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Inheritance pattern of yield attributes in spring wheat at grain filling stage under different temperature regimes

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Abstract

One hundred spring wheat accessions were assessed for heat tolerance under plastic sheet tunnel resulting in seven parents with diverse heat tolerance. Tolerant and susceptible genotypes were graded on the bases of their relative cell injury percentages and relative values for different yield components. The analysis of variance for relative cell injury % revealed highly significant differences among the genotypes with a range from 28 to 98 %. These 7 parents were crossed in a full diallel system to evaluate the inheritance pattern of some spike related yield attributes (spike length, spikelets per spike, spike density, spike weight, grains per spike and grain yield per plant) under different temperature regimes at grain filling stage. Preliminary ANOVA revealed significant genotypic variation (P<0.01) for all the traits studied under both environments. Spike length, spikelets per spike and spike density revealed partial fitness of data for additive dominance model under normal conditions while other traits like spike weight, grains per spike and grain yield per plant showed full adequacy. Under heat stress all traits showed partial adequacy except for grains per spike which showed full adequacy. Formal ANOVA displayed significant effects for both additive and dominance effects in most characters under both regimes. Grain yield per plant showed significancy for only 'a' item under normal conditions and both 'a' and 'b' under high temperature regime. The additive component of variance (D) was significant and more than dominance variance H_1 and H_2 for spike length, spike density and grain yield per plant under both temperature regimes showing preponderance of additive effects. Grains per spike showed prevalence of dominant gene action under both conditions. Spikelets per spike and spike weight showed dominance effects under normal conditions and additive ones under heat stress. Estimates of narrow sense heritability were moderate to high in almost all the traits except for spikelets per spike under normal conditions in which it was low. Predominance of additive genetic effects in majority of traits under heat stress suggested early generation selection through pedigree method while presence of non-additive effects may respond to heterosis breeding.

Keywords: Spring wheat, Additive-dominance model, Inheritance pattern, Heat tolerance.
Abbreviations: RCI%= Relative cell injury percentage, a = additive, b= over all dominance effects, c= maternal effects, and d= reciprocal affects, b_1= directional dominance effects, b_2= effects due to parents contributing varying degree of dominant alleles, b_3= specific gene interaction, D= estimate of additive effects, H_1 and H_2= variation due to dominance effects of genes, F= estimate of the relative frequency of dominant to recessive alleles in the parental lines. F= positive when-ever the dominant alleles are more frequent than the recessive alleles, h^2= direction of dominance, $(H_1/D)^{0.5}$=mean degree of dominance, $H_2/4H_1$= proportion of genes with positive and negative effects in the parents, $[(4DH1)^{0.5}+F]/[(4DH1)^{0.5}–F]$= proportion of dominant and recessive genes in the parents.

Introduction

Spring wheat (*Triticum aestivum*) is the most important and widely consumed cereal at national level and Pakistan is one of the leading wheat producing countries of the world. Grain yield in wheat is a complicated quantitative parameter and is the product of its interaction with environment and several yield attributes affecting grain yield (Anwar et al., 2009). Grain yield is highly affected by environmental stresses like drought stress due to unavailability of water and less rainfall and heat stress because over 50% of the total wheat is sown late which results in terminal heat stress. High temperature and drought are the key stress factors which have influential impact on crop yield when they act collectively. Both these factors when applied at post- anthesis, reduced duration of maturation, grain filling, grain yield, mean grain weight, grain number and 1000-grain weight (Kaur and Behl, 2010). Terminal heat stress is an alarming factor causing significant yield reduction because of temperature stress at the critical stages like anthesis and grain filling (Ortiz-Ferrera et al.,

Table 1. Different lines/varieties used for 7x7 diallel crossing scheme in *Triticum aestivum* L.

S. No	*Acc. No*	*LINES/VARIETIES (Parentage)*	*RCI %age*	*RV (GPS)*	*RV (1000 KW)*	*RV (YP)*	*Av. RV*	*Stay green/ grain formation*	*REMARKS*
1	87	MAYA/PAVON	28.81	0.45	0.55	0.30	0.43	Stayed green with moderate grain formation	Tolerant
2	91	SHALIMAR 88 (PB81/HD2182//PB81)	32.77	0.40	0.51	0.45	0.45	Stayed green with bold grains	Tolerant
3	80	CHENAB-2000 (CHUMA18/BAU)	35.87	0.46	0.51	0.24	0.40	Stayed green with bold grains	Tolerant
4	54	INQILAB-91 (CROW/WL-711)	46.50	0.29	0.35	0.25	0.30	Stayed green with less grains	Moderately Tolerant
5	32	UQAB-2000 (CROW'S'/NAC//BOW'S')	68.73	0.05	0.10	0.15	0.10	Not remained green with few grains	Susceptible
6	58	PUNJAB-85 (KVZ/TRM//PTM/ANA)	78.30	0.11	0.15	0.09	0.12	Not remained green with few grains	Susceptible
7	21	WEEBLI-1	66.40	0.13	0.17	0.15	0.15	Not remained green with few grains	Susceptible

*S. No: Serial No, Acc No: Accession No

Table 2. Mean squares of various plant traits in a 7x7 diallel cross under normal and heat stress conditions of *Triticum aestivum* L.

Characters	*Mean squares*	
	Normal conditions	Heat stress conditions
Spike length	0.85**	1.015**
Spikelets per spike	1.96**	1.40**
Spike density	0.018*	0.015**
Spike weight	0.31**	0.41**
Grains per spike	83.82**	230.62**
Grain yield per plant	10.65**	3.057**

1993, Rehman et al., 2009a). During reproductive phase of wheat, the photosynthetic apparatus become damaged which results in the damage of source activity and sink capacity which ultimately reduces yield (Harding et al., 1990). In Pakistan, terminal temperature stress is a main reason of yield reduction in wheat due to delayed planting. The grain filling proceeds stable within temperatures of 25-28°C. The flowering and grain filling are routinely exposed to warming temperatures (maximum 28-38°C) in the months of March and April. A survey covering nineteen developing countries including major wheat producers, prior to the 2006 International Symposium on Increasing Wheat Yield Potential, to ascertain substantial yield losses concluded that heat stress is one of the most important constraint on wheat production, affecting up to 57% of the entire wheat area in the surveyed countries (Kosina et al. 2007). Short heat stresses (≥35°C) during grain filling period reduce starch contents decreasing the grain quality as well as grain weight (Sial et al. 2005). Therefore, there is a dire need to explore germplasm that can either tolerate heat stress at terminal stage or that mature early without yield reduction and thus escape the stress. Keeping in view, these changing climates and global warming prospects, the enhancement in yield potential must be of an elementary concern for plant breeders especially wheat breeders all over the world. The main objective of wheat breeding is to improve yield and related parameters by selecting and improving yield components including spike characteristics like spike length, number of spikelets per spike, number of grains per spike, spike weight, spike density. Additive gene action was found to be involved in controlling spike length (Chowdhry et al., 2005; Malik et al., 2005) and non-additive genetic effects under normal conditions (Rahim et al., 2006). However, according to some researchers, over-dominance is involved in spike length and spikelets per spike (Habib and Khan, 2003). Additive type of gene action was found for spikelets per spike (Siddique et al., 2004; Malik et al., 2005). Partial dominance was also reported by some researchers (Habib and Khan 2003). For spike density, additive type of gene action along with partial dominance was involved (Khan et al., 2003) and for number of grains per spike and grain yield per plant over dominance was reported by (Khan et al., 2003). Number of grains per spike was controlled by partial dominance (Habib and Khan, 2003), while non-additive gene action was also reported by Saeed et al. (2001). All of these reports are from the studies undertaken under normal conditions. The wheat improvement programs mainly focused at the manipulation and characterization of germplasm accessions and precise perceptive of the genetic mechanisms involved in the inheritance of important economic characters must be initiated for coping with heat stress. Until now no study has been carried out for finding the inheritance basis for heat tolerance in wheat at grain filling stage. The present studies primarily designed not only to explore sources of terminal heat tolerance in bread wheat germplasm for exploitation in the breeding program but also to know the effect of different temperature regimes on the genetic mechanism involved in the inheritance of spike related traits.

Results and discussion

Screening of parents and preliminarily analysis of variance

Sufficient temperature was provided to screen heat tolerant spring wheat genotypes under artificial plastic tunnel environment (Fig. 1). Seven parents were screened from the assessed germplasm and different criteria was used for screening of heat tolerant parents including RCI%, relative ratio (ratio of stressed/non-stressed) for each variety/ line for different yield components ability to stay green (Rehman et al., 2009a) and seed development (Table 1). RCI% in terms of electrolyte leakage is the suitable method to determine cell membrane thermo stability (Sullivan and Ross, 1979). Cellular membrane stability is one of the efficient methods of screening germplasm against heat and drought stresses on physiological basis (Ibrahim and Quick, 2001; Ali et al. 2009a). This method was used in wheat as a modified method to develop heat tolerant lines (Saadalla et al., 1990; Tahir and Singh, 1993). The analysis of variance for relative cell injury % revealed highly significant differences (mean square value of 646.20** at 0.05 probability level) among the genotypes giving a range from 28 to 98 % (Fig. 3A). The yield related characters, grains per spike, 1000 kernal weight and grain yield per plant demonstrated different range for the values of relative ratio (Fig. 3B, C & D). Few accessions showed high average relative ratios for these traits including MAYA/PAVON, SHALIMAR 88 and CHENAB-2000 however most of the lines (almost > 90%) exhibited low values for all the traits and their RCI% was really high and they did not stayed green for longer time. The lines, MAYA/PAVON, SHALIMAR 88 and CHENAB-2000 showed good promise against heat stress regarding relative ratio of yield traits, RCI% (28%, 32% and 35% respectively) and stay green ability with normal grain formation. So these genotypes were rated as heat tolerant. Staying green ability of the genotypes in PST with good cell membrane stability indicated that their photosynthetic system is more stable under heat stress (Rehman et al. 2009a). Chen et al. (2000) reported that the late sown conditions and plastic sheet tunnel could simulate heat stress and concluded grain weight per spike and yield per plant as reliable selection criterion against heat stress. On the other hand, INQILAB-91 demonstrated almost modest value for RCI% and relative ratios but it stayed green with reasonable seed formation. So it was rated as moderately tolerant to heat stress. Similarly, from the susceptible genotypes three genotypes were selected (PUNJAB-85, UQAB-2000 and WEEBLI-1) which were quite opposite to MAYA/PAVON, SHALIMAR-88 and CHENAB-2000 for all the screening criteria. Rehman et al. (2009b) used also mirror parents for yield traits in mungbean for 8×8 diallel crossing system. After the screening of these 7 parents, a full diallel crossing scheme was followed. The replicated data of yield traits from 49 genotypes (including 7 parents and 42 F1 hybrids) were assessed for preliminary ANOVA which indicated significant differences for all the traits among 49 genotypes under both regimes (Table 2). This significant variability rendered the data adequate to go further for genetic analysis of the data by using additive-dominance model (Ali et al., 2008).

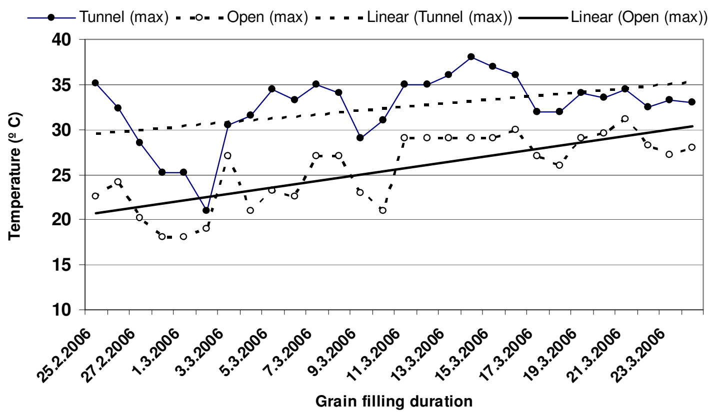

Fig 1. The difference of temperature inside the plastic tunnel and outside the tunnel during anthesis and grain filling stage. It showed a clear elevation of temperature inside the tunnel for the efficient screening of parents for crossing program.

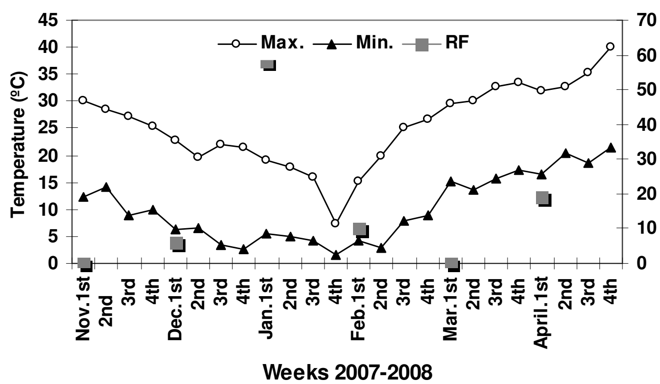

Fig 2. Maximum and minimum temperature through the growing season of the crop in 2007-2008. It showed high temperature stress (>30ºC) at grain filling stage which started from third week of March 2008.

Adequacy tests for additive-dominance (AD) model

Additive-dominance model for various plant traits under normal and heat stress conditions and the validity of some of the assumptions underlying the genetic model, were tested by joint regression analysis, and analysis of variance of (Wr + Vr) and (Wr – Vr) (Table 3). The regression coefficient 'b' for all the traits under both environments departed significantly from zero but not from unity. This property of the regression line indicated the presence of intra-allelic interaction, independent distribution of the genes among the parents for the trait, and independency of genes in their action (Ali and Awan, 2009). The unit slope of regression lines for all the studied traits suggested that all assumptions underlying the additive-dominance model were met (Mather and Jinks, 1982). The mean squares of analysis of variance of (Wr + Vr) and (Wr – Vr) (Table 2) showed significant differences ($P \leq 0.05$ - 0.01) between the arrays (Wr + Vr) and non-significant ($P > 0.05$) differences within the arrays (Wr – Vr) for spikelets per spike, spike weight, grains per spike and grain yield under normal conditions and for trait grains per spike under heat stress indicating that dominance was present and epistasis was absent. Thus, the results of both tests proposed that the simple genetic model was fully adequate for these traits. However, non-significant differences ($P > 0.05$) between the arrays (Wr + Vr) for traits like spike length, spike density under normal conditions and the all other traits except grains per spike under stress conditions showed the absence of dominant effects and presence of epistasis. Thus, based upon the results of two tests, simple genetic model was partially adequate for analyzing the data set for the traits showing presence of dominance and non-significant (Wr + Vr). The partially adequate models for the above mentioned traits may be due to the presence of non-allelic interaction, linkage and non-independent distribution of the genes in the parents as suggested by Mather and Jinks (1982). The traits, qualifying one test for additive dominance model were reported by (Ali and Awan, 2009; Rehman et al., 2009; 2010).

Table 3. Scaling tests for adequacy of additive-dominance (AD) model for various plant traits under normal and heat stress conditions of *Triticum aestivum* L.

Traits	*Regression slope*		*Mean squares*		*Adequacy to AD model*	*Joint regression coefficient*
Normal conditions	b_0	b_1	Wr + Vr	Wr - Vr		
Spike length	2.68*	0.66^{NS}	0.17^{NS}	0.0055^{NS}	partially adequate	b=0.801±0.299
Spikelets per spike	2.83*	1.06^{NS}	4.38*	0.30^{NS}	fully adequate	b=0.727±0.257
Spike density	5.07*	-0.72^{NS}	0.000067^{NS}	0.0000049^{NS}	partially adequate	b=1.164±0.229
Spike weight	5.41*	0.12^{NS}	0.033**	0.0013^{NS}	fully adequate	b=0.979±0.180
Grains per spike	2.92*	0.80^{NS}	477.42**	53.22^{NS}	fully adequate	b=0.783±0.268
Grain yield per plant	10.28*	-1.92^{NS}	26.46**	0.83^{NS}	partially adequate	b=1.23±0.120
Heat stress						
Spike length	3.17*	0.27^{NS}	0.17^{NS}	0.036^{NS}	partially adequate	b=0.920±0.290
Spikelets per spike	7.73*	-0.13^{NS}	0.40^{NS}	0.043^{NS}	partially adequate	b=1.016±0.131
Spike density	4.38*	0.47^{NS}	0.000012^{NS}	0.87^{NS}	partially adequate	b=0.903±0.206
Spike weight	3.05*	-0.09^{NS}	0.10^{NS}	0.0022*	partially adequate	b=1.03±0.340
Grains per spike	6.15*	0.49^{NS}	29508.58*	932.93^{NS}	fully adequate	b=0.925±0.150
Grain yield per plant	4.47*	-0.60^{NS}	0.30^{NS}	0.025^{NS}	partially adequate	b=1.155±0.258

Where: $b_{0=}$ is coefficient of regression deviating from zero, b_1= coefficient of regression deviating from unity, Mean squares are from analysis of variance of values (Wr+Vr between arrays) and (Wr-Vr with in arrays). In the presence of dominance, Wr+Vr may change from array to array and if Wr-Vr will be significant there will be the presence of non-allelic interactions (Ali et al., 2008& 2009b, Ali and Awan 2009, Rehman et al., 2009b & 2010).

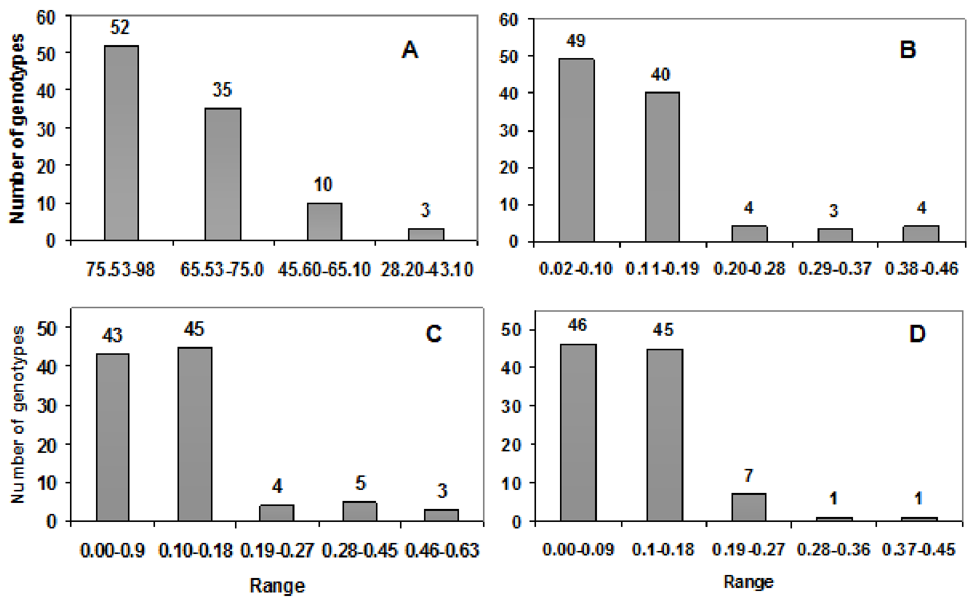

Fig 3. Range of Relative Cell Injury %age (A), relative ratios for grains per spike (B), 1000 kernal weight (C) and grain yield per plant (D) in 100 different wheat germplasm accessions. Most of the lines clustered towards high relative injury percentage.

Formal analysis of variance

Formal analysis of variance partitioned the total variance into additive (a), over all dominance effects (b), maternal (c), and reciprocal affects (d) (Table 4). The b item was further divided into directional dominance effects (b_1), effects due to parents contributing varying degree of dominant alleles i.e. asymmetrical gene distribution among the parents (b_2) and specific gene interaction (b_3) i.e. residual dominance or specific combining ability (Rehman et al., 2010). Spike length and grains per spike revealed significant effect for both 'a' and 'b' under both normal and heat stress conditions which indicated the involvement of both additive and dominance components of heritable variation for these traits. On the other hand, spikelets per spike and spike weight showed that both 'a' and 'b' items were significant under normal conditions while under heat stress regime significant effect of 'a' revealed that heat stress has somehow changed the inheritance pattern of these traits. Spike density exhibited significant effect of 'a' under both regimes while grain yield per plant showed significant effect for only 'a' under normal conditions and for both 'a' and 'b' under high temperature regime. This concluded that heat stress has an affect on the inheritance pattern of spikelets per spike, spike weight and grain yield per plant. Further separation of components of dominance (b) displayed that b_1 was significant for spikelets per spike and grains per spike in both normal and stress regimes whereas it was significant for spike weight and grain yield per plant in heat stress and normal conditions, respectively. This showed unidirectional dominance for these traits. The items b_2 and b_3 were significant for spike length under heat stress whereas spike weight, grains per spike and grain yield per plant presented significant b_2 and b_3 values under both temperature regimes. This resulted due to the

Table 4. Formal analysis of variance for earliness related traits for 8×8 diallel cross in spring wheat

Item	df	Spike length		Spikelets per spike		Spike density		Spike weight		Grains per spike		Grain yield per plant	
		Nor.	HS	Nor.	HS	Nor.	HS	Nor.	HS	Nor.	HS	Nor.	HS
a	6	3.74**	3.59**	3.06*	5.04**	0.0615**	0.0627**	1.038**	2.234**	401.4**	927.39**	63.84**	20.26**
b	21	0.38*	0.77**	2.96**	0.70^{NS}	0.0070^{NS}	0.0057^{NS}	0.401**	0.144^{NS}	66.05**	261.99**	4.61^{NS}	0.59**
b_1	1	0.22^{NS}	1.28^{NS}	17.96**	2.76**	0.00002^{NS}	0.0008^{NS}	3.129^{NS}	0.053**	272.0**	17.60**	0.53**	0.02^{NS}
b_2	6	0.14^{NS}	1.00**	5.47**	0.67^{NS}	0.0061^{NS}	0.0038^{NS}	0.075**	0.111**	42.49**	116.55**	4.01**	0.22*
b_3	14	0.50^{NS}	0.63*	0.82^{NS}	0.56^{NS}	0.0079^{NS}	0.0068^{NS}	0.346**	0.168**	61.44**	341.77**	5.16**	0.79**
c	6	0.47*	1.12**	0.42^{NS}	1.55^{NS}	0.0131^{NS}	0.0197^{NS}	0.011^{NS}	0.151**	5.40*	0.189^{NS}	2.37^{NS}	1.09**
d	15	0.51^{NS}	0.28^{NS}	0.74^{NS}	0.87^{NS}	0.0181*	0.0080^{NS}	0.010^{NS}	0.160**	13.00**	0.179^{NS}	1.14^{NS}	0.41*
Total	48	0.85	1.01	1.96	1.40	0.0180	0.0153	0.310	0.414	83.81	230.62	10.65	3.06
a× blocks	12	0.23	0.13	1.08	0.86	0.0120	0.0037	0.023	0.364	1.32	8.92	0.24	0.17
b_1 × blocks	42	0.50	0.31	0.86	0.68	0.0061	0.0064	0.024	0.037	1.87	9.39	1.28	0.17
b_2 × blocks	2	0.04	0.83	0.16	0.21	0.0108	0.0006	0.005	0.016	0.79	1.37	0.85	0.07
b_3 × blocks	12	0.80	0.18	1.41	0.71	0.0075	0.0034	0.032	0.021	2.36	11.62	0.69	0.08
b × blocks	28	0.41	0.33	0.68	0.70	0.0051	0.0081	0.023	0.046	1.74	9.009	1.56	0.22
c × blocks	12	0.19	0.24	0.49	0.77	0.0064	0.0104	0.005	0.026	2.03	10.304	1.45	0.12
d × blocks	30	0.47	0.27	0.60	1.09	0.0044	0.0071	0.008	0.019	1.68	4.042	1.92	0.15
Block interaction	96	0.42	0.27	0.76	0.84	0.0063	0.0086	0.017	0.030	1.76	7.775	1.37	0.16

Where Nor.= normal conditions, HS= Heat stress, ** = P<0.01, * = P<0.05 and ns= Not-significant

Table 5. Estimation of the components of genetic variation under different temperature regimes

Character	*Condition*	*D*	H_1	H_2	*F*	$\hat{h}^2$	*E*	$(H1/D)^{0.5}$	$4DH_1^{0.5}+F/$ $4DH_1^{0.5}-F$	$H_2/4H_1$	$h^2_{(n.s)}$
Spike length	Normal	0.34±0.036*	-0.11±0.09	-0.037±0.076	-0.040±0.086	-0.036±0.051	0.15±0.01*	0.56	0.81	0.086	0.53
	H. stress	0.98±0.052*	0.49±0.13*	0.32±0.11*	0.83±0.13*	0.16±0.075*	0.096±0.018*	0.71	4.01	0.16	0.47
Spikelets per spike	Normal	1.93±0.29*	2.54±0.70*	1.43±0.62*	2.82±0.70*	2.80±0.42*	0.27±0.10*	1.15	4.51	0.14	0.14
	H. stress	0.69±0.030*	-0.17±0.073*	-0.12±0.064	0.24±0.07*	0.31±0.04*	0.29±1.08	0.51	2.05	0.18	0.43
Spike density	Normal	0.0083±0.00055*	0.00005±0.001	0.0002±0.001	0.0029±0.001*	-0.001±0.0009	0.002±0.0002*	0.079	-2.60	0.95	0.53
	H. stress	0.0052±0.00033*	-0.002±0.0008*	-0.001±0.0007	-0.001±0.0008	-0.001±0.0005*	0.002±0.0001*	0.61	0.76	0.14	0.55
Spike weight	Normal	0.14±0.016*	0.27±0.038*	0.25±0.033*	0.059±0.038	0.51±0.023*	0.0062±0.005	1.37	1.36	0.24	0.41
	H. stress	0.21±0.016*	0.087±0.038*	0.070±0.034*	0.022±0.038	0.0036±0.023	0.011±0.0057	0.64	1.17	0.20	0.79
Grains per spike	Normal	26.77±3.20*	52.46±7.70*	42.79±6.78*	-1.61±7.67	44.10±4.56*	0.62±1.13	1.40	0.96	0.20	0.63
	H. stress	152.96±13.28*	194.78±31.97*	169.03±28.17*	91.18±31.86*	1.50±18.92	2.81±4.69	1.13	1.72	0.22	0.49
Grain yield per plant	Normal	8.78±0.34*	2.71±0.83*	2.09±0.73*	3.45±0.82*	-0.15±0.49	0.49±0.12*	0.55	2.09	0.19	0.74
	H. stress	2.25±0.063*	0.29±±0.15	0.28±0.13*	0.35±0.15*	-0.023±0.090	0.055±0.022*	0.36	1.54	0.24	0.88

Where * = P<0.05 and values with no star are Not-significant presence of asymmetrical distribution of dominant genes among the parents and specific gene interaction, i.e. specific combining ability of the parents for these characters. In case of spike length, b_2 and b_3 were non-significant under normal conditions while under heat stress b_2 and b_3 showed significance. This was the same with b_2 under different temperature regimes for spikelets per spike. Significant effects of c and d items under heat stress for spike weight and grain yield per plant and under normal conditions for grains per spike suggested the retesting of a mean square against c and that of b, b_1, against d. This revealed that maternal and reciprocal effects had played role in the genetic mechanism controlling these characters which were more prominent under heat stress regime. Conversely, spike length showed significant effect for c and not-significant effect for d under both conditions and significant d value for spike density revealed contribution of some reciprocal effects under normal conditions.

Estimation of components of variation and graphical representation

The genetic components of variation showed that value of D was positive and significant under both temperature regimes for spike length, spike density and grain yield per plant indicating the presence of additive effects in controlling the inheritance pattern and this was confirmed by the low value of H_1 and H_2 as compared to D (Table 5). This was soundly supported by the values degree of dominance ($(H_1/D)^{0.5}$) for these traits which was less than unity showing partial dominance . The values of H_1 and H_2 components were significant and more than D value for grains per spike under both conditions and for spikelets per spike and spike weight under normal conditions. This demonstrated the presence of dominance effects controlling the gene action of these traits and this was in agreement with the values of $(H_1/D)^{0.5} > 1$, however, both these characters showed additive control of inheritance under heat stress conditions with $(H_1/D)^{0.5} < 1$. This suggested that heat stress resulted in altering the inheritance pattern for these characters by converting it from dominance gene action towards additive one thus making the selection easier for plant breeders working for improvement under high temperature. The F value was an estimate of the relative frequency of dominant to recessive alleles in the parental lines. Negative F values signified the important role of recessive genes for spike length and grains per spike under normal conditions and positive F value under stress showing the importance of dominant genes for these traits. All other characters showed positive value under both conditions except spike density which displayed negative value for F and this again pointed out that heat stress had an effect on inheritance of spike length, spike density and grains per spike. This was robustly supported by the values $[(4DH_1)^{0.5}+F]/[(4DH_1)^{0.5}-F]$ which were more than unity for the characters showing positive value for F thus pointing toward high proportion of dominant to recessive genes in the parents and vice versa. The value of $h\wedge^2$ denoting the dominance effect due to heterozygous loci was negative for spike length under normal conditions while it was positive under heat stress. However, spike density and grain yield per plant exhibited negative value of $h\wedge^2$ under both conditions whereas spikelets per spike, spike weight and grains per spike demonstrated positive value under both conditions. $h\wedge^2$ indicated the direction of dominance mean that positive sign showed dominance of genes with increasing effect at most of loci and negative sign illustrated dominance of genes with decreasing effect (Ali et al. 2008). Similarly, value of $H_2 / 4H_1$ ratio < 0.25 and the information, $H_1 - H_2 \neq 0$, showed unequal gene frequencies in the parents which indicated unequal distribution of genes for all the traits among the parents under both regimes. Spike length, spike density and grain yield per plant displayed significant environmental variation component (E) which suggested that genetics of these traits are highly influenced by environmental factors. According to Fehr (1978), the influence of environment and complex inheritance are responsible for variation in quantitative characters like grain yield and its components. Heritability is a technique used by the plant breeders for effectively isolating the magnitude of genetic variation from total phenotypic variation. Selection efficiency for a plant trait depends on magnitude of heritability and genetic variation (Falconer and Mackay, 1996). The estimates of narrow sense heritability ($h^2_{(ns)}$) were high under both conditions for grain yield per plant, hence, indicating better chance for improvement following selection procedure aimed at increasing grain yield per plant under different temperature regimes. However, grains per spike presented high $h^2_{(ns)}$ under normal conditions and medium under heat stress. Collaku (1994) obtained low heritability during experiments that included drought stress for grains per spike but Rana et al. (1999) concluded that under different water regimes, grains per spike is a significant property for the phenotypical selection due to its high heritability. Spike weight had moderately low $h^2_{(ns)}$ under normal and high under high temperature regime suggesting improvement by using simple selection method under heat stress conditions and this was firmly sustained and conditioned by strong additive gene action ($a>b+b_1+b_2+b_3$ and $D>H_1$ and H_2) involved in the inheritance of spike weight and grain yield per plant under heat stress. Spike length showed moderate heritability recommending some chances of improvement following selection under both conditions. Similarly spike density showed moderately high estimates for $h^2_{(ns)}$ under both conditions. Spikelets per spike displayed low heritability under normal conditions and moderate under stress conditions. Normally the traits having high $h^2_{(ns)}$ were accustomed by additive gene effects. Ali et al. (2009b) and Rehman et al. (2009b) also showed high heritability due to the preponderance of additive effects and low heritability due to the presence of dominance effects for yield related traits in cotton (*Gossypium hirsutum*) and mungbean (*Vigna radiata*), respectively. The graphical representation of spike related traits under heat stress agreed with the results of formal ANOVA and components of variation (Fig. 4). The regression line for all characters under heat stress conditions passed above the origin showing the presence of additive gene action except for spike weight and grains per spike for which the regression line cut the vertical axis below the origin, hence demonstrating the existence of over-dominance for these traits. This suggested that under heat stress conditions, pedigree selection procedures could be utilized for genetic improvement in spike length, spikelets per spike, spike density and grain yield per plant. On the other hand, over-dominance in case of spike weight and grains per spike proposed the use of heterosis breeding for evolution of cultivars with heavy spikes and more number of grains per spike. Previously different mode of inheritance has been reported for these characters but only under normal temperature conditions. According to Kaur and Behal (2010), effect of high temperature and drought on grain yield is additively controlled. Inamullah et al., (2006) reported that over-dominance is involved in controlling the inheritance of spike length; however, additive genetic control was observed for spikelets per spike by Gurmani et al. (2007) and Samiulallah et al. (2010). Similarly, additive effects were involved in the inheritance of spike density (Altinbas and Bilgen 1996) and Hall and Van Sanford (2003) reported additive control for number of grains per spike.

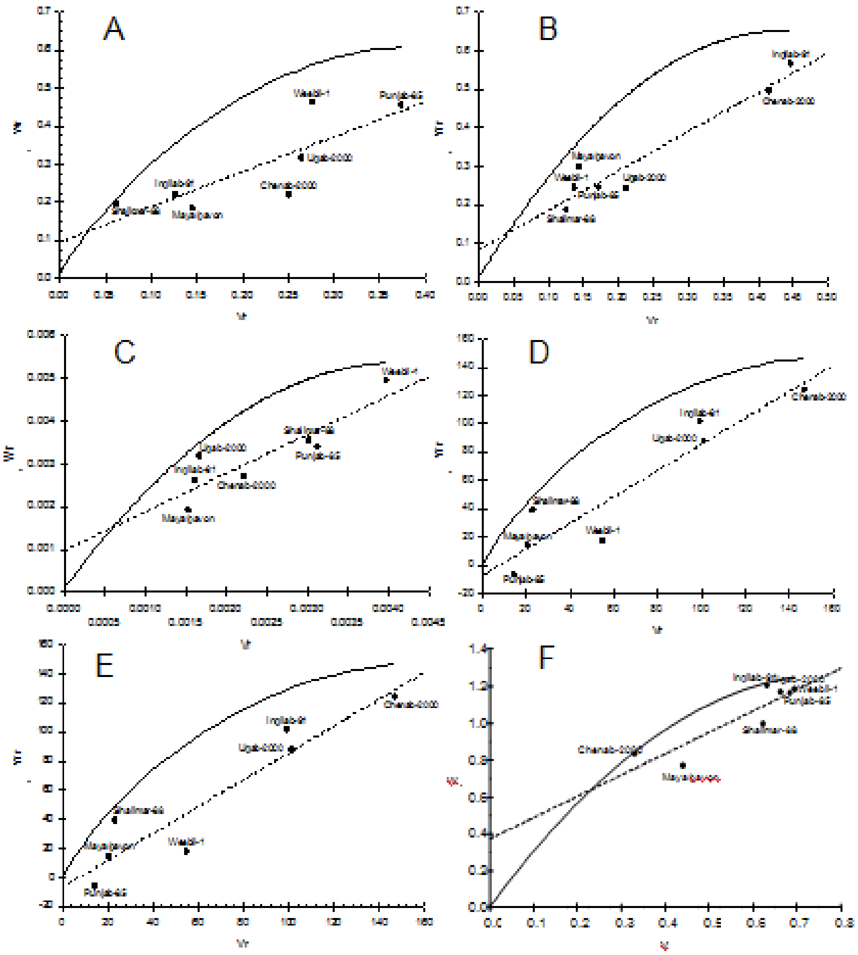

Fig 4. The graphical representation of spike relates traits under heat stress. The regression passed above the origin for spike length (A), spikelets per spike (B), spike density (C) and grain yield per plant (F) while for spike weight (D) and grains per spike (E) the regression line cut the vertical axis below the origin.

Partial dominance with additive gene action was reported for grain yield per plant (Samiulallah et al., 2010; Khan et al, 2000).

Material and Methods

Screening of parents and development of experimental material

A germplasm of 100 spring wheat accessions was evaluated for heat tolerance at Wheat Research Institute, Faisalabad during crop season of 2005-06. For this purpose, germplasm accessions were exposed to heat stress in plastic sheet tunnel (PST) by using the technique developed by (Rehman et al., 2009a). The germplasm was sown in two sets in randomized complete block design (RCBD) with three replications, one in plastic tunnel and one in open adjacent to the tunnel. As the experiment comprising a number of genotypes, there existed a great variability regarding heading dates. Some of the genotypes head earlier and some head later. So the genotypes that head earlier were sown later and the genotypes that head later were sown earlier to get synchronization in heading. Each genotype was sown in a single meter row with 30cm and 7.5cm inter and intra row spacing. Four seeds per hill were placed at the time of planting and later thinned to single seedling at two leaf stage. The genotypes sown under tunnel were exposed to heat stress at the stages of anthesis and grain filling for a period of almost one month (Rehman et al., 2009a). Daily temperature was noted both inside and outside the tunnel and maintained at almost > 32°C inside the tunnel (Fig. 1). Three criteria were used for screening the parents for crossing program; first, measurement of relative cell injury percentage (RCI%), second, the heat tolerance of different genotypes was measured as relative ratio (ratio of stressed/non-stressed) for each variety/ line for spike traits like grains/ spike, 1000 kernel weight, and yield/ spike and third, ability to stay green (Rehman et al., 2009a) and seed development.

Measurement of relative cell injury percentage (RCI%)

For estimating relative cell injury percentage, artificial desiccation of wheat leaves was induced by polyethylene glycol (PEG-6000) method as proposed by Sullivan (1971) and followed by Shanahan et al. (1990). For this purpose, a 10 fully expanded flag leaves of 10 randomly selected guarded plants were collected at 11:00 am from the plots under plastic sheet tunnel (PST). Samples were rinsed twice with deionized water to remove surface contamination and then blotted dry. Two groups of fifteen leaf discs of 1.0 cm^2 size were made from the selected leaves samples for all the 100 genotypes. One group was exposed to 30% polyethylene glycol (PEG-6000) in 25 ml test tubes and the second group was submerged in 15 ml deionized water in the test tubes (control sample). These test tubes were covered by aluminum foil. For this purpose, one set of leaf discs were used as a control and kept at room temperature (25ºC) and second set was treated at (49ºC) in water bath (MEMMERT-WB1, Germany) for 1 hour. After treatment the readings of both control and treated leaf discs were taken by using conductivity meter (Model No. JENWAY- 4510 Sr. No-02370 Barlow World Scientific Limited, UK) and after this, the samples were kept in test tubes overnight. In the next day, both controlled and treated test tubes were placed in autoclave (Model No. HVA-85 HRAYAMA Manufacturing Company, Japan) at 1200ºC and 0.10 Mpa, for a period of 10 minutes to kill tissues completely and leakage from the leaf discs from the test tubes was taken by using the conductivity meter. Then the relative cell injury percentage was calculated by using the formula;

Relative Cell Injury percentage = 1 – {(1 – T1 / T2)/ (1 – C1 / C2)} × 100

Where, T1 and T2 = Conductivity reading at 49ºC and conductivity reading at 120ºC, respectively, C1 and C2= Conductivity reading at room temperature and conductivity reading at 120ºC, respectively.

After screening against heat stress, experimental material was developed by crossing 7 divergent parents (Table 2) including five locals Shalimar-88 (Tolerant), Chenab-2000 (Tolerant), Inqilab-91(Moderately tolerant), Uqab-2000 (Susceptible) and Punjab-85 (Susceptible) and two exotic CIMMYT originated cultivars Weebli-1 (Susceptible) and Maya/Pavon (Tolerant) which were sown in the field on 5th of November, 2006 in the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad and later hybridized in all possible combinations including reciprocals following full diallel mating system. During next crop season, seven wheat varieties/lines (parents) and their hybrids (F_1) were planted in field in two sowing dates on 10th of November, 2007 (normal condition) and 25th of December (heat stress condition) following a triplicated RCBD. In late sowing, the crop was subjected to natural heat stress regime around 30-40º C at grain filling stage (Fig. 2). Thirty plants of each genotype were grown in a 5 m long row in each replication. The plants were spaced 15 and 30 cm apart within and between the rows, respectively. Two seeds were dibbled per hole and after germination, one healthy seedling was retained at each hole after thinning. All standard agronomic practices i.e., hoeing, weeding and irrigation etc. were adopted uniformly. For data collection, 10 guarded plants for each parent and cross were tagged at random for each replication in both regimes and data was recorded for spike length of mother shoot of selected plants in centimeters from base to the tip of spike excluding awns. Spikelets were counted from the mother spike of selected plants and spike density for each genotype was calculated by dividing number of grains per spike over spike length. For spike weight, mother shoot of each selected plant was weighed on electronic balance (Compax- Cx-600). Similarly, the spike of the mother shoot was thrashed manually and numbers of grains per spike were counted for each genotype and for grain yield, all spikes of individual selected plants were threshed manually and weighed using the electric balance. Finally average of all the traits was obtained.

Genetic analysis

The collected data were analyzed to determine significant varietal differences among the 49 genotypes under both regimes following Steel et al. (1997). The simple additive-dominance (AD) model developed by Hayman (1954) and Jinks (1954), modified by Mather and Jinks (1982), adopted by Singh and Chowdhary (1985) and very recently employed by Ali and Awan (2009) and Rehman et al. (2009b, 2010) was utilized for genetic analysis. Heritability was rated as low, medium and high following Stansfield (1986).

Conclusion

The results concluded that relative cell injury percentage enables us to screen breeding material for heat tolerance. Late sowing provided sufficient heat stress at grain filling stage in F_1 generation which allowed us to study the genetic basis of heat tolerance in wheat at terminal growth stage. The F_1 crosses and parents showed significant variability under heat stress which suggested ample chances for improvement of heat tolerance in segregating generations. The results from the genetic studies revealed the preponderance of additive genetic effects for most of the traits with the exception of spikelets per spike, spike weight and number of grains per spike in which dominance effects were predominant along with additive control. This proposed that inheritance of heat tolerance is a complicated and could be conditioned by different inheritance patterns. However, in this study, the traits controlled by additive genetic effects and high heritability may be improved through pedigree selection and heterosis breeding may be utilized for the characters controlled by dominance effects.

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