

GENETIC ANALYSIS OF RELATIVE CELL INJURY PERCENTAGE AND SOME YIELD CONTRIBUTING TRAITS IN WHEAT UNDER NORMAL AND HEAT STRESS CONDITIONS

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Several wheat genotypes were screened against heat stress. Seven wheat (*Triticum aestivum* L.) cultivars obtained after screening against heat classified as tolerant, moderately tolerant, and susceptible to heat stress, were mated in a complete diallel mating system to study the inheritance pattern of relative cell injury percentage (cell injury %) and some yield contributing parameters under normal and heat stress conditions. Significant genotypic differences were found ($P < 0.01$) for all the studied traits under both regimes. The scaling test disclosed partial adequacy for traits such as days to heading and days to maturity, but for flag leaf area and relative cell injury %, it showed full sufficiency under both environments. The model for grain yield per plant and biomass per plant were fully adequate under normal conditions, but partially adequate under stress. The harvest index showed partial adequacy under normal conditions, but was fully adequate under stress. The additive component of genotypic variation (D) was significant for all studied traits and more significant than the H_1 and H_2 dominance components. Values of the gene proportion with positive and negative effects in the parents ($H_2/4H_1$) demonstrated an unequal distribution of dominant genes in the parents for almost all the traits except for flag leaf area, grain yield per plant, and harvest index which showed an equal distribution of dominant genes under stress conditions. High heritability estimates were found for days to heading, days to maturity, flag leaf area, grain yield, and relative cell injury percentage under both regimes. Moderately high estimates were found for biomass per plant and harvest index.

Key words: Relative cell injury percentage, additive components, adequacy test, heritability, wheat, diallel.

Human beings directly depend on plants to obtain their food. Common bread wheat (*Triticum aestivum* L.) is among the major crops widely grown in Pakistan and throughout the world as a principal food cereal. We are far from meeting the demands of an ever-increasing population through efficient resource management which includes breeders who work to create new varieties that can also produce better yields in diverse environments. Wheat is best adapted to cool growing conditions (Modhej *et al.*, 2008). Its cultivation is expanding into regions that are too warm for optimal growth and yield. Many parameters, such as early sowing, judicious use of fertilizer, timely irrigation, and temperature, affect yield and directly influence wheat production. Of these, temperature stress or heat shocks are the most important and especially in regions where temperature fluctuations are abrupt. Lower productivity is due to shorter crop duration and grain-filling period as well as higher temperatures during crop growth, particularly during the grain-filling period which

is the most critical stage of grain development. Short heat stress (≥ 35 °C) during this period reduces starch contents, thus decreasing grain quality and weight (Sial *et al.*, 2005).

Wheat is autogamous and attains homozygosity after continuous inbreeding. It is generally agreed that germplasm diversification and genetic closeness among elite breeding material is the basic element in plant breeding (Mukhtar *et al.*, 2002). Consequently, to evolve high-yielding, heat-tolerant varieties, special attention must be given to understanding various morpho-physiological traits such as flag leaf area, relative cell injury %, and yield related parameters. The proper choice of parents for crossing would be equally important. In any breeding program, it is quite complicated to achieve higher yields because yield is a multigenic control character. Wheat germplasm greatly varies all over the world for yield and its related characters. Many researchers found this diversity in their genetic material (Ambreen *et al.*, 2002). These findings, related to variability in germplasm, help plant breeders to develop efficient breeding programs where multi-diverse genetic material can adapt everywhere and yield better in different environments. Gene action and inheritance studies employing the diallel technique, developed by Hayman (1954a; 1954b), provide valuable information about the nature and magnitude of

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the gene action involved in inheritance. The aim of the present study was to explore new combinations for heat tolerance by using a diallel mating system and the mode of gene action that is operative for different physiological traits related to heat and yield contributing parameters in wheat.

MATERIALS AND METHODS

The experimental material developed after screening against heat was comprised of seven wheat cultivars: five locals including 'Shalimar-88' (Tolerant), 'Chenab-2000' (Tolerant), 'Inqilab-91' (Moderately tolerant), 'Uqab-2000' (Susceptible but yielder), and 'Punjab-85' (Susceptible but yielder) and two exotic CIMMYT originated cvs. Weebli-1 (Susceptible but yielder) and Maya/Pavon (Tolerant) that were sown in the field on 5 November 2006 in the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan, and later hybridized in all the possible combinations, including reciprocals, with a diallel mating system. During the following crop season, the seven wheat varieties/lines (parents) and their hybrids (F1) were planted in the field at two sowing dates, 10 November 2007 at normal sowing time and 25 December at late sowing, to receive heat stress at anthesis applying a randomized complete block design with three replicates. Thirty plants of each genotype were grown in a 5 m long row in each replicate. Plants were spaced 15 and 30 cm apart within and between the rows, respectively. A template was used to ensure uniformity in the sowing distance and depth. Two seeds were dibbled in each hole and, after germination and thinning, only one healthy seedling was retained. For data collection, 10 guarded plants for each parent and cross were randomly tagged for each replicate in both regimes, and days to heading were obtained from the time of complete emergence to the date when 60% of the plants had completed heading. The stage when ears emerged after the unfolding of the flag leaf was regarded as the heading stage. Days to maturity were recorded as the period from the sowing date to the heading stage when plants were physiologically mature. From the fully developed flag leaf of selected mother shoots, maximum length and breadth were measured (cm²). Data were recorded in the morning hours when the leaf was fully turgid. Flag leaf area was measured with the following function by Muller (1991).

Flag leaf area = Flag leaf length × Flag leaf width × 0.74

At harvest, 10 randomly selected plants were weighed separately with an electric balance (Compax-Cx-600) before threshing to obtain their biological yield in grams and calculate their mean. For grain yield, all the spikes of individually selected plants were threshed manually and weighed with an electric balance (Compax-Cx-600). Mean grain yield per plant was estimated for each genotype in each replicate. The harvest index for each of

the genotypes was computed with the following formula: Harvest index % = (Grain yield per plant/Biological yield per plant) × 100

To estimate relative cell injury %, the age of the parent's artificial desiccation was induced by the polyethylene glycol (PEG-6000) method as proposed by Sullivan (1971). At anthesis, flag leaves of 10 randomly selected plants were taken from field-grown plants to study the electrolyte leakage from leaves with a conductivity meter according to the technique used by Shanahan *et al.* (1990). Samples were rinsed twice with deionized water to remove surface contamination and then blotted dry.

Two groups of 15 leaf discs 1.0 cm² in size were formed from the selected leaf sample of both regimes, including normal and heat stress of all the parents. One group was exposed to 30% polyethylene glycol (PEG-6000) in 25 mL test tubes, while the second group was submerged in test tubes with 15 mL deionized water (control sample). These test tubes were covered with aluminum foil. One set of leaf discs was used as a control and kept at room temperature (25 °C), while the second set was treated at 49 °C in a water bath (Memmert-WB1, Germany) for 1 h. After treatment, readings of the control and treated leaf discs were taken with the conductivity meter (Model N° Jenway- 4510 Sr. No-02370 Barlow World Scientific Limited, UK) after leaving the test tubes overnight. The following day, both controlled and treated test tubes were placed in an autoclave (Model N° HVA-85 Hrayama Manufacturing Company, Japan) at 120 °C and 0.10 MPa for 10 min to completely kill tissues, and leakage from the leaf discs from the test tubes was taken with the conductivity meter. Then the relative cell injury % was calculated with the formula:

Relative Cell Injury % = $1 - (1 - T1/T2)/(1 - C1/C2) \times 100$
where T1 = conductivity reading at 49 °C, T2 = conductivity reading at 120 °C, C1 = conductivity reading at room temperature, and C2 = conductivity reading at 120 °C.

Collected data were analyzed to determine significant varietal differences among 42 genotypes under both regimes according to Steel *et al.* (1997). The simple additive-dominance (AD) model, suggested by Hayman (1954a; 1954b) and Jinks (1954) and modified by Mather and Jinks (1982) for diallel analysis, was employed for further investigations.

RESULTS

Genotypic differences among parents

ANOVA indicated significant differences ($P < 0.01$) for all the traits among 49 genotypes under both regimes. The mean squares for the traits are shown in Table 1 and describe the high significance of the F-test for all the traits under study. The relative cell injury % of the parents selected for crossing is given in Figure 1.

Table 1. Mean squares of various *Triticum aestivum* plant traits in a 7 × 7 diallel cross under normal and heat stress conditions.

	DF	Days to heading	Days to maturity	Flag leaf area	Biomass per plant	Grain yield per plant	Harvest index	RCI%
Source (normal)								
Replicate	2	30.74 ^{NS}	15.31 ^{NS}	4.31 ^{NS}	13.39 ^{NS}	1.44 ^{NS}	13.97 ^{NS}	15.26 ^{NS}
Genotypes	48	38.22**	45.96**	15.72**	68.43**	10.65**	40.23**	269.78**
Error	96	11.64	7.09	1.76	14.93	1.37	19.77	14.93
Mean		91.42	146.41	24.60	46.37	18.64	40.74	43.82
CV, %	3.73	1.82	5.39	8.33	6.28	10.92	7.34	
Source (heat stress)								
Replicate	2	3.62 ^{NS}	6.76 ^{NS}	0.15 ^{NS}	3.43 ^{NS}	0.174 ^{NS}	1.59 ^{NS}	1.13 ^{NS}
Genotypes	48	13.49**	23.96**	8.09**	18.94**	3.057**	80.57**	22.33**
Error	96	6.49	10.80	1.34	3.82	0.156	8.23	9.04
Mean		73.68	106	16.15	19.44	5.63	29.36	51.31
CV, %		3.46	3.10	7.16	10.07	7.03	9.77	5.86

CV: Coefficient of variation; RCI: relative cell injury.

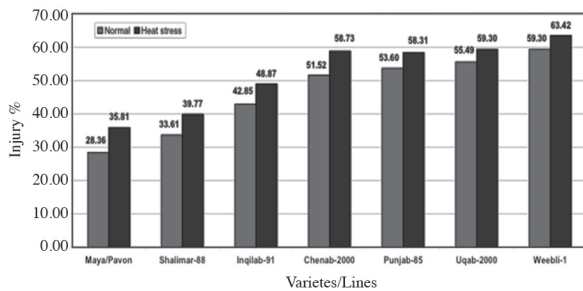


Figure 1. Relative cell injury percentage of parents used in a 7 × 7 diallel cross under normal and heat stress conditions.

Adequacy test of studied traits

The additive-dominance model for various plant characters 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 ANOVA of (Wr + Vr) and (Wr - Vr). Results of two tests under normal and stress conditions are shown in Table 2. The regression coefficient ‘b’ for all the characters departed significantly from zero, but did not deviate from unity under both conditions. 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 that genes were independent in their action. The unit slope of the regression lines for all the plant traits under study suggested that all the assumptions underlying the additive-dominance model were met (Mather and Jinks, 1982).

The mean squares of ANOVA for (Wr + Vr) and (Wr - Vr) (Table 2) showed significant differences (P ≤ 0.05 - 0.01) between the arrays (Wr + Vr) and non-significant (P > 0.05) differences within the arrays (Wr - Vr) for flag leaf area, RCI (%), biomass per plant, and grain yield under normal conditions; characters, such as flag leaf area, RCI (%), days to maturity, and harvest index under heat stress, indicated that there was dominance and no epistasis. 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 such as days to heading, days to maturity, and harvest index under normal conditions, and traits such as days to heading, grain yield per plant, biomass per plant under stress conditions showed no dominant effects and the presence of epistasis. Thus, based on the results of two tests, the simple genetic model was partially adequate for analyzing the data set for plant traits such as days to heading, days to maturity, and harvest index under normal conditions, and traits

Table 2. Scaling tests for adequacy of additive-dominance model for various *Triticum aestivum* plant traits under normal and heat stress conditions.

Traits (normal)	Regression slope		Mean squares		Remarks	Joint regression(b)
	b ₀	b ₁	Wr + Vr	Wr - Vr		
Days to heading	3.57*	0.054 ^{NS}	231.83 ^{NS}	20.46 ^{NS}	Model is partially adequate	b = 0.984 + 0.275
Days to maturity	3.51*	1.17 ^{NS}	314.95 ^{NS}	137.51 ^{NS}	Model is partially adequate	b = 0.749 + 0.213
Flag leaf area	7.14*	0.29 ^{NS}	49.20**	2.13 ^{NS}	Model is fully adequate	b = 0.960 + 0.134
Grain yield per plant	10.28*	-1.92 ^{NS}	26.46**	0.83 ^{NS}	Model is fully adequate	b = 1.23 + 0.12
Biomass per plant	3.91*	1.74 ^{NS}	2409.49**	172.04 ^{NS}	Model is fully adequate	b = 0.691 + 0.176
Harvest index	5.50*	0.18 ^{NS}	88.23 ^{NS}	28.63 ^{NS}	Model is partially adequate	b = 0.968 + 0.175
Relative cell injury, %	6.09*	0.50 ^{NS}	15024.02**	496.93 ^{NS}	Model is fully adequate	b = 0.924 + 0.151
Traits (heat stress)						
Days to heading	4.63*	0.58 ^{NS}	26.54 ^{NS}	4.71 ^{NS}	Model is partially adequate	b = 0.889 + 0.192
Days to maturity	4.84*	0.14 ^{NS}	79.03 ^{NS}	10.66 ^{NS}	Model is partially adequate	b = 0.971 + 0.200
Flag leaf area	6.15*	0.68 ^{NS}	15.11**	0.87 ^{NS}	Model is fully adequate	b = 0.901 + 0.146
Grain yield per plant	6.32*	-0.63 ^{NS}	37.56 ^{NS}	1.72 ^{NS}	Model is partially adequate	b = 1.155 + 0.258
Biomass per plant	2.85*	0.10 ^{NS}	607.82*	69.70 ^{NS}	Model is fully adequate	b = 1.11 + 0.175
Harvest index	5.49*	0.06 ^{NS}	5862.64**	301.79 ^{NS}	Model is fully adequate	b = 0.964 + 0.338
Relative cell injury, %	4.63*	0.58 ^{NS}	26.54 ^{NS}	4.71 ^{NS}	Model is partially adequate	b = 0.987 + 0.179

b: Regression-coefficient; Wr: covariance; Vr: variance.

such as days to heading, grain yield per plant, biomass per plant under heat stress conditions.

Estimating genetic components and graphical representation under normal and heat stress conditions

The D component was positive and significant for days to heading (Table 3). The values of H_1 and H_2 are less than D, indicating that genes showing additive effects are more important than dominance effects for days to heading under normal and heat stress conditions. The $H_2/4H_1$ ratio was < 0.25 , which indicated an unequal distribution of genes for days to heading among parents under both regimes. The positive F-value denoted the important role of dominant genes and was supported by a high value of $\sqrt{4DH_1 + F}/\sqrt{4DH_1 - F} = 1.58$ under normal conditions; a negative F-value was found under stress, indicating that the role of dominant genes was unimportant. The negative value of h^2 , the dominance effect due to heterozygous loci, was noted under both environments. The degree of dominance was < 1 , suggesting the presence of partial dominance in the F_1 hybrid under both environments. The estimate of narrow-sense heritability was 67 and 62% under normal and stress conditions, respectively. The graph in Figure 2 shows that the Maya/Pavon and Shalimar-88 parents contain maximum dominant genes. However, the Inqilab-91 and Weebli-1 varieties possess maximum recessive genes since they are far from the origin under normal conditions. The graph of the under stress conditions (Figure 3) shows that the Maya/Pavon and Inqilab-91 parents contain maximum dominant genes. However, the Punjab-85 and Weebli-1 varieties possess maximum recessive genes since they are the farthest from the origin.

For the days to maturity trait, D is positive and significant under both regimes, thus indicating additive effects since its value is higher than H_1 and H_2 (Table 3). However, H_1 and H_2 values were negative under stress. The degree of dominance was < 1 , thus suggesting partial dominance in the expression of days to maturity under

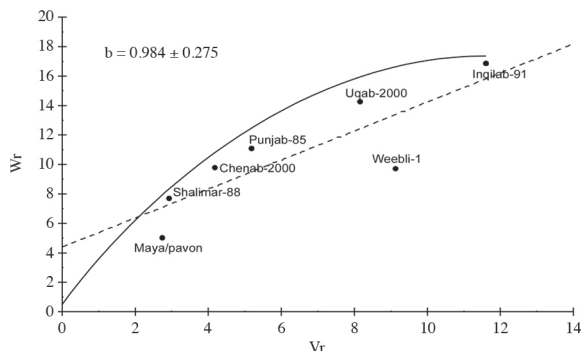


Figure 2. Covariance/Variance (W_r/V_r) graph for days to heading under normal conditions

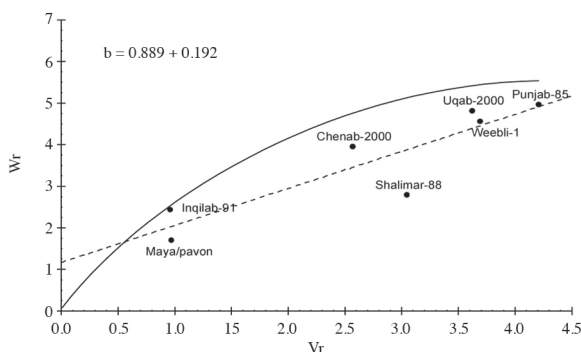


Figure 3. Covariance/Variance (W_r/V_r) graph for days to heading under heat stress conditions.

both conditions, this was supported by the slope on the regression line in Figures 3 and 4. The $H_2/4H_1$ ratio value was < 0.25 , which indicated an unequal distribution of genes for the trait among parents under both regimes. The positive F-value denoted the important role of dominant genes which was favored by the high value of $\sqrt{4DH_1 + F}/\sqrt{4DH_1 - F} = 1.48$ under normal conditions, but a negative value was found under stress environments. The estimate of narrow-sense heritability was 77 and 64% under normal and stress conditions, respectively. The graph in Figure 4 shows that Chenab-2000 and Shalimar-88 parents contain

Table 3. Estimation of the components of genetic variation under normal and heat stress conditions.

Character	Condition	D	H_1	H_2	F	h^2	E	$(H_1/D)^{0.5}$	$\frac{4DH_1^{0.5} + F}{4DH_1^{0.5} - F}$	$H_2/4H_1$	$h^2_{(m)}$
Days to heading	Normal	21.72 ± 1.59	-2.81 ± 3.81	-0.99 ± 3.36	3.50 ± 3.80	-1.99 ± 2.26	4.27 ± 0.56	0.36	1.58	0.088	0.67
	Heat stress	5.68 ± 0.44	-1.71 ± 1.06	-1.03 ± 0.93	-1.72 ± 1.05	-1.11 ± 0.63	2.28 ± 0.15	0.55	0.57	0.15	0.62
Days to maturity	Normal	31.66 ± 2.35	13.13 ± 5.67	11.42 ± 4.99	7.91 ± 5.65	-0.40 ± 3.35	2.58 ± 0.83	0.64	1.48	0.22	0.77
	Heat stress	11.15 ± 0.65	-3.59 ± 1.57	-1.13 ± 1.38	-3.96 ± 1.57	-1.71 ± 0.93	3.80 ± 0.23	0.57	0.52	0.079	0.64
Flag leaf area	Normal	7.14 ± 0.45	2.38 ± 1.08	2.20 ± 0.94	7.41 ± 1.45	-0.015 ± 0.64	0.64 ± 0.16	0.57	0.62	0.23	0.79
	Heat stress	3.37 ± 0.31	0.79 ± 0.75	0.75 ± 0.66	-1.60 ± 0.75	0.36 ± 0.45	0.47 ± 0.11	0.48	0.34	0.24	0.79
Biomass per plant	Normal	48.84 ± 6.19	22.01 ± 14.89	20.23 ± 13.12	19.59 ± 14.84	-2.20 ± 8.81	5.29 ± 2.19	0.67	1.84	0.23	0.60
	Heat stress	10.89 ± 0.52	4.35 ± 1.25	4.95 ± 1.10	1.03 ± 1.25	0.66 ± 0.74	1.35 ± 0.18	0.63	1.16	0.28	0.64
Harvest index	Normal	13.13 ± 0.94	-6.11 ± 2.27	-2.94 ± 2.00	-5.12 ± 2.26	-2.95 ± 1.34	6.98 ± 0.33	0.68	0.55	0.12	0.55
	Heat stress	45.28 ± 3.79	12.14 ± 9.13	12.09 ± 8.04	0.55 ± 9.10	-1.38 ± 5.40	2.87 ± 1.34	0.52	1.02	0.25	0.79
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
	Heat 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
Relative cell injury%	Normal	134.40 ± 9.35	56.92 ± 22.51	46.89 ± 19.83	-15.03 ± 22.43	24.68 ± 13.32	3.71 ± 3.30	0.65	0.84	0.21	0.84
	Heat stress	111.88 ± 6.70	39.34 ± 16.13	29.43 ± 14.21	-18.24 ± 16.07	0.50 ± 9.55	3.15 ± 2.37	0.59	0.76	0.19	0.87

D: additive variance; H_1 : dominance variance; H_2 : proportion of positive and negative genes in the parents; F: Relative frequency of dominant and recessive alleles in the parent; h^2 : dominance effect (over all loci in heterozygous phase), E: environmental variance; $(H_1/D)^{0.5}$: mean degree of dominance; $\sqrt{4DH_1 + F}/\sqrt{4DH_1 - F}$: proportion of dominant and recessive genes in the parents; $H_2/4H_1$: proportion of genes with positive and negative effects in the parents; $h^2_{(m)}$: heritability.

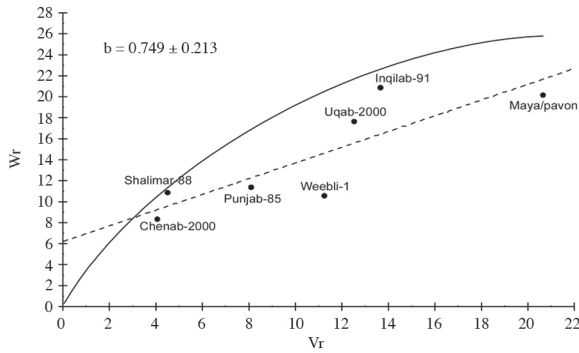


Figure 4. Covariance/Variance (W_r/V_r) graph for days to maturity under normal conditions.

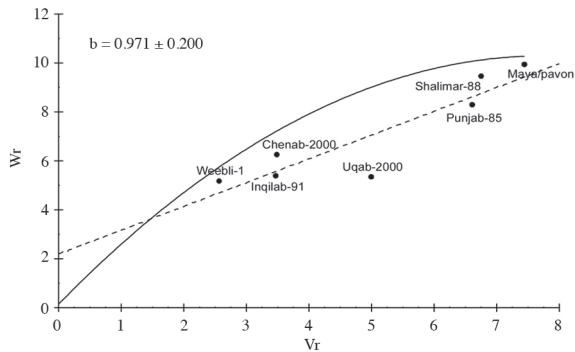


Figure 5. Covariance/Variance (W_r/V_r) graph for days to maturity under heat stress conditions.

the maximum number of dominant genes. However, 'Maya/Pavon' and 'Inqilab-91' possess the maximum number of recessive genes since they are farthest from the origin under normal sowing conditions. Figure 5 indicated that 'Weebli-1', 'Inqilab-91', 'Uqab-2000', and 'Chenab-2000' possessed the maximum number of dominant genes responsible for inheritance of days to heading under stress. The maximum number of recessive genes were carried by 'Maya/Pavon' and 'Shalimar-88'.

Estimating genetic components of variation for flag leaf area under normal conditions showed that the value for D was positive and significant under both conditions, thus indicating additive effects (Table 3) which were further evidenced by H_1 and H_2 values which were lower than D. The value of $H_2/4H_1$ ratio was < 0.25 under normal conditions, which indicated an unequal distribution of genes for the trait among parents. However, the value was almost equal to 0.25 under stress and demonstrated an equal distribution of genes. A positive F-value denoted the important role of dominant genes under normal conditions, while the under stress value was negative, thus showing the important role of recessive alleles. The negative value of h^2 was noted under normal conditions and was positive under stress. The degree of dominance was < 1 , suggesting the presence of partial dominance in the F_1 hybrid; this was supported by the regression slope in Figure 6. The estimate of narrow-sense heritability was 79% under both conditions. Figure 6 showed that

'Chenab-2000' and 'Punjab-85' had the maximum number of dominant genes for flag leaf area, while 'Inqilab-91' and 'Maya/Pavon' had the maximum number of recessive genes for flag leaf area under normal sowing conditions. The W_r/V_r graph (Figure 7) for under stress conditions shows that 'Chenab-2000' and 'Uqab-2000' had the maximum number of dominant genes for flag leaf area under heat stress conditions, while 'Inqilab-91' and 'Maya/Pavon' had the maximum number of recessive genes for control the flag leaf area.

The H_1 , H_2 , and D genetic components for grain yield per plant were positive and significant. Component D is higher than H_1 and H_2 under both environments and shows additive genetic effects in controlling grain yield. The value of the $H_2/4H_1$ ratio was < 0.25 , which indicated an unequal gene distribution for the trait among the parents, but this value is almost equal to 0.25 under stress, which shows the equal gene distribution. The Positive F-value denoted the important role of dominant genes under both conditions. The negative value of h^2 was noted. The degree of dominance was < 1 , suggesting partial dominance in the F_1 hybrid, this was supported by the regression slope in Figure 8. The estimate of narrow-sense heritability was 74 and 88% under normal and stress conditions, respectively. Figure 10 shows that 'Maya/Pavon' and 'Uqab-2000' had the maximum number of dominant genes for grain yield per plant. However, 'Chenab-2000' and 'Weebli-1' had the maximum number

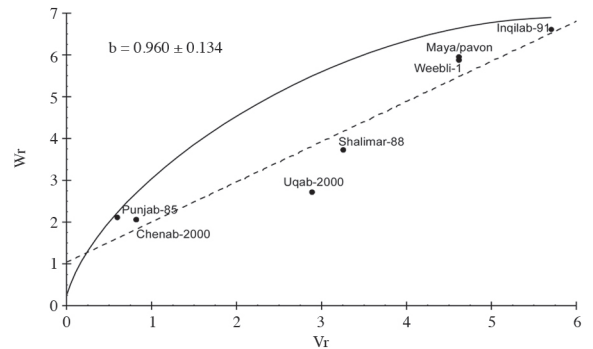


Figure 6. Covariance/Variance (W_r/V_r) graph for flag leaf area under normal conditions.

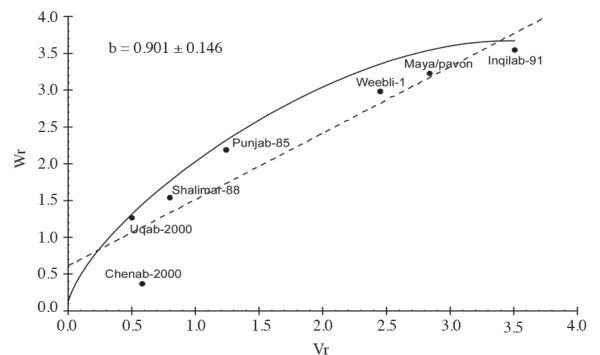


Figure 7. Covariance/Variance (W_r/V_r) graph for flag leaf area under heat stress conditions.

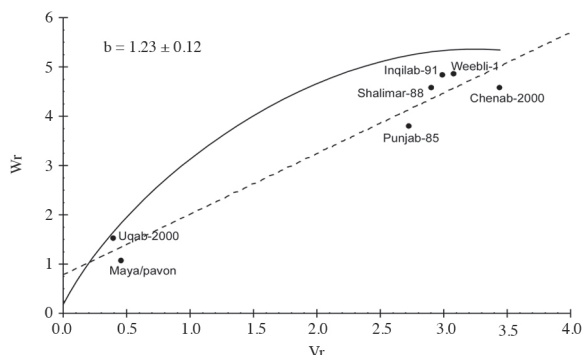


Figure 8. Covariance/Variance (W_r/V_r) graph for grain yield per plant under normal conditions.

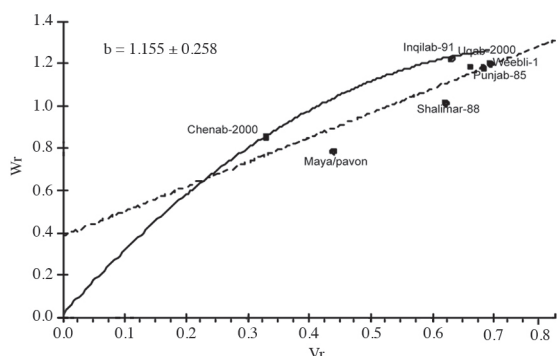


Figure 9. Covariance/Variance (W_r/V_r) graph for grain yield per plant under heat stress conditions.

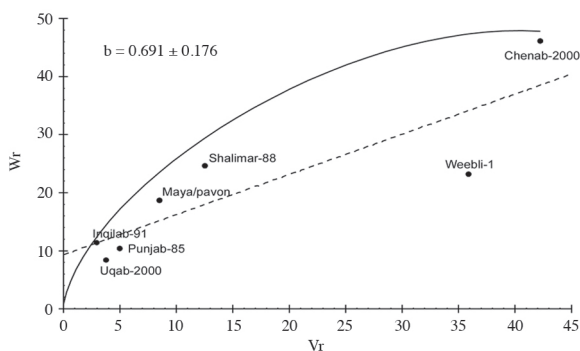


Figure 10. Covariance/Variance (W_r/V_r) graph for biomass per plant under normal conditions.

of recessive genes to control grain yield under normal conditions. The W_r/V_r graph (Figure 9) for grain yield under stress conditions, 'Weebli-1' and 'Punjab-85' had the maximum number of recessive genes for grain yield under heat stress conditions.

The value of D was positive and significant and higher than H_1 and H_2 , thus indicating additive effects in controlling biomass per plant under both regimes (Table 3). The value of the $H_2/4H_1$ ratio was < 0.25 under normal conditions and > 0.25 under stress conditions; both values indicated an unequal gene distribution for the trait among

the parents. The positive F -value denoted the important role of dominant genes. The negative value of h^2 was noted. The degree of dominance was < 1 , suggesting partial dominance in the F_1 hybrid; this was supported by the regression slope in Figure 10. The estimate of narrow-sense heritability was 60 and 64% under normal and stress conditions, respectively. Figure 12 shows that 'Uqab-2000' had the maximum number of dominant genes for biomass per plant. 'Chenab-2000' had the maximum number of recessive genes for biomass per plant under normal conditions. Figure 11 shows that 'Punjab-85' and 'Shalimar-88' had the maximum number of dominant genes for biomass per plant. The 'Maya/Pavon' and 'Inqilab-91' lines had the maximum number of recessive genes for biomass per plant under stress conditions.

The value of D was greater than H_1 and H_2 , which confirmed that additive gene action was involved in the inheritance of the harvest index under both conditions. The ratio of $H_2/4H_1$ is < 0.25 , which provides the unequal gene distribution in the parents under normal conditions. H_1 and H_2 were almost equal under stress conditions and the gene distribution for the harvest index was equal. The value of the $H_2/4H_1$ ratio was 0.25, which provides further evidence of equal gene distribution in the parents. The negative value of F was found under normal conditions and revealed the presence of more recessive genes, but it was positive with more dominant genes under stress.

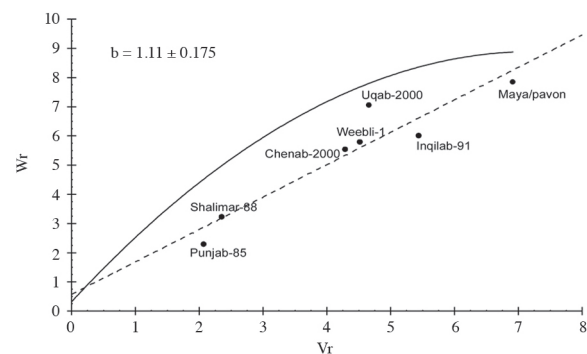


Figure 11. Covariance/Variance (W_r/V_r) graph for biomass per plant under heat stress conditions.

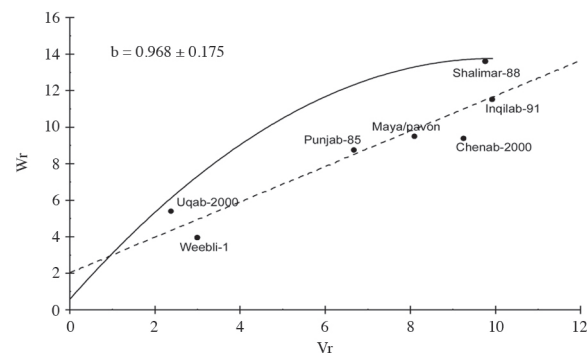


Figure 12. Covariance/Variance (W_r/V_r) graph for harvest index under normal conditions.

The negative sign of h^2 was observed. The degree of dominance was < 1 , supporting partial dominance in the F_1 hybrids; this was confirmed by the slope of the regression line in Figures 12 and 13 under both conditions. The estimate of narrow-sense heritability for the harvest index was 55 and 79% under normal and stress conditions, respectively. The distribution of varietal points along the regression line (Figure 12) shows 'Weebli-1' and 'Uqab-2000' with the highest number of dominant genes plus 'Shalimar-88' and 'Inqilab-91' in the farthest position along the regression line with the maximum number of recessive genes. The graph (Figure 13) of the harvest index under stress indicated that 'Shalimar-88' and 'Inqilab-91' contain the maximum number of dominant genes as compared to other parents. However, the 'Weebli-1' and 'Chenab-2000' parents are far from the origin so they contain the maximum number of recessive genes to control the harvest index.

The component of variation D showed that it was positive and significant under both conditions. The H_1 and H_2 values were not equal and less than D, thus showing the importance of additive effects and the unequal gene distribution. The $H_2/4H_1$ ratio was < 0.25 , which indicated an equal distribution of dominant genes for the trait among the parents under both conditions. The negative F-value denoted the important role of recessive genes, which was supported by a low value of $\sqrt{4DH_1 + F}/\sqrt{4DH_1 - F}$. The positive value of h^2 was noted. The degree of dominance was < 1 under both regimes, suggesting partial-dominance in the F_1 hybrid. The estimate of narrow-sense heritability was 87 and 84% under normal and stress conditions, respectively. The distribution of varietal points along the regression line (Figure 14) shows that 'Maya/Pavon' and 'Inqilab-91' had the maximum number of dominant genes for relative cell injury %. 'Uqab-2000' and 'Weebli-1' had the maximum number of recessive genes to control this trait. Figure 15 shows 'Maya/Pavon' and 'Shalimar-88' with the maximum number of dominant genes for relative cell injury (%). 'Weebli-1' and 'Uqab-2000' carried the maximum recessive genes to control relative cell injury (%).

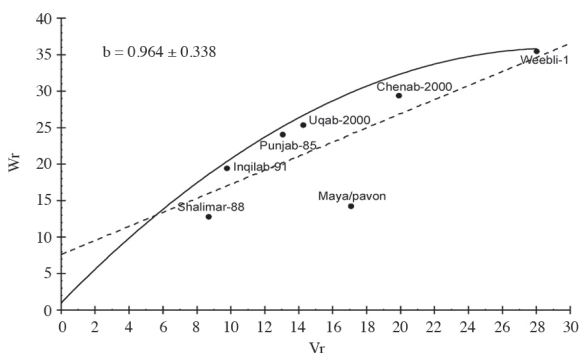


Figure 13. Covariance/Variance (Wr/Vr) graph for harvest index under heat stress conditions.

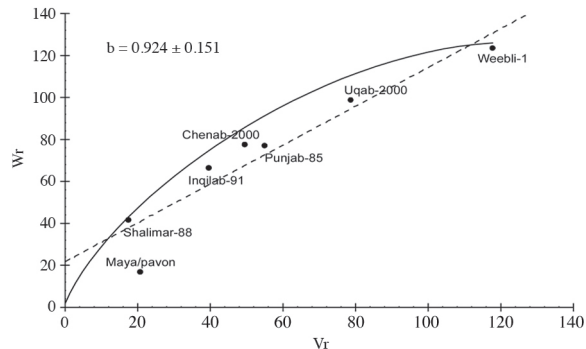


Figure 14. Covariance/Variance (Wr/Vr) graph for relative cell injury % under normal conditions.

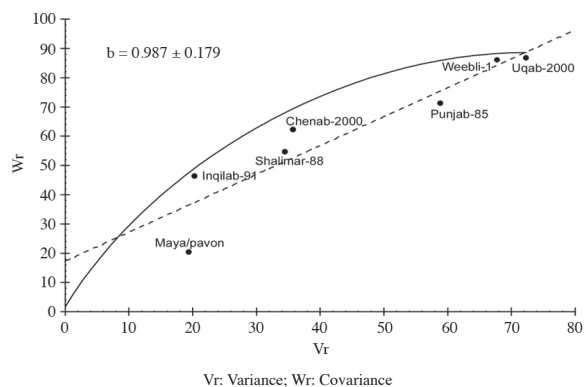


Figure 15. Covariance/Variance (Wr/Vr) graph for relative cell injury % under heat stress conditions.

DISCUSSION

Extensive wheat cultivation poses many problems. Among these, terminal heat stress is a serious threat. In Pakistan, late-sown wheat crops are vulnerable to this risk resulting in severe yield loss. It is well known that for every 1°C increase in ambient temperature during the grain-filling period, yield is reduced by up to 4% (McDonald *et al.*, 1983). According to DuPont *et al.* (2006), heat stress during grain-filling reduces grain weight by 50%. So, there is a need to develop varieties that not only have the ability to escape, avoid, or tolerate this stress, but also to produce higher yields in these conditions. For this purpose, knowledge about plant and heat-related traits provide an opportunity to select the best parents and their cross-combinations to develop high-yielding varieties which can perform better in heat stress conditions. Electrolyte leakage is a measure of cell membrane thermo stability (Sullivan and Ross, 1979). This method is used in wheat as a modified method to develop heat tolerant lines (Saadalla *et al.*, 1990a; 1990b; Tahir and Singh, 1993). Wheat varieties with a better genetic potential perform better in conducive and non-conductive environment ecosystems (Calderini and Slafer, 1999; Reynolds and Borlaug, 2006). There is a correlation between yield improvement and increased dry matter, other than grain,

but less attention was given to above-ground mass (Sayre *et al.*, 1997). Crop plants have various mechanisms to improve yield (Singh *et al.*, 1998). A good source and sink relationship is one way of improving yield. Researchers explain this relationship with good results (Slafer *et al.*, 1996).

The present sample of genetic material, developed after screening against heat via relative cell injury % of the parents, was used to generate information on the genetic mechanism of relative cell injury % and some yield-related traits. Cellular membrane stability is one of the effective screening methods against heat tolerance on a physiological basis (Ibrahim and Quick, 2001). However, yield and its related parameters in stress environments are mainly effective to evaluate stress. The cell membrane thermostability (CMT) method on flag leaves of field-grown plants resulted in thermo tolerant lines, resulting in a significant spring wheat yield increase (Shanahan *et al.*, 1990). They also concluded that the cell membrane thermostability test is a useful screening procedure to select heat-tolerant spring wheat genotypes. Similarly, Saadalla *et al.* (1990a; 1990b) advocated that the technique is a reliable method to explore heat-tolerant germplasm in wheat. Some studies regarding heat tolerance with respect to cell injury (%) revealed that the genotypes with less injury to plasma membranes are tolerant as compared to the genotypes with more injury to cell membrane (Renu *et al.*, 2004). Membrane thermostability is heritable (Fokar *et al.*, 1998) and highly correlated to yield.

The genotypic variation was found for all the traits under both conditions. Significant differences among genotypes for grain yield and related traits in different wheat varieties were also reported by Ambreen *et al.* (2002). Early-maturing genotypes can have higher grain weight and a longer grain formation period, and thereby have the ability to tolerate heat stress as compared to long-duration genotypes (Singh *et al.*, 2005). Some of the wheat genotype experiments to overcome heat indicate that short-duration genotypes show low heat susceptibility as compared to the long-duration genotypes (Sharma *et al.*, 2004).

Data assessment revealed partial adequacy for traits such as days to heading and days to maturity under both regimes, but they showed full adequacy under both environments for flag leaf area and relative cell injury %. Models for grain yield per plant and biomass per plant were fully adequate under normal conditions but partially adequate under stress. The harvest index showed partial adequacy under normal conditions, but it was fully adequate under stress. The partially adequate models for the abovementioned traits can be due to non-allelic interaction, linkage, and non-independent gene distribution in the parents as suggested by Mather and Jinks (1982). In spite of the partial adequacy of the simple genetic model to the data set, the model analyzed the diallel cross data in wheat (Hussain, 1991). The

significant variation among genetic components, additive and dominant for all the characters under study indicated the efficient creation of genetic variability. The breeding value of a line is a function of the additive genetic effects that were evident from the significant and higher D value than the dominance variance H_1 and H_2 for all traits. Some of the studies in late conditions revealed that days to heading, days to maturity, grain yield per plant, biomass per plant, and harvest index were controlled by additive genetic effects; direct selection methodologies can be adopted to select these traits (Chandrashekhar and Kerketta, 2004). Some researchers reported partial dominance for this trait and concluded that early-maturing genotypes are very useful in late-sown conditions (Patil *et al.*, 1995), but others contradict this finding because of the large variation in the wheat germplasm (Sabouri *et al.*, 1996; Yang *et al.*, 1997). Studies on days to heading under normal and late-sown conditions revealed that days to heading were significantly higher under early sowing than late-sown conditions (Renu *et al.*, 2004). Genotypes and sowing dates are significantly correlated with membrane thermostability (Sandeep *et al.*, 2000). Comparing the mean of two sowing extremes revealed that days to heading, days to maturity, and grain yield are greatly reduced as a result of the difference in sowing times (Mahboob *et al.*, 2005). Similarly, yield is greatly reduced by late sowing as reported by Arain *et al.* (2002). The inheritance pattern study for the flag leaf area was demonstrated by many researchers, but some concluded that additive gene action was involved in the expression of this trait (Joshi *et al.*, 2002), while others found partial dominance with additive gene action (Ambreen *et al.*, 2002). Dominance was also reported by some researchers (Ejaz-ul-Hassan and Khaliq, 2008). The harvest index was controlled by additive gene action (Ullah, 2004; Joshi *et al.*, 2004).

The magnitude of H_1 and H_2 was not equal for all the studied traits under both conditions, except for flag leaf area, grain yield, and harvest index under stress environments that showed an equal gene distribution. F, which indicates the relative frequency of dominant and recessive alleles in the parents, was positive for days to heading, days to maturity, and flag leaf area under normal conditions, but it was negative under stress. The harvest index was negative under heat stress and positive under normal conditions, but grain yield was positive and relative cell injury % was negative under both environments. The degree of dominance was lower for almost all the traits showing partial dominance under both regimes. Heritability estimates were moderate to high for all the traits under normal and stress conditions. Some researchers reported high heritability estimates for grain yield per plant (Riaz and Chowdhry, 2003), intermediate estimates were reported by Mahmood and Chowdhry (1999), Fida *et al.* (2001), whereas Aycicek and Yildirim (2006) found low heritability in wheat. High heritability was found in

the flag leaf area in wheat cultivars (Ahmed *et al.*, 2004), low to moderate heritability estimates were found for the flag leaf area by Riaz and Chowdhry (2003) and Ejaz-ul-Hassan and Khaliq (2008). Low heritability values for biomass per plant and harvest index were reported by Subhani *et al.* (2000). Thus, this genetic umbrella of different physiological and yield-related parameters would continue to achieve a high yield potential.

CONCLUSIONS

Actual genetic studies about days to heading, days to maturity, flag leaf area, grain yield per plant, biomass per plant, harvest index, and relative cell injury % would be helpful to develop material against heat stress. The presence of additive effects along with moderate to high heritability in almost all the traits is indicative of early generation trait selection. Similarly, sowing dates and relative cell injury % for screening purposes will be efficient criteria to develop heat tolerant lines.

Análisis genético del porcentaje relativo de daño celular y algún rasgo que contribuye al rendimiento en trigo bajo condiciones normales y de estrés térmico. Varios genotipos de trigo se discriminaron para estrés térmico. De ellos siete cultivares de trigo (*Triticum aestivum* L.) incluyendo tolerantes, moderadamente tolerantes, y susceptibles a estrés térmico obtenidos después de discriminar con calor se aparearon en un sistema de apareamiento de diallelo completo para estudiar el patrón de heredabilidad del porcentaje de daño celular relativo (daño celular %) y algunos parámetros que contribuyen al rendimiento bajo condiciones normales o de estrés térmico. Se encontraron diferencias genotípicas significativas ($P < 0.01$) para todos los rasgos estudiados bajo ambas condiciones. Pruebas de ajuste revelaron adecuación parcial para rasgos como días a espigadura y días a madurez en ambas condiciones pero mostraron suficiencia completa para área hoja bandera y daño celular % en ambas condiciones. El modelo para producción de grano por planta y biomasa por planta fue completamente suficiente bajo condiciones normales y completamente adecuado en estrés. El componente aditivo de variación genotípica (D) fue significativo para todos los rasgos estudiados y más que los componentes de dominancia H_1 y H_2 . Los valores de la proporción de genes con efectos positivos y negativos en los progenitores ($H_2/4H_1$) demostraron distribución desigual de genes dominantes en los progenitores para casi todos los rasgos excepto área de hoja bandera, producción de grano, y daño celular % en ambas condiciones. Se encontraron estimaciones relativamente altas para biomasa por planta e índice de cosecha.

Palabras clave: Porcentaje de daño celular relativo, componentes aditivos, test de adecuación, heredabilidad, trigo, diallelo.

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