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Genetic Analysis of Some Spring Wheat Genotypes for Terminal Heat Stress Tolerance

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DIALLEL analysis is a mating design used in quantitative genetics to find superior genotypes for hybridization and selection programmes. This competition evaluated 15 F_1 hybrids and their six parental lines for a range of morphological and physiological traits, including days to 50% heading, days to 75% maturity, plant height (cm), grains per spike, grain yield per plant (g), grain filling duration, cell membrane thermostability (%), leaf area (cm²), SPAD chlorophyll content, and relative water content (%). At the Botanical Garden of Sindh Agriculture University Tandojam, the experiment was conducted using a factorial design with two sowing regimes: an ideal sowing date and a late sowing date. Under both normal and late sowing conditions, the variances for general combining ability (GCA) and specific combining ability (SCA) were found to be significant for nearly all the traits under study. This suggests that both additive and non-additive gene actions were supporting the traits under investigation. Three parents like TD-1, Benazir, Kiran-95 and TJ-83 were found exceptionally high general combiners by manifesting higher GCA estimates for yield and physiological characters studied; therefore such parents are expected to prove excellent in the improvement of bread wheat, specifically with regard to heat stress environments. Concerning SCA effects, the F_1 hybrids such as TD-1×Kiran-95, NIA-Sarang × TJ-83, Benazir × AS-2002 under heat stress circumstances, AS-2002, TD-1 × Kiran-95, NIA-Sarang × Benazir, and TJ-83 × AS-2002 shown rewarding SCA effects for the characteristics under study; as a result, they could be chosen for use in next wheat breeding programs.

Keywords: Combining ability; heat stress; wheat genotypes.

Introduction

A vital staple crop, wheat (*Triticum aestivum* L.) provides a significant portion of the world's calories and protein (Mishra et al., 2021). Because of its large area, excellent productivity, and leading position in the food grain trade, it is referred to as the "King of Cereals." Being among the earliest grain crops to be domesticated, it has long been regarded as a basic staple meal in many European, Asian, and African civilizations. With 60–68% carbs, 6-21% proteins, 1.5–2% fats, 2-2.5% cellulose, and 1.8% minerals, it is a remarkable boon and a singular gift from nature to humanity (Das, 2008; Fu et al., 2023). Increasing wheat output is essential to feeding the world's growing population. From 9,168 thousand hectares in 2020–21 to 8,976 thousand hectares in 2021–22, Pakistan's wheat-sown area decreased by 2.1 percent. Consequently, wheat production fell from 27.464 million tonnes to 26.394 million tonnes, a 3.9 percent decrease. Reduced planting area, scarce irrigation water, dry sowing conditions, less fertilizer application, and a heat wave in March and April were some of the factors that led to this drop (PBS 2021–22). The wheat growth season is severely impacted by high temperature stress, especially during the final heat stress of grain filling. A major factor in the decrease in single seed weight and, consequently, the reduction in grain production in wheat (*Triticum aestivum* L.) worldwide is terminal high-temperature stress during the grain-filling stage. Developing resistant cultivars through conventional breeding, which entails finding tolerant lines and introducing these qualities into commercial varieties, is one efficient way to counteract the negative impacts of

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high temperatures (Fu et al., 2023). According to Giraldo et al. (2019), the demand for wheat would increase by 60% from 2010 levels by 2050, when the world's population is predicted to surpass 9 billion. The yearly worldwide yield growth must quicken from 1% (2001–2010) to 1.6% (2011–2050) in order to satisfy this higher demand. Seven nations currently produce 79% of the world's wheat, producing around 751 million tonnes annually: China, the United States, Turkey, Canada, Australia, India, and Argentina (FAOSTAT, 2018). However, current estimates of wheat yield gains range from 0.5% to 1% annually, a far less range than the 2.4% growth required for satisfying global demand (Crespo-Herrera et al., 2018). China is the largest producer of wheat with 17.6% share in the world production and is planted on about 222 million hectares. It is also a major food grain of Pakistan and per capita utilization is around 124 kg per year. In Pakistan, terminal heat stress / drought stress is a major cause of yield decrease in bread wheat and other crops (Jatoi et al., 2024). It is grown in practically every region of the country, with 70% of the irrigated land and 30% rain-fed (Hossain et al., 2018). Temperature is the main restraining aspect that influences yield production of wheat especially during the grain filling period. Heat tolerance is a complex phenomenon, thus it is very hard to make a reliable assessment about it. High temperature stress is a chief ecological constraint hampering productivity of hexaploid wheat in most parts of the globe. Al-Khatib & Paulsen (1989) suggested that the ideal heat for all physio-chemical processes of wheat from vegetative to reproductive stages is 20^{o}C or below. Wheat crops grow best at temperatures ranging from 15 to 25^{0} degrees Celsius, but it can also grow at temperatures ranging from 3 to 4 degrees Celsius or 30 to 32^{0} degrees Celsius (Rind et al., 2023). Information on wheat genotypes' general and specific combining abilities is required to initiate a successful wheat breeding strategy (Fasahat et al., 2016; Parveen et al., 2023). Wheat researchers place a high priority on studying the genetic makeup, the tendency of combining ability, and plant behaviour under high temperatures in order to increase wheat output. Knowledge of GCA, SCA, and the gene activation in available breeding material, is critical for launching an efficient wheat breeding programme. The evaluation of SCA impacts on grain production and its component qualities is critical for selecting prospective parents in order to evolve high yielding hybrids. Most of Wheat breeders around the world are continuously working to develop wheat cultivars with a suitable tolerance to heat stress. Joshi et al. (2003) assessed wheat combining ability using 10 different parental lines and 45 F_1s and F_2s and found substantial differences among parental GCA and crosses SCA for all the variables observed. For all characteristics, the SCA and GCA components of variance were found significant. In contrast, the GCA was prominent, showing the frequency of additive genes for the parameters tested. Some parents were observed to be best combiner for seed yield while, moderate to other essential characters. Thus, present investigation is aimed to identify the best combiners for the traits like yield and physiological traits.

Materials and Methods

The 15 F_1 hybrids (Table 1a) developed from half diallel mating design with 6 parental lines were grown under two treatments i.e. non-stress (normal sowing on 15th November at normal temperatures and no heat stress) and heat stress (late sowing on 15th December at high temperatures) in natural field conditions so as to collect the data for genetic analysis. The factorial RCBD was trailed in the experiment with four replications. A total of 21 genotypes including six parents and 15 F_1 hybrids were grown to estimate combining ability. Every suggested agricultural technique was used to ensure robust crop development. General combining ability (GCA) and specific combining ability (SCA) differences between physiological and yield characteristics were determined by analyzing the data. Variances were analyzed in compliance with Gomez & Gomez (1984). The Griffing's numerical technique (1956) was used to determine combining ability by genetic analysis of parents and F_1 hybrids for days to 50 percent heading, days to 75 percent maturity, plant height (cm), grains spike^{-1}, grain yield plant^{-1} (g), grain filling duration, cell membrane thermostability (CMT %), leaf area (cm^2), SPAD Chlorophyll content and relative water content in leaf (RWC %).

TABLE 1a. Crossing pattern of F_1 hybrids obtained through half diallel crossing fashion.

Females/males	NIA-Sarang	Kiran-95	Benazir	TJ-83	AS-2002
TD-1	TD-1 × NIA-Sarang	TD-1 × Kiran-95	TD-1 × Benazir	TD-1 × T.J-83	TD-1 × AS-2002
NIA-Sarang	-	NIA-Sarang × Kiran-95	NIA-Sarang × Benazir	NIA-Sarang × TJ-83	NIA-Sarang × AS-2002
Kiran-95		-	Kiran -95 × Benazir	Kiran -95 × TJ-83	Kiran -95 × AS-2002
Benazir			-	Benazir × TJ-83	Benazir × AS-2002
TJ-83				-	TJ-83 × AS-2002
AS-2002					-

Result

Days to 50% heading

Regarding days to 50% heading under optimum sowing conditions, Benazir and Kiran-95 recorded upmost and lowermost positive GCA effects of 0.74 and 0.08, correspondingly (Table 2), similarly parent NIA-Sarang (-0.39) and TJ-83 (-0.23) exposed negative but desirable GCA effects. However, in high temperature environment, the parents AS-2002 (0.44) and TD-1 (0.13) demonstrated the highest and lowest positive yet undesirable GCA effects respectively. While under the same conditions, the parents AS-2002 (0.44) and TD-1 (0.13) displayed the largest and lowest positive yet undesired GCA effects, respectively. NIA-Sarang (-0.50) had shown most desirable GCA effects, while Kiran-95 (-0.09) revealed least negative but rewarding GCA effects. The cross TD-1 x Kiran-95 (0.20) produced the least beneficial SCA effects. The cross Benazir x AS-2002 (-1.02) revealed the most desirable negative SCA effects, whereas the cross Kiran-95 x Benazir (-0.05) revealed the least ideal negative SCA effects. Under heat stress planting, six F_1 hybrids showed adverse progressive SCA effects, while the other nine F_1 hybrids showed desired negative SCA effects. However, in delayed sowing (Fig. 1), the crosses TJ-83 x AS-2002 (3.69) and TD-1 x Kiran-95 (0.47) showed the less beneficial SCA effects. The highest negative effects were exhibited Benazir x AS-2002 (-1.34) and TD-1 x AS-2002 (-1.31), whereas the crosses Kiran-95 x Benazir (-0.06) and Benazir x TJ-83 (-0.28) demonstrated the minimum negative SCA effects.

Days to 75% maturity

Benazir and TD-1 revealed the most unfavorable positive GCA impacts of 0.67 and 0.60 for 75% maturity in normal as well as stress conditions respectively (Table 2). AS-2002 established the highest negative yet desirable GCA effects of -0.52, while TD-1 observed the minimum negative GCA impacts of -0.14 under optimal sowing conditions. In late sowing conditions, the parent TJ-83 expressed the most negative GCA effects (-0.45), while the parent NIA-Sarang showed the least negative GCA effects (-0.09). In non-stressed planting, the cross TJ-83 x AS-2002 (2.10) recorded the greater but unfavorable positive SCA effects, followed by the crosses TD-1 x Benazir (1.04) and TD-1 x AS-2002 (0.81), and Kian-95 x Benazir (0.17). Under heat stress circumstances, 6 F_1 hybrids exhibited non-beneficial positive SCA effects. The highest beneficial negative SCA effects in non-stressed conditions were revealed by the cross NIA-Sarang x Benazir (-1.27), while the minimum value of rewarding negative SCA effects (-0.20) was represented by the cross TD-1 x NIA-Sarang. In stressed situations, the cross NIA-Sarang x Kiran-95 (1.23) demonstrated the greatest positive but undesirable SCA effects (Fig. 2), whereas the cross NIA-Sarang x Benazir (0.04) had the least positive SCA effects. Under the same delayed sowing, the cross Kiran-95 x TJ-83 revealed the highest desired negative SCA effects (-0.96), while the cross Benazir x TJ-83 expressed the least (-0.05) SCA impacts.

Plant height

The parent Kiran-95 manifested highest undesirable positive GCA effects in normal (3.86) as well as in heat environment (2.33), nevertheless the parents AS-2002 (0.37) and Benazir (0.30) exhibited (Table 2) the minimum yet beneficial positive GCA effects for plant height. However, the parent TD-1 expressed the maximum negative yet beneficial GCA effects of -3.53 in normal sowing and -3.00 in late sowing growing timings, respectively, whereas minimum yet desirable negative GCA effects was recorded by Benazir (-0.84) and TJ-83 (-0.14) under both sowing seasons. Under heat stress circumstances, 8 F_1 hybrids revealed desired positive SCA effects, though the further 7 F_1 hybrids revealed desirable negative SCA effects. Concerning consequences of SCA effects under normal growing season, TD-1 x Kiran-95 showed the highest positive but non-beneficial SCA effects (5.24). The cross Kiran-95 x TJ-83 presented the maximum negative SCA effects (-3.80), however TJ-83 x AS-2002 accomplished the minimum negative SCA effects (-0.30). About SCA effects under heat stress conditions, the hybrids NIA-Sarang x Benazir, Kiran-95 x TJ-83 and NIA-Sarang x TJ-83 exhibited the minimum positive SCA effects and displaying the effects as 0.10, 0.43 and 0.55, respectively. The hybrid TD-1 x AS-2002 found the most ideal negative SCA effects of -2.39 (Fig. 3), whereas TJ-83 x AS-2002 revealed the least desirable negative SCA effects of -0.02.

Grains spike^{-1}

Concerning GCA effects for grains spike^{-1}, the parent TD-1 performed better than rest of the parents by manifesting higher positive GCA effects under optimum (3.09) and stress environment (1.81), whereas the parent Kiran-95 expressed the minimum desirable GCA effects in normal non-stress (1.19) and in heat stress conditions (1.25) (Table 3). The greater as well as less negative GCA effects were demonstrated by Benazir (-1.34) then TJ-83 (-0.38). While Benazir and TJ-83 (-1.57) also showed at par GCA effects (Table 3), AS-2002 showed the least negative GCA impacts (-1.22). The prime positive SCA effects under normal environment were reported in NIA-Sarang x Benazir and NIA-Sarang x AS-2002, while lowest positive SCA effects were identified in TD-1 x TJ-83 (0.43). Moreover hybrids TD-1 x Kiran-95 and Benazir x TJ-83 manifested the most unfavourable SCA effects, with -2.13 and -0.69, respectively. Under heat stress conditions, 11 hybrids exposed the positive SCA effects whilst other 4 hybrids exhibited the negative SCA effects. Three hybrids such as NIA-Sarang x Benazir (8.85), Benazir x AS-2002 (3.79) and NIA-Sarang x TJ-83 (2.88) presented the maximum desirable positive SCA effects. However, under late planting heat stress circumstances, Kiran-95 x AS-2002 (1.01) disclosed the lowest beneficial SCA effects. Under heat stress (Fig. 4), TD-1 x NIA-Sarang (-7.33) and Kiran-95 x Benazir (-1.52) showed the greatest negative SCA effects.

Grain yield plant^{-1}

The parent TD-1 revealed the strongest positive GCA effects in both normal (0.44) and heat stress (0.52) circumstances, whereas the parent Kiran-95 showed less positive GCA effects in both normal (0.06) and heat stress (0.23) settings. The parents NIA-Sarang and Benazir both expressed the similar GCA value (-0.28) yet gave maximum negative GCA effects in normal sowing. The highest negative GCA effects under late sowing heat stress conditions were also demonstrated by the same parent NIA-Sarang (-0.53). The parent AS-2002 displayed (Table 3) the lowest negative GCA effects of -0.13 under non-stressed conditions and lower GCA effects (-0.31) under stressed conditions was exhibited by Benazir. Under heat stress conditions, 8 F_1s out of 15 exposed the positive SCA effects and the rest 7 F_1 hybrids exhibited the negative SCA effects. For SCA effects, the cross Kiran-95 x Benazir (0.91) manifested the maximum positive SCA effects value in optimum environment, whereas the crosses Benazir x TJ-83 expressed less but the same (0.63). In both normal and heat stressed conditions, the less but same positive SCA effects were manifested by NIA-Sarang x TJ-83 (0.12) and NIA-Sarang x Benazir (0.12). Under normal conditions, the largest yet unrewarding negative SCA effects were presented by TD-1 x Benazir (-1.35), while D-1 x Benazir (1.19) and TD-1 x NIA-Sarang (-0.76) expressed the maximum SCA effects. Under both growing circumstances, the least negative SCA impacts were seen in Kiran-95 x AS-2002 (-0.16) and Benazir x AS-2002 (-0.21) (Fig. 5) under both growing circumstances.

Grain filling duration

With respect to grain filling duration, Kiran-95 displayed the maximum positive GCA effects under normal sowing time (0.38) and in delayed heat stress sowing (0.32), however NIA-Sarang (0.36) and TJ-83 (0.01) demonstrated the maximum and minimum positive GCA effects (Table 3). In terms of GCA effects, TD-1 and Benazir attained highest progressive negative GCA effects of -0.41 and -0.31, correspondingly, while AS-2002 and TD-1 achieved minimum negative GCA effects of -0.07 and -0.01, correspondingly. Under normal sowing time, Kiran-95 x Benazir (0.82) and Kiran-95 x TJ-83 (0.06) exhibited the most and least positive SCA effects, respectively, while NIA-Sarang x Benazir (-0.78) and Benazir x TJ-83 (-0.43) showed the highest and lowest negative SCA effects. Out of 15 F_1 hybrids, 9 showed favorable SCA impacts under delayed sowing (heat stress), whereas 6 showed negative SCA effects. In the late sowing season, NIA-Sarang x Kiran-95 and TD-1 x NIA-Sarang showed the most positive SCA effects (0.75 and 1.01, respectively), whereas TD-1 x TJ-83 showed the lowest positive SCA effects (0.01). Under late heat stress sowing circumstances (Fig. 6), TJ-83 x AS-2002 showed the largest negative SCA effects (-0.64), whereas NIA-Sarang x AS-2002 showed the lowest negative SCA effects (-0.06).

Cell membrane thermo stability (CMT)

Under optimum and heat stress environment for CMS, the greatest positive GCA effects of 102.08 and 140.91 were expressed by TD-1 respectively (Table 4), whereas the lowest positive GCA effects were displayed by TJ-83 (49.30) and Kiran-95 (68.69). The greatest negative GCA effects of -113.73 and -142.47 were exhibited by the same parent NIA-Sarang in both the growing times, while the minimum negative GCA effects were seen in Benazir (-59.79) under normal conditions and in AS-2002 (-36.97) in heat stress conditions. Regarding SCA estimates, out of 15 F_1 hybrids under normal planting, 4 F_1 hybrids exhibited the positive SCA effects whereas 11 F_1 hybrids achieved the negative SCA effects. The hybrid TD-1 x Kiran-95 manifested the maximum positive SCA (4.81) value under normal conditions, while the maximum positive SCA estimates were observed in TD-1 x Kiran-95 (7.01) and Kiran-95 x AS-2002 (2.88) under late sowing. However, Kiran-95 x TJ-83 exposed the minimum positive SCA effects under normal planting (0.21) and in high temperatures (1.95). NIA-Sarang x AS-2002 showed the extreme negative SCA effects (-12.99) for normal growing season and Kiran-95 x Benazir (-12.01) for heat stress growing times, however the less negative SCA effects (Fig. 7) were noticed in the same parent TD-1 x TJ-83 under non-stressed (-0.97) and in stressed conditions (-0.17).

Leaf area

The highest and smallest positive GCA effects under optimum conditions for leaf area were noticed in TJ-83 (0.76) and Benazir (Table 4) (0.06), respectively, whereas AS-2002 (-1.08) and NIA-Sarang (-0.58) exposed the biggest and lowest negative GCA impacts, respectively. Under heat stress, Kiran-95 (0.89) and Benazir (0.06) revealed the highest and smallest positive GCA effects, respectively, whereas AS-2002 (-1.34) and NIA-Sarang (-0.54) established the biggest and smallest negative GCA effects. Pertaining to SCA effects, the highest and smallest positive SCA effects of 1.51 and 0.20 were observed in hybrids TD-1 x NIA-Sarang and NIA-Sarang x Kiran-95, respectively, under normal plantings, however the highest and smallest negative SCA effects were recorded in TJ-83 x AS-2002 (-1.20) and Kiran-95 x AS-2002 (-0.11), respectively in same growing conditions. Eight F_1s from 15 F_1 hybrids proved the positive SCA effects under heat stress, seven F_1 hybrids expressed the negative SCA effects and one zero effects. The crosses NIA-Sarang x Kiran-95 (1.51) and TD-1 x TJ-83 (1.41) however exhibited the highest positive SCA effects in nonstress and heat stress plantings correspondingly (Fig. 8), while NIA-Sarang x Benazir (0.08) expressed the smallest positive SCA effects. The highest and the lowest, but negative SCA effects were manifested by TD-1 x AS-2002 (-1.62) and Kiran-95 x AS-2002 (-0.18) under thrombotic stress.

Chlorophyll (SPAD)

Under non-stressed planting, for SPAD chlorophyll, the maximum positive GCA effects were noted (Table 4) in TJ-83 (0.99), nonetheless the most positive GCA effects under stressed sowings were expressed by the same parent TJ-83 (1.22). The minimum positive GCA effects were exposed by AS-2002 in non-stressed planting (0.30) and in stressed sowing period (0.50). The variety Benazir under normal (-0.87) and in heat stress sowing, displayed the highest negative (-1.26) GCA effects, where the minimum negative GCA effects in non-stress and in heat stress were observed in Kiran-95 (-0.82) and NIA-Sarang (-0.30), respectively. Out of 15 F_1s, 11 F_1s demonstrated the positive SCA effects and the rest 4 F_1 hybrids disclosed the negative SCA effects under the heat stress plantings. NIA-Sarang x Kiran-95 (4.23) showed the most positive SCA effects in normal sowing, while NIA-Sarang x Kiran-95 (2.54) and Kiran-95 x TJ-83 (2.04) expressed the maximum positive SCA effects under heat stress conditions. The lowest positive SCA effects of 0.06 and 0.03 in NIA-Sarang x AS-2002 and TD-1 x AS-2002 were explored under both the sowing conditions. With respect to negative SCA effects under normal and heat stress plantings (Fig. 9), Kiran-95 x AS-2002 (-3.05) and TD-1 x Kiran-95 (-2.89) demonstrated the highest SCA effects, nevertheless the lowest negative SCA effects were observed in NIA-Sarang x Benazir (-0.47) and in Kiran-95 x AS-2002 (-1.16).

Relative water content (RWC %)

In optimum sowing environment, TD-1 and TJ-83 attained maximum and minimum positive GCA effects of 1.11 and 0.12, respectively, while Benazir (-1.43) and AS-2002 (-0.08) accomplished desirable maximum (Table 4) and minimum negative yet deleterious GCA effects, respectively. In high temperature sowing environment, positive GCA effects with more and less GCA values were recorded by T.J-83 (1.77) and TD-1 (0.75), whereas in Benazir and AS-2002, the largest and smallest negative GCA impacts of -2.30 and -0.11, were noted respectively. About SCA effects at optimum sowing time, NIA-Sarang x AS-2002 (2.10) and NIA-Sarang x TJ-83 (0.30) demonstrated the maximum and minimum positive SCA effects, respectively, while TD-1 x NIA-Sarang (-4.42) and Kiran-95 x AS-2002 (-0.15) established the more and less negative SCA effects (Fig. 10), respectively. Whilst in delayed sowing under heat stress, 7 F_1 from 15 F_1 hybrids played the positive SCA effects whereas 8 F_1 hybrids exhibited the negative SCA effects. Under high temperatures, NIA-Sarang x AS-2002 (5.68) and Kiran-95 x Benazir (3.29) showed the maximum desirable positive SCA effects, whereas Benazir x AS-2002 exhibited the least positive SCA effects (0.49). The most significant negative SCA effects were observed in the cross between TD-1 and NIA-Sarang (-8.76), while the least negative SCA effects were noted in the cross between NIA-Sarang and Benazir (-0.36).

Discussions

Days to 50% heading

According to (Table 1b), GCA and SCA were not significant for 50% of the heading in stress and non-stress situations. In this study, the parent NIA-Sarang showed the most negative GCA effects, while the parent TD-1 showed the smallest negative GCA effects. Under typical sowing dates, in days to 50% heading, Benazir recorded the maximum positive GCA and Kiran-95 the minimum positive GCA effects. The parents AS-2002 and TD-1 showed the highest and lowest beneficial GCA impacts under late sowing dates. NIA-Sarang, on the other hand, showed negative but maximal GCA effects, whereas Kiran-95 showed minimal GCA (Table 2). With respect to SCA, the maximum positive SCA effects under controlled conditions were shown by the crosses TJ-83 x AS-2002, NIA-Sarang x Kiran-95 and TD-1 x AS-2002, while the minimum positive SCA effects were exhibited by the cross TD-1 x Kiran-95. The cross Benazir x AS-2002 manifested the maximum negative SCA effects (Fig. 1). Among 15 F_1 hybrids evaluated, 6 F_1 hybrids manifested the positive SCA effects and 9 F_1 hybrids exhibited negative SCA estimates under heat stress conditions. Under heat stress conditions, the maximum and minimum positive SCA effects were exhibited by the crosses TJ-83 x AS-2002 and TD-1 x Kiran-95, respectively. The maximum negative effects were taken by Benazir x AS-2002 and TD-1 x AS-2002, whereas the crosses Kiran-95 x Benazir and Benazir x TJ-83 revealed the minimum negative SCA effects. The results demonstrated that crosses Benazir, Kiran-95 and AS-2002 manifested positive GCA estimates being good general combiners under normal and stress growing conditions. Six hybrids revealed positive SCA estimates under both normal and late sowing conditions. The hybrids like TJ-83, NIA-Sarang x Kiran-95 and TD-1 x AS-2002 proved to be good specific combiners for developing wheat varieties in future breeding programmes under heat stress conditions for this character. Coinciding to our findings, the similar importance of GCA and SCA estimates for days to 50% heading was recorded by Qabil (2017) and Ishaq et al. (2018) who suggested that dominant genes were prevailing for this trait. The GCA of parents (Fig. 1) and SCA of the hybrids for each character under normal and late sowing conditions are discussed in the following paragraphs.

Days to 75% maturity

The analysis of variance and mean squares for general combining ability (GCA) and specific combining ability (SCA) were not significant for both days to 75% maturity under non-stress and heat stress conditions, but GCA was significant and SCA was non-significant for this trait under heat stress (Table 1b). The results presented in Table 2, demonstrated the maximum positive GCA effects under both normal and late sowing conditions for days to 75% maturity were unveiled by Benazir and TD-1, whereas the lowest positive GCA effects were obtained by NIA-Sarang and Kiran-95, respectively.

The maximum desirable negative GCA effects were achieved by AS-2002; yet minimum negative GCA was observed in TD-1 under normal sowing conditions (Table 2). In late sowing conditions, the parent TJ-83 demonstrated the maximum desirable negative GCA effects and minimum negative GCA by NIA-Sarang. In normal sowing time, the higher positive SCA effects were demonstrated by the crosses TJ-83 x AS-2002, TD-1 x Benazir and TD-1 x AS-2002 and lowest positive SCA by Kian-95 x Benazir. Six out of 15 F_1 hybrids exposed the positive SCA effects and the remaining 9 F_1 hybrids articulated the negative SCA effects under late sowing and heat stress (Fig. 2). The maximum yet desirable negative SCA effects under non-stressed conditions were shown by the hybrids NIA-Sarang x Benazir and minimum negative SCA estimates by TD-1 x NIA-Sarang. Under stressed conditions, the cross NIA-Sarang x Kiran-95 revealed the highest positive SCA effects while minimum positive SCA by NIA-Sarang x Benazir. The highly negative and rewarding SCA effects were observed by Kiran-95 x TJ-83 and minimum negative SCA effects by Benazir x TJ-83 under heat stress conditions. Ishaq et al. (2018) also demonstrated similar results for days to 75% maturity. Current results indicated that parents TD-1, Kiran-95 and Benazir displayed as good general combiners for crossing and selection under both seasons but especially under late sowing conditions. Singh et al. (2014) and Parveen et al. (2023) also identified some good specific combiners for the development of hybrids. Six crosses like TJ-83 x AS-2002 (Fig. 2), TD-1 x Benazir and NIA-Sarang x Kiran-95 expressed positive SCA effects demonstrating more contribution of additive and dominant genes for days to 75% maturity and can be used for further evaluation.

Plant height

When comparing the plant height trait under non-stress and heat stress circumstances, the mean squares for the general combining ability (GCA) and specific combining ability (SCA) analysis of variances were very significant. (Table 2) The parent AS-2002 and Benazir showed the least desirable positive GCA effects, while the parent Kiran-95 showed the most unwanted positive GCA effects under both normal and heat stress circumstances. However, the parent Benazir and TJ-83TD-1 expressed the maximum negative yet rewarding GCA effects (normal sowing) and (late sowing) growing seasons. Under heat stress conditions, 8 F_1 hybrids out of 15 demonstrated undesirable positive SCA effects and the rest of 7 F_1 hybrids showed the negative but desirable SCA effects. The hybrids, Kiran-95 x TJ-83 and TD-1 x AS-2002 exhibited maximum negative SCA effects, while TJ-83 x AS-2002 revealed the minimum but desirable negative SCA effects. For SCA effects under heat stress conditions, NIA-Sarang x Benazir, Kiran-95 x TJ-83 and NIA-Sarang x TJ-83 exhibited the minimum yet desirable positive SCA effects, nonetheless, TJ-1 x AS-2002 and Kiran-95 x AS-2002 disclosed the maximum and desirable negative SCA effects, while TJ-83 x AS-2002 revealed the minimum SCA effects (Fig. 3). Six parents were evaluated from which only three parents such as TD-1, Kiran-95 and TJ-83 manifested desirable negative GCA estimates under normal conditions and three parents TD-1, TJ-83 and AS-2002 exhibited negative results of GCA estimates in stress conditions. Such results indicated that TD-1, Benazir and TJ-83 were good general combiners for crossing purpose (Fig. 3). While 15 hybrids, seven showed desirable negative SCA effects under heat stress while crosses Kiran-95 x TJ-83, TD-1 x AS-2002 and Kiran-83 x AS-2002 revealed good specific combiners so as to develop either shorter or medium tall plants for both the conditions. Singh et al. (2014), El-Nahas & Ali (2021) and Joshi et al. (2023) observed some of the parents and crosses with higher desirable negative SCA estimates for plant height.

Grains spike^{-1}

Both the general combining ability (GCA) and specific combining ability (SCA) analyses of variance were highly significant for trait grains spike^{-1} in both heat stress and non-stress scenarios (Table 3). In terms of GCA effects, the parent TD-1 outperformed the other parents in terms of high positive GCA effects for grains spike^{-1} in both controlled and heat stress circumstances, while the parent Kiran-95 provided the second highest positive GCA effects under both normal and heat stress situations. Crosses NIA-Sarang x Benazir and NIA-Sarang x AS-2002 showed the highest positive SCA effects under late planting circumstances, whereas TD-1 x TJ-83 showed the highest positive SCA effects. TD-1 x Kiran-95, Benazir x TJ-83. Under high temperatures, from 15 F_1 hybrids, 11 F_1s exposed the positive SCA effects and the rest 4 F_1s demonstrated negative SCA effects. The hybrids such as NIA-Sarang x Benazir, Benazir x AS-2002 and NIA-Sarang x TJ-83 presented the maximum positive SCA effects indicating prevalence of dominant genes. The highest negative SCA effects were presented by TD-1 x NIA-Sarang and Kiran-95 x Benazir, however TD-1 x TJ-83 displayed the minimum negative SCA effects under heat stress conditions (Fig. 4). To conclude the results, parents TD-1 and Kiran-95 proved to be the best general combiners suitable for crossing and selection while hybrids NIA-Sarang x Benazir, NIA-Sarang x AS-2002 and NIA-Sarang x TJ-83 being good specific combiners are suitable to be grown in both growing conditions. Fellahi et al. (2013) recognized a Line-A901 and tester Wifak which was good combiners for the number of grains spike^{-1} while cross A901 x Wifak with high SCA effects, was the best specific combiner for grains spike^{-1}. Similar estimates of GCA and SCA were also achieved by Kumar et al. (2017) and Rind et al. (2023) who revealed the expression of dominant genes for yield and many yield contributing attributes. The results of good parents and crosses indicated that this investigation can be used for the improvement of wheat cultivars and development of hybrids in the up-coming breeding programmes.

Grain yield plant^{-1}

The variance analysis for general combining ability (GCA) and specific combining ability (SCA) showed highly significant results for the grain yield per plant under both non-stress and heat stress conditions (Table 3). Under both normal and late sowing conditions, the parents TD-1, Kiran-95, and TJ-83 showed greater positive GCA effects for grain yield per plant. The parents NIA-Sarang and Benazir expressed the equal value of maximum negative GCA effects under normal sowing conditions. Under high temperatures of late sowing conditions, 8 among 15 F_1 hybrids displayed positive SCA estimates exhibiting their superiority for hybrid wheat development. Regarding SCA effects, Benazir x TJ-83 and NIA-Sarang x AS-2002 crosses exhibited maximum positive SCA effects under heat stress environmental conditions (Table 3). The greatest negative SCA effects were observed in the TD-1 x Benazir cross under normal conditions, while both the TD-1 x Benazir and TD-1 x NIA-Sarang crosses exhibited the highest negative SCA effects under heat stress conditions (Fig. 5). The results of present results indicated that Kiran-95 and TD-1 were good general combiners while hybrids Kiran-95, Benazir x TJ-83 and NIA-Sarang x AS-2002 were good specific combiners expressing the importance of additive and non-additive genes for this trait. For grain yield plant^{-1}, Punia et al. (2011) identified four lines were to be good combiners for different heat tolerant parameters along with grain yield, yet three combinations expressed high SCA effect for grain yield under both normal and late sowing conditions. Similarly (Fig. 5), nine crosses showed favourable and significant SCA effects in both heat stress and non-stress circumstances, according to Morgan et al. (2018), El-Nahas & Ali (2021) and Riaz et al. (2021). The GCA impacts of the genotypes RAJ 3777, RAJ 4120, HD 2967, DBW 173, and GW 451 on grain yield and heat tolerance traits were found to be significant by Kumari et al. (2022). Furthermore, seven crossings showed noteworthy SCA impacts for characteristics related to heat tolerance and grain yield. Under late planting or heat stress circumstances, selection within the segregating generations of these crosses may successfully give lines with high producing potential.

Grain filling duration

Under both non-stress and heat stress circumstances, the analysis of variances for the trait grain filling duration was highly significant for both general combining ability (GCA) and specific combining ability (SCA). Kiran-95 had the greatest favourable GCA effects for grain filling duration in both normal and late sowing heat stress scenarios. Not so much GCA estimates were revealed by the parents, thus except Kiran-95 (Table 3), none of the parents seem to be suitable for crossing and selection purpose. Somehow parent Benazir with negative GCA may be considered worthwhile for hybridization if short duration breeding material is to be developed. Under normal conditions, the crosses NIA-Sarang x Benazir, TD-1 x Benazir, NIA-Sarang x Benazir, NIA-Sarang x AS-2002 and Benazir x TJ-83 with higher negative SCA estimates may be rewarding to develop shot grain filling duration breeding material. Under heat stress conditions, TD-1 x AS-2002, NIA-Sarang x Benazir and TJ-83 x AS-2002 with higher negative effects are good specific combiners, hence they are considered as potential hybrids for shortening grain filling duration time. Analogous to present results, Ko et al. (2017) noted superb results for grain filling duration while experimenting with 11 Korean lines for SCA estimates. Morgan et al. (2018) and Mahdy et al. (2022) identified the best outcomes for grain filling duration in their experiments consisted of 8 lines along with 28 hybrids for the estimation of GCA and SCA under both growing conditions. Hence, these hybrids could be used as superior hybrids for the betterment of wheat development schemes. While summarizing the GCA effects of parents, it was observed that under normal and late sowing (heat stress) conditions, parents revealed desirable GCA effects for various traits like NIA-Sarang and TJ-83 for days to 50% flowering; TJ-83 and AS-2002 for days to 75% maturity; TD-1 and AS-2002 for plant height;, grains spike^{-1}; TD-1, Kiran-95 and TJ-83 for grain yield plant^{-1} and grain filling duration. These parents with high general combining ability and additive genes are promising parents to be used in hybridization and selection schemes so as to develop improved wheat breeding material for different traits. Concerning SCA estimates of hybrids for various traits, the crosses such as TD-1 x NIA-Sarang, Kiran-95 x TJ-83 and Benazir x AS-2002 revealed desirable negative yet higher SCA for days to 50% flowering and days to 75% maturity; TD-1 x Benazir, TD-1 x AS-2002, NIA-Sarang x Kiran-95 for plant height. The higher but desirable effects were demonstrated by crosses TD-1 x Kiran-95, NIA-Sarang x TJ-83 and Benazir x AS-2002 for grains spike^{-1}; TD-1 x Kiran-95, NIA-Sarang x Benazir and TJ-83 x AS-2002 for grain yield plant^{-1} (Fig. 6). These results suggested that though not many hybrids manifested consistently higher SCA for most of the traits, yet many hybrids were reliable in expressing higher SCA for several traits simultaneously.

Cell membrane thermo stability

Under normal and delayed sowings, the highest affirmative GCA impacts were expressed by TD-1 and TJ-83 for cell membrane thermostability (Table 4). The supreme but undesirable GCA estimates were exhibited by the parents NIA-Sarang, Benazir and AS-2002 under both growing conditions. Three F_1 hybrids amongst 15 F_1s under heat stress, demonstrated the progressive SCA value while 12 F_1s revealed deleterious SCA. For SCA, TD-1 x Kiran-95 manifested the maximum value of positive SCA impacts in timely sowing, while the supreme value with constructive SCA impacts were observed in TD-1 x Kiran-95 and Kiran-95 x AS-2002 under late sowing conditions (Fig. 7). The present results revealed that out of six parents, three of them like TD-1, Kiran-95 and TJ-83 articulated positive GCA estimates under non-stress and heat stress conditions for membrane thermal stability. From 15 hybrids, four under optimal and three in delayed sowing played a prominent role for SCA effects. Farooq et al. (2011) perceived noteworthy differences among wheat genotypes for relative cell injury% and noted 28 to 98% of cell injury due to heat stress. Similar to present findings, El-Rawy et al. (2018) also reported the striking GCA and SCA estimates advocating the cell membrane thermostability due to additive genes in parents and dominant in hybrids. Because these hybrids demonstrated exceptional cell membrane thermostability in hot conditions, these results indicated that heat tolerance based on cell membrane thermostability could be enhanced using the current genetic variation in combinations TD-1 x Kiran-95, Kiran-95 x AS-2002, and Kiran-95 x TJ-83.

Leaf area

The higher positive GCA effects under optimum and high temperature conditions for leaf area were noticed in TJ-83 and Benazir, whereas the maximum negative GCA estimates were noted by NIA-Sarang and AS-2002 under both the sowing dates. Pertaining to SCA effects, the positive SCA effects were seen in TD-1 x NIA-Sarang, TD-1 x TJ-83 and NIA-Sarang x Kiran-95 under the conditions of normal and high temperature (Table 4). Four from 15 F_1s, under high temperature demonstrated the progressive SCA effects yet 11 F_1s expressed the negative SCA effects. TD-1 x TJ-83 and NIA-Sarang x Kiran-95 exhibited the supreme positive SCA estimates, while NIA-Sarang x Benazir expressed the minimum positive SCA effects. These results revealed that parents Kiran-95, Benazir and TJ-83 were tagged as potential general combiners with additive genes under both growing seasons; therefore these parents are useful for crossing and selection schemes. The high ranking hybrids with positive SCA estimates were; TD-1 x NIA-Sarang, TD-1 x TJ-83 and NIA-Sarang x Kiran-95 in optimum and late sowing conditions. These findings indicated that a sufficient number of hybrids might be created for hybrid wheat by using dominant genes and being good specific combiners (Fig. 8). According to Golparvar et al. (2013), both additive and non-additive genes roles impart a substantial influence in wheat combining ability under late sowing conditions. A variety with a small leaf area can achieve good yield due to greater light-use efficiency per unit leaf area (Li et al., 2023)

Chlorophyll (SPAD)

Both in optimum and in heat stress sowing conditions, higher positive GCA effects were probed in TD-1, TJ-83 and AS-2002 however manifested maximum positive GCA effects for SPAD chlorophyll, thus such parents are tagged as good general combiners (Table 4). Conversely, variety Benazir and Kiran-95 manifested negative GCA estimates being un-reliable parents to improve heat stress tolerance in wheat breeding schemes. 11 F_1 hybrids amongst 15 F_1s, demonstrated the positive SCA effects and the rest of 4 F_1 hybrids revealed negative SCA effects under planting in heat stress. The hybrids NIA-Sarang x Kiran-95, Kiran-95 x TJ-83, Benazir x AS-2002 and TJ-83 x AS-2002 displayed the higher positive SCA effects in both optimum and delayed planting in high temperature environment. Un-rewarding higher negative SCA effects under normal and heat stress conditions were observed in crosses TD-1 x Kiran-95, NIA-Sarang x TJ-83 and Kiran-95 x AS-2002 (Fig. 9). The current results about SPAD chlorophyll showed that parents like TD-1, TJ-83 and AS-2002 performed superbly as good general combining parents being most suitable for crossing and selection programmes. However, hybrids NIA-Sarang x Kiran-95, TD-1 x TJ-83, Kiran-95 x TJ-83, Kiran-95 x Benazir and Benazir x AS-2002 which expressed higher SCA effects with dominant genes evidenced that they are good specific combiners under both normal and late sowing conditions. These results further advocated that SPAD chlorophyll may be improved by exploring potential hybrids. Analogous to the current findings, Islam et al. (2014) were successful in determining the role of SPAD chlorophyll in wheat under heat stress circumstances. As a result, it was proposed that such hybrids possessed dominant and over dominant genes, making them likely for hybrid wheat exploitation.

Relative water content (RWC %)

In optimum and delayed sowings, relative water contents, the maximum positive GCA effects were obtained by TD-1 and TJ-83 however the greater and minimum negative GCA impacts were noted in Benazir and AS-2002, respectively. In the environment of higher temperature, positive GCA effects with maximum and minimum value were observed in TJ-83 and TD-1, respectively (Table 4). Concerning SCA effects under the environment of optimum and heat stress environment, the crosses TD-1 x Kiran-95, NIA-Sarang x AS-2002 and NIA-Sarang x TJ-83 manifested relatively higher positive SCA effects, respectively. Under late sowing in heat stress, 7 F_1s showed advantageous SCA estimates, while 8 F_1s showed deleterious SCA estimates. The heat tolerant hybrids with higher SCA together with dominant genes are highly rewarding to improve RWC%. Parents like as TD-1 and TJ-83 that demonstrated positive GCA estimations for relative water content in stress circumstances are good general combiners and hence suitable candidates to be involved in hybridization programmes so as to improve RWC. For SCA estimates, hybrids such as NIA-Sarang x AS-2002, TD-1 x Kiran-95, NIA-Sarang x TJ-83, Kiran-95 x Benazir and Benazir x AS-2002 were high ranking hybrids with good specific combining ability for RWC% (Fig. 10). According to Balouchi (2010), dominant and additive genes advocate relative water content of wheat leaves. The hybrids with higher SCA values retained largely dominant genes, which could be highly useful for the production of hybrid crops with increasing relative water content when subjected to higher temperatures.

Table 1b. Mean squares of general combining ability (GCA) and specific combining ability (SCA) from analysis of variance for various morpho-physiological traits of F_1 hybrids of wheat grown under non-stress and heat stress conditions.

Yield traits	Non-stress G.C.A D.F=5	Non-stress S.C.A D.F= 14	Non-stress Error D.F. = 60	Heat stress G.C.A D.F=5	Heat stress S.C.A D.F= 14	Heat stress Error D.F. = 60
Days to 50% heading	1.27*	0.41	0.82	0.81	1.78	1.08
Days to 75% maturity	1.79*	0.96	1.08	1.70*	0.39	0.62
Plant height	51.09**	6.52**	1.43	25.36**	2.40**	1.17
Grains spike^1	20.72**	8.42**	0.95	26.02**	22.37**	2.12
Grain yield plant^1	0.65**	0.42**	0.03	1.54**	0.39**	0.03
Grain filling duration	0.78**	0.30**	0.04	0.32**	0.33**	0.04
*CMT (%)	154.85**	106.33**	0.26	149.93**	106.61**	0.15
Leaf area (cm^2)	4.00**	0.84**	0.04	5.49**	1.24**	0.07
SPAD chlorophyll	4.24**	3.53**	0.06	7.77**	3.42**	0.05
RWC %	6.23**	4.02**	0.19	23.01**	14.60**	0.20

*CMT% = Cell membrane thermo stability

Table 2. General combining ability (GCA) effects of parents for Days to 50% heading, Days to 75% maturity, Plant height (cm) of wheat grown under normal and heat stress conditions.

Parents	Days to 50% heading		Days to 75% maturity		Plant height (cm)	
	Normal	Heat stress	Normal	Heat stress	Normal	Heat stress
TD-1	-0.01	0.13	-0.14	0.60	-3.53	-3.00
NIA-Sarang	-0.39	-0.50	0.01	-0.09	1.44	1.02
Kiran-95	0.08	-0.09	0.43	0.55	3.86	2.33
Benazir	0.74	0.16	0.67	-0.27	-0.84	0.30
TJ-83	-0.23	-0.13	-0.44	-0.45	-1.29	-0.14
AS-2002	-0.20	0.44	-0.52	-0.34	0.37	-0.50
SE (gi)	0.29	0.33	0.33	0.25	0.39	0.35

Table 3. General combining ability (GCA) effects of parents for grains spike^{1}, grain yield plant^{-1} and grain filling duration of wheat grown under normal and heat stress conditions.

Parents	Grains spike^{1}		Grain yield plant^{-1}		Grain filling duration	
	Normal	**Heat stress**	**Normal**	**Heat stress**	**Normal**	**Heat stress**
TD-1	3.09	1.81	0.44	0.52	-0.41	-0.01
NIA-Sarang	-1.44	1.31	-0.28	-0.53	0.36	-0.04
Kiran-95	1.19	1.25	0.06	0.23	0.38	0.32
Benazir	-1.34	-1.57	-0.28	-0.31	-0.14	-0.31
TJ-83	-0.38	-1.57	0.19	0.42	-0.12	0.01
AS-2002	-1.13	-1.22	-0.13	-0.32	-0.07	0.02
SE (gi)	0.31	0.47	0.05	0.05	0.06	0.06

Table 4. General combining ability (GCA) effects of parents for cell membrane thermostability, leaf area, SPAD chlorophyll and relative water contents of wheat grown under normal and heat stress conditions.

Parents	CMT		Leaf area		SPAD chlorophyll		Relative water contents	
	Normal	Heat stress	Nor mal	Heat stress	Normal	Heat stress	Normal	Heat stress
TD-1	102.08	140.91	0.25	0.23	0.40	0.77	1.11	0.75
NIA-Sarang	-113.73	-142.47	-0.58	-0.54	0.00	-0.30	-0.38	-1.69
Kiran-95	74.93	68.69	0.59	0.89	-0.82	-0.93	0.66	1.58
Benazir	-59.79	-101.34	0.06	0.06	-0.87	-1.26	-1.43	-2.30
TJ-83	49.30	71.19	0.76	0.71	0.99	1.22	0.12	1.77
AS-2002	-52.79	-36.97	-1.08	-1.34	0.30	0.50	-0.08	-0.11
SE (gi)	0.16	0.12	0.07	0.09	0.08	0.07	0.14	0.14

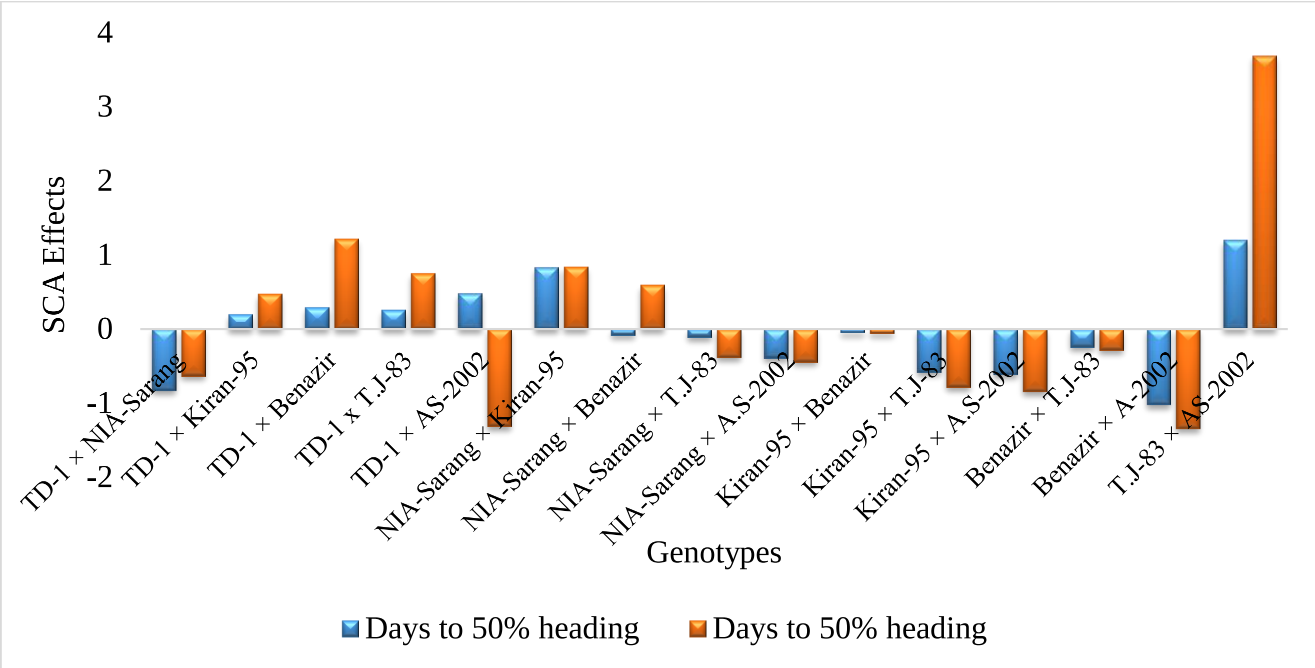

Fig. 1. (SCA) effects of hybrids for Days to 50% heading of wheat grown under normal and heat stress conditions.

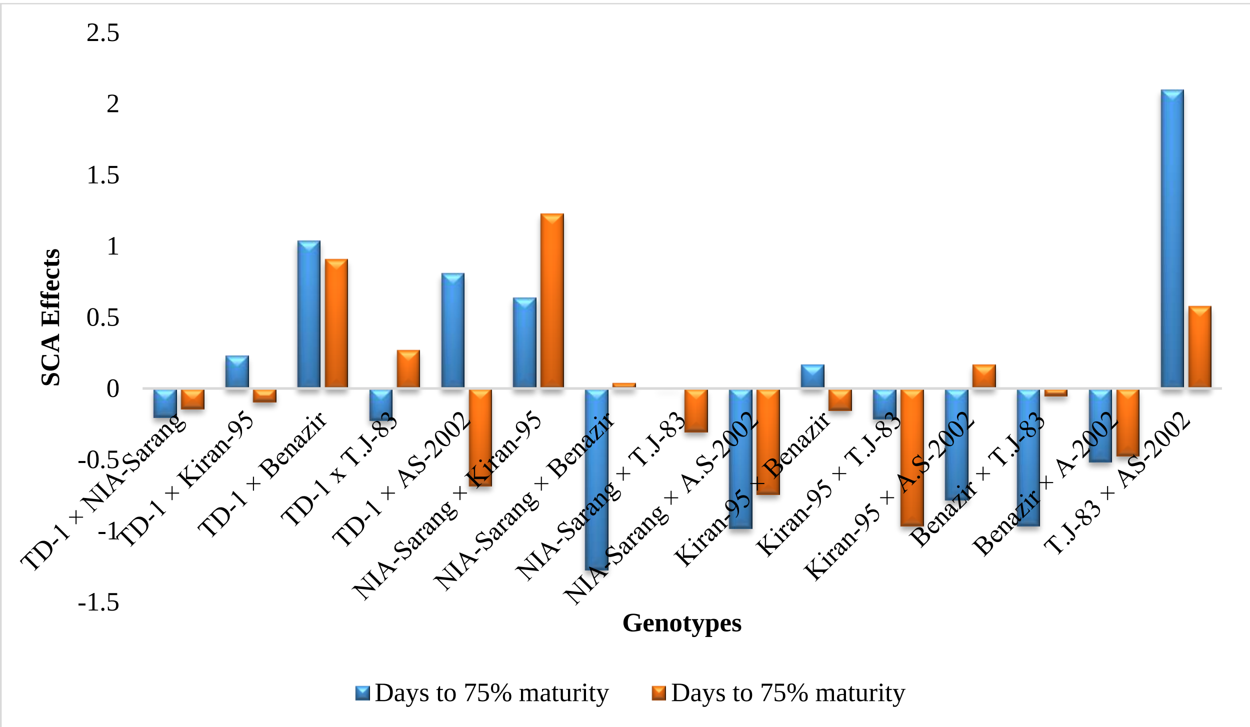

Fig. 2. (SCA) effects of hybrids for Days to 75% maturity of wheat grown under normal and heat stress conditions.

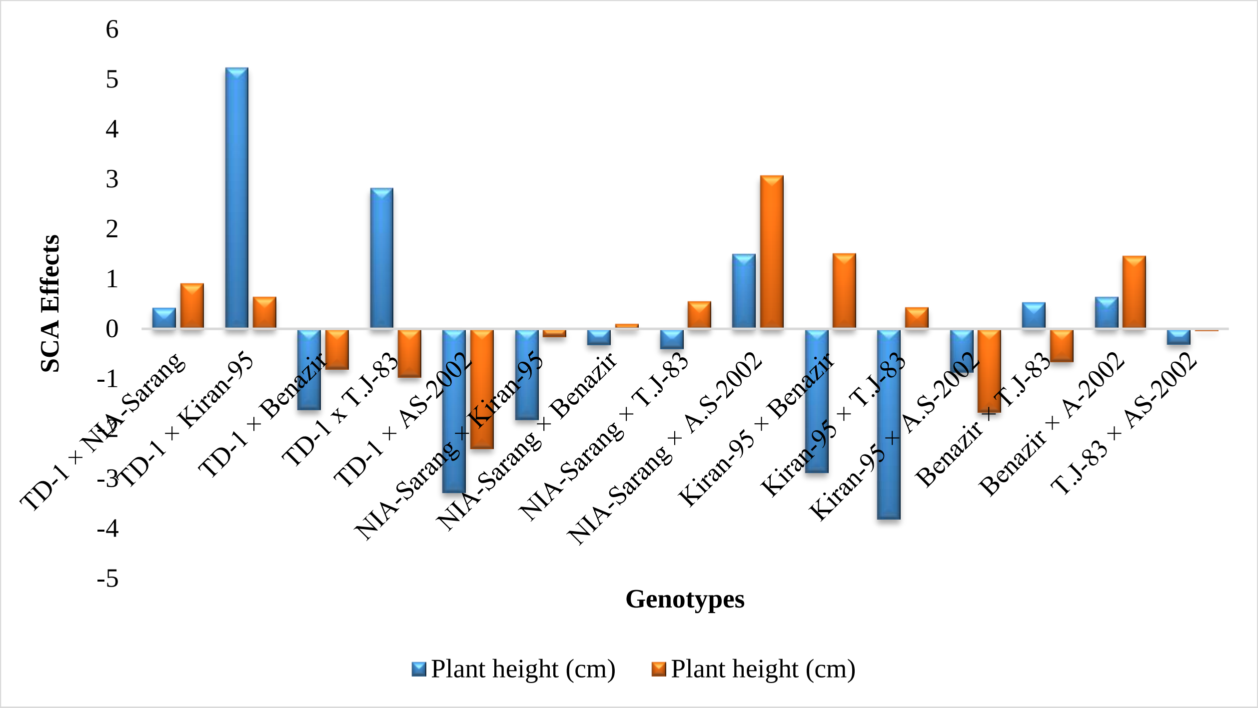

Fig. 3. (SCA) effects of hybrids for Plant height (cm) of wheat grown under normal and heat stress conditions.

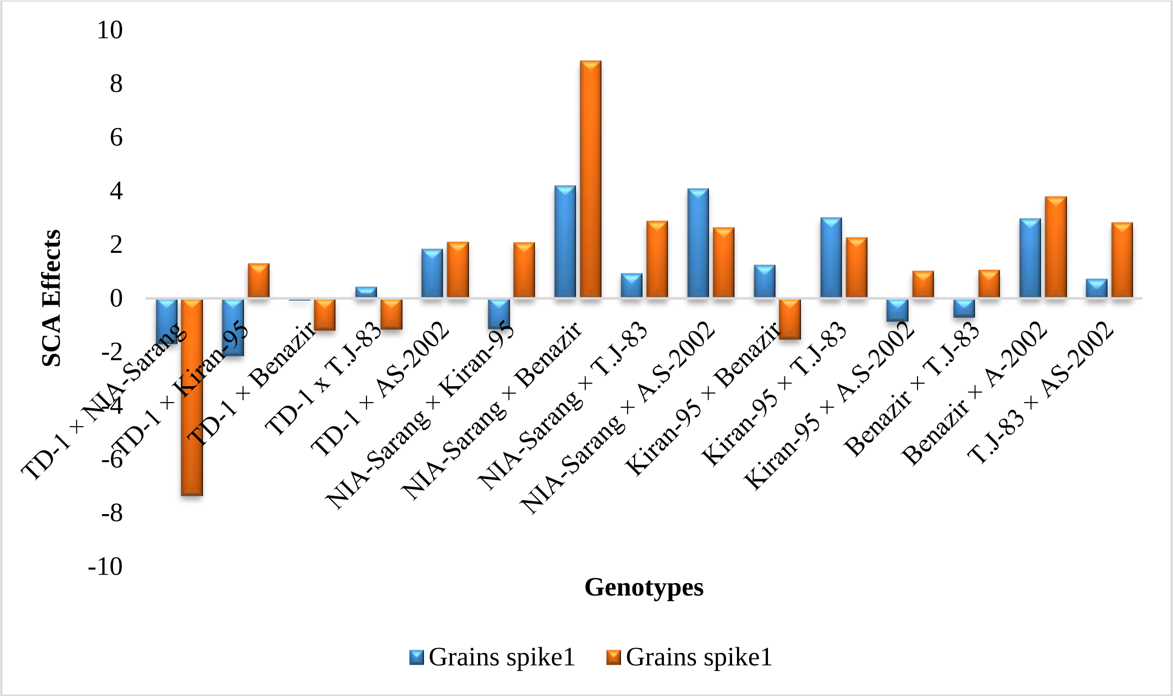

Fig. 4. (SCA) effects of hybrids for grains spike^{-1} of wheat grown under normal and heat stress conditions.

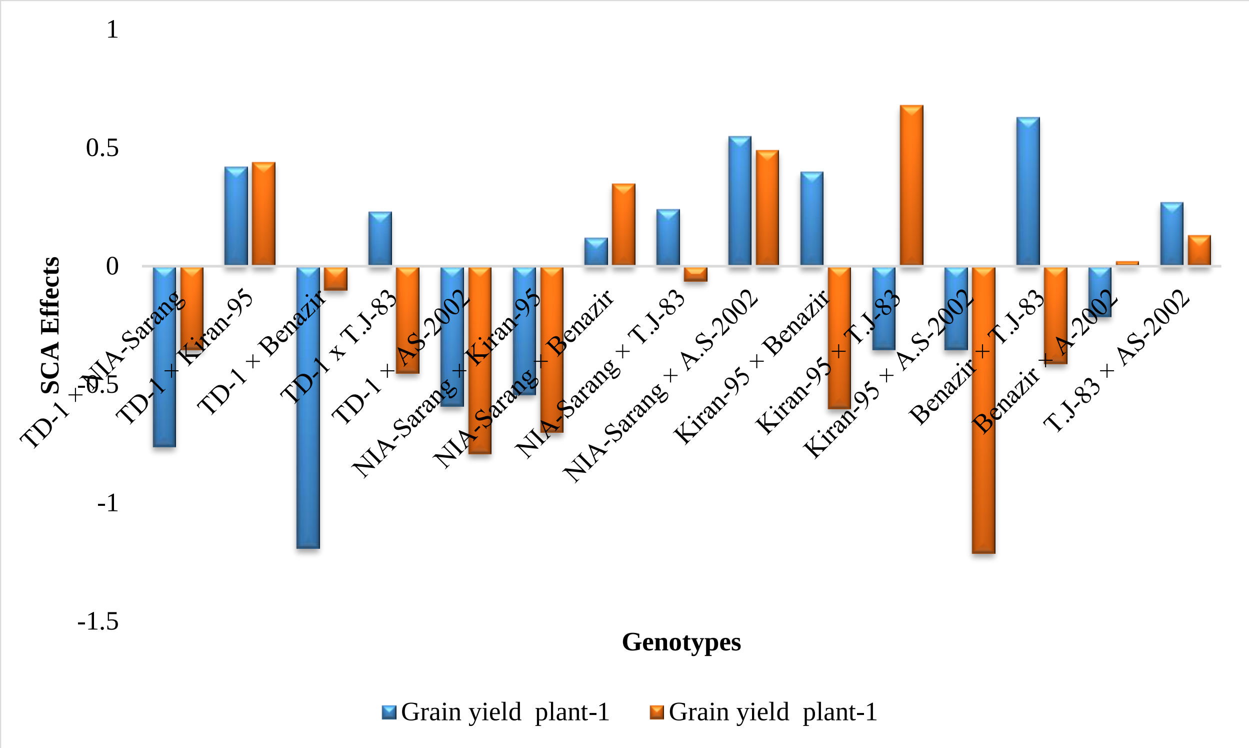

Fig. 5. (SCA) effects of hybrids for grain yield-1 of wheat grown under normal and heat stress conditions.

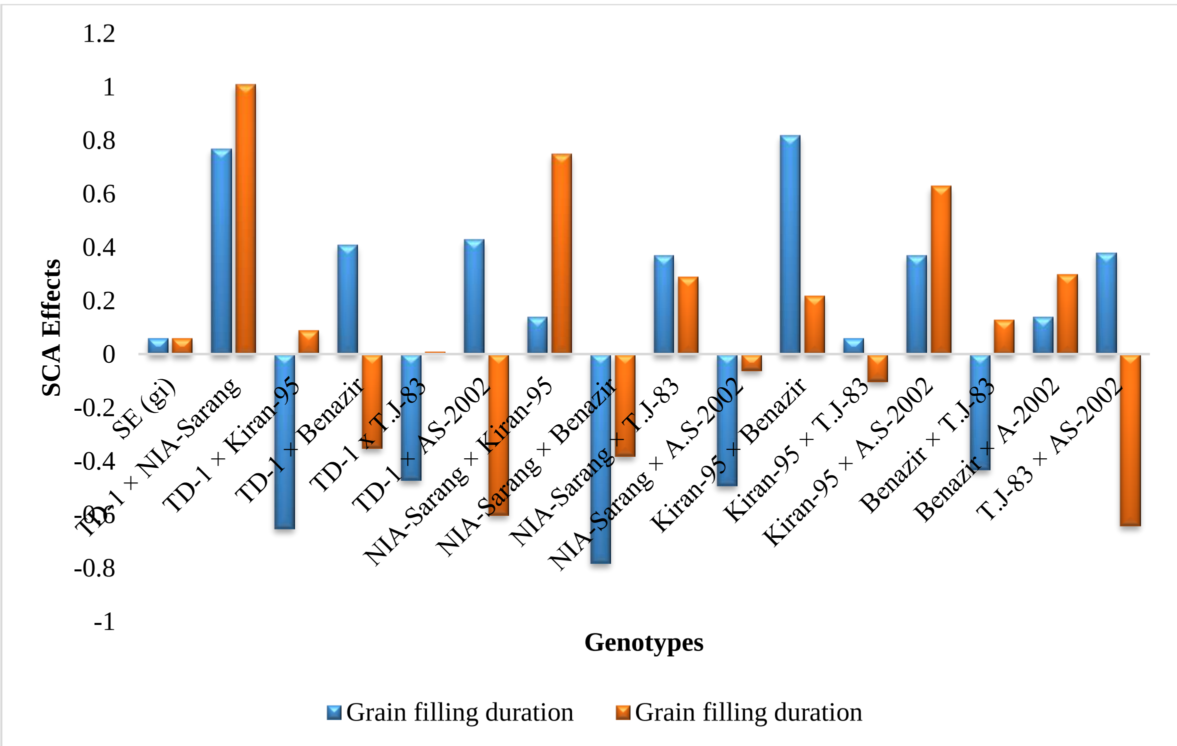

Fig. 6. (SCA) effects of hybrids for grain filling duration of wheat grown under normal and heat stress conditions.

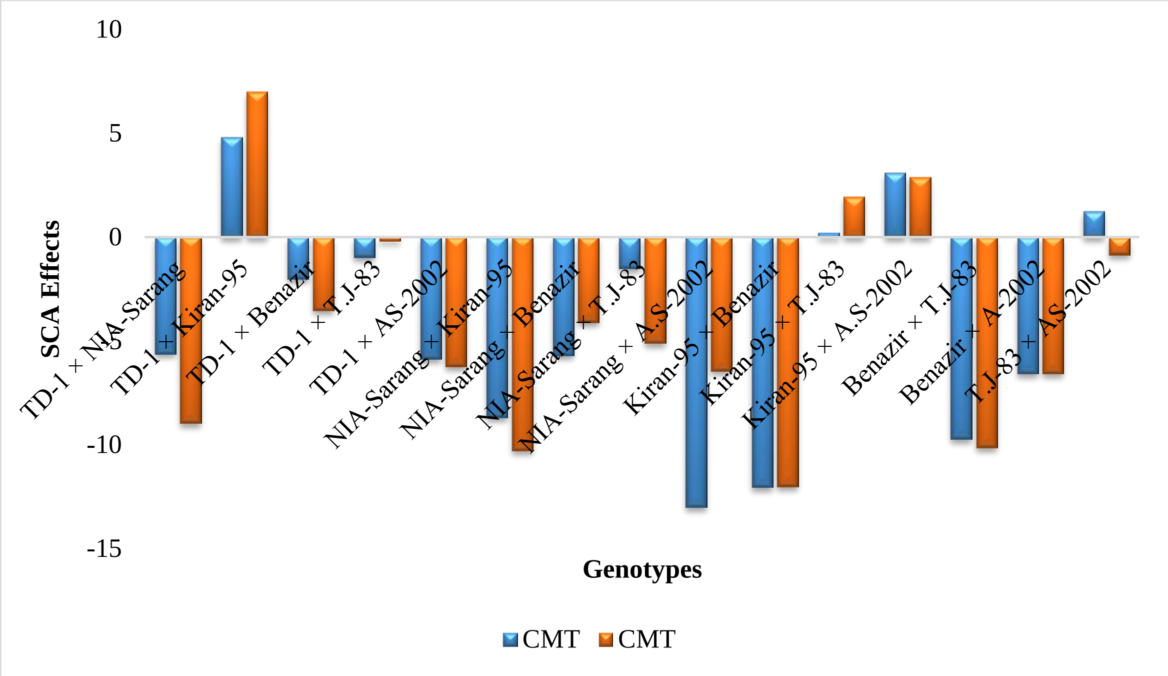

Fig. 7. (SCA) effects of hybrids for cell membrane thermostability% of wheat grown under normal and heat stress conditions.

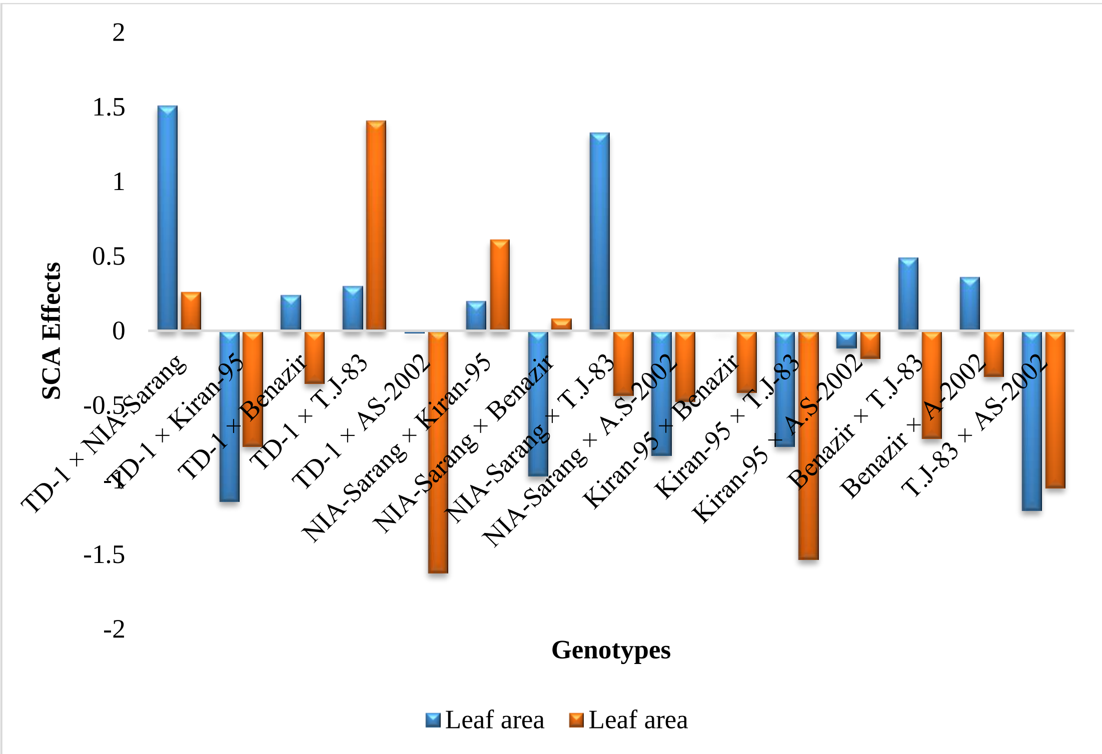

Fig. 8. (SCA) effects of hybrids for leaf area (cm) of wheat grown under normal and heat stress conditions.

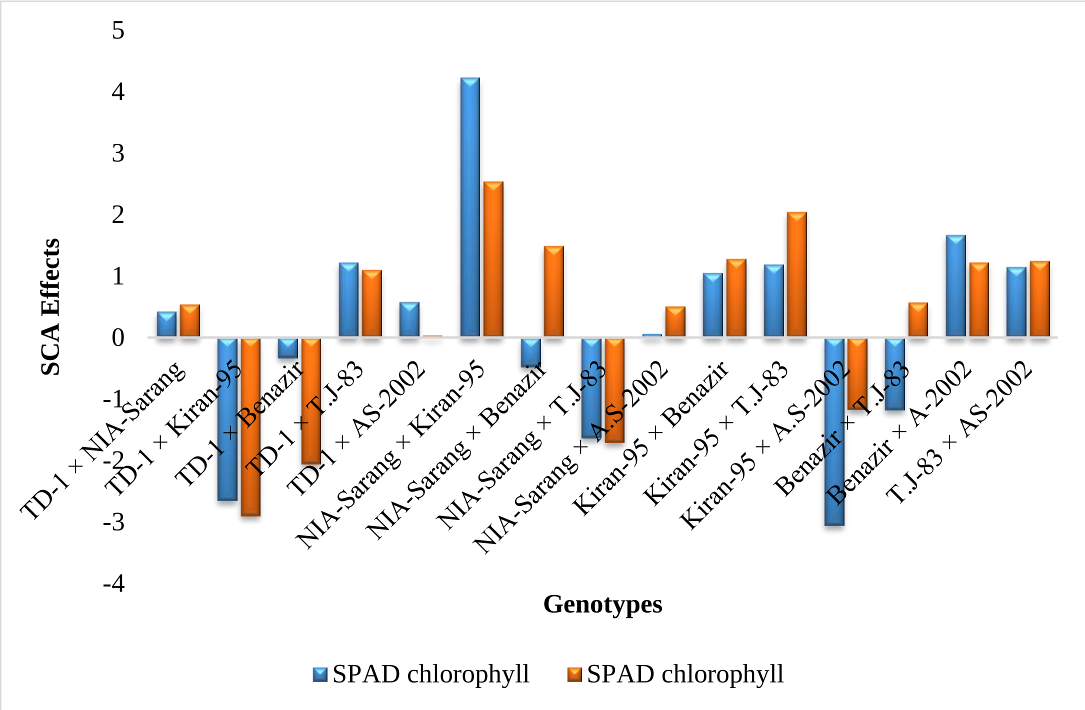

Fig. 9. (SCA) effects of hybrids for SPAD chlorophyll of wheat grown under normal and heat stress conditions.

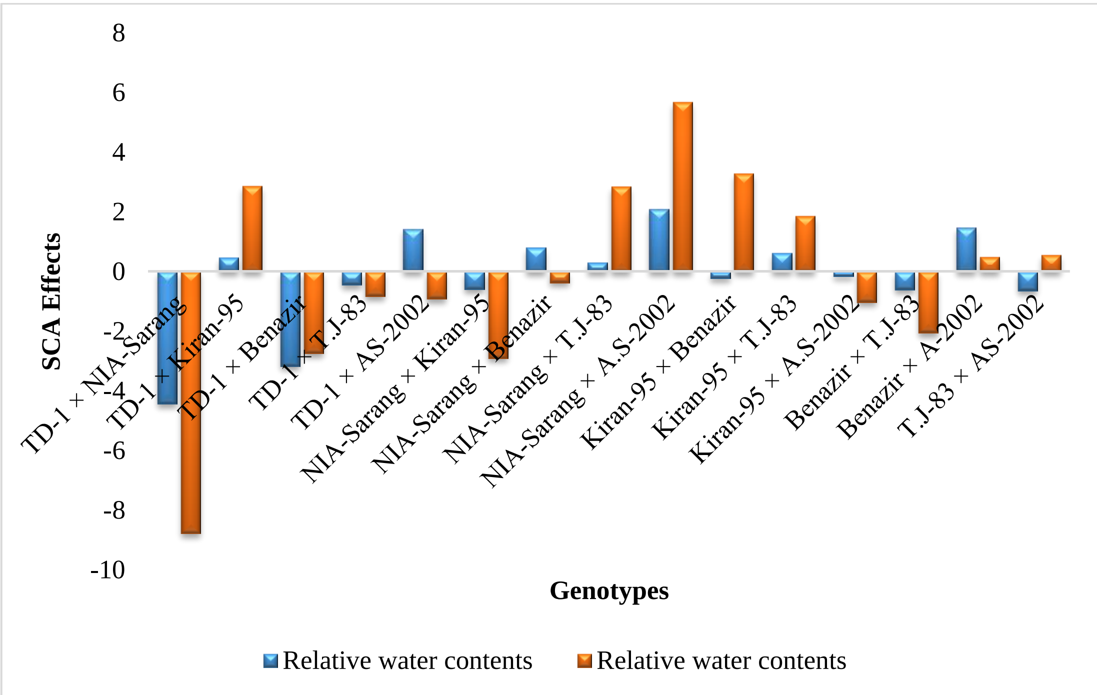

Fig. 10. (SCA) effects of hybrids for relative water contents% of wheat grown under normal and heat stress conditions.

Conclusions

The parents like TD-1, Benazir, Kiran-95 and TJ-83 with desirable general combining ability and additive genes for majority of the traits under study are promising parents to be used in hybridization and selection schemes so as to develop heat tolerant wheat breeding material for different traits. The results suggested that though not many hybrids manifested consistently higher SCA for most of the traits, yet many hybrids such TD-1 x Kiran-95, NIA-Sarang x TJ-83 and Benazir x AS-2002 for grains spike^{-1}; TD-1 x Kiran-95, NIA-Sarang x Benazir and TJ-83 x AS-2002 for grain yield plant^{-1} were reliable hybrids in expressing higher SCA effects for several traits simultaneously.

Author's contribution

TA Baloch and WA Jatoi conducted the research experiment and wrote up the manuscript, M Tahir helped during experiment for recording the observations and finalized the data, M Hanif, ZA Baloch and IA Jatoi analyzed the data.

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