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Combining ability and heterosis of maize (*Zea mays* L.) populations from the Algerian Sahara Desert under Mediterranean drought conditions

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Keywords: *Maize; Algerian germplasm; varietal effect; heterosis; drought*

Abstract

Drought causes significant yield reduction in maize (*Zea mays* L.), and germplasm from the Saharan Desert offers potential sources of drought tolerance. Our objectives were to estimate heterosis and combining ability among Algerian maize populations under drought conditions and to identify populations and crosses as sources of drought tolerance for breeding programs in temperate environments. A diallel design without reciprocal of six populations was used. The populations *per se*, their respective crosses, and checks were evaluated in Algiers (Algeria) in 2016, 2017 and 2018. Algerian maize populations exhibited high phenotypic variability and genetic divergence under water stress. The populations IGS and AOR *per se* could provide favorable alleles for higher early vigor under drought, MST for reducing anthesis-silking interval (ASI), and both AOR and SHH for increasing yield under water stress. Among all crosses, IGS × MST was the most outstanding cross for reducing ASI, and IGS × SHH and BAH × SHH for increasing yield under water stress. Our results confirm the existence of heterotic relationships among Algerian maize populations from diverse origins under water stress

Abbreviations

AOR – population from Aougrout
ASI – Anthesis-Silking Interval
BAH – population from Bechar
DZ – code for Algerian accessions
IGS – population from Ain Salah
IZM – population from Inzgmir
MST – population from K'sar M'sehel
SHH – population from Sidi Maamar

Introduction

Maize (*Zea mays* L.) is one of the most important crops in the World (Barrière, 2000, Shiferaw *et al.*, 2011, Scott and Emery, 2016) with around 1,000 million tons per year. Maize is the major source of calories and protein especially for Africa's people (Shiferaw *et al.*, 2011). It is a versatile crop with wider genetic variability and able to grow successfully throughout the world covering tropical, subtropical and temperate agro-climatic conditions.

Maize production is subjected to many constraints causing yield reduction (Kouakou *et al.*, 2010). Drought is the factor most frequently limiting maize production (Edmeades *et al.*, 1992, Betrán *et al.*, 2003, Bänziger *et al.*, 2006). Maize grain losses due to drought may average 24 million Mg per year, equivalent to 17% of the potential production (Edmeades *et al.*, 1992) and such loss is expected to increase with climate change. Drought has become more frequent, severe and widespread across Africa over the last 50 years (Badu-Apraku *et al.*, 2010, Menkir *et al.*, 2016). Therefore, the improvement of maize for drought tolerance is of paramount importance. To meet these goals, evaluating collections of maize populations adapted to drought is critical for selecting the adequate genotypes for breeding programs (Flint-Garcia *et al.*, 2005).

Maize populations are considered primary donors of resistance genes (Katna and Sood, 2015). Comparison of diversity in equivalent samples of inbreds and open-pollinated landraces revealed that maize inbred capture <80% of the alleles in the landraces, suggesting that landraces can provide additional genetic diversity for maize breeding (Liu *et al.*, 2003). Algerian maize populations were collected from a subtropical area in

Table 1 - Name, origin and genetic cluster and geographic areaa of the six Algerian populations used in the diallel mating design

Population	Origin	Cluster and Algerian area
DZ-AOR	Aougrout, Adrar	II Center
DZ-BAH	Bechar	III West
DZ-IGS	Ain Salah, Tamanrasset	I South
DZ-IZM	Inzgmir, Adrar	II Center
DZ-MST	K'sar M'sehel, Timimoune, Adrar	II Center
DZ-SHH	Sidi Maamar, Saida	North

Cherchali *et al.* (2018)

the Algerian Sahara Oases (Aci *et al.*, 2013). Saharan maize had been adapted to extreme conditions and could have developed resistance to extreme stresses. However, gene banks and breeding collections have poor representation from the Saharan germplasm and, particularly, from Algeria (Djemel *et al.* 2012), and there are few studies on the genetic material of maize form Algeria. In particular, Djemel *et al.*, (2012) reported a preliminary approach using 10 open-pollinated populations based only on agronomic performance. The authors concluded that Algerian populations could be incorporated into breeding programs. Djemel *et al.* (2018) evaluated eighteen maize populations from the Algerian Sahara along with three European and two American hybrids under drought at flowering stage. Some Algerian populations were able to maintain their yield under drought conditions. Recently, Aci *et al.* (2018) revealed that Algerian maize population has a wide genetic diversity, offering a source of novel favorable alleles useful for maize breeding programs to face the climate changes related stresses. Furthermore, Algerian maize populations were adapted to Sahara conditions and could provide new alleles for tolerance to extreme conditions such as drought (Djemel *et al.*, 2019).

To exploit genetic diversity in all maize programs, heterosis is considered as the main factor in yield breeding schemes (Betrán *et al.*, 2003). Recently, Cherchali *et al.* (2018) studied the heterotic patterns among Algerian, US Corn Belt, and European flint maize populations under the Mediterranean conditions of North Africa. These authors identified a high degree of genetic divergence among Algerian maize populations and between Algerian maize populations and Corn Belt dent and European flint germplasm from northern and southern Spain. The authors suggested that Algerian maize could be considered as a novel source to increase the narrow genetic basis, exploited nowadays especially under drought conditions. Our objectives were (i) to estimate the heterosis and combining ability of six Algerian maize populations under drought conditions by using a diallel design, and (ii) to select the most promising populations and crosses for breeding for stress tolerance.

Material and methods

Germplasm

Six Algerian maize populations representing the main genetic and geographic maize groups of Algeria were evaluated in this study (Table 1). These populations were crossed in a diallel mating design without reciprocals in 2013 to produce 15 hybrids (Cherchali *et al.*, 2018). Based on Aci *et al.* (2013) results, Algerian maize populations were classified into three groups: Cluster I includes IGS that comes from the most southern area (province of Tamanrasset); Cluster II includes accessions coming from the center of the prospected area, Adrar (AOR, IZM, and MST), with a smaller group including the SHH population from the north of Algeria; and Cluster III includes populations from Bechar province (BAH). The diallel crossing system was made by Cherchali *et al.* (2018). For each cross, 60 pairs of plants were used to produce 60 crosses and all kernels were bulked to represent one hybrid

Experimental design and field measurement

The 25 genotypes (6 populations, 15 crosses and 4 checks: the breeding populations from dry Spain [EPS14(FR)C3] and humid Spain [EPS13(FR)C3]) that represent the main heterotic group in Spain, their respective cross EPS13(FR)C3 × EPS14(FR)C3 and EP42 × EP17 hybrid) were evaluated under water stress following a 5 × 5 lattice design with 3 replications at Algiers, Algeria (36°43’16" N, 3°09’03"E, 36 m altitude, with 600 mm of annual rainfall) in 2016, 2017 and 2018. Trials under well water conditions received 600 mm of water from sowing to post-flowering. However, only 200 mm was applied under drought conditions. Irrigation was applied every week and, when the trials received water from rainfall, the exact amount was removed from the irrigation supply. Plots were planted and harvested manually. Each plot consisted of two 3 m

Table 2 - Analysis of variance combined across environments for four agronomic traits analyzed in a diallel among six Algerian maize populations evaluated along with four checks in three environments in Algiers under drought.

Source of variation	df	Early vigor (1–9 scale)[a]	Plant height (cm)	ASI[b] (days)	Grain yield ($Mg.h^{-1}$)
Environments (Env)	2	55.78**	11234.74**	24.02**	16.26**
Treatments	1	177.49**	158558.96**	554.95**	114.04**
Block (Env × Group)	52	2.43**	421.08*	2.93**	0.83*
Env × Treatments	2	18.44**	9672.74**	26.47**	17.43**
Genotypes	24	8.64**	9394.26**	8.15**	2.74**
Env × Genotypes	46	2.44*	6362.15**	6.90**	1.51**
Treatments × Genotypes	24	2.31^{ns}	509.37*	6.53**	0.80^{ns}
Error					
df		285	285	280	275
ms		1.53	306.47	1.83	0.54

[a] scale from 1 to 9: 1 = weak plant to 9 = strong plant.

[b] ASI: Anthesis-silking interval

*, ** Significant at the 0.05, and 0.01 probability levels, respectively; ns: not significant

long rows. The rows were spaced 0.80 m apart, and the hills were spaced 0.20 m apart to obtain a final density of 60,000 $plants.ha^{-1}$.

For all field trials, the following data were recorded: early vigor five weeks after sowing (1-9 scale: 1=weak plant, 9=strong plant); anthesis-silking interval (ASI) was calculated as the difference between anthesis (from planting to 50% of plants shedding pollen) and silking (days from planting to 50% of plants showing silks). Two weeks after the pollen shed, plant height was measured as the distance from ground level to the first tassel branch of 10 plants per plot, and finally, the grain yield (weight of kernels per hectare at 140 g kg^{-1} kernel moisture).

Statistical Analysis

The PROC MIXED procedure of SAS Institute (2015) was used to analyse the data, considering genotypes (populations *per se* and crosses) and water regime as fixed effects, whereas environment, replicates, and blocks as random factors. Analyses were performed using the following linear model:

$$Y = Mean + Env + Rep\ (Env) + Block\ (Rep \times Env) + Entry + Entry \times Env + Error$$

where Y is the observed value, Mean is the mean of the values observed in the experiment, Env is the environmental effect, $Rep\ (Env)$ is the effect of repetition within environment, $Block$ is the effect of a block within $(Rep \times Env)$, $Entry$ is the effect of populations or hybrids, $Entry \times Env$ is the effect of *Entry × environment interaction*, and $Error$ is the residual term.

Analysis of diallel crosses was made according to Gardner and Eberhart (1966) Analysis II, excluding checks. The linear model is as follows:

$$Yij = E + b\ (e) + Uv + 1/2(vi + vj\ ) + 1/2(evi + evj\ ) + k(hij + ehij) + Error$$

where Yij is the value observed for the cross of populations i and j; Uv is the mean of all parental populations; E is the effect of environment; $b(e)$ is the effect of repetition within environment; and vi and vj are the varietal effects for populations i and j, respectively; evi and evj are the effects of interaction of environment and population i and j, respectively; $k = 0$ when $i = j$ and $k = 1$ $i \neq j$; hij is the deviation from mean heterosis observed in the cross of populations i and j; and $ehij$ is the interaction of environment and heterosis of populations i and j. Varietal effect was calculated as the difference between a particular population mean and the mean of all populations, whereas heterosis effect was calculated as the difference between the mean of two parental populations and their cross and is presented as a percentage, as well as in units of measurement for each trait. Furthermore, hij was partitioned as follows:

$$hij = h + hi + hj + s\ ij$$

Where h is the average heterosis, hi and hj are the varietal heterosis effects or deviations from the mean heterosis due to the varieties i and j; and sij is the specific heterosis in the population cross between i and j. All data were analyzed with the DIALLEL-SAS05 program of Zhang *et al.* (2005).

Fig. 1 -

Table 3 - Means of the agronomic traits analyzed in the diallel systems with six Algerian maize populations evaluated along with four checks in three environments in Algiers under well-watered conditions and water stress.

Entry	Early vigor (scale 1-9)[a]		Plant height (cm)		ASI (days)		Grain yield (t.ha^{-1})	
	Well water	Water stress	Well water	Water stress	Well water	Water stress	Well water	Water stress
Algerian populations								
AOR	6.44	3.66	173.64	126.21	2.44	3.88	2.24	1.41
BAH	6.22	4.88	164.87	131.53	1.66	4.22	2.06	1.31
IGS	7.00	5.22	193.61	139.73	1.88	4.44	2.39	1.02
IZM	6.11	3.77	181.03	127.17	3.77	6.11	1.97	0.75
MST	5.88	4.00	170.37	119.24	2.44	3.00	1.73	0.79
SHH	6.33	4.88	178.01	127.04	2.33	4.22	2.72	1.79
Populations' crosses								
AOR × BAH	7.00	6.44	172.34	139.10	2.66	3.33	2.69	1.86
AOR × IGS	7.55	6.33	202.15	140.22	1.55	4.55	2.49	1.56
AOR × IZM	7.44	6.00	187.76	140.00	2.55	4.88	3.34	1.59
AOR × MST	7.11	5.88	187.45	129.75	3.00	4.33	2.84	1.36
AOR × SHH	7.11	6.33	173.78	137.64	2.22	4.11	2.15	1.47
BAH × IGS	6.22	5.11	179.45	129.65	2.66	5.62	2.55	1.32
BAH × IZM	8.00	5.55	180.44	140.12	2.33	5.12	2.80	1.33
BAH × MST	6.66	5.33	177.67	130.01	1.77	2.77	3.03	1.40
BAH× SHH	7.66	5.55	174.21	131.47	2.55	4.22	3.41	2.37
IGS× IZM	5.94	6.11	160.88	125.60	2.22	5.33	1.88	1.71
IGS × MST	6.88	5.77	177.98	133.61	2.44	2.88	2.88	1.08
IGS × SHH	8.44	6.33	187.71	145.92	1.77	5.12	3.40	2.39
IZM × MST	6.88	5.00	187.57	132.06	2.66	5.12	2.88	1.25
IZM × SHH	7.44	5.22	189.36	134.38	2.11	5.22	2.87	1.67
MST × SHH	6.77	5.33	171.02	137.41	1.55	3.87	2.06	1.41
Checks								
EPS13(FR)C3	6.11	6.44	123.33	134.64	3.00	8.00	1.35	0.72
EPS14(FR)C3	6.83	4.33	183.85	124.66	2.16	9.33	1.94	0.63
EPS13(FR)C3 × EPS14(FR)C3	8.00	7.20	200.46	144.51	2.66	7.50	2.04	1.62
EP42 × EP17	6.55	5.44	231.66	176.33	3.88	5.55	2.70	1.92
Means	6.89	5.43	166.15	122.39	2.41	4.81	2.51	1.43
LSD $_{(0.05)}$	1.20	1.11	13.70	18.52	0.84	1.45	0.82	0.54

[a] scale from 1 to 9: 1=weak plant to 9=strong plant

Results

Analysis of variance and means' comparisons

Combined analysis of variance across years and treatments revealed significant differences between environments and interactions of the environment with genotypes and treatments for all traits (Table 2). Significant differences among genotypes and irrigation were revealed for all traits. Treatment × genotypes interaction was significant only for ASI and plant height.

Agronomic performance of populations *per se* and their crosses is presented in Table 3. Under control conditions, early vigor ranged from 5.88 (MST) to 7.00 (IGS) for parental populations and from 5.94 to 8.44 for their crosses, and from 6.11 to 8.00 for the checks. IGS × SHH was the most vigorous cross (8.44), followed by BAH × IZM (8.00). IGS had the highest early vigor *per se*, though this population had significantly lower vigor than the most vigorous hybrid IGS × SHH, and its crosses were among those with the highest vigor. MST was the popu-

Table 4 - Mean squares from the Analysis II of Gardner and Eberhart (1966) of the diallel made among Algerian populations evaluated under well-watered conditions and water stress in three environments in Algiers.

Sources of variation	df	Early vigor (scale 1-9)[a]	Plant height (cm)	ASI (days)	Grain yield (t.h^{-1})
Well-watered					
Environment (Env)	2	120.32**	6000.18**	21.25**	41.63**
Rep (Env)	6	6.71**	1279.98**	2.34*	3.04**
Entry	20	4.22**	875.91**	2.49**	2.25**
Varietal effects (V)	5	2.13	873.63	3.72	0.64
Heterosis (H)	15	4.92**	876.68	2.08	2.79*
Average heterosis (Ha)	1	25.37*	536.86	0.88	12.38
Varietal heterosis (Hv)	5	1.68	405.55	2.43	0.84
Specific heterosis (Hs)	9	4.44	1176.17	2.01*	2.81*
Env × Entry	40	1.31	841.37**	2.06**	1.03
Env × V	10	1.3	295.4	3.88**	0.32
Env × H	30	1.31	1023.37**	1.45*	1.27*
Env × Ha	2	0.3	837.6*	5.59**	0.7
Env × Hv	10	0.52	646.52**	1.88*	1.77**
Env × Hs	18	1.86	1253.37**	0.76	1.05
Error	120	1.55	232.59	0.83	0.71
Water stress					
Environment (Env)	2	24.66**	38405.08**	24.58**	8.92**
Rep (Env)	6	4.82**	1264.49**	1.92	0.75*
Entry	20	5.58**	358.26	7.42**	1.52**
Varietal effects (V)	5	4.08	353.05	20.19**	3.08
Heterosis (H)	15	6.56**	409.37	2.90	0.99
Average heterosis (Ha)	1	69.78*	1936.64	0.39	4.44
Varietal heterosis (Hv)	5	4.17*	299.25	0.60	0.42
Specific heterosis (Hs)	9	1.08	306.79	4.48	0.93*
Env × Entry	40	1.48	393.00	3.90**	0.58**
Env × V	10	2.05	717.88*	3.15	0.96**
Env × H	30	1.11	258.03	4.30**	0.50*
Env × Ha	2	3.13	163.22	1.43	0.35
Env × Hv	10	0.46	240.39	3.60*	0.67*
Env × Hs	18	1.12	329.08	5.02**	0.36
Error	119	1.40	333.95	1.80	0.30

[a] scale from 1 to 9: 1=weak plant to 9=strong plant

lation with the lowest vigor *per se*; however, differences among populations *per se* were not significant for early vigor under well water. Conversely, differences among populations *per se* were significant for early vigor under water stress, ranging from 3.66 (AOR) to 5.22 (IGS). The crosses varied from 5.00 (IZM × MST) to 6.44 (AOR × BAH), and vigor varied from 4.33 to 7.20 for the checks. The crosses involving IGS with AOR (6.33), SHH (6.33) and IZM (6.11); along with AOR × BAH and AOR × SHH (6.33) were the most vigorous crosses and their performance was similar to the most vigorous check EPS13(FR) C3 × EPS14(FR)C3, though most crosses were not significantly different from AOR × BAH for early vigor.

For plant height, under control conditions, EP17 × EP42 exhibited the tallest plants (231.66 cm), followed by AOR × IGS (202.15 cm) and EPS13(FR)C3 × EPS14(FR) C3 (200.46 cm). Among the populations *per se*, IGS had the tallest plants (193.61 cm) along with IZM. It was remarkable IGS had the greatest early vigor. Under water

Table 5 - Genetic parameters from the analyses of Gardner and Eberhart II (1966) (varietal effects, varietal heterosis, average heterosis and specific heterosis) for early vigor, plant height, ASI and grain yield in the diallel made among six Algerian maize populations evaluated in three environments in Algiers under water stress and well water.

Populations	Early vigor (1-9 scale)[a]		Plant height (cm)		ASI (days)		Grain yield (t/ha)	
	Well water	Water stress	Well water	Water stress	Well water	Water stress	Well water	Water stress
Varietal effect								
AOR	0.11	-0.77	-3.28	-4.75	0.01	-0.33	0.05	0.45*
BAH	-0.11	0.48	-12.04	3.53	-0.75*	-0.11	-0.12	0.09
IGS	0.66	0.82*	16.68*	11.73	-0.53	0.11	0.20	-0.20
IZM	-0.22	-0.62	4.10	-0.82	1.35**	1.77**	-0.21	-0.47*
MST	-0.44	-0.40	-6.54	-8.74	0.01	-1.33**	-0.45	-0.43
SHH	0	0.48	1.08	-0.94	-0.09	-0.11	0.53	0.57*
Varietal Heterosis								
AOR	0.06	0.94**	6.69	5.14	0.14	-0.07	-0.08	-0.24
BAH	0.01	-0.43	1.23	-3.09	0.53*	-0.21	0.24	0.04
IGS	-0.5	-0.18	-7.11	-6.03	0.09	0.28	-0.24	0.13
IZM	0.11	0.08	-1.36	-0.46	-0.54*	-0.01	0.11	0.14
MST	-0.12	-0.16	2.88	1.17	0.009	-0.12	0.20	-0.13
SHH	0.43	-0.24	-2.33	3.27	-0.24	0.14	-0.23	0.05
Specific heterosis								
AOR×BAH	-0.22	0.32	-8.58	2.52	0.07	-0.58	-0.18	0.20
AOR×IGS	0.45	-0.20	15.21**	2.48	-0.70*	0.02	-0.06	-0.03
AOR×IZM	0.17	-0.08	1.36	2.97	-0.005	-0.18	0.64*	0.12
AOR×MST	0.18	-0.06	2.13	-4.94	0.55	0.93*	0.17	0.14
AOR×SHH	-0.58	0.02	-10.12	-3.04	0.07	-0.17	-0.57	-0.43*
BAH× IGS	-0.71	-0.67*	2.35	-3.99	0.41	1.12*	-0.24	-0.39*
BAH× IZM	-0.89	-0.21	-3.88	-7.18	0.22	-0.08	0.13	0.24
BAH× MST	-0.08	0.13	2.19	-0.59	-0.67*	-0.58	0.11	0.08
BAH×SHH	0.13	0.00	0.13	-5.12	0.41	-0.03	0.44	0.34*
IGS×IZM	-1.03*	0.35	-21.68**	-8.49	-0.005	-0.31	-0.73*	0.18
IGS×MST	0.25	0.16	-3.5	1.84	0.32	-1.08*	0.28	-0.17
IGS×SHH	1.03*	0.35	7.62	8.15	-0.03	0.25	0.75	0.42*
IZM× MST	0.09	-0.17	6.62	1.00	0.24	0.60	0.14	0.11
IZM×SHH	-0.13	-0.31	9.81	-2.66	-0.005	-0.18	0.07	-0.16
MST×SHH	-0.45	-0.06	-7.44	2.68	-0.45	0.14	-0.70	-0.16
Average heterosis	0.81*	1.35**	3.73	7.13	0.15	0.10	0.56**	0.36**

a scale from 1to 9: 1=weak plant to 9=strong plant.

* and ** Significant at the 0.05 and 0.01 probability levels respectively

stress, EP17 × EP42 was the tallest with 176.33 cm followed by the IGS × SHH (145.92 cm) and most crosses, along with two populations *per se*, IGS (139.73 cm) and BAH, which were not significantly different from IGS × SHH.

Under control conditions, ASI varied from 1.66 days (BAH) to 3.77 days (IZM) for populations *per se*, and from 1.55 days for both (MST × SHH and AOR × IGS) to 3.00 days (AOR × MST) for crosses. Among the checks, only EPS14(FR)C3 (2.16 days) was not significantly different from the crosses having the shortest ASI. Under water stress, ASI varied from 3.00 days (MST) to 6.11 days (IZM) for populations *per se*, and from 2.77 days (BAH × MST) to 5.62 days (BAH × IGS) for crosses. Neither MST, AOR, BAH and SHH *per se*, nor IGS × MST (2.88 days), AOR × BAH (3.33 days), MST × SHH (3.87 days), AOR × SHH, and BAH × SHH were significantly different from BAH × MST for ASI under water stress. Most crosses and populations had lower ASI than the checks that varied from 5.55 days (EP17 × EP42) to 9.33 days (EPS14(FR)C3).

Finally, the grain yields of the populations *per se* under well water ranged from 1.73 t.ha^{-1} (MST) to 2.72 t.ha^{-1} (SHH) and differences were not significant for yield among populations *per se*. Variation was from 1.88 t.ha^{-1} (IGS × IZM) to 3.41 t.ha^{-1} (BAH × SHH) for their crosses, and from 1.35 t.ha^{-1} (EPS13(FR)C3) to 2.70 t.ha^{-1} (EP17 × EP42) for the checks under control conditions. The highest yielding crosses were BAH × SHH, IGS × SHH, AOR × IZM, and BAH × MST, though differences were not significant with five more crosses and the population SHH *per se*. In general, most crosses exhibited higher grain yield than the checks. Under water stress, grain yield ranged from 0.75 t.ha^{-1} (IZM) to 1.79 t.ha^{-1} (SHH) for populations *per se*, from 1.08 t.ha^{-1} (IGS × MST) to 2.39 t.ha^{-1} (IGS × SHH) for their crosses, and from 0.63 t.ha^{-1} (EPS14(FR)C3) to 1.92 t.ha^{-1} (EP17 × EP42). The mean value of most crosses was superior to that of the checks. The highest yielding crosses were IGS × SHH, BAH × SHH, and AOR × BAH.

Genetic parameters among Algerian Maize Populations

Analysis of diallel crosses was done separately for each treatment (Table 4). Combined analysis of variance over year of all agronomic traits measured in the diallel design showed significant differences among environments and among entries. Entries were significantly different for all treatments except plant height under water stress. Environments × entry interactions were significant for plant height and ASI under well-watered conditions, and for yield and ASI under water stress conditions. Varietal effect was significant only for ASI under water stress. Heterosis was significant for early vigor under both conditions and for yield under well-watered conditions. Average heterosis was significant only for early vigor in both conditions. Specific heterosis was significant for yield under both conditions and for ASI under well-watered conditions. Environment × varietal effect was significant for ASI under well water and for plant height and yield under water stress. Environment × specific heterosis interaction was highly significant only for plant height under well water and for ASI under water stress. Environment × heterosis and Environment × varietal heterosis were significant for all traits except early vigor under well water, and for early vigor and plant height under water stress. Environment × average heterosis interaction was significant for plant height and ASI under well water.

Genetic parameters estimated from the analyses of Gardner and Eberhart (1966) are presented in Table 5. For early vigor, under well-watered conditions, IGS × IZM (-1.03) presented a significant and negative specific heterosis, while IGS × SHH (1.03) had a significant and positive specific heterosis. Under water stress, IGS × BAH had a significant and negative specific heterosis (-0.67). The varietal effect was positive and significant only for IGS (0.82), and varietal heterosis was significant and positive for AOR (0.94). Average heterosis was significant and positive under both treatments, showing the superiority of the crosses over the populations. For plant height, under well-watered conditions, specific heterosis was significant and positive (15.21 cm) for AOR × IGS and significant and negative (-21.68 cm) for IGS × IZM. In addition, the varietal effect was significant for IGS (16.68 cm). Under water stress, none of the populations or crosses had significant effects for any of the genetic parameters, and average heterosis was not significant under any of the treatments. For ASI and under well-watered conditions, AOR × IGS and MST × BAH presented significant and negative specific heterosis (-0.70 day and -0.67 day respectively). Varietal effect was significant and positive for IZM (1.35 days) but negative for BAH (-0.75 day). Moreover, varietal heterosis was significant and positive for BAH (0.53 day) and negative for IZM (-0.54 day). Under water stress, AOR × MST and IGS × BAH exhibit significant and positive specific heterosis (0.93 day and 1.12 days, respectively), while IGS × MST presented a significant and negative value (-1.08 days). Varietal effect was significant and positive for IZM (1.77 days) but significant and negative for MST (-1.33 days). Average heterosis was not significant for this character.

Finally, under well-watered conditions, the most outstanding cross for grain yield was AOR × IZM, which presented positive and significant specific heterosis (0.64 t.ha^{-1}). Contrarily, IGS × IZM exhibited negative and significant specific heterosis (-0.73 t.ha^{-1}). None of the populations had significant varietal effect or varietal heterosis for yield. Average heterosis was significant and positive (0.56 t.ha^{-1}). Under water stress, IGS × SHH and BAH × SHH showed significant and positive specific heterosis (0.42 t.ha^{-1} and 0.34 t.ha^{-1} respectively) whereas AOR × SHH and IGS × BAH were significant and negative (-0.43 and -0.39 respectively). Furthermore, the varietal effect was significant and positive for AOR and SHH (0.45 t.ha^{-1} and 0.57 t.ha^{-1} respectively) but significant and negative for IZM (-0.47 t.ha^{-1}). The average heterosis was significant and positive (0.36 t.ha^{-1}).

Discussion

Analysis of variance and means' comparisons

Our results confirm that the performance of all populations and their crosses was reduced under drought conditions, with mean yield reduction of 43% that is much larger than previous reports (Edmeades *et al.*, 1992; Betrán *et al.*, 2003; Bänziger *et al.*, 2006). Mean ASI increased 50% from control to drought conditions, and the effect of drought was smaller for mean early vigor (21%) and mean plant height (26%). Drought is the main climatic change related factor that reduces the maize production; therefore, improving grain yield under stress environments needs the exploitation of new genetic variation (Flint-Garcia *et al.*, 2005); however only 10% of total maize diversity has been used (Hallauer *et al.*, 2010). Information about the type of gene action controlling agronomic traits under stress is of paramount importance to identify useful parents and hybrids (Nasser *et al.*, 2020). Knowledge of the genetic parameters for traits with agronomic relevance allows the breeder to recognize the additive and non-additive effects responsible for each trait (Coelho *et al.*, 2020). This is important for setting a breeding strategy to improve a target trait (Ertiro *et al.*, 2017). In this context, maize populations from Algerian Sahara were evaluated using diallel design under water stress to identify the most promising populations that could be incorporated as potential sources of drought tolerance into maize breeding programs for drought tolerance. Significant differences were detected among populations and their crosses under drought and optimum conditions. These results reveal substantial and adequate genetic variability among the Algerian maize germplasm for all the measured traits. That variability allows genetic progress under stressed conditions as reported by Akaogu *et al.* (2017). High degree of genetic diversity among Algerian populations was reported previously by Djemel *et al.* (2012) and Aci *et al.* (2013). This variability makes breeding programs possible in temperate environments and allows the increase of the narrow genetic basis used nowadays. The significant treatment × genotype interactions for both ASI and and plant height were generally of rank, indicating that the relative performance of genotypes was different under well-watered conditions and under drought for all traits. In addition, the lack of significant environment × specific heterosis interactions (for early vigor, ASI and yield under well-watered conditions and for early vigor, plant height and yield under drought) and environment × varietal heterosis interactions (for early vigor under both conditions and for plant height under drought) indicated the stability of heterotic effects across environments as reported by (Wegary *et al.*, 2014). This finding would increase genetic gain in breeding programs and allows the selection of stable and outstanding genotypes under drought conditions (Yan and Hunt, 1998).

Genetic parameters among Algerian Maize Populations

Under well-watered conditions, the significant heterosis variation indicated that non-additive gene action was more important in the inheritance of early vigor and yield. Varietal effects were not significant for any trait. Our results concur with Soengas *et al.* (2003) who found nonsignificant varietal effects for grain yield. However, other authors have found that most of the variability is under the control of varietal effects (Noldin *et al.*, 2017, Cherchali *et al.*, 2018). Specific heterosis was significant for ASI and yield indicated the important role of non-additive genetic effect for the traits most strongly affected by drought. Moreover, our results show that specific heterosis explained more variation of heterosis than varietal heterosis both under control and drought conditions, except for early vigor under drought; accordingly, Begum *et al.* (2018) reported that the contribution was higher for specific heterosis than for varietal heterosis for plant height and grain yield.

Under drought, heterosis effect was significant only for early vigor indicating that non-additive gene action controlled mainly this trait. Varietal effect was significant for ASI indicating that additive genetic was the main genetic effect. This implies that appreciable breeding progress could be made using breeding methods, which capitalize additive gene action such as intrapopulation selection for population improvement, as well as for the development of drought-tolerant hybrids. Significant specific heterosis for yield indicated the importance of the non-additive gene action in the inheritance of this trait. The expression of heterosis was greater under drought stress than under non-stressed environments (Betrán *et al.*, 2003). However, Badu-Apraku *et al.* (2011) also reported that additive gene action mainly contributed to the inheritance of grain yield under drought. In addition, Derera *et al.* (2008) showed that only general combining ability was significant for yield, indicating the predominance of additive effects. Only early vigor exhibited significant average heterosis, indicating that the early vigor of the crosses was, on average, greater than the early vigor of the populations *per se* under both treatments.

Early vigor and yield are the best indicators for existing heterotic groups and ASI is considered as the best secondary trait related to yield improvement under drought conditions. Under drought conditions, early vigor is the principal adaptive factor (Welcker *et al.*, 2007, Ruta *et al.*, 2010, Araus *et al.*, 2012, Jiang *et al.*, 2012) followed by ASI. Under our stressed conditions, IGS and AOR presented a significant and positive varietal effect and varietal heterosis, respectively. For ASI, MST presented significant and negative varietal effects and both AOR and SHH exhibited significant and positive varietal effects for grain yield. These populations could be considered as invaluable sources of favorable alleles to improve grain yield and plant growth-related traits under drought conditions, though each of them has different potential favorable contributions. These results indicate that it is possible to use these populations in intrapopulation or interpopulation selection, depending on the breeding objective. In addition, Gardner and Eberhart (1966) suggested that for reciprocal recurrent selection program, populations that exhibited the largest varietal effects should be employed. Furthermore, Nasser *et al.* (2020) also reported that the presence of high varietal heterosis effects indicates the existence of great genetic potential. Based on specific heterosis, IGS × MST, for ASI, and IGS × SHH and BAH × SHH, for yield production, were the most promising crosses with significant favorable specific heterosis under water stress. Our results indicated that these crosses had the potential for improving germplasm under stress conditions and could be incorporated into a reciprocal recurrent selection program as suggested by Saif-ul-Malook *et al.* (2016).

Among Algerian maize populations, SHH (population from the north of Algeria) presented a positive and significant varietal effect for grain yield and produced promising crosses with IGS and BAH. Maize populations were classified into three groups according to Aci *et al.* (2013): IGS (Cluster I) comes from the most southern area (province of Tamanrasset); Cluster II includes accessions coming from the center of the prospected area, Adrar, with a smaller group including the SHH population from the north of Algeria and Cluster III includes populations of Bechar province (BAH). There was a clear pattern of relationship between early vigor and yield and genetic distance, based on the geographical origins of the populations, as the most promising crosses were made between populations from diverse groups and regions.

Conclusions

Algerian populations exhibited a high genetic variability under water stress. IGS and AOR (for improving early vigor), MST (for reducing ASI) and both AOR and SHH (for increasing yield) could be incorporated into maize drought tolerance breeding programs as a new sources of drought tolerance. Moreover, IGS × MST was the most outstanding cross for reduced ASI, and both IGS × SHH and BAH × SHH for increasing yield, under water stress. These crosses can be employed in reciprocal recurrent selection to improve drought tolerance. Finally, the populations cited above could be used in breeding programs to enhance tolerance to water stress.

Funding

This research was funded by École Nationale Supérieure Agronomique d'Alger, PRIMA, a program supported by the European Union under H2020 framework programme, PCI2021-121912 and PID2019-108127RB-I00 funded by MCIN/AEI/ 10.13039/501100011033

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