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Genetic Analysis of Heat Stress Tolerance and Association of Traits in Tropical Maize (*Zea mays* L.)

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Abstract Maize is more affected by abiotic stress especially heat stress as compared to other crop plants. In the present study, eight females and four males were crossed in NCD-II design to get 32 hybrids and these hybrids were evaluated for their combining ability, mode of gene action and association of heat adaptive traits under natural heat stress condition. The combining ability analysis revealed that the predominance of non-additive gene action for heat tolerant traits as GCA/SCA variance ratio was very low except grain yield. Among the parents, L_1 and L_2 were good general combiners for heat tolerance component traits like leaf firing, tassel blast and also for yield contributing traits. Two hybrids, $L_1 \times T_3$ and $L_4 \times T_1$ showed desirable sca effects for maximum number of traits. Association studies revealed that yield was positively associated with plant height and number of grains per cob and negatively associated with tassel blast and leaf firing under heat stress condition.

Keywords Tropical maize, Heat stress tolerance, Combining ability, Gene action, Association.

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Introduction

Maize (*Zea mays* L.) is an important cereal crop worldwide, serving as a major staple for both human consumption and animal feed. It has also become a key resource for industrial applications and bioenergy production [1]. Maize is highly productive under optimal environmental and crop management conditions. However, maize cultivation is severely affected by both biotic and abiotic stresses. Each year, an average of 15 to 20% of the potential world maize production is lost due to these stresses [2].

According to the report of Intergovernmental Panel on Climatic Change [3], global mean temperature would rise 0.3°C per decade reaching to approximately 1°C and 3°C above the present value by years 2025 and 2100, respectively and leading to global warming. Maize is at highest risk of extreame temperature compared to wheat and soybean worldwide

Table 1. List of inbred lines used as parents in generating 32 hybrids using NCD-II design.

Parental lines	Pedigree	Reaction to heat stress
L_1	(CA14515 / CA14502)-F2-10-2-B*9	Tolerant
L_2	POOL16BNSEQC3F32×37-4-1-2-1-B*8	Tolerant
L_3	POOL16BNSEQC3F37×3-2-2-3-2-B*5	Tolerant
L_4	P31C4S5B-6-*-*-3-1-B*8-3-B*6	Tolerant
L_5	DTPYC9-F46-3-9-1-2-2-1-3-B*9	Tolerant
L_6	CA14514-8-3-2-B*6	Susceptible
L_7	POOL16BNSEQC3F22×1-3-2-2-2-B*5	Susceptible
L_8	DTPYC9-F46-1-7-1-2-1-2-2-B*7	Tolerant
T_1	(DT/LN/EM-46-3-1×CML311-2-1-3)-B-F216-1-1-1-B*5	Tolerant
T_2	WLS-F190-2-1-1-B-2-B*5	Tolerant
T_3	(CML20×CML329)-17-3-3-1-B*11	Susceptible
T_4	CA14514-9-6-3-B*4	Susceptible

[4]. High temperatures have profound impact on yield compared to drought in maize [5]. Increase in temperature by 2°C would reduce maize yield by 13% while a 20% increase in intraseasonal variation in rainfall, would reduce maize yield by only 4.5% [6].

The total yield loss depends on the occurrence of stress during crop growth, as well as the duration and the severity of the stress. The optimal temperatures for growth of tropical maize is between 25°C to 33°C , while night temperatures range between 17°C to 23°C [7]. The temperature above 35°C for a long period is considered to be unfavorable for maize cultivation and over 40°C cause irreversible damage to yield levels.

High temperatures during flowering reduce the quantity and viability of pollen produced resulting in reduced fertilization of ovules and therefore reduced sink capacity [5]. Increasing temperature also accelerated developmental rates for both anthesis and maturity [8]. Kaur et al. [9] reported that traits like tassel blast, leaf firing and leaf senescence expressed under heat stress showed significant negative association with grain yield.

The adverse effects of heat stress can be mitigated by developing crop plants with improved thermotolerance using various genetic approaches. For this purpose, however, a through understanding of physiological responses of plants to high temperature, mechanisms of heat tolerance and possible strategies for improving crop thermotolerance is imperative [10]. Further, there is no extensive breeding effort especially for heat stress in tropical and subtropical maize [11]. Genetic improvement in tropical maize under heat stress can be achieved by identification of diverse population and going for selection for primary traits such as yield in a target environment and for secondary traits like flowering, cell membrane stability, chlorophyll content and senescence that show strong association with the yield [12]. Thus, there is a need to undertake breeding work to develop heat stress tolerant inbreds / hybrids. In the present study, an attempt was made to elucidate the genetics of heat tolerance and characters associated with heat tolerance.

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Materials and Methods

The experiment was carried out at Agriculture College Farm, Bheemarayanagudi (16°44´N latitude and 76°47´E longitude with an altitude of 458 m above mean sea level) of University of Agriculture Sciences-Raichur, Karnataka, India during spring 2015. The ex-

Table 2. ANOVA and Variance component for different traits of tropical maize hybrids under heat stress condition. * and **Significance at p = 0.05 and p = 0.01, respectively, AD–Anthesis date, SD–Silking date, ASI–Anthesis to silking interval, TB–Tassel balst (%), LF–Leaf firing (%), PH–Plant height (cm), EH–Ear height (cm), EL–Ear length (cm), EG–Ear girth (cm), NGC–No. of grains per cob, SP–Shelling %, TW–Test weight (g), GY–Grain yield per plant (g).

Source of	df	AD	SD	ASI	TB	LF	PH	EH
Replication	1	1.27	0.00	1.26	8.45	40.08	870.25*	123.77
Hybrids	31	13.36	15.99*	10.64	1114.05*	402.88**	419.83**	122.28*
Females	7	7.84	9.89	12.06	1348.19	356.97	413.42	81.46
Males	3	34.01	37.04	10.56	1054.69	499.63	1818.43**	448.30**
F × M	21	12.25	15.01*	10.18	1044.48	404.37**	222.17	89.30
Errors	31	9.85	7.55	7.14	609.24	114.47	158.05	63.93
Total	63	11.44	11.58	8.77	848.10	255.21	298.17	93.59
σ^2 GCA		0.03	0.03	0.01	2.07	1.04	5.90	0.98
σ^2 SCA		1.20	3.73	1.52	217.61	14.94	32.06	12.69
σ^2GCA / σ^2SCA		0.02	0.08	0.06	0.09	0.06	0.18	0.07

Table 2. Continued.

Source of	df	EL	EG	NGC	SP	T W	GY
Replication	1	2.68	0.60	1359.76	21.12	4.10	15.64
Hybrids	31	5.13**	1.37**	6838.12**	33.03	14.51*	637.69
Females	7	5.03	1.07	4615.98	41.01	15.62	916.07
Males	3	21.34**	0.76	24512.06*	52.60	42.59*	1277.20
F×M	21	2.85**	1.55**	5053.99	27.57	10.14	453.52
Errors	31	0.89	0.55	3445.93	18.97	6.00	456.82
Total	63	3.00	0.95	5081.99	25.92	10.16	538.82
σ^2 GCA		0.06	0.05	53.18	0.16	0.13	5.48
σ^2 SCA		0.97	0.50	804.03	4.30	2.06	1.64
σ^2GCA / σ^2SCA		0.06	0.10	0.06	0.03	1.64	3.34

perimental material consist 32 hybrids developed at CIMMYT–Asia Regional Program-Hyderabad, India using eight tropical female lines and four male lines crossed in NCD-II design (Table 1). These hybrids were evaluated with three checks viz., 31Y45, BIO9544, D2244 in alpha lattice design with two replications. Each plot consisted of two rows of 4m length with spacing of 60 cm×20 cm. The recommended cultural practices were followed during crop growth period to raise a healthy crop.

The following traits viz., days to 50% anthesis, days to 50% silking and ears per plot were recorded on plot basis. Whereas, plant height (cm), ear height (cm), number of grains per cob, ear length (cm), ear girth (cm), test weight (g) and shelling per cent were recorded on five selected representative plants as per the standard procedures mentioned in the manual [13]. Grain yield per plant (g) was calculated by dividing the grain yield per plot by total number of plants in the plot and finally it was adjusted to the moisture content of 12.5% and scaled to tons ha^{-1}.

The estimates of general combining ability (GCA) for females, males and specific combining ability (SCA) for crosses were estimated according to Comstock and Robinson [14] and the phenotypic correlation coefficients for various characters were calculated as per the method suggested by Al-Jibouri et al. [15]. The analysis was performed using WINDOSTAT 9.2. The weather data during crop growth period indicated that the most of the cropping period was under heat stress, which was indicated by the combination of high temperature (Tmax > 35°C and Tmin > 22°C) and RH (< 40%) leading to proper evaluation of hybrids under high temperature.

Table 3. General combining ability (gca) effects of parents for various traits under heat stress condition. *, ** Significant at 5% and 1%, respectively.

Sl. No.	Parents	Anthesis date	Silking date	ASI	Tassel blast (%)	Leaf firing (%)	Plant height (cm)	Ear height (cm)
				Females				
1	L_1	–0.39	–0.93	– 0.54	5.96	– 14.29**	– 7.97	– 3.82
2	L_2	1.73	0.56	– 1.17	– 24.64**	– 5.97	4.03	0.54
3	L_3	–1.39	0.18	1.57	4.07	– 1.26	– 10.09*	– 5.70
4	L_4	– 0.76	–0.06	0.70	– 7.16	– 3.72	0.40	0.54
5	L_5	0.23	0.06	– 0.17	– 8.78	– 0.71	9.28	1.54
6	L_6	0.98	0.56	– 0.42	13.24	4.42	0.03	1.23
7	L_7	– 0.01	1.68	1.70	14.43	– 1.07	– 4.34	1.42
8	L_8	– 0.39	–2.06*	– 1.67	2.85	– 5.97	8.65	4.17

Table 3. Continued.

Sl. No.	Parents	Ear length (cm)	Ear girth (cm)	No. of grains/ cob	Shelling (%)	Test weight (g)	Grain yield/ plant (g)
				Females			
1	L_1	– 0.31	– 0.04	– 33.36	–1.63	0.30	16.23*
2	L_2	–0.20	0.78**	28.14	4.30**	1.88*	18.87*
3	L_3	0.68*	– 0.18	12.39	1.12	– 0.54	– 1.28
4	L_4	0.58	– 0.33	– 4.10	– 1.68	– 0.56	0.59
5	L_5	0.04	– 0.31	15.89	– 1.98	– 2.57**	– 7.01
6	L_6	–1.70**	0.14	– 33.86	– 1.38	1.64	3.13
7	L_7	0.20	0.14	– 7.60	– 0.77	0.06	– 6.73
8	L_8	0.70*	– 0.21	22.51	2.03	– 0.21	8.67

Table 3. Continued.

Sl. No.	Parents	Anthesis date	Silking date	ASI	Tassel blast (%)	Leaf firing (%)	Plant height (cm)	Ear height (cm)
				Males				
9	T_1	– 0.26	0.43	0.70	– 7.47	– 0.48	– 3.34	1.35
10	T_2	– 0.64	–1.68*	– 1.04	5.08	– 3.18	15.59**	6.92**
11	T_3	2.11*	1.87*	– 0.23	– 6.33	– 4.35	– 3.72	– 4.07*
12	T_4	– 1.20	–0.62	0.57	8.71	– 8.02**	– 8.53*	– 4.20*
CD at 5% female		2.26	1.98	1.93	17.79	7.71	9.06	5.76
CD at 1% female		3.04	2.66	2.60	23.94	10.38	12.19	7.75
SEm±		1.10	0.97	0.94	8.72	3.78	4.44	2.82
CD at 5% male		1.59	1.40	1.36	12.58	5.45	6.41	4.07
CD at 1% male		2.15	1.88	1.83	16.93	7.33	8.62	5.48
SEm±		0.78	0.68	0.66	6.17	2.67	3.14	1.99

Table 3. Continued.

Sl. No.	Parents	Ear length (cm)	Ear girth (cm)	No. of grains/ cob	Shelling (%)	Test weight (g)	Grain yield/ plant (g)
				Males			
9	T_1	0.24	– 0.07	– 10.92	– 1.61	– 0.36	0.29

Table 3. Continued.

Sl. No.	Parents	Ear length (cm)	Ear girth (cm)	No. of grains/ cob	Shelling (%)	Test weight (g)	Grain yield/ plant (g)
				Males			
10	T_2	0.75**	0.27	48.07**	0.85	– 1.03	8.60
11	T_3	0.70**	– 0.24	8.57	– 1.38	– 1.00	12.37*
12	T_4	– 1.69**	0.04	– 45.73**	2.14	2.40**	3.47
CD at 5% female		0.68	0.53	42.32	3.14	1.76	15.41
CD at 1% female		0.91	0.72	56.95	4.22	2.37	20.73
SEm±		0.33	0.26	20.75	1.54	0.86	7.55
CD at 5% male		0.48	0.37	29.93	2.22	1.25	10.89
CD at 5% male		0.64	0.51	40.27	2.98	1.68	14.66
SEm±		0.23	0.18	14.67	1.08	0.61	5.34

Further, Vapor Pressure Deficit (VPD) was also calculated [16] to measure drying power of the air around crop canopy which plays a key role in the overall effect of high temperatures on plant tissues as it indicates the deficit between the amount of moisture present in the air at a given air temperature and the amount of moisture the air can hold when it is fully saturated [13]. VPD at experimental site was > 3.00 k Pa (>2.5 k Pa is considered to be under heat stress) during 8th, 9th and 10th weeks which coincided with flowering period of the crop (data not shown).

Results and Discussion

Analysis of variance for combining ability revealed that variance due to males was highly significant for most of the traits indicating that wide variability among the male parents for different traits. The female × male interaction was highly significant for silking date, leaf firing and ear girth indicating the presence of heterosis in the hybrids (Table 2).

The variance due to SCA were higher than the GCA variances for all the traits indicating preponderance of non-additive gene action in the inheritance of these traits except grain yield (Table 2). This fact was supported by low GCA variance to SCA variance ratio. The predominance of non-additive gene action for controlling these traits were also reported by Kaur et al. [9] for plant height, ear height, anthesis date, silking date, leaf firing, tassel blast ; Kaur and Saxena [17] for anthesis date, silking date and 75% brown husk maturity ; Tassawer et al. [18] for plant height, tassel blast and leaf firing. This suggests that greater importance of non-additive gene action in expression of these traits and further the opportunity for exploitation of heterosis for heat stress tolerance.

Combining ability analysis revealed that (Table 3) parent L_1 recorded desirable gca effects for grain yield (16.43) and leaf firing (-14.29). L_2 possessed highly desirable gca effects for tassel blast (-24.64), ear girth (0.78), shelling percentage (4.30), test weight (1.88) and grain yield per plant (18.87). Hence, L_1 and L_2 were identified as good general combiners for heat tolerant traits and grain yield. Parent L_8 was a good combiner for silking date and ear girth but was poor combiner for grain yield and heat tolerance thus of restricted use. The results indicated the presence of good and poor combiners in the present study. Parents viz., L_5 and L_3 also exhibited significant gca effects for plant height and ear length, respectively. Exploitation of these parents in breeding program would be effective to exploit non-additive component of genetic variation for heat tolerance traits and also grain yield in spring maize by developing heat tolerant hybrids.

Hybrids viz., $L_1 \times T_2$, $L_1 \times T_3$, $L_6 \times T_4$, and $L_7 \times T_2$, possessed highest negative sca effects for leaf firing and tassel blast (Table 4). The hybrid, $L_1 \times T_3$ was a desirable cross for most of the traits viz., plant height,

Table 4. SCA effects of top three crosses for different characters in desirable directions under heat stress condition. *, **Significant at 5% and 1%, respectively.

Characters	Crosses	SCA effects
Anthesis date	$L_4 \times T_3$, $L_6 \times T_1$, $L_6 \times T_2$	4.48, -3.86, -2.98
Silking date	$L_1 \times T_4$, $L_6 \times T_2$, $L_3 \times T_3$	3.87, -3.31, -2.50
Anthesis to silking interval	$L_6 \times T_3$, $L_1 \times T_1$, $L_4 \times T_2$	5.14*, -2.45, -3.45
Tassel blast %	$L_7 \times T_2$, $L_1 \times T_2$, $L_4 \times T_2$	37.56*, -26.98, -26.77
Leaf firing %	$L_6 \times T_4$, $L_1 \times T_2$, $L_1 \times T_3$	18.41*, -17.09*, -15.91*
Plant height (cm)	$L_1 \times T_3$, $L_4 \times T_1$, $L_1 \times T_1$	23.53*, -21.28*, 16.09
Ear height (cm)	$L_1 \times T_3$, $L_4 \times T_1$, $L_2 \times T_2$	15.92*, -13.73*, 11.79*
Ear length (cm)	$L_4 \times T_4$, $L_3 \times T_3$, $L_7 \times T_1$	2.66*, 1.56*, 1.09
Ear girth (cm)	$L_2 \times T_2$, $L_1 \times T_4$, $L_6 \times T_2$	1.31*, 1.09*, 1.02
No. of grains per cob	$L_4 \times T_4$, $L_4 \times T_3$, $L_1 \times T_2$	96.23*, 37.92, 37.67
Shelling percentage (%)	$L_4 \times T_1$, $L_1 \times T_3$, $L_6 \times T_3$	7.45*, 6.39*, 5.60
Test weight (g)	$L_1 \times T_4$, $L_1 \times T_3$, $L_3 \times T_3$	4.10*, 3.83*, 3.36
Grain yield per plant (g)	$L_4 \times T_1$, $L_1 \times T_3$, $L_2 \times T_3$	33.19*, 32.04*, -24.97

ear height, shelling percentage, test weight, grain yield as well as heat tolerance and it could be used for further evaluation under heat stress as it is high yielding and heat tolerant till stature hybrid. Another hybrid, $L_4 \times T_1$ exhibited high significant sca effects for plant height, ear height, shelling percentage and grain yield. Only $L_{36} \times L_2$ combination was desirable for ASI, which is an important trait for synchronous maturity. The cross combinations viz., $L_4 \times T_4$ and $L_3 \times T_3$ were good specific combiners for ear length and $L_2 \times T_2$ and $L_1 \times T_4$ combinations were good for ear girth. Only one hybrid $L_4 \times T_4$ exhibited desirable sca effects for number of grains per cob under heat stress condition.

Association of traits under heat stress condition

The association of traits under heat stress condition indicated that important heat tolerant traits viz., tassel blast and leaf firing exhibited negative association with yield and yield contributing traits (Data not shown). Leaf firing showed negative significant correlation with plant height (-0.260) and number of grains per cob (-0.242). Thus, as stress increased substantially plant height decreased and very low number of grains per cob could be observed resulting into significant decrease in grain yield. Tassel blast showed positive correlation with leaf firing (0.268) indicating the occurrence of these two traits under heat stress condition as a rule. The negative association of grain yield with leaf firing and tassel blast were also reported by Dinesh et al. [19]. ASI is positively correlated with plant height (0.426) and negatively correlated with yield (-0.235) indicating requirement of low ASI to get high yield. Ranganatha [20] also reported negative association of ASI with grain yield. Positive significant associations were observed between plant height and yield (0.383), number of grains per cob and yield (0.511) and also between plant height and number of grains per cob (0.576). Thus, evaluation of crosses revealed that selection of hybrids with tall, with no tassel blast and leaf firing and also with high number of grains per cob would be desirable to get high yield under heat stress conditions.

From the present study, it is concluded that most of the traits of tropical maize under heat stress conditions are controlled by non-additive gene action. Further, the traits viz., plant height and number of grains per cob could be considered as positive traits and tassel blast and leaf firing could be considered as negative traits for selection of tropical maize lines/ hybrids under heat stress condition. On the basis of gca effects of parents, L_2 (POOL16BNSEQC3F32×37-4-1-2-1- B*8) was most desirable heat tolerant parent followed by L_1 (CA14515/CA14502)-F_2-10-2-B*9). Hybrids viz., $L_1 \times T_3$, $L_4 \times T_1$ and $L_1 \times T_2$ could be exploited commercially as they showed considerable degree of heat tolerance with high yield. Further, promising hybrids could be evaluated in multilocation trials over seasons to assess their stability and potentiality for commercial cultivation besides their use in isolation of second cycle inbred lines.

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