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CELL MEMBRANE THERMO-STABILITY STUDIES THROUGH JOINT SEGREGATION ANALYSIS IN VARIOUS WHEAT POPULATIONS

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Abstract

Using joint segregation analysis (JSA) technique as statistical approach, mixed inheritance analysis for cell plasma membrane as membrane thermal stability (MTS) was assayed in two parental lines (P_1, P_2) and their four populations (F_1, BC_1, BC_2, F_2) of four wheat crosses, viz., Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver and TD-1 × D-97603 at Faculty of Agriculture, Gomal University, Dera Ismail Khan, Pakistan during crop season 2011-12. Results revealed that MTS was under control of two mixed groups of genes i.e., additive-dominant-epistatic major genes plus additive–dominant-epistasis of polygenes (model E) in Hashim-08 × LU-26 and Farid-06 × Shafaq crosses, respectively. In cross Parula × Blue Silver, it was governed by mixed genes i.e. one major-gene and additive-dominance-epistatic polygenes (model D). However, in cross TD-1 × D-97603, the MTS was under the influence of mixed epistasis of two major genes plus polygenes (model E-1). Polygene variation and polygene heritability were higher than major gene variation and heritability in crosses Hashim-08 × LU-26 and Farid-06 × Shafaq. In crosses Parula × Blue Silver and TD-1 × D-97603, the major gene variation and heritability were higher than polygene variation and heritability, indicating maximum contribution of the major genes. While in cross TD-1 × D-97603, epistatic components were also positive and due to which the polygene heritability was almost zero. Moderate to high environmental variation in the MTS for segregating generations revealed that the said trait was highly persuaded by the environment. However, the genetic behavior of the MTS suggested that early selection for MTS in the crosses Hashim-08 × LU-26 and Farid-06 × Shafaq would be efficient. Whereas, the delayed selection in crosses Parula × Blue Silver and TD-1 × D-97603 until the accumulation of maximum favorable genes will be effective.

Introduction

Heat stress is the major production constraint to wheat in arid, semiarid, tropical and subtropical regions of the world (Ashraf & Haris, 2005). Heat stress has various severe effects at different growth stages of wheat, especially at the anthesis and grain filling stages in almost all the environments (Reynolds *et al.,* 1994). At the time of anthesis during spikelets development, it reduces the potential number of grains. At post anthesis during grain filling stage, it affects the availability and translocation of photosynthates to developing seed and starch synthesis, thus adversely affecting the grain weight and quality (Mohammadi *et al*., 2004). Therefore, the development of heat tolerant cultivars is the major concern in wheat breeding programmes.

Exposure to high temperature reduces the yield and quality in several different ways (Maestri *et al*., 2002; Wardlaw *et al*., 2002) like reduction in photosynthesis, either due to damage of photosystem II (Paulsen, 1994) or inhibition of rubisco activase (Law & Crafts-Brander, 1999), increase in respiration (Berry & Bjorkman, 1980) or disruptions of the respiratory mechanism (Lin & Markhart, 1990) and also decrease in starch synthesis in developing the grain (Bhullar & Jenner, 1985).

Different physiological characters related with heat tolerance including canopy temperature depression (CTD), spike temperature depression (STD), cell membrane thermostability (CMT), triphenyltetrazolium chloride (TTC) staining, chlorophyll fluorescence, and reflectance spectroscopy have been studied for heat tolerance mechanism. In the cell membrane thermostability, electrolyte leakage from leaf tissue is measured after exposure to high temperatures (Ibrahim & Quick, 2001).

Although resistance to high temperatures involves several complex tolerance and avoidance mechanisms, the membrane is thought to be a site of primary physiological injury by heat (Blum, 1988), and measurement of solute leakage from tissue can be used to estimate the damage to membranes. Since membrane thermostability is moderately heritable (Fokar *et al*., 1998) showed high genetic correlation with yield and potential application in breeding. Determining mechanisms associated with heat tolerance and identifying efficient screening assays associated with these mechanisms are vital for heat tolerance improvement in wheat germplasm (Ristic *et al*., 2007). Further, it is also crucial to know the association between these variables and grain yield under heat stress to justify their use as a selection tool.

The choice of selection and breeding procedure for genetic improvement of any crop mainly depends upon the information and knowledge about type of gene action and magnitude of genetic components for various characters in the plant materials under investigation (Ojaghi & Akhundova, 2010). The present study was thus designed to evaluate the genetic behavior and inheritance pattern of cell MTS and to select the desirable genotypes for future breeding strategies.

Materials and Methods

Eight genetically diverse parents selected from wheat germplasm were crossed in the combinations viz., Hashim-08 × LU-26, Farid-06 × Shafaq, Parula × Blue Silver and TD-1 × D-97603 during crop season 2011-12 at the Faculty of Agriculture, Gomal University, Dera Ismail Khan, Pakistan (Dera Ismail Khan, 31°, 49 ′N; 70°,

55′E). Two parental genotypes (P_1, P_2) and their four populations (F_1, BC_1, BC_2 and F_2) of each cross were developed during 2009-10 and 2010-11. The P_1, P_2 and four populations of each cross combination planted in a randomized complete block (RCB) design with two replications. Keeping row length of four meters, two rows were planted for P_1, P_2 and F_1 populations, three rows each for back cross populations (BC_1, BC_2) and four rows for F_2 populations in each replication. The plants and rows spacing were kept at 10 and 30 cm, respectively.

Cell membrane thermal stability: From P_1, P_2, and four populations, eight fully expended leaves were cut from randomly tagged plants in each replication. The leaves were thoroughly washed with de-ionized water, and each leaf was divided into two parts to use as control and heat treatment. One gram sample of these leaves was placed into two different test tubes containing 20 ml de-ionized water. One of the test tubes was kept at 25°C and the other at 46°C for one hour in water bath. To stabilize the content of the liquid compounds after treatment, the test tubes were kept for two hours at room temperature. Conductivity readings were recorded at 25°C using an electrical conductivity meter for control (C_1) and heat treated (T_1) tubes. Both the test tubes were further autoclaved at 120°C for 20 minutes. The second conductivity reading of the aqueous phase (C_2 and T_2) was taken after the samples were cooled to room temperature. The MTS values were estimated using the following equation as suggested by Blum and Ebercon (1981).

$$\text{Relative Injury (RI) \%} = 100-\{[1-(T_1/T_2)]/[1-(C_1/C_2)] \times 100\}$$

Where C and T refers to electrical conductivity of control and heat treated samples and the subscript 1 and 2 refer to electrical conductivity readings before and after autoclave, respectively.

Data recording and analysis: The data regarding MTS (relative injury %) were subjected to the five groups consisting of 24 different genetic models of the Joint Segregation Analysis (JSA) designed for the P_1, P_2 and four basic populations (Gai & Wang, 1998; Gai *et al*., 2003, 2007) (Tables 1 & 2). Suitable genetic models for each cross combination were determined by using maximum log of likelihood estimates (McLachlan, 1988; Wang & Gai, 1997) and Akaike's information criterion (Akaike, 1977) (Table 3). Selection of best-fit model was made on the basis of all non-significant or least number of significant values of the three chi-square statistics i.e. U_1^2, U_2^2 and U_3^2 (Tables 4a, b). Two other important completely distribution free tests i.e. Smirnov's statistics (nW^2) and Kolmogorove's statistics (Dn) were used as goodness of fit tests to determine whether the selected model sufficiently explains the data (Tables 4a, b). If, for a particular genetic model, none of these five statistics were significant, then the data were considered to adequately fit the model (Gai & Wang, 1998). The data were analyzed by using sin.exe software and the major genes-polygenes mixed inheritance model to a joint analysis of multi-generations (Gai *et al*., 2003). In case of the best-fit model, the values of second order genetic parameters as well as σ_{mg}^2 and σ_{pg}^2 for BC_1, BC_2 and F_2 were worked out with the help of proposed formulae (Gai *et al*., 2003; Zhang *et al*., 2003). Under the second order genetic parameters, the phenotypic variation (σ_p^2) partitioned into genetic (σ_g^2) and environmental variations (σ_e^2) for each cross. The genetic components of variation in turn were subdivided into variation due to major genes (σ_{mg}^2) and polygenes (σ_{pg}^2). Based on Mather and Jinks (1982), the values from μ1 to μ69 exhibited different means of component distributions (Wang *et al*., 2001; Zhang *et al*., 2003) regarding six generations which are to be put in the formulae as suggested by Gai *et al*., (2003) for calculating 1st and 2nd order genetic parameters (Tables 5 & 6).

Results

Occurrence of cell MTS in various wheat populations: The frequency distribution of cell membrane stability in P_1, P_2 and four populations is presented in Table 2. The F_1 of cross Hashim-08 × LU-26 tended towards the parent one indicating higher MTS. However, in crosses Farid-06 × Shafaq and TD-1 × D-97603, it was equally distributed between the parents. The cross Parula × Blue Silver exhibited higher MTS having low damage percentage. The tendency of BC_1 in crosses Hashim-08 × LU-26 and Farid-06 × Shafaq was towards parent one. The F_2 exhibited high membrane stability by having low damage percentage against F_1 and back cross populations in crosses Hashim-08 × LU-26, Farid-06 × Shafaq and TD-1 × D-97603 whereas in cross Parula × Blue Silver, it was equally distributed between the parents.

Gene action for cell MTS in various wheat populations: For cross Hashim-08 × LU-26, the best-fit model for cell membrane stability was found to be model E. Model E indicated two mixed gene complexes viz., additive-dominant-epistatic major genes plus additive-dominant-epistasis of polygenes (Tables 3 & 4a). In cross Hashim-08 × LU-26, the additive (d_a, d_b) and dominant (h_a, h_b) effects contributed by two major genes (A & B) were estimated to be -0.20, 0.12 and 0.09, 0.07, respectively (Tables 5 & 6). The dominant ratios (h_a/d_a and h_b/d_b) of the genes A and B in cross Hashim-08 × LU-26 were -0.46 and 0.55, respectively (no dominance due to major gene A and partial dominance due to major gene B). Positive dominant ratios obtained for major gene B indicating partial dominance due to said gene in controlling the MTS. The additive × additive effects (i) of the major genes plus polygenes were recorded as 0.07 for cross Hashim-08 × LU-26. The additive × dominant effects of gene A over gene B (J_{ab}) and that of B over A (J_{ba}) were 0.11 and -0.20 for cross Hashim-08 × LU-26, respectively. The dominant × dominant type of non-allelic interaction (l) was recorded as -0.03 for cross Hashim-08 × LU-26. The second order genetic parameters given in Tables 5 & 6 revealed the phenotypic variation for cell membrane stability in segregating populations of BC_1, BC_2 and F_2. This phenotypic variance was divided into genetic and environmental variances while, genetic variation is further divided into variation due to major genes and polygenes. In cross Hashim-08 × LU-26, variation due to polygenes was more than variation due to major genes. Similarly,

maximum polygene heritability i.e., 12.83, 41.99 and 8.90 were estimated in cross Hashim-08 × LU-26 for BC_1, BC_2 and F_2 populations, respectively.

For cross Farid-06 × Shafaq, the best-fit genetic model for MTS was found to be model E, indicating two mixed gene groups i.e. additive-dominant-epistatic major genes plus additive–dominant-epistasis of polygenes (Tables 3 & 4a). In cross Farid-06 × Shafaq, each of d_a, d_b were estimated as 0.02 and h_a, h_b were estimated as -0.03, -0.02, respectively. In cross Farid-06 × Shafaq, dominant ratios (h_a/d_a and h_b/d_b) were -1.21 and -0.74, respectively. The additive × additive effect (*i*) of the major genes plus polygenes were recorded as 0.02 for cross Farid-06 × Shafaq. The additive × dominant effect of gene A over gene B (J_{ab}) and that of B over A (J_{ba}) estimated to be -0.02 and -0.03, respectively. The dominant × dominant type of non-allelic interaction (*l*) value was 0.03. The second order genetic parameters indicated the phenotypic variation for cell membrane stability in segregating populations i.e. BC_1, BC_2 and F_2 (Tables 5 & 6). The genetic and environmental variances derived phenotypic variance, and in turn, the genetic variation is subdivided into variation due to major genes and polygenes. Polygene variation excelled the major gene variation. Similarly, in cross Farid-06 × Shafaq the maximum polygene heritabilities i.e. 69.01, 29.28 and 43.53 were estimated for segregating generations BC_1, BC_2 and F_2, respectively.

Table 1. Estimable first order genetic parameters in various genetic models (A-1 to E-6).

Models	Model groups, code, and implication of model type	First order genetic parameters	
		Major genes	Polygenes
Group 1: One major gene			
A-1	Additive-dominant	*m, d, h*	σ^2
A-2	Additive	*m, d,* (*h=0*)	σ^2
A-3	Completely dominant	*m*, *d* (*h* = *d*)	σ^2
A-4	Completely negative dominant	*m*, *d* (*h* = -*d*)	σ^2
Group 2: Two major genes			
B-1	Additive-dominance-epistasis	*m*, *da*, *db*, *ha*, *h*b, *i*, *jab*, *jba*, *l*	σ^2
B-2	Additive-dominant	*m*, *d*a, *db*, *ha*, *hb*, *i*, *jab*, *jba*, *l*	σ^2
B-3	Additive	*m*, *da*, *db* (*ha*=*hb*= 0)	σ^2
B-4	Equally additive	*m*, *d* (*da*= *db*, *ha*=*hb*=0)	σ^2
B-5	Completely dominant	*m*, *da* (= *ha*), *db* (=*hb*)	σ^2
B-6	Equally dominant	*m*, *d* (= *da*= *db*= *ha*= *hb*)	σ^2
Group 3: Polygene			
C	Additive-dominant-epistasis	*M*	[d], [h], [*i*], [*j*], [l]
C-1	Additive-dominant	*M*	[d], [h]
Group 4: One major gene plus polygene			
D	Additive-dominant one major gene and additive-dominant-epistasis of polygene	*m*, *d*, *h*	[d], [h], [*i*], [*j*], [*l*]
D-1	Additive-dominant one major gene and additive-dominant polygene	*m*, *d*, *h*	[d], [h]
D-2	Additive one major gene and additive-dominant polygene	*m*, *d*, (*h* = 0)	[d], [h]
D-3	Completely dominant one major gene and additive-dominant polygene	*m*, *d* (*h* = *d*)	[d], [h]
D-4	Completely negative dominant one major gene and additive-dominant polygene	*m*, *d* (*h*= -*d*)	[d], [h]
Group 5: Two major genes plus polygene			
E	Additive-dominant-epistatic of two major genes and additive-dominant-epistasis of polygene	*m1* ~ *m6*, *da*, *db*, *ha*, *hb* , *i*, *jab*, *jba*, *l*	[d], [h], [*i*], [*j*], [*l*]
E-1	Additive-dominant epistasis of two major genes and additive-dominant polygene	*m*, *da*, *db*, *ha*, *hb* , *i*, *jab*, *jba*, *l*	[d], [h]
E-2	Additive-dominant two major genes and additive-dominant polygene	*m*, *da*, *db*, *ha*, *hb* , *i*= *jab*= *jba*, *l*	[d], [h]
E-3	Additive two major genes and additive-dominant polygene	*m*, *da*, *db*, *ha* = *hb* = 0	[d], [h]
E-4	Equally additive two major genes and additive-dominant polygene	*m*, *d* (= *da* = *db* , (*ha* = *hb* = 0)	[d], [h]
E-5	Completely dominant two major genes and additive-dominant polygene	*m*, *da* = *ha*, *db* = *hb*	[d], [h]
E-6	Equally dominant two major genes and additive-dominant polygene	*m*, *d* = *da* = *db* = *ha* = *hb*	[d], [h]

m: Population mean. *d*, [d]: Additive effect due to major gene(s) and polygenes, respectively. *h,* [h]: Dominant component due to major gene(s) and polygenes, respectively. *i*, [*i*]: Additive ×Additive component due to major gene(s) and polygenes, respectively. *jab*: *da* × hb: First major gene with additive × second major gene with dominant effect. *jba*: *db* × h*a*: Second major gene with additive × first major gene with dominant effect. [*j*]: Additive-dominance epistasis. Source of different model groups and model types (Gai and Wang, 1998; Gai *et al*., 2003; Zhang *et al*., 2003).

Table 2. Frequency distribution in plant population of cell MTS in P_1, P_2, F_1, B_1, B_2 and F_2 of four bread wheat crosses.

Crosses	Generations	Range of relative injury % of cell membrane												Size	Mean	Variance
		15-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75			
Hashim-08 × LU-26	P_1	-	-	-	12	12	12	24	-	-	-	-	-	60	41.06	25.81
	F_1	-	-	-	36	18	36	-	-	-	-	-	-	90	37.59	18.81
	P_2	-	-	-	-	-	-	-	-	24	24	12	-	60	60.89	25.26
	BC_1	-	-	60	60	30	-	-	-	-	-	-	-	150	30.52	15.23
	BC_2	-	-	-	-	30	90	30	-	-	-	-	-	150	41.79	12.11
	F_2	-	-	40	80	80	-	-	-	-	-	-	-	200	32.76	18.88
Farid-06 × Shafaq	P_1	-	-	-	-	24	12	24	-	-	-	-	-	60	42.29	27.61
	F_1	-	-	12	12	12	24	-	-	-	-	-	-	90	36.76	33.51
	P_2	-	-	12	24	24	-	-	-	-	-	-	-	60	32.32	14.43
	BC_1	-	-	-	-	-	30	60	30	-	30	-	-	150	48.81	57.57
	BC_2	-	-	-	60	30	60	-	-	-	-	-	-	150	36.60	13.8
	F_2	-	40	80	40	40	-	-	-	-	-	-	-	200	29.53	12.43
Parula × Blue Silver	P_1	-	-	-	-	-	-	12	24	24	-	-	-	60	53.36	19.54
	F_1	-	-	18	36	36	-	-	-	-	-	-	-	90	31.75	14.92
	P_2	-	-	-	-	-	-	-	-	12	12	12	24	60	65.21	45.95
	BC_1	-	-	60	30	60	-	-	-	-	-	-	-	150	31.81	23.89
	BC_2	-	-	30	60	30	30	-	-	-	-	-	-	150	33.55	17.39
	F_2	-	-			40	40	120	-	-	-	-	-	200	43.86	27.97
TD-1 × D-97603	P_1	-	-	-	-	-	-	-	-	12	24	12	12	60	63.58	24.48
	F_1	-	-	-	-	-	-	36	18	18	18	-	-	90	52.25	41.48
	P_2	-	-	-	-	-	-	12	36	12	-	-	-	60	51.26	13.96
	BC_1	-	-	60	30	30	30	-	-	-	-	-	-	150	52.25	41.30
	BC_2	30	-	60	-	60	-	-	-	-	-	-	-	150	52.25	41.30
	F_2	40	-	40	80	40	-	-	-	-	-	-	-	200	52.25	41.23

In cross Parula × Blue Silver, the best-fit genetic model for MTS was to be model D showing two mixed genes viz., one major-gene and additive-dominance-epistasis polygenes (Tables 3 & 4b). As evident from the 1st order genetic parameters (Tables 5 & 6), the negative additive effect (-4.40) and positive dominant effect (3.26) were observed in the said cross for MTS. The additive effects due to polygenes were negative whereas the dominant effects were positive due to polygenes. Epistatic effects of major genes were positive which revealed that the MTS was under control of epistatic nature of major genes. As evident from the second order genetic parameters, the major gene heritability was higher in segregating generations BC_1, BC_2 and F_2 as compared to polygene heritability, and revealed more contribution of major genes.

For cross TD-1 × D-97603, the best-fit genetic model was found to be E-1 representing two mixed gene complexes viz., two major additive-dominance epistatic genes plus additive-dominant polygenes (Tables 3 & 4b). In said cross, the additive and dominant effects contributed by two major genes (A & B) were estimated to be 3.10, -1.80 and 3.70, -2.60, respectively. In the said cross, the dominant ratios (h_a/d_a and h_b/d_b) of the genes A and B were 1.20 and 1.40, respectively. The additive × additive effect (*i*) of the major genes plus polygenes was recorded as 2.60. The additive × dominant effects of gene A over gene B (J_{ab}) and that of B over A (J_{ba}) were -3.2 and -9.4, respectively. The dominant × dominant type of non-allelic interaction (*l*) was recorded as 8.00. The second order genetic parameters indicated the phenotypic variation for cell membrane stability in segregating populations BC_1, BC_2 and F_2 (Tables 5 & 6). The phenotypic variance was partitioned into genetic and environmental variances, while genetic variation was further subdivided into variation due to major genes and polygenes. In cross TD-1 × D-97603, the variation due to polygenes was almost negligible than variation due to major genes. However, the variation due to environment was prominent in the segregating populations showing that the MTS was highly influenced by the environment.

Discussion

Both membrane thermal stability (MTS) and relative cell injury (RCI %) have been used in past studies to evaluate the heat stress (Sairam & Srivastava, 2001; Dhanda & Munjal, 2006). The MTS/RCI measurements can be reliably used to determine electrolytic conductivity at growing stages in wheat genotypes. However, MTS can be favored to relative injury (RI) to save time and laboratory facilities. The F_2 populations exhibited high membrane stability by having low damage percentage than F_1 and back cross populations in crosses Hashim-08 × LU-26, Farid-06 × Shafaq and TD-1 × D-97603 whereas in cross Parula × Blue Silver it was equally distributed between the parents. Yildirim *et al*., (2009) investigated membrane stability of four spring wheat parents and their six half F_2 diallel cross progenies grown in the field. Their findings also revealed that membrane stability parameters of genotypes decreased during the later developmental stages, and the membrane thermal stability was mediated mainly by non-additive gene actions. The components of genetic variance indicated considerable influence of dominance variance in determining inheritance of MTS (Dhanda & Munjal, 2009). However, in present material the selection for heat tolerant populations based on MTS may be more effective by reducing the dominance variance after a few generations of selfing.

Table 3. Maximum log likelihood values and AIC values for cell MTS under various genetic models estimated through IECM algorithm.

Models	Max. Log of likelihood	AIC	Models	Max. Log of likelihood	AIC
	Hashim-08 × Lu-26			**Farid-06 × Shafaq**	
A-1	-2347.18	4702.37	A-1	-2309.83	4627.67
A-2	-2442.49	4890.98	A-2	-2336.74	4679.49
A-3	-2359.81	4725.62	A-3	-2474.21	4954.41
A-4	-2623.12	5252.24	A-4	-2306.39	4618.79
B-1	-2081.89	4183.79	B-1	-2160.32	4340.65
B-2	-2247.02	4506.04	B-2	-2203.02	4418.04
B-3	-2455.15	4918.31	B-3	-2378.78	4765.57
B-4	2432.88	4871.77	B-4	-2378.15	4762.31
B-5	-2255.26	4518.53	B-5	-2464.28	4936.57
B-6	-2255.26	4516.53	B-6	-2464.28	4934.57
C	-2017.2	4054.41	C	-2101.02	4222.04
C-1	-2247.91	4509.83	C-1	-2361.46	4736.92
D	-2025.96	4075.92	D	-2117.86	4259.72
D-1	-2147.79	4313.59	D-1	-2181.34	4380.68
D-2	-2147.78	4311.57	D-2	-2181.09	4378.18
D-3	-2147.74	4311.48	D-3	-2181.39	4378.78
D-4	-2027.31	4070.62	D-4	-2181.34	4378.69
E	-2025.96	4087.92	E	-2117.86	4271.73
E-1	-2044.03	4118.06	E-1	-2134.55	4387.89
E-2	-2299.31	4620.62	E-2	-2194.56	4423.34
E-3	-2238.13	4494.26	E-3	-2387.79	4767.87
E-4	-2245.54	4512.23	E-4	-2468.12	4885.61
E-5	-2299.31	4616.62	E-5	-2469.56	4943.45
E-6	-2300.81	4617.63	E-6	-2518.49	5089.76
	Parula × Blue Silver			**TD-1 × D-97603**	
A-1	-2215.33	4438.67	A-1	-2310.54	4629.09
A-2	-2718.25	5442.51	A-2	-2343.45	4692.91
A-3	-2572.33	5150.66	A-3	-2370.11	4746.23
A-4	-2795.99	5597.98	A-4	-2309.57	4625.14
B-1	-2171.61	4363.22	B-1	-2240.07	4500.14
B-2	-2210.34	4432.69	B-2	-2294.95	4601.90
B-3	2722.42	5452.84	B-3	-2374.73	4757.47
B-4	-2717.16	5440.33	B-4	-2345.34	4696.69
B-5	-2577.33	5162.66	B-5	-2369.64	4747.29
B-6	-2577.33	5160.66	B-6	-2369.64	4745.29
C	-2128.15	4276.30	C	-2287.32	4594.64
C-1	-2427.35	4868.70	C-1	-2323.57	4661.14
D	-2121.71	4267.43	D	-2287.31	4598.63
D-1	-2245.59	4509.18	D-1	-2319.18	4656.36
D-2	-2245.58	4507.17	D-2	-2259.18	4534.37
D-3	-2253.42	4522.84	D-3	-2319.38	4654.77
D-4	-2252.99	4521.98	D-4	-2319.37	4654.75
E	-2119.46	4274.92	E	-2221.71	4479.43
E-1	-2154.49	4338.99	E-1	-2182.46	4394.92
E-2	-2427.45	4876.91	E-2	-2247.88	4517.77
E-3	-2337.51	4693.01	E-3	-2256.63	4531.26
E-4	-2389.22	4722.11	E-4	-2316.55	4649.11
E-5	-2427.45	4872.91	E-5	-2323.51	4665.00
E-6	-2443.32	4902.64	E-6	-2384.85	4785.71

AIC - Akaike's information criterion (Akaike, 1977), IECM - Iterated expectation and conditional maximization

Table 4a. Test for goodness of fit regarding cell MTS of models C, D and E.

Models	Generations	U_1^2	U_2^2	U_3^2	nW^2	Dn
Hashim-08 × Lu-26						
C	P_1	0.54 (0.46)	2.21**	9.64**	1.26	0.34
	F_1	0.01 (0.89)	0.21 (0.63)	1.79*	0.79	0.22
	P_2	0.90 (0.34)	0.55 (0.45)	0.49 (0.48)	0.60*	0.22
	BC_1	0.08 (0.77)	0.51(0.47)	3.02 (0.08)	0.78*	0.17*
	BC_2	0.74 (0.38)	1.21 (0.27)	1.14 (0.28)	1.46	0.22
	F_2	0.005 (0.94)	0.11 (0.73)	1.14 (0.28)	0.99	0.15*
D	P_1	0.91 (0.33)	4.82*	25.82***	1.61	0.37
	F_1	0.003 (0.84)	1.16 (0.28)	12.68***	1.06	0.25
	P_2	1.44 (0.22)	0.47 (0.49)	3.62*	0.68	0.21
	BC_1	0.06 (0.79)	0.17 (0.67)	0.42 (0.51)	0.71*	0.16*
	BC_2	0.35 (0.54)	0.02 (0.88)	2.97 (0.08)	1.37	0.23
	F_2	0.005 (0.94)	0.11 (0.73)	1.14 (0.28)	0.99	0.15*
E	P_1	0.91 (0.33)	4.82*	25.83***	1.16	0.37
	F_1	0.03 (0.84)	1.16 (0.28)	12.68***	1.06	0.25
	P_2	1.44 (0.22)	0.47 (0.49)	3.62 (0.056)	0.68	0.21
	BC_1	0.06 (0.79)	0.17 (0.67)	0.42 (0.51)	0.71	0.16*
	BC_2	0.35 (0.54)	0.02 (0.88)	2.97 (0.08)	1.37	0.23
	F_2	0.005 (0.94)	0.11 (0.73)	1.14 (0.28)	0.99	0.15*
Farid-06 × Shafaq						
C	P_1	0.02 (0.88)	0.15 (0.69)	4.61*	0.42	0.19
	F_1	0.01 (0.89)	0.80 (0.37)	16.98***	0.96	0.24
	P_2	0.14 (0.70)	0.04 (0.82)	5.48*	0.63	0.23
	BC_1	1.77 (0.18)	1.32 (0.24)	0.31 (0.57)	1.86	0.28
	BC_2	0.20 (0.65)	0.33 (0.56)	16.40***	2.21	0.26
	F_2	0.35 (0.55)	0.03 (0.86)	2.58 (0.10)	0.89	0.14
D	P_1	0.04 (0.83)	0.89 (0.34)	21.23***	0.73	0.23
	F_1	0.06 (0.80)	2.31 (0.12)	49.49***	1.54	0.28
	P_2	0.33 (0.56)	0.16 (0.68)	0.36 (0.54)	0.57	0.21
	BC_1	1.77 (0.18)	1.32 (0.24)	0.31 (0.57)	1.86	0.28
	BC_2	0.10 (0.74)	0.001 (0.97)	1.23 (0.26)	1.76	0.23
	F_2	0.16 (0.68)	0.71 (0.39)	3.33 (0.06)	0.84	0.14
E	P_1	0.04 (0.83)	0.89 (0.34)	21.23***	0.73	0.23
	F_1	0.06 (0.80)	2.31 (0.12)	12.21 (0.23)	1.54	0.28
	P_2	0.33 (0.56)	0.16 (0.68)	0.36 (0.54)	0.57	0.21
	BC_1	1.77 (0.18)	1.32 (0.24)	0.31 (0.57)	1.86	0.28
	BC_2	0.10 (0.74)	0.001 (0.97)	1.23 (0.26)	1.76	0.23
	F_2	0.16 (0.68)	0.71 (0.39)	3.33 (0.06)	0.84	0.14

Variations due to polygenes were more pronounced as compared to variation due to major genes in cross Hashim-08 × LU-26. Similarly, the maximum polygene heritabilities were observed in the said cross for BC_1, BC_2 and F_2 populations. Yildrim *et al*., (2009) also observed that MTS was controlled by non-additive gene action. Considerable amount of dominance variance in inheritance of MTS suggesting that selection for heat tolerance may be more effective by reducing the dominance variance after a few generations of selfing (Dhanda & Munjal, 2009). However, Ibrahim and Quick (2001) mentioned that mean squares due to GCA were four times to that of SCA, indicating the importance of additive gene effects in acquired thermal tolerance. Results suggested that heat tolerance based on MTS can be improved using the existing genetic variability available within the germplasm evaluated in this study.

For cross Farid-06 × Shafaq, the polygene variation excelled the major gene variation with maximum polygene heritabilities in segregating generations i.e., BC_1, BC_2 and F_2. In F_5 populations, the progeny means of relative injury values determined, and due to transgressive segregations the parent contributed different genes for heat tolerance and the MTS was not simply inherited (Saadalla *et al*., (1990). Farooq *et al*., (2011) findings revealed that relative cell injury % would be helpful to develop material against heat stress, and found additive components with moderate to high heritability for genetic variation in heat tolerance and that were in close analogy with these findings. Dhanda and Munjal (2009) also obtained higher GCA values than SCA indicating additive type of gene action for inheritance in wheat crosses.

Table 4b. Test for goodness of fit regarding cell MTS of models C, D, E, E-1 and B-1.

Models	Generations	U_1^2	U_2^2	U_3^2	nW^2	*Dn*
Parula × Blue silver						
E	P_1	0.007 (0.93)	0.75 (0.38)	10.01**	0.59*	0.25
	F_1	0.25 (0.61)	0.42 (0.51)	0.41 (0.52)	0.84	0.23
	P_2	0.17 (0.67)	5.82*	64.78***	1.42	0.30
	BC_1	0.12 (0.72)	0.10 (0.74)	0.003 (0.95)	0.73	0.15*
	BC_2	0.09 (0.76)	0.04 (0.84)	0.13 (0.71)	0.92	0.16*
	F_2	0.19 (0.65)	0.16 (0.68)	0.005 (0.94)	1.89	0.23
D	P_1	0.006 (0.93)	0.64 (0.42)	8.43**	0.56	0.24
	F_1	0.23 (0.62)	0.32 (0.57)	0.14 (0.70)	0.83	0.23
	P_2	0.16 (0.68)	5.53*	61.51***	1.37	0.29
	BC_1	0.45 (0.50)	0.90 (0.34)	1.46 (0.22)	0.82	0.19
	BC_2	0.09 (0.76)	0.04 (0.84)	0.13 (0.71)	0.92	0.16
	F_2	0.07 (0.78)	0.41 (0.52)	2.27 (0.13)	2.10	0.24
C	P_1	0.004 (0.95)	0.02 (0.87)	0.17 (0.67)	0.36	0.21
	F_1	0.10 (0.74)	0.03 (0.84)	4.11*	0.83	0.21*
	P_2	0.09 (0.76)	2.90 (0.08)	31.83***	0.90	0.25
	BC_1	0.13 (0.71)	0.02 (0.87)	4.18*	0.98	0.21
	BC_2	0.09 (0.76)	0.04 (0.84)	0.13 (0.71)	0.91	0.16*
	F_2	1.34 (0.24)	3.82*	11.03***	2.76	0.28
TD-1 × D-97603						
E	P_1	2.90 (0.08)	0.47 (048)	14.64***	1.23	0.35
	F_1	1.59 (0.20)	4.79*	186.33***	4.08	0.38
	P_2	0.19 (0.66)	0.61 (0.43)	2.09 (0.14)	0.55	0.23
	BC_1	4.04*	5.82*	3.49 (0.06)	1.83	0.22
	BC_2	0.24 (0.62)	0.35 (0.55)	18.55***	2.54	0.27
	F_2	11.89***	11.09***	0.00 (0.97)	2.9	0.26
E-1	P_1	9.00**	2.03 (0.15)	35.01***	2.09	0.42
	F_1	4.99*	3.07 (0.07)	245.68***	5.21	0.42
	P_2	0.81 (0.36)	0.15 (0.69)	3.65*	0.63	0.23
	BC_1	1.09 (0.29)	0.81 (0.36)	0.18 (0.66)	1.71	0.21
	BC_2	1.39 (0.23)	2.70 (0.10)	3.99*	1.58	0.20
	F_2	0.02 (0.88)	0.10 (0.74)	0.53 (0.46)	1.93	0.21
B-1	P_1	4.74*	4.93*	0.19 (0.65)	0.83	0.23
	F_1	0.10 (0.74)	8.89**	113.47***	2.87	0.38
	P_2	5.97*	7.55**	2.32 (0.12)	1.11	0.29
	BC_1	0.45 (0.50)	0.16 (0.68)	0.98 (0.32)	1.51	0.22
	BC_2	0.03 (0.86)	0.53 (0.46)	12.93***	2.07	0.26
	F_2	1.05 (0.30)	1.65 (0.19)	1.38 (0.23)	2.26	0.25

According to genetic parameters, the additive effects were negative while dominant effects were positive for MTS in cross Parula × Blue Silver. The epistatic effects of major genes were positive which revealed that MTS was under control of epistatic nature of major genes. The SCA effects surpassed the GCA effects for all the variables, which indicating that MTS was mediated mainly by non-additive gene action (Dhanda & Munjal, 2009). Ibrahim and Quick (2001) concluded that both the GCA and SCA effects for MTS at 8-10 day wheat seedlings were significant, accounting for 44% and 19% of the total variability, respectively.

In consideration of cross TD-1 × D-97603, the two major additive-dominance epistatic genes plus additive-dominant polygenes were controlling the MTS. In the said cross, the variations due to polygenes were almost negligible as compared to variation due to major genes. However, the variation due to environment was prominent in the segregating populations showing that the MTS was highly influenced by the environment. Dhanda and Munjal (2009) reported higher GCA than SCA indicating additive type of gene action for cell MTS in wheat. The findings of Farooq *et al*., (2011) revealed that additive components of genetic variation for cell membrane were significant in wheat crosses. Both additive and dominant type of gene action were reported at the genetic direction of MTS (Dhanda & Munjal, 2006). Results indicated that MTS could be used as balancing tool in breeding programs for screening of heat tolerance potential in spring wheat and evaluation of genetic variation for membrane stability among genotypes.

Table 5. Maximum likelihood estimates of component parameters regarding cell MTS in four wheat crosses in their respective best fit model.

Variables	Hashim-08 × Lu-26	Farid-06 × Shafaq	Parula × Blue Silver	TD-1 × D-97603
	Model Type: E	Model Type : E	Model Type: D	Model Type: E-1
M_1	41.06	42.28	53.36	64.26
M_2	37.58	36.76	31.75	53.16
M_3	60.89	32.32	65.21	51.94
M_{41}	30.48	48.87	28.21	58.59
M_{42}	30.47	48.80	35.88	47.15
M_{43}	30.51	48.78	-	47.15
M_{44}	30.62	48.80	-	58.83
M_{51}	41.77	36.60	32.98	58.91
M_{52}	41.80	36.60	34.12	59.76
M_{53}	41.80	36.60	-	47.34
M_{54}	41.79	36.59	-	46.19
M_{61}	32.68	29.61	38.09	58.63
M_{62}	32.67	29.53	45.75	47.19
M_{63}	32.31	29.53	46.89	47.20
M_{64}	32.70	29.51	-	47.19
M_{65}	32.81	29.53	-	58.87
M_{66}	32.84	29.53	-	59.72
M_{67}	32.97	29.53	-	47.20
M_{68}	32.84	29.53	-	47.30
M_{69}	32.83	29.52	-	46.16
Σ^2	17.18	17.84	16.88	11.11
Σ_4^2	17.18	39.33	16.88	11.11
Σ_5^2	17.18	17.84	16.94	11.11
Σ_6^2	18.76	17.84	16.88	11.11

Table 6. Estimates of first and second order genetic parameters for cell MTS in four wheat crosses.

First Order Genetic Parameter				2nd Order Genetic Parameter			
Hashim-08 × LU-26 (model E)							
-	-	-	-	-	BC_1	BC_2	F_2
M_1	41.07	h_a	0.09	σ_p^2	15.23	12.1	18.9
M_2	37.46	h_b	0.07	σ_{mg}^2	0.00	0.00	0.02
M_3	60.75	h_a/d_a	-0.46	σ_e^2	17.18	17.18	17.18
M_4	30.49	h_b/d_b	0.55	σ_{pg}^2	1.95	5.08	1.68
M_5	41.64	I	0.07	h_{mg}^2(%)	0.02	0.00	0.10
m_6	30.45	j_{ab}	0.11	h_{pg}^2(%)	12.83	41.99	8.90
d_a	-0.20	j_{ba}	-0.20	-	-	-	-
d_b	0.12	L	-0.03	-	-	-	-
Farid-06 × Shafaq (model E)							
-	-	-	-	-	BC_1	BC_2	F_2
M_1	42.32	h_a	-0.03	σ_p^2	57.57	13.8	12.4
M_2	36.78	h_b	-0.02	σ_{mg}^2	0.0	0.00	0.00
M_3	32.35	h_a/d_a	-1.21	σ_e^2	17.84	17.84	17.84
M_4	48.81	h_b/d_b	-0.74	σ_{pg}^2	39.73	4.04	5.41
M_5	36.62	I	0.02	h_{mg}^2(%)	0.00	0.00	0.00
M_6	27.53	j_{ab}	-0.02	h_{pg}^2(%)	69.01	29.28	43.53
d_a	0.02	j_{ba}	-0.03	-	-	-	-
d_b	0.02	L	0.03	-	-	-	-
Parula × Blue Silver (Model D)							
-	-	-	-	-	BC_1	BC_2	F_2
m_1	57.76	D	-4.40	σ_p^2	23.89	17.39	27.97
m_2	28.49	H	3.26	σ_{mg}^2	7.00	0.45	11.09
m_3	60.81	-	-	σ_e^2	16.88	16.88	16.88
m_4	32.61	-	-	σ_{pg}^2	0.00	0.06	0.00
m_5	29.72	-	-	h_{mg}^2(%)	29.34	2.59	39.65
m_6	42.49	-	-	h_{pg}^2(%)	0.00	0.35	0.00
TD-1 × D-97603 (Model E-1)							
-	-	-	-	-	BC_1	BC_2	F_2
M	55.5	I	2.6	σ_p^2	41.3	41.3	41.2
d_a	3.1	j_{ab}	-3.2	σ_{mg}^2	30.2	30.2	30.1
d_b	-1.8	j_{ba}	-9.4	σ_e^2	11.1	11.1	11.1
h_a	3.7	L	8.0	σ_{pg}^2	0.0	0.0	0.0
h_b	-2.6	[d]	24.9	h_{mg}^2(%)	73.1	73.1	73.1
h_a/d_a	1.2	[h]	-11.4	h_{pg}^2(%)	0.0	0.0	0.0
h_b/d_b	1.4	-	-	-	-	-	-

Conclusion

Genetic behavior of the membrane thermal stability suggested that early selection in the crosses Hashim-08 × LU-26 and Farid-06 × Shafaq would be efficient, while in Parula × Blue Silver and TD-1 × D-97603, the delayed selection until accumulation of maximum favorable genes will be effective. However, the influence of the environment may vary and could not be avoided.

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