Genetic analysis of water-deficit response traits in maize

M. Ahmad[1], M. Saleem[1], M. Ahsan[1] and A. Ahmad[2]

[1]Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan
[2]Department of Agronomy, University of Agriculture, Faisalabad, Pakistan

Corresponding author: M. Ahmad
E-mail: mahmadpbg@gmail.com

Genet. Mol. Res. 15 (1): gmr.15017459
Received August 17, 2015
Accepted November 13, 2015
Published March 28, 2016
DOI http://dx.doi.org/10.4238/gmr.15017459

ABSTRACT. A set of sixty inbred lines of maize (*Zea mays* L.) were screened in the greenhouse at the seedling stage under both normal and water-deficit conditions. Six water deficit-tolerant inbred lines were selected based on root to shoot ratios. These selected lines were crossed in a diallel pattern. The parental, F_1, and reciprocal cross plants were planted in a field under both normal and water-deficit conditions. Normal irrigation was applied to the control set, while the water-deficit set received 50% of normal irrigation levels. Analyses of variance of various morpho-physiological parameters identified significant differences among the selected lines under both conditions, indicating the presence of significant genetic variability. Variance components for general combining ability (GCA), specific combining ability (SCA), and reciprocal effects for all the parameters were estimated to determine the relative importance of additive and non-additive or dominance type of gene action. Variance components for GCA were larger than for SCA indicating the preponderance of additive types of gene action for all the traits under study. Hybrids developed from inbred lines W-10 and W-64SP proved to have the best grain yield under normal and water-deficit conditions. Under water-deficit conditions, the best performing cross was B-34 x W-10. Hence, these inbred lines and the hybrids might be of value in future breeding programs.

Key words: Maize; Genetic study; General combining ability; Specific combining ability; Water-deficit maize

INTRODUCTION

Maize (*Zea mays* L.) is an important cereal plant and is one of the most productive and versatile crop species worldwide. The species has a large range of genetic and phenotypic traits that allow it to be cultivated under a wide variety of soil and ecological conditions. Maize is currently grown in conditions ranging from tropical to temperate regions, from 50° North latitude to 40° South and from sea level to an altitude of 3300 m. It is mainly grown for human consumption, but is also important for animal/poultry feed and fodder both as green forage and silage. Maize is a carbohydrate-rich food and its kernel has been likened to a “starch factory”. It is used as food in both fresh and processed forms. The kernel provides raw material for various industrial applications such as fermentation, textiles, corn refineries, foundries, and food industries. In Pakistan, maize is the third most important cereal crop after wheat and rice; it is cultivated on an area of over 1 million hectares and has an annual production of approximately 4.6 million tons and an average yield of about 4268 kg/ha (Anonymous, 2012-2013). Globally, maize is grown on 175.93 million ha with a total grain production of 862.85 million metric tons (USDA-FAS 2012-2013). The major corn-producing areas are the United States, China, the European Union, Brazil, Mexico, and India (USDA/FAS /GRAIN 2012-2013).

Water deficiency adversely affects the growth of maize plants, causing poor crop stand, low plant density, stunted growth, wilting, top firing, tassel blast, silk delay, poor seed set, and barrenness, which results in reduced grain yield. The plants exhibit a variety of physiological, morphological, and biological adaptations in response to water deficits. Some traits contribute to enhanced tolerance to stressful growing conditions, for example, a short anthesis-silking interval (ASI) is a good indicator of general tolerance to reduced photosynthesis at flowering induced by abiotic stresses. The low heritability of drought tolerance and the lack of an effective selection strategy limit the development of tolerant cultivars to environmental stresses. Maize has a range of morpho-physiological seedling traits that could potentially be utilized for screening genotypes against moisture deficit conditions (Taiz and Zeiger, 2006). Since water availability has a key role in crop production, there is considerable interest in breeding varieties that are tolerant of water deficits (Edmeades, 2008). Water stress affects plant height, leaf temperature, days taken to tasseling, days taken to silking, ASI, number of kernels per ear, 100 grain weight, grain yield per plant, number of kernels per row, ear height, relative leaf water content, and number of ears per plant (Tabassum et al., 2005; Akbar et al., 2008; Chohan, 2012; Wattoo, 2013).

An essential approach for the development of water deficit-tolerant genotypes is to select locally adapted germplasms with sufficient genetic variability for high yield potential and drought adaptive characters. There is good evidence that hybrids maintain their advantages over open-pollinated varieties in both stress and non-stress environments. Water deficit tolerance involves a complex polygenic mechanism associated with epistasis. General (GCA) and specific combining ability (SCA) provide estimates for the contributions of additive and non-additive components respectively to this mechanism. An improved understanding of the gene interactions that influence economically important attributes would be helpful to maize breeders and would allow the screening of fewer generations. The present research was initiated to explore the genetic mechanisms controlling various traits under water-deficit conditions.

MATERIAL AND METHODS

Sixty inbred lines of maize of diverse origins were obtained from national and international research organizations. After an initial screen based on root to shoot ratios, six inbred lines were selected. The selected inbred lines were planted in the research area (field) at the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad. All possible crosses among the selected inbred lines were made in a diallel fashion during Spring 2012. To avoid foreign contamination during crossing, male and female parts of plants were bagged with kraft paper and butter paper bags, respectively. The female parents were hand emasculated and pollinated to produce a maximum number of seeds. The six parental lines, 15 F_1 progeny, and the progeny of reciprocal crosses were planted in the field during Autumn 2012 under both normal and water-deficit conditions using the randomized complete block design. The experimental unit consisted of two 12.5-m rows with 75-cm inter-row distance and 23-cm inter-plant distance. The recommended agronomic, cultivation and plant protection measures were applied equally to both experimental groups, with the exception of irrigation water. The normal level of irrigation was applied to one group of plants, while the other received half this amount (water-deficit group). Ten equally competitive plants were selected from each treatment and used for analyses of morpho-physiological traits.

Leaf temperature (°C)

Leaf temperatures were measured in leaves fully exposed to sunlight between 12:00 and 15:30 h. The measurements were made from three leaves of each plant with an infrared thermometer (RAYPRM 30 CFRJ, RAYTEK, USA) and averaged for statistical analysis.

Relative water contents

Relative water contents were determined using the method described by Garcia-Mata and Lamattina (2001). Under water-deficit conditions, leaf samples were detached from plants and placed in polythene bags. Fresh leaf weights were recorded using an electronic balance in the laboratory. The leaf samples were then kept in water overnight and turgid leaf weights were recorded. Then, the leaves were oven dried at 70°C for 24 h and dry leaf weights were recorded. Relative water content (RWC) was determined as follows:

$$\text{RWC\%} = [\text{fresh weight - dry weight}] / [\text{turgid leaf weight - dry leaf weight}] \times 100$$

Plant height

The heights of mature plants were measured as the distance from ground level to the apex of the tassel using a measuring steel rod. The average was used for the statistical analysis.

Anthesis-silking interval

ASI is a key indicator of the response of maize plants to water deficiency during flowering.

ASI is defined as the time between pollen shedding and silk emergence. ASI was determined as time (days) to 50% silking - time (days) to 50% anthesis.

Grain yield per plant

Grain yield per plant was determined by weighing the shelled grains from the plants after drying to a constant moisture level (15%); the average was used for statistical analysis.

Statistical and biometrical analysis

Data pertaining to various physiological and agronomic traits were statistically analyzed (Steel et al., 1987) to identify significant differences among the genotypes. Combining ability was estimated by diallel analysis using Griffing's (1956) method I, model I. Genetic variability in the germplasm was partitioned into GCA, SCA, reciprocal effects, and the error mean squares for these parameters. Sums of squares for these components were calculated.

RESULTS AND DISCUSSION

Significant mean squares ($P \leq 0.05$) were found for the parental inbred lines and diallel cross-combinations for various traits under both normal and water-deficit conditions (Table 1).

Table 1. Mean squares due to general (GCA) and specific combining ability (SCA), and reciprocal effects in six maize inbred lines in a diallel cross under normal and water-deficit conditions.

Trait	GCA		SCA		Reciprocal		Error	
	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit
Plant height	286.31**	290.52**	8.74**	5.43**	10.71**	17.82**	1.552	4.416
Leaf temperature	6.96**	4.83**	0.856**	0.316**	0.690**	0.962**	0.177	0.168
Anthesis-silking interval	0.929**	6.032**	3.45**	0.708**	0.707**	1.166**	0.226	0.387
Grain yield per plant	351.80**	451.13**	18.578**	6.03**	50.807**	71.898**	2.689	7.841
Relative leaf water content	0.009**	0.0119**	0.0008**	0.0005**	0.02**	0.001**	0.0003	2.963

Analyses of variance of the data on the studied traits revealed highly significant mean squares due to GCA, SCA, and reciprocal effects under normal and water deficit conditions, indicating the importance of both additive and non-additive genetic effects. Relative GCA, SCA, and reciprocal effects were also calculated for all characters using method I, model I of Griffing (1956), and are presented in Table 1.

Estimates of variance components for GCA, SCA, and reciprocal effects for all the studied traits under normal and water-deficit regimes are shown in Table 2. These components were computed in order to obtain an estimate of the relative importance of additive and non-additive genetic effects and of dominance gene action. The estimation of components of variation indicated larger values of GCA variance (g) compared to SCA variance (s), indicating a preponderance of additive genetic effects for all the traits except for the number of kernels per ear. Under water-deficit conditions, leaf temperatures showed larger values for SCA variance (s) than GCA variance (g), indicating a higher level of non-additive genetic effects. The presence of significant mean squares due to reciprocal effects indicated the presence of cytoplasmic effects in the experimental material.

Table 2. Estimates of variance components for general (GCA) and specific combining ability (SCA), and reciprocal effects under normal and water-deficit conditions.

Trait	σ^2 GCA		σ^2 SCA		σ^2 Reciprocal		GCA/SCA ratio		σ^2 A		σ^2 D	
	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit	Normal	Water deficit
Plant height	120.56	23.76	41.746	6.58	-4.105	6.7	2.888	3.61	241.13	47.52	41.746	6.58
Leaf temperature	0.51	0.377	0.394	0.213	0.256	0.3969	1.29	1.76	1.02	0.7545	0.394	0.231
Anthesis-silking interval	0.074	0.361	0.115	0.186	0.24	0.3897	0.643	1.94	0.148	0.7222	0.115	0.1867
Grain yield per plant	27.811	37.08	9.225	11.04	24.05	32.029	3.014	3.36	55.62	72.17	9.225	11.04
Relative leaf water content	0.0007	0.0009	0.0003	0.001	0.0009	0.0008	2.333	0.9	0.001	0.001	0.0003	0.001

σ^2 A = additive variance; σ^2 D = dominance variance.

Analysis of plant height variation

Analysis of plant height variations found highly significant mean squares due to GCA and SCA under normal and water-deficit conditions, showing the importance of additive and non-additive genetic effects (Table 1). Estimates of the components of variation showed greater GCA variance (σ^2g) than SCA variance (σ^2s) under both normal and water-deficit regimes, indicating a preponderance of additive genetic effects for plant height (Table 2). The results are in agreement with those of Malik et al. (2004), Rezaei et al. (2005), and Hussain (2009). Plant height has previously been reported to be under the control of additive and non-additive gene effects (Bello and Olaoye, 2009; Chohan, 2012; Wattoo, 2013).

The inbred line Q-67 had a GCA of 9.463, whereas inbred line W-64SP had the highest (-3.954) negative GCA effects and was the poorest general combiner. The cross Q-67 x W-64SP showed the highest SCA effects (3.815) followed by the crosses Q-67 x B-34 and Q-67 x W-10 with values of 2.565 and 2.009, respectively. The cross 53P4 x W-64SP had a poor SCA effect with a high negative value of -1.991. The maximum reciprocal effect was displayed by the cross 53P4 x Q-67 (5.667) followed by 53P4 x W-10 (3.167) and the maximum negative effect (-2.5) was found in the cross W-64SP x N-18 (Table 3).

Table 3. Estimates of general combining ability (diagonal, red font), specific combining ability (above diagonal), and reciprocal effects (below diagonal) for plant height.

	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.
Inbred lines	Q-67		N-18		W-10		B-34		53P4		W-64SP	
Q-67	9.463	7.004	-0.71	-2.054	2.009	1.413	2.565	0.852	-1.407	-1.126	3.815	1.682
N-18	-1.833	5.917	0.074	5.206	-0.269	1.96	-1.88	1.116	1.981	-0.995	0.037	3.013
W-10	1.833	2.75	-1.17	3.7	-0.315	-3.594	-0.491	-0.234	-0.796	-0.012	0.259	-1.754
B-34	2.5	5.7	1	3.6	-0.667	-0.55	-2.87	-0.682	0.426	0.16	0.315	-0.731
53P4	5.667	3.433	1.667	2.233	3.167	1.083	0.167	0.333	-2.398	-4.071	-1.991	-0.176
W-64SP	1.333	1.083	-2.5	-2.117	2.333	-0.217	1.833	0.85	-1.667	-2.683	-3.954	-3.863

W. Def. = water-deficit conditions.

The three parental inbred lines displayed positive GCA effects under water-deficit conditions (Table 3). A higher GCA effect (7.004) was found for genotype Q-67, which was a good general combiner for plant height, followed by N-18 (5.206). The lowest GCA effect (-4.071) was displayed by 53P4, which was the poorest combiner.

Positive SCA effects were shown by 7 cross-combinations, including N-18 x W-64SP (3.013), N-18 x W-10 (1.960), and Q-67 x W-64SP (1.682). The cross Q-67 x N-18 showed the highest negative (-2.054) SCA effect, closely followed by W-10 x W-64SP (-1.754). Eleven cross-combinations exhibited positive values for reciprocal effects and four showed negative reciprocal effects under water-deficit conditions. The maximum positive reciprocal effects were recorded from the reciprocal cross N-18 x Q-67 (5.917), followed by the reciprocal cross B-34 x Q-67 (5.700); a poor reciprocal effect (-2.683) was shown by the cross W-64SP x 53P4.

Analysis of leaf temperature variations

Analyses of leaf temperatures found significant mean squares for GCA, SCA, and reciprocal effects under normal and water-deficit regimes (Table 1). Estimation of the components of variation showed that a greater proportion was due to GCA variance (σ^2 g) than SCA variance (σ^2 s) expressing additive genetic effects for leaf temperature (Table 2). These results are consistent with those of Chohan (2012) and Wattoo (2013) who reported additive genetic effects for this trait. However, they differ from those of Hussain (2009) who suggested greater SCA variance than GCA variance and indicated the importance of non-additive effects for leaf temperature.

Under normal water conditions, the parental genotypes N-18 and W-10 had the highest GCA: 1.205 for N-18 and 0.607 for W-10 (Table 4). The highest negative GCA (-0.745) was present in the genotype W-64SP. Nine crosses had positive SCA effects. The most useful specific combinations were W-10 x W-64SP (1.354) and N-18 x 53P4 (0.940). The cross 53P4 x W-64SP had the maximum negative GCA effect (-0.944). Ten crosses exhibited positive reciprocal effects while five crosses had negative effects. Cross W-64SP x N-18 had the highest positive reciprocal effect (1.133), followed by the crosses 53P4 x Q-67 (0.983) and W-64SP x 53P4 (0.833). The highest negative reciprocal effects under normal water conditions were found in the crosses B-34 x Q-67 (-0.700) and 53P4 x N-18 (-0.400).

Under water-deficit conditions, two parental lines, W-10 (0.978) and N-18 (0.531), had positive GCA effects (Table 4). W-64SP had the highest negative GCA effect (-0.700) and was the poorest general combiner. Seven cross-combinations had positive SCA effects. The most useful specific combinations were W-64SP x W-10 (0.725) followed by N-18 x 53P4 (0.378) and 53P4 x Q-67 (0.317), whereas W-64SP x 53P4 had the highest negative SCA effects (-0.658) for leaf temperature. Ten crosses had positive and five crosses had negative reciprocal effects for this trait under water-deficit conditions. The highest positive reciprocal effect were found in the cross-combinations 53P4 x W-64SP (1.967) and B-34 x 53P4 (1.067); the highest negative effect was present in N-18 x B-34 (-0.783).

Table 4. Estimates of general combining ability (diagonal, red font), specific combining ability (above diagonal), and reciprocal effects (below diagonal) for leaf temperature.

	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.
Inbred lines	Q-67		N-18		W-10		B-34		53P4		W-64SP	
Q-67	-0.515	-0.408	-0.607	-0.286	-0.627	-0.500	0.087	0.106	0.609	0.317	0.376	0.061
N-18	0.783	0.183	1.205	0.531	-0.596	-0.122	-0.199	-0.183	0.940	0.378	0.106	0.156
W-10	0.033	0.417	0.550	0.300	0.607	0.978	0.165	-0.381	0.120	-0.419	1.354	0.725
B-34	-0.700	-0.133	-0.067	-0.783	-0.200	-0.433	-0.506	-0.344	-0.582	0.286	0.084	-0.036
53P4	0.983	0.467	-0.400	-0.067	0.450	-0.183	0.433	1.067	-0.045	-0.056	-0.944	-0.658
W-64SP	0.217	0.733	1.133	0.267	-0.150	0.117	0.400	0.467	0.833	1.967	-0.745	-0.700

W. Def. = water-deficit conditions.

Analysis of anthesis-silking interval variation

Under normal water conditions, significant mean squares were found for GCA and SCA effects for ASI, showing the importance of both additive and non-additive genetic effects (Table 1). GCA variance (σ^2 g) was larger than SCA (σ^2 s) showing the predominance of additive genetic effects (Table 2). These results are consistent with those of Hussain (2009), Chohan (2012), and Wattoo (2013) who demonstrated that this trait was controlled by additive gene action.

Three parental lines had positive GCA effects while the remainder displayed negative GCA effects under normal water conditions (Table 5). The parental line N-18 was the best general combiner with a positive value of 0.278, while parental line W-64SP had the lowest GCA effect of -0.444. Nine crosses exhibited positive SCA effects, the six showed negative effects. Cross W-64SP x B-34 displayed the highest SCA effect (0.167) and 53P4 x B-34 had the lowest (-0.194). In the reciprocal crosses, 13 had positive and 2 had negative SCA effects. The highest reciprocal effect (1.667) was present in W-10 x B-34, while the lowest (-0.333) was found in Q-67 x 53P4.

Table 5. Estimates of general combining ability (diagonal, red font), specific combining ability (above diagonal), and reciprocal effects (below diagonal) for anthesis-silking interval.

	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.
Inbred lines	Q-67		N-18		W-10		B-34		53P4		W-64SP	
Q-67	-0.194	-0.315	0.083	-0.852	-0.139	-0.352	0.083	0.87	-0.056	0.481	-0.028	0.12
N-18	0.5	0	0.278	-0.731	-0.111	-0.102	0.111	0.954	0.139	0.565	0	-0.13
W-10	0.333	0.333	-0.17	-0.5	0	-0.565	0.056	0.12	0.083	0.231	0.111	-0.46
B-34	0.667	1.667	0.5	-0.167	1.167	0.5	0.111	0.38	-0.194	-1.046	0.167	-0.24
53P4	-0.33	1.667	0.667	1	0.333	-0.833	0.167	-0.167	0.25	0.269	-0.139	0.204
W-64SP	1	1	0.5	0	0.333	0.833	0.833	0.667	0.333	0.333	-0.444	0.963

W. Def. = water-deficit conditions.

Under water-deficit conditions, both GCA and SCA showed significant mean squares suggesting the presence of both additive and non-additive genetic effects. GCA variance (σ^2 g) was greater than SCA variance (σ^2 s), indicating the presence of additive genetic effects. Under water-deficit conditions, half of the parental lines had positive GCA effects, the other half had negative effects. Parental genotype W-64SP was considered the best combiner on account of the highest positive value (0.963), whereas N-18 was the poorest combiner with a negative value of -0.731. Eight of 15 crosses showed positive SCA effects while 7 displayed a negative SCA effect. Cross B-34 x N-18 had the highest positive SCA effect (0.954), while 53P4 x B-34 had the lowest (-1.046). Eleven crosses showed positive reciprocal effects and four crosses had negative reciprocal effects. The highest positive reciprocal effect was found in Q-67 x B-34 (1.667), while the lowest negative reciprocal effect (-0.833) was present in cross W-10 x W-64SP (Table 5).

Analysis of grain yield per plant variation

Under normal water conditions, GCA and SCA showed significant mean squares indicating the involvement of additive and non-additive genetic effects (Table 1).

Estimation of the components of variation (Table 2) showed that GCA variance (σ^2 g) was greater than SCA variance (σ^2 s) indicating the presence of additive genetic effects, as has been reported by Bello and Olaoye (2009), Chohan (2012), and Wattoo (2013). Three parental genotypes namely 53P4 (6.544), W-10 (3.797), and B-34 (3.322) were good GCA combiners due to their large positive GCA effects, while three others namely W-64SP (-6.342), N-18 (-6.033), and Q-67 (-1.289) were considered to be poor combiners on account of their negative GCA effects. Eight cross-combinations displayed positive SCA effects and seven had negative SCA effects. Cross W-64SP x W-10 had the highest SCA effect (5.794) while W-64SP x 53P4 showed lowest negative value (-3.469). In reciprocal crosses, ten combinations had positive effects and five showed negative reciprocal effects for grain yield per plant under normal water conditions. Among these combinations, the maximum positive value for reciprocal effects (10.483) was shown by W-10 x 53P4, while Q-67 x W-10 displayed the minimum value (-7.417).

Under water-deficit conditions, GCA and SCA displayed highly significant mean squares (Table 1); the former was larger (Table 2) indicating additive genetic effects (σ^2 s). Two of the parental genotypes had positive GCA effects, while the other four showed negative effects. Parental genotype W-10 had the largest positive value (11.575) and was considered the most useful general combiner; N-18 had the largest negative GCA effect (-5.514) and was considered the poorest general combiner (Table 6). Positive SCA effects were present in seven crosses. The cross B-34 x N-18 had the largest positive SCA (3.292), while 53P4 x N-18 had the largest negative effect (-2.519) and was considered the poorest specific combiner for grain yield per plant under water-deficit conditions (Table 6).

Table 6. Estimates of general combining ability (diagonal, red font), specific combining ability (above diagonal), and reciprocal effects (below diagonal) for grain yield per plant.

	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.
Inbred lines	Q-67		N-18		W-10		B-34		53P4		W-64SP	
Q-67	-1.289	-2.186	-0.944	0.753	-1.758	-0.003	-1.917	-1.769	2.844	1.886	0.897	-0.292
N-18	-5.933	-4.667	-6.033	-5.514	1.903	2.325	3.661	3.292	3.639	-2.519	-3.225	0.736
W-10	-7.417	-7.667	9.067	9.667	3.797	11.575	-2.419	-0.947	-2.625	0.692	5.794	0.031
B-34	5.017	1.000	-0.250	0.267	-0.300	-13.750	3.322	1.342	1.067	-0.042	1.919	-0.569
53P4	0.967	0.067	1.583	-2.000	10.483	7.033	3.467	-1.333	6.544	-3.914	-3.469	-0.231
W-64SP	-1.433	0.500	0.633	1.533	5.017	-10.083	0.300	-3.917	5.500	-0.500	-6.342	-1.303

W. Def. = water-deficit conditions.

Analysis of relative water content variation

Analysis of relative water contents of leaves identified significant mean squares for GCA and SCA effects under normal conditions, showing that this trait was under the control of additive and non-additive genetic effects (Table 1).

Estimation of components of variation revealed greater GCA (σ^2 g) than SCA variance (σ^2 s) under normal conditions indicating a preponderance of additive effects (Table 2). Chohan (2012) and Wattoo (2013) similarly reported additive genetic effects for relative water content. Three parental genotypes had positive GCA effects, while the other three showed negative effects (Table 7). The genotype N-18 had the highest GCA effect (0.040) and was considered the most useful general combiner; parental line B-34 had the lowest GCA effect (-0.031) and was considered the poorest general combiner. Seven crosses showed positive SCA effects while the remaining eight crosses exhibited negative SCA effects. Cross B-34 x N-18 was the best specific combiner (0.044), while cross 53P4 x B-34 was the poorest (-0.032). Ten reciprocal crosses had positive effects and 5 had negative effects. The highest reciprocal effect (0.040) was present in the cross 53P4 x W-64SP, while the lowest (-0.108) was present in N-18 x 53P4.

Table 7. Estimates of general combining ability (diagonal, red font), specific combining ability (above diagonal), and reciprocal effects (below diagonal) for relative water contents.

	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.	Normal	W. Def.
Inbred lines	Q-67		N-18		W-10		B-34		53P4		W-64SP	
Q-67	-1.289	-2.186	-0.944	0.753	-1.758	-0.003	-1.917	-1.769	2.844	1.886	0.897	-0.292
N-18	-5.933	-4.667	-6.033	-5.514	1.903	2.325	3.661	3.292	3.639	-2.519	-3.225	0.736
W-10	-7.417	-7.667	9.067	9.667	3.797	11.575	-2.419	-0.947	-2.625	0.692	5.794	0.031
B-34	5.017	1.000	-0.250	0.267	-0.300	-13.750	3.322	1.342	1.067	-0.042	1.919	-0.569
53P4	0.967	0.067	1.583	-2.000	10.483	7.033	3.467	-1.333	6.544	-3.914	-3.469	-0.231
W-64SP	-1.433	0.500	0.633	1.533	5.017	-10.083	0.300	-3.917	5.500	-0.500	-6.342	-1.303

W. Def. = water-deficit conditions.

Analysis of relative leaf water contents showed significant mean squares for GCA effects under water-deficit conditions, indicating the presence of additive genetic effects (Table 1). The magnitude of the GCA effects was greater than that for SCA revealing the predominance of additive effects.

GCA variance (σ^2 g) was greater than SCA variance (σ^2 s) indicating additive genetic effects (Table 2). Three parental genotypes had positive GCA effects and three had negative effects (Table 7). The parental line N-18 showed the highest positive GCA effect (0.051) and was considered a good general combiner, while line B-34 had the lowest GCA effect (-0.031) was considered a poor general combiner. Seven crosses showed positive SCA effects and eight displayed negative effects. The maximum SCA effect (0.019) was found in cross B-34 x W-10 and the minimum SCA effect (-0.019) was present in 53P4 x B-34. The highest reciprocal effects (0.028) were displayed in the cross Q-67 x 53P4 and the lowest (0.085) in the cross N-18 x 53P4.

CONCLUSION

Under both normal and water-deficit conditions, our analyses of trait variation identified highly significant mean squares revealing the presence of considerable genetic variability in the gene pool. On the basis of mean grain yield performance under normal conditions, the best combinations were B-34 x W-10, 53P4 x W-10, W-10 x 53P4 and its reciprocal, and B-34 x 53P4. Under water stress conditions, the best performing crosses were B-34 x W-10, 53P4 x W-10 and its reciprocal, and W-10 x Q-67. Hence, the cross B-34 x W-10 can be utilized for future breeding programs under water-deficit conditions. The information obtained here can also be used to identify the best parental inbred lines for cross-combinations to increase the economic yield on a sustainable basis in water deficit areas.

Conflicts of interest

The authors declare no conflict of interest.

REFERENCES

Akbar M, Saleem M, Azhar FM, Ashraf MY, et al. (2008). Combining ability analysis in Maize under normal and high temperature conditions. *J. Agric. Res.* 46: 27-38.

Anonymous (2012-2013). Economic Survey of Pakistan. Economic Adviser's Wing, Finance Division, Government of Pakistan. Islamabad.

Bello OB and Olaoye G (2009). Combining ability for maize grain yield and other agronomic characters in typical southern guinea savanna ecology of Nigeria. *Afr. J. Biotechnol.* 8: 2518-2522.

Chohan MSM (2012). Genetic basis of drought tolerance and other plant traits in *Zea mays* L. PhD thesis, Dept. Plant Breeding and Genetics, University of Agri., Faisalabad, Pakistan.

Edmeades GO (2008). Drought tolerance in maize: an emerging reality. A feature in James, Clive. Global status of commercialized Biotech/GM crops 2008/ISAAA Brief No. 39.ISAAA: Ithaca, NY.

García-Mata C and Lamattina L (2001). Nitric oxide induces stomatal closure and enhances the adaptive plant responses against drought stress. *Plant Physiol.* 126: 1196-1204.http://dx.doi.org/10.1104/pp.126.3.1196

Griffing B (1956). Concept of general and specific combining ability in relation to diallel/crossing systems. *Aust. J. Biol. Sci.* 9: 463-493.

Hussain I (2009). Genetics of drought tolerance in maize (*Zea mays* L). PhD thesis, Dept. Plant Breeding and Genetics, University of Agri., Faisalabad, Pakistan.

Malik SI, Malik H, Minhas NM and Munir M (2004). General and specific combining ability studies in maize diallel crosses. *Int. J. Agric. Biol.* 6: 856-859.

Rezaei AH, Yazdisamadi B, Zali A, Rezaei AM, et al. (2005). An estimate of heterosis and combining ability in corn using diallel crosses of inbred lines. *Indian J. Agric. Sci.* 36: 385-397.

Steel RGD, Torrie JH and Discky DA (1987). Principles and procedures of statistics: A biometrical approach. 3rd ed. McGraw Hill Book Co., New York.

Tabassum MI, Saleem M, Ali A and Malik MA (2005). Genetic mechanisms of leaf characteristics and grain yield in maize under normal and moisture stress conditions. *Biotechnology* 4: 243-254. http://dx.doi.org/10.3923/biotech.2005.243.254

Taiz L and Zeiger E (2006). Stress physiology. In: Plant physiology. 4th ed. (Taiz L and Zeiger E, eds.). Sinauer Associates, 671-681.

Wattoo FM (2013). Genetics of physio-agronomic traits in maize under water deficit conditions. PhD thesis, Dept. Plant Breeding and Genetics, University of Agri. Faisalabad, Pakistan.