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Combining ability studies of high-temperature stress tolerant attributes of advance lines of spring wheat under a hot and dry climate of Bhakkar

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Abstract

An expected increase in world temperature requires us to better know the scope of heat stress experienced by plants. So, we highlighted the combining ability of wheat plant to combine successfully with another wheat plant, resulting desirable traits in next generation and it also provides information about the controlling of genetic mechanisms of quantitative traits that helps in the selection of suitable parents under a hot and dry climate. Combining ability analysis was used to get progenies with desirable traits under agro ecological zone of Thal. These analyses were applied to 21 (direct crosses) hexaploid spring bread wheat F_1 populations according to 7×7 diallel fashion biometrical approach under three heat stress regimes at Arid Zone Research Institute, Bhakkar, Pakistan during 2018-19 to 2020-21, i.e., TWS12464, TWS1335-1, TWS11510, TWS15105, TWS1578, TWS12245, Gold-16. Spring bread wheat is also known as spring wheat that is planted in spring and harvested in late summer. Results indicated that the mean squares of most traits proved highly significant due to the general combining ability (GCA) and specific combining ability (SCA). The variance ratios of GCA/SCA revealed all of the traits were predominantly under additive genetic control. TWS12464 was the best combiner with a maximum mean performance of all the traits in all temperature stresses followed by the parent namely Gold-16. Moreover, crosses TWS12464 × Gold-16 and TWS1335-1× TWS12464 were the best F1 hybrids. These crosses depicted good positive effects of SCA along with maximum mean performance for dry biomass per plant at anthesis, spikelets per spike, spike length, grain yield per plant in three test environments. These outperforming strains could be used to develop high-yielding temperature stress-resilient wheat cultivars to mitigate the grain yield gap in country terminal heat-prone ecological zone.

Keywords: Combining ability, Diallel, Grain yield, Heat stress, Thermotolerance, Wheat

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Introduction

Wheat crop is a symbol of food security across the world as well as in Pakistan, where it has no alternative to any other strategic food commodity (Khan et al., 2016; Anser et al., 2018; Shafqat et al., 2019). It is cultivated annually in 9 million hectares area, with 14.4% share in value addition and 3.0% of GDP in agriculture. In the developing world, its production is projected to increase 60% by 2050. In Pakistan, to meet the wheat grain demand is still a challenge. Total area and production of wheat was 8976 thousand hectares and 26394 thousand tones, respectively during 2021-22. The inconstant wheat production and its projected demand deserve to focus future wheat research towards heat stress management. It is the second important crop that provides a major element of the total food resource and dietary protein that is grown in a wide range of environments (Mehmood et al., 2020; Shehzad et al., 2022; Shafqat et al., 2023). Wheat is ever first plant grown by the humans, and cultivated throughout the globe because of its wider adaptability (Ali et al., 2013; Shaheen et al., 2023; Shehzad et al., 2023). Tangible yield appreciation is call of the day to fulfill food and feed demand and it invites the attention of scientists to work for humanity well-being by evolving high-yielding temperature stress-tolerant wheat varieties (Abbas et al., 2014; Zameer et al., 2015). The major grain yield production constraint in Pakistan as well as in the world is temperature stress (Ullah et al., 2020). It has a major role in pollination and grain filling. The combining ability is a potential study that provides important information about the genetic processes which control quantitative characteristics and allows the selection of suitable parents for seed multiplication in hot and dry climates. The term is used to describe the potential for two parents' plants to produce offspring with desirable traits such as disease resistance, high yield with improved quality. General combining ability provides valuable assessment for additive gene accomplishment, and conversely it is precise merely indicative of non-additive gene action. Combining ability analysis provides explicitly the insight picture of quantitative traits. This technique is of cardinal importance for result-oriented breeding programs to develop high temperature stress tolerant wheat cultivars. Combining ability is important tool for analysis by involving thirty F1 generations of 6x6 diallel cross in major cereal crops in both stress free and heat stress environments where significant heterogeneity was attributed to cultivars with additive, non-additive and reciprocal. The SCA: GCA variance ratio for all the studied traits in the temperature stress environment indicated the presence of non-additive gene effects. Sometimes there are high genetic and phenotypic coefficients of variability (Tahmasebi et al., 2013) are associated with high SCA & GCA effects on grain production (Kapoor et al., 2011) and GCA and SCA ratios for 1000 grain weight and yield/plant. GCA and SCA are very important estimates to assess the yield performance of inbred lines and hybrids (Ali et al., 2013). Genetic improvement is the best solution as temperature stress cultivars once developed would be a low-cost input technique that would be easily available to farmers. The main aim of this wheat research orientation was to utilize local genetic variables to get deeper comprehension of the phenomena of low yield in high temperature and to develop thermo tolerant wheat cultivars for growers. These genotypes could be helpful to bridge up the yield gap in hot irrigated areas of the country.

Materials and Methods

Experiment was carried out at Arid Zone Research Institute at Bhakkar, Pakistan in cereal experimentation block during the three wheat crop seasons 2018-19 to 2020-21.

Germplasm Screening (2018-19)

Wheat germplasm screening nursery (2018-19) comprising 150 wheat genotypes was laid out in three conditions, one each stress free and two heat stress environment (early and late planting) according to RCBD with three replications during Rabi 2018-19. Timely and late plantings were carried out on 10th November and 20th December, respectively in 2018. Late planting treatment was eventually subjected to temperature stress to identify heat stress tolerant and susceptible strains to be used as parental genotypes for hybridization during the next crop season by following the methodology adopted by (Rane & Nagarajan, 2004).

Hybridization (2019-20)

Seven parental genotypes viz TWS12464, Gold-2016, TWS1335-1, TWS11510, TWS15105, TWS1578 and TWS12245 were selected for high temperature stress tolerance studies during the crop season 2018-19 from the material obtained from CIMMYT (The International Maize and Wheat Improvement Center). A crossing block comprising four high temperature stress tolerant and three high temperature stress susceptible genotypes were laid out on 15th November 2019 for the hybridization program. Hybridization was carried out as per diallel fashion biometrical technique (7×7). F_0 seed of twenty-one direct recombinants along with parental genotypes was reserved to study F1 generations in heat stress environment during wheat crop season 2020-21.

Genetic Material Evaluation (2020-21)

Twenty-one direct F_1 generations resulting from 7×7 diallel fashion hybridization along with seven parental strains of hexaploid bread wheat were laid out for combining ability analysis in a stress-free (timely planting) and two heat stress climates (timely planting in polyhouse and late planting in open field) at Arid Zone Research Institute, Bhakkar, Pakistan during wheat crop season 2020-21. Timely planting to serve as a stress-free and polyhouse planting with the objective to create temperature stress were simultaneously carried out on 10th November whereas; late planting was made on 20th December 2020. Experiment was sown according to diallel biometrical approach with three replications. Gross plot size was 5.0 m×1.8m having line-line and plant-plant distance of 0.30 m and 0.15 m, respectively. This experiment was subjected to indirect high temperature stress by sowing one set at belated stage for the assessment of heat stress with reference to 80% late sowing being practiced by wheat growers in Pakistan. Timely planting in polyhouse was carried out to measure the net heat stress quantum to avoid the issue of reduction in kelvin heat units. Kelvin heat units (KHU) is used to express the amount of heat required to bring plants to a certain temperature over a period of time to predict crop growth and development. Hence all three experimental sub units were sown in field and a polyhouse was erected 60 days after timely planting. Polyhouse day time temperature was maintained 41 ± 5 ºC above the ambient temperature. All agronomic requirements were provided uniformly. Six high temperature associated traits, i.e., days to 50% earing, biomass/ plant at anthesis (gm), spike length (cm), Spikelets per spike, Tillers per plant (No.) and grain yield were estimated at different growth stages. Experiment data were subjected to combining ability analysis to explore inbuilt genetic capability with reference to aforesaid six attributes in no heat stress as well in two high temperature stress environments.

Heading (Days)

50% earing was noticed from the date of germination to 50% heading stage of concerned genotypes.

Biomass plant^{-1} (g)

Ten protected plants of each genotype were picked from the second row on day anthesis and then after oven drying, these were weighed to calculate their mean values.

Spike length (cm)

Five plants were selected to measure spike length of main culm was at maturity; measured by taking it from the base to the tip of head excluding awns and mean value was computed.

Spikes plant^{-1} (No.)

Ten plants from each cultivar were selected to calculate mean value.

Spikelets spike^{-1} (No.)

Ten plants from each cultivar were selected to calculate mean value. Where spikelets of mother shoot were recorded.

Grain yield plant^{-1} (g)

Ten plants were selected randomly from each genotype. Spikes were threshed manually and grain yield was measured with help of electronic balance and there after mean yield per plant of each genotype was taken. General combining ability (GCA) and specific combining ability (SCA) methods were used to study genetic variability in all cultivars (Griffing, 1956).

Results and Discussion

Germplasm screening

Two sets of field experiment comprising 150 wheat genotypes were laid out under normal and high temperature stress condition having RCBD design with three replications during Rabi season 2018-19 (From November 2018-pril 2019). One set of experiment was planted on 10th November 2018 under normal field environment to attain stress free environment. While planting of second set of experiment was delayed up to 15th December 2018 to provide high temperature stress during critical stages of plant development (Dwivedi et al., 2017; Elbasyoni, 2018; Dubey et al., 2020; Poudel & Poudel, 2020). According to relative tolerance index %, relative performance ratio and reduction in grain yield % under heat stress in comparison with optimal situation four terminal heat tolerant and three thermos-labile (Table 1) wheat genotypes were identified and selected (Ali & El-Sadek, 2016; Mohammadi, 2016; Schmidt et al., 2020) for further studies.

Table 1 Germplasm screening under normal and heat stress conditions

S. No.	Genotypes	Grain yield per plant (g)		RTI. %*	RPR%**	Yield Red.%***	Attribute
		Normal temp.	Heat stress				
1	TWS12464	30	19.67	34.43	65.66	34.34	Tolerant
2	GOLD-16	31	20.63	33.32	66.54	33.45	Tolerant
3	TWS1335-1	30	19.67	34.33	65.66	34.43	Tolerant
4	TWS15110	29	21	29.89	72.41	27.58	Tolerant
5	TWS15105	22.33	8.67	61.12	38.82	61.17	Susceptible
6	TWS1578	25	11.33	54.66	45.32	54.68	Susceptible
7	TWS12245	25	11.67	53.46	46.48	53.32	Susceptible

* = Relative tolerance index %; ** = Relative performance ratio %; *** = Yield reduction percentage in heat stress as compared with normal temperature condition

Hybridization

Seven wheat genotypes selected for study of high temperature stress tolerance inheritance were planted in field on 12th November 2019 during crop season 2019-20. Similarly for execution of efficient and successful hybridization program a second set of crossing block was laid out on 20th November 2019. First irrigation was applied twenty five days after germination while 2nd, 3rd, 4th and 5th irrigations were applied at booting, dough and grain filling stages respectively. During hand pollination period two special irrigations were applied to get maximum and healthy pollen grains and ensure maximum seed setting. At suitable boot stage central spikelets of spike were retained while others were removed with the help of a pair of scissors. One third part of the top floret were cut with the help of a pair of scissors by holding tiny floret between thumb and fore finger and three immature anthers in each floret were removed with the help of pointed forceps avoiding pistil damage. After completion of emasculation the entire spike was covered with a glycine bag. Depending on environmental conditions after 2 to 3 days when bifid ovaries were full receptive, hand pollination of emasculated spikes was done by using fresh pollen grains from the respective male parent and spike was covered again with butter paper bag till seed setting. Forty spikes per cross combination were hybridized to get maximum F_0 seed. Twenty one direct crosses were made by hybridizing seven parents. Sufficient quantity of F_0 seed (about 900-100) was obtained to carry out the study smoothly. At physical maturity harvesting was done and harvested seed of 21 crosses alongwith parents (Table 2) was reserved for evaluation and screening for high temperature tolerance during next crop season (2020-21).

Table 2 List showing 21 recombinants alongwith seven parents produced by hybridizing in 7×7 diallel fashion during crop season 2019-20

S. No.	Recombinants/ parents	S. No.	Recombinants/ parents
1	TWS12464 (Parent)	15	TWS1335-1 × TWS11510

2	TWS12464 × Gold-16	16	TWS1335-1 × TWS15105
3	TWS12464 × TWS1335-1	17	TWS1335-1 × TWS1578
4	TWS12464 × TWS11510	18	TWS1335-1 × TWS12245
5	TWS12464 × TWS15105	19	TWS11510 (Parent)
6	TWS12464 × TWS1578	20	TWS11510 × TWS15105
7	TWS12464 × TWS12245	21	TWS11510 × TWS1578
8	Gold-16 (Parent)	22	TWS11510 × TWS12245
9	Gold-16 × TWS1335-1	23	TWS15105 (Parent)
10	Gold-16 × TWS11510	24	TWS15105 × TWS1578
11	Gold-16 × TWS15105	25	TWS15105 × TWS12245
12	Gold-16 × TWS1578	26	TWS1578 (Parent)
13	Gold-16 × TWS12245	27	TWS1578 × TWS12245
14	TWS1335-1 (Parent)	28	TWS12245 (Parent)

Genetic material evaluation

Two separate experiments were conducted during wheat crop season 2020-21 (November 2020-April 2021). First experiment was laid out on November 10th, 2020 under normal field conditions (timely planting) and second experiment was laid out on 20th December 2020 under high temperature stress (late planting) condition. In each set of experiments twenty one F_1 hybrids along with seven parents were laid out according to randomized complete block design with three replications. Plot size was kept 1.50 m × 2.50 m with plant to plant distance pf 0.15m. Uniformity in distance and depth of seeds was maintained with a template. To ensure uniform population two seeds per whole were maintained and after germination at each plant position one healthy seedling was retained through thinning. All the standard agronomic practices were adapted uniformly. During evaluation of heat tolerance as it was desirable to avoid water stress therefore adequate irrigation regime was applied during the crop season. Data were recorded on randomly selected 10 guarded plants of each genotype per replication per treatment for different physio-morphological traits. Most of the parameters studied were indicator of high temperature tolerance (Cossani & Reynolds, 2012; Cao et al., 2015; Saxena et al., 2016).

Heading (Days)

In all three environments, mean squares due to GCA and SCA were extremely significant for days to heading. In all regimes, the GCA mean squares were higher. Variations in means square attributes among genotypes at heading in GCA and SCA were 277.2:10.04, 107.5:9.74, 345.7:13.30 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in table 1. Significant mean squares due to both GCA and SCA for days to heading in present work are similar as reported by (Ahmed & EL-Hosary, 2021; M. Ali, Hassan, & Ali, 2020) while (Rajput & Kandalkar, 2018) resulted significant mean squares attributable to GCA only. The variance component analysis demonstrated that this trait has large GCA variance, resulting in additive variance in both temperature stress scenarios showing that additive genetic control is the dominant mode of regulation for this trait. Estimates of variance components among genotypes at heading in GCA and SCA were 19.1: 5.5, 7.0: 5.48, and 26.5: 11.70 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 2. This character has been linked to additive genetic effects (Sharma et al., 2019; Semahegn et al., 2021). However, a majority of non additive gene action was found by (Kamara et al., 2021). Wheat cultivars having early heading always support grain filling and survival better under heat stress. As a result, for days to heading negative combining ability consequences are desirable. Under stress free condition, four of the seven parents i.e., TWS12464, Gold-16, TWS1335-1 and TWS11510 exhibited negative GCA effects and two genotypes i.e., TWS1578 & TWS12245 showed highest positive GCA effects. Ten out of twenty one crossings had SCA negative values where cross Gold-16 × TWS1578 and TWS11510 × TWS12245 displayed maximum negative SCA display. Under heat stress condition, similar four parents i.e. TWS12464, Gold-16, TWS1335-1 and TWS11510 showed negative GCA values having maximum in Gold-16 while TWS1578, TWS12245 & TWS15105 depicted positive GCA effects. Seven crosses showed negative SCA values having maximum in TWS11510 × TWS12245. However TWS1578 × TWS12245 cross had maximum positive SCA effects in table 6. Similarly, Kamara et al. (2021) also noted that high GCA values were scattered amongst the parentage and altered across tested atmospheres, which proves the impacts of atmospheres on GCA estimates. A significant and negative GCA impacts for DTH exhibited by different parents across tested atmospheres, indicated that these parentages could be imperative sources of favorable alleles for earliness. Al-Ashkar et al. (2020) also observed the early heading has a significant benefits for avoiding terminal heat stress under late sown wheat.

Spike length (cm)

Spike length showed that GCA mean squares were higher than SCA and were highly significant under stress free as well as heat stress environment. Variations in means square attributes among genotypes in spike length due to GCA and SCA were 24.6: 1.66, 36.3: 1.68, 27.4: 1.76 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 3. Estimates of variance components among genotypes at spike length due to GCA and SCA were 1.64: 0.9, 2.47: 0.89 and 1.83: 0.95 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 4. Where greater values showed the presence of additive gene effects in both environmental conditions. These findings are supported by Ahamed et al. (2018); Parveen et al. (2018); Shah et al. (2018); Dedaniya et al. (2019); Sharma et al. (2019); Abro et al. (2021); Kumar et al. (2022). Parveen et al. (2018) results slighty differ as mean squares due to SCA and GCA were highly significant for all the characters while GCA were highly significant for all the traits except for spike length for which GCA effects were significant. Genotypes 9802 (-0.67) and 9801 (-0.07) showed GCA negative valus and proved spike length poor combiner. Additive genes are genes whose effects on a trait are independent of other genes and add up in a predictable manner. Non-additive genes, on the other hand, are genes whose effects on a trait are dependent on other genes or the environment (Sibolibane & Weis, 2022). Mwadzingeni et al. (2018) revealed that presence of at least one best general combiner is important for acquiring good specific cross combinations. Remarkably, none of the tested hybrids had a significant SCA effects for all studied traits table 6. Although, the hybrid Gold-16 × TWS15110 was a good hybrid combination for spike length. Additionally, TWS12464 × TWS1578, TWS1335-1 × TWS15105, and TWS12464 × TWS15105 were excellent combiner for spike length. Thus, a desirable segregants could be expected from crosses (Kamara et al., 2021).

Spikes plant^{-1}

Combining ability studies for spikes per plant showed that GCA mean squares were higher than SCA and were highly significant under stress free as well as heat stress environment. Variations in means square attributes among genotypes in spike per plant due to GCA and SCA were 25.5:3.3, 18:2.25 and 26.2:3.23 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 3. Estimates of variance components among genotypes at spikes per plant due to GCA and SCA were 1.59:1.69, 1.13:1.18 and 1.65:1.68 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively where SCA values are greater than GCA as given in Table 4. These finding are supported by Sharma et al. (2019); El-Nahas et al. (2021); El Nahas and Ali (2021). They found non additive effects of gene for spikes per plant in their findings. Saeed et al. (2016) & Ahmad et al. (2017) reported similar results. While Mwadzingeni et al. (2018); Shah et al. (2018) reported additive effects for spikes per plant which differs with our findings. Hei et al. (2016) reported both additive as well as dominance for spikes per plant. Combining ability analysis revealed that cultivar TWS12464 showed highest positive GCA effects while TWS12245 depicted poor values and proved poor combiner. TWS15105 × TWS1578 F1 hybrids showed highest SCA effects while negative SCA effects were maximum in cross combination TWS11510 × TWS12245. Under heat stress condition best GCA performer was TWS11510 while TWS12245 displayed the poorest performance under similar situation. In case of SCA effects maximum positive effects were revealed by F_1 hybrid TWS12464 × TWS11510 however cross combination TWS1335-1 × TWS1578 showed poor SCA effects as give in the Table 5 & 6. These studies also confirmed by Desale et al. (2014) where the analysis of variance for combining ability showed mean squares due to both SCA and GCA. They were highly significant for tillers per plant, length of spike, number of spikelets per spike, length of spike, number of grains per spike, grain weight per spike, 100 grain weight and grain yield per plant. This indicated both additive and non additive genetics variance which played important role in the inheritance of all these characters.

Table 3 Mean square attributed to general and specific combining abilities and reciprocal effects of genotypes

Variation	Heading (Days)			Spike length (cm)			Spikes/plant (No.)		
	A	B	C	A	B	C	A	B	C
GCA	277.2**	107.5**	345.7**	24.60**	36.3**	27.4**	25.5**	18*	26.2**
SCA	10**	9.74**	13.30**	1.66**	1.68**	1.7**	3.3**	2.25**	3.23**
Error	0.31	0.1	0.18	0.08	0.11	0.09	0.4	0.2	0.27

Table 4 Estimates of variance components relative to GCA, SCA and reciprocal effects of parental genotypes following Griffing approach method 1 model II

Variation	Heading (Days)			Spike length (cm)			Spikes/plant (No.)		
	A	B	C	A	B	C	A	B	C
GCA	19.1	7.0	26.5	1.6	2.4	1.8	1.59	1.13	1.65
SCA	5.5	5.4	11	0.90	0.89	0.95	1.69	1.18	1.68
Error	0.3	0.11	0.34	0.08	0.12	0.94	0.39	0.17	0.27
SE	3.4	1.2	2.3	1.8	2.7	1.02	0.94	0.96	0.97

Table 5 Estimates of general combining ability for the traits under studied in three temperature regimes

Parents	Heading (Days)			Spike length (cm)			Spikes/plant (No.)		
	A	B	C	A	B	C	A	B	C
TWS12464	-3.64	-2.32	-4.87	0.90	1.08	0.91	1.71	1.42	1.72
Gold-16	-6.00	-3.15	-7.32	1.18	1.30	1.19	0.11	0.08	0.14
TWS1335-1	-1.77	-1.30	-1.94	0.87	1.15	0.80	0.76	0.68	0.81
TWS11510	-0.82	-0.65	-0.44	1.27	1.61	1.45	1.02	0.82	1.00
TWS15105	0.89	0.93	1.86	-1.38	-1.71	-1.39	-1.48	-1.00	-1.58
TWS1578	6.16	5.05	7.29	-1.24	-1.63	-1.09	-0.07	-0.03	-0.08
TWS12245	5.18	1.46	5.43	-1.59	-1.79	-1.89	-2.05	-1.75	-2.01
SE (gi-gj)	0.21	0.12	0.22	0.10	0.13	0.11	0.24	0.16	0.19

Biomass plant^{-1} at anthesis (g)

Dry biomass of complete foliage showed that GCA mean squares were higher than SCA and were highly significant under stress free as well as heat stress conditions. These findings were strongly supported by (Nazir, Sarfraz, et al., 2021). Variations in means square attributes among genotypes in dry biomass at anthesis due to GCA and SCA were 407.5:34.95, 267.5:39.61, 261.2:68.44 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 7, while estimates of variance components among genotypes at heading due to GCA and SCA were 26.6:19.86, 16.34:19.89, and 13.8:38.9 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 8. Under stress conditions variance components of GCA were greater than SCA variance but vice versa in case of heat stress conditions. (Nazir, Mahmood, Shah, Ali, & Ahmad, 2021) reported that SCA had higher dominance variance than GCA due to lack of heat stress environment. Additive genetic effects were the cause of the genetic control for this feature. It was revealed that under heat stress conditions genotype TWS1335-1 had best GCA performance while TWS12245 poor display. Genotypes cross TWS15105 × TWS1578 showed maximum SCA positive effects with minimum effects in genotypes cross TWS11510 × TWS12245 as shown in Table 9 & 10. These results were confirmed by Iqbal and Khan (2006) where it was reported greater GCA variance values as compared to SCA which was the predominance of non additive gene effects. Importance of both additive and non additive genetic effects for biomass/plant was observed by Iqbal and Khan (2006). Khan et al. (2007) noted that the genotype V-00055 was a good general combiner for plant height, biomass, grains per spike and grain yield, similarly, Uqab 2000 is also good combiner for plant height, tillers per plant, biomass, 1000 grain weight and grain yield per plant but it was a negative combiner for number of grains per spike.

Table 6 Estimates of specific combining ability for the traits studied in three temperature regimes

Crosses	Heading (Days)			Spike length (cm)			Spikes/plant (No.)		
	A	B	C	A	B	C	A	B	C
1×2	-0.92	-2.84	-5.38	-0.61	-0.83	-1.12	-1.16	-0.61	-0.62
1×3	-1.65	-2.03	-1.93	-0.22	-0.22	0.06	-1.14	-0.87	-0.96
1×4	0.38	0.32	1.73	0.47	0.40	0.37	1.43	1.49	1.51
1×5	-0.82	2.73	0.42	0.28	-0.11	0.30	-1.23	-0.97	-1.22
1×6	1.91	0.27	2.65	-0.27	0.40	-0.25	0.86	0.51	0.78
1×7	2.38	1.87	5.85	0.66	1.22	0.89	0.50	0.22	0.37
2×3	3.03	0.96	6.68	1.09	0.10	0.15	1.62	1.30	1.61
2×4	1.07	0.99	2.51	0.96	1.26	1.46	-1.14	-0.85	-0.91
2×5	2.03	2.06	1.70	0.84	1.17	0.94	0.03	0.20	0.02
2×6	-6.06	1.44	-1.38	-0.46	-0.45	-0.69	-0.21	-0.16	-0.32
2×7	2.41	-0.95	2.30	-0.28	0.04	0.23	-1.07	-0.78	-1.05
3×4	-0.99	-2.03	-0.19	0.59	0.29	0.39	1.72	1.39	1.58
3×5	-0.707	1.04	-0.50	-0.19	0.61	-0.00	-0.28	-0.23	-0.48
3×6	3.53	0.42	2.06	-0.32	0.33	0.32	-2.35	-1.92	-2.48
3×7	-1.49	1.35	-1.57	0.15	0.40	0.45	0.79	0.63	0.78
4×5	-0.65	2.56	-0.34	0.00	0.35	-0.24	-0.04	0.30	0.16
4×6	0.91	0.77	0.39	-1.43	-0.93	-1.12	-0.12	-0.39	-0.17
4×7	-612.82	-625.2	-616.6	-1.60	-2.61	-660.6	-1.64	-1.65	-664.69
5×6	-0.63	-3.81	-0.24	1.34	1.23	1.93	1.88	1.29	1.92

5×7	-0.87	-1.48	1.94	-2.31	-3.06	-2.44	-1.52	-1.82	-2.01
6×7	5.14	7.18	3.54	-2.30	-2.34	-2.23	1.12	1.25	1.30
SE	0.51	0.31	0.54	0.26	0.32	0.28	0.58	0.39	0.48

SF = Stress free (Timely planting); HS = Heat stress (Late planting); HS = Heat stress (Timely planting in Polyhouse)

Spikelets spike^{-1}

Combining ability studies for spikelets per spike showed that GCA mean squares were higher than SCA and were highly significant under stress free as well as heat stress environment. Variations in means square attributes among genotypes in spikelets per spike due to GCA and SCA were 36.2:5.35, 57.1:11.7 and 46.9:7.69 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 7. These results were supported by Kalhoro et al. (2015); Dedaniya et al. (2019). Where variance value of trait SCA were greater than GCA resulted in dominance of variance in all conditions. Estimates of variance components among genotypes at spikelets per spike due to GCA and SCA were 2.2:2.7, 3.2:6.1 and 2.8:4.3 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 8. These results were supported by Saeed and Khalil (2017) who reported non additive effects in spikelets per spike. Parveen et al. (2018) revealed mean squares due to GCA, SCA and RCA were highly significant while mean squares due to SCA were greater than GCA. Highest SCA effects were exhibited by the cross 9801 × Chakwal-50. But some researches reported additive effects for the spikelets per spike (Kutlu & Olgun, 2015; Ahamed et al., 2018). Parental genotype TWS11510 showed the highest GCA positive effects while TWS11505 was proved a poor combiner. F1 hybrid TWS11510 × TWS15105 showed highest SCA effects while maximum negative TWS15105 × TWS12245 recombinant SCA effects. Genotype TWS11510 showed maximum performance however TWS15105 proved poor combiner in heat stress environment. In case of SCA effects maximum positive effects were recorded for the hybrid TWS12464 × Gold-16, while the poorest SCA effects were displayed by F_1 hybrid TWS1335-1 × TWS1578 as shown in Table 9 & 10.

Plant grain yield^{-1} (g)

Combining ability studies for grain yield per plant showed that GCA mean squares were higher than SCA and were highly significant under stress free as well as heat stress environment. Variations in means square attributes among genotypes in grain yield per plant due to GCA and SCA were 102.8: 13.3, 77.3: 9.02 and 81.2: 10.1 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 7. Ahmed et al. (2017) reported similar findings. Variations in variance showed that GCA mean squares were higher than SCA, which exhibited importance of additive gene effects for grain yield per plant in all conditions. Estimates of variance components among genotypes at grain yield per plant due to GCA and SCA were 6.6:6.4, 4.8:4.4 and 5.1:5 at stress free timely sowing, heat stress late plantation and heat stress timely plantation, respectively as given in Table 8. These findings were also affirmed by the ratios of GCA to SCA mean squares being greater than one indicating the importance of additive gene effects. The results of these studies were supported by Khiabani et al. (2015); Ahmad et al. (2016). TWS12464 displayed the highest positive GCA effects along with best field performance in all test regimes. Highest positive SCA performance was observed in crosses TWS1335-1 × TWS11510, while negative SCA effects were maximum in TWS11510 × TWS12245 in stress free condition (Table 10). Maximum positive SCA effects were recorded in F_1 hybrid TWS15105 × TWS12245 in both heat stress climates. Parveen et al. (2018) concluded higher SCA mean squares than GCA. He indicated non additive type of gene action for grain yield per plant. Variance components also showed similar behavior. Four parents positive GCA effect of which Chakwal-50 was best general combiner for grain yield per plant.

Table 7 Mean square attributed to general and specific combining abilities and reciprocal effects of genotypes

Variation	Biomass/plant			Spikelets/spike			Grains/plant (g)		
	A	B	C	A	B	C	A	B	C
GCA	407.5**	267.5**	261.2**	36.2**	57.1**	46.9**	102.8**	77.3**	81.2**
SCA	34.95**	39.6**	68.4**	5.35**	11.70**	7.69**	13.3**	9.02**	10.1**
Error	0.08	4.7	0.11	0.57	0.9	0.11	1.7	1.3	1

Table 8 Estimates of variance components relative to GCA, SCA and reciprocal effects of parental genotypes following Griffing approach method 1 model II

Variation	Biomass/plant			Spikelets/spike			Grains/plant (g)		
	A	B	C	A	B	C	A	B	C
GCA	26.6	16.3	13.8	2.2	3.2	2.81	6.6	4.8	5.1
SCA	19.8	19.8	38.9	2.7	6.1	4.31	6.4	4.4	5
Error	0.08	4.6	0.11	0.57	0.88	0.12	1.7	1.3	1
SE	1.3	0.82	0.35	0.81	0.53	0.65	0.97	1.1	0.98

Table 9 Estimates of general combining ability for the traits under studied in three temperature regimes

Parents	Biomass/plant			Spikelets/spike			Grains/plant (g)		
	A	B	C	A	B	C	A	B	C
TWS12464	6.77	3.59	4.31	1.18	1.16	1.40	3.44	3.09	3.01
Gold-16	1.34	2.37	1.41	0.52	1.49	0.89	0.11	-0.11	0.22
TWS1335-1	3.17	4.25	3.86	0.74	1.43	1.13	1.54	1.47	1.56
TWS11510	3.96	3.33	3.88	2.33	2.27	2.26	2.09	1.56	1.77
TWS15105	-4.33	-2.60	-4.15	-2.013	-2.52	-2.18	-2.94	-2.27	-2.87
TWS1578	-2.06	-5.05	-4.13	-1.52	-1.82	-1.91	-0.13	-0.01	-0.25
TWS12245	-8.85	-5.89	-5.18	-1.24	-2.02	-1.59	-4.11	-3.72	-3.44
SE (gi-gj)	0.11	0.82	0.12	0.29	0.35	0.13	0.49	0.38	0.38

Table 10 Estimates of specific combining ability for the traits studied in three temperature regimes

Crosses	Biomass/plant			Spikelets/spike			Grains/plant (g)		
	A	B	C	A	B	C	A	B	C
1×2	0.45	5.46	5.49	2.04	3.06	2.04	-2.37	-1.54	-1.22
1×3	8.11	4.91	7.37	1.00	1.91	1.48	-2.63	-1.44	-1.56
1×4	4.16	4.34	5.35	-0.93	-2.84	-1.07	2.65	3.30	3.06
1×5	-1.55	-5.40	-6.77	1.15	0.86	1.79	-1.99	-2.54	-2.46
1×6	2.35	-1.61	-2.79	-2.61	-2.18	-2.48	1.70	0.70	0.92
1×7	-7.36	-6.95	-8.74	-0.31	-1.31	-0.79	1.18	0.25	0.78
2×3	-3.63	0.63	-0.88	1.48	2.58	1.56	2.87	2.58	2.73
2×4	0.92	1.39	1.92	1.48	1.67	1.56	-2.51	-2.18	-1.65
2×5	3.21	1.65	5.14	-2.21	-3.46	-2.37	0.01	0.82	0.49
2×6	-1.72	-2.73	-2.72	-1.14	-2.42	-2.14	0.20	-0.61	-0.80
2×7	-0.94	-6.40	-9.84	-1.25	-2.30	-1.37	-1.99	-1.39	-1.94
3×4	0.42	-0.33	-1.03	0.18	1.80	1.03	3.72	2.58	2.51
3×5	-0.29	1.77	0.52	-0.88	-2.41	-1.27	-0.75	-0.59	-0.84
3×6	-0.89	-3.11	-6.34	-2.02	-3.78	-3.38	-4.73	-3.51	-3.96
3×7	-2.77	-0.78	5.71	0.20	-0.08	0.15	1.91	0.87	1.39
4×5	-3.08	-2.97	-6.01	2.37	2.42	1.76	0.03	0.32	0.28
4×6	-1.67	-4.68	-3.53	0.34	-0.11	0.07	-0.44	-0.78	-0.34
4×7	-6.37	-6.47	-641.27	-2.57	-2.59	-657.85	-4.92	-0.37	2.94
5×6	0.95	8.08	9.35	2.22	2.84	2.26	3.58	3.56	3.47
5×7	5.61	2.70	0.80	-3.69	-3.40	-4.28	-3.20	-3.66	-3.56
6×7	-3.44	-1.28	2.66	0.46	2.28	1.25	2.03	2.37	2.32
SE	0.26	2.00	0.31	0.70	0.87	0.32	1.21	1.06	0.93

SF = Stress free (Timely planting); HS = Heat stress (Late planting); HS = Heat stress (Timely planting in Polyhouse)

Conclusion

These parental genotypes viz TWS12464, Gold-16 and TWS11510 proved as good general combiners for most of the test attributes. Similarly F1 hybrids TWS12464 × TWS11510 and TWS12464 × TWS1335-1exhibited good SCA effects with excellent mean field performance for grain yield and most of the traits studied in both stress free and heat stress regimes.

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