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SUPERIOR WHEAT HYBRIDS DEVELOPMENT FOR PHYSIOLOGICAL AND YIELD-RELATED TRAITS UNDER ADVERSE ENVIRONMENTAL CONDITIONS

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SUMMARY

Late sowing of wheat (*Triticum aestivum* L.) crop correlates with high temperatures. Thus, temperature is one of the main restraining factors influencing wheat yield productivity, especially during the grain-filling period. The best solution to this problem is to evolve heat-tolerant genotypes. Yet, heat tolerance is a complicated issue, causing it a challenge to make a reliable assessment of it. High-temperature stress is a chief ecological constraint hampering the productivity of hexaploid wheat in most parts of the globe. Wheat genotypes, which persist against abiotic stresses, especially at terminal stress periods, are options to meet Pakistan's food requirements in the coming years. In the current study, concerning SCA effects, the F_1 hybrids, such as TD-1 × Kiran-95, NIA-Sarang × TJ-83, Benazir × AS-2002, TD-1 × Kiran-95, NIA-Sarang × Benazir, and TJ-83 × AS-2002, expressed rewarding SCA effects for several characteristics under the heat-stress environment; hence, they could be alternatives in future wheat breeding programs. Heterosis may further be a pursuit for these crosses to get the advantage of hybrid vigor.

Keywords: Wheat (*Triticum aestivum* L.), heterosis, yield, heat stress, genotypes, physiological and yield traits

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Key findings: Regarding SCA effects, the F_1 hybrids, such as TD-1 × Kiran-95, NIA-Sarang × TJ-83, Benazir × AS-2002, TD-1 × Kiran-95, NIA-Sarang × Benazir, and TJ-83 × AS-2002, articulated rewarding SCA effects for several traits under heat-stress environment. Hence, they can be options in future wheat (*T. aestivum* L.) breeding programs.

INTRODUCTION

Temperature is the main restraining factor influencing wheat (*T. aestivum* L.) yield production, especially during a grain-filling stage. Heat tolerance is a complex phenomenon; thus, it is difficult to make a reliable assessment to overcome this problem. High-temperature stress is a chief ecological constraint hampering the productivity of hexaploid wheat worldwide. Al-Khatib and Paulsen (1989) suggested that the ideal heat for all physio-chemical processes of wheat from vegetative to reproductive stages is 20 °C or below. The wheat crop grows best at temperatures ranging from 15 °C to 25 °C, but it can also grow at temperatures ranging from 3 °C to 4 °C or 30 °C to 32 °C (Sial and Khalil, 2012; Rind *et al*., 2023a).

High temperatures during anthesis and grain maturity had shown significant decreases in carbohydrate accumulation of developing grains compared with plants sown under optimum conditions (Hurkman *et al*., 2003; Reddy *et al*., 2023; Rind *et al*., 2023b; Sakran *et al*., 2022; and Singh *et al*., 2020). High temperatures at pre-anthesis and post-anthesis caused immense effects on wheat growth, reducing the wheat crop's photosynthetic efficiency (Wang *et al*., 2011). Higher temperatures also instigated a negative impact on bread wheat production for an extended period (Wardlaw and Wrigley, 1994), yet heat shock response for a few days triggered higher air temperatures (> 32 °C), particularly during the reproductive phase (Blumenthal *et al*., 1994; Stone and Nicolas, 1994).

The wheat response to high temperatures around anthesis can induce a non-recoverable reduction in yield by adversely affecting ovary development and pollen viability, thus reducing grain setting (Pradhan *et al*., 2012). Reports stated the association of many morpho-physiological variables with wheat genotype performance under heat stress. Meanwhile, heat tolerance has a link with increased leaf chlorophyll retention, canopy temperature depression, photosynthetic rate, and leaf senescence (Rees *et al*., 1993; Reynolds *et al*., 1997; Al-Khatib and Paulsen, 1999). The remaining characteristics, such as biomass, 1000-seed weight, and seed yield, were highly susceptible to heat stress.

Tillering capacity, the head spike grain weight, spike fertility, tiller number, seeds spike^{-1}, and harvest index appeared, causing negative impacts on yield under heat stress. An estimation has shown that an ascent in the temperature of only 1 °C in wheat during the growing season declines its yields by around 3%–10%. Yield losses of 33.6% were evident in wheat's major cultivars, owing to heat stress during late sowing conditions, revealing the need to incorporate heat-tolerant traits/genes in wheat cultivars to achieve sustainable production (Chatrath *et al.*, 2007; Burdak *et al*., 2023; Choudhary *et al*., 2022; Joshi *et al*., 2023). Under high temperatures, specific heat shock properties incur activation, causing an amalgamation of heat shock proteins even though other solvent and insoluble proteins demonstrated alternations (in abundance) in high-temperature stress (Simmonds 1995).

Likewise, high temperatures can badly influence cellular membranes, injuring an essential photosynthetic apparatus and changing lipid structure, causing protein denaturation (Wahid *et al*., 2007). An expected increase in global atmospheric carbon dioxide concentration and average ambient temperature (due to climate change) instigate an ascent in heat wave frequency that may severely increase terminal drought for many cropping regions (Kumar *et al*., 2020; Kumar *et al*., 2021). Given the exposure of bread wheat to extreme temperatures, the responses to heat entailed accelerated senescence, less greenness in the leaves, lowered carbon dioxide assimilation, and increased photorespiration (Farooq *et al*., 2011). Similarly, enhancing grain yield in high temperatures can result from selecting genotypes based on grain filling and size. High-temperature stress also resulted in destroying chlorophyll-a and chlorophyll-b. The chlorophyll and stomatal performance, badly influenced by high-temperature stress in different plant parts, reduced the rubisco activity (Morales *et al*., 2003).

Heterosis is the ability of a hybrid to outperform the mid-parent value or better parents. Under the influence of a fickle environment, the gene's allelic or non-allelic relationships show hybrid vigor. In many crop species, heterosis has been effective but crucial in enhancing agricultural plants' productivity. Nowadays, it is a well-established fact that heterosis does arise with suitable parental combinations (Baloch *et al*. 2015). Grain-yield heterotic effects often show a correlation with cross-pollinated crops. In wheat, hybrid vigor has a direct association with the effective selection of potential parents. Wheat breeders working on various aspects of hybrid wheat discovered that the conventional heterotic effect for grain yield ranged from 6% to 41% on a large plot basis (Yadav and Murty, 1976; Borghi *et al*., 1986; Kumar *et al*., 2021; Mahmood *et al*., 2021; Panhwar *et al*., 2022). The current study aimed to learn more about the impact of high temperatures on crop development, physiological and yield characteristics, and combining capacity, as well as detect heat-tolerant wheat cultivars for obtaining better grain yields. Furthermore, it aims to identify hybrids with high heterosis in F_1 with superior heat-stress characteristics.

MATERIALS AND METHODS

Six potential and heat-tolerant wheat (*T. aestivum* L.) cultivars, viz., TD-1, NIA-Sarang, Kiran-95, Benazir, TJ-83, and AS-2002, bore screening for hybridization in the growing season of 2016–2017 at the Sindh Agriculture University, Tandojam, Pakistan. Crosses creation was in a 6 × 6 half diallel pattern (Griffing, 1956, Method-II, Model-I). The 15 F_1 hybrids developed from half diallels entailed growth with six parental lines in natural field conditions under two treatments, i.e., non-stress (regular sowing time on November 15 at standard temperatures and no heat stress) and heat stress (late sowing on December 15 at high temperatures during anthesis time) to collect data for genetic analysis. The meteorological data showed no rainfall during all the experiments, especially at anthesis until grain formation (January 15 to February 15). Thus, experiments proceeded successfully under field conditions (Table 1).

The experiment had four replications using a factorial randomized complete block design. The genetic study required producing genotypes totaling 21 comprising six parents and 15 F_1 hybrids. All implemented agronomic practices helped promote vigorous crop growth. Data analysis to identify the heterotic impacts of F_1 hybrids included productive tillers plant^{-1}, spike length (cm), spikelets spike^{-1}, grains spike^{-1}, grain yield plant^{-1} (g), 1000-grain weight (g), cell membrane stability (CMS), stomatal density (mm^2) and dimensions, leaf area (cm^2), and grain-filling duration.

Statistical analysis

The analysis of variance followed the procedures of Gomez and Gomez (1984), while the applied LSD test helped compare treatments and genotypes. The heterosis calculation relied on the method suggested by Fehr (1987).

RESULTS AND DISCUSSION

Significant variations across parental lines, F_1s, and parents vs. hybrids showed that the data are valuable for determining the parents' capacity of hybrids for heterotic effects (Table 2).

Table 1. Meteorological data taken at experimental site (natural field conditions).

Year	Month	Temperature			Total Rainfall	Relative Humidity
2017	January	7.27	22.15	14.71	00	60.81
	February	10.07	28.20	19.14	00	48.82
	March	14.79	34.88	24.84	00	47.07
	April	19.91	40.11	30.01	00	42.14
	May	24.63	41.75	33.19	00	50.25
	June	26.11	39.25	32.68	00	59.29
	July	25.34	36.66	31.00	00	67.54
	August	24.75	36.50	30.63	00	65.75
	September	22.98	36.64	29.81	00	65.46
	October	19.13	38.50	28.82	00	52.50
	November	12.23	30.84	21.54	00	50.89
	December	7.39	24.52	15.96	00	52.54
2018	January	8.00	26.48	17.24	00	51.39
	February	11.50	28.82	20.16	00	51.32
	March	15.61	36.39	26.00	00	44.86
	April	20.09	40.25	30.17	00	41.04
	May	23.52	42.05	32.79	00	40.43
	June	25.54	38.93	32.24	00	58.29
	July	25.18	36.84	31.01	00	63.46
	August	23.86	35.95	29.91	00	65.71
	September	22.38	36.98	29.68	00	60.14
	October	17.61	37.27	27.44	00	49.25
	November	14.89	31.36	23.13	00	57.25
	December	8.90	25.30	17.10	00	59.57

Table 2. Mean squares from analysis of variance for different morpho-physiological traits of wheat genotypes under normal and heat-stress conditions.

Parameters	Mean squares				
	Replication	Treatment (T)	Genotypes (G)	T × G	Error
	d.f. = 3	d.f. = 1	d.f. = 20	d.f. = 20	d.f. = 123
CMT (%)	2.40	2508.69**	933.20**	4.80**	0.21
Stomatal density	0.567	942.881**	100.918**	3.998**	0.135
Stomatal dimension	0.35	1275.90**	71.75**	4.08**	0.16
Leaf area	0.045	601.853**	13.446**	1.887**	0.056
Productive tillers plant^{-1}	0.0619	43.8499**	2.6334**	0.1523**	0.0894
Spike length	0.019	101.931**	2.537**	0.186**	0.011
Spikelets spike^{-1}	0.097	235.554**	12.896**	2.754**	0.029
Grains spike^{-1}	7.60	3928.92**	111.75**	20.98**	1.50
Grain yield plant^{-1}	0.053	232.957**	4.220**	0.235**	0.027
1000-grain weight	2.04	1205.20**	21.57**	9.30^{ns}	6.62
Grain-filling duration	0.015	856.857**	1.915**	0.938**	0.041

**,* Significant at 1% and 5% level of probability, d.f. = Degree of freedom, N.S. = Nonsignificant

Heterosis

The prime objective of any breeding scheme is to accumulate desirable genes from two or more parental lines into a single hybrid, which usually yields more than the parents. Such hybrids become specimens for direct exploitation of hybrid vigor or forwarded to future filial generations for selecting desirable progenies after achieving a desirable level of homozygosity. The amount of hybrid vigor's improvement can result when involving divergent parental lines in the crossing program. Diverse parents with different genes at different loci may influence yield by demonstrating dominant effects at many yield-influencing loci (Khanishova and Azizov, 2023; Ali *et al*., 2024).

Cell membrane thermostability (CMS)

Under timely sowing conditions, the higher and lower deleterious relative heterosis was evident in wheat (*T. aestivum* L.) crosses, NIA-Sarang × A.S-2002 and TD-1 × Kiran-95, respectively (Table 3). Similarly, the highest and lowest negative heterobeltiosis occurred in crosses, NIA-Sarang × A.S-2002 and TD-1 × Kiran-95, respectively. Likewise, in late sowing under heat-stress conditions, cross TD-1 × Kiran-95 displayed positive relative heterosis, while remaining F1s showed deleterious negative heterosis, with the maximum and minimum negative heterobeltiosis noted in crosses, NIA-Sarang × AS-2002 and TD-1 × Kiran-95 for cell membrane thermostability, respectively. The crosses included parents with poor × poor and high × high GCA impacts in manifesting

Table 3. Heterotic effects of F_1 hybrids of wheat genotypes for cell membrane thermostability and stomatal density under normal and heat-stress conditions.

F_1 hybrids	Cell membrane thermostability			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-22.90	-27.39	-31.45	-35.75
TD-1 × Kiran-95	-0.97	-2.69	2.12	-0.86
TD-1 × Benazir	-18.14	-21.52	-23.43	-27.46
TD-1 × T.J-83	-8.06	-10.42	-9.77	-11.64
TD-1 × AS-2002	-18.25	-21.32	-20.22	-24.11
NIA-Sarang × Kiran-95	-28.69	-31.71	-33.98	-36.33
NIA-Sarang × Benazir	-33.57	-34.81	-35.32	-36.05
NIA-Sarang × T.J-83	-18.12	-20.94	-27.10	-30.29
NIA-Sarang × A.S-2002	-38.57	-39.94	-41.28	-42.18
Kiran-95 × Benazir	-33.36	-35.00	-36.87	-38.45
Kiran-95 × T.J-83	-7.61	-8.41	-6.37	-7.19
Kiran-95 × A.S-2002	-7.30	-9.25	-6.24	-8.19
Benazir × T.J-83	-29.77	-30.93	-35.09	-37.26
Benazir × A-2002	-29.35	-29.62	-31.68	-31.97
T.J-83 × AS-2002	-9.29	-10.43	-13.38	-15.91
F_1 hybrids	Stomatal density			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	20.90	9.95	16.46	11.73
TD-1 × Kiran-95	-5.60	-12.45	-6.84	-13.03
TD-1 × Benazir	8.37	-4.40	3.40	-5.94
TD-1 × T.J-83	-1.70	-10.32	-3.94	-9.43
TD-1 × AS-2002	23.87	11.39	22.12	12.88
NIA-Sarang × Kiran-95	10.70	8.38	12.87	9.69
NIA-Sarang × Benazir	7.16	3.59	12.86	6.75
NIA-Sarang × T.J-83	3.04	2.68	6.47	4.55
NIA-Sarang × A.S-2002	11.26	9.88	11.76	7.50
Kiran-95 × Benazir	-0.60	-5.87	-3.09	-5.75
Kiran-95 × T.J-83	0.00	-1.76	3.57	2.49
Kiran-95 × A.S-2002	-6.92	-9.99	-11.50	-12.44
Benazir × T.J-83	4.03	0.22	4.85	0.93
Benazir × A-2002	-4.36	-6.41	-2.14	-0.38
T.J-83 × AS-2002	-13.49	-14.87	-8.41	-10.32

* = Relative heterosis, ** = Better parent heterosis

high heterotic effects under both sowing conditions, indicating that dominant × dominant and additive × additive gene interactions were active for this trait. In an experiment for CMS in wheat breeding, Thomas *et al*. (2017) researched and well-versed high amounts of relative heterosis and heterobeltiosis observed in crosses HD-2733 × HUW-468, HD-2733 × AAI-16, and NW-1014 × NW-4035.

Stomatal density

The maximum yet desirable negative relative heterosis and heterobeltiosis resulted in the cross TJ-83 × AS-2002, and the minimum negative mid and better parent heterosis was apparent in Kiran-95 × Benazir and Kiran-95 × TJ-83, respectively, under optimal sowing conditions (Table 3). Of 15 F_1 hybrids, nine presented undesirable positive heterosis, and six showed rewarding negative heterosis over the mid-parents in heat-stress conditions. Over mid-parent heterosis, crosses TD-1 × AS-2002 and Kiran-95 × AS-2002 showed the most undesired positive and desirable negative heterosis, respectively. The highest and lowest positive better parent heterosis were distinct in the crosses, TD-1 × AS-2002 and Benazir × T.J-83, respectively. Under heat-stress circumstances, TD-1 × Kiran-95 and Benazir × AS-2002 exhibited desired maximum and minimal negative better parent heterotic effects. These combinations of parents are significant for hybrid wheat development since they showed advantageous negative mid-parent and high-parent heterosis under heat-stress conditions. Parents TD-1, AS-2002, Kiran-95, and Benazir served to create hybrids with high × high and low × low GCA effects. The results suggested high vigor was due to additive × additive and dominant × dominant gene actions. Thus, the hybrids with good and poor GCA parents are reliable for hybrid development or selection schemes. Baloch *et al*. (2013) also articulated outstanding results in their experiments for stomatal density in breeding programs to improve wheat for heat-stress conditions.

Stomatal dimension

Regarding the stomatal dimension, the highest and lowest yet desirable negative heterosis appeared over mid-parent in crosses TD-1 × Kiran-95 and Kiran-95 × Benazir, respectively, for regular sowings (Table 4). However, with high temperatures, the maximum and minimum negative unwanted heterotic effects surfaced from Kiran-95 × T.J-83 and NIA-Sarang × T.J-83 for the stomatal dimension. Furthermore, under heat-stress circumstances, crosses TD-1 × Kiran-95 and Benazir × AS-2002 exhibited desirable maximum and minimal negative heterosis over better parents. The characters' gene action, like additive × additive and additive × dominant, is notable in heterotic estimates. Assessing the GCA of parents involved in crosses was necessary to determine the types of genes operating for hybrid vigor. The cross combinations with high GCA parents suggested that additive × additive gene interactions were responsible for the expression of high relative heterosis and heterobeltiosis. Thus, hybrids with superior performance can be beneficial in the selection process to improve the stomatal dimension. Baloch *et al*. (2013) articulated the results that were also outstanding in their experiment for the stomatal dimension.

Leaf area

Varied positive and negative mid- and better-parent heterosis emerged in normal and heat-stress conditions (Table 4). Under controlled conditions, the calculated maximum positive and negative heterosis over mid-parent manifested in crosses TD-1 × NIA- Sarang and T.J-83 × AS-2002, respectively. Similarly, in NIA-Sarang × Kiran-95 and Benazir × AS-2002, the minimal positive and negative relative heterosis was evident. Furthermore, high and low positive heterobeltiosis was visible in TD-1 × NIA- Sarang and NIA-Sarang × T.J-83 hybrids, respectively, under optimum sowings. Additionally, under delayed sowings, the TD-1 × T.J-83 and TD-1 × AS-2002 hybrids showed the highest positive and

Table 4. Heterotic effect of F_1 hybrids of wheat genotypes for stomatal dimension and leaf area grown under normal and heat-stress conditions.

F_1 hybrids	Stomatal dimension			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	25.28	7.40	17.49	2.30
TD-1 × Kiran-95	-6.66	-17.11	-5.53	-15.77
TD-1 × Benazir	18.67	3.40	10.26	-3.03
TD-1 × T.J-83	2.29	-10.05	3.00	-8.14
TD-1 × AS-2002	11.53	-0.50	7.12	-3.75
NIA-Sarang × Kiran-95	0.24	-3.73	-2.06	-4.67
NIA-Sarang × Benazir	0.82	-1.09	-6.36	-7.43
NIA-Sarang × T.J-83	3.78	0.75	-0.41	-3.09
NIA-Sarang × A.S-2002	0.87	-3.61	-1.36	-4.80
Kiran-95 × Benazir	-2.00	-4.11	-5.88	-7.34
Kiran-95 × T.J-83	-5.97	-7.00	-6.78	-6.81
Kiran-95 × A.S-2002	5.36	4.81	1.16	0.28
Benazir × T.J-83	0.06	-1.01	-1.61	-3.16
Benazir × A-2002	7.81	4.95	2.10	-0.34
T.J-83 × AS-2002	-2.57	-4.14	-4.14	-4.94
F_1 hybrids	Leaf area			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	8.81	4.69	0.06	-4.87
TD-1 × Kiran-95	-5.43	-9.11	-7.21	-11.02
TD-1 × Benazir	2.05	2.01	-4.90	-4.97
TD-1 × T.J-83	2.25	-0.53	2.55	-0.97
TD-1 × AS-2002	-0.99	-3.70	-13.69	-17.48
NIA-Sarang × Kiran-95	0.27	-7.14	0.28	-8.37
NIA-Sarang × Benazir	-2.66	-6.38	-1.60	-6.37
NIA-Sarang × T.J-83	7.00	0.25	-4.70	-12.34
NIA-Sarang × A.S-2002	-4.26	-5.32	-7.03	-7.57
Kiran-95 × Benazir	-1.65	2.46	-6.28	-10.19
Kiran-95 × T.J-83	-4.58	-3.37	-11.61	-12.25
Kiran-95 × A.S-2002	-4.09	2.96	-7.72	-15.23
Benazir × T.J-83	2.26	-0.49	-7.79	-11.02
Benazir × A-2002	-0.24	-3.00	-7.96	-11.93
T.J-83 × AS-2002	-6.65	-11.61	-11.93	-18.55

negative heterosis over mid-parents, respectively. However, in the case of better parent heterosis, all F1 hybrids showed negative heterosis for leaf area. The results showed that two hybrids, TD-1 × NIA-Sarang, and TD-1 × T.J-83, remarkably displayed superior heterotic effects under both environmental circumstances. As a result, these hybrids can be effective in breeding projects to enhance hybrid wheat schemes. The crosses involved high × poor, poor × high, and high × high GCA parents, demonstrating that additive × dominant, dominant × additive and additive × additive gene interactions correlate in heterosis expression. Thus, these two hybrids are options for hybrid crops and hybridization and selection in later segregating generations. Farooq *et al*. (2013) also acquired the best mid-parent and better heterosis values in some of their cross combinations like Inqilab-91 × Shalimar-88, Shalimar-88 × Maya/Pavon, Chenab-2000 × Punjab-85, Maya/Pavon × Chenab-2000, Shalimar-88 × Uqab-2000, and Uqab-2000 × Maya/Pavon for leaf area.

Productive tillers per plant

During timely sown crop conditions, Benazir × AS-2002 manifested the maximum advantageous heterobeltiosis, while TD-1 × Kiran-95 showed the lowest affirmative relative heterosis and NIA-Sarang × Kiran-95 exposed the lowest positive better-parent heterosis (Table 4). Under timely sowing conditions, TD-1 × Benazir exhibited the most deleterious relative and heterobeltiosis, and NIA-Sarang × AS-2002 and Kiran-95 × Benazir presented the least negative mid-parent and better-parent heterosis. Furthermore, under heat-stress circumstances, 13 of the 15 F_1 hybrids showed negative heterosis, with just two hybrids showing progressive mid-parent heterosis and heterobeltiosis. The utmost affirmative and negative heterosis was visible in crosses Benazir × AS-2002 and TD-1 × AS-2002 over mid-parent heterosis. In contrast, minimal positive and negative mid-parent heterosis was prominent in TD-1 × Kiran-95 and NIA-Sarang × Kiran-95 for productive tillers plant^{-1}. In delayed sowing in heat conditions, simultaneously computing the higher and lower progressive heterobeltiosis resulted in crosses Benazir × AS-2002 and TD-1 × AS-2002, respectively. Comparatively, potential hybrids in both environments demonstrated their appropriateness under favorable and unfavorable conditions. The genes displaying increased heterosis were distinguishable by the integration of parents involved in those possible crosses. Such hybrids may be appropriate only for hybrid crop development to enhance the number of tillers in wheat plants. The hybrid Benazir × AS-2002 with relative heterosis and heterobeltiosis in typical sowing time involving parents with poor × poor GCA estimates suggested that dominant × dominant gene interactions expressed high heterosis. This hybrid could be optimal for hybrid wheat development. Under heat-stress conditions, two hybrids, such as Benazir × AS-2002 and TD-1 × AS-2002, showed higher relative heterotic and heterobeltiotic effects with a non-additive × non-additive gene action because the parents had poor × poor GCA estimates. Farooq *et al*. (2014) reported high and desirable relative and high-parent heterosis in some hybrids developed by 7 × 7 diallel crosses.

Spike length

All the crosses showed negative heterosis except NIA-Sarang × T.J-83, which showed positive heterosis over mid-parent. However, maximum and minimum undesirable heterotic effects surfaced over mid-parent by the crosses Kiran-95 × A.S. 2002 and Kiran-95 × TJ-83 under the optimal sowing period (Table 5). Similarly, under delayed sowing with high temperatures, the highest positive and highest negative heterosis occurred over mid-parent in crosses NIA-Sarang × Benazir and Kiran-95 × AS-2002, respectively, for spike size. Moreover, all 15 F_1s revealed deleterious heterobeltiosis under regular sowing conditions. Nevertheless, the high, positive, and deleterious heterobeltiosis in heat-stress conditions appeared from crosses Kiran-95 × T.J-83 and Kiran-95 × AS-2002, respectively. Under heat-stress environments, cross combinations, like Kiran-95 × T.J-83 and Kiran-95 × A.S-2002, which expressed the highest heterosis, used parents with high × poor and poor × poor general combining ability, respectively, demonstrating that the additive × dominant gene action from better and poor parents and dominant × dominant genes from both meager combiners showed high heterosis for the manifestation of spike length. These results further indicated that hybrids, such as Kiran-95 × T.J-83 and Kiran-95 × A.S-2002, with the same gene interactions, are equally productive for hybrid wheat production and selecting desirable plants from segregating populations. Ilker *et al*. (2010) also obtained better results in some hybrids, revealing relative heterosis and heterobeltiotic effects for ear head size.

Spikelets per spike

Under timely sowing conditions, all the 15 F_1s exhibited negative relative heterosis for spikelets spike^{-1}. The largest and smallest negative relative heterosis were apparent in TD-1 × Benazir and NIA-Sarang × AS-2002, respectively (Table 5). Nevertheless, under

Table 5. Heterotic effect of F_1 hybrids of wheat genotypes for productive tillers plant^{-1} and spike length grown under normal and heat-stress conditions.

F_1 hybrids	Productive tillers plant^{-1}			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-2.83	-15.21	-13.90	-27.22
TD-1 × Kiran-95	0.79	-10.85	0.57	-13.41
TD-1 × Benazir	-18.73	-29.12	-21.32	-32.56
TD-1 × T.J-83	-16.27	-24.08	-14.84	-25.19
TD-1 × AS-2002	-14.94	-27.55	-22.15	-34.08
NIA-Sarang × Kiran-95	3.06	1.46	-0.02	-2.20
NIA-Sarang × Benazir	-2.67	-2.72	-3.22	-4.82
NIA-Sarang × T.J-83	7.04	2.53	-1.49	-5.80
NIA-Sarang × A.S-2002	-0.10	-2.89	-4.27	-4.48
Kiran-95 × Benazir	1.00	-0.63	-4.87	1.50
Kiran-95 × T.J-83	-8.75	-11.25	-7.60	-9.73
Kiran-95 × A.S-2002	-2.06	-6.23	-5.15	-7.02
Benazir × T.J-83	-6.28	-10.28	-4.78	-7.45
Benazir × A-2002	15.24	12.09	7.70	6.15
T.J-83 × AS-2002	-3.42	-9.94	-6.17	-10.08
F_1 hybrids	Spike length			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-3.11	-7.09	-7.84	-14.81
TD-1 × Kiran-95	-1.80	-4.62	-2.34	-7.47
TD-1 × Benazir	-2.45	-7.61	-6.38	-12.69
TD-1 × T.J-83	-5.45	-6.78	-8.14	-10.95
TD-1 × AS-2002	-8.21	-9.73	-14.98	-19.19
NIA-Sarang × Kiran-95	-5.49	-6.74	-12.72	-14.98
NIA-Sarang × Benazir	-0.48	-1.75	1.17	0.20
NIA-Sarang × T.J-83	1.19	-1.63	-1.80	-6.51
NIA-Sarang × A.S-2002	-3.89	-6.34	0.88	-2.06
Kiran-95 × Benazir	-7.49	-9.87	-12.67	-14.12
Kiran-95 × T.J-83	-0.13	-1.63	3.22	0.82
Kiran-95 × A.S-2002	-14.05	-15.13	-20.86	-21.13
Benazir × T.J-83	-7.32	-11.02	-6.79	-10.43
Benazir × A-2002	-1.82	-5.51	-5.59	-7.46
T.J-83 × AS-2002	-3.20	-3.44	-2.50	-4.45

* = Relative heterosis, ** = Better parent heterosis

typical sowing, the utmost and least negative heterobeltiosis were demonstrative of TD-1 × Benazir and T.J-83 × AS-2002. Under late sowing in heat-stress conditions, the crosses NIA-Sarang × T.J-83 and TD-1 × Benazir presented the most positive and negative heterosis over mid-parent. Nonetheless, all F_1 hybrids demonstrated negative better-parent heterosis, except for the cross NIA-Sarang × T.J-83, which displayed positive heterosis for spikelets spike^{-1}. The gene action with the highest heterosis gained evaluation by the general combining ability of the parents engaged in said specific combination. The cross NIA-Sarang × T.J-83, which expressed higher heterotic effects under late sowing conditions, contained parents with poor × poor GCA estimates, suggesting that dominant × dominant genes from both parents made distinguishing combinations. Therefore, such a hybrid may be appropriate for only hybrid evolution to expand this trait in wheat. Ahmad *et al*. (2016) concluded that three hybrids demonstrated substantial heterotic effects under normal and heat-stress sowing conditions for this trait.

Grains per spike

Most of the F_1s displayed positive mid-parent heterosis for grains spike^{-1}. The maximum advantageous relative heterosis was noteworthy in the cross NIA-Sarang × Benazir, while the lowest positive heterosis materialized in the cross NIA-Sarang × Kiran-95. However, maximum negative and relative heterosis was evident in cross TD-1 × Kiran-95 under normal sowing time (Table 6). Furthermore, in heat stress, the crosses NIA-Sarang × Benazir and TD-1 × NIA-Sarang presented the most positive and negative heterosis over mid-parent for grains spike^{-1}. Nonetheless, the cross Benazir × AS-2002 showed the highest positive heterobeltiosis. Under the optimal sowing, the cross TD-1 × Benazir revealed the maximum negative better-parent heterosis. Both above-mentioned probable hybrids combined the parents with good × good and good × poor general combiners. These results demonstrated that high heterosis of mid- and better parents under both environmental

Table 6. Heterotic effect of F_1 hybrids of wheat genotypes for spikelets spike^1 and grains spike^{-1} grown under normal and heat-stress conditions.

F_1 hybrids	Spikelets spike^1			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-4.05	-7.20	-14.14	-19.48
TD-1 × Kiran-95	-2.44	-6.37	-3.32	-8.59
TD-1 × Benazir	-18.01	-21.52	-18.27	-23.64
TD-1 × T.J-83	-12.02	-19.35	-10.19	-18.57
TD-1 × AS-2002	-10.40	-17.90	-13.95	-21.97
NIA-Sarang × Kiran-95	-15.91	-16.58	-16.98	-17.70
NIA-Sarang × Benazir	-7.77	-8.75	-10.10	-10.46
NIA-Sarang × T.J-83	-1.94	-7.24	28.35	23.80
NIA-Sarang × A.S-2002	-0.66	-6.06	-1.32	-4.81
Kiran-95 × Benazir	-2.76	-3.03	-7.20	-8.36
Kiran-95 × T.J-83	2.48	-2.33	2.49	-1.98
Kiran-95 × A.S-2002	-5.98	-10.41	-10.01	-13.93
Benazir × T.J-83	-8.53	-12.59	-9.34	-12.23
Benazir × A-2002	-4.90	-9.15	-6.42	-9.39
T.J-83 × AS-2002	-1.06	-1.09	-5.62	-5.61
F_1 hybrids	Grains spike^{-1}			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-0.79	-4.56	-12.59	-24.59
TD-1 × Kiran-95	-3.86	-5.32	1.78	-6.15
TD-1 × Benazir	2.41	-6.46	0.00	-14.34
TD-1 × T.J-83	1.85	-5.70	-1.39	-12.70
TD-1 × AS-2002	6.03	-3.04	6.95	-8.61
NIA-Sarang × Kiran-95	0.80	-1.57	11.75	3.88
NIA-Sarang × Benazir	13.37	7.41	31.62	30.51
NIA-Sarang × T.J-83	6.21	2.06	15.62	12.23
NIA-Sarang × A.S-2002	8.94	7.82	18.29	16.95
Kiran-95 × Benazir	5.41	-2.35	5.26	-2.91
Kiran-95 × T.J-83	6.89	0.39	11.17	6.31
Kiran-95 × A.S-2002	2.33	-5.10	11.35	2.43
Benazir × T.J-83	4.20	2.68	12.71	8.51
Benazir × A-2002	11.45	12.84	22.19	21.84
T.J-83 × AS-2002	7.24	5.80	17.45	12.77

* = Relative heterosis, ** = Better parent heterosis

conditions in both hybrids had control by additive × additive and additive × dominant types of gene interactions. Hence, the crosses NIA-Sarang × Benazir, NIA-Sarang × Benazir, TD-1 × NIA- Sarang, and Benazir × AS-2002 are vital for measuring, either for hybrid wheat improvement or an assortment of advantageous plants from earlier filial generations. Patel *et al*. (2018) reported that five hybrids, which articulated high relative heterosis and heterobeltiosis for seeds spike^{-1}, gave higher grain yields.

Grain yield per plant

F_1 hybrids demonstrated positive heterosis over mid-parents, while seven F_1s presented negative heterosis over mid-parents in a series of crosses assessed (Table 6). Furthermore, the highest positive and negative heterosis over mid-parent came from Benazir × TJ-83 and TD-1 × Benazir, respectively. Similarly, the calculated highest positive heterobeltiosis was in Benazir × TJ-83, and the maximum negative heterosis over better parent appeared in the cross TD-1 × Benazir under regular sowing time. Nonetheless, in late sowing under heat-stress conditions, most crosses showed negative heterosis over mid-parent, while several hybrids offered positive heterosis over mid-parent. The utmost positive and negative heterosis over mid-parent was remarkable in Benazir × T.J-83 and TD-1 × Benazir for grain yield, respectively. In addition, the maximum positive and negative heterosis over better parents was evident in crosses Benazir × TJ-83 and TD-1 × Benazir, respectively. The cross Benazir × T.J-83 was the only one performing better in both the sowing conditions for mid-parent and better-parent heterosis. Thus, this cross can serve as low × good GCA parents, establishing that better heterosis was attainable by a dominant × additive complementary gene interaction, suggesting that such hybrids may be worthwhile in favor of hybrids' evolution or single-plant selections. This promising hybrid can help increase grain production under normal and heat-stress planting conditions. Dedaniya *et al*. (2018) performed line × tester mating crosses and reported sizeable heterotic effects for agronomic attributes and grain yield in four hybrids.

1000-grain weight

Except for Benazir × TJ-83, all other F_1s presented undesirable heterosis over mid-parent. The highest and lowest negative heterosis over mid-parent appeared in crosses NIA-Sarang × T.J-83 and NIA-Sarang × Benazir, respectively (Table 7). Similarly, the cross Benazir × AS-2002 showed maximum positive better-parent heterosis in optimum sowing conditions. The most positive heterosis computation emerged under heat-stress circumstances in the cross NIA-Sarang × T.J-83 over mid-parent; however, the utmost negative heterosis was prominent in the cross Kiran-95 × A.S-2002 over mid-parent. Only one cross (NIA-Sarang × T.J-83) showed maximum positive relative heterosis, while the remaining crosses displayed negative heterobeltiosis. These results demonstrated that high mid-parent and better parent heterosis in NIA-Sarang × T.J-83, Benazir × AS-2002, and NIA-Sarang × T.J-83 had apportioning with additive × additive and additive × dominant gene interactions under both non-stressed and stressed environmental conditions. Hence, these three crosses are crucial for hybrid wheat improvement or development via selecting good plants from earlier segregating generations. Ilker *et al*. (2010) observed noteworthy results for mid- and better-parent heterosis in the seed index while studying 15 hybrids of first filial generation to improve this trait in wheat breeding programs.

Grain-filling duration

Positive and negative heterotic effects were evident for mid- and better parents in both sowing conditions (Table 8). Furthermore, maximum and minimum positive effects were notable in crosses Kiran-95 × Benazir and Kiran-95 × T.J-83, respectively, over the mid-parent under non-stress conditions. Moreover, the highest positive and negative heterosis over better parents had manifestations from crosses Kiran-95 × Benazir and NIA-Sarang ×

Benazir, respectively. Under heat stress, the highest positive and negative heterosis over better parent was indicative in crosses NIA-Sarang × Kiran-95 and TJ-83 × AS-2002, respectively. The top-scoring hybrids were Kiran-95 × Benazir and NIA-Sarang × Kiran-95, demonstrating greater mid-parent and better-parent heterosis during optimum and heat-stress conditions. Hence, they proved themselves candidates for hybrid wheat development under a versatile atmosphere for grain-filling duration. Concerning gene action in demonstrating high heterotic effects, these crosses related with poor × poor GCA parents, articulating that heterosis was due to dominant × dominant gene interactions; hence, such scrupulous cross combinations are appropriate only for hybrid wheat to increase the grain-filling duration. The study findings agreed with those presented by Singh *et al*. (2014), who experimented on 45 crosses under optimum and heat-stress conditions. Numerous hybrids occurred expressing desirable relative heterosis and heterobeltiosis under both conditions for the grain-filling period.

Table 7. Heterotic effect of F_1 hybrids of wheat genotypes for grain yield plant^{1} and 1000-seed weight grown under normal and heat-stress conditions.

F_1 hybrids	Grain yield plant^{-1}			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-4.77	-10.84	-10.58	-17.75
TD-1 × Kiran-95	0.16	-4.41	-1.07	-4.87
TD-1 × Benazir	-10.54	-16.72	-13.50	-19.88
TD-1 × T.J-83	0.49	-4.72	0.94	-4.04
TD-1 × AS-2002	-4.96	-9.96	-7.65	-15.15
NIA-Sarang × Kiran-95	-4.20	-6.11	-6.53	-10.76
NIA-Sarang × Benazir	2.20	1.57	-2.79	-3.54
NIA-Sarang × T.J-83	2.32	0.96	2.36	-1.14
NIA-Sarang × A.S-2002	2.79	1.51	2.57	2.45
Kiran-95 × Benazir	6.73	3.97	1.20	-2.67
Kiran-95 × T.J-83	-1.21	-1.90	-0.75	-1.93
Kiran-95 × A.S-2002	-1.33	-2.10	-2.69	-7.20
Benazir × T.J-83	8.14	6.07	6.21	3.35
Benazir × A-2002	-2.70	-4.49	-3.57	-4.42
T.J-83 × AS-2002	3.03	2.94	3.82	0.15

F_1 hybrids	1000-seed weight			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	-2.53	-1.33	-3.92	-7.16
TD-1 × Kiran-95	-1.74	-1.36	-0.07	-0.28
TD-1 × Benazir	-2.87	-4.17	-4.27	-7.59
TD-1 × T.J-83	-0.41	-0.75	-0.66	-1.90
TD-1 × AS-2002	-2.61	-2.25	-6.01	-8.97
NIA-Sarang × Kiran-95	-3.11	-4.17	-4.87	-8.27
NIA-Sarang × Benazir	-0.17	-0.03	-2.93	-3.03
NIA-Sarang × T.J-83	-10.03	-11.65	22.97	20.29
NIA-Sarang × A.S-2002	-3.36	-1.53	-1.90	-2.15
Kiran-95 × Benazir	-0.89	-2.38	-1.36	-4.97
Kiran-95 × T.J-83	-2.32	-2.48	-5.08	-6.46
Kiran-95 × A.S-2002	-6.08	-5.89	-6.49	-9.62
Benazir × T.J-83	0.97	-2.21	-2.85	-5.06
Benazir × A-2002	-1.77	1.47	-4.42	-4.75
T.J-83 × AS-2002	-3.42	-3.27	-5.07	-3.15

* = Relative heterosis, ** = Better parent heterosis

Table 8. Heterotic effect of F_1 hybrids of wheat genotypes grain-filling duration grown under normal and heat-stress conditions.

F_1 hybrids	Grain-filling duration			
	Normal		Heat-stress	
	R.H. *(%)	B.P. **(%)	R.H. *(%)	B.P. **(%)
TD-1 × NIA-Sarang	2.45	0.00	4.59	3.29
TD-1 × Kiran-95	-0.96	-2.92	1.64	1.55
TD-1 × Benazir	1.58	0.58	-1.06	-1.81
TD-1 × T.J-83	-1.05	-2.24	-0.09	-0.50
TD-1 × AS-2002	2.13	1.42	-2.04	-2.52
NIA-Sarang × Kiran-95	0.89	0.45	4.93	3.71
NIA-Sarang × Benazir	-2.00	-3.41	0.01	-0.49
NIA-Sarang × T.J-83	0.95	-0.27	1.94	0.26
NIA-Sarang × A.S-2002	-0.75	-2.46	0.78	-0.97
Kiran-95 × Benazir	2.86	1.82	1.88	1.20
Kiran-95 × T.J-83	0.61	-0.18	0.69	0.19
Kiran-95 × A.S-2002	2.09	0.76	2.89	2.29
Benazir × T.J-83	-1.14	-1.36	0.11	-1.05
Benazir × A-2002	1.07	0.77	0.58	-0.67
T.J-83 × AS-2002	1.56	1.04	-2.53	-2.61

* = Relative heterosis, ** = Better parent heterosis.

CONCLUSIONS

The results suggested only a few wheat (*T. aestivum* L.) hybrids manifested consistently higher heterosis for most traits. Several hybrids, such as TD-1 × Kiran-95, NIA-Sarang × TJ-83, and Benazir × AS-2002, were superior for productive tillers plant^{-1}, spike length, spikelets spike^{-1}, grains spike^{-1}. TD-1 × Kiran-95, NIA-Sarang × Benazir, and TJ-83 × AS-2002, for grain yield plant^{-1} and yield ha^{-1}, were reliable hybrids for expressing simultaneously higher SCA effects for several traits. Some F_1 hybrids expressed vigor for many traits; therefore, such hybrids may require further exploration under late sowing heat-stress conditions to confirm their performance for heat tolerance.

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