

GENETIC ANALYSIS FOR TERMINAL HEAT STRESS IN BREAD WHEAT (*TRITICUM AESTIVUM* L. EM THELL)

MANOHAR RAM*, R. M. SINGH AND R. K. AGRAWAL
Department of Genetics and Plant Breeding,
Institute of Agricultural Sciences, BHU, Varanasi - 221 005
e-mail: manoharbhu07@gmail.com

KEYWORDS

Terminal heat stress
Gene Action
Cell membrane
thermostability
Canopy temperature
depression
Heat susceptibility index

Received on :

10.12.2013

Accepted on :

24.04.2014

*Corresponding
author

ABSTRACT

High temperature during reproductive and grain filling phases causes significant yield losses to wheat in South Asia and many other parts of the world. In present investigation out of 54 wheat cultivars/lines screen for terminal heat stress ten cultivars/lines classified as highly tolerant, tolerant, moderately tolerant, and susceptible to heat stress were mated in diallel fashion to generate 45 F₁ hybrids which were evaluated using RBD in both normal and heat stress conditions at BHU, Varanasi, India. Genetic parameters for morpho-physiological traits viz. days to 50% heading, plant height, 1000 grain weight, grain yield plant⁻¹, canopy temperature depression (CTD), cell membrane thermostability (CMS) and heat susceptibility index (HSI) were estimated. Parents HUW-234 followed by PBW-175, HD-2888 and DBW-14 in both normal and stress environment having good GCA along with high *per se* performance for canopy temperature depression and cell membrane thermostability could be used as donor for terminal heat tolerance in breeding programme. For CTD and CMS h²(ns) estimate were high. Since the identified genotypes can cope up the effect of heat stress, they can be utilized for developing heat tolerant genotypes.

INTRODUCTION

Wheat (*Triticum aestivum* Em. Thell) is the most widely consumed cereal crop worldwide. Approximately 40% of wheat areas in the temperate environments face terminal heat stress, which cover 36 million ha. (Reynolds *et al.*, 2001). Heat stress or high temperature during crop growing period restricts wheat production and productivity, particularly at germination and grain filling stage (Monu Kumar *et al.*, 2013). The optimum temperature required for growth and development of wheat is in the range 18-24°C and even short periods (5-6 days) of exposure of wheat crops to temperatures of 28-32°C may result up to 20 percent decrease in yield (Rane *et al.*, 2007). It is reported that between 2020-2050 between 26-51% of Indo Gangetic Plain may be transformed by climate changes to a heat-stressed, sub-optimal wheat production zone (Ortiz *et al.*, 2008). A number of high temperature stress-related traits have received considerable attention, in particular membrane thermostability (Saadalla *et al.*, 1990), canopy temperature depression (Blum *et al.*, 1982), heat susceptibility index for thousand grain weight (Paliwal *et al.*, 2012). The present investigation was undertaken to understanding the genetic control of these traits would aid in choosing parents for heat tolerance breeding programmes.

MATERIALS AND METHODS

In present investigation 54 wheat genotypes were screened

against heat stress out of which ten varieties (DBW-14, HUW-234, T-190, HD 2285, PBW-175, HD-2888, VEERY S, HUW-468, PAVON 76, and PBW 343) were selected on the basis of their response to heat stress using cell membrane thermostability and canopy temperature depression (Table 2). These parents were mated in diallel fashion to produce 45 F₁s. Experiment was conducted in Randomized Block Design (RBD) at two different sowing dates: 5th, December (Normal environment) and 1st January (Stress environment). Ten parents and 45 F₁s were sown in four rows (spacing 25 cm) of 3 metre length. Data on various morph-physiological parameters included day to 50% heading, plant height, grain yield⁻¹, cell membrane thermostability, canopy temperature depression and HSITGW were recorded to assess the effect of terminal heat stress on yields and yield contributing traits.

Cell membrane thermostability (CMS)

CMS was determined by the procedure suggested by Blum and Ebercon (1981) using following formula:

$$CMS (\%) = \frac{1 - (T_1/T_2)}{1 - (C_1/C_2)} \times 100$$

Where, T and C refer to treatment and control, respectively, and 1 and 2 refer to initial and final conductance readings, respectively.

Heat susceptibility index for thousand grain weight (HSITGW) was calculated using following formula suggested by Fischer and Maurer, (1978).

$$HSITGW = [(1-TGW_{HS}/TGW_{control})/D]$$

Where

$Y_{heat\ stress}$ = TGW in heat stress duration $Y_{control}$ = TGW in control duration

D (stress Intensity) = $(1 - X_{HS}/X_{control})$ X_{HS} = mean of TGW_{heat stress} of all genotypes $X_{control}$ = mean of TGW_{control} of all genotypes

Canopy temperature depression (CTD)

CT was recorded using infra red thermometer (MIKRON IR + MAN, USA). CTD was calculated as per Bahar *et al.*, 2008.

$$CTD = \text{Air temperature } (^{\circ}C) - \text{Canopy temperature } (^{\circ}C)$$

Mean values were subjected to analysis of variance to test the significance for each character as per methodology advocated by Panse and Sukhatme (1967). The estimation of components of variations, carried out by the methods of Jinks (1956) and Hayman (1954). Combining ability effects and variances of diallel crosses were carried out according to Griffing (1956) following Model I and Method II.

RESULTS AND DISCUSSION

Body weight

Breeding for terminal heat stress tolerance is becoming more important day by day owing to global warming in wheat. Unlike the breeding for biotic stresses, breeding for heat tolerance is more challenging because of complex character, which cannot be measured on its own. It has to be measured in terms of its manifestation towards changing performance of a genotype for a given trait. Knowing the fact that stress accelerates the phenological development of the plant, thereby affecting all plant characters, it becomes imperative to study the comparative changes experienced in heat stress versus non stress environments.

Wide range of variability was found for all the traits in entries (varieties and checks) and in check vs varieties which significantly differed for all the traits except grain yield plant¹ and heat susceptibility index for thousand grain weights (Table 1). Wide range of variation was found for varieties/genotypes for canopy temperature depression (2.04-7.57°C), cell membrane thermostability (28.67-70.57) and heat susceptibility index (0.31-2.08) for thousand grain weight in wheat lines offering immense scope of selection for terminal heat tolerance parameters in wheat improvement programme

under heat stress. Earlier researchers also reported significant variation among characters like CTD and CMTS (Kaur *et al.*, 2007), CTD and HSITGW (Paliwal *et al.*, 2012 and Tiwari *et al.*, 2012) and Day to 50% heading and plant height (Santosh Arya *et al.*, 2013 and Binod Kumar *et al.*, 2013).

Positive and significant value of GCA effects for all character except day to 50% heading, plant height and HSITGW are considered desirable. The mean sum of squares due to GCA and SCA were highly significant for all the traits (Table 3), which are also reported by Kamaluddin *et al.* (2007) and Dhanda and Munjal (2012). The significance of both GCA and SCA variances suggested that the both additive and non-additive types of gene action played an important role for inheritance of the traits. Patil *et al.* (1995) noticed that both GCA and SCA variances were significant for grain yield and its components pooled over three environments where as Yildirim *et al.* (2009) reported significant GCA and SCA effects for CMS. The estimates of mean sum squares due to GCA was higher for all the traits in comparison of SCA mean sum of squares in both normal and stress environments except grain yield plant¹ in normal environment and plant height in stress environment. Larger magnitude of GCA variance than SCA was also reported by Nanda *et al.*, (1983) and Kamaluddin *et al.*, (2007). Preponderance of additive gene effects was also reported by Singh *et al.*, (1990) in diallel analysis of induced mutants of bread wheat. Dhanda and Mumjal (2012) has also reported similar results for heat susceptibility index for thousand grain weight. Parents DBW-14, HUW-234, HD-2285, HUW-468 and VERRY S in both normal and stress environments were good general combiners for earliness (Table 2). Parents DBW-14 and HUW-234 in both normal and stress environments; HD-2285 in normal environment; VERRY S in stress environment were good combiners for short stature of plant. Negative and significant GCA effect was reported for plant height by Ivanovska *et al.* (2003) and Irshad *et al.* (2012). Reduced height is a very effective trait in terms of increased grain yield lodging resistance and more fertilizer responsiveness (Borlaug 1968). Parents HD-2285 and PBW-175 (normal and stress environment) having positive significant GCA for 1000-grain weight should be used for enhancing grain yield. The best general combiner for grain yield plant¹ was HUW-234 followed by T-190 as it showed highly significant and positive GCA effects in normal and stress environments. A number of workers (Kamaluddin *et al.* 2007, Rehman *et al.*, 2002 and

Table 1: Analysis of variance of 54 genotypes/ varieties (including 6 checks) using Augmented RBD for 6 traits in bread wheat

Source of Variation	DF	Mean sum of square					
		Days to 50% heading	Plant height (cm)	1000-grains weight (g)	Canopy Temperature depression	Cell membrane thermostability (%)	Heat Susceptibility Index for thousand grain weight
Block (eliminating Check + Var.)	2	1.05	0.98	0.20	0.05	2.26	0.08
Entries (ignoring Blocks)	53	68.68**	159.97**	13.60**	2.52**	118.36**	0.23*
Checks	5	161.29**	268.87**	11.42**	9.44**	770.83**	1.27**
Varieties	47	43.61**	142.57**	14.12**	1.71**	44.34**	0.12*
Checks vs. Varieties	1	783.46**	433.13**	0.18	6.14**	334.69**	0.002
ERROR	10	1.06	4.01	0.11	0.21	0.78	0.04
Mean	84.11	96.45	11.32	5.29	44.36	0.99	
Range	69.00-98.00	59.80-126.40	3.97-21.16	2.04-7.57	28.67-70.57	0.31-2.08	
SE ±	1.57	3.06	0.50	0.69	1.35	0.29	

Note; *, ** significant at 5% and 1% levels, respectively; DF = Degrees of freedom; SE = Standard Error,

Table 2: Estimates of GCA effects of 10 parents along with their mean performance, pedigree and heat response for 6 traits of diallel (excluding reciprocals) generations in bread wheat under normal and stress environments

Parents	Pedigree	E	DH	Mean	PH	Mean	GYP	Mean
			GCA		GCA		GCA	
DBW-14	RAJ-3765/PBW-343	N	-1.78**	67.33	-7.78**	64.7	-0.69**	8.24
		S	-1.29**	65.67	-2.88**	57.2	0.06 *	5.49
HUW-234	HUW-12*2/CPAN-166	N	-2.20**	64.33	-1.13**	79.7	0.35**	9.44
		S	-1.62**	65	-1.97**	60.8	0.13 **	6.2
T-190	<i>T. aestivum</i> 'Selkirk'	N	4.22**	85.67	1.97**	88.6	0.76**	6.96
		S	0.72**	74	0.22	72.2	0.34 **	4.69
HD-2285	249/HD-2160/ HD-2186	N	-2.01**	68.33	-5.83**	75.7	0.85**	6.3
		S	-1.17**	65	0.36	63.4	0.04	3.99
PBW-175	HD2160/4/JN/GAGE// JN/KAL/3/PV18/C273	N	1.11**	77	0.44	95.6	0.03	9.96
		S	-0.48*	72.67	-0.09	79.8	-0.39**	4.73
HD-2888	C-306/ <i>Triticum sphaerococcum</i> // HW 2004	N	2.58**	83.33	5.67**	90.2	-1.18**	6.34
		S	1.52**	76	0.16	73.4	0.58 **	5.68
HUW-468	CPAN1962/TONI//LIRA"S"/ PRL"S"	N	-2.36**	71.67	0.41	78	0.09 0.52 **	7.4
		S	-0.78**	67.67	0.35	67.2		4.89
Veery S	KAVKAZ/ (SIB) BUHO// KALYANSONA/BLUEBIRD/	N	-3.78**	64.67	2.60**	76	-1.11**	5.98
		S	-1.14**	63	-1.41**	58.8	-0.58 **	4.71
PAVON-76	VICAM71/CIANO67/SIETERRS66// KALYANSONA/BLUEBIRD	N	1.05**	74.33	3.70**	85.4	-0.09	6.56
		S	1.55**	75.33	3.86**	71.2	-0.49 **	3.57
PBW-343	ND/VG 1944//KAL// BB/3/YACO'S'/ 4/ VEE # 5	N	3.19**	86.33	-0.05	82.1	0.98**	7.78
		S	2.63**	76.67	1.39**	63.6	-0.21 **	3.69
SE(gi) ±		N	0.18		0.39		0.06	
		S	0.18		0.31		0.03	
SE(gig) ±		N	0.27		0.59		0.08	
		S	0.26		0.46		0.04	
Mean		N		74.3		81.6		7.5
		S		70.1		66.76		4.76

Table 2: cont.....

Parents	Pedigree	CTD		CMS		HSITGW		Heat Response
		GCA	Mean	GCA	Mean	GCA	Mean	
DBW-14	RAJ-3765/PBW-343	0.72 ***	6.97	4.96**	70.71	0.10**	0.45	Highly tolerant
		0.67**	6	5.10**	67.34			
HUW-234	HUW-12*2/CPAN-166	0.69**	6.59	4.57**	70.03	-0.15**	0.35	Highly tolerant
		0.66**	5.19	4.51**	67.75			
T-190	<i>T. aestivum</i> 'Selkirk'	0.42**	6.29	1.58** 0.66 *	62.24	0.09**	0.77	Tolerant
		0.08**	4.78		60.72			
HD-2285	249/HD-2160/ HD-2186	-0.045	6.16	3.28**	62.81	-0.15**	0.72	Tolerant
		-0.06**	5.31	3.83**	61.68			
PBW-175	HD2160/4/JN/GAGE// JN/KAL/3/PV18/C273	0.23**	6.09	2.85**	55.48	-0.17**	0.72	Moderately tolerant
		0.41**	5.52	3.28**	57.21			
HD-2888	C-306/ <i>Triticum sphaerococcum</i> // HW 2004	0.28**	6.12	0.68 *	56.3	-0.24**	1	Moderately tolerant
		0.49**	5.71	1.38**	50.7			
HUW-468	CPAN1962/TONI//LIRA"S"/ PRL"S"	0.04	6.12	2.60**	52.18	-0.15**	1.1	Moderately tolerant
		0.07**	5.06	2.74**	50.7			
Veery S	KAVKAZ/ (SIB) BUHO// KALYANSONA/BLUEBIRD/	0.21**	5.71	-0.3	53.57	-0.12**	0.96	Moderately tolerant
		0.29**	5.08	-0.99**	46.69			
PAVON-76	VICAM71/CIANO67/SIETERRS66// KALYANSONA/BLUEBIRD	-1.10**	3.23	11.34*	34.99	0.41**	2.13	Susceptible
		-1.21**	2.1	-11.53**	31.3			
PBW-343	ND/VG 1944//KAL// BB/3/YACO'S'/ 4/ VEE # 5	-1.45**	2.98	-8.88**	35.96	0.38**	2.06	Susceptible
		-1.41**	2.73	-8.99**	32.24			
SE(gi) ±		0.04		0.33		0.03		
		0.02		0.26				
SE(gig) ±		0.06		0.5		0.04		
		0.03		0.38				
Mean			0.63		55.43		1.03	
			4.75		2.97			

Note: DH = Days to 50% heading, PH = Plant height (cm), GYP = Grain yield plant⁻¹ (g), CTD = Canopy Temperature depression, CMS = Cell membrane thermostability (%), HSI TGW = Heat Susceptibility Index for thousand grain weight. N = Normal environment, S = Stress environment and *, ** significant at 5% and 1% levels, respectively.

Farooq et al., 2011) also reported positive and significant GCA for 1000-grain weight and grain yield plant⁻¹. CTD is an efficient parameter for stress diagnostic and selection

of heat stress adapted genotypes. It works on the principle that surface temperature of the canopy is related to the amount of transpiration resulting in evaporative cooling. The positive

Table 3: ANOVA of combining ability analysis for 6 traits of bread wheat in F₁ generations under normal and stress environments

Source of Variation	Degrees of freedom	Environment	Mean sum of square					
			Days to 50% heading	Plant height (cm)	1000-grains weight (g)	Canopy Temperature depression	Cell membrane thermostability (%)	Heat Susceptibility Index for thousand grain weight
GCA	9	N	91.83**	203.52**	7.36**	6.22**	375.71**	0.66**
		S	26.42**	41.81**	2.01**	6.47**	395.44**	
SCA	45	N	10.80**	41.16**	11.10**	0.19**	32.94**	0.23**
		S	8.07**	46.70**	1.04**	0.39**	34.99**	
Error	108	N	0.44	2.08	0.04	0.02	1.47	0.01
		S	0.42	1.29	0.01	0.01	0.88	

Note:*,** significant at 5% and 1% levels, respectively.

Table 4: Genetic components and proportion of genetic variation in 10x10 diallel crosses (excluding reciprocals) in F₁ generations under normal and stress environments

Parameters Environment	D		\hat{H}_1		\hat{H}_2		h ²		F	
	N	S	N	S	N	S	N	S	N	S
DH	71.36**	27.93**	53.83**	38.76**	35.75**	27.61**	4.2	0.15	64.08**	32.34**
PH	75.92**	51.50*	197.84**	218.86**	139.72**	164.29	7.71	13.09	58.69	90.90*
GYP	1.82	0.73*	36.81**	4.80**	32.07**	3.81**	105.38**	0.07	3.2	0.89*
CTD	1.86**	1.65**	0.79**	1.58**	0.65**	1.25**	0.15	1.67**	-0.14	0.33
CMS	149.54**	168.45**	146.75**	157.03**	118.30**	127.52**	5.12	5.76	53.27	68.79*
HSI TGW	0.36**		1.03**		0.81**		0.02		0.36*	

Table 4: Cont.....

Parameters Environment	E		\hat{H}_1/D		$\hat{H}_2/4\hat{H}_1$		h ² / \hat{H}_2		K _D /K _R		h ² (ns)	
	N	S	N	S	N	S	N	S	N	S	N	S
DH	0.43	0.42	0.87	1.18	0.17	0.18	0.12	0.01	3.14	2.93	0.58	0.32
PH	2.08	1.3	1.61	2.06	0.18	0.19	0.06	0.08	1.63	2.5	0.51	0.15
GYP	0.04	0.01	4.5	2.56	0.22	0.2	3.29	0.02	1.49	1.63	0.17	0.3
CTD	0.02	0.01	0.65	0.98	0.21	0.2	0.23	1.33	0.89	0.81	0.85	0.78
CMS	1.5	0.88	0.99	0.97	0.2	0.2	0.04	0.05	1.44	1.54	0.67	0.66
HSI TGW	0.01		1.69		0.2		0.03		1.85		0.35	

Note; DH = Days to 50% heading, PH = Plant height (cm), GYP = Grain yield plant⁻¹ (g), CTD = Canopy Temperature depression, CMS = Cell membrane thermostability (%), HSI TGW = Heat Susceptibility Index for thousand grain weight D = Variation due to additive effects of genes, \hat{H}_1 = Variation due to dominance effects of genes (Corrected dominance effect), \hat{H}_2 = Uncorrected dominance effect, h² = Dominance effect (as algebraic sum over all loci in the heterozygote phase in all the crosses), F = Mean of Fr(Covariance of additive and dominance effects in a single array/over the arrays or gene distribution and E = Expected environment component of variation \hat{H}_1/D = Mean degree of dominance, $\hat{H}_2/4\hat{H}_1$ = Proportion of genes with positive and negative effects in parents, h²/ \hat{H}_2 = Number of group(s) of gene which control the trait and exhibit dominance, K_D/K_R = Proportion of dominant and recessive genes in the parents and h²(ns) = Heritability in narrow sense, N = Normal environment; S = Stress environment and *, ** significant at 5% and 1% levels, respectively;

and highly significant GCA effects were showed by DBW-14 and HUW-234 in both normal and stress environments and therefore, DBW-14, HUW-234 showing consistent performance in respect of canopy temperature depression and cell membrane thermostability should be utilized in terminal heat tolerance breeding program. A number of workers (Saadalla *et al.*, 1990, Yaldirim *et al.*, 2009 and Ibrahim and Quick 2001) also reported positive and desirable GCA effects in different lines showing tolerance against heat stress. Heat susceptibility index is a measure of the heat tolerance of genotypes. Lower the index greater the heat tolerance (Ibrahim and Quick, 2001). Therefore, negative and significant GCA effects are desirable to heat tolerance. The best general combiner was HD-2888 followed by PBW-175, HD-2285, HUW-468 HUW-234 and VERRY S. Dhanda and Munjal (2012) also reported negative and desirable GCA effects in different lines showing less effect of heat stress.

The significance of SCA effect indicates that dominance and epistasis were also involved in the expression of the traits studied. The crosses showing negative and significant SCA

effects in both normal and stress environments for day to 50% heading were DBW-14 x HD-2888, HUW-234 x PBW-175, T-190 x PBW-234, PBW-175 x HUW-468 and HD-2888 x PBW-343. Therefore, these crosses were considered as good specific combiners for earliness. Kamaluddin *et al.* (2011) and Kumar *et al.* (2012) also reported negative and significant SCA effects for day to 50% heading. The negative and significant SCA effects were observed in 6 crosses suggesting good specific combining ability for dwarf stature of the plants. Short stature of plants in wheat imparts lodging resistance sustaining yield and thus considered desirable trait. Significant negative SCA effects for plant height were reported by Ivanovska *et al.* (2003) and Farooq *et al.* (2011).

Out of 45 crosses 15 crosses had highly significant and desirable SCA effects for grain yield plant⁻¹. Five, in order of *per se* performance with positive and significant SCA were HD-2285 x HD-2888, HD-2285 x HUW-468, HUW-234 x HD-2285, T-190 x HD-2285 and T-190 x PAVON-76 in both normal and stress environments. These results are in agreement with findings of Sharma and Singh (1983) and Joshi *et al.*

(2004). Out of 45 crosses 7 crosses viz., DBW-14 x HUW-234, DBW-14 x HD-2285, HUW-234 x T-190, T-190 x PBW-175, HD-2888 x PAVON-76, VERRY-S x PAVON-76 and PAVON-76 x PBW-343 exhibited significant and positive SCA effects in both normal and stress environments for canopy temperature depression indicating good specific combining ability. Canopies may be cooler because of their ability to transfer relatively more heat back to atmosphere by reflection and convection (Blum, 1988). Cell membrane thermostability (CMS) is commonly used assays for evaluating thermotolerance at cellular level (Wu and Wallner 1983). It is rapid and flexible in terms of stage of plant development and is amenable to use in breeding for heat tolerance. Sixteen crosses out of forty five had positive and significant SCA in which five, crosses viz., DBW-14 x HUW-234, DBW-14 x T-190, T-190 x PBW-175, HD-2285 x HUW-468, PBW-175 x HUW-468, in order of *per se* performance with positive and significant SCA in both normal and stress environments can be useful in terminal heat tolerance breeding programme. Yildirim *et al.* (2009) reported that significant SCA effects for membrane thermostability suggested that it is mediated by dominance effects.

High heat susceptibility index is indicative of susceptibility of crosses. Negative and significant SCA effects therefore will be desirable for selection of tolerant combinations. Eighteen cross combinations exhibited significant and negative SCA effects having less susceptibility to terminal heat. Dhanda and Munjal (2012) also found negative SCA effects in different cross combinations for heat susceptibility index.

Nature and magnitude of genetic components

The estimates of $5\sigma^2_{\bar{U}}$ were highly significant for all the traits except grain yield plant⁻¹, in normal environment and $5\sigma^2_{\bar{U}}$, and $5\sigma^2_{\bar{U}_2}$ highly significant for all the traits in both normal and stress environments except plant height in stress environment. These results elucidate that genetic control of all the traits except plant height were governed by genes having both additive and dominance effects (Table 4).

The direction of dominance was positive for grain yield plant⁻¹ in normal environment, whereas, in stress environment also the direction of dominance was positive and significant for canopy temperature depression which suggested that traits were under the control of positive dominance effects. The value of $5\sigma^2_{\bar{U}}$ were significant and positive for days to 50% heading and heat susceptibility index for thousand grain weight in normal environment and all the traits except, grain yield plant⁻¹ and canopy temperature depression in stress environment suggesting an excess of positive genes. The error component (*E*) was non-significant for all the traits in both normal and stress environments except spike harvest index. Nazeer *et al.* (2004) reported similar results for grain yields traits in wheat.

The estimates of degree of dominance $5\sigma^2_{\bar{U}_1}/5\sigma^2_{\bar{U}}$ indicated that traits plant height, grain yield plant⁻¹, heat susceptibility index for thousand grain weight in normal environment and for all the traits except canopy temperature depression and cell membrane thermostability (%) in stress environment were under the control of over-dominance. The degree of dominance for cell membrane thermostability (%) in normal environment and canopy temperature depression and cell

membrane thermostability (%) in stress environment showed presence of complete dominance. The trait number of days to 50% heading in normal environment was under influence of partial dominance.

Proportions of genes $5\sigma^2_{\bar{U}_2}/45\sigma^2_{\bar{U}_1}$ with positive and negative effects in parents approached theoretical value (0.25). For the trait grain yield plant⁻¹ in normal environment had symmetry of positive and negative alleles at loci, whereas, all other traits in normal environment showed asymmetry of positive and negative alleles. All the traits exhibited asymmetry of proportion of genes with positive and negative effects in stress environment. Hussain *et al.* (2004) also reported asymmetrical gene distribution for plant height, number of grains spike⁻¹, and symmetrical distribution for harvest index. The ratio of $1^2/5\sigma^2_{\bar{U}_2}$ ranged from 0.01 to 3.29 which indicated that at least 1 to 4 genes or group of genes showing dominance were present for different traits. Similar finding were reported by Kumar (2012) and Nazeer *et al.* (2004). The ratio of dominance to recessive genes $5\sigma^2_{\bar{U}}/5\sigma^2_{\bar{U}_1}$ was greater than unity for all the traits except canopy temperature depression in the normal and stress environments, indicating an excess of dominant genes in the parents.

The heritability (narrow sense) in general was lower to high in both the normal and stress environments for different traits. Heritability was higher in normal environment than stress environment (Tiwari *et al.*, 2012). High narrow sense heritability in normal environment was recorded for canopy temperature depression followed by cell membrane thermostability in that order, while it was high in stress environment for canopy temperature depression and membrane thermostability. A number of workers (Rathey *et al.*, 2011; Lopes *et al.*, 2012 and Tiwari *et al.*, 2012) have also reported heritability estimates ranging from 0.4-0.9 for canopy temperature depression. Foker *et al.* (1998) reported high heritability for cell membrane thermostability and suggested that canopy temperature depression and cell membrane thermostability trait can be effectively used in breeding programmes.

High temperatures causing heat stress in wheat are expected to increase in frequency across the globe. Heat stress substantially affects grain filling duration, its rate, and ultimately grain yield. Nonetheless the timing, duration and intensity of heat stress determine its impact on grain yield. By using CMS, CTD and HSITGW the adversities of heat stress can be minimized by developing tolerant genotypes.

ACKNOWLEDGEMENT

The first author gratefully acknowledges the financial assistance provided by the UGC, Govt. of India and the infrastructure facilities by the Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi (UP) for completion of the research work.

REFERENCES

- Bahar, B., Yildirim, M., Celaledin, B. and Ibrahim, G. 2008. Effect of canopy temperature depression on grain yield and yield Components in bread and durum wheat, *Not. Bot. Hort. Agrobot. Cluj*. **36(1)**: 34-37.

- Binod, K., Singh, C. M. and Jaiswal K. K. 2013.** Genetic variability, association and diversity studies in bread wheat (*Triticum aestivum* L.) *The Bioscan* **8(1)**: 143-147.
- Blum, A. 1988.** Plant Breeding for Stress Environments, CRC Press, FL.
- Blum, A. and Ebercon, A. 1981.** Cell membrane stability as a measure of drought and heat tolerance in wheat. *Crop Sci.* **21**: 43-47.
- Blum, A., Mayer, J. and Gozlan, G. 1982.** Infrared thermal sensing of plant canopies as a screening technique for dehydration avoidance in wheat, *Field Crops Res.* **5**: 137-146.
- Borlaug, N. E. 1968.** Wheat breeding and its impact on world food supply. In K.W. Finlay and K.W. Shephard, eds. *Proceedings of the 3rd International Wheat Genetics Symposium*, Australian Academy of Sciences, Canberra, Australia. p. 1-36.
- Dhanda, S. S. and Munjal, R. 2012.** Heat tolerance in relation to acquired thermotolerance for membrane lipids in bread wheat. *Field Crops Res.* **135**: 30-37.
- Farooq, J., Khaliq, I., Kashif, M., Ali, Q. and Mahpara, S. 2011.** Genetic analysis of relative cell injury percentage and some yield contributing traits in wheat under normal and heat stress conditions, *Chilean J. Agricultural Research* **71(4)**: 511-520.
- Fischer, R. A. and Maurer, R. 1978.** Drought resistance in spring wheat cultivars. I. Grain yield responses, *Aust. J. Agric. Res.* **29**: 897-907.
- Griffing, B. 1956.** Concept of general and specific combining ability in relation to diallel crossing system, *Aust. J. Biol. Sci.* **9**: 463-93.
- Hayman, B. I. 1954.** The theory and analysis of diallel crosses, *Genetics*. **43**: 789-809.
- Hussain, F., Ashraf, M., Mehdi, S. S. and Ahmad, M. T. 2004.** Genetics of leaf rust and agronomic traits in wheat (*Triticum aestivum* L.), *International J. Biology and Biotechnology*. **1(4)**: 549-561.
- Ibrahim, A. M. H. and Quick J. S. 2001.** Genetic control of high temperature tolerance in wheat as measured by membrane thermal stability, *Crop Science*. **41**: 1405-1407.
- Irshad, M., Khaliq, I., Khan, A. S. and Ali A. 2012.** Genetic Studies For Some Agronomic Traits In Spring Wheat Under Heat Stress, *Pakistan J. Agricultural Science*. **49(1)**: 11-20.
- Ivanovska, S., Balalic, M. K. and Stojkovski, C. 2003.** Diallel Analysis For Plant Height In Winter Wheat, *Genetika*. **35(1)**: 11-19.
- Jinks, J. L. 1956.** The F_2 and backcross generations from a set of diallel crosses, *Heredity*. **10**: 1-30.
- Joshi, S. K., Sharma, S. N., Sinnghania, D. L. and Sain, R. S. 2004.** Combining ability in the F_1 and F_2 generations of diallel cross in hexaploid wheat (*Triticum aestivum* L. Em. Thell). *Hereditas*. **141**: 115-121.
- Kamaluddin Singh, R. M., Prasad, L. C., Abidin, M. Z. and Joshi, A. K. 2007.** Combining ability analysis for grain filling duration and yield traits in spring wheat (*Triticum aestivum* L. em. Thell.) *Genetics and Molecular Biology*. **30(2)**: 411-416.
- Kamaluddin Singh, R. M. and Khan, M. A. 2011.** Combining ability Analyses for Protein Content and Maturity Traits in Spring Wheat (*Triticum aestivum*). *J. Phytology*. **3(7)**: 38-43
- Kaur, A., Sohu, V. S. and Mavi, G. S. 2007.** Genotypic variation for physiological traits associated with heat tolerance in bread wheat (*Triticum aestivum* L.). *Crop Improve.* **34(2)**: 117-123.
- Kumar, M. 2012.** Genetics of partial leaf rust resistance and yield components in bread wheat (*Triticum aestivum* L. em Thell), *Ph. D. Thesis, Banaras Hindu University, Varanasi*.
- Lamalakshmi Devi, E., Swati, Goel, P., Singh, M., Jaiswal, J. P. 2013.** Heterosis studies for yield and yield contributing traits in bread wheat (*Triticum aestivum* L.). *The Bioscan* **8(3)**: 905-909.
- Lopes, M. S., Renolds, M. P., Jalal-Kamali, M. R., Moussa, M., Feltaous Y., Tihar, I. S. A., Barma, N., Vargas, M., Mannes, Y. and Baum, M. 2012.** The yield correlation of selectable physiological traits in a of populations advance spring wheat lines grown in warm and drought environment, *Field Crops Res.* **128**: 129-136.
- Monu, K., Sharma, R. K., Kumar, P., Singh, G. P., Sharma, J. B. and Rahul, G. 2013.** Evaluation of bread wheat (*Triticum aestivum* L.) genotypes for terminal heat tolerance under different environments. *Indian J. Genet.* **73**: 446-449.
- Nanda, G. S., Virk, P. S. and Gill, K. S. 1983.** Diallel analysis over environments in wheat-plant characters and harvest index, *Indian J. Genet.* **43**: 21-27.
- Nazeer, A. W., Hassan, M. S. and Akram, Z. 2004.** Genetic architecture of some agronomic traits in diallel cross of bread wheat, *Pakistan J. Biological Sciences*. **7(8)**: 1340-1342.
- Ortiz, R., Sayre, K. D., Govaerts, B., Gupta, R., Subbarao, G. V., Ban, T., Hodson, D., Dixon, J. M., Ortiz-Monasterio, J. I. and Reynolds, M. 2008.** Climate change: can wheat beat the heat?, *Agr Ecosyst Environ.* **126**: 46-58.
- Paliwal, R., Roder, M. S., Kumar, U., Srivastava, J. P. and Joshi, A. K. 2012.** QTL mapping of terminal heat tolerance in hexaploid wheat (*Triticum aestivum* L.). *Euphytica*. **153**: 135-151.
- Panse, V. G. and Sukhatme, P. V. 1967.** Statistical methods for agricultural workers, 2nd Ed, Indian Council of Agricultural Research, New Delhi.
- Patil, H. S., Manake, B. S., Chavan, V. W. and Kachole, U. G. 1995.** Diallel analysis in bread wheat, *Indian J. Genet.* **55(3)**: 320-323.
- Rane, J., Pannu, R. K., Sohu, V. S., Saini, R. S., Mishra, B., Shoran, J., Crossa, M., Vargas, J. and Joshi, A. K. 2007.** Performance of yield and stability of advanced wheat genotypes under heat stressed environments of Indo-Gangetic plains. *Crop Sci.* **47**: 1561-1573.
- Rathey, A. R., Shorter, R. and Chapman, S. C. 2011** Evaluation of CIMMYT conventional and synthetic spring wheat germplasm in rainfed- sub tropical environments. II. Grain yield components and physiological traits. *Field Crops Res.* **124**: 195-204.
- Rehman, A., Khaliq, I., Chowdhry, M. A. and Khushnood, R. I. 2002.** Combining ability studies for polygenic characters in *Aestivum* species. *Int. Journal Argic. Biol.* **4**: 171-174.
- Reynolds, M. P., Ortiz-Monasterio, J. I. and McNab, A. 2001.** Application of physiology in wheat breeding, (ed) CIMMYT, El Batan, Mexico. (Chapter 10) p. 124.
- Saadalla, M. M., Quick, J. S. and Shanahan, J. F. 1990.** Heat tolerance in wheat. II. Membrane thermo stability and field performance, *Crop Sci.* **30**: 1248-1251.
- Arya, S., Mishra, D. K. and Bornar, S. S. 2013.** Screening genetic variability in advance lines for drought tolerance of bread wheat (*Triticum aestivum*). *The Bioscan*. **8(4)**: 1193-1196.
- Sharma, S. K. and Singh R. K. 1983.** Combining ability for harvest index and its components in wheat. *Indian J. Genet.* **43**: 229-231.
- Singh, S. P., Singh, R. M., Singh, J. and Agarwal, R. K. 1990.** Combining ability for yield and some of its important components in induced mutants of bread wheat, *Indian J. Genet.* **50(2)**: 167-170.
- Tiwari, C., Wallwork, H., Dhari, R., Arun, B., Mishra, V. K. and Joshi, A. K. 2012.** Exploring the possibility of obtaining terminal heat tolerance in a doubled haploid population of spring wheat (*Triticum aestivum* L.) in the eastern Gangetic plains of India, *Field Crops Res.* **135**: 1-9.
- Wu, M. T. and Wallner, S. J. 1983.** Heat stress responses in cultured plant cells: Development and comparison of viability tests. *Plant Physiol.* **72**: 817-820.
- Yildirim, M., Bahar, B., Koc, M. and Barutcular C. 2009.** Membrane thermal stability at different developmental stages of spring wheat genotypes and their diallel cross populations, *Tarim Bilimleri Dergisi*. **15(4)**: 293-300.