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COMBINING ABILITY STUDIES FOR PHYSIOLOGICAL AND GRAIN YIELD TRAITS IN MAIZE AT TWO TEMPERATURE REGIMES

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Abstract

The F_1 generation obtained from a 6×6 diallel cross was evaluated for combining ability effects at normal and high temperature regimes for various physiological and grain yield parameters. The mean squares due to genotypes, general combining ability (GCA), specific combining ability (SCA) and reciprocal effects were highly significant for all the traits at both temperature regimes while GCA effects were non–significant for stomatal conductance and transpiration rate at high temperature. The GCA: SCA variance ratio exhibited that all traits were controlled by the non-additive genes except for growing degree-days to 50% maturity that was predominantly under the control of additive genes at both temperature regimes. The inbred line 935006 was found to be the best general combiner with better mean performance for grain yield plant^{-1} with lesser growing degree days to 50% silking growing degree days to 50% physiological maturity and higher turgor potential at normal and high temperature regimes. The best single cross hybrid was 935006 × R2304-2 and its reciprocal followed by F165-2-4 × R2304-2 and F165-2-4 × 935006 for good specific combining ability, reciprocal effects, better grain yield plant^{-1} and some other desirable traits.

Introduction

Plants with 4-carbon assimilation pathway or Hatch Slack pathway are efficient user of CO_2. Maize is a C_4 plant that is grown from tropical to temperate regions and geographically from 58° North latitude (in Canada and Russia) to 40° South latitude (in Southern hemisphere). In Pakistan it is mainly grown in provinces of Punjab and NWFP in spring and summer. Its world average yield is much higher than that of Pakistan (Anon., 2005-2006).

Maize has gained a special position in the crop husbandry of Pakistan and its area, under cultivation and yield have significantly increased during the last few years (Anon., 2005-2006). The optimum day temperature ranges from 25 to 32°C and night temperature ranges 16.7 to 23.3°C for maize plant. At optimum temperature, the photosynthetic rate is more rapid than respiration resulting in enhanced plant growth. The crop faces high temperature stress particularly at reproductive stage in spring which is a serious problem causing drastic grain yield reduction so potential grain yield cannot be achieved from the crop. Therefore, breeders need to develop maize genotypes tolerant to high temperature stress in tropical and subtropical regions including Pakistan for getting potential grain yield.

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Growth is affected adversely when temperature decreases to 5°C or increases from 32°C. Net photosynthesis is inhibited at the leaf temperature above 38°C due to thermal inactivation of enzymes. Activity of RUBISCO decreases at the temperature exceeding 32.5°C with nearly complete inactivation at 45°C if temperature increases rapidly. At 54°C, maize plant dies (Steven *et al*., 2002). High temperature stress and low humidity can desiccate exposed silk and pollen grains when they are released from the anthers due to thin outer membranes (Sinsawat, 2004). Prolonged exposure to higher temperature above 32.5°C reduced pollen germination of many genotypes near to a zero level in maize. The degree of damage depends upon the intensity and the duration of high temperature spell (Herrero *et al*., 1980; Hussain *et al*., 2006). Continuously rising temperature, less frequency and uneven distribution of rainfall coupled with usual canal–closure in Pakistan has been significantly reducing the grain yield. Smith (1996) also reported that corn could survive brief exposures to 112 °F (44°C). Corn yield may be reduced by 1.5 bushels acre^{-1} (101 kg ha^{-1}.) for each day if the temperature reaches 95°F (35°C) or higher during pollination and grain filling (Smith, 1996). This problem could be overcome by developing high temperature tolerant maize hybrids.

Genetic variations are the basis of improvement in any crop. Success in hybridization program depends upon the choice of suitable parental material, which will combine well to generate superior hybrids. A knowledge of general and specific combining abilities (GCA, SCA) influencing yield and its components has become increasingly important for plant breeders in the choice of suitable parents for developing potential hybrids in many crop plants (Kruvadi, 1991). Crossing of diverse inbred lines provides sufficient genetic variability for an effective selection of desirable traits. Suitable inbred lines thus may be selected on the basis of general combining ability effects with their better mean performance to produce productive synthetics/ cultivars. The average performance of a particular inbred line in a series of crosses/ hybrid combinations is called its general combining ability, which is due to additive genes effect while performance of two specific inbred lines in a particular cross, which is due to non-additive genes effect is called specific combining ability. The success to identify the parental inbred lines that combine well to produce productive single /double cross hybrids depends on the specific combining ability effects and gene actions that control the traits to be improved. The variance of GCA/SCA ratio is useful in estimating the existing variability whether due to additive or non- additive or both types of gene actions.

Therefore, understanding of genetic mechanism for high temperature tolerance is necessary for the development of heat tolerant hybrids and synthetics for sustainable agriculture.

Materials and Methods

The research was conducted at the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad and Nuclear Institute for Agriculture and Biology (NIAB) during 2005-06. Two high temperature tolerant (935006, R2205-5-4), two moderately tolerant (F-165-2-4, F101-7-2-6) and two high temperature susceptible maize lines (F113-1-1-1 and R2304-2) were chosen on the basis of cell membrane thermostability from 77 inbred lines. The six selected lines were crossed in a complete diallel fashion during winter, 2005. Seeds of F_0 including reciprocal crosses and parental lines were sown in triplicate RCBD in two sets after seed treatment with Benomyl 50 W.P. mixed with Confidar 70 WS @ 5 g per kg seed for the control of shoot fly. One set was sown on February 08, 2006 (sowing time of spring maize) in the field while 2nd on March 14, 2006 to expose it to high temperature stress at reproductive stage. Two seeds per hill were planted with a dibbler, keeping plant-to-plant and line-to-line distances of 18 and 75 cm, respectively. After germination, thinning was done to have a single healthy seedling per hole. All cultural practices were kept uniform for both the sets. Twelve irrigations were applied to avoid both the trials from drought stress. Nitrogen, P_2O_5 and K_2O @ 75, 130, 100 kg ha^{-1} respectively were applied at the time of sowing. Nitrogen @ 85 kg ha^{-1} at the time of second irrigation and 100 kg ha^{-1} at tasseling stage was also applied. Premextra gold 720 S.C. @ 1200 m*L* $ha^{-1}$was applied for control of weeds. Data regarding physiological traits *viz.*, cell membrane thermostability percentage, stomatal conductance, transpiration rate and turgor potential, growing degree days (GDDs) to 50% tasseling, growing degree days to 50% physiological maturity and grain yield $plant^{-1}$ were recorded from both the sets in the field. First set was harvested on June 14, 2008 and second set on July 13, 2006. The measurement for cell membrane thermostability (CMT) at high temperature stress was determined (Sullivan, 1972) using the formula:

$$\text{CMT \%age} = \text{Percent injury} = [1- (1-T_1 / T_2) \div (l - C_1 / C_2)]\times l00$$

where T_1 = First conductivity measurement of plant sample treated at 45°C before autoclave, T_2= Second conductivity measurement of plant sample treated at temperature 45°C after autoclave, C_1 = First conductivity measurement at room temperature (22°C) before autoclave and C_2 = Second conductivity measurement at room temperature (22°C) after autoclave.

Diffusible resistance was measured with the help of steady state porometer (Model L-1 1600 SSP1674 Li Cor. Inc, USA). Stomatal conductance was measured as reciprocal of diffusible resistance. Third leaf from top of two plants in each treatment was used to determine the leaf water potential (ψ_w) with Scholander type pressure chamber.

Leaves used for water potential were frozen at –20°C for 7 days then thawed and cell sap was extracted with the help of a disposable syringe. The sap so extracted was directly used for the determination of osmotic potential with the help of osmometer using formula:

$$\text{Osmotic potential} = (\text{mili osmoles}/1000)\times 0.0832(°K /10)=\text{MPa}$$

where °K = absolute temperature in Kelvin.

Turgor potential (ρ) was calculated as the difference between osmotic potential (π) and water potential values (ψ). Where $\rho = -\psi w + \psi s$. Transpiration rate was measured with the help of steady state porometer mentioned above after adjusting it with the prevailing environment with the help of null gain adjustment at prevailed temperature and light quantum from set-1 grown in February 08, 2006 and from set-2 grown in March 14, 2006. Most commonly used calculation method for growing degree-days for corn is the 30/10 cutoff method. Growing degree-days for days to 50% tasseling and maturity were calculated as the average daily temperature minus 10 according to the formula given below:

$$\text{GDDs} = ½ (\text{T max.} + \text{T min.}) –10$$

If the maximum daily temperature ($T_{max.}$) was greater than 30°C, then this temperature was used to determine the daily average. Similarly, if the minimum daily temperature ($T_{min.}$) was less than 10°C, then this temperature was used to determine the daily average. Growing degree-days were calculated daily and summed over time to define thermal time for a particular stage of the crop. Analysis of variance was carried out to test the significant differences among 36 genotypes resulting from 6×6 diallel cross following Steel & Torrie (1984). Combining ability analysis was computed following Griffing's approach method 1, model 1 (Griffing, 1956).

Results and Discussion

Mean performance, least significant difference (LSD) and coefficient of variation of all traits studied is given in Table 1a & b. Genotypic mean squares showed highly significant differences among genotypes (parents, their crosses and reciprocals) for all the traits studied (Table 2a, b). The mean squares attributable to GCA, SCA and reciprocal were highly significant for all the traits at both temperature regimes except GCA mean square for stomatal conductance and transpiration rate at high temperature. Significant mean squares attributable to GCA, SCA and reciprocal for the traits depicted significant variability. The GCA/SCA variance ratio less than one further exhibited that all traits were controlled mainly by non-additive genes at both temperature regimes except GDDs to 50% maturity, which was predominantly under additive genes effect (Table 3a, b). Earlier, plant breeders used combining ability analysis for evaluating their breeding materials to find out lines/varieties having good combining ability for various agronomic traits for the improvement of self and cross pollinated crops (Barati *et al*., 2004; Borghi & Perenzin, 1994; Choukan, 1999; Hussain *et al*., 2006; Khan *et al*., 2008; Khan *et al*., 2009; Prakash & Ganguli, 2004; Sain *et al*., 1992; Talleei & Kochaksaraei, 1999).

A lot of information on physiological traits for high temperature tolerance in maize is available (Herrero & Johnson, 1980; Sinsawat *et al*., 2006; Smith, 1996; Steven *et al*., 2002) but the literature regarding genetic evaluation of these traits is scanty. Leaf conductance was reported under control of both additive and non-additive genetic effects (Rebetzke, 2003). Number of days to 50% tasseling was reported under additive gene action (Prakash *et al*., 1999). GCA and SCA effects were significant for days to pollen shedding (GDDs to 50% tasseling) depicting importance of both additive and non-additive genes effect for the control of this trait (Barati *et al.,* 2004). Reciprocal effects were significant for all the traits at high temperature stress depicting the significant contribution of cytoplasmic inheritance in controlling these traits (Talleei & Kochaksaraei, 1999). Contradictory results may be due to different genetic background of the cultivars used and different environmental conditions.

The inbred line "935006" was found best general combiner for grain yield plant^{-1} and turgor potential due to positive GCA effects along with better mean performance but poor combiner for cell membrane thermostability, growing degree days to 50% tasseling and maturity due to negative GCA effects for these traits (Table 4a, b). Negative values for CMT % age depicted tolerance to high temperature stress, less growing degree-days to tasseling and maturity denoted short vegetative and maturity durations, respectively at both the temperature regimes. The inbred line "R2304-2" was found good general combiner for grain yield plant^{-1}, cell membrane thermostability % age (good general combining ability for cell membrane thermostability was undesirable because it depicted susceptibility against high temperature stress) but negative GCA effects for growing degree-days to 50% tasseling and physiological maturity (desirable at high temperature stress due to short duration of vegetative and maturity periods). Negative GCA effects for stomatal conductance and transpiration rate at both temperature regimes showed poor general combining ability of this line for these traits.

Table 1a. Means, LSD and Coefficient of variation of physiological traits of maize in a 6×6 diallel cross maize diallel crosses.

Sr. No.	Inbred lines/crosses	CMT %age		Stomatal conductance (S cm^{-1})		Transpiration rate (µg cm^{-2} S^{-1})	
		N T	HTS	NT	H TS	NT	HTS
1.	**F 165-2-4**	**62.07**	**54.12**	**0.099**	**0.693**	**1.346**	**7.389**
2.	F 165-2-4 × 935006	54.96	47.87	**0.065**	**0.524**	**0.952**	**6.297**
3.	F 165-2-4 × F 101-7-2-6	61.43	55.80	0.064	0.702	0.997	7.372
4.	F 165-2-4 × R 2205-5-4	58.60	50.83	0.079	0.596	1.090	7.029
5.	F 165-2-4 × F 113-1-1-1	57.91	52.47	0.054	0.585	0.885	6.991
6.	F 165-2-4 × R 2304-2	67.15	52.17	0.081	0.702	1.096	7.505
7.	935006 × F 165-2-4	60.03	48.03	0.073	0.590	0.925	8.315
8.	**935006**	**53.28**	**44.67**	**0.068**	**0.915**	**1.037**	**9.537**
9.	935006 × F 101-7-2-6	69.37	46.50	**0.080**	**0.602**	**1.069**	**7.131**
10.	935006 × R 2205-5-4	68.88	65.90	0.069	0.708	1.026	8.223
11.	935006 × F 113-1-1-1	61.45	53.3	0.067	0.634	0.974	7.382
12.	935006 × R 2304-2	75.24	50.63	**0.057**	**0.768**	**1.002**	**7.738**
13.	F 101-7-2-6 × F 165-2-4	66.33	65.00	0.052	0.561	0.991	7.052
14.	F 101-7-2-6 × 935006	68.17	63.17	0.065	0.537	0.765	6.375
15.	**F 101-7-2-6**	**66.24**	**64.65**	**0.057**	**0.659**	**1.142**	**7.366**
16.	F 101-7-2-6 × R 2205-5-4	72.90	62.33	0.080	0.578	1.329	6.855
17.	F 101-7-2-6 × F 113-1-1-1	73.50	61.82	0.073	0.822	1.059	8.586
18.	F 101-7-2-6 × R 2304-2	74.75	65.63	0.063	0.567	1.078	6.692
19.	R 2205-5-4 × F 165-2-4	67.13	56.70	0.097	0.649	1.980	6.148
20.	R 2205-5-4 × 935006	74.80	68.37	0.069	0.524	1.082	6.453
21.	R 2205-5-4 × F 101-7-2-6	64.99	60.13	0.116	0.573	2.302	6.707
22.	**R 2205-5-4**	**46.00**	**43.08**	**0.088**	**0.781**	**2.606**	**6.928**
23.	R 2205-5-4 × F 113-1-1-1	57.21	56.60	0.076	0.601	3.313	6.963
24.	R 2205-5-4 × R 2304-2	53.48	44.90	0.089	0.664	2.160	7.513
25.	F 113-1-1-1 × F 165-2-4	50.81	47.97	0.047	0.633	0.552	7.503
26.	F 113-1-1-1 × 935006	65.78	60.60	0.058	0.596	0.819	6.887
27.	F 113-1-1-1 × F 101-7-2-6	78.96	69.13	0.051	0.554	0.746	7.724
28.	F 113-1-1-1 × R 2205-5-4	63.84	59.88	0.046	0.582	1.131	6.744
29.	**F 113-1-1-1**	**78.65**	**70.40**	**0.045**	**0.636**	**0.543**	**6.665**
30.	F 113-1-1-1 × R 2304-2	71.96	56.37	0.042	0.543	0.517	6.784
31.	R 2304-2 × F 165-2-4	73.19	52.90	0.053	0.652	0.757	7.864
32.	R 2304-2 × 935006	68.63	55.50	**0.046**	**0.577**	**0.658**	**5.543**
33.	R 2304-2 × F 101-7-2-6	77.12	68.43	0.045	0.742	0.630	9.020
34.	R 2304-2 × R 2205-5-4	67.87	63.12	0.060	0.604	0.835	7.880
35.	R 2304-2 × F 113-1-1-1	74.75	70.47	0.065	0.583	0.893	7.670
36.	**R 2304-2**	**84.40**	**79.16**	**0.048**	**0.594**	**0.672**	**6.004**
	Grand mean	66.44	58.24	0.066	0.634	1.1338	7.242
	CV %	5.39	5.23	8.23	13.18	13.33	13.18
	LSD at 0.05	5.835	6.386	0.0089	0.1691	0.247	1.555

NT = Normal temperature, HTS = High temperature stress

Table 2a. Mean squares attributed to genotypes, general combining ability and specific combining ability and reciprocal effects of parental inbred lines.

Variation due to	CMT %		Stomatal conductance		Transpiration rate		Turgor potential	
	NT	HTS	NT	HTS	NT	HTS	NT	HTS
Genotypes	230.9606**	228.8362**	0.0009**	0.0233**	1.0997**	0.0538**	0.0561**	0.2182**
GCA	242.2995**	192.3979**	0.0009**	0.0021^{NS}	1.2834**	0.252 ^{NS}	0.0588**	0.0478**
SCA	76.7057**	76.9023**	0.0002**	0.0102**	0.1222**	0.8046**	0.0129**	0.0786**
Reciprocal	22.1643**	36.9489**	0.0002**	0.0072**	0.3053**	0.7088**	0.0111**	0.0752**
Error	8.4740	8.5300	0.00001	0.0036	0.0077	0.3039	0.0050	0.0076

*Significant ($p \leq 0.05$), **Highly significant ($p \leq 0.01$), NT=Normal temperature, HTS=High temperature stress

Table 2b. Mean squares attributed to genotypes, general combining ability and specific combining ability and reciprocal effects of parental inbred lines.

Variation due to	GDDs to 50% tasseling		GDDs maturity		Grain yield plant^{-1}	
	NT	HTS	NT	HTS	NT	HTS
Genotypes	11465.79**	10223.29**	9239.172**	12148.36**	1350.58**	1529.382**
GCA	10584.5**	8939.783**	15779.41**	20644.05**	547.494**	1213.44**
SCA	4282.317**	4031.814**	1084.054**	1757.192**	739.028**	675.898**
Reciprocal	1109.6**	938.1953**	829.984**	813.7043**	128.923**	109.145**
Error	113.5270	265.384	564.282	164.615	10.062	11.6689

*Significant ($p \leq 0.05$), **Highly significant ($p \leq 0.01$), NT=Normal temperature, HTS=High temperature stress

Table 3a. Estimates of variance components relative to general, specific combining ability and reciprocal effects of parental inbred lines following Griffing's approach method 1 model 1.

Variation due to	CMT %		Stomatal conductance		Transpiration rate		Turgor potential	
	NT	HTS	NT	HTS	NT	HTS	NT	HTS
□^{2} **g**	13.994	9.82631	0.0001	-0.001	0.1063	-0.004	0.0045	0.0034
□^{2} **s**	42.054	42.8687	0.0002	0.0066	0.1145	0.5007	0.0079	0.0710
□^{2} **r**	10.945	16.9380	0.0001	0.0018	0.1488	0.2025	0.0030	0.0338
□^{2} **e**	8.474	8.5300	0.00001	0.0036	0.0077	0.3039	0.0050	0.0076
□^{2} **g**/□^{2} **s**	0.33	0.2300	0.500	-0.020	0.930	-0.010	0.570	0.0500

NT=Normal temperature, HTS=High temperature stress. GDDs= Growing degree days

Table 3b. Estimates of variance components relative to general, specific combining ability and reciprocal effects of parental inbred lines following Griffing's approach method 1 model 1.

Variation due to	GDDs to 50% tasseling		GDDs to 50% maturity		Grain yield plant^{-1}	
	NT	HTS	NT	HTS	NT	HTS
□^{2} **g**	872.58	722.87	1267.97	1706.62	44.786	46.580
□^{2} **s**	6168.79	3776.34	519.77	1592.58	728.965	385.68
□^{2} **r**	489.04	336.41	132.845	324.54	59.431	48.74
□^{2} **e**	113.5	265.38	564.300	164.600	10.062	11.669
□^{2} **g**/□^{2} **s**	0.2100	0.1900	2.4400	1.0700	0.0600	0.012

NT=Normal temperature, HTS=High temperature stress. GDDs= Growing degree days

Table 4a. Estimates of general combining ability effects for physiological traits at normal and high temperature stress.

Inbred line	CMT %		Stomatal conductance		Transpiration rate		Turgor potential	
	NT	HTS	NT	HTS	NT	HTS	NT	HTS
F 165-2-4	-4.632	-4.852	0.006	-0.003	-0.061	-0.007	-0.005	0.026
935006	-1.952	-3.916	-0.001	0.0230	-0.0192	0.206	0.114	0.046
F 101-7-2-6	3.561	4.254	0.001	-0.004	-0.034	0.108	-0.032	-0.054
R 2205-5-4	-4.631	-1.772	0.013	0.003	0.651	-0.215	0.030	0.028
F 113-1-1-1	1.350	2.776	-0.011	-0.017	-0.140	-0.032	-0.009	-0.101
R 2304-2	6.305	3.520	-0.008	-0.002	-0.224	-0.061	-0.097	0.056
SE (g_i-g_j)	1.655	1.4027	0.0025	0.0480	0.070	0.441	0.0567	0.0700

NT = Normal temperature, HTS = High temperature stress

Table 4b. Estimates of general combining ability effects for physiological traits at normal and high temperature stress.

Inbred lin	GDDs to 50% tasseling		GDDs to 50% maturity		Grain yield plant^{-1}	
	NT	HTS	NT	HTS	NT	HTS
F 165-2-4	28.432	27.546	46.13	60.102	2.464	2.100
935006	-41.244	-41.782	-44.896	-57.518	6.694	13.414
F 101-7-2-6	13.260	22.744	19.703	16.778	-8.383	-11.48
R 2205-5-4	6.022	-3.820	-1.687	-8.054	-7.101	-5.760
F 113-1-1-1	25.592	16.066	21.027	19.546	-1.110	-7.948
R 2304-2	-32.117	-20.754	-40.161	-30.865	7.437	9.443
SE (g_i-g_j)	8.5260	13.035	19.010	10.2660	2.5380	2.7329

NT = Normal temperature, HTS = High temperature stress

The inbred line “F165-2-4” had positive GCA effect for grain yield plant^{-1}, growing degree-days to 50% tasseling and maturity but negative GCA effects for CMT %age and transpiration rate at both temperature regimes. Therefore it proved good general combiner for grain yield plant^{-1}, growing degree-days to 50% tasseling and physiological maturity but poor combiner for CMT % age and transpiration rate at both temperature regimes. It means that its manipulation in hybridization might produce higher grain yield with more growing degree-days to 50% tasseling and physiological maturity. It had positive GCA effects for stomatal conductance at normal temperature but negative at high temperature which depicted that utilization of this inbred line at normal temperature might produce crosses of higher stomatal conductance but at high temperature stress it may give forth cross combination of low transpiration rate also. It also had negative GCA effects for turgor pressure at normal temperature but positive at high temperature. Therefore, this inbred line would maintain turgor pressure in crosses at high temperature. Higher turgor pressure at high temperature stress is an excellent trait for effective growth rate at high temperature stress. That is why it was excellent cross at high temperature stress. All other inbred lines were recorded as poor combiners for grain yield plant^{-1} along with some other traits due to negative GCA effects. Therefore, these crosses proved worthless for grain yield improvement at both temperature regimes. The earlier breeding efforts were also made looking for best general combiners for utilizing in development of higher yielding hybrids/synthetics/varieties (Borghi & Perenzin, 1994; Choukan, 1999; Griffing, 1956; Khan *et al*., 2009; Prakash *et al.*, 2004**;** Sain, *et al.*, 1992 and Sain *et al.*, 1997).

The hybrid "F165-2-4×935006" proved good specific combiners for grain yield plant^{-1} and growing degree-days to 50% maturity due to positive SCA effects for these traits but poor combiner for growing degree days to tasseling (GDDs for vegetative phase) and cell membrane thermostability % age at both temperature regimes (Table 5a, b). This cross proved higher yielder with shorter vegetative growth period, medium crop period for physiological maturity and tolerant to high temperature stress (as it gave less values for cell membrane thermostability % age), optimal stomatal conductance and turgor pressure.

The hybrid "F165-2-4×F113-1-1-1" was also good specific combiners for grain yield plant^{-1} but poor combiner for cell membrane thermostability % age (Table 5a, b), stomatal conductance, growing degree-days to tasseling (GDDs for vegetative phase), growing degree-days to 50% maturity at both temperature regimes. This cross recorded higher mean performance for grain yield plant^{-1} with shorter vegetative and physiological maturity phases and tolerant to high temperature stress (due to negative SCA effects for cell membrane thermostability % age), higher stomatal conductance, transpiration rate and turgor pressure and lesser growing degree days to tasseling and growing degree days to 50% maturity. Other crosses F165-2-4 × R2304-2, F165-2-4 × F113-1-1-1, 935006 × F101-7-2-6, 935006 × R2304-2 and R2205-5-4 × R2304-2 had also good specific combining ability and better mean performance for grain yield plant^{-1} along with optimum mean performances for some other traits studied at both temperature regimes.

The good specific combining ability crosses for grain yield plant^{-1} involved at least one of the good general combining parents (935006, R2304-2 or F165-2-4) for this trait. Therefore, high × high and low × high GCA parents performed better in SCA estimation. It was inferred that the utilization of parent with best GCA produces good hybrid combinations. In case of mean values, the hybrids having maximum SCA also showed appreciable mean values for the traits. Parents with high GCA were found more effective to produce high yielding hybrids. Other crosses were poor combiners and did not show consistency in their performance for grain yield plant^{-1} and other traits. Therefore, these were of least interest for the breeders.

The reciprocals of the crosses F165-2-4 × F101-7-2-6, F165-2-4 × R2205-5-4, F165-2-4 × F113-1-1-1, F165-2-4 × R2304-2 and 935006 × F113-1-1-1 had positive reciprocal effects but only F165-2-4 × F113-1-1-1 and F165-2-4 × R2304-2 had better grain yield plant^{-1} (grand mean+Cd_1) due to maternal effects. Therefore, lateral two crosses may also be considered for grain yield plant^{-1} (Table 6a, b).

Conclusion

935006 followed by R2304-2 and F165-2-4 proved good general combiners for grain yield plant^{-1}. 935006 followed by R2304-2 were also tolerant to high temperature stress due to poor GCA for CMT % age. 935006 **×** R2304-2, F 1652-4 × 935006, F165-2-4 × F113-1-1-1, F165-2-4 × R2304-2, 935006 × F101-7-2-6 and R2205-5-4 × R2304-2 had good SCA effects with excellent mean performances for grain yield plant^{-1} along with most of the traits studied at both the temperature regimes. 935006 × R2304-2, F165-2-4 × F113-1-1-1 and F165-2-4 × R2304-2 including their reciprocals performed better for SCA and reciprocal effects with better mean performance for grain yield improvement at both temperature regimes. Good performing crosses involved at least one good general combing parent in most of the cases. 935006 × R2304-2 and its reciprocal proved best at both temperature regimes for improvement in grain yield plant^{-1} and other physiological traits.

Table 5a. Estimates of specific combining ability effects for physiological traits at normal and high temperature stress.

Cross no.	CMT %		Stomatal conductance		Transpiration rate		Turgor potential	
	NT	HTS	NT	HTS	NT	HTS	NT	HTS
1×2	-2.362	-1.298	-0.002	-0.098	0.054	-0.138	-0.102	0.163
1×3	-1.484	2.981	-0.014	0.004	-0.049	-0.134	0.001	-0.155
1×4	5.689	2.774	-0.003	-0.012	-0.192	-0.435	-0.027	0.214
1×5	-8.796	-5.714	-0.011	-0.006	-0.218	0.041	0.075	-0.242
1×6	2.058	-4.151	0.003	0.047	0.074	0.507	-0.088	0.191
2×3	0.722	-3.521	0.007	-0.084	0.005	-0.807	0.099	-0.087
2×4	11.982	14.805	-0.010	-0.044	-0.542	0.101	0.062	-0.271
2×5	-2.225	0.084	0.007	-0.026	0.091	-0.285	0.040	0.220
2×6	1.139	-4.554	-0.006	0.017	0.108	-0.750	-0.082	0.086
3×4	3.577	0.733	0.018	-0.057	0.061	-0.358	-0.107	0.216
3×5	4.879	0.438	0.006	0.076	-0.062	0.833	-0.106	0.037
3×6	-0.370	1.243	-0.005	0.026	-0.027	0.563	0.070	0.123
4×5	-2.631	-0.769	-0.008	-0.028	0.573	-0.145	0.040	0.111
4×6	-7.441	-5.755	0.003	-0.001	-0.067	0.726	-0.020	-0.052
5×6	-0.735	-0.886	0.006	-0.052	-0.069	0.074	-0.003	0.092
SE($S_{ij}-_{ik}$)	3.7013	3.1365	0.006	0.1073	0.1566	0.441	0.1267	0.1564

NT = Normal temperature, HTS = High temperature stress
1 = F165-2-4, 2 = 935006, 3 = F101-7-2-6, 4 = R2205-5-4, 5 = F113-1-1-1 and 6 = R2304-2

Table 5b. Estimates of specific combining ability effects for physiological traits at normal and high temperature stress.

Cross no.	GDDs to 50% tasseling		GDDs to 50% maturity		Grain yield plant^{-1}	
	NT	HTS	NT	HTS	NT	HTS
1×2	-49.034	-43.674	4.036	18.043	11.476	6.366
1×3	4.262	-0.149	12.254	2.020	-11.632	-1.028
1×4	-16.250	-15.185	9.386	-2.455	4.120	8.413
1×5	-45.270	-35.555	-34.003	-52.555	21.406	11.308
1×6	-35.161	-39.519	-29.224	6.440	6.425	13.730
2×3	-51.109	-69.388	-31.454	-20.893	12.845	20.211
2×4	5.963	2.909	9.941	31.115	-2.820	-5.149
2×5	2.592	5.173	26.380	37.431	0.768	5.002
2×6	-11.657	7.009	11.659	9.793	15.282	14.813
3×4	16.650	18.801	12.512	21.476	20.167	-10.043
3×5	30.855	21.998	3.357	3.309	7.890	-10.503
3×6	-21.128	6.583	28.894	15.854	2.871	8.531
4×5	-1.524	8.145	5.355	6.151	-1.991	8.376
4×6	-8.551	-18.452	13.218	6.796	16.736	14.459
5×6	-22.510	-35.271	-6.246	1.946	-0.576	2.960
SE($S_{ij}-_{ik}$)	19.064	29.148	42.502	22.9562	5.6760	6.1109

NT =Normal temperature, HTS = High temperature stress
1 = F165-2-4, 2 = 935006, 3 = F101-7-2-6, 4 = R2205-5-4, 5 = F113-1-1-1 and 6 = R2304-2

Table 6a. Estimates of reciprocal effects for physiological traits at normal and high temperature stress.

Reciprocal cross	CMT %		Stomatal conductance		Transpiration rate		Turgor potential	
	NT	HTS	NT	HTS	NT	HTS	NT	HTS
2×1	-2.533	-0.083	-0.004	-0.033	0.013	-1.009	-0.005	-0.173
3×1	-2.450	-4.600	0.006	0.071	0.003	0.160	0.026	-0.158
4×1	0.600	-8.333	0.007	0.033	0.152	0.378	-0.025	0.227
5×1	-4.265	-2.933	-0.009	-0.026	-0.445	0.441	0.144	0.093
6×1	-2.958	-1.233	0.000	0.092	-0.028	0.885	0.048	0.275
3×2	3.955	1.098	-0.018	0.002	-0.486	0.074	-0.129	0.272
4×2	3.550	2.250	0.004	-0.024	0.167	-0.256	0.073	-0.198
5×2	-2.165	-3.650	0.005	0.019	0.078	0.247	0.094	0.137
6×2	-2.728	-3.658	0.011	0.134	0.157	0.431	-0.073	0.283
4×3	-3.317	-1.642	0.015	0.009	1.091	0.110	0.068	-0.227
5×3	-3.017	-0.367	0.014	0.025	0.169	-0.179	0.030	0.035
6×3	3.305	-2.433	0.005	0.095	0.172	1.098	-0.073	-0.060
5×4	-1.182	-1.400	0.009	-0.088	0.224	-1.1664	0.012	-0.260
6×4	-7.195	-9.110	0.015	0.030	0.663	-0.183	0.070	0.193
6×5	-1.395	-7.050	-0.011	-0.020	-0.188	-0.443	-0.073	0.012
SE(r_{ij}-r_{ik})	4.055	3.436	0.006	0.118	0.1716	1.080	0.139	0.173

NT =Normal temperature, HTS = High temperature stress
1 = F165-2-4, 2 = 935006, 3 = F101-7-2-6, 4 = R2205-5-4, 5 = F113-1-1-1 and 6 = R2304-2

Table 6b. Estimates of reciprocal effects for physiological traits at normal and high temperature stress.

Reciprocal cross	GDDs to 50% tasseling		GDDs to 50% maturity		Grain yield plant^{-1}	
	NT	HTS	NT	HTS	NT	HTS
2×1	8.633	2.050	-24.142	-3.017	-7.718	-0.218
3×1	-7.100	-17.500	-9.892	-9.900	1.280	1.253
4×1	6.133	9.733	-2.792	-5.767	3.447	6.247
5×1	2.500	11.933	-24.417	-25.883	9.180	6.632
6×1	-64.017	-56.833	-28.383	-33.067	15.190	19.47
3×2	1.158	11.917	10.433	12.600	0.460	-1.765
4×2	12.550	11.917	-3.742	2.617	-2.072	-1.352
5×2	-6.900	-11.950	-44.700	-43.650	18.003	7.057
6×2	0.000	17.167	-3.125	3.167	-1.102	-1.923
4×3	4.667	12.250	4.600	6.133	4.015	-14.25
5×3	-9.800	-28.867	-34.550	13.700	-2.017	-6.145
6×3	27.225	5.300	-13.958	-11.067	-9.170	3.822
5×4	45.242	-24.067	5.408	3.167	8.662	-4.895
6×4	-28.487	-27.533	7.975	12.067	-1.368	-3.423
6×5	11.458	13.733	-22.392	-4.183	-8.235	-2.290
SE(r_{ij}-r_{ik})	20.864	32.000	46.559	25.147	6.217	6.694

NT =Normal temperature, HTS = High temperature stress
1 = F165-2-4, 2 = 935006, 3 = F101-7-2-6, 4 = R2205-5-4, 5 = F113-1-1-1 and 6 = R2304-2

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