8	15.6	31.0	34.7	1.2	1.1	13.8	13.2
L18 X L28	15.8	22.4	35.2	38.7	1.1	1.0	12.4	12.2
L18 X Sd7	10.6	14.8	30.3	34.3	1.2	1.1	13.9	13.4
L28 X Sd7	9.7	11.4	28.5	32.0	1.2	1.2	14.4	14.2
Average (C)	10.0	12.8	28.3	31.6	1.2	1.2	14.6	14.0

Genotypes	WW	WS	WW	WS	WW	WS	WW	WS
	DTA		**ASI**		**PH (cm)**		**EH (cm)**	
				Inbreds				
LSD 0.05	1.5	1.9	1.5	1.9	0.1	0.1	0.5	0.9
	KPP		**KPR**		**100-KW (g)**		**GYPP (g)**	
				Inbreds				
L20	681.1	504.1	37.4	32.0	34.1	30.1	106.6	57.7
L53	755.1	670.4	42.4	39.4	35.4	33.4	132.1	85.5
Sk5	575.1	454.2	33.7	30.7	31.7	29.0	77.6	46.9
L18	492.1	423.9	29.1	28.2	26.4	27.7	46.7	34.8
L28	458.1	390.2	28.2	26.1	25.6	25.5	44.4	21.2
Sd7	524.6	338.1	30.9	25.0	28.1	24.4	55.1	13.2
Average (P)	581.0	463.5	33.6	30.2	30.2	28.3	77.1	43.2
				F_1 crosses				
L20 X L53	1001.4	914.8	54.0	50.9	40.6	37.0	277.4	242.7
L20 XSK5	851.2	771.0	46.5	43.3	35.8	31.7	221.7	166.8
L20 X L18	800.6	694.5	44.6	42.0	35.4	31.9	219.2	182.1
L20 X L28	829.1	748.9	45.7	43.8	36.3	33.2	232.8	171.7
L20 X Sd7	818.5	734.1	45.5	43.1	35.9	32.7	226.7	179.9
L 53 X Sk5	903.1	846.6	48.5	45.5	38.1	35.0	245.5	203.0
L53 X L18	743.2	635.3	42.5	39.4	33.9	29.9	197.5	138.9
L53 X L28	862.1	775.9	46.9	44.8	37.2	33.8	237.5	171.6
L53 X Sd7	885.4	810.4	47.7	45.1	37.6	34.3	241.0	197.3
Sk5 X L18	844.8	762.4	46.3	44.3	36.7	33.4	234.8	183.7
Sk5 X L28	806.2	722.6	45.1	42.5	35.6	32.4	223.2	177.2
Sk5 X Sd7	773.0	659.1	43.4	40.6	34.6	30.6	207.2	147.7
L18 X L28	668.0	543.5	40.6	37.1	31.8	27.3	171.1	124.0
L18 X Sd7	777.9	674.4	43.8	41.1	34.8	31.2	213.3	154.2
L28 X Sd7	811.3	713.9	46.0	43.6	36.3	33.5	227.6	177.2
Average (C)	825.0	733.8	45.8	43.1	36.0	32.5	225.1	174.5
LSD 0.05	64.5	66.0	2.1	2.5	1.6	1.8	13.8	10.5

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

Under well-watered (WW) and water stress (WS) 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 optimum irrigation and tolerant to deficit irrigation. 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 water stress and non-stress 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. Several investigators emphasized the role of maize genotypes in drought tolerance. Tolerant genotypes of maize were characterized by having shorter anthesis-silking interval (ASI) [30], more ears/plant [31] and greater number of kernels/ear [4,13,31,32].

3.3 Genetic Correlations

Estimates of genetic correlation coefficients between each of GYPP or drought tolerance index (DTI) and other studied traits across the two seasons under each environment (WW and WS) 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 DTI (r_g= 0.97) under WS environment; that is why the estimates of genetic correlation coefficients between grain yield per plant (GYPP) and other traits are very close to those between drought tolerance index (DTI) and the same traits (Table 4). The exception was only the genetic correlation between GYPP and EPP, which was high and significant (0.98**) under WW, but was not significant under WS and between DTI and EPP (0.71).

Table 4. Genetic correlation coefficients between GYPP under well watering (WW) and water stress (WS) or drought tolerance index (DTI) with other studied traits under water stress conditions for parental inbred lines across 2013 and 2014 seasons

Trait	WW	WS	WS
	GYPP		DTI
DTA	-0.15	0.15	0.14
ASI	-0.21	-0.41	-0.35
PH	0.74	0.35	0.58
EH	0.68	0.70	0.73
BS	0.42	-0.52	-0.51
LANG	-0.67	-0.58	-0.60
EPP	0.98**	0.58	0.71
RPE	0.99**	0.98**	0.93**
KPR	0.99**	0.99**	0.99**
KPP	0.99**	0.98**	0.99**
100-KW	0.97**	0.99**	0.97**
GYPP	----	----	0.97**

**and ** indicate that r_g estimate exceeds once and twice its standard error, respectively*

In general, GYPP or DTI of inbreds showed very strong and positive genetic association with all grain yield components, namely rows/ear, kernels/row, kernels/plant and 100-kernel weight under the two environments; stressed and non-stressed. Genetic correlations between either GYPP or DTI and each of DTA, ASI, PH, EH, BS and LANG traits of inbreds were not significant. The strong relationships between grain yield and all yield components are in harmony with many reports [12,33-39].

3.3.2 Across crosses

Grain yield/plant of crosses had a perfect and positive genetic association with drought tolerance index (DTI) under WS environment (r_g = 0.99**) (Table 5). Grain yield/plant or DTI of crosses showed very strong and positive genetic correlations (r_g = ≥ 0.92) 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 or DTI of crosses showed significant (P≤ 0.01) but negative genetic correlation coefficients (r_g = ≥ 0.91) with DTA, PH, EH, BS, and LANG in both environments (Table 5). This indicates the importance of these traits in drought tolerance. Moreover, GYPP or DTI showed a negative (but not significant) genetic correlation with ASI under both environments, however irrespective of non-significant r_g (ranging from -0.42 to -0.45), this trait is also important in tolerance to drought stresses.

Table 5. Genetic correlation coefficients between GYPP under well watering (WW) and water stress (WS) or drought tolerance index (DTI) with other studied traits under water stress conditions for 15 F_1 crosses across 2013 and 2014 seasons

Trait	WW	WS	WS
	GYPP		DTI
DTA	-0.96**	-0.91**	-0.93**
ASI	-0.42	-0.45	-0.43
PH	-0.98**	-0.93**	-0.95**
EH	-0.98**	-0.95**	-0.97**
BS	-0.98**	-0.94**	-0.95**
LANG	-0.99**	-0.91**	-0.93**
EPP	0.94**	0.92**	0.95**
RPE	0.98**	0.95**	0.97**
KPR	0.96**	0.96**	0.99**
KPP	0.98**	0.93**	0.95**
100-KW	1.00**	0.95**	0.96**
GYPP	----	----	0.99**

**and ** indicate that r_g estimate exceeds once and twice its standard error, respectively*

Significant and negative r_g values detected between GYPP or DTI of hybrids and DTA, PH, EH, BS and LANG traits in both environments, indicate that early anthesis, shorter plant, lower ear placement, low barrenness and narrow leaf angle of F_1 crosses are the reason of high yielding of these crosses under drought conditions, *i.e.* drought tolerance. These results are in agreement with those reported by other investigators [12,40-42].

3.4 Heritability

Broad-sense heritability (h^2_b) was of high magnitude (> 90%) for eight out of 12 studied traits (DTA, PH, EH, LANG, RPE, KPP, 100KW and GYPP) under WW and WS 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 and 80.81%) and ASI (79.31 and 69.23%) under WW and WS, respectively, indicating that the environment and genotype × environment interaction had considerable effects on the phenotype for these two traits. In general, the magnitude of h^2_b was higher under WS than WW in eight out of 12 studied traits. Banziger et al. [43] 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. Moreover, under three moisture regimes, studies based on S_1 to S_3 progenies in six tropical maize populations indicated increased broad sense heritability with decreased stress for most traits [4]. According to Dabholkar [44], 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 [9,45]. Furthermore, it should be kept in mind that the estimate of heritability applies only to environments sampled [16,44,46,47].

Table 6. Heritability (%) estimates in broad-sense (h^2_b) and narrow-sense (h^2_n) under well watering (WW) and water stress (WS) across two seasons

Trait	h^2_b%		h^2_n%	
	WW	WS	WW	WS
DTA	93.22	96.95	35.16	26.15
ASI	79.31	69.23	3.45	15.38
PH	97.5	95.36	13.03	4.20
EH	97.95	98.01	13.96	9.72
BS	48.48	80.81	3.68	9.10
LANG	91.77	92.85	47.92	25.46
EPP	80.00	87.07	66.67	0.86
RPE	93.82	94.02	64.88	42.19
KPR	99.41	84.00	20.16	15.78
KPP	96.53	97.37	21.39	17.20
100-KW	98.57	98.11	35.11	28.78
GYPP	99.22	99.31	7.48	4.93

Narrow-sense heritability (h^2_n) was generally of medium magnitude, but ranged from 0.86% for EPP under WS to 66.67% for ASI (3.45%) under WW (Table 6). It is observed that 10 out of 12 characters, showed higher h^2_n under WW than that under WS environment, but only two traits, namely ASI and BS exhibited higher estimates of h^2_n under water stressed than well watering environment. Under WS, the highest h^2_n was recorded by RPE (42.19%) followed by 100-KW (28.78%), DTA (26.15%) and LANG (25.46%). 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.

A number of reports on heritabilities are available for different traits of maize under drought stress and low N conditions [4,12,43]. However, many investigators reported a decline in heritability for grain yield under stress [9,45]. In general, our results are in agreement with those reported by some researchers [9,43,48,49] who support that heritability is higher under good (non-stressed) environment. However, these results are in disagreement with other investigators [39,45,50-52], who support the idea that heritability is higher under stressed than non-stressed environment. Different conclusions of different reports might be attributed to the differences in germplasm and the environments used by different investigators [44].

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 WS and at the same time showing much higher narrow-sense heritability than GYPP (> 3 fold) are DTA, LANG, RPE, 100KW, KPR and KPP. These traits are qualified to be considered secondary traits to drought tolerance.

3.5 Predicted Selection Gain

The expected genetic advance for studied traits under the two studied environments (WW and WS) 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 than WS for eight traits, namely DTA, PH, EH, LANG, EPP, RPE, 100 KW and GYPP , but showed higher value under WS than WW for four traits, namely ASI, BS, KPR, and KPP. Thus, based on the present results, it is recommended to practice selection for improving ASI, BS, KPR and KPP traits under water stressed environment , but for the remaining studied traits, it is better to practice selection under optimum irrigation 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 [9,12,43,48]. 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 [45,50-53].

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 WW and WS and PH under WS 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 = 240.1 and 238.1% under WS and WW, respectively) and for low PH under WS (RE = –160.6%) was significantly superior to direct selection for grain yield itself. We therefore conclude that KPP and PH traits are valuable adjunct in increasing the efficiency of selection for grain yield under water stress and KPP is a valuable secondary trait in increasing the efficiency of selection for grain yield under well watering conditions. These characters are related to genotypic drought stress tolerance. Tolerant genotypes of maize were characterized by greater number of kernels/ear [31,32].

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 [16] 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 [17].

Choosing the optimal environment in which to achieve maximum genetic gain is important factor for crop breeders. Falconer [8] and Allen et al. [54] 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 water stressed and non-stressed environments were calculated for direct and indirect selection using 10% selection intensity for inbreds (Table 8) and crosses (Table 9).

3.5.2.2.1 Across inbreds

For the three traits of inbreds ASI, BS and 100KW under both environments and DTA, PH, LANG, EPP and RPE of inbreds under WW, 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 water stress or non-stress environment would improve the trait under consideration in a way better than the indirect selection.

On the contrary, the traits EH, KPR, KPP and GYPP of inbreds under both environments and DTA, PH, LANG, EPP and RPE of inbreds under WW 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 or WS environment would improve the trait of interest in a way better than the direct selection. Maximum expected gain for inbreds was obtained for EPP trait from indirect selection under WS for the use under WW environment (RE = 424.1%) followed by GYPP from indirect selection under WW for the use under WS environment (RE = 326.9%) and then the same trait (GYPP) from indirect selection under WS for the use under WW environment.

3.5.2.2.2 Across hybrids

For the studied traits of F_1 crosses ASI, KPR, KPP, 100 KW, and GYPP under both environments, DTA, PH, EH, LANG, EPP and RPE under WW, and BS under WS, 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 water stress or non-stress environment would improve the trait under consideration in a way better than the indirect selection.

The direct selection under water deficit would ensure the preservation of alleles for drought [55] and the direct selection under optimal environment would take advantage of the high heritability [45,54,56,57].

Table 7. Estimates of genetic gain from direct selection and indirect selection, *i.e.* secondary trait vs. yield in maize under well watering (WW) and water stress (WS) across two seasons

Trait	Direct selection gain %	WS	Indirect selection gain (%), *i.e.* secondary trait vs. yield and relative efficiency (RE%)	
	WW		**WW**	**WS**
DTA	3.6	3.0	-0.5 (-14.4)	-0.5 (-17.7)
ASI	1.4	4.8	0.0 (-0.8)	0.0 (-0.5)
PH	5.9	1.9	-5.5 (-92.0)	-3.0 (-160.6)
EH	10.2	6.7	-3.8 (-37.6)	-3.1(-45.9)
BS%	1.6	7.2	-0.1 (-7.5)	-0.5 (-6.3)
LANG	24.4	9.9	-1.4 (-5.77)	-0.9 (-8.95)
EPP	11.7	0.2	0.0 (0.2)	0.0 (1.9)
RPE	12.8	9.3	0.3 (2.6)	0.3 (3.3)
KPR	9.9	77.3	1.3 (13.45)	11.9 (15.45)
KPP	11.6	12.7	27.5 (238.1)	30.4 (240.1)
100-KW	12.3	9.5	1.0 (8.5)	0.8 (8.9)
GYPP	10.0	5.8	--	--

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 vs.WS	2.6	0.0	3.9	10.6	-0.5	17.7
(RE%)	(72.8)	(2.0)	(65.2)	(104.6)	(-30.5)	(72.4)
WS vs. WW	3.1	0.0	3.3	9.0	-1.3	15.2
(RE%)	(103.9)	(0.6)	(175.1)	(133.9)	(-18.4)	(154.3)
	EPP	**RPE**	**KPR**	**KPP**	**100-KW**	**GYPP**
WW vs.WS	0.6	9.9	11.6	15.3	11.7	30.1
(RE%)	(5.5)	(77.3)	(117.4)	(132.3)	(94.9)	(326.9)
WS vs. WW	0.8	10.0	97.2	14.5	9.5	15.4
(RE%)	(424.1)	(107.8)	(125.7)	(114.7)	(99.3)	(207.2)

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 vs.WS	2.9	0.5	3.2	7.9	1.9	15.4
(RE%)	(80.3)	(37.9)	(54.2)	(78.0)	(118.4)	(63.0)
WS vs. WW	3.5	0.6	3.0	7.1	5.6	14.3
(RE%)	(114.0)	(13.2)	(157.0)	(105.4)	(77.8)	(145.1)
	EPP	**RPE**	**KPR**	**KPP**	**100-KW**	**GYPP**
WW vs.WS	1.2	10.4	8.6	10.7	11.6	7.6
(RE%)	(10.5)	(81.7)	(86.9)	(92.7)	(94.3)	(82.6)
WS vs. WW	1.6	10.7	75.3	11.3	9.1	5.4
(RE%)	(844.3)	(115.4)	(97.4)	(89.7)	(95.0)	(72.3)

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

On the contrary, the traits of hybrids DTA, PH, EH, LANG, EPP and RPE under WS environment and BS under WW 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 or WW environment would improve the trait of interest in a way better than the direct selection. Maximum expected gain was obtained for EPP trait from indirect selection under WS for the use under WW environment (RE = 844.3%) followed by PH from indirect selection under WS for the use under WW environment (RE = 157.0%) and then LANG from indirect selection under WS for the use under WW environment (RE = 145.1%).

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 WS is WW 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 ultimately be produced, namely a certain type of stress environment, to minimize genotype x environment interaction. Ceccarelli [58] 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. [57] have 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 [59]. 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, low barrenness and narrow leaf angle of F_1 crosses are correlated with high yielding under drought conditions, *i.e.* with drought tolerance of these crosses. The results on genetic correlations between GYPP or DTI and other studied traits and on narrow-sense heritability, concluded that the traits showing strong correlations with yield or DTI under WS and at the same time show much higher narrow-sense heritability than GYPP (> 3 fold) are DTA, LANG, RPE, 100 KW, KPR and KPP. These traits could be considered secondary traits to drought tolerance. Results also concluded that KPP and PH traits are valuable adjunct in increasing the efficiency of selection for grain yield under water stress conditions. These characteristics are related to genotypic drought stress tolerance. Results concluded that choosing the optimum selection environment to achieve maximum gain is dependent on the maize genotype (inbred or hybrid) and the trait of interest. With respect of GYPP of hybrids, the direct selection is better than the indirect one, *i.e.* the optimum selection environment is the target environment, while for inbreds, the indirect selection is better than the direct one, *i.e.* the optimum selection environment for high yield under WS is the optimum environment (WW) and *vise versa*. Further investigations should be conducted on identification of the best secondary trait(s) and the optimum selection environment for drought 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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