



Genetics of drought tolerance at seedling and maturity stages in *Zea mays* L.

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Abstract

Shortage of irrigation water at critical growth stages of maize is limiting its production worldwide. Breeding drought-tolerant cultivars is one possible solution while identification of potential genotypes is crucial for genetic improvement. To assess genetic variation for seedling-stage drought tolerance, we tested 40 inbred lines in a completely randomized design under glasshouse conditions. From these, two contrasting inbred lines were used to develop six basic generations (P_1 , P_2 , F_1 , F_2 , BC_1F_1 , BC_2F_2). These populations were then evaluated in a triplicated factorial randomized complete block design under non-stressed and drought-stressed conditions. For statistical analyses, a nested block design was employed to ignore the replication effects. Significant differences ($p \leq 0.01$) were recorded among the genotypes for investigated seedling-traits. Absolute values of fresh root length, fresh root weight, and dry root weight lead to select two genotypes, one tolerant (WFTMS) and one susceptible (Q66). Estimates of heritability, genetic advance, and genotypic correlation coefficients were higher and significant for most of the seedling-traits. Generation variance analysis revealed additive gene action. Narrow-sense heritability [$F_2 \geq 65$; $F_\infty \geq 79$] revealed the same results. Generation mean analysis signified additive genetic effects in the inheritance of cob girth, non-additive for plant height, grains per ear row and grain yield per plant, and environmental for ear leaf area, cob length, grain rows per ear, biomass per plant, and 100-grain weight under drought-stressed conditions. For conferring drought-tolerance in maize, breeders can adopt the recombinant breeding strategy to pyramid the desirable genes.

Additional key words: genetic effects; maize; morphological and seedling traits; water stress.

Abbreviations used: BPP (biomass per plant); CG (cob girth); CL (cob length); CRD (completely randomized design); DRW (dry root weight); DS (drought-stressed); DSW (dry shoot weight); E (emergence); ELA (ear leaf area); FRCBD (factorial randomized complete block design); FRL (fresh root length); FRW (fresh root weight); FSL (fresh shoot length); FSW (fresh shoot weight); GPER (grains per ear row); GRPE (grain rows per ear); GYPP (grain yield per plant); HGW (100-grain weight); NS (non-stressed); PH (plant height).

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Introduction

Maize (*Zea mays* L.), commonly known as corn, is a major staple consumed as food, feed, and raw materials in many industrial products worldwide. Its grains are a rich source of starch, protein, oil, fiber, sugar, and ash (Chaudhry, 1983). Globally, maize is grown on an area of about 183 Mha with 1021 Mt production annually (<http://faostat.fao.org/>). Its demand in the international market, especially in developing countries, is expected to rise from 526 to 784

Mt owing to reduced cropland and increased growth rate (Chen *et al.*, 2012).

Among cereals, maize is highly productive under suitable environmental and better management conditions. At the same time, it is also very sensitive to drought and heat-stresses and may result in yield losses of 15-20% annually (Lobell *et al.*, 2011). However, these yield losses depends upon stress severity, duration and occurrence at the crop stage. Drought-stress during V_8 to V_{17} plant growth stages affects maize plant development, architecture, ear size and kernels

number severely (Heiniger, 2001; Farré & Faci, 2006). Drought occurring two weeks before and during silking phase reduces seed setting and kernel size, causing 20-50% significant yield losses (Schussler & Westgate, 1991; Nielsen, 2007). Negative effects of drought on crop productions are likely to increase in the outlook due to unpredictable global climatic changes (Sanderson *et al.*, 2011). Improvement in water-use efficiency through management practices and evolution of stress-tolerant crop varieties will likely play an effective role in mitigating damaging effects of abiotic plant stresses on agricultural production (Tester & Langridge, 2010).

As drought is quantitative in nature, therefore, requires an understanding of genetic mechanisms controlling various plant traits for adopting different breeding approaches (Khan *et al.*, 2004; Ahsan *et al.*, 2013). Assessment of crop genotypes at seedling-stage is an imperative feature of plant breeding for developing drought-tolerant cultivars. Vigorous maize seedlings lead to healthy crop and ultimately good production under water-deficit conditions. Potential variations exist in maize genetic stocks for drought-tolerance. Identification and characterization of genotypes for the said purpose is the primary step in developing drought-tolerant cultivars (Chen *et al.*, 2012; Naveed *et al.*, 2016a). This requires an understanding of gene action controlling various seedling and morphological plant traits. Various biometrical techniques could be used for appraising genetic effects. Among these, generation mean analysis is the one which determines the type of epistasis at digenic level using scaling test, accurately and efficiently (Naveed *et al.*, 2016b). In view of the above, we conducted this study to identify the contrasting inbred lines at seedling-stage drought-stress and to find the inheritance pattern of gene or genes involved in the drought-tolerance using six basic generations.

Material and methods

Plant material and other experimental details

Drought-tolerance studies in maize at seedling and maturity stages were carried out in the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan during the years 2010-13. For this purpose, 40 out of 200 maize inbred lines, collected from different research organizations were selected based on characterization/information provided by the contributors.

As the screening experiments were conducted inside the glasshouse, the design used for laying out the plant material was completely randomized (CR). However, for the evaluation of six basic generations in non-stressed and drought-stressed conditions, we applied a

factorial randomized complete block design (FRCBD) with three repeats. Row to row and plant to plant distances maintained were 75 and 25 cm, respectively. Agronomic and crop husbandry practices were followed according to experimental needs.

Screening at seedling stage

This experiment was conducted in a glasshouse during autumn, 2010. A total of 36 seeds of each test entry were sown in all 3 replications using the same number of polythene bags (20×15 cm each) in two separate sets: Set-I, irrigation was applied to the 100% of the field capacity or crop need, while in Set-II irrigation was applied to the 50% of the field capacity.

Seven days after the sowing of seeds in polythene bags, 150 mL of water was applied to both the experimental sets. Fifteen days following the sowing, another irrigation of 150 mL of water was given just once to Set-I only. However, 21 days after the sowing and for uprooting the seedlings, 150 mL of water was applied to both the experimental sets. After uprooting and washing with tap water cautiously, the seedlings were dried by wrapping them in blotting papers for 10 minutes.

To select the desirable parents, assessment of the germplasm was done on absolute genotypic performances for investigated seedling-traits. This selection procedure had extensively been employed by other researchers (Azhar *et al.*, 2005; Akhter *et al.*, 2007; Iqbal *et al.*, 2011). We measured the following plant characters by using the procedures given in Table 1: fresh root length (FRL), fresh root weight (FRW), dry root weight (DRW), emergence% (E), shoot length, fresh shoot weight (FSW), and dry shoot weight (DSW) under the contrasting conditions (Matsui & Singh, 2003; Qayyum *et al.*, 2012). Data were recorded on 8 seedlings/genotype selected randomly and analyzed using analysis of variance (Steel *et al.*, 1997). Phenotypic and genotypic correlation coefficients between pairs of seedling traits were calculated using individual plant data of F₂ population (Kwon & Torrie, 1964). Broad-sense heritability (Weber & Moorthy, 1952) and genetic advance (Falconer & Mackay, 1996) were also worked out for seedling-traits.

Studies at physiological plant maturity

Based on seedling-traits, two contrasting inbred lines were selected and used as parents (P₁ and P₂) to develop F₁ seed during autumn, 2011. P₁ was used as pollen parent while P₂ as female parent. During autumn 2012, both parents (P₁ and P₂) and their hybrids (F₁) were raised under field conditions. Some of the F₁ plants were selfed

Table 1. Various seedling and morphological plant traits of maize recorded under non-stressed and drought-stressed conditions.

Variables	Abbreviation	Procedure / Methodology
Emergence%	E%	Ratio of germinated seeds to number of seeds sown multiplied by 100.
Fresh root length	FRL	Measured in centimeters (cm).
Fresh shoot length	FSL	Fresh shoot lengths obtained from each selected seedling were measured in cm.
Fresh root weight	FRW	The roots of each selected plant were separated from the plant and fresh root weight was recorded in grams.
Fresh shoot weight	FSW	The shoots of each plant were separated from the plant and fresh root weight was recorded in grams.
Dry root weight	DRW	Fresh roots detached from selected seedlings were put in a kraft paper bag and dried in an electric oven at $65 \pm 5^\circ\text{C}$ for 72 hours for complete drying. The dried roots were weighed in grams.
Dry shoot weight	DSW	Fresh shoots detached from the seedlings were put in a kraft paper bag and dried in an electric oven at $65 \pm 5^\circ\text{C}$ for 72 hours for complete drying. The dried shoots were weighed in grams.
Plant height	PH	At physiological plant maturity, the lengths were measured in cm from ground level to the apex of tassels of randomly selected plants using a measuring rod (Guzman & Lamkey, 2000).
Ear leaf area	ELA	Leaves were collected from randomly selected competitive plants in each treatment and leaf area of each was measured in cm^2 using a leaf area meter (Model CI-203 CID, Inc. USA).
Cob length	CL	The length of cobs from each selected plant was measured in cm using a measuring tape.
Cob girth	CG	The diameter of cobs from each selected plant was measured from base, middle and top with the help of a Vernier Caliper (Model, RS232) and averaged.
Grain rows per ear	GRPE	These were counted from the cobs of each selected plant and averaged.
Grains per ear row	GPER	Grains were counted from ear rows of each selected plant and averaged.
Plant biomass	BPP	The weight of total air dried selected plants was recorded and converted into kg/ha. This, together the grain yield, was used to calculate the plant biomass.
100-grain weight	HGW	Three sets, each comprising 100 grains, were collected from each selected plant and weighed in grams.
Grain yield per plant	GYPP	The grains obtained from each selected plant were weighed in grams.

as a source for raising F_2 population while the remaining F_1 plants were backcrossed with P_1 and P_2 to develop BC_1F_1 and BC_2F_2 generations, respectively.

During autumn 2013, seeds of these six basic generations (P_1 , P_2 , F_1 , F_2 , BC_1F_1 , and BC_2F_2) were planted in two sets, one under field (non-stressed) and the other under drought-stressed conditions. Per replication, 30 plants were sown of each parent (P_1 , P_2) and their hybrids (F_1), 60 of each backcross (BC_1F_1 , BC_2F_2), and 200 of the F_2 generation. To record the data in a replication, randomly guarded 15 plants were selected each of P_1 , P_2 & F_1 while 30 plants each of BC_1F_1 , BC_2F_2 , and 60 plants of F_2 generations, separately both from non-stressed and drought-stressed experiments. Data were recorded on various plant traits, such as plant height, ear leaf area, cob length, cob girth, grain rows per ear, grains per ear row, biomass per plant, 100-grain weight, and grain yield per plant at physiological plant maturity.

Statistical analysis

Observations recorded on different plant traits of six basic generations were analyzed using nested block

design to ignore the replication effects. Variance analysis of each character was done according to Steel *et al.* (1997). Generation mean and variance analyses were performed to find the type of genetic effects and components of variance associated with inheritance of traits for each regime, separately (Mather & Jinks, 1982). Mean and variances of parents (P_1 & P_2), backcrosses (BC_1 & BC_2), and segregating generations (F_1 & F_2) for each trait were averaged over replications before use in statistical and biometrical analyses. A weighted least square analysis was done on generation mean using simplest residual (m) model and tested for goodness of fit. If chi-square value of one-factor model [m] was significant then further models of increasing complexity [md, mdh, etc.] were tried and tested for goodness of fit. The best model was the one which had significant estimates of all the variables along with non-significant chi-square value. The parent with higher value was always taken as P_1 in the model fitting for each trait. Sum of squares (SS) for those comparisons were generated following Little & Hills (1978). Estimates of narrow-sense heritability of various morphological traits were also computed (Mather & Jinks, 1982).

Results

Selection of parents on the basis of seedling traits

Mean squares acquired from analysis of variance of experiments conducted under non-stressed and drought-

stressed environments revealed significant differences among the genotypes for the traits investigated (Table 2). The responses of genotypes varied for all the measured traits under both the experimental regimes. Inbred line WFTMS exhibited, in non-stressed vs drought-stressed conditions: the highest FRL (35.5 vs 34.0 cm), FSL (40.9 vs 30.1 cm), FRW (38.7 vs 15.2 g),

Table 2. Mean performance and statistical significance for various seedling-traits in 40 maize inbred lines under non-stressed and drought-stressed conditions.

Entry	Traits ^[1]													
	E%		FRL		FSL		FRW		FSW		DRW		DSW	
	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS
WFTMS	5.0	5.0	35.5	34.0	40.9	30.1	38.7	15.2	16.8	11.8	27.3	13.2	4.1	3.4
B34	5.0	4.0	33.7	28.1	35.3	29.0	35.8	13.3	16.9	10.9	25.9	2.0	4.1	3.3
W187R	5.0	4.0	35.1	29.8	34.1	26.6	36.7	2.5	15.8	7.4	27.4	0.4	6.7	1.9
AES204	5.0	3.5	27.3	22.3	27.3	23.9	15.6	6.2	10.1	4.3	9.6	2.5	3.8	2.8
A427-2	5.0	3.0	23.7	18.6	22.3	17.1	16.2	10.6	11.7	6.4	13.3	9.7	3.6	2.4
Q67	4.5	3.5	29.3	21.7	31.4	28.1	26.9	11.3	14.7	5.9	14.7	7.0	2.7	2.1
Antigua1	5.0	4.0	26.9	29.8	26.1	22.4	16.6	14.5	11.2	9.2	11.3	13.3	2.5	2.1
N48-94	5.0	2.5	26.8	18.4	33.2	21.1	26.4	7.2	10.8	4.5	21.0	5.3	3.2	2.0
A521-1	5.0	4.5	27.6	22.4	30.2	24.8	17.3	13.6	8.5	4.0	9.3	7.5	2.4	2.0
A239	5.0	3.5	29.6	25.1	29.6	22.4	18.2	11.2	9.3	3.5	10.2	6.2	3.9	2.0
K55TMS	5.0	2.5	28.2	31.1	31.6	22.0	19.6	9.7	9.2	5.7	17.4	6.1	2.5	1.9
USSR150	5.0	4.0	27.3	20.7	30.5	17.1	15.2	5.0	10.4	5.3	7.8	4.4	2.7	1.7
G.PF-9	5.0	4.0	28.5	21.9	30.1	20.0	17.3	7.7	7.3	2.4	15.4	5.0	2.2	1.7
OH28	4.5	3.5	28.9	26.6	30.8	23.3	7.5	7.1	9.6	10.7	6.4	6.0	2.4	1.5
PB77	5.0	2.5	28.5	24.7	31.8	23.9	15.1	6.5	11.7	4.2	11.4	4.7	2.5	1.4
W64SP	5.0	5.0	26.2	24.8	28.6	24.4	23.2	5.8	9.5	4.5	11.7	4.3	1.8	1.4
OH54-3A	4.5	3.5	23.7	22.2	30.5	23.3	18.8	8.1	9.9	6.2	12.4	5.1	1.5	1.4
N18	5.0	3.0	28.1	17.7	32.1	15.1	24.4	10.0	12.7	1.9	12.8	4.8	1.9	1.3
OH8	5.0	3.0	28.1	21.8	28.9	26.1	8.1	4.1	8.7	3.5	4.7	1.9	2.7	1.2
WF-9	5.0	2.0	23.4	15.9	33.4	25.6	11.4	9.2	10.0	2.0	6.8	5.5	1.8	1.2
A556	5.0	3.0	26.2	25.8	25.7	25.4	14.1	5.6	10.8	4.3	8.5	4.4	1.6	1.2
A495	5.0	4.0	27.1	22.3	24.2	21.0	14.0	5.9	9.5	3.2	7.1	3.6	4.0	1.2
OH41	4.5	4.5	28.0	26.8	28.1	26.9	16.0	7.2	8.7	1.6	9.8	5.9	1.7	1.1
A545	5.0	3.5	28.1	15.5	31.0	15.7	26.7	7.6	10.6	5.3	18.5	6.3	2.2	1.0
W10	5.0	3.5	24.6	24.3	30.5	18.0	17.9	10.7	7.2	2.9	16.6	6.8	1.5	1.0
B34-2B	5.0	3.5	28.0	19.3	29.1	19.9	15.9	3.9	7.9	2.9	14.5	3.0	1.9	0.8
WM13RA	5.0	4.0	24.8	29.2	30.5	29.0	21.0	3.3	11.3	4.0	8.9	2.3	1.3	0.8
B42	5.0	3.5	26.8	21.9	30.0	18.9	16.8	5.6	9.8	6.0	15.1	3.6	1.6	0.7
A509	5.0	3.5	24.8	24.7	27.6	24.5	28.3	7.2	14.1	2.6	17.7	4.4	1.6	0.7
WA3748	5.0	3.5	27.2	22.3	31.1	20.8	21.3	6.6	12.1	5.9	12.8	8.7	1.4	0.7
A638	5.0	3.5	27.3	25.3	28.2	25.3	18.7	6.4	9.5	4.3	11.5	2.7	1.2	0.7
OH33-1	5.0	3.0	26.6	22.8	30.7	21.6	17.2	8.0	8.7	2.4	13.0	4.8	1.1	0.7
USSR40	5.0	3.5	24.3	24.3	21.6	17.2	15.5	5.8	9.1	3.8	12.7	4.6	1.0	0.7
PB7-1	5.0	3.5	28.5	18.9	29.3	23.8	9.0	4.0	9.9	5.0	7.9	3.0	1.4	0.6
W82-3	5.0	4.0	19.7	17.5	19.0	12.8	7.2	3.0	6.8	2.3	3.3	1.9	3.5	1.6
A50-2	5.0	4.0	33.6	26.6	28.4	21.4	15.0	13.7	8.1	2.9	8.6	7.3	2.8	1.4
M14	5.0	3.5	24.9	26.2	20.1	17.5	9.3	3.1	7.0	3.0	7.1	3.0	2.5	1.4
Q97	4.0	3.5	28.0	23.2	30.2	23.1	29.7	4.5	10.0	5.5	7.7	3.1	0.9	0.4
Q66	4.0	2.5	21.8	20.4	19.8	12.9	10.5	2.7	6.4	1.2	4.9	1.1	0.7	0.4
W64TMS	4.5	3.0	24.9	21.8	30.5	24.1	12.3	5.6	10.1	3.2	9.4	5.4	3.1	1.3
Mean	4.89	3.53	27.29	23.42	29.11	22.15	18.64	7.48	10.31	4.67	12.31	5.02	2.40	1.43
SE	0.04	0.10	0.51	0.66	0.68	0.68	1.22	0.54	0.40	0.40	0.92	0.44	0.19	0.11
MS	0.14	0.32	22.39	33.24	38.56	36.09	12.50	2.31	12.87	14.58	73.23	32.30	1.73	1.34
p<0.01	**	**	**	**	**	**	**	**	**	**	**	**	**	**

[1]: For traits, see Table 1. SE: standard error; MS: mean square; **: significant at 1% level.

FSW (16.8 vs 11.8 g), DRW (27.3 vs 13.2 g) and DSW (4.1 vs 3.4 g). Inbred line Q66, however, presented the lowest values for FRL (20.8 vs 21.4 cm), FSL (19.8 vs 12.9 cm), FRW (10.5 vs 2.7 g), FSW (6.4 vs 1.2 g), DRW (4.9 vs 1.1 g), and DSW (0.7 vs 0.4 g). WFTMS and W64SP displayed the highest E%, while WF-9, the lowest. Some experimental lines, B34 and W187R revealed encouraging results for some traits, but not for others. Among all the tested genotypes, two inbred lines, WFTMS and Q66 appeared most divergent under both conditions, therefore, they were selected to develop breeding material for conducting genetic studies of drought-tolerance. On overall basis, estimates of root length, shoot length, fresh root weight and dry root weight under drought-stressed regime were greater than the non-stressed one.

Assessment of genetic variability

Various descriptive statistics regarding genetic variability are given in Table 3. The coefficient of variability (CV) was highest for DRW (55.45%) while lowest for FRL (17.76%) in drought-stressed conditions. However, under the non-stressed regime, DSW (49.06%) and E% (5.43%) revealed the highest and least CV values, respectively. The magnitudes of genotypic variances were lesser in comparison to phenotypic variances for the traits studied. The variance estimates under drought-stressed condition were higher than the respective variances under the non-stressed regime. Estimates of broad-sense herit-

ability were high (>60%) for all the investigated traits in both conditions except for E% in the non-stressed environment which was low (<60%). The genetic advance was low for E% and moderate for FRL under non-stressed conditions, while high (>20%) for all the other traits under both the environmental conditions.

Association studies among seedling traits

In non-stressed conditions, most of the seedling-traits exhibited positive and significant associations among each other except for DRW with FRL, FRW and FSW, and for DRW with DSW at genotypic and phenotypic levels (Table 4). Similarly in the drought-stressed regime, correlation coefficients recorded were positive and significant for most of the traits except for FRL with FSL, FSL with FRW and DSW, and for FSW with DRW (Table 5).

Drought tolerance studies at maturity stage

The selected inbred lines, WFTMS, a tolerant male parent (P_1), and Q66, a susceptible female parent (P_2), were used to develop six basic generations. The generation means for various traits indicated significant differences ($p < 0.01$) among parents (P_1 , P_2), their hybrids (F_1) and segregating (F_2 , BC_1F_1 , BC_2F_2) populations for the traits studied under both non-stressed and drought-stressed conditions (Table 6). Filial-generation one (F_1) means fell outside the range of both the parents

Table 3. Genetic parameters for various maize seedling-traits in 40 inbred lines under non-stressed and drought-stressed conditions.

Traits ^[1]		CV%	σ_g^2	GCV %	σ_p^2	PCV %	σ_e^2	ECV %	H ² %	GA %
E (%)	NS	5.43	0.04	4.01	0.07	5.43	0.03	3.65	54.28	5.16
	DS	18.44	0.26	14.51	0.42	18.44	0.16	11.38	62.09	20.08
FRL (cm)	NS	11.77	6.91	9.68	11.20	12.32	4.29	7.63	61.69	13.34
	DS	17.76	12.60	14.97	16.62	17.20	4.02	8.45	75.83	22.89
FSL (cm)	NS	14.74	15.97	13.76	19.28	15.12	3.31	6.26	82.86	21.98
	DS	19.41	13.54	16.54	18.04	19.10	4.51	9.54	75.03	25.15
FRW (g)	NS	41.55	56.03	41.08	62.28	43.31	6.25	13.72	89.96	68.38
	DS	46.00	4.99	37.59	6.15	41.71	1.15	18.08	81.23	59.46
FSW (g)	NS	24.59	5.17	22.12	6.44	24.67	1.26	10.93	80.38	34.81
	DS	53.71	6.53	54.71	7.29	57.81	0.76	18.68	89.56	90.86
DRW (g)	NS	47.03	34.02	45.71	36.61	47.42	2.59	12.62	92.92	77.33
	DS	55.45	13.90	57.05	16.15	61.51	2.26	22.99	86.04	53.55
DSW (g)	NS	49.06	0.65	40.30	0.86	46.54	0.22	23.27	75.00	61.24
	DS	50.44	0.54	55.33	0.67	61.49	0.13	26.82	81.04	65.96

[1]: For traits, see Table 1. CV: coefficient of variability; ECV: environmental coefficient of variation; GA: genetic advance; GCV: genotypic coefficient of variation; PCV: phenotypic coefficient of variation; σ_e^2 : environmental variance; σ_g^2 : genotypic variance; H²: heritability in broad-sense; h²: heritability in narrow-sense; σ_p^2 : phenotypic variance.

Table 4. Genotypic and phenotypic correlation coefficients among various maize seedling-traits under non-stressed conditions.

Traits ^[1]		FRL	FSL	FRW	FSW	DRW	DSW
E (%)	r _g	0.723*	0.560*	0.799*	0.585*	0.306*	0.876*
	r _p	0.619**	0.502**	0.636**	0.518**	0.186	0.686**
FRL	r _g		0.671*	0.640*	0.852*	0.153	0.748*
	r _p		0.586**	0.580**	0.783**	0.133	0.559**
FSL	r _g			0.494*	0.720*	0.458*	0.524*
	r _p			0.444**	0.693**	0.332**	0.433**
FRW	r _g				0.672*	0.084	0.878*
	r _p				0.640**	0.113	0.706**
FSW	r _g					-0.023	0.699*
	r _p					0.013	0.606**
DRW	r _g						0.169
	r _p						0.172

[1]: For traits, see Table 1. r_g: genotypic correlation; r_p: phenotypic correlation. *, **: significant at 5% and 1% levels, respectively.

Table 5. Genotypic and phenotypic correlation coefficients among various maize-seedling traits under drought-stressed conditions.

Traits ^[1]		FRL	FSL	FRW	FSW	DRW	DSW
E (%)	r _g	0.829*	0.342*	0.520*	0.352*	0.357*	0.337*
	r _p	0.683**	0.257*	0.425**	0.303**	0.265*	0.321**
FRL	r _g		0.079	0.494*	0.195*	0.407*	0.564*
	r _p		0.086	0.444**	0.154	0.304**	0.470**
FSL	r _g			-0.097	0.432*	0.376*	0.022
	r _p			-0.006	0.384**	0.270*	-0.026
FRW	r _g				0.331*	0.426*	0.694*
	r _p				0.223*	0.257*	0.513**
FSW	r _g					-0.011	0.260*
	r _p					0.021	0.170
DRW	r _g						0.595*
	r _p						0.431**

[1]: For traits, see Table 1. r_g: genotypic correlation; r_p: phenotypic correlation. *, **: significant at 5% and 1% levels, respectively.

Table 6. Generation means for various morphological traits of maize under non-stressed and drought-stressed conditions.

Traits ^[1]		Generations						p<0.01	LSD (0.05)
		P ₁	P ₂	F ₁	F ₂	BC ₁ F ₁	BC ₂ F ₂		
PH	N	149.33	148.68	149.92	131.17	143.20	141.26	**	0.78
	D	138.95	138.53	138.49	116.39	128.36	124.22	**	0.36
ELA	N	392.49	378.39	382.65	313.35	371.74	373.47	**	9.19
	D	283.88	260.71	289.20	202.33	304.13	290.95	**	20.37
CL	N	17.44	16.62	16.33	15.63	16.35	16.61	**	0.23
	D	14.97	14.23	13.47	12.83	12.93	12.85	**	0.33
CG	N	6.21	6.77	5.73	4.36	5.16	5.13	**	0.20
	D	5.33	5.07	4.43	4.34	5.22	5.41	**	0.13
GRPE	N	15.63	15.57	14.53	14.63	14.89	14.53	**	0.48
	D	11.97	11.70	12.10	12.98	11.59	12.75	**	0.25
GPER	N	39.03	37.23	36.30	34.82	37.35	36.41	**	0.44
	D	28.70	27.00	26.60	31.97	24.65	25.22	**	0.53
BPP	N	1082.3	1115.5	1032.1	1023.4	1107.0	1055.7	**	5.95
	D	646.07	630.27	653.55	591.16	602.13	632.97	**	13.20
HGW	N	32.20	30.13	29.07	26.13	26.95	25.47	**	0.49
	D	22.00	20.07	21.63	20.53	22.60	20.80	**	0.47
GYPP	N	78.03	74.56	72.30	73.17	69.80	65.93	**	0.70
	D	64.57	61.03	72.47	64.03	63.37	58.46	**	1.32

[1]: For traits, see Table 1. **: significant at 1% level.

for traits like ELA, GRPE, BPP and GYPP in drought-stressed conditions, and PH in the non-stressed regime, suggesting a transgressive segregation. Mean estimates of six basic generations for the investigated traits were higher in the non-stressed regime than in the respective drought-stressed conditions. Differences in mean values of F_1 , F_2 and backcrosses (BC_1F_1 and BC_2F_2) for all the traits were due to the parental contribution in a particular trait. These results pointed sufficient differences among the genetic material developed which led to perform generation mean analysis.

Estimates of genetic effects controlling inheritance pattern of various plants are given in Table 7. Dominance with epistatic additive-additive gene interaction was predominant in controlling PH under both the conditions, while GYPP, only under the drought-stressed regime. Epistatic additive-additive digenic effects controlled the inheritance of ELA in non-stressed conditions. The simply mean value best fitted to data of CL and GRPE under both the conditions, and of ELA and GPER in the non-stressed regime, while to data of BPP and HGW only under drought-stressed environments. Non-allelic additive-additive gene action was recorded for CG and HGW of this crossed material under the non-stressed regime. Duplicate dominance with additive-additive and additive-dominance interactions was crucial in controlling GPER under the drought-stressed regime. For BPP under the non-stressed conditions, we observed addi-

tive gene action with non-allelic dominance-dominance interaction.

Estimates of components of genetic variance and narrow sense heritability are given in Table 8. Under the drought-stressed conditions for plant traits such as PH, ELA, GRPE, GPER and HGW, additive [D], environmental [E], and interaction [F] components of genetic variance were important in contrast to only [D] and [E] component for CL, CG, BPP and GYPP. In non-stressed conditions, [D] and [E] variances predominated for traits like PH, ELA, CL, CG, GRPE, HGW and GYPP in comparison to three variance components [D, E, and F] for GPER and BPP. Narrow sense heritability under non-stressed conditions ranged 69% (GPER) to 92% (PH) in comparison to the range of 65% (PH) to 90% (CG, GYPP) under drought-stressed conditions. The estimates for CL, CG, HGW and GYPP were higher under drought-stressed than under non-stressed conditions. Estimates of heritability for infinity-generation (F_∞) were high in contrast to the F_2 population for all the traits under both non-stressed and drought-stressed environments.

Discussion

Drought is one of the leading abiotic plant stresses that affect plants at various levels of their organization (Yordanov *et al.*, 2000). Building tolerance against it,

Table 7. Genetic effects for various morphological traits of maize under non-stressed and drought-stressed conditions.

Trait ^[1]		Mean [m]	Additive [d]	Dominance [h]	Additive × Additive [i]	Additive × Dominance [j]	Dominance × Dominance [l]	Chi-square χ^2 (df)
PH	NS	114.58 ± 3.98		35.4 ± 4.27	34.54 ± 4.04			1.19(3)
	DS	93.41 ± 3.92		45.06 ± 4.16	45.01 ± 4.29			1.86(3)
ELA	NS	293.98 ± 43.03	6.87 ± 3.35	88.97 ± 44.05	91.62 ± 43.29			1.46(2)
	DS	283.07 ± 4.33						8.29(5)
CL	NS	16.54 ± 0.3						1.86(5)
	DS	13.83 ± 0.31						3.65(5)
CG	NS	5.45 ± 0.27			0.91 ± 0.41			3.88(4)
	DS	4.62 ± 0.08	0.41 ± 0.09					3.24(4)
GRPE	NS	15.29 ± 0.32						2.10(5)
	DS	11.98 ± 0.38						0.85(5)
GPER	NS	37.75 ± 0.55						5.00(5)
	DS	43.54 ± 5.05		-29.38 ± 8.45	-15.66 ± 5.07	-6.79 ± 2.43	12.44 ± 3.82	1.54(1)
BPP	NS	1094.63 ± 9.01	20.34 ± 9.19				-60.81 ± 18.6	1.74(3)
	DS	639.18 ± 15.3						1.06(5)
HGW	NS	27.42 ± 1.31			3.51 ± 1.75			3.45(4)
	DS	21.44 ± 0.34						3.87(5)
GYPP	NS	75.82 ± 0.91		-14.59 ± 4.78			11.04 ± 4.69	3.63(3)
	DS	46.31 ± 8.15		26.05 ± 8.47	17.44 ± 8.24			2.99(3)

[1]: For traits, see Table 1. df: degrees of freedom; χ^2 : chi-square.

Table 8. Genetic variance components for various morphological traits of maize under non-stressed and drought-stressed conditions.

Trait ^[1]		Additive [D]	Environment [E]	Interaction [F]	χ^2 (df)	h ² (%)	
						F ₂	F _∞
PH	NS	15.41 ± 1.44	0.66 ± 0.1		4.12(4)	92	96
	DS	8.3 ± 1.47	2.21 ± 0.32	2.08 ± 0.95	1.92(3)	65	79
ELA	NS	1 206.5 ± 152.5	58.48 ± 3.35		5.13(4)	91	95
	DS	1 110.8 ± 195.8	68.68 ± 10.22	-401.09 ± 129.79	3.48(3)	89	94
CL	NS	3.16 ± 0.38	0.38 ± 0.06		5.52(4)	81	89
	DS	5.45 ± 0.59	0.46 ± 0.07		8.25(4)	86	92
CG	NS	1.32 ± 0.16	0.15 ± 0.02		4.39(4)	81	90
	DS	1.44 ± 0.15	0.084 ± 0.01		5.62(4)	90	94
GRPE	NS	6.54 ± 0.67	0.44 ± 0.07		0.08(4)	88	94
	DS	4.31 ± 0.58	0.65 ± 0.09	1.51 ± 0.35	3.89(3)	77	87
GPER	NS	9.91 ± 1.6	2.21 ± 0.32	-4.08 ± 0.95	1.70(3)	69	82
	DS	4.53 ± 0.75	1.05 ± 0.15	1.6 ± 0.46	0.19(3)	68	81
BPP	NS	11 235.76 ± 1 266.6	632.92 ± 84.71	-1 892.24 ± 586.36	1.38(3)	90	95
	DS	10 450.8 ± 1 132.5	900.57 ± 133.22		1.08(4)	85	92
HGW	NS	19.13 ± 2.4	2.55 ± 0.37		1.08(4)	79	88
	DS	7.36 ± 0.78	0.48 ± 0.07	-2.61 ± 0.46	0.34(3)	88	94
GYPP	NS	30.45 ± 4.19	2.04 ± 0.29		3.68(4)	88	94
	DS	38.87 ± 5.22	2.1 ± 0.22		4.87(4)	90	95

^[1]: For traits, see Table 1. df: degrees of freedom; F₂: filial-generation two; F_∞: filial-infinity generation; h²: heritability in narrow-sense; χ^2 : chi-square.

therefore, requires genetic improvement of crop plants without any cost in yield potential. Plants cope the dry soils by employing different mechanisms ranging avoidance to tolerance. One way of managing adverse effects of drought is the development of deep-rooted genotypes by altering the carbon distribution models (Lopes & Reynolds, 2011). Longer roots displayed clear benefit in soils with deep water availability (Sponchiado *et al.*, 1989). Previously, research efforts remain focused more on improving shoot traits linked with photosynthesis and stay-green characteristics than on the root traits (Lopes *et al.*, 2011).

Drought affected maize plant right from seedling to grain filling stages (Haq *et al.*, 2015). At seedling stage, it reduced root and shoot growth in maize (Thomas & Howarth, 2000). It increased root length and root weight (Rao & Singh, 2004) while decreased shoot length and its fresh weight (Thakur & Rai, 1984), and root and shoot dry weights in maize (Matsuura *et al.*, 1996; Ali *et al.*, 2011). Drought tolerant cultivars had higher fresh and dry shoot weights in comparison to susceptible ones (Ashraf, 1989). Water-stress, not only dwindled the maize plant height but also decreased ear leaf area causing reduction in ear length and grain yield (El-Hifny *et al.*, 2003; Ross *et al.*, 2006; Moosavi, 2012). Decrease in grains per ear row and 100-grain weight was also noticed under drought conditions (Saeed *et al.*, 1997; Khayatnezhad *et al.*, 2011). The

causes of reduction in grains per ear may either be embryo abortion or delayed silk appearance under drought-stressed conditions (Wasson *et al.*, 2000).

In the present study, assessment of various seedling traits for drought tolerance revealed significant variability among the 40 maize inbred lines. The estimates pertaining to different traits exhibited significant reduction under the drought-stressed regime in contrast to non-stressed conditions. This is in agreement to the observations of Ali *et al.* (2013). The selection of drought-tolerant (WFTMS) and susceptible (Q66) genotypes was done on the basis of FRL and other seedling traits under both the environments which were further used for the genetic studies of various morphological traits. The choice of the contrasting genotypes was made by considering actual performance under both the environments. The method of relative performance or percentage increase or decrease for each trait was not employed due to its ineffectiveness in selecting the potential genotypes. The reason is that the actual performance of some the genotypes were far better under both the conditions than those favored by percentage increase/decrease method. The study of genetic components for seedling-traits revealed higher values for most traits in drought-stressed than non-stressed conditions, implying that choice of criterion is vital for pyramiding drought-tolerance in maize. Components of genetic variability and association stud-

ies suggested that traits such as FRL, FRW and DRW could be considered for developing drought-tolerant maize genotypes while for non-stressed conditions, traits like FSL, FRL, FRW and DRW might be considered.

Dissection of genetic variation into different components using biometric methods is important for a plant breeder to exploit the potential genetic resources through plant selections and hybridization schemes. The procedure of generation mean and variance analyses had extensively been used for drought-tolerance studies in cotton (Khan *et al.*, 2014), wheat (Munir *et al.*, 2007) and maize (Ahsan *et al.*, 2013). Generation mean analysis for PH revealed involvement of dominance genetic effects in its inheritance under both the environments. Yadav *et al.* (2003) also reported such gene action for PH. However, positive [i] complicated the situation, therefore, requires further progeny testing under both conditions. Significance of only residual [m] effects for CL and GRPE under both environments while for ELA, BPP and HGW in drought-stressed conditions and for GPER in non-stressed environments suggested the potential role of environment in the inheritance of these traits. These findings are in agreement to the observations of Bernardo *et al.* (1992), Blum *et al.* (2001), Aslam *et al.* (2006), Jabeen *et al.* (2008) and Taheri *et al.* (2011). Additive-dominance along with epistatic (additive-additive) interaction effects were recorded for ELA under non-stressed environments. Iqbal *et al.* (2012) suggested postponement of plant selections till the later generations for plant traits with such type of gene action. For CG and HGW, epistatic additive-additive interaction was predominant under the non-stressed conditions in comparison to additive genetic effects under the drought-stressed environments. Similar results were reported by Chen *et al.* (1996), Singh *et al.* (2000), Tripathy *et al.* (2000), Malik *et al.* (2004) and Aslam *et al.* (2006). Positive values of genetic effects and epistatic interactions indicate the possibility to fix cob girth and 100-grain weight in the later generations. Dominance and epistatic [ij] gene action for GPER under drought-stressed conditions suggested postponement of plant selections to later generations. Tabassum *et al.* (2007) and Jabeen *et al.* (2008) also made similar suggestions. Negative [dhi] values for grain per ear row under drought-stressed conditions revealed that conducting plant selections might be ineffective for this trait. Positive l suggests that dominance-dominance interaction is responsible for the increase in grains per ear row under drought-stressed conditions. For BPP, additive gene action with dominance-dominance interaction was found crucial under the non-stressed conditions. These results are in agreement to the observations of Taheri

et al. (2011). Positive d indicated increase while negative l suggested decrease in plant biomass, implying that the model is complex and further progeny testing is required for the improvement of this trait. Involvement of duplicate gene action in the inheritance of GYPP under the non-stressed environments offered a complex situation and suggested delaying the plant selections to later generations. These findings are similar to the one reported by Afarinesh *et al.* (2005) and Kanagarasu *et al.* (2010). Iqbal *et al.* (2015) suggested usefulness of crossing among the desirable segregants in the segregating populations for those traits where early selection cannot be exercised.

Dissection of total variance into D (additive), H (dominance), E (environmental), and F (interaction) components had been used previously for genetic studies (Haq *et al.*, 2015; Iqbal *et al.*, 2015). Contribution of additive (D) variance in contrast to other components was much higher in all the investigated traits. However, the interaction (F) variance for traits such as PH, ELA, GRPE, GPER, and HGW under drought-stressed conditions complicated their inheritance pattern. Larger and significant estimates of additive (D) variance for CL, CG, BPP and GYPP under drought and PH, ELA, CL, CG, GRPE, HGW and GYPP under the non-stressed environments indicated involvement of positive and negative alleles from the two parents in the developed genetic material (Rahman & Malik, 2008; Khan *et al.*, 2014). Higher estimates of narrow-sense heritability under both non-stressed and drought-stressed regimes are encouraging for maize breeders implying that plant selections for drought-tolerant recombinants could be conducted in the segregating progeny of this particular crossed material.

We may conclude that root traits like length, fresh and dry weights can be vital for effective screening of maize genotypes at seedling-stage drought-stress. Further, hybridization and adoption of recombinant breeding strategy could be the way forward for developing drought-tolerant genotypes.

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