INNSPUB

International Journal of Biosciences | IJB |
ISSN: 2220-6655 (Print), 2222-5234 (Online)
http://www.innspub.net
Vol. 15, No. 5, p. 443-461, 2019

RESEARCH PAPER OPEN ACCESS

Quantitative genetic analysis of yield, fibre and physiological traits for drought tolerance of elite cotton cultivars

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Key words: General and specific combining ability, Drought tolerance, and Upland cotton.

http://dx.doi.org/10.12692/ijb/15.5.443-461 Article published on November 28, 2019

Abstract

Classification of water stress tolerant cotton genotypes is a big challenge for breeders and physiologists. Thus present studies was taken up to identify potential cultivars which have the ability to combine their favourable genes on crossing and produce water stress tolerant progenies. For this purpose, the experiment was carried-out in a factorial design with two irrigation regimes (non-stress *vs.* water stress at reproductive stage) in four replications at Department of Plant Breeding and Genetics, Sindh Agriculture University, Tandojam, Pakistan. Six cotton genotypes were crossed in a 6 × 6 half diallel mating design during 2010, thus 15 F_1s were developed for genetic analysis in 2011. The parent Sadori expressed significantly greater general combining ability for bolls plant^{-1} (4.04** in non-stress and 4.06** in water stress) and seed cotton yield in Kg ha^{-1} (165.83** in non-stress and 277.85** in water stress), thus Sadori is regarded as good general combiner parent suitable for hybridization and selection programmes. While many hybrids manifested significantly higher specific combining ability (SCA) effects, yet cross CIM-496 × CIM-534 exhibited maximum SCA for bolls plant^{-1} (13.94** in non-stress and 12.89** in stress) and yield (850.09** in non-stress and 1185.35** in stress, thus considered as good specific combiner hence is suitable for hybrid cotton development in stress and non-stress conditions. The correlation coefficients (r) determined from pooled data revealed that, by and large, the correlations were higher in moisture stress than in non-stress environment. In stress conditions, the higher positive associations between yield, fibre and physiological traits were noted.

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Introduction

The world is experiencing from water abundance epoch to water deficient era, yet currently water shortage is about 12.0 Million Acre Foot and probable rise is expected up to 30.5 Million Acre Foot by the time 2025 (GOP, 2016). Characterization of moisture stress tolerant genotypes is also a big issue because that requires identifying and developing some unique phenotypic characters in crop plants which contribute towards stress tolerance and establish their comparative significance. Generally, plant breeders use elite plant varieties as parents to evolve new drought tolerant breeding material through hybridization and selection programmes which eventually decreases the genetic distance of newly evolved cotton varieties. Hence, it is indispensable to discover potential alleles for moisture tolerance which may be found in adapted genetic stock or transmit unique genes from exotic germplasm so as to widen genetic base for water stress tolerance. In the past, difficulties were realized in lacking the knowledge regarding physiological traits which are associated with water stress tolerance and can reliably be used as sound indicators for drought tolerance. Quite a number of physiological attributes were considered as prospective indicators for water stress tolerance for instance reticence of photosynthesis and low stomatal conductance (Pettigrew, 2004; Athar and Ashraf, 2005). Length of fresh roots and shoots and their biomass, chlorophyll and proline contents, rate of photosynthesis and expression of drought responsive genes are considered as reliable indicators of plant response to moisture stress conditions (Kohli *et al.*, 1999; Sperdouli *et al.*, 2012). It is observed that a genotype which maintains normal water status usually do not permit high transpiration from the surface of leaves or develops smaller stomatal size and density without declining net chlorophyll content, such genotypes may help produce higher yields under water stress environments (Freeman, 2014). Thus, genotypes with decreased water loss from excised leaves, lower transpiration rate due to smaller stomatal dimension and density and retain higher water content in leaves are suggested as reliable selection criteria to breed plants against water stress (Clarke and McCaig, 1982; Malik and Wright, 1997; Malik *et al.*, 1999; Rahman *et al.*, 2000). It is argued that stomatal conductance is not a desirable trait as it affects productivity under non-stress conditions (Manavalan and Nguyen, 2017).

Studies on the genetic control of drought tolerance require integrative efforts of both geneticists and physiologists for evaluating huge lot of characters on many genotypes. While identifying prospective parents for hybridization and selection scheme for drought tolerance, it becomes important to determine breeding value of parents involved in hybridization. Crossing of potential parents is therefore first step towards the genetic improvement for water stress environments. In genetic analysis, combining ability of parents is characterized as the ability of parents to bring together the favourable genes during crossing programme so that they are simultaneously transmitted from parents to their offspring (Allard, 1960; Mir *et al.*, 2016). By definition, when two parents generate potential progenies, such parents are said to have good combining ability (Vasal *et al.*, 1986; Baloch *et al.*, 2014). Two concepts of combining ability are proposed to determine the potentiality of parents, 1) general combining ability (GCA), and 2) specific combining ability (SCA) which are known to have important implications on pure line and hybrid variety development. The GCA is the performance of a particular genotype with many other crosses, while SCA was elucidated as the performance of parents in specific combinations (Sprague and Tatum (1942). Recognition of potential parents for hybridization in future breeding programmes is foremost objective of cotton breeders (Okey *et al.*, 2006; Kulembeka *et al.*, 2012; Sana *et al.*, 2018). In this context, a diallel mating design is regarded as powerful genetic analysis being adapted to obtain information about the legacy of polygenic characters (Parviz, 2016). Crosses among selected set of inbred parents can provide information on the genetic variability and their combing ability. The Diallel technique uses a universal approach in the selection of inbreds and hybrids with superior characters under exploitation. The decline of 42% in yield under drought and both additive and dominant genes advocating seed cotton yield, lint% and boll weight is observed by Gamal *et al.* (2009). Batao *et al.* (2016) found that yield and its associated characters in substitution lines were advocated by integrated effects of additive and non-additive genes, while Rathva *et al.* (2017) observed that ginning outturn% was chiefly advocated by additive genes, yet boll mass, total fruits plant^{-1}, seed cotton and lint yields were largely governed by dominant genes. Correlation is a statistical technique which imitates the associated response of a meticulous trait with its corresponding characters, thus endow with a superior indicator to envisage the analogous alteration that may arise in one trait at the cost of the balanced modification in another character (Naqibullah, 2003; Ahmad *et al.*, 2008; Ahmad *et al.*, 2011; Ali *et al.*, 2011). The present investigation is aimed at obtaining the information regarding combining ability of cotton varieties for drought tolerance based on their yield, fibre quality and physiological characters.

Materials and methods

Plant material and methodology of evaluating F_1 hybrids

The research was carried-out in the experimental area of the Department of Plant Breeding and Genetics at Sindh Agriculture University Tandojam, Pakistan. Six most popular cultivars such as CRIS-134, Sadori, Sindh-1, CIM-496, CIM-506 and CIM-534 were identified as drought tolerant based on previous screening experiment by studying physiological, yield and fibre traits. Crosses among these cultivars were attempted during 20110 in 6 × 6 half diallel fashion (Griffing, 1956) and the seed of 15 F_1 hybrids was obtained.

The experiment was carried- out in a factorial design with two irrigation treatments, non-stress and water stress with four replications during 2011. The water regimes were considered as the main factor while varieties as sub-factor. All agricultural inputs and practices like spraying, fertilization, wee××ding, irrigation and cotton production technology were adopted as recommended for the cotton crop. The analysis of variance was determined following statistical procedures of Gomez and Gomez (1984) and using Statistix software 8.1 version, while determining general combining ability (GCA) and specific combing ability (SCA) variances and their effects were estimated as suggested by Griffing (1956) and adopted by Singh and Choudhry (1979) and correlation coefficients were estimated by following the method of Raghavrao (1983). All the recommended agricultural practices were applied for healthy crop. The data were collected from ten tagged plants in each replication. Six irrigations in non-stress treatment were applied according to the crop requirement whereas in water stress treatment, the water stress was imposed at reproductive stage from 75 till 110 days of planting. The soil type of the experimental area was loam and sandy loam in texture. For the cotton experiment area, water content at field capacity varied from 20.3 to 27.6 %, and wilting point varied from 7.2 to 9.7 % on dry weight basis. The dry soil bulk densities ranged from 1.42 to 1.50 g cm-3 throughout the 1.2 m deep profile and there was no precipitation during the experimentation period. The data were recorded for sympodial branches plant^{-1}, bolls plant^{-1}, boll weight (g), seed cotton yield (Kg ha^{-1}), lint%, staple length (mm), fibre strength (tppsi), leaf area (cm^2), relative water content (%) and stomatal conductance (mmol m^{-2}s-1).

Results and discussion

Analysis of variance of parents and F_1 hybrids for yield, fibre quality and physiological traits

Analysis of variance (mean squares) from combined data of parents and F_1 hybrids revealed that irrigation treatments induced significant variation in sympodial branches plant^{-1}, number of bolls plant^{-1}, boll weight, seed cotton yield (kg ha^{-1}), lint (%), staple length, fiber strength, leaf area, relative water content and stomatal conductance (Table 1). The genotypes also performed variably due to water stress for all the traits studied. The significance of genotype × treatment interactions for all the studied characters indicated that varietal performance was inconsistent over the irrigation treatments.

Table 1. Combined analysis of variance for yield and fiber traits of cotton genotypes grown under non-stress and water stress conditions.

Traits	Replication (D.F.=3)	Treatment (T) (D.F.=1)	Genotypes (G) (D.F.=20)	T × G (D.F.=11)	Parents (P) (D.F.=5)	Hybrids (H) (D.F.=14)	P vs. H (D.F.=1)	Error (D.F.= 123)
Sympodia plant^{-1}	0.16	993.77**	29.01**	9.96**	10.23**	32.37**	75.87**	0.47
Bolls plant^{-1}	1.15	1755.05**	341.96**	12.94**	148.78**	417.30**	253.03**	1.06
Boll weight	0.03	13.91**	1.71*	0.24*	1.21**	1.75*	3.71**	0.07
Seed cotton yield	4716.17	51950007**	1587418**	187199**	253713**	1849909**	4581067**	2864.82
Lint (%)	3.08	267.52**	22.07**	1.33*	43.12*	15.90**	3.18**	1.01
Staple length	4.95	132.14**	3.12**	0.84*	2.68**	2.83**	9.31**	0.64
Fiber strength	1.74	2958.48**	124.67**	31.99**	149.77**	58.07**	931.55**	0.96
Leaf area	2.06	5833.93**	572.12**	28.44**	669.72**	557.82**	284.30**	1.06
Relative water content	4.90	62833.30**	147.40**	104.70**	125.30**	125.40**	564.60**	0.80
Stomatal conductance	29.00	330461**	1586.00**	1608.00**	826.40**	619.00**	18920.10**	6.00

**,* = Significant at 1 and 5% probability levels respectively, DAP*=Days after planting.

The degrees of freedom for genotypes were divided into parents, F_1 hybrids and parents *vs.* F_1 hybrids. Significance of all these three sources of variations suggested that considerable quantum of genetic variability was present among the parents and their hybrids while the significance of parents *vs.* hybrids revealed the scope of hybrid cotton development. The variances among the genotypes were independent in both non-stress and water stress imposed at reproductive stage. It was noted that the mean squares in non-stress were greater than water stress conditions for the characters such as bolls per plant, boll weight, lint%, staple length, fibre strength and stomatal conductance (Table 2).

Table 2. Mean squares from analysis of variance for yield and fibre quality traits of parents and F_1 hybrids of cotton grown under non-stress and water stress conditions.

Characters	Non-stress			Water stress at reproductive stage		
	Replication D.F. = 3	Genotype D.F. =20	Error D.F. = 60	Replication D.F. =3	Genotype D.F. =20	Error D.F.= 60
Sympodia plant^{-1}	0.19	5.52**	0.47	0.03	33.45**	0.49
Bolls plant^{-1}	0.13	153.34**	0.70	3.04	201.55**	1.37
Boll weight	0.29	1.05**	0.07	0.14	0.89**	0.04
Seed cotton yield (kg ha^{-1})	2271	689914**	2144	6074	1084703**	3548
Lint (%)	3.69	13.59**	1.32	0.61	9.80**	0.67
Staple length	3.98	2.51**	0.68	2.09	1.45**	0.58
Fiber strength	1.74	109.59**	1.16	0.45	47.06**	0.78
Leaf area	0.77	258.97**	0.94	2.13	341.58**	1.18
Relative water content	1.41	38.48**	0.92	4.83	213.63**	0.72
Stomatal conductance	35.25	1789.06**	11.00	3.13	1404.84**	1.04

** = Significant at 1% probability level.

While the effects of water stress were different in drought stress and in that case, drought caused the variations in sympodial branches plant^{-1}, seed cotton yield kg ha^{-1}, leaf area and relative water content. Different abiotic stresses, especially water stress significantly influenced the yield and its associated characters all over the world (Basal *et al.*, 2005). Moderate to severe water stress affects various morpho-physiological traits such as affects leaf size, stems extension, root production, chlorophyll fluorescence, water use efficiency dry matter yield, water content, stomatal conductance, water potential and cell membrane stability (Al-Hamdani *et al.*, 2003).

The mean squares for general combining ability (GCA) and specific combining ability (SCA) were significant for the yield, fibre quality and physiological traits in both stress and non-stress conditions excluding that GCA was non-significant for boll weight under non-stress.

The significance of GCA and SCA for almost all the studied traits under water stress as well as non-stress conditions demonstrated that additive as well as dominant genes were equally essential in advocating the characters under study.

However under normal irrigation regime, GCA variances were predominant against the SCA for sympodia plant^{-1}, lint%, staple length, fibre strength, and stomatal conductance while the SCA variances were greater than GCA for the other traits (Table 3).

Table 3. General combining ability (GCA) and specific combining ability (SCA) mean squares for yield, fiber and physiological traits of cotton genotypes grown under non-stress and water stress conditions.

Traits	Non-stress			Water stress at reproductive stage		
	GCA D.F. =5	SCA D.F. =15	Error D.F. = 60	GCA D.F. =5	SCA D.F. =15	Error D.F. = 60
Sympodia plant^{-1}	2.47**	1.66**	0.48	9.80**	7.88**	0.4978
Bolls plant^{-1}	38.22**	38.37**	0.71	54.87**	47.35**	1.373
Boll weight	0.10	0.31**	0.07	0.10**	0.26**	0.049
Seed cotton yield	103212.1**	195567.2**	2144.0	280110.4**	268229.9**	3548.0
Lint (%)	5.73**	2.62*	1.327	3.59*	2.09**	0.673
Staple length	2.65**	1.62**	0.271	2.42**	1.006**	0.254
Fiber strength	32.83**	25.59**	1.163	21.61**	8.48**	0.781
Leaf area	55.36**	67.87**	0.949	53.76**	95.94**	1.181
Relative water content	9.13**	9.78**	0.921	19.76**	64.61**	0.729
Stomatal conductance	731.39**	352.55**	11.00	168.22**	412.20**	1.040

**,* = P≤0.01 and 0.05 respectively.

Under water stress condition at reproductive stage, the SCA variances were at upper edge over GCA for boll weight, leaf area, relative water content and stomatal conductance, nonetheless the GCA variances for other traits such sympodia plant^{-1}, seed cotton yield in kg ha^{-1}, GOT%, fibre length and fibre strength were greater than SCA. The higher portion of SCA indicated the prevalence of non-additive genes while larger portion of GCA revealed the preponderance of additive genes in the interdictory of characters studied. When the additive estimates are greater than the dominant, then phenotypic selection in earlier filial generations would be successful; nonetheless when additive genes are larger than non-additive genes, the progress of such characters require meticulous selection in later segregating generations (Ali *et al.* 2008). Similar to our results, Cheatham *et al.* (2003) and Imran *et al.* (2016) reported that though additive as well as dominant genes caused differences for water stress resistance, however the additive gene influence was very prominent and degree of dominance for fibre length, fiber strength, and fineness was also less than unity. Contrary to our results, Hassan *et al.* (2000) and Ahuja and Dhayal (2007) and Khokhar *et al.* (2018) reported that non-additive genes were more important for fiber quality traits than additive genes. Though GCA and SCA variances were equally essential, nonetheless the extent of SCA was much greater than GCA demonstrating the predominance of non-additive genes advocating bolls formed, lint% and yield as reported by Deshphande and Baig (2003). Similarly, combining ability analysis by El-Mansy *et al.* (2010) exposed considerable GCA and SCA variances for most of the studied traits revealing the important role of both additive and dominant genes for those traits. Analogous to results of above mentioned workers, Rokaya *et al.* (2005) and Jatoi *et al.* (2010) also found substantial variances for GCA and SCA supporting the value of additive and dominant genes, nonetheless the proportion of GCA over the SCA was higher than 1.0 demonstrating the prevalence of additive genes in the inheritance of yield, 100-seed weight and GOT% (Rehana *et al.*, 2018). Bushra *et al.* (2015) reported that GCA variances were greater than SCA for bolls per plant, seed cotton yield and lint % while, SCA variances were higher than GCA for sympodial branches plant^{-1} and fibre length. With little disagreements, our results revealed that GCA and not the SCA was important for sympodial branches plant^{-1}, staple and fibre strength and yield.

Apart from these results, Khokhar *et al.* (2018) noted that the ratio of δ^2GCA/δ^2SCA being lower than unity indicated the predominance of non-additive types of gene action for number of sympodial branches, numbers of bolls, boll weight, seed cotton yield, lint%, fiber length and fiber strength.

Table 4. General combining ability (GCA) effects of parents for yield and its component traits of cotton grown under stress and non- stress conditions.

Parents	Sympodial branches plant^{-1}		Bolls plant^{-1}	
	Non-stress	Water stress	Non-stress	Water stress
CRIS-134	0.18	0.61*	0.45	1.72**
Sadori	0.09	1.43**	4.04**	4.06**
Sindh-1	0.01	0.07	-0.15	-0.22
CIM-496	-0.26	-0.64**	-1.15**	-1.22**
CIM-506	-0.35	-1.79**	-2.27**	-3.56**
CIM-534	0.33	0.31	-0.93**	-0.78*
S.E.(gi.)	0.22	0.23	0.27	0.38
S.E. (gi-gj)	0.34	0.35	0.42	0.59
Parents	Boll weight		Seed cotton yield (kg ha^{-1})	
	Non-stress	Water stress	Non-stress	Water stress
CRIS-134	-0.12	0.03	-37.29*	27.23
Sadori	0.11	0.04	165.83**	277.85**
Sindh-1	0.01	-0.19	-71.35**	-88.46**
CIM-496	-0.06	-0.04	-30.10*	50.04*
CIM-506	-0.10	-0.01	-134.48**	-293.40**
CIM-534	0.15	0.16*	107.40**	26.73
S.E. (gi.)	0.09	0.07	14.94	19.22
S.E. (gi-gj)	0.14	0.11	23.15	29.78

**,* = P≤0.01 and 0.05 respectively.

General combining ability (GCA) and specific combining ability (SCA) estimates for yield, fibre quality and physiological traits

Genetic analysis for determining GCA and SCA of parents for water stress tolerance are very essential attributes to develop new drought resistant breeding material. The GCA determines the varietal performance in series of crosses whilst SCA connotes those instances where certain hybrids perform better or poor against average performance in hybrids. Thus, specific combining ability is vital for developing hybrids, whereas general combining ability is valuable for crossing and selection schemes. In quantitative traits, gene action is determined as additive, dominance and epistatic with their interactions (Saleem *et al.*, 2015; Sana *et al.*, 2018). The GCA and SCA effects of yield, fibre quality, and physiological traits are depicted in Tables 4 to 11. The character wise results are presented here under:

Sympodial branches plant^{-1}

Though variances attributable to GCA and SCA were significant for sympodia per plant under both non-stress and water stress environments, nevertheless, GCA variances in both the conditions were higher than the SCA (Table 3). These results demonstrated that additive genes were obvious in controlling sympodial branches per plant. Rana *et al.* (2009) evaluated six F_1 and F_2 crosses under moisture stress circumstances and that additive and non-additive genes advocated the legacy of sympodia per plant. Out of six parents, only two parents Sadori and CRIS-134 exhibited higher positive GCA estimates in moisture deficit environment while none of the parental lines manifested significant GCA effects under non-stress environments (Table 4).

These results revealed that parents Sadori and CRIS-134 being good general combiners due to higher GCA estimates are worthwhile for hybridization and selection programs so as to develop new breeding material for drought tolerance so as to increase sympodial branches under water shortage conditions. Among the 15 hybrids, seven of them expressed desirable positive SCA estimates in non-stress ranging from 0.08 to 1.67 by the hybrids CRIS-134 × CIM-496 and Sadori × CIM-534, nonetheless only five hybrids manifested desirable positive SCA effects under water stress environments ranging from 0.13 to 2.95 (Table 5).

Table 5. Specific combining ability (SCA) effects of F_1 hybrids of yield and its component traits of cotton grown under water stress conditions.

F_1 hybrids	Sympodial branches plant^{-1}		Bolls plant^{-1}	
	Non-stress	Water stress	Non-stress	Water stress
CRIS-134 × Sadori	0.08	1.91**	8.38**	8.61**
CRIS-134 × Sindh-1	-1.09	-2.23**	-1.43	-2.86*
CRIS-134 × CIM-496	1.67*	-1.02	-5.43**	-5.36**
CRIS-134 × CIM-506	-0.23	0.13	-1.81	-4.01**
CRIS-134 × CIM-534	-1.41*	-3.46**	-4.65**	-5.79**
Sadori × Sindh-1	1.49*	2.95**	5.72**	4.30**
Sadori × CIM-496	-0.49	-3.09**	-4.53**	-8.20**
Sadori × CIM-506	0.11	-1.19	-1.40	-5.36**
Sadori × CIM-534	1.67*	2.72**	7.75**	7.11**
Sindh-1 × CIM-496	-1.66*	-1.73*	-0.59	-2.42*
Sindh-1 × CIM-506	0.93	-2.33**	-0.46	-2.58*
Sindh-1 × CIM-534	-1.50*	-2.67*	-1.56*	-4.61**
CIM-496 × CIM-506	-0.80	-0.62	2.29**	-1.08
CIM-496 × CIM-534	0.77	2.79**	13.94**	12.89**
CIM-506 × CIM-534	-1.39*	-3.06**	-2.93**	-6.01**
S.E. (si.)	0.61	0.62	0.75	1.04
S.E.(sii-sjj)	0.69	0.70	0.84	1.17

**,* =P≤0.01 and 0.05 respectively.

The four top ranker F_1 hybrids such as Sadori × Sindh-1, Sadori × CIM-534, Sadori × Sindh-1 and Sindh-1 × CIM-506 manifested greater SCA estimates of in optimum environments respectively, while in drought environments, the three high SCA scoring hybrids were; Sadori × Sindh-1, CIM-496 × CIM-534 and Sadori × CIM-534 gave even increased SCA estimates. Present results indicated that hybrids which scored higher SCA in both the environment may be choice crosses for hybrid cotton development. Two types of genes those were additive and dominant were involved in the inheritance of sympodia per plant depending on the GCA and SCA effects of the parents' involved in cross combinations (Rana *et al.*, 2009).

Bolls plant^{-1}

The general and specific combining ability variances were significant for number of bolls per plant in optimum and moisture stress conditions, yet general combining ability and specific combining ability were almost similar in magnitude under normal irrigation while in drought stress, the GCA was much greater than SCA (Table 3). Such results indicated that under water stress, additive genes were preponderant over the non-additive ones for bolls per plant. Kiani *et al.* (2007) evaluated 6 × 6 diallel crosses and reported substantial control of additive and dominant genes for bolls per plant, while Kalsy and Garg (1988) observed that additive, dominance and epistasis genes played an imperative role in the inheritance of number of bolls per plant in cotton.

Two out six parents, i.e. Sadori and CRIS-134 manifested greater positive GCA effects estimates in water stress conditions (Table 4), nevertheless, the other four parents expressed undesirable negative GCA estimates in both the environments.

Table 6. Specific combining ability (SCA) effects of F_1 hybrids for yield traits of cotton grown under non-stress and water stress conditions.

F_1 hybrids	Boll weight		Seed cotton yield (kg ha^{-1})	
	Non-stress	Water stress	Non-stress	Water stress
CRIS-134 × Sadori	0.86*	0.90**	528.84**	374.54**
CRIS-134 × Sindh-1	-0.64*	-0.37	-8.97	-59.15
CRIS-134 × CIM-496	-0.37	-0.72**	-107.72**	-112.65*
CRIS-134 × CIM-506	-0.10	-0.25	-55.85	41.29
CRIS-134 × CIM-534	-0.53*	-0.37	-75.22**	-189.34**
Sadori × Sindh-1	0.55*	0.20	482.90**	782.72**
Sadori × CIM-496	-0.61*	-0.50*	-285.85**	-552.78**
Sadori × CIM-506	-0.54*	-0.81**	-161.47**	-114.84*
Sadori × CIM-534	0.28	-0.13	504.15**	667.54**
Sindh-1 × CIM-496	0.12	-0.15	-108.66**	-389.46**
Sindh-1 × CIM-506	0.59*	0.25	98.21*	-163.53**
Sindh-1 × CIM-534	0.53*	0.11	21.34	-328.65**
CIM-496 × CIM-506	-0.52*	-0.15	251.96**	15.47
CIM-496 × CIM-534	-0.10	-0.07	850.09**	1185.35**
CIM-506 × CIM-534	-0.15	-0.13	299.46**	-256.21**
S.E. (si.)	0.25	0.20	41.04	52.80
S.E. (sii-sjj)	0.28	0.22	46.30	59.57

**,* = P≤0.01 and 0.05 respectively.

The negative GCA estimates in drought conditions were greater as compared to optimum irrigation situation indicating that drought caused negative impact on bolls formed per plant. From 15 F_1 hybrids, only five in optimum and four in drought stress manifested positive SCA estimates (Table 5). In both the environments, nearly similar parents expressed positive SCA estimates that suggested the reliability of the parents in the performance under moisture deficit and optimum irrigation environments and the favourable genes advocating the bolls per plant. The maximum positive SCA effects, nonetheless was recorded by CIM-496 × CIM-534, CRIS-134 × Sadori, Sadori × CIM-534 and Sadori × Sindh-1 under normal and in drought environments. The findings of Abro *et al.* (2009) are in consonance with ours in that, they observed parent Sadori as good general combiner with high GCA estimates while two hybrids like Sadori × CIM-448 and Sadori × CRIS-134 with greater SCA estimates were identified as good specific combiners, hence such hybrids may be exploited for hybrid cotton development.

Table 7. General combining ability (GCA) effects of parents for yield, fiber quality and physiological traits of cotton grown under non-stress and water stress.

Parents	Lint (%)		Staple length	
	Non-stress	Non-stress	Non-stress	Water stress
CRIS-134	1.43**	-0.24**	-0.24**	-0.19*
Sadori	0.15	0.14	0.14	0.34**
Sindh-1	-0.39	-0.36**	-0.36**	-0.19*
CIM-496	-0.39	0.14	0.14	-0.03
CIM-506	-1.07*	-0.08	-0.08	-0.16
CIM-534	0.27	0.42**	0.42**	0.22*
S.E. (gi.)	0.37	0.08	0.08	0.09
S.E. (gi-gj.)	0.57	0.13	0.13	0.38
Parents	Fiber strength		Leaf area	
	Non-stress	2.80**	Non-stress	Water stress
CRIS-134	1.46**	0.08	-3.98**	-3.54**
Sadori	-0.01	-2.01**	1.27**	0.83*
Sindh-1	-3.54**	-0.89**	-1.95**	-1.07**
CIM-496	-1.01*	0.65*	3.02**	3.55**
CIM-506	1.49**	-0.64*	-0.39	-1.70**
CIM-534	1.61**	0.29	2.02**	1.93**
S.E. (gi)	0.35	0.44	0.31	0.35
S.E. (gi-gj)	0.45	2.80**	0.48	0.45

Parents	Relative water content	
	Non-stress	Water stress
CRIS-134	-0.31	-0.16
Sadori	1.06**	2.66**
Sindh-1	-0.53	-1.28**
CIM-496	1.59**	0.81*
CIM-506	-1.00*	-1.69**
CIM-534	-0.81*	-0.34
S.E. (gi)	0.31	0.27
S.E. (gi-gj)	0.48	0.42

**,* = P≤0.01 and 0.05 respectively.

Boll weight

Mean squares due to GCA were non-significant while SCA was significant in non-stress, however the GCA as well as SCA variances were significant in water stress conditions (Table 3). Thus, none of the parents expressed striking GCA estimates for boll weight, yet parents Sadori and CIM-534 revealed positive but non-significant GCA estimates in non-stress as well as under drought stress conditions. The other parents which expressed either positive or negative estimates were at negligible GCA range (Table 4). The significant variances owing to additive and non-additive genes have played an important role to identify parents suitable for hybridization or for hybrid crop development. Coinciding to our findings, Memon *et al.* (2016) also estimated negligible GCA effects for parents and SCA for hybrids in boll weight. Converse to our findings, Kiani *et al.* (2007) and Rana *et al.* (2009) reported prominent role of GCA and SCA genes advocating boll weight. From 15 F_1 hybrids examined six hybrids in non-stress and four hybrids under drought stress displayed enviable positive SCA estimates (Table 6). From these hybrids, four hybrids *viz.*, CRIS-134 × Sadori, Sindh-1 × CIM-506, Sadori × Sindh-1 and Sindh-1 × CIM-534 manifested superior SCA estimates under optimum and in drought stress situations, yet SCA estimates of these hybrids were not essential because of their non-significance variances and effects. Contrary to our results, Bhushra *et al.* (2015) observed significant SCA effects in four out of ten hybrids for boll weight.

Table 8. Specific combining ability (SCA) effects of F_1 hybrids for lint% and staple length of cotton grown under water stress conditions.

F_1 hybrids	Lint (%)		Staple length	
	Non-stress	Non-stress	Non-stress	Water stress
CRIS-134 × Sadori	0.99	1.18	0.90**	-0.58*
CRIS-134 × Sindh-1	0.02	-1.57*	-0.10	-0.55*
CRIS-134 × CIM-496	-1.98	-1.41	-0.10	-0.71*
CRIS-134 × CIM-506	-1.79	-2.04*	-0.38	-0.08
CRIS-134 × CIM-534	-1.14	-1.10	0.12	0.04
Sadori × Sindh-1	2.30*	1.65*	0.53*	0.92**
Sadori × CIM-496	-0.70	-0.19	-1.47**	-0.74**
Sadori × CIM-506	-0.01	-0.82	-1.25**	-0.62*
Sadori × CIM-534	1.39	0.87	0.25	0.26
Sindh-1 × CIM-496	0.83	0.31	-0.97*	-0.21
Sindh-1 × CIM-506	-0.48	0.68	0.50*	0.42
Sindh-1 × CIM-534	-0.83	0.12	-1.00**	-0.46
CIM-496 × CIM-506	-0.98	-0.41	0.25	0.51*
CIM-496 × CIM-534	2.17*	1.78*	0.25	-0.12
CIM-506 × CIM-534	-1.14	1.15	-0.04	0.01
CRIS-134 × Sadori	1.02	0.73	0.23	0.24
CRIS-134 × Sindh-1	1.15	0.82	0.26	0.29
CRIS-134 × CIM-496	-1.14	1.15	0.90**	-0.58*
S.E. (si.)	1.02	0.73	-0.10	-0.55*
S.E. (sii-sjj)	1.15	0.82	-0.10	-0.71*

**,* = $P \leq 0.01$ and 0.05 respectively.

Seed cotton yield (kg ha^{-1})

The mean squares (variances) owing to general and specific combining ability in normal and water shortage situations were significant suggesting that additive and dominant genes were advocating seed cotton yield. The extent of variances concerning to SCA however were higher than GCA in non-stress, yet GCA was much greater than SCA under water stress condition (Table 3). These results revealed the greater importance of additive genes in controlling seed cotton yield under drought stress environment. Shakoor *et al.* (2010) conducted generation mean analysis of parents, F_1s, F_2s and backcrosses under optimum and water stress environments. They observed that both additive and dominant genes were advocating seed cotton yield in both the environments and further concluded that since SCA variances were lower than GCA, hence suggested selection in delayed generations. Similar to our results and the findings of Shakoor *et al.* (2010), Naqibullah (2013) who carried-out 6 × 6 diallel crosses and observed that though variances for both GCA and SCA were significant, yet GCA (additive genes) were prevailing for seed cotton yield. Two out of six parents displayed affirmative GCA estimates in non-stress whereas four parents manifested desirable positive GCA effects in water stress conditions (Table 4).

Table 9. Specific combining ability (SCA) effects of F_1 hybrids for fiber and physiological traits of cotton grown under water stress conditions.

F_1 hybrids	Fiber strength		Leaf area	
	Non-stress	Non-stress	Non-stress	Water stress
CRIS-134 × Sadori	2.86**	0.57	5.52**	7.05**
CRIS-134 × Sindh-1	8.39**	4.16**	-2.01*	-2.04
CRIS-134 × CIM-496	1.36	2.29*	-15.48**	-16.67**
CRIS-134 × CIM-506	-1.64	-1.25	2.17*	0.58
CRIS-134 × CIM-534	-0.76	0.54	-5.23**	-8.29**
Sadori × Sindh-1	0.61	4.63**	8.49**	9.83**
Sadori × CIM-496	-0.67	-0.75	-2.73*	-9.04**
Sadori × CIM-506	1.58	1.72*	1.17	-2.54*
Sadori × CIM-534	6.96**	3.75**	11.52**	11.33**
Sindh-1 × CIM-496	2.11*	0.85	1.74	-2.88*
Sindh-1 × CIM-506	-1.14	-1.43	-0.11	0.62
Sindh-1 × CIM-534	3.24**	-1.15	3.49**	-2.01*
CIM-496 × CIM-506	3.83**	-0.31	-5.58**	-4.76**
CIM-496 × CIM-534	2.71*	0.47	5.52**	8.37**
CIM-506 × CIM-534	3.71**	-2.56**	-8.83**	-13.88**
S.E. (si)	0.95	0.78	0.86	0.96
S.E. (sii-sjj)	1.08	0.88	0.97	1.09
F_1 hybrids	Relative water content		Stomatal conductance	
	Non-stress	Water stress	Non-stress	Water stress
CRIS-134 × Sadori	2.89**	3.82**	11.47**	-5.90**
CRIS-134 × Sindh-1	-0.76	-7.24**	0.94	15.20**
CRIS-134 × CIM-496	-2.64**	-6.33**	11.88**	1.26
CRIS-134 × CIM-506	0.21	-5.83**	-4.28	7.57**
CRIS-134 × CIM-534	0.77	-7.68**	-10.59**	22.48**
Sadori × Sindh-1	2.11*	6.45**	18.38**	-14.15**
Sadori × CIM-496	-4.01**	-11.15**	-11.43**	27.92**
Sadori × CIM-506	-0.92	-4.90**	3.16	8.73**
Sadori × CIM-534	4.89**	1.26	16.60**	-17.62**
Sindh-1 × CIM-496	-1.92	-8.21**	-3.96	8.76**
Sindh-1 × CIM-506	2.42*	-3.21**	10.63**	4.07**
Sindh-1 × CIM-534	1.74*	-2.05*	3.82	9.23**
CIM-496 × CIM-506	1.55	-2.05*	21.07**	26.13**
CIM-496 × CIM-534	2.11*	6.35**	34.00**	-23.21**
CIM-506 × CIM-534	2.46	-4.90**	8.10*	21.10**
S.E. (si)	0.85	0.75	2.94	0.90
S.E. (sii-sjj)	0.96	0.85	3.32	1.02

**,* = P≤0.01 and 0.05 respectively.

The parent Sadori expressed extraordinarily higher GCA estimates followed by CIM-534 in non-stress and water stress conditions. Whereas under stress, the parents like Sindh-1 and CIM-506 expressed maximum adverse GCA effects for seed cotton yield in Kg ha^{-1}. Thus, GCA estimates suggested that parents Sadori and CIM-534 render as higher combiners with additive genes; therefore they fit very well for hybridization and selection programmes. Comparable to our results, Rauf *et al.* (2006) succeeded in identifying parents like NIAB-999, CIM-473 and Acala as good general combiners for seed cotton yield. Among 15 F_1 hybrids evaluated, eight in non-stress and six in drought stress expressed affirmative SCA estimates. Positive GCA estimates in non-stress ranged from 21.34 to 850.09 whereas the same range in water stress was from 15.47 to 1185.35 (Table 6). The top four high scoring SCA hybrids such as CIM-496 × CIM-534, CRIS-134 × Sadori, Sadori × CIM-534 and Sadori × Sindh-1 exhibited elevated SCA estimates in both non-stress and in water stress environments. Kiani *et al.* (2007) and Bhushra *et al.* (2015) recognized three hybrids with higher SCA estimates were good specific combiners, hence were suitable for hybrid cotton so as to improve seed cotton yield. Sivia *et al.* (2017) recorded significant SCA effects for seed cotton yield from the cross combinations AC726 × H1236, H1476 × H1226, Luxmi PKV × H1226, H1470 × H 1098-I and H1470 × H1236. These cross combinations involved at least one parent with high or average GCA effect for a particular trait.

Table 10. General combining ability (GCA) effects of parents for stomatal conductance of cotton grown under non-stress and water stress conditions.

Parents	Stomatal conductance	
	Non-stress	Water stress
CRIS-134	-15.13**	-1.60**
Sadori	8.19**	-8.01**
Sindh-1	0.22	0.90*
CIM-496	-0.22	4.83**
CIM-506	-4.81**	3.77**
CIM-534	11.75**	0.11
S.E. (gi.)	1.07	0.33
S.E. (gi-gj.)	1.66	0.51

** = P≤0.01 and 0.05 respectively.

Lint%

The significant variances owing to GCA and SCA were found in both optimum irrigation and in water deficit situations revealed that additive and dominant genes were supporting seed cotton yield in both the environments. The scope of variances due to GCA however was more obvious than the SCA in normal irrigation and in drought environment (Table 3). These results revealed the importance of additive genes controlling lint%. Naqibullah (2013) determined combining ability from six parent half diallel and noted that although GCA and SCA variances were significant, yet GCA variances were much greater than the SCA signifying that additive genes were advocating lint%. On the contrary, El-Seoudy *et al.* (2014) observed that SCA variances being greater than GCA indicated that non-additive genes were playing prominent role for lint%. With regard to lint%, three, out of six parents such as CRIS-134, CIM-534 and Sadori exhibited positive GCA estimates in optimum irrigation whilst in drought, only two parents such as CRIS-134 and Sadori expressed positive estimates (Table 7), nonetheless other three parents in non-stress and four parents in drought stress exposed undesirable negative GCA estimates for lint %. Three parents possessing higher combining ability may be rewarding for crossing purpose. Regarding SCA estimates of F_1 hybrids, six hybrids exhibited desirable positive SCA estimates for lint% in non-stress conditions and seven hybrids expressed positive GCA effects in water stress conditions. The positive SCA estimates in optimum irrigations varied from 0.02 to 2.30. In stress conditions, out of 15 hybrids examined, the positive SCA estimates ranged from 0.12 to 1.78 (Table 8). The top scoring four hybrids viz., Sadori × Sindh-1 closely followed by CIM-496 × CIM-534, CRIS-134 × Sadori and Sindh-1 × CIM-496 expressed higher SCA estimates in non-stress. While under stress, the three similar out of four hybrids CIM-496 × CIM-534, Sadori × Sindh-1 and CRIS-134 × Sadori with small alteration in rank order expressed higher positive SCA estimates. Majority of the hybrids however still expressed significantly positive SCA estimates, hence stood at good specific combiners for lint%. Comparable to our findings, Naqibullah (2013) and Bhushra *et al.* (2015) accomplished five good specific combiners extracted from half diallel crosses of cotton with higher SCA estimates.

Staple length

The significant variances were found owing to GCA and SCA in optimum irrigation and in water stress conditions revealing that both additive and dominant genes were sustaining staple length. Significant estimates of additive and dominance regarding for fiber length were observed by Nasimi *et al.* (2016) which suggested the significance of both additive and dominant genes were advocating fibre length in both water stress and optimum irrigation (Table 3). It was further evident that H2 /4H1 was less than 0.25 and √4DH1 +F/√4DH1-F was more than 1.0, indicating that there was an excess of dominant genes in the parents. The scopes of variances owing to GCA variances however were more obvious than the SCA in optimum and in drought environments. These results suggested preponderance role of additive genes controlling staple length. Comparable to present findings, Madhuri *et al.* (2015) also reported that 2.5% span length was controlled by non-additive genes while Aguado *et al.* (2010) carried-out genetic analysis of five parents and their ten F_1s. They observed that though both additive and non-additive variances were significant, yet additive variances were prevailing for fibre length. Only three out of six parents in non-stress and two in drought stress articulated positive GCA estimates. Whereas all the other parents in either environments manifested negative GCA effect (Table 7). Analogous to present results, Madhuri *et al.* (2015) identified parents like AK-032 and AK-053 from lines and DR-7R from testers as good general combiners due to higher GCA estimates and additive genes. Seven crosses from 15 F_1 hybrids expressed positive SCA estimates in optimum irrigation varying from 0.12 to 0.90 while six hybrids displayed positive SCA effects ranging from 0.04 to 0.92 in drought stress conditions. Higher SCA effects however were observed in F_1 hybrids like CRIS-134 × Sadori, Sadori × Sindh-1 and CIM-496 × CIM-506 under non- stress conditions (Table 9). While in stress treatment, the higher positive SCA effects were recorded by crosses Sadori × Sindh-1, CIM-496 × CIM-506 and Sindh-1 × CIM-506. The SCA estimates in stress conditions nevertheless were by and large lower in normal irrigation environment. Similar to our results, Bhushra *et al.* (2015) succeeded in identifying three crosses like CRIS-134 × MG-6, IR-3701 × FH-113 and IR-3701 × MG-6 with higher estimates of SCA and greater heterotic effects for staple length suggested that such hybrids possess dominant and over dominant genes, hence may be potential hybrids for the exploitation of heterosis in cotton.

Fibre strength

The mean squares indicated that GCA and SCA variances were significant in both normal and in water stress conditions revealing that both additive and dominant genes were advocating fibre strength. Similar to present findings, Nasimi *et al.* (2016) observed significant estimates of additive and dominant genes revealed the importance of additive as well as non-additive were involved in the genetic control of fiber strength under normal and drought conditions. The magnitude of additive and dominant appeared to be almost equal under both irrigation regimes, which indicated that about equal number of genes were involved in the inheritance of fibre strength. The significance of GCA variance being greater than SCA in both the environments was very apparent (Table 3). Such results indicated preponderance role of additive genes advocating fibre strength. Parallel to present findings, Rana *et al.* (2009) and Aguado *et al.* (2010) noted that although both additive and non-additive variances were essential, the magnitude of additive variances were predominance revealing that fibre strength is primarily controlled by additive genes. Three out of six parents expressed positive GCA estimates in both the environments. The parents like CIM-534, CIM-506 and CRIS-134 expressed significantly higher positive GCA estimates in non-stress environment, while Sadori, Sindh-1 and CIM-496 manifested undesirable negative GCA effects (Table 7). In drought stress conditions, again three but with addition of one dissimilar parent like CRIS-134, CIM-506 and Sadori and CIM-534 revealed positive GCA estimates. For fibre strength, Mehmet and Aydin (2015) conducted genetic analysis and observed some parents like Sahin-2000, BA-308 as good general combiners with higher GCA estimates and additive genes. While parents CRIS-134, CIM-506 and Sadori and CIM-534 from our studies proved their being good general combiners thus their suitability for crossing programmes to improve fibre strength under moisture stress conditions. Eleven, out of 15 F_1 hybrids, manifested positive SCA estimates which varied from 0.95 to 8.39. Under drought stress conditions, nine out of 15 expressed positive SCA estimates and the values of positive SCA varied from 0.47 to 4.16 (Table 9). By and large, in normal irrigation conditions, the hybrids expressed higher SCA against water stress.

The top four F_1 hybrids demonstrating higher SCA effects in non-stress were; CRIS-134 × Sindh-1, Sadori × CIM-534, CIM-496 × CIM-506 and CIM-506 × CIM-534. While the high ranking, four hybrids in drought stress were; CRIS-134 × Sindh-1, Sadori × Sindh-1, Sadori × CIM-534 and CRIS-134 × CIM-496.

The high ranking hybrids expressed greater SCA estimates in non-stress against water stress environment. These results indicated that hybrids with non-additive genes and expressing higher SCA estimates under stress may be useful to develop hybrids with better fibre potency under low moisture environments. Imran *et al.* (2016) determined genetic control of fibre strength under non-stress and water stress conditions. They observed that degree of dominance was less than unity for fibre potency.

Leaf area

The general and specific combining ability mean squares indicated that were significant in optimum irrigation as well as in drought conditions illuminating those both additive and non-additive genes were controlling the leaf area. The importance of SCA variances was greater than GCA under non-stress and water stress environment (Table 3). These results suggested that non-additive variances and the genes were prevailing role of leaf area. From six parents, three parents such as CIM-496, CIM-534 and Sadori manifested superior and positive GCA estimates in both non-stress and water stress conditions (Table 7). The range of positive GCA effects in parents ranged from 1.27 to 3.02 in non-stress, while it ranged from 0.83 to 3.55 in water stress environment. The positive GCA estimates indicated that parents CIM-496, CIM-534 and Sadori possess additive genes, hence are good general combiners to improve leaf area through hybridization and selection programmes. Eight out of 15 hybrids displayed positive SCA estimates in non-stress varying from 1.17 to 11.52 while under stress, the positive SCA effects varied from 0.62 to 11.33. The values of negative or positive estimates were, by and large, greater in water stress than in non-stress environment (Table 9). However, four F_1 hybrids like Sadori × CIM-534 scored higher SCA effects followed by Sadori × Sindh-1, Sadori × Sindh-1 and CIM-496 × CIM-534 and CRIS-134 × Sadori with similar GCA effects in non-stress conditions. Likewise in stress, the greater but positive SCA effects were scored by Sadori × CIM-534, Sadori × Sindh-1, CIM-496 × CIM-534 and CRIS-134 × Sindh-1. These results indicated that sufficient number of hybrids with dominant genes and being good specific combiners may be exploited for the development of hybrid cotton.

Relative water content %

The significant mean squares concerning to GCA and SCA in both non-stress and in water stress situations revealed that both additive and non-additive genes were advocating relative leaf water content.

The variances owing to GCA and SCA were almost equal in optimum irrigation, yet they were very different in water stress conditions where SCA variances was about three times greater than GCA indicating predominance of non-additive variances and non-additive genes controlling relative water content under stress environment (Table 3). The significant role of both additive and non-additive genes was also observed by Rana *et al.* (2009) under water deficit conditions. Two parents like CIM-496 and Sadori revealed positive GCA in optimum irrigation and exactly alike parental lines also manifested significant GCA effects in water stress treatment also (Table 7). This result suggested that parents CIM-496 and Sadori were marked as revealing potential combining ability with additive genes hence are useful parents for crossing and selection schemes. While other four parents either in optimum irrigation or in water stress environment exposed negative GCA effects. Ten out of 15 F_1 hybrids in optimum irrigation and 4 hybrids in water stress environment manifested positive SCA estimates (Table 9).

In non-stress, the positive estimates varied from 0.21 to 4.89 whereas the same range in water stress ranged from 1.26 to 6.35. In non-stress, the maximum SCA effects however were manifested by the crosses Sadori × CIM-534, CRIS-134 × Sadori and Sindh-1 × CIM-506. In stress treatment, higher SCA effects were observed in Sadori × Sindh-1, CIM-496 × CIM-534 and CRIS-134 × Sadori.

The positive SCA estimates of high ranking hybrids were greater in non-stress than the water stress environment. Amjad *et al.* (2016) carried out generation mean analysis of parents F_1, F_2, BC_1 and BC_2 populations developed from crosses between FH-207 (drought tolerant) and FH-901 (drought susceptible) parents. They observed that additive and dominant genes were advocating the relative water content of leaves in cotton. The hybrids which manifested high SCA retained predominantly dominant genes and such genes could be useful for hybrid crop development retaining more relative water content when imposed to moisture deficiency.

Stomatal conductance

The GCA and SCA variances relating to normal and water stress conditions were significant, implying that both additive and non-additive genes were controlling the stomatal conductance in cotton. The GCA variances were greater than SCA under non-stress while it was *vice versa* in water stress where SCA variance was far greater than GCA suggesting that non-additive genes and variances were more important under drought stress conditions (Table 3). Three out of six parents displayed desirable positive GCA effects for stomatal conductance in non-stress while four parents manifested enviable negative SCA estimate under water stress conditions.

The maximum desirable positive GCA effects were recorded by the parents CIM-534 and Sadori in non-stress environment (Table 10). Under drought stress, the parents Sadori expressed maximum desirable negative GCA effects closely persuaded by CRIS-134. The parent CRIS-134 is the only parent that manifested maximum undesirable positive GCA effects however the same parent expressed maximum desirable negative GCA effects under drought stress conditions being the most drought tolerant parent.

These results suggested that parents Sadori and CRIS-134 by expressing desirable negative GCA estimates in water stress with additive genes are good general combiners; hence they are suitable parents for developing drought tolerant material via lower stomatal conductance. Eleven from 15 F_1 hybrids demonstrated positive desirable SCA effects in non-stress conditions while under stress, four hybrids manifested advantageous negative SCA estimates (Table 11).

The four potential hybrids expressed positive SCA effects in optimum irrigation and also desirable negative SCA in drought stress were nominated as CIM-496 × CIM-534, Sadori × CIM-534, Sadori × Sindh-1 and CRIS-134 × Sadori. Baodi *et al.* (2008) suggested that leaf water use efficiency under stress conditions may be achieved by choosing breeding material with more photosynthesis, low transpiration rate and low stomatal conductance.

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