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Genetic variability predicting breeding potential of upland cotton (*Gossypium hirsutum* L.) for high temperature tolerance

FAROOQ Amjad[1*], SHAKEEL Amir[2], SAEED Asif[2], FAROOQ Jehanzeb[1], RIZWAN Muhammad[1], CHATTHA Waqas Shafqat[2], SARWAR Ghulam[1] and RAMZAN Yasir[1]

Abstract

Background High temperature stress at peak flowering stage of cotton is a major hindrance for crop potential. This study aimed to increase genetic divergence regarding heat tolerance in newly developed cultivars and hybrids. Fifty cotton genotypes and 40 F_1 (hybrids) were tested under field conditions following the treatments, viz., high temperature stress and control at peak flowering stage in August and October under April and June sowing, respectively.

Results The mean squares revealed significant differences among genotypes, treatments, genotype × treatment for relative cell injury, chlorophyll contents, canopy temperature, boll retention and seed cotton yield per plant. The genetic diversity among 50 genotypes was analyzed through cluster analysis and heat susceptibility index (HSI). The heat tolerant genotypes including FH-Noor, NIAB-545, FH-466, FH-Lalazar, FH-458, NIAB-878, IR-NIBGE-8, Weal-AG-Shahkar, and heat sensitive, i.e., CIM-602, Silky-3, FH-326, SLH-12 and FH-442 were hybridized in line × tester fashion to produce F_1 populations. The breeding materials' populations (40 F_1) revealed higher specific combining ability variances along with dominance variances, decided the non-additive type gene action for all the traits. The best general combining ability effects for most of the traits were displayed by the lines, i.e., FH-Lalazar, NIAB-878 along with testers FH-326 and Silky-3. Specific combining ability effects and better-parent heterosis were showed by the crosses, viz., FH-Lalazar × Silky-3, FH-Lalazar × FH-326, NIAB-878 × Silky-3, and NIAB-878 × FH-326 for seed cotton yield and yield contributing traits under high temperature stress.

Conclusion Heterosis breeding should be carried out in the presence of non-additive type gene action for all the studied traits. The best combiner parents with better-parent heterosis may be used in crossing program to develop high yielding cultivars, and hybrids for high temperature stress tolerance.

Keywords High temperature, Upland cotton, Peak flowering, Heterosis, Gene action, Combining ability

Introduction

Cotton (*Gossypium hirsutum* L.) is an important crop being cultivated in more than eighty countries due to its products and socio-economic scope. The 80% of world cotton production share comes from top five countries, i.e., India, China, USA, Brazil, and Pakistan, respectively (Statista 2020). Cotton crop provides raw materials for several industries to produce edible oil, clothes, and seed cakes for livestock, organic matter, and several other products (Khan et al. 2020). Annually cotton crop

*Correspondence:
Farooq Amjad
amjad.cri@gmail.com
[1] Cotton Research Station, Ayub Agricultural Research Institute, Faisalabad 38000, Pakistan
[2] Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad 38040, Pakistan

overall contributes 0.6% in GDP of Pakistan in terms of foreign exchange earnings (Economic Survey of Pakistan 2021). Seed cotton yield facing severe decline in present climate change scenario involving a key factor, i.e., high temperature. The temperature trend revealed that global mean temperature may be increased (1–4 °C) at the end of twenty-first century (Driedonks et al. 2016). In Pakistan, during a period from 1960 to 2007, the average high temperature 0.87 °C per annum has been increased and similar trend predicted up to 2050. This trend of higher temperature may be prolonged and more expected in the major cotton zones of Pakistan (Pakistan Meteorological Department 2009; Salman et al. 2016). Under biotic and abiotic factors, the seed cotton yield of Pakistan revealed decline trends from 11.9 million bales to 8 million bales during the last five years since 2017–2021 (Economic Survey of Pakistan 2021). In Pakistan, overall 80% cotton sown in May due to late harvesting of previous crop of the cropping scheme, i.e., wheat-cotton, chickpea-cotton, and fodder-cotton (Ali et al. 2019). Therefore, cotton sowing in April and May always comes under high temperature stress starting from seedling to flowering. Pakistan's maximum daily temperature may range from 45 °C to 50 °C in June, July, and August, which is 20 °C higher than the optimum temperature for cotton production (Rahman et al. 2004; Abro et al. 2015).

Principally, high temperature stress is a major threat for sustainable cotton production, due to its negative impact on morpho-physiological traits (Yousaf et al. 2023). High temperature stress may cause malformation to the reproductive organs, viz., embryo, style, and ovaries, thus resulting less seed setting and low crop yield (Ekinci et al. 2017; Hatfield et al. 2018; Raja et al. 2019). The commercially approved cotton cultivars have low to moderate seed cotton yield and have not much high temperature tolerance. These cultivars depicted narrow genetic base that resulting in limited genetic gain and may be highly susceptible to stressed environment (McCarty et al. 2008; Wang et al. 2017; Ma et al. 2018). Hence, stabilized cotton productivity may be achieved by pyramiding of favorable diverse genes for heat tolerance in modern cultivars (Rani et al. 2022). Therefore, higher genetic variability in available germplasm may be useful against high temperature stress. The genetic variability in existing germplasm may be exploited through hybridization of desired traits to improve seed cotton yield and heat tolerance in new cultivars. Furthermore, genetically diverse parents and their combinations may be evaluated based on combining abilities for desired traits, viz., relative cell injury, chlorophyll contents, plant height, the number of bolls, boll weight, and bolls retention under high temperature stress (Brown and Oosterhuis 2010; Liu et al. 2006; Karademir et al. 2012; Singh et al. 2018). The study of high temperature stress under field conditions was also reported in several crops like maize (Wu et al. 2020), cotton (Saleem et al. 2020; Abro et al. 2022), wheat (Schmidt et al. 2020), pea (Mohapatra et al. 2020), rice (Karwa et al. 2020), and sugarcane (Amna et al. 2020). The treatment designs, viz., control and high temperature stress were applied at peak flowering time following different sowing time (Zhao et al. 2012; Ban et al. 2015; Mahdy et al. 2017; Saleem et al. 2020). The higher general combining ability (GCA), specific combining ability (SCA) effects, and heterosis would be effective approaches to improve the desired traits in cotton for developing excellent varieties (Abdel-Aty et al. 2023). This study may confer the variability and identification of distinct heat tolerant and heat sensitive genotypes. The genetic materials (hybrids) were assessed based on combining abilities, gene action and heterosis manifestation in favor of various traits to get maximum seed cotton yield under high temperature stress.

Materials and methods

Plant materials

The screening phase against high temperature stress was conducted in 2019 under field conditions. A diverse germplasm of 50 genotypes of upland cotton were collected from different public and private sectors (Figs. 1, 2, and 3). Based on heat susceptibility index (HSI) and cluster analysis, the heat tolerant (FH-Noor, FH-458, FH-466, FH-Lalazar, IR-NIBGE-8, Weal-AG-Shahkar, NIAB-545, and NIAB-878) and heat sensitive genotypes (Silky-3, FH-326, SLH-12, CIM-602, and FH-442) were selected for hybridization as females (lines) and males (testers) parents, respectively. The parental genotypes were raised in a glasshouse in November to produce (F_1) hybrid seed. The glasshouse temperature was maintained at 30/20 °C (day/night) along with 50%–60% relative humidity. Hybridization was started at anthesis/flowering stage to develop all possible cross combinations following line × tester design ($8 \times 5 = 40$ F_1). The breeding phase was conducted on 40 F_1 + 13 parents in 2020 under field conditions and studied the genetic basis of temperature tolerance in upland cotton.

Treatments/experimental design

The consecutive experiments, viz., screening phase (50 genotypes) and breeding phase (40 F_1 + 13 parents) were planned and executed at Cotton Research Station, Faisalabad, Pakistan (longitude 73.1°E, latitude 31.43°N). The experiments were arranged under randomized complete block design (RCBD) following split-plot layout scheme with three replications. The air temperature was given out as a main factor, whilst genotypes as sub-factor for each treatment. The treatments, i.e., high and control

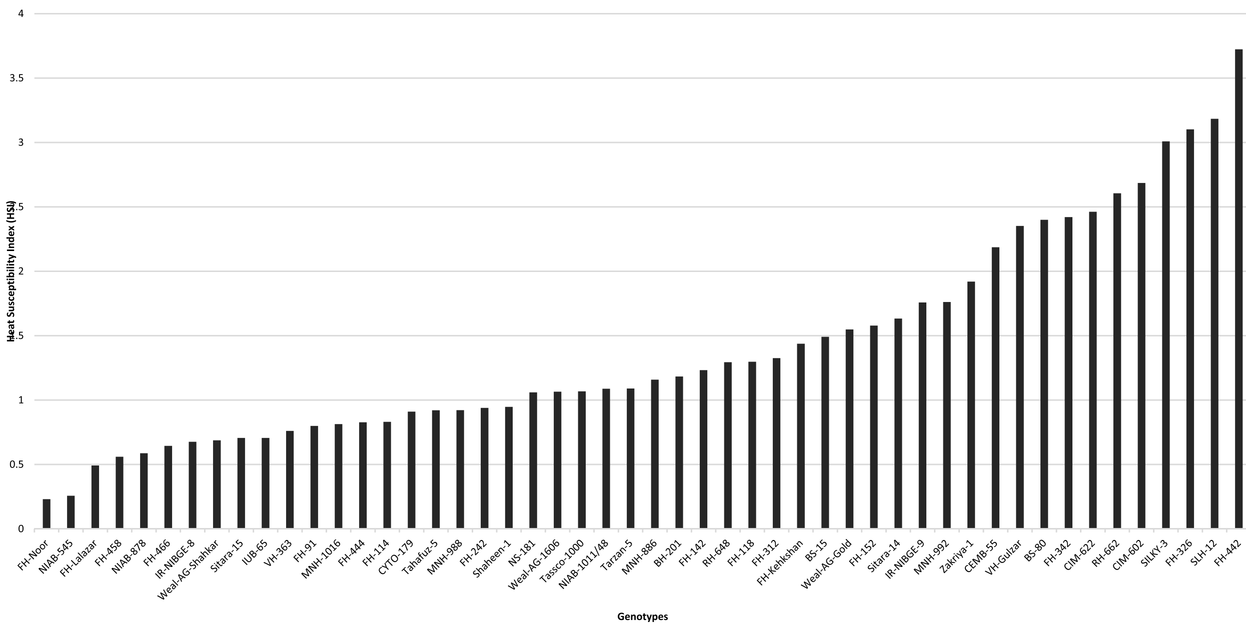

Fig. 1 Heat susceptibility index (HSI) for seed cotton yield per plant

temperature were applied at peak flowering time under field conditions. High temperature stress was applied in August following the April-sowing. The control temperature was applied in October following the June-sowing. Plant population was managed in separate rows comprising 15 plants for each genotype following 75 cm row-to-row and 30 cm plant-to-plant spacing. The fertilizers including nitrogen 200 kg·hm^{-2}, phosphorus 60 kg·hm^{-2} and potash 100 kg·hm^{-2} were applied to fulfill the nutritional requirements of experiments. Phosphorus and potash were applied at bed preparation with 1/4th of nitrogen, while the remaining 1/4th nitrogen applied after 30 days of germination, 1/4th at flowering, and 1/4th at boll formation stage, respectively (Rahman et al. 2008). The experiments were sprayed adequately whenever plant protection required for controlling different insect-pests. All irrigations were applied to justify the crop water requirements throughout the season, especially at flowering and bolls maturation time.

Collection of seasonal weather data

Seasonal meteorological data were collected from observatory of Agronomic Research Institute, Faisalabad, which was located near to the experimental site. Mean maximum temperature was ranged from 24.4 to 40.2 °C in 2019 and 27.1 °C to 39.6 °C in 2020, respectively. Mean maximum temperature on peak flowering was recorded 38.5 °C and 37.8 °C in August under the April-sowing in 2019 and 2020, respectively. Similarly, mean maximum temperature 34.2 °C and 33.7 °C was recorded on peak flowering time in October under the June-sowing for the consecutive years of study (Table 1).

Relative cell injury

Relative cell injury percentage (RCI %) was measured following the method that proposed by Sullivan (1972). The younger leaves (20–22 days old) from 10 plants were used to prepare sampling discs at peak flowering time in falcon tubes. Leaf discs (diameter 10 mm) were punched from each lobe of leaf on either side of mid-rib. The leaves' discs were collected from the attached leaves at daytime between 13:00–15:00. Leaf discs were rinsed with deionized water to remove adhering electrolytes from cut surface. A set of 5 falcon tubes was prepared as control and other set of 5 tubes as heat-treated for each genotype. Each falcon tubes of both sets were contained ten leaf discs and filled with 20 ml deionized water. The heat-treated set was incubated in water bath at 50 °C for 30 min. Both sets were placed at room temperature up to 24 h for maximum electrolytes diffusion. After 24 h both sets of falcon tubes were mixed gently, and EC (Electric Conductivity) values were recoded using EC meter (HANNA Instruments, HI, USA). Both sets of falcon tubes were autoclaved at pressure of 0.10 MPa for diffusion of maximum electrolytes. Then falcon tubes were placed at room temperature for measuring final EC values. Relative cell injury procedure was carried out separately for

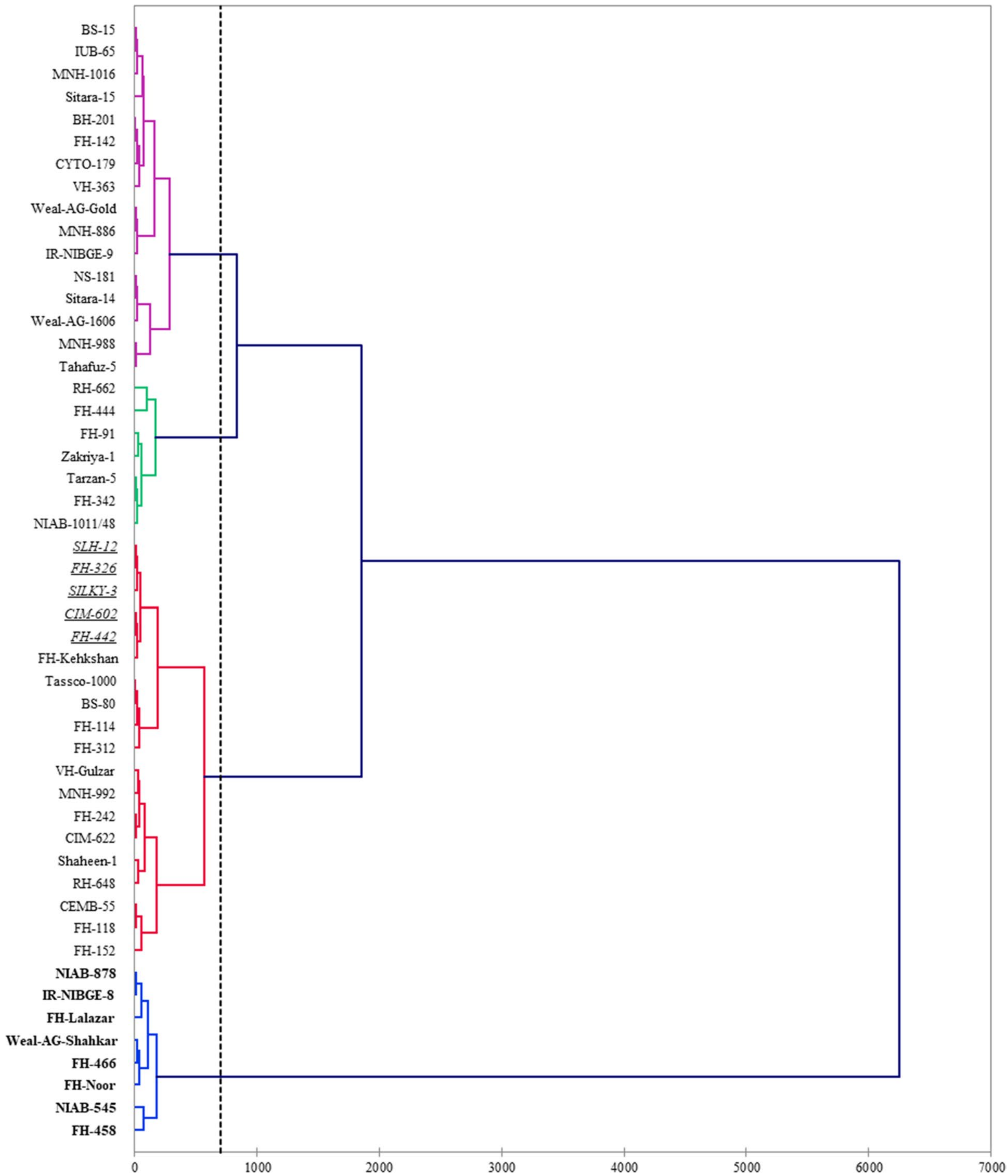

Fig. 2 Dendrogram of 50 cotton genotypes for relative cell injury, chlorophyll contents, canopy temperature, bolls retention and seed cotton yield in June-sowing (control)

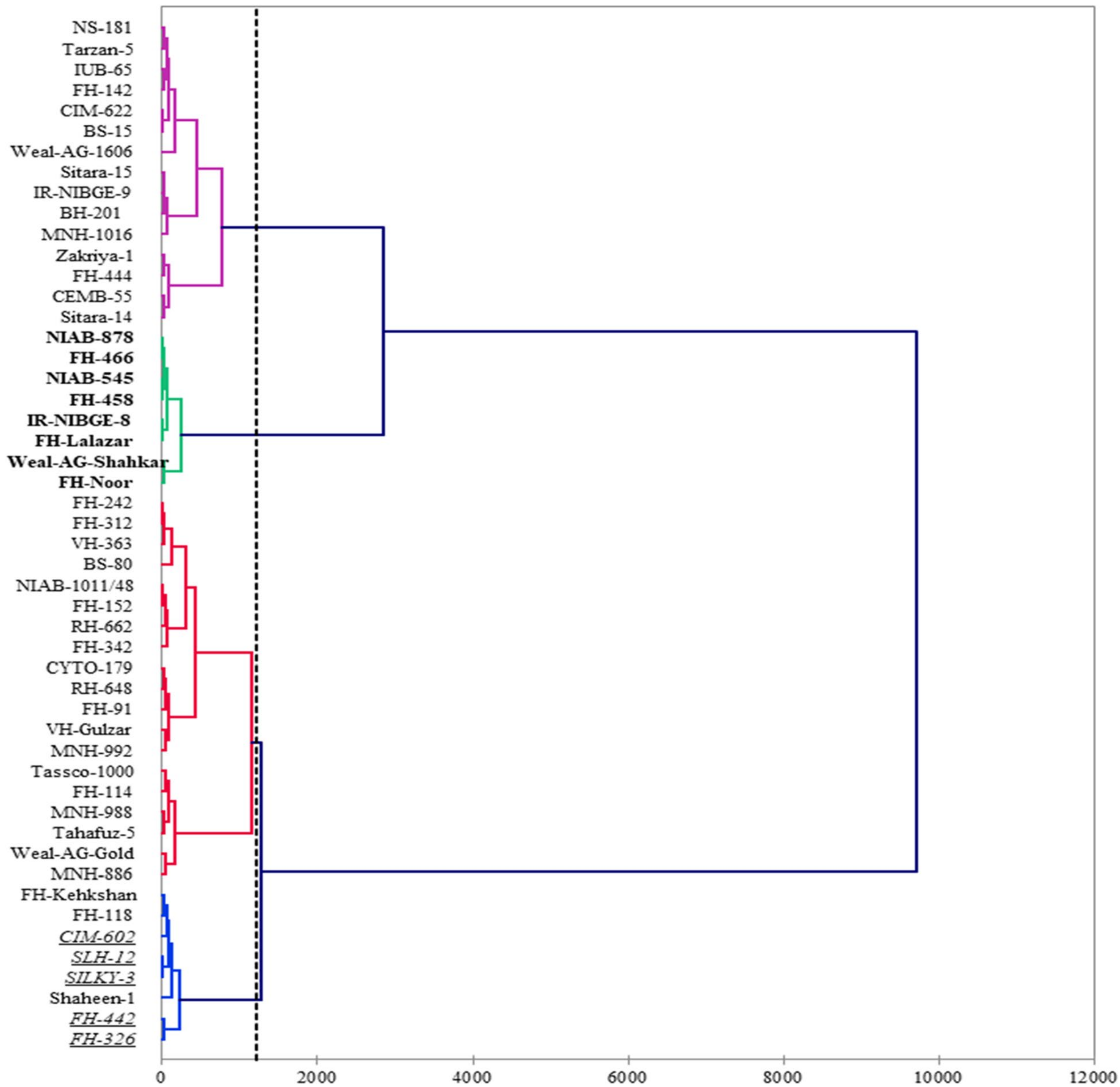

Fig. 3 Dendrogram of 50 cotton genotypes for relative cell injury, chlorophyll contents, canopy temperature, bolls retention and seed cotton yield in April-sowing (high temperature stress)

each date of sowing. Relative cell injury percentage was calculated by the following formula.

$$\mathrm{RCI}(\%) = [1 - (1 - \frac{\mathrm{T1}}{\mathrm{T2}})/(1 - \frac{\mathrm{C1}}{\mathrm{C2}})] \times 100\%$$

whereas: T1 = EC value of heat-treated/water-bath, C1 = EC value of control set, T2 = EC value after autoclaving of heat-treated set, C2 = EC value after autoclaving of control set.

Chlorophyll contents

The chlorophyll contents ($\mu\mathrm{mol}\cdot\mathrm{m}^{-2}$) were determined from surface of leaf by using a hand-held optical chlorophyll contents meter (CCM-200 Plus,Opti-Sciences, Inc., Hudson, NH, USA). The observations were taken on daytime from 14:00 to 15:00 under field conditions. The expanded green leaves from three positions, i.e., top 4$^{\mathrm{th}}$ leaf, middle, and bottom leaves were selected for recording observations.

Table 1 Climatic conditions of cotton growing seasons in 2019 and 2020

Months	2019				2020			
	Mean max. temp. /°C	Mean mini. temp. /°C	Mean R. H /%	Total Rainfall / mm	Mean max. temp. /°C	Mean mini. temp. /°C	Mean R. H /%	Total Rainfall / mm
April	35.4	18.8	68.6	20.2	36.3	18.4	52.4	15.4
May	40.2	23.5	52.5	18.4	39.6	24.0	54.4	11.0
June	39.0	25.8	62.8	68.9	39.0	25.6	60.2	110.8
July	37.6	27.5	70.4	130.6	37.2	26.8	70.4	240.3
August	38.5	28.1	75.8	134.7	37.8	26.9	69.4	5.2
September	37.1	25.3	73.3	9.9	35.6	25.5	73.2	29.4
October	34.2	17.0	66..1	0.0	33.7	19.1	70.5	0.3
November	24.4	10.2	81.4	0.8	27.1	11.0	80.4	0.0

Note: *Max.* Maximum, *Mini.* Minimum, *Temp.* Temperature, *R.H.* Relative Humidity

Canopy temperature

Canopy temperature was recorded on sunny day, from 14:00 to 15:30, under field conditions. The observations were recorded using an infrared thermometer (IR-880A, UK) positioning at the angle 30°–45° from 0.5 m edge and 50 cm above canopy of plants.

Boll retention

Boll retention was determined by counting the total numbers of retained bolls and tagged flowers or fruiting sites per plant. The observations were recorded on ten selected plants of all genotypes in each replication. Boll retention percentage was also calculated by Liu et al. (2006), Cottee et al. (2010), and Lokhande and Reddy (2014) using following formula:

$$\text{Boll retention (BR\%)} = \frac{\text{Total numbers of retained bolls per plant}}{\text{Total numbers of fruiting sites per plant}} \times 100$$

Yield and yield components

The average of bolls per plant and sympodial branches per plant were calculated by counting their total number per plant on 10 randomly selected plants at harvesting time. The boll weight recorded from a sample's weight containing 50 bolls by using simple calculation of arithmetic mean. Seed index was calculated by randomly counted 100 seeds of each genotype and weighed in grams on electronic balance. Plant height were taken at harvesting time and measured from ground level to apical bud with the help of centimeter scale. The data of seed cotton yield per plant were recorded after accumulating the yield of 10 selected plants and the average was calculated to get final seed cotton yield per plant in grams.

Statistical analysis

The experiments conducted under randomized complete block design (RCBD) following split-plot scheme of treatments along with three replications. The data under screening traits were subjected into analysis of variance following the Steel et al. (1997). The significance was analyzed among treatments, genotypes, and interactions at *, $P \leq 0.05$ (significant) and **, $P \leq 0.01$ (highly significant). Descriptive statistics was performed by using software Statistix 8.1. The grouping of genotypes was carried out on Xlstat software following the method of cluster analysis as described by Ward (1963). Fischer and Maurer (1978) described the heat susceptibility index (HSI), which was calculated following the modified formula as under:

$$\text{Heat susceptibility index} = \frac{(1 - \text{Ys}/\text{Yn})}{(1 - \bar{\text{Y}}\text{s}/\bar{\text{Y}}\text{n})}$$

whereas: Ys = Mean seed cotton yield of a genotype under high temperature stress. Yn = Mean seed cotton yield of a genotype under control condition. $\bar{\text{Y}}$s = Mean of all genotypes under high temperature stress. $\bar{\text{Y}}$n = Mean of all genotypes under control condition.

Based on HSI calculations the genotypes were kept in four classes, viz., highly heat tolerant (HSI ≤ 0.50); heat tolerant (HSI ≥ 0.51–0.75); moderate heat tolerant (HSI ≥ 0.76–1.00), or heat susceptible (HSI ≥ 1.00).

Analysis of variance for combining ability under line × tester design

Combining abilities of selected parents and their crosses estimated following line × tester scheme of Kempthorne (1957) provided that genetic information regarding gene action and heterosis.

Estimation of general combining ability (GCA) effects

General combining ability (GCA) effects for lines and testers were calculated following formula:

$$\text{GCA effects of lines}: \ \text{gi} = \{(\text{xi}\ldots/\text{tr}) - (\text{x}\ldots/\text{ltr})\}$$

$$\text{GCA effects of testers}: \text{gt} = \{(\text{x.j.}/\text{lr}) - (\text{x}\ldots/\text{ltr})\}$$

whereas: l = number of lines, t = number of testers, r = number of replications, xi… = total of the F_1 resultant from crossing the i^{th} line with all the testers, x.j. = total of all the crosses of j^{th} testers with all the lines, x… = total of all crosses.

Estimation of specific combining ability (SCA) effects

$$\text{Sij} = \{(\text{xij.}/\text{r}) - (\text{xi..}/\text{tr}) - (\text{x.j.}/\text{lr}) + (\text{x}\ldots/\text{ltr})\}$$

whereas: Xij. = total of F_1 resultant from crossing of i^{th} lines with j^{th} testers.

Significance of the effects was calculated with t-test as given below:

$$\text{t} - \text{calculated} = (\text{Effects}/\text{SE})$$

The above effects were considered significant if t-calculated exceeds from t-tabulated under the error degree of freedom at level of 5%.

Calculation of standard error (S.E.)

$$\text{S.E.(GCA for lines)} = \sqrt{\text{MSE}/\text{r} \times \text{t}}$$

$$\text{S.E.(GCA for testers)} = \sqrt{\text{MSE}/\text{r} \times \text{l}}$$

$$\text{S.E.(SCA)} = \sqrt{\text{MSE}/\text{r}}$$

Genetic components

Estimation of genetic components of variation following the GCA and SCA variances is given below:

$$\text{General combining ability variance (Vgca)} = \frac{\text{MSl} - \text{MSlt} + (\text{MSt} - \text{MSlt})}{\text{r}(1+\text{t})}$$

$$\text{Spesific combining ability variance (Vsca)} = \frac{\text{MSlt} - \text{MSE}}{\text{r}}$$

While:

$$\text{Additive variance } (\text{V}_\text{A}) = 2\text{V}_{\text{gca}}$$

$$\text{Dominance variance } (\text{V}_\text{D}) = \text{V}_{\text{sca}}$$

whereas: MSl = Mean squares of lines, MSt = Mean squares of testers, MSl t = Mean squares of lines and testers, MSE = Mean squares of error, r = Replications.

Heterosis

Heterosis manifestation of cross combinations over better parent was calculated following the formula:

$$\text{Heterosis over better} - \text{parent } (\%) = \frac{\text{F1} - \text{Better} - \text{ parent value}}{\text{Better} - \text{ parent value}} \times 100$$

Heterosis significance was calculated through *t*-test according to formulae given by Wynne et al. (1970) as under:

$$\text{t} - \text{test for better} - \text{parent heterosis} = (\text{F}1 - \text{BP})/$$

Results

The means squares of 50 cotton genotypes revealed the significant differences among genotypes, treatments, genotypes × treatments interaction for the traits like relative cell injury, chlorophyll contents, canopy temperature, boll retention, and seed cotton yield (Table 2). The most tolerant and sensitive genotypes were selected for crossing based on heat susceptibility index

Table 2 Mean squares for screening traits of 50 genotypes studied under control and high temperature stress in 2019

S.O.V	df	RCI	CC	CT	BR	SCY
Replications	2	24.4	35.83	0.18	36.12	12.37
Treatments	1	3192.2[b]	659.8[a]	208.3[b]	247.9[b]	2453.9[b]
Error (a)	2	9.74	18.9	0.13	41.11	11.23
Genotypes	49	480.7[b]	166.4[b]	6.22[b]	293.52[b]	572.8[b]
Genotypes × Treatments	49	88.28[b]	35.2[b]	2.50[b]	135.27[b]	103.6[b]
Error (b)	196	10.75	6.5	0.42	8.23	6.28
Total	299					

[a] = Significance at 5%, [b] = Significance at 1%, *S.O.V* Source of variation, *df* Degree of freedom, *RCI* Relative cell injury, *CC* Chlorophyll contents, *CT* Canopy temperature, *BR* Boll retention, *SCY* Seed cotton yield/plant

(HSI) and cluster analysis as selection criteria. Heat susceptibility index (HSI) for 50 cotton genotypes was observed from 0.23 to 3.72. The lower values of HSI as selection criteria of heat tolerance were observed in 8 genotypes including FH-Noor (0.23), NIAB-545 (0.25), FH-Lalazar (0.49), FH-458 (0.56), NIAB-878 (0.58), FH-466 (0.64), IR-NIBGE-8 (0.67), and Weal-AG-Shahkar (0.68). Based on higher values of HSI the five genotypes, viz., CIM-602 (2.68), Silky-3 (3.00), FH-326 (3.10), SLH-12 (3.18), and FH-442 (3.72) were found heat sensitive (Fig. 1). Cluster analysis demonstrated genotypic variability under control and high temperature stress. Based on the highest and lowest mean values of studied traits the genotypes were further classified as heat tolerant in one cluster and heat sensitive genotypes in another cluster (Figs. 2 and 3). The heat tolerant genotypes were selected as lines (female) and testers as heat sensitive (male) parents. The breeding materials of 40 F_1 generations were assessed for combining ability effects, heterosis and gene action under Line × Tester mating design. The mean squares values following line × tester design for the June- (control) and the April-sowing (high temperature stress) depicted significant variations among genotypes, crosses, lines, testers, L × T, parents, and cross vs parent for various traits, viz., relative cell injury, chlorophyll contents, boll retention, sympodial branches per plant, bolls per plant, plant height, and seed cotton yield. Boll weight remained non-significant under both treatments. Under control, mean square values of seed index for L × T, parents, and cross vs parents also remained non-significant. Similarly, L × T revealed non-significance for canopy temperature under control. While, under high temperature stress seed index showed non-significant results for L × T and cross vs parents (Table 3).

GCA and SCA variances predicting gene action

The results of general combining ability (GCA) variance, specific combining ability (SCA) variance, additive variance and dominance variance presented in Table 4. GCA and additive variances as well as SCA and dominance variances were used to determine the type of gene action for all the traits. This study showed that SCA and dominance variances were higher than GCA and additive variances for all studied traits. These results predicted that non-additive type of gene action controlling the expression of all traits under control and high temperature stress (Table 4).

GCA, SCA effects, and heterosis for relative cell injury

The values of relative cell injury may be the least/negatively preferred for improvement of such trait. The parents and crosses showed significantly negative general and specific combining ability (GCA & SCA) effects were

Table 3 Mean square values of line × tester analysis for various traits under control and high temperature stress in 2020

SOV	df	RCI	CC	CT	BR	SB	PH	B/P	BW	SI	SCY
Control											
Rep	2	0.09	12.5	3.44	3.5	2.5	83.1	4.5	0.05	0.18	10.6
Gen	52	319.4^b	113.4^b	4.27^b	254.3^b	22.4^b	423.4^b	94.1^b	0.32^{ns}	1.74^a	1240.1^b
Cross	39	231.3^b	75.3^b	2.95^b	186.7^b	19.3^b	313.9^b	104.1^b	0.29^{ns}	1.95^a	445.7^b
Line	7	371.7^b	207.9^b	5.64^b	135.2^b	13.7^b	602.2^b	77.6^b	0.46^{ns}	4.59^b	785.9^b
Tester	4	739.8^b	32.8^b	5.89^b	1200.9^b	43.7^b	205.0^b	256.2^b	0.98^{ns}	5.80^b	376.3^b
L×T	28	123.5^b	48.3^b	1.86$^{n.s}$	1531.2^b	17.2^b	257.5^b	89.0^b	0.15^{ns}	0.73^{ns}	370.5^b
Parents	12	598.8^b	135.7^b	7.64^b	459.3^b	32.5^b	607.1^b	68.9^b	0.47^{ns}	1.19^{ns}	3007.8^b
Cross vs Parent	1	404.0^b	1328.3^b	15.03^b	431.2^b	19.6^b	2486.8^b	7.0^a	0.003^{ns}	0.01$^{n.s}$	11,010.9^b
High temperature stress											
Rep	2	7.5	2.5	1.3	13.8	3.8	115.5	0.9	0.01	0.19	4.59
Gen	52	387.0^b	103.9^b	6.14^b	303.9^b	57.3^b	1197.6^b	167.8^b	0.37 ns	2.25^b	3474.2^b
Cross	39	231.3^b	75.3^b	2.95^b	186.7^b	19.3^b	313.9^b	104.1^b	0.29^{ns}	1.95^a	445.7^b
Line	7	371.7^b	207.9^b	5.64^b	135.2^b	13.7^b	602.2^b	77.6^b	0.46^{ns}	4.59^b	785.9^b
Tester	4	739.8^b	32.8^b	5.89^b	1200.9^b	43.7^b	205.0^b	256.2^b	0.98^{ns}	5.80^b	376.3^b
L×T	28	123.5^b	48.3^b	1.86$^{n.s}$	1531.2^b	17.2^b	257.5^b	89.0^b	0.15^{ns}	0.73^{ns}	370.5^b
Parents	12	598.8^b	135.7^b	7.64^b	459.3^b	32.5^b	607.1^b	68.9^b	0.47^{ns}	1.19^{ns}	3007.8^b
Cross vs Parent	1	404.0^b	1328.3^b	15.03^b	431.2^b	19.6^b	2486.8^b	7.0^a	0.003^{ns}	0.01$^{n.s}$	11,010.9^b

Rep Replication, *Gen* Genotype, *L × T* Line × tester, ^{a} = Significance at 5%, ^{b} = Significance at 1%, *df* Degree of freedom, *RCI* Relative cell injury percentage, *CC* Chlorophyll contents, *CT* Canopy temperature, *BR* Boll retention, *B/P* Bolls per plant, *BW* Boll weight, *SB* Sympodial branches/plant, *SI* Seed index, *PH* Plant height, *SCY* Seed cotton yield/plant

Table 4 Estimation of genetic components of variation under control and high temperature stress

Trait	Control				High temperature stress			
	GCA Var	SCA Var	Additive Var	Dominance Var	GCA Var	SCA Var	Additive Var	Dominance Var
RCI	1.900	40.92	3.80	40.92	2.261	58.03	4.522	58.03
CC	0.477	9.58	0.95	9.58	-0.152	19.69	-0.304	19.69
CT	0.019	-0.05	0.038	-0.05	0.0009	1.402	0.0018	1.402
BR	2.33	18.07	4.66	18.07	2.955	22.768	5.91	22.768
SB	0.037	5.37	0.074	5.37	-0.113	14.323	-0.226	14.323
PH	0.996	80.37	1.99	80.37	3.722	244.843	7.444	244.843
B/P	0.27	28.55	0.54	28.55	0.255	50.275	0.51	50.275
BW	0.003	0.04	0.006	0.04	0.003	0.047	0.006	0.047
SI	0.021	0.22	0.042	0.22	0.025	0.201	0.050	0.201
SCY	1.325	122.12	2.65	122.12	2.327	541.404	4.654	541.404

Note: *GCA* General combining ability, *SCA* Specific combining ability, *Var.* Variance, *RCI* Relative cell injury, *CC* Chlorophyll contents, *CT* Canopy temperature, *BR* Boll retention, *B/P* Bolls per plant, *BW* Boll weight, *SB* Sympodial branches/plant, *SI* Seed index, *PH* Plant height, *SCY* Seed cotton yield/plant

preferred against heat stress. Under control condition, female parents, namely FH-Lalazar (-6.79), FH-Noor (-2.22), NIAB-545 (-1.7), NIAB-878 (-1.57), Weal-AG-Shahkar (-1.64), and the male parents, viz., FH-326 (-3.78), Silky-3 (-3.45), and SLH-12 (-3.2) displayed significantly negative GCA effects. Under high temperature stress conditions, the female parents, i.e., FH-Lalazar (-7.49), NIAB-545 (-2.47), FH-Noor (-1.66), and male parents including SLH-12 (-4.32), FH-326 (-5.41), Silky-3 (-3.25) showed maximum negative GCA effects (Table 5). Under control condition, the crosses, viz. FH-466 × CIM-602 (-15.20), FH-Lalazar × FH-442 (-8.03) showed significantly negative SCA effects (Table 6). While, under high temperature stress the crosses, viz., FH-466 × CIM-602 (-17.10), NIAB-878 × CIM-602 (-9.36) indicated the significantly negative SCA effects (Table 7). For better-parent heterosis, significantly negative results were displayed by the crosses, viz., FH-Lalazar × FH-326 (-49.36%) and NIAB-545 × FH-326 (-47.03%) under control condition. Under high temperature stress the crosses, namely NIAB-545 × FH-326 (-46.74%) and FH-Lalazar × Silky-3 (-46.34%) depicted significantly negative better-parent heterosis in favor of relative cell injury (Tables 6 and 7).

GCA, SCA effects, and heterosis for chlorophyll contents

Maximum chlorophyll contents may be claimed following the significantly positive GCA and SCA effects. Under control temperature condition the female parents including IR-NIBGE-8 (4.02) and FH-Noor (3.98) revealed significantly positive GCA effects. Under high temperature stress a female, i.e., FH-458 (3.46), while a male, i.e., CIM-602 (1.30) indicated significantly positive GCA effects (Table 5). Significantly positive SCA effects were observed in a cross combination, i.e., IR-NIBGE-8 × Silky-3 (6.45) under control condition. The crosses, namely NIAB-545 × FH-442 (7.33) and NIAB-878 × SLH-12 (6.25) under high temperature stress, revealed significantly positive SCA effects (Tables 6 and 7). The significantly positive better-parent heterosis was not depicted by any cross combination.

GCA, SCA effects, and heterosis for canopy temperature

Canopy temperature with significantly negative GCA and SCA effects was claimed for improving heat tolerance in cotton. Under control temperature condition none of the female parents showed significantly negative GCA effects.

Whereas, male parent, i.e., FH-326 (-0.67) revealed significantly negative GCA effects for canopy temperature. Under high temperature conditions only the female parents, viz., NIAB-545 (-0.75) and Weal-AG-Shahkar (-0.63) showed significantly negative GCA effects (Table 5). Under control condition the crosses, namely FH-Noor × SLH-12 (-1.86) and FH-Lalazar × Silky-3 (-1.79) showed significantly negative SCA effects. Under high temperature stress some crosses, viz., FH-466 × FH-442 (-2.18), and FH-Lalazar × FH-326 (-2.14) revealed significantly negative SCA effects (Tables 6 and 7). Significantly negative better-parent heterosis was found in crosses, namely FH-Lalazar × FH-326 (-16.56%) and FH-458 × FH-326 (-14.08%) under control condition. While the combinations, viz., NIAB-878 × Silky-3 (-14.39%) and FH-Lalazar × FH-326 (-12.61%) exhibited significantly negative better-parent heterosis under high temperature stress (Tables 6 and 7).

GCA, SCA effects, and heterosis for boll retention

Boll retention percentage could be improved through significantly positive aGCA and SCA effects. Under control condition, the female parents, i.e., FH-Noor (1.87),

Table 5 Estimation of general combining ability (GCA) effects for various traits under control and high temperature stress

Lines	RCI	CC	CT	BR	SB	PH	B/P	BW	SI	SCY
Control										
FH-Noor	-2.22**	3.98**	-0.33 ^{ns}	1.87**	-0.46 ^{ns}	-8.84**	1.02*	0.04 ^{ns}	0.08 ^{ns}	-3.7**
FH-458	4.06**	0.86 ^{ns}	-0.15 ^{ns}	2.15**	-1.03**	0.45 ^{ns}	-2.91**	-0.18**	-0.23**	-0.11 ^{ns}
FH-466	9.89**	-1.88 ^{ns}	-0.1 ^{ns}	-3.68**	0.26 ^{ns}	-0.23 ^{ns}	-2.91**	0.03 ^{ns}	-0.71**	-8.6**
FH-Lalazar	-6.79**	-6.31**	-0.72 ^{ns}	4.64**	-1.45**	2.22*	3.09**	0.31**	0.93**	0.39 ^{ns}
Weal-AG-Shahkar	-1.64**	1.37 ^{ns}	-0.27 ^{ns}	-4.2**	0.00 ^{ns}	12.13**	0.96*	0.08**	-0.71**	12.62**
NIAB-545	-1.7**	-3.93**	-0.12 ^{ns}	0.9**	1.12**	-2.84**	-0.77 ^{ns}	0.08**	0.27**	-7.34**
IR-NIBGE-8	-0.02 ^{ns}	4.02**	0.37 ^{ns}	-1.02**	1.29**	-5.82**	-0.98*	-0.24**	0.00 ^{ns}	-1.28*
NIAB-878	-1.57**	1.89 ^{ns}	1.32**	-0.66**	0.26 ^{ns}	2.93**	2.49**	-0.12**	0.38**	8.01**
S.E.	0.23	1.14	0.37	0.18	0.27	1.04	0.473	0.02	0.06	0.53
Testers										
FH-326	-3.78**	-0.66 ^{ns}	-0.67*	9.5**	0.01 ^{ns}	2.64**	3.65**	0.31**	0.71**	6.37**
Silky-3	-3.45**	-0.25 ^{ns}	-0.09 ^{ns}	5.55**	-0.81**	-4.2**	-0.31 ^{ns}	0.02 ^{ns}	0.31**	-2.54**
SLH-12	-3.2**	1.67 ^{ns}	-0.21 ^{ns}	-3.52**	-1.8**	2.32**	-3.6**	-0.24**	-0.30**	-3.05**
CIM-602	1.18**	0.6 ^{ns}	0.58*	-5.31**	1.19**	1.02 ^{ns}	2.98**	-0.1**	-0.45**	1.35**
FH-442	9.25**	-1.36 ^{ns}	0.39 ^{ns}	-6.21**	1.41**	-1.78*	-2.72**	0.01 ^{ns}	-0.28**	-2.14**
S.E.	0.184	0.902	0.289	0.141	0.21	0.83	0.374	0.023	0.050	0.43
High temperature stress										
FH-Noor	-1.66**	1.10 ^{ns}	0.09 ^{ns}	1.99**	0.52 ^{ns}	-12.8**	3.28**	0.06*	-0.27**	-5.59**
FH-458	1.83**	3.46**	-0.31 ^{ns}	3.21**	0.06 ^{ns}	5.16**	-2.58**	-0.18**	-1.05**	-1.27*
FH-466	9.06**	-0.46 ^{ns}	1.16**	-3.62**	-1.54**	0.11 ^{ns}	-5.45**	0.03 ^{ns}	-0.3**	-18.3**
FH-Lalazar	-7.49**	0.13 ^{ns}	0.23 ^{ns}	5.81**	-0.74**	-6.27**	4.95**	0.34**	0.73**	-8.28**
Weal-AG-Shahkar	0.38 ^{ns}	-0.56 ^{ns}	-0.63*	-4.04**	2.59**	7.86**	0.75 ^{ns}	0.03 ^{ns}	-0.52**	30.62**
NIAB-545	-2.47**	-1.22 ^{ns}	-0.75**	0.37 ^{ns}	0.46 ^{ns}	17.6**	1.62**	0.05 ^{ns}	0.62**	6.3**
IR-NIBGE-8	0.68**	-1.65*	0.68*	-2.18**	-0.34 ^{ns}	-13.7**	-2.18**	-0.25**	0.17**	-3.09**
NIAB-878	-0.33 ^{ns}	-0.81 ^{ns}	-0.46 ^{ns}	-1.53**	-1.01**	2.13*	-0.38 ^{ns}	-0.08**	0.61**	-0.46 ^{ns}
S.E.	**0.24**	**0.79**	**0.28**	**0.19**	**0.31**	**0.93**	**0.40**	**0.03**	**0.06**	**0.55**
Testers										
FH-326	-5.41**	-0.14 ^{ns}	-0.10 ^{ns}	10.73**	1.02**	7.28**	4.47**	0.36**	0.7**	7.01**
Silky-3	-3.25**	-1.46*	-0.03 ^{ns}	6.07**	-0.82**	7.78**	0.51 ^{ns}	0.02 ^{ns}	0.2**	-1.61**
SLH-12	-4.32**	1.13 ^{ns}	0.66**	-4.02**	-0.94**	-4.34**	-3.24**	-0.19**	-0.14**	0.83 ^{ns}
CIM-602	1.41**	1.30*	-0.18 ^{ns}	-5.64**	0.47 ^{ns}	-5.12**	1.55**	-0.21**	-0.47**	-2.91**
FH-442	11.56**	-0.82 ^{ns}	-0.35 ^{ns}	-7.14**	0.27 ^{ns}	-5.6**	-3.28**	0.02 ^{ns}	-0.29**	-3.32**
S.E	**0.19**	**0.63**	**0.22**	**0.15**	**0.25**	**0.73**	**0.32**	**0.02**	**0.05**	**0.43**

Note: *RCI* Relative cell injury, *CC* Chlorophyll contents, *CT* Canopy temperature, *BR* Boll retention, *B/P* Bolls per plant, *BW* Boll weight, *SB* Sympodial branches, *SI* Seed index, *PH* Plant height, *SCY* Seed cotton yield/plant

*=Significant, **=Highly significant, ^{ns}=Non-significant, S.E.= Standard error

FH-458 (2.15), FH-Lalazar (4.64), and NIAB-545 (0.9) as well as male parents FH-326 (9.5) and Silky-3 (5.55) showed significantly positive GCA effects. While, under high temperature stress, female parents, viz., FH-Noor (1.99), FH-458 (3.21), FH-Lalazar (5.81), and male parents including FH-326 (10.73) and Silky-3 (6.07) revealed significantly positive GCA effects for boll retention (Table 5). Under control condition among crosses, namely FH-Noor × FH-442 (11.60) and FH-458 × CIM-602 (6.10), showed significantly positive SCA effects. Under high temperature stress, the best crosses, viz., FH-Noor × FH-442 (12.95) and FH-458 × CIM-602 (6.20) revealed significantly positive SCA effects (Tables 6 and 7). The crosses including FH-Lalazar × FH-326 (14.07%) and FH-Lalazar × Silky-3 (8.32%) displayed significantly positive better-parent heterosis under control condition. Under high temperature stress condition, the crosses, i.e., FH-Lalazar × FH-326 (11.25%) and FH-Lalazar × Silky-3 (7.59%) indicated significantly positive better-parent heterosis in favor of boll retention (Tables 6 and 7).

Table 6 Calculation of specific combining ability (SCA) and heterosis (Better-parent) in different promising crosses for each trait under control condition

Traits	Crosses	SCA	Crosses	Heterosis (Better-parent)
RCI	FH-466 × CIM-602	-15.20	FH-Lalazar × FH-326	-49.36
	FH-Lalazar × FH-442	-8.03	NIAB-545 × FH-326	-47.03
CC	IR-NIBGE-8 × Silky-3	6.45	-	-
	-	-	-	-
CT	FH-Noor × SLH-12	-1.86	FH-Lalazar × FH-326	-16.56
	FH-Lalazar × Silky-3	-1.79	FH-458 × FH-326	-14.08
BR	FH-Noor × FH-442	11.60	FH-Lalazar × FH-326	14.07
	FH-458 × CIM-602	6.10	FH-Lalazar × Silky-3	8.32
B/P	Weal-AG-Shakar × SLH-12	9.67	IR-NIBGE-8 × FH-326	26.92
	NIAB-878 × Silky-3	8.18	NIAB-878 × Silky-3	21.51
BW	NIAB-878 × FH-326	0.51	NIAB-878 × FH-326	14.55
	FH-466 × FH442	0.42	FH-466 × FH442	11.13
SI	FH-Noor × FH-442	0.90	NIAB-878 × FH-326	16.43
	NIAB-878 × FH-326	0.74	FH-458 × FH-326	11.57
SB	IR-NIBGE-8 × SLH-12	4.58	IR-NIBGE-8 × SLH-12	22.23
	FH-Lalazar × SLH-12	4.09	IR-NIBGE-8 × CIM-602	13.46
PH	FH-Noor × FH-326	18.89	Weal-AG-Shahkar × CIM-602	22.97
	FH-Noor × FH-442	13.31	FH-Lalazar × CIM-602	6.12
SCY	Weal-AG-Shahkar × SLH-12	21.90	NIAB-878 × Silky-3	18.42
	NIAB-878 × Silky-3	18.87	NIAB-878 × FH-326	5.58

Note: *RCI* Relative cell injury, *CC* Chlorophyll contents, *CT* Canopy temperature, *BR* Boll retention, *B/P* Bolls per plant, *BW* Boll weight, *SB* Sympodial branches per plant, *SI* Seed index, *PH* Plant height, *SCY* Seed cotton yield/plant

GCA, SCA effects, and heterosis for bolls per plant

The number of bolls per plant is an important yield component, which may be improved through positive general and specific combining abilities effects. Among females the genotypes, i.e., FH-Noor (1.02), FH-Lalazar (3.09), Weal-AG-Shahkar (0.96), and NIAB-878 (2.49), as well as the male parents including FH-326 (3.65) and CIM-602 (2.98) showed significantly positive GCA effects under control condition. Under high temperature stress the female genotypes, namely FH-Noor (3.28), FH-Lalazar (4.95) and NIAB-545 (1.62) indicated GCA significantly positive effects. The male parents, viz., FH-326 (4.47) and CIM-602 (1.55) displayed significantly positive GCA effects under high temperature stress (Table 5). The crosses, namely Weal-AG-Shakar × SLH-12 (9.67) and NIAB-878 × Silky-3 (8.18) were found desirable based on significantly positive SCA effects under control condition. Under high temperature stress, the best crosses, i.e., Weal-AG-Shakar × SLH-12 (17.71) and NIAB-878 × Silky-3 (13.43) displayed significantly positive SCA effects for improving bolls per plant (Tables 6 and 7). The crosses including IR-NIBGE-8 × FH-326 (26.92%) and NIAB-878 × Silky-3 (21.51%) displayed significantly positive better-parent heterosis under control condition. The crosses including FH-Lalazar × Silky-3 (55.56%) and FH-Lalazar × FH-326 (50.00%) showed significantly positive better-parent heterosis under high temperature stress condition in favor of bolls per plant (Tables 6 and 7).

GCA, SCA effects, and heterosis for boll weight

Significantly positive GCA & SCA effects may contribute towards higher boll weight. Among female parents under control condition the genotypes, i.e., FH-Lalazar (0.31), Weal-AG-Shahakar (0.08), NIAB-454 (0.08) and a male parent FH-326 (0.31) displayed significantly positive GCA effects. Under high temperature stress condition female parents, viz., FH-Lalazar (0.34) and FH-Noor (0.06), whereas male parent FH-326 (0.36) indicated significantly positive GCA effects for boll weight (Table 5). The best crosses under control condition included NIAB-878 × FH-326 (0.51) and FH-466 × FH-442 (0.42) followed significantly positive SCA effects. Similarly, under high temperate stress also included these crosses, i.e., NIAB-878 × FH-326 (0.46) and FH-466 × FH-442 (0.36) for improving boll weight (Tables 6 and 7). Under control condition the crosses, namely NIAB-878 × FH-326 (14.55%) and FH-466 × FH-442 (11.13%) indicated significantly positive better-parent heterosis. Under high temperature stress the crosses, i.e., NIAB-878 × FH-326

Table 7 Calculation of specific combining ability (SCA) and heterosis (Better-parent) in different promising crosses for each trait under high temperature stress condition

Traits	Crosses	SCA	Crosses	Heterosis (Better-parent)
RCI	FH-466 × CIM-602	-17.10	NIAB-545 × FH-326	-46.74
	NIAB-878 × CIM-602	-9.36	FH-Lalazar × Silky-3	-46.34
CC	NIAB-545 × FH-442	7.33	-	-
	NIAB-878 × SLH-12	6.25	-	-
CT	FH-466 × FH-442	-2.18	NIAB-878 × Silky-3	-14.39
	FH-Lalazar × FH-326	-2.14	FH-Lalazar × FH-326	-12.61
BR	FH-Noor × FH-442	12.95	FH-Lalazar × FH-326	11.25
	FH-458 × CIM-602	6.20	FH-Lalazar × Silky-3	7.59
B/P	Weal-AG-Shakar × SLH-12	17.71	FH-Lalazar × Silky-3	55.56
	NIAB-878 × Silky-3	13.43	FH-Lalazar × FH-326	50.00
BW	NIAB-878 × FH-326	0.46	NIAB-878 × FH-326	12.75
	FH-466 × FH-442	0.36	NIAB-545 × FH-326	9.91
SI	FH-Noor × SLH-12	0.78	NIAB-545 × FH-326	8.17
	FH-458 × FH-442	0.72	NIAB-878 × FH-326	7.14
SB	Weal-AG-Shakar × SLH-12	8.07	Weal-AG-Shahakar × SLH-12	40.68
	NIAB-878 × Silky-3	5.88	FH-Noor × FH-326	14.81
PH	Weal-AG-Shahkar × SLH-12	32.44	FH-458 × Silky-3	9.55
	FH-Noor × CIM-602	30.11	-	-
SCY	Weal-AG-Shahkar × SLH-12	21.90	NIAB-878 × Silky-3	31.90
	NIAB-878 × Silky-3	18.87	NIAB-878 × FH-326	8.44

Note: *RCI* Relative cell injury, *CC* Chlorophyll contents, *CT* Canopy temperature, *BR* Boll retention, *B/P* Bolls per plant, *BW* Boll weight, *SB* Sympodial branches per plant, *SI* Seed index, *PH* Plant height, *SCY* Seed cotton yield/plant

(12.75%), and NIAB-545 × FH-326 (9.91%) revealed significantly positive better-parent heterosis for boll weight (Tables 6 and 7).

GCA, SCA effects, and heterosis for sympodial branches per plant

Sympodial branches per plant required higher in numbers which could be improved through positive GCA and SCA effects. Under control condition, the female parents, viz., NIAB-545 (1.12) and IR-NIBGE-8 (1.29), and the male parents, viz., CIM-602 (1.19) and FH-442 (1.41) showed highly significantly positive GCA effects. Under high temperature stress the female parent, i.e., Weal-AG-Shahkar (2.59), and male parent FH-326 (1.02) depicted significantly positive GCA effects regarding sympodial branches per plant (Table 5). The SCA among crosses, viz., FH-Lalazar × SLH-12 (4.09), and IR-NIBGE-8 × SLH-12 (4.58) revealed better performance because of significantly positive effects. Similarly, under high temperature stress the crosses, viz., Weal-AG-Shahakar × SLH-12 (8.07) and NIAB-878 × Silky-3 (5.88) displayed significantly positive SCA effects through which the number of sympodial branches may be increased (Tables 6 and 7). Significantly positive better-parent heterosis determined by the crosses, viz., IR-NIBGE-8 × SLH-12 (22.23%) and IR-NIBGE-8 × CIM-602 (13.46%) under control condition. The crosses including Weal-AG-Shahkar × SLH-12 (40.68%) and FH-Noor × FH-326 (14.81%) showed significantly positive better-parent heterosis under high temperature stress regarding sympodial branches per plant (Tables 6 and 7).

GCA, SCA effects, and heterosis for Seed Index

Under control significantly positive GCA effects were indicated by female parents, viz., FH-Lalazar (0.93), NIAB-545 (0.27), and NIAB-878 (0.38). Whereas, male parents, namely FH-326 (0.71) and Silky-3 (0.31) showed significantly positive GCA effects. Under high temperature stress female parents including FH-Lalazar (0.73), NIAB-545 (0.62), IR-NIBGE-8 (0.17) and NIAB-878 (0.61) showed significantly positive GCA effects. The male parents, viz., FH-326 (0.7) and Silky-3 (0.2) indicated significantly positive GCA effects regarding seed index (Table 5). Under control some crosses, viz., FH-Noor × FH-442 (0.90) and NIAB-878 × FH-326 (0.74) were predicting significantly positive SCA effects. Under high temperature stress the crosses including FH-Noor × SLH-12 (0.78) and FH-458 × FH-442 (0.72) indicated significantly positive SCA effects for seed index (Tables 6 and 7). For better-parent heterosis the significantly positive results were displayed by the crosses, viz., NIAB-878 × FH-326 (16.43%) and FH-458 × FH-326 (11.57%). The crosses including NIAB-545 × FH-326 (8.12%) and NIAB-878 × FH-326 (7.14%) determined significantly positive better-parent heterosis under temperature stress in favor of seed index (Tables 6 and 7).

GCA, SCA effects, and heterosis for plant height

For plant height the female parents, namely FH-Lalazar (2.22), Weal-AG-Shahakar (12.13) and NIAB-878 (2.93) depicted significantly positive GCA effects. The male parents, viz., FH-326 (2.64) and SLH-12 (2.32) revealed significantly positive GCA effects under control condition. Under high temperature stress, GCA effects were found significantly positive among females, viz., FH-458 (5.16), Weal-AG-Shahkar (7.86), NIAB-545 (17.6), and NIAB-878 (2.13). The male parents, viz., FH-326 (7.28) and Silky-3 (7.78) indicated significantly positive GCA effects for plant height (Table 5). Under control positive significant SCA effects were observed amongst the crosses, viz., FH-Noor × FH-326 (18.89), FH-Noor × FH-442 (13.31). Under high temperature stress, the crosses, viz., Weal-AG-Shahkar × SLH-12 (32.44), and FH-Noor × CIM-602 (30.11) described significantly positive SCA effects regarding plant height (Tables 6 and 7). Under control condition crosses, viz., Weal-AG-Shahkar × CIM-602 (22.97%) and FH-Lalazar × CIM-602 (6.12%) revealed significantly positive better-parent heterosis. Under high temperature stress condition the cross FH-458 × Silky-3 (9.55%) displayed significantly positive better-parent heterosis (Tables 6 and 7).

GCA, SCA effects, and heterosis for seed cotton yield per plant

Significantly positive general and specific combining abilities (GCA & SCA) effects are important regarding improvement in seed cotton yield. Under control condition the female parents, viz., Weal-AG-Shahkar (12.62), NIAB-878 (8.01), and male parents including FH-326 (6.37) and CIM-602 (1.35) indicated significantly positive GCA effects. Under high temperature stress the female parents, namely Weal-AG-Shahkar (30.62), NIAB-545 (6.34), and a male parent FH-326 (7.01) revealed significantly positive GCA effects for improving seed cotton yield (Table 5). Under control condition, SCA were observed in some promising crosses, viz., Weal-AG-Shahkar × SLH-12 (21.90) and NIAB-878 × Silky-3 (18.87) which showed significantly positive SCA effects. Under high temperature stress, among elite crosses, viz., Weal-AG-Shahkar × SLH-12 (21.90) and NIAB-878 × Silky-3 (18.87) indicated highly significantly positive SCA effects with improved seed cotton yield per plant (Tables 6 and 7). The crosses including NIAB-878 × Silky-3 (18.42%), NIAB-878 × FH-326 (5.58%) revealed significantly positive better-parent heterosis under control condition. The crosses, viz., NIAB-878 × Silky-3 (31.90%) and NIAB-878 × FH-326 (8.44%) depicted significantly positive better-parent heterosis for seed cotton yield under high temperature stress condition (Tables 6 and 7).

Discussion

High temperature stress mostly affected seedling, flowering, which may cause irreversible damage to seed cotton yield and yield related traits (Wahid et al. 2007; Lokhande and Reddy 2014; Kaushal et al. 2016). Screening approaches of different sowing times have been carried out under field conditions to study the effects of temperature on cotton crop (Zhao et al. 2012; Saleem et al. 2014; Ban et al. 2015; Mahdy et al. 2017). Cotton researchers preferred early screening of cotton genotypes at peak flowering stages based on relative cell injury (Rahman et al. 2004; Khan et al. 2008), chlorophyll contents (Bibi et al. 2008; Hejnak et al. 2015), canopy temperature (Khan et al. 2014; Purushothaman and Krishnamurthy 2014). Delayed screening approaches may include agronomic traits, i.e., boll retention, seed cotton yield, and other yield related traits (Cottee et al. 2010; Lokhande and Reddy 2014; Ban et al. 2015; Ullah et al. 2016; Singh et al. 2018). Therefore, treatment of high temperature stress in August was synchronized at peak flowering stage under the April-sowing. Similarly, control temperature was synchronized at peak flowering stage in October under the June-sowing. The analysis of variance during screening of 50 genotypes revealed the significant difference among genotypes, treatments, genotypes × treatments interaction for the traits including relative cell injury, canopy temperature, chlorophyll contents, boll retention, and seed cotton yield.

The degree of temperature sensitivity and tolerance among genotypes was assessed through heat susceptibility index (HSI) as described by Fischer and Maurer (1978). The estimates of HSI demonstrated variability in cotton genotypes and categorized them into heat tolerant and heat sensitive. Based on the least HSI values (HSI $\leq$ 0.50) eight genotypes including FH-Noor, NIAB-545, FH-Lalazar, FH-458, NIAB-878, FH-466, IR-NIBGE-8, and Weal-AG-Shahkar were selected as highly heat tolerant, while the heat sensitive genotypes, viz., CIM-602, Silky-3, FH-326, SLH-12, and FH-442 were selected due to high HSI values $\geq$ 1.00 (Fig. 1). Similarly, some cotton scientists also used HTI (heat tolerant index) as synonymous of HSI as the selection criteria (Rahman 2006; Pakniyat 2010; Abro et al. 2015). The cluster analysis distinguished the variability of 50 genotypes in different clusters. Heat tolerant and sensitive genotypes were found in separate clusters from which the extreme variants were selected as female and male parents (Figs. 2 and 3). Based on genotypic variability among 50 genotypes the cross combinations were developed among selected heat tolerant and heat sensitive parents following line × tester scheme (Kempthorne (1957)). Different F_1 hybrids presented wide range of results for gene action, combining abilities, and heterosis for studied traits against high temperature stress. Mean square values under line × tester analysis revealed significant genetic variability among genotypes, crosses, lines, testers, L × T, parents, and cross vs parent for the traits, viz., relative cell injury, chlorophyll contents, canopy temperature, boll retention, bolls per plant, sympodial branches, seed index, plant height, and seed cotton, whilst boll weight remained non-significant (Table 3).

The type of gene action was estimated through the values of SCA variances and dominance variances for all traits. The higher values of SCA variance along with dominance variance indicated preponderance of non-additive/dominant type of gene action for all traits as it was earlier reported upon by Ahuja and Dhayal (2007), Khan et al. (2009), and Bankar et al. (2020). The non-additive gene action following heterosis may be used for improving relative cell injury and chlorophyll contents, whilst the presence of additive gene action for such traits were proposed by Jamil et al. (2020). Contrary to present study, the relative cell injury being controlled by additive genes may be used as a selection criterion for developing heat tolerant cultivars (Shakeel et al. 2001; Rahman 2006; Salman et al. 2019). Non-additive gene action may be utilized for improving the boll retention against high temperature stress through heterosis breeding program (Sawan 2014; Tariq et al. 2017; Singh et al. 2018). For canopy temperature, genotypic differences and non-additive gene action under high temperature stress may be improved through heterosis breeding as described by Mohammadi et al. (2012), Purushothaman and Krishnamurthy (2014), and Khan et al. (2014). Khokhar et al. (2018) and Yehia et al. (2023) endorsed this study regarding non-additive gene action for the traits, viz., plant height, monopodial branches, sympodial branches, bolls per plant, boll weight, and seed cotton yield. The study of different populations revealed that seed cotton yield and yield components being the complex characters may be controlled equally by additive (fixable) or dominance/epistatic (non-fixable) genes (Bibi et al. 2011).

Combining ability (GCA & SCA) estimates were utilized to find out the potential of parents and their combinations for improving the desired traits (Memon et al. 2014; Chaudhary et al. 2019). The good general combiner parents may not always produce good specific combinations for all traits. Higher estimates of GCA and SCA towards negative direction were claimed for improving relative cell injury. GCA effects for relative cell injury were showed by female parents, i.e., FH-Lalazar, NIAB-545, and FH-Noor, and male parents included SLH-12, Silky-3, and FH-326. SCA effects of crosses, viz., FH-Lalazar × FH-442, FH-466 × CIM-602, and NIAB-878 × CIM-602 depicted significantly negative effects under both treatments. Therefore, the involved GCA parents may be combined as high × high, high × low or low × low to determined high SCA combinations (Yehia et al. 2023). For canopy temperature female parents, i.e., NIAB-545 and Weal-AG-Shahkar were found good for GCA effects. While, among crosses the most desirable included FH-Lalazar × FH-326 and FH-466 × FH-442, which showed negative and significant SCA effects for improving canopy temperature under high temperature stress. These results revealed that good specific combinations may be the product of poor × poor, combiners (Bankar et al. 2020). Chlorophyll contents displayed significantly positive GCA effects, which indicated by a female parent, i.e., FH-458 and a male parent, i.e., CIM-602 under high temperature stress. Significantly positive SCA effects for chlorophyll contents shown by crosses, viz., NIAB-545 × FH-442 and NIAB-878 × SLH-12 performed well under high temperature. Similarly, Karademir et al. (2016) also stated that higher GCA and SCA may be involved for improving chlorophyll contents under temperature stress. GCA effects regarding boll retention, bolls per plant, and boll weight revealed significantly positive by the female parents, viz., FH-Noor and FH-Lalazar along with a male parent, i.e., FH-326 (Table 5). Higher SCA effects desirable for improving boll retention, which displayed by crosses, namely FH-Noor × FH-442 and FH-Lalazar × CIM-602. For bolls per plant significantly positive SCA effects were shown by the crosses including Weal-AG-Shakar × SLH-12 and NIAB-878 × Silky-3. Under high temperature stress boll weight revealed significantly positive SCA effects in crosses, viz., NIAB-878 × FH-326 and FH-466 × FH-442. Therefore, a combination of good and poor general combiner may perform better as described by Bankar et al. (2020). For sympodial branches under high temperature stress conditions the best female parent was Weal-AG-Shahkar which had positive GCA effects, whereas among male parents, FH-326 indicated significantly positive GCA effects. SCA effects for sympodial branches per plant involving one of the best general combiner parents were showing better performance in the crosses, i.e., Weal-AG-Shahakar × SLH-12 and NIAB-878 × Silky-3. Under high temperature stress the female parents, namely Weal-AG-Shahkar (30.62), NIAB-545

(6.34), and male parent FH-326 (7.01) revealed the best significantly positive GCA effects for seed cotton yield (Table 5). For seed index among the desired general combiners the best female parents, i.e., FH-Lalazar, NIAB-545, and NIAB-878 showed positive GCA effects along with male parents, viz., FH-326 and Silky-3. Whereas the best SCA effects for seed index showed by crosses, namely FH-Noor × SLH-12 and FH-458 × FH-442 as product of poor × poor. Under high temperature stress the good GCA effects for plant height showed by female parents, viz., FH-458, Weal-AG-Shahkar, NIAB-545, NIAB-878 and the males FH-326 and Silky-3. Under high temperature stress the SCA effects for plant height were significantly positive showed by crosses, viz., Weal-AG-Shahkar × SLH-12 and FH-Noor × CIM-602 as combinations of good × poor and poor × poor, respectively (Table 7).

Under high temperature stress the female parents, namely Weal-AG-Shahkar and NIAB-545, and the male parent FH-326 revealed the best significantly positive GCA effects regarding seed cotton yield (Table 5). The best crosses Weal-AG-Shahkar × SLH-12 and NIAB-878 × Silky-3 were found best for seed cotton yield following significantly positive SCA effects under high temperature stress (Table 7). High yielding crosses always possessed higher SCA effects and contribute higher performance for most of the yield related traits (Yehia et al. 2023). Similarly, significantly positive GCA/SCA effects of parents and crosses could be used for improving seed cotton yield and other yield related components against temperature stress (Koebernick et al. 2019; Udaya and Patil 2020). It was earlier suggested by Ali et al. (2016) and Kaleem et al. (2016) that based on higher SCA effects along with non-additive gene action, such traits may be improved through developing different hybrid combinations. Whereas higher GCA variance indicated additive gene action, which described that improvement may be possible through simple selection process (Memon et al. 2014; Chaudhary et al. 2019).

Heterosis breeding may be used to develop hybrids for different morpho-physiological traits against high temperature stress (Zeng et al. 2012). Significant and positive better-parent heterosis was considered for all traits except relative cell injury, and canopy temperature. Under high temperature stress significantly negative better-parent heterosis regarding relative cell injury found in crosses, namely NIAB-545 × FH-326, and FH-Lalazar × Silky-3. The desired negative heterotic effects among hybrids for improving relative cell injury were reported by Abro et al. (2022). Canopy temperature improvement was claimed through significantly negative better-parent heterosis, which observed in crosses including NIAB-878 × Silky-3, FH-Lalazar × FH-326. Boll retention percentage could be improved through significantly positive better-parent heterosis that found among crosses, namely FH-Lalazar × FH-326 and FH-Lalazar × Silky-3. Significantly positive better-parent heterosis was desirable regarding different seed cotton yield and yield attributes under high temperature stress conditions. Seed cotton yield and yield attributes including boll weight and seed index may be improved together for better-parent heterosis using cross combinations, viz., NIAB-545 × FH-326 and NIAB-878 × FH-326. Similarly, positive heterotic effects for seed cotton yield, boll weight, and yield related traits were suggested earlier by Solongi et al. (2019). Bolls per plant revealed higher better-parent heterosis in crosses, viz., FH-Lalazar × Silky-3 and FH-Lalazar × FH-326, while sympodial branches per plant could be improved using crosses, viz., Weal-AG-Shahakar × SLH-12 and FH-Noor × FH-326. Under high temperature stress, significantly positive better-parent heterosis was showed by a cross FH-458 × Silky-3, which could be used for increasing plant height. Based on maximum significantly positive better-parent heterosis, the best crosses were suggested for improving seed cotton yield under heat stress (Abro et al. 2022). Similarly, seed cotton yield could be improved by selecting the crosses, viz., NIAB-878 × Silky-3 and NIAB-878 × FH-326. Therefore, better-parent heterosis for seed cotton yield, plant height, sympodial branches per plant, bolls per plant, and boll weight may be exploited to develop commercial cultivars as earlier suggested by Campbell et al. (2008) and Vavdiya et al. (2019).

Conclusion

Cotton crop during peak summer season usually expose to high temperature at peak flowering stage. The genetic variability in local germplasm was bifurcated into heat tolerant and heat sensitive genotypes based on heat susceptibility index. Therefore, genetic study following hybridization (heat tolerant × heat sensitive) showed higher specific combining ability and better-parent heterosis. The crosses including FH-Lalazar × Silky-3, FH-Lalazar × FH-326, NIAB-878 × Silky-3, and NIAB-878 × FH-326 revealed improvement for seed cotton yield and yield components under high temperature stress. Moreover, higher SCA variance for all traits revealed non-additive type of gene action. Therefore, heterosis breeding technique may be exploited for improving all such traits to develop heat tolerant genetic materials like cultivars, and hybrids.

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Authors' contributions

Farooq A, performed experiments, analyzed data, and wrote the manuscript. Shakeel A, assisted in planning of experiments. Saeed A, did grammar editing and proofread of manuscript. Farooq J, provided the cotton germplasm. Chattha WS, assisted for data analysis. Rizwan M, assisted during hybridizing and data collection. Sarwar G, provided the experiment place at his station. Ramzan Y, managed the crop husbandry. The author(s) read and approved the final manuscript.

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Availability of data and materials

All data generated or analyzed during this study are included in this published article and its additional files.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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