GENETIC ARCHITECTURE OF RELATIVE CELL INJURY AND SOME YIELD RELATED PARAMETERS IN *Gossypium hirsutum* L.

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ABSTRACT

Although cotton is sun loving crop but its production is adversely affected due to biotic and abiotic stress, heat stress contributed significantly in this loss around the globe. The present research work on heat tolerance in cotton is a step forward to understand the genetic basis of heat tolerance in upland cotton. The presence and identification of genetic variation for certain traits is one of the pre-requisite to start research work. There are several techniques for the screening of germplasm for heat tolerance. Relative cell injury was used for the identification of the most heat tolerant and susceptible cotton genotypes i.e. VH-259, VH-142 and DNH-40, VH-282 respectively. The identified genotypes were used for the development of F_1, F_2, BC_1 and BC_2 populations for genetic studies. The biometrical analysis revealed that selected traits i.e. relative cell injury, chlorophyll contents, boll shedding percentage, plant height, number of bolls per plant, number of seeds per boll, seed cotton yield were controlled by additive and non-additive type of gene action including epistatic effects. It is suggested that selection in these populations should be done in later generations for the development of new germplasm with enhanced heat tolerance.

Keywords: Generation means analysis, Gene action, Heat stress, Screening, Upland Cotton.

INTRODUCTION

Upland cotton is an important fiber crop which is cultivated in more than hundred countries and covering more than 32 million hectares worldwide. It is an important source of oil and livestock feed, even as low-protein food for humans in some third-world countries (Singh et al., 2007). USA, China, India and Pakistan are top four cotton producing countries and collectively provide about 2/3 cotton of the world. Its production accounts for 1.5% in GDP, 7.1% in agricultural value addition and it also plays a major role in foreign exchange for Pakistan and during July-March 2014-15, textile industry fetched foreign exchange of 10.22 billion dollars. The cotton crop is planted on an area of 2961 thousand hectares, showing an increase of 5.5 percent over area of i.e. 2806 thousand hectares last year's and its production stood at 13.983 million bales against 12.769 million bales of last year showing an increase of 9.5% for the year 2014-15 (Govt. of Pakistan, 2014-15).

Production of cotton is adversely effected by various biotic and abiotic stresses among them heat stress is one of the major factors that affects its growth and development which directly effects on yield of seed cotton. Global warming due to increase of greenhouse gases has significantly changed the world climate and this

is one of the sources of increase in global temperature by 0.4-0.8 °C/year. Loss of 4.2 billion dollars was recorded in agriculture sector due to heat and drought stress (Pachauri et al., 2014). This warns the plant breeders and scientists to identify and design strategy that could minimize the losses due to these stresses. High temperature induces irreversible changes/damage to plant development and growth such as wilting of leaf, flower and fruit shedding. This damage depends on intensity and duration of temperature as well as growth stage of plant (Mittler, 2006; Wahid et al., 2007; Viola et al., 2010).

In Pakistan, cotton is grown in the Punjab and Sindh provinces (Ahmad and Makhdum, 1992). In Punjab and Sindh, during plantation, germination and growth stage temperature reaches to 45-50°C, and this high temperature significantly reduce plant population by reducing germination percentage, poor pollen germination, production of low quality fiber and finally reduction of yield (Rahman et al., 2004). According to some researchers, seedlings and floral stages are the most sensitive stages to high temperature (Howarth and Ougham, 1993; Ismail and Hall, 1998; Foolad, 2005). In addition, high temperatures also exerts adverse effects by modifying physiological functions of cellular organelles while modification in cell membranes either by

denaturation of proteins or by transformation of saturated fatty acid to unsaturated fatty acid in membrane lipids (Larkindale and Huang, 2004). In fact, high temperature loosens the chemical bonds (covalent or non- covalent bonds) between molecules within membrane and enhances mobility of molecules across membranes. Increase in membrane fluidity can lead to leakage of organic and inorganic solutes that leads to loss of physiological functions of cellular membranes. This membrane stability percentage can be used as important criteria for the identification of heat tolerant and susceptible lines (Wahid et al., 2007), and this techniques has been used by various researches in various crops like cotton (Azhar et al., 2009; Khan et al., 2014), wheat (Blum and Ebercon, 1981; Bajji et al., 2002; Dhanda et al., 2004), rice (Ali et al., 2013) and maize (Naveed et al., 2014).

If temperature exceed from 36°C, it adversely affects on reproductive phase, including 65-70% shedding of squares. buds and flowers, pollen sterility and consequently decrease the plant yield (Kittock et al., 1988; Baloch et al., 2000; Liu et al., 2006). Moreover, high temperature slows down rate of photosynthesis and respiration (Christiansen, 1978). The breeding for heat tolerant cotton genotype depends upon the presence of genetic and significant amount of variability in the available germplasm. The susceptibility to high temperatures varies for developmental and reproductive stages in crop plants (Sakata and Higashitani, 2008). Several reports are available about the presence of genetic variation in heat related parameters in various field crops i.e. wheat (Shanahan et al., 1990; Ali and Khan, 2007), rice (Mackill et al., 1982), cowpeas (Mutters and Hall, 1992; El-kholy et al., 1997), and mungbean (Collins et al., 1995). Although information on the occurrence of variability for heat tolerance in crop species is available but this knowledge on genetic basis of that variation is not fully utilized. However a few genetic studies on wheat (Ibrahim and Quick, 2001a, b), cowpea (Ismail and Hall, 1998) and cotton (Trolinder and Shang, 1991; Baloch et al., 2000; Rahman et al., 2004) provide evidence that heat tolerance is genetically controlled, and suggesting the opportunities for further improvement in heat tolerance through selection and breeding.

Keeping in view the impact of heat stress on yield and physiology of cotton plant, the present study was designed to determine the genetic basis of heat tolerance and other economic traits in upland cotton.

MATERIALS AND METHODS

Assessment of germplasm for relative cell injury (RCI)

Eighty genotypes of upland cotton were collected from various Agricultural Research stations/ institutes of Pakistan to identify heat tolerant and susceptible parents. The collected germplasm was sown on 23 May, 2012 at cotton research farm of the Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad (Pakistan). All cultural and agronomic practices approved by Government of Punjab were adopted to get healthy population. Relative cell injury (RCI) percentage was

measured from ten fully developed young leaves during peak flowering season. A steel punch having a diameter of 10 mm was used for sample collection from selected leaves. Two sets of samples were collected from both sides of midrib of each leaf. One set was used as control and other for heat treatment. Leaf disks were collected at about 12 pm to 2 pm and samples were immediately kept in falcon tubes having 2ml of distilled water and were taken to laboratory as quickly as possible. They were washed twice with distilled water to remove dust and other inert material present on the leaf surface. After washing, 12 ml of distilled water was added in sterilized falcon tubes and covered with lid to avoid evaporation during heat treatment. One set of falcon was kept at room temperature and other at 50^0C in water bath for 1 hour (Rahman et al., 2004). After heat treatment, 10 ml of distilled water was added to each tube and kept at 10^0C for 24 hours to allow diffusion of electrolytes. On the next day, tubes were kept at room temperature and shaken three times for mixing of electrolytes. Initial electrical conductivity (EC) was noted with the help of EC meter. Falcon tubes were autoclaved at 0.10 MPa pressure to release all of electrolytes present in leaf disk. Tubes were placed on working bench when room temperature was attained then relative reading of EC was noted again with the help of same EC meter as used previously (Sullivan, 1972).

Relative cell injury (RCI) percentage was calculated by using the following formula proposed by

$$RCl \% = [1-[(1-(T_1-T_2))] / (1-(C_1/C_2))]] \times 100$$

Where T and C are respective EC values of heat treated and controlled tubes and subscripts 1 and 2 represent initial and final EC readings, respectively.

Development of various populations for genetic studies

Two heat tolerant (VH-259 and VH-142) and two heat susceptible genotypes (VH-282 and DNH-40) were selected on the basis of the data recorded for RCI percentage. These four genotypes were sown in cotton growing season 2013 for the development of F_1 population. During the next cropping season 2013-14, F_1 generations and their parents were grown in the field for developing back crosse1, back cross 2 and F_2 generations. All preliminary measures were adopted to avoid self-pollination during hybridization.

Assessment of populations for heat stress and other economic traits

On 7 May 2015 and 1 June 2015, fours parents (VH-282, VH-142, DNH-40, and VH-259) along with F_1, F_2, BC_1 and BC_2 populations from each cross were grown in triplicate using randomized complete block design in field conditions of the department. Each replication was comprised of five rows with ten plants for each of parent, F_1, backcross and six rows of each F_2 generation. Plant to plant and row to row distance was kept 30 cm and 75 cm respectively. Data on cell membrane stability (%) and Chlorophyll contents (SPAD-502) was recorded during August, 2015 for both late and early sown trial. Data was

collected during mid-day from all tagged one month old plants (three fully developed leaves from each plant were used). SPAD-502 Chlorophyll meter was placed on each leaf and waited until reading was stabilized. Average of three leaves was used as per plant reading. In addition, data on plant height (cm), boll shedding percentage (%), number of bolls per plant, number of seeds per boll and seed cotton yield (g) were recorded at maturity from 30 plants of each parent, F_1, backcrosses while 150 plants of each F_2 population.

Statistical Analysis

Analysis of variance among the generations was conducted as in (Steel et al., 1997). The data collected for the traits showing significant differences, was used to conduct generation means analysis following the method described by (Mather and Jinks, 1982).

Response of germplasm against heat stress

Eighty cotton genotypes were grown in field conditions for screening against heat stress using relative cell injury percentage. The mean values of all genotypes under heat stress were given in Table 1. Analysis of variance revealed the presence of significant differences among the genotypes for the trait. Values of RCI% was ranged from 39.1 to 85.9 in the available germplasm of cotton. In this study two cultivars namely VH-259 and VH-142 having values 39.1 and 40.3 respectively were identified to be most heat tolerant while DNH-40 and VH-282 having RCI % of 85.9 and 83.8 respectively were identified as most heat susceptible genotypes (Table 1).

Table 1. Mean values of 80 genotypes of cotton for RCI % in green house conditions.

Sr. No	Genotypes	RCI	Sr. No	Genotypes	RCI	Sr. No	Genotypes	RCI	Sr. No	Genotypes	RCI
1	DNH 40	85.9	21	CIM 109	77.2	41	NIAB	71.8	61	VH 281	62.4
2	VH 282	83.8	22	FH 114	77.2	42	MNH93	71.4	62	MNH 147	61.9
3	MNH 465	82.5	23	CRWAS 310	77.1	43	CIM 70	70.8	63	VH-250	61.8
4	CIM 608	82.2	24	C 26	76.7	44	BH 163	70.7	64	MNH 888	61.7
5	MNH 506	81.7	25	BH 96	76.5	45	NS 131	69.0	65	BP 900	61.1
6	CIM 534	81.2	26	BH 121	76.1	46	FH 113	68.8	66	RED ACALA	60.7
7	CIM 499	81.1	27	FH 2015	76.1	47	KZ 191	68.2	67	VH 144	59.3
8	VH 291	80.6	28	GR 156	76.1	48	DNH29	68.1	68	B 557	58.2
9	NIAB 86	80.6	29	RIBA B50	76.0	49	FH 682	67.7	69	MNH 554	57.7
10	AA 802	79.9	30	NF 801/7	75.8	50	BH 160	67.3	70	FH 115	57.6
11	KZ 181	79.7	31	SV 322	75.7	51	VH 297	66.2	71	MNH 700	57.6
12	CIM 707	79.7	32	CRWAS 134	75.4	52	BS 1	66.1	72	SLH 257	57.6
13	NIAB 98	79.5	33	BH 147	74.5	53	CIM 496	65.7	73	CRWAS 379	56.3
14	FH 87	79.1	34	DPL 70010	74.3	54	DPL2775	65.0	74	BT 701	56.0
15	NIAB 999	78.9	35	FH 942	74.2	55	DPL 26	64.1	75	VH 141	54.4
16	IR 3701IR 3701	78.8	36	CRWAS 5A	73.5	56	DPL 28	63.4	76	BP 630	54.0
17	SV 857	78.7	37	VH 61	72.5	57	BH 162	63.2	77	VH 300	52.8
18	VH 268	78.7	38	FH900	72.4	58	VH 255	63.0	78	Marvi	49.1
19	KZ 189	78.5	39	FH 4243	72.0	59	CRWAS 402	62.7	79	VH 142	40.3
20	CIM 448	78.1	40	VH 256	72.0	60	MNH 786	62.6	80	VH 259	39.1

Gene action

The six generations from both crosses were planted in field conditions for the collection of observations on all traits under study. Mean values and ANOVA were biometrically analyzed using generation mean analysis approach proposed by (Mather and Jinks, 1982). The interpretation of the results of each agronomic trait is mentioned in following paragraphs.

Relative Cell Injury

Mean values of relative cell injury of F_1 generation was higher than mean values obtained from population of F_2, BC_1 and BC_2 in normal and heat stress conditions for both the crosses of cotton indicated that heterozygosity could be exploited for decrease of this trait. Mean value for relative cell injury was ranged from 62.83 to 78.53 in

this study from six generations i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2 for each cross (Table 2).Analysis of the data by generation mean analysis showed that relative cell injury was under the influence of multiple genes. This trait was controlled by [mjl] in cross-1 in normal conditions while under heat stress condition it was controlled by [mdhjl]. Additive component [d] was more than dominant component [h] for cross-1 under heat stress conditions. Analysis of the data also revealed that duplicate epistasis existed under heat stress conditions because dominant component [h] and dominant × dominant component [l] have opposite signs. Relative cell injury was controlled by [mhijl] and revealed that for cross-2 in normal condition duplicate epistasis existed because dominant component [h] and dominant × dominant component [l] have opposite signs in normal condition for cross-2 whereas heat stress

condition of cross-2 it was controlled by [mdhjl]. Additive component [d] was higher than dominant component [h]

and duplicate epistasis also plays its role to control this trait under heat stress condition (Table 3).

Table 2. Generation means for plant height, number of bolls per plant, boll shedding percentage, number of seeds per boll, seed cotton yield, relative cell injury percentage and chlorophyll contents in two crosses VH-282 × VH-142 and DNH-40 × VH-259 under normal and heat stress conditions.

Traits	Stress Levels	Generation Means						Pop Effect
		P_1	P_2	F_1	BC_1	BC_2	F_2	
RCI	N1	28.30	28.45	21.86	26.66	26.57	26.97	**
	H1	24.27	37.17	25.67	35.23	36.73	32.48	**
	N2	25.36	25.32	21.47	31.27	29.94	28.34	**
	H2	24.78	35.02	25.72	33.79	33.93	32.01	**
CC	N1	30.90	30.02	28.44	31.14	30.38	29.94	**
	H1	16.56	27.80	23.40	22.89	24.54	25.78	**
	N2	30.72	31.08	30.35	30.95	30.99	30.84	**
	H2	26.35	29.16	25.53	26.74	25.81	27.43	**
PH	N1	109.53	107.10	112.43	103.47	107.00	106.36	**
	H1	101.47	99.57	106.47	101.60	102.33	101.48	**
	N2	106.93	106.70	108.83	107.50	108.63	107.68	**
	H2	102.30	94.10	102.03	100.70	93.60	107.38	**
B/P	N1	12.97	11.43	12.67	12.20	11.63	11.47	*
	H1	10.13	7.01	8.57	8.57	9.37	7.76	*
	N2	21.73	19.94	19.03	19.08	20.83	18.33	**
	H2	12.60	11.57	11.23	11.67	11.90	11.40	**
BSP	N1	81.03	89.10	84.00	83.90	89.20	79.36	**
	H1	81.20	89.17	85.30	82.70	88.97	79.16	**
	N2	83.47	86.30	82.70	82.67	82.40	84.09	**
	H2	69.97	80.20	73.10	70.80	80.03	72.50	**
NSB	N1	26.60	22.83	23.40	24.10	24.93	23.21	**
	H1	20.56	20.55	19.80	20.15	20.13	20.22	**
	N2	24.88	24.97	23.23	24.10	24.20	24.16	**
	H2	24.17	21.50	22.70	22.91	23.53	22.20	* *
SCY	N1	50.54	34.50	46.75	35.23	35.08	41.78	**
	H1	35.49	23.69	35.47	27.98	25.08	25.13	**
	N2	79.51	59.52	75.22	62.26	59.23	62.05	**
	H2	43.75	34.82	38.66	36.54	36.86	39.02	**

RCI: Relative Cell Injury, CC: Chlorophyll Contents, PH: Plant height, B/P: Number of Bolls per Plant, BSP: Boll Shedding Percentage, NSB: Number of Seeds per Boll, SCY: Seed Cotton Yield,
N1 and N2: Cross 1 and Cross 2 under normal conditions respectively, H1 and H2: Cross 1 and Cross 2 under heat stress conditions respectively.

Chlorophyll contents

Mean values for chlorophyll contents of F_2 was higher than F_1, BC_1 and BC_2 in both the crosses in normal as well as heat stress conditions, so homozygosity could result in improvement of this trait. Chlorophyll contents were ranged from 16.56 to 31.14 in this study conducted in field conditions for both crosses having six generations i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2 (Table 2). Generation mean analysis showed that chlorophyll contents were controlled by polygenes. This trait was controlled by [mdhi] and [mdh] in normal conditions and under heat stress condition respectively in cross-1. Additive component [d] was higher than dominant component [h] in normal and under heat stress conditions. Chlorophyll contents were controlled by [ml] and [mdh] in normal conditions and under heat stress conditions respectively in cross-2. Additive component [d] again was higher than dominant

component [h] for this trait under heat stress conditions (Table 3).

Plant height

For plant height under both stress conditions in both crosses, (VH-282 × VH-142 was considered as cross-1 while DNH-40 × VH-259 was cross-2) F_1 mean value was higher than F_2, BC_1 and BC_2 mean values, so heterozygosity could result in taller plants (Table 2).

In this study plant height ranged from 93.60 to 112.43cm for both crosses under normal and heat stress conditions in 12 generations (six from each cross i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2). Generation mean analysis showed that plant height was controlled by polygenes. In cross-1 under normal condition it was controlled by [mdhi], while in heat stress conditions, it was controlled by [mdl] (Table 3). Here dominant component was higher

than additive component in normal conditions while in cross-2, this trait was controlled by [mdh] in normal condition, but in heat stress condition, it was controlled by [mdhj]. Here additive component was more than dominant component in heat stress. Dominant component was higher than additive component in normal condition. Epistatic components [i], [j] and [l] were also contributing under both conditions.

Table 3. Estimates of the best fit model for generation means parameters (±, standard error) by weighted least squares analysis in respect for plant height, number of bolls per plant, boll shedding percentage, number of seeds per boll, seed cotton yield, relative cell injury percentage and chlorophyll contentsin two crosses VH-282 × VH-142 and DNH-40 × VH-259 under normal and heat stress conditions.

Traits	Stress Condition	Genetic Effects						X^2(DF)
		m±S.E.	[d]±S.E.	[h]±S.E.	[i]±S.E.	[j]±S.E.	[l]±S.E.	
RCI	N1	71.623±0.499	--	--	--	0.821±2.771	6.513±1.026	0.019(3)
	H1	66.786±6.226	6.451±0.554	-15.613±14.357	--	-21.411±3.319	23.157±8.454	0.871(1)
	N2	66.170±6.812	--	-2.110±16.310	8.490±6.783	-3.198±3.941	14.471±9.856	0.121(1)
	H2	66.833±7.166	5.118±0.635	-9.940±16.839	--	-14.078±4.086	17.384±10.027	0.809(1)
CC	N1	33.753±0.356	0.438±0.126	-5.363±0.497	-3.325±0.394	--	--	0.774(2)
	H1	20.375±0.140	9.837±0.136	-0.700±0.264	--	--	--	2.374(3)
	N2	30.991±0.123	--	--	--	--	-0.575±0.286	2.242(4)
	H2	27.764±0.148	1.436±0.147	-2.211±0.268	--	--	--	0.311(3)
PH	N1	94.224±2.045	1.142±0.537	18.154±2.568	14.063±2.158	--	--	0.202(2)
	H1	100.398±0.368	0.938±0.432	--	--	--	5.992±0.799	0.295(3)
	N2	106.823±0.527	0.160±0.528	2.025±0.947	--	--	--	0.206(3)
	H2	98.236±0.276	4.098±0.282	3.864±0.474	--	-36.183±2.904	--	0.419(2)
B/P	N1	12.200±0.184	0.767±0.184	-2.449±0.819	--	-0.872±0.700	2.916±0.842	1.226(1)
	H1	8.560 ±0.107	1.577±0.176	--	--	--	--	0.017(4)
	N2	19.070±0.267	0.892±0.175	--	1.760±0.336	3.592±0.853	-0.039±0.357	0.014(1)
	H2	12.086±0.479	0.512±0.141	-0.857±0.638	-0.005±0.523	--	--	0.006(2)
BSP	N1	83.973±0.192	4.033±0.247	--	1.102±0.331	27.748±1.053	--	0.073(2)
	H1	80.957±0.932	3.982±0.238	4.430±1.122	4.273±0.982	29.019±1.271	--	1.971(1)
	N2	82.698±0.203	1.475±0.222	--	2.187±0.342	--	--	0.267(3)
	H2	53.211±2.401	5.116±0.238	50.465±5.537	--	25.293±1.291	-30.577±3.271	0.572(1)
NSB	N1	24.730±0.165	1.852±0.163	-1.301±0.298	--	--	--	0.177(3)
	H1	20.559±0.221	--	-0.750±0.416	--	--	--	0.053(4)
	N2	24.950±0.148	--	-1.659±0.285	--	--	--	0.272(4)
	H2	22.831±0.102	1.327±0.146	--	--	--	--	0.364(4)
SCY	N1	29.724±4.691	8.017±0.738	5.010±10.778	--	-29.442±2.654	12.016±6.527	1.006(1)
	H1	41.063±5.319	5.900±0.733	-46.754±12.252	--	-11.896±2.963	41.164±7.356	0.982(1)
	N2	76.003±7.516	9.993±0.640	-54.178±17.283	--	-25.629±3.951	53.395±10.14	1.231(1)
	H2	33.682±6.339	4.465±0.630	6.451±14.574	--	-13.256±3.371	-1.470±8.591	0.892(1)

RCI: Relative Cell Injury, CC: Chlorophyll Contents, PH: Plant height, B/P: Number of Bolls per Plant, BSP: Boll Shedding Percentage, NSB: Number of Seeds per Boll, SCY: Seed Cotton Yield, N1 and N2: Cross 1 and Cross 2 under normal conditions respectively, H1 and H2: Cross 1 and Cross 2 under heat stress conditions respectively.

Number of bolls per plant

For number of bolls per plant in F_1 generation mean value was higher than F_2, BC_1 and BC_2 for cross-1 and cross-2 in normal and heat stress conditions. Heterozygosity could result in improvement of this trait (Table 2). In this study number of bolls per plant was ranged from 7.01 to 21.73 for both crosses under normal and heat stress conditions, for 12 generations (six from each cross i.e.P_1, P_2, F_1, F_2, BC_1 and BC_2).

Generation mean analysis showed that this trait was controlled by polygenes. In cross-1 under normal condition it was controlled by [mdhjl], while it was controlled by [md] in heat stress conditions. Here dominant component was negative, showing that genes responsible for decrease of this trait are dominant over the genes increasing the trait. In cross-2, this trait was controlled by [mdijl] in normal condition, while it was controlled by [mdhi] in heat stress condition. Again

additive component was negative and showing the same results as noted in cross-1 in normal conditions. The results of cross-1 under normal condition revealed that duplicate epistasis existed as [h] and [l] showed the presence of opposite signs (Table 3).

Boll shedding percentage

For boll shedding percentage inF_1generation was higher than F_2, BC_1 and BC_2 for both the crosses under normal and stress conditions and heterozygosity could result in increase of boll shedding, so homozygosity should be preferred to decrease boll shedding. Boll shedding percentage was ranged from 69.97 to 89.20 for cross-1 and 2 under normal and heat stress conditions (Table 2).

Generation mean analysis showed that this trait was controlled by polygenes. In cross-1 under normal condition it was controlled by [mdij], while it was

controlled by [mdhij] in heat stress condition. Here epistatic component [i] was again positive. In cross-2, boll shedding percentage was controlled by [mdi] in normal condition, while [mdhjl] in heat stress condition. In heat stress condition for both the crosses dominance component was more than additive component. The analysis of cross-2 in heat stress condition revealed the presence of duplicate epistasis due to positive and negative signs of [h] and [l] respectively. This observation indicated that epistatic component [i] played its role in controlling the boll shedding percentage in normal condition for both the crosses whilst for cross 1 in heat stress conditions (Table 3).

Number of seeds per boll

For number of seeds per boll mean value of F_1 was higher than population of F_2, BC_1 and BC_2 in both crosses. The range for mean value for number of seeds per boll was 19.80 to 26.60 under normal and heat stress conditions for cross-1 and cross-2 from six generations i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2 of each cross (Table 2). Generation mean analysis showed that this trait was controlled by polygenes. It was controlled by [mdh] and [mh] under normal condition and heat stress condition in cross-1 respectively. In cross-1, additive component [d] was higher than dominance component [h] in normal conditions. In cross-2, this trait was controlled by [mh] in normal conditions, while [md] in heat stress condition (Table 3).

Seed cotton yield

For seed cotton yield, mean value of F_1 was higher than F_2, BC_1 and BC_2 population in normal and heat stress condition in both crosses revealed that heterozygosity could be amenable for this trait. The range for mean value for seed cotton yield was 23.69 to 79.51 under normal and heat stress conditions for both crosses from six generations i.e. P_1, P_2, F_1, F_2, BC_1 and BC_2 for each cross (Table 2). Generation mean analysis showed that seed cotton yield was under the influence of multiple genes and controlled by [mdhjl] in cross-1 and cross-2 in normal and heat stress conditions. Additive component [d] was more than dominant component [h] for cross-1 in both conditions and for cross-2 only in normal condition. Dominant component [h] was higher than additive component [d] for cross-2 under heat stress condition.

The results for this trait revealed that dominant component [h] and dominant × dominant component [l] have same signs, which indicate that complementary epistasis also involved in the inheritance of this trait in normal condition for cross-1. The analysis for this trait also revealed that duplicate epistasis exists because dominant component [h] and dominant × dominant component [l] have opposite signs for cross-2 in normal and heat stress condition and cross-1 under heat stress condition (Table 3).

DISCUSSION

Temperature is a physical parameter that influences proteins and membranes structures through simple thermodynamic effects. Usually these influences are rapid and every molecule can be affected by temperature. It is documented and reported that shifts in climatic temperature can be perceived by cells in terms of changes in membrane rigidity (Vigh et al., 2007a b). High temperatures cause considerable pre- and post-harvest damages including scorching and sun burns of leaves, branches, stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration and damage, and reduction in yield of field crops (Vollenweider and Günthardt Goerg, 2005). Plants respond to stress through physiological and biochemical processes resulting in alteration of gene expression (Wahid et al., 2007; Chaves et al., 2009; Payton et al., 2011).

Although adverse temperatures can affect all stages of development, the cotton crop seems to be particularly sensitive to adverse temperatures during reproductive phase. It was reported that there was no clear consensus about the optimum temperature for growth and development of cotton, as plant response varies with plant developmental stage and environment in which cultivar was developed (Oosterhuis, 2002; Kumar et al., 2012; Sezener et al., 2015). Relative cell injury has been considered as a reliable parameter for screening against abiotic stress tolerance (Shafeeq and Zafar, 2006; Khan et al., 2008; Moussa and Abdel-Aziz, 2008; Azhar et al., 2009; Brito et al., 2011). Two identified tolerant genotypes VH-259 and VH-142 could be used in further breeding programs planned to improvise heat stress. These genotypes could be recommended for heat stress areas.

It was suggested that all the traits were controlled by additive, dominance and epistatic type of gene action. It could be suggested that selection should be done in later generations in order to improve these traits. It was also noted that number of bolls per plant, boll shedding percentage and relative cell injury percentage were controlled by duplicate type of epistasis as signs of [h] and [l] were opposite for these traits, while seed cotton yield showed complementary type of epistasis as signs of [h] and [l] were similar. Similar kind of results were presented by (Ahmad et al., 2009; Khan et al., 2009; Ullah et al., 2010; Gillani et al., 2015; Saleem et al., 2015; Shakeel et al., 2015) while contradictory results were presented by (Farooq et al., 2011; Ghobadi et al., 2011; Khan and Qasim, 2012; Iqbal et al., 2013).

CONCLUSION

Two identified tolerant genotypes VH-259 and VH-142 could be used in further breeding programs. All the traits under study showed complex type of gene action. So it could be suggested that selection should be done in later generations in order to improve these traits. This F_2 population could be used as good source population for further breeding programs focusing on heat stress tolerance.

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