



RESEARCH ARTICLE

Assessment of heterosis for grain yield and component traits in bread wheat (*Triticum aestivum* L. em Thell)

B L Dhaka^{1*}, D K Gothwal¹, A C Shivran², S S Rajput¹, R R Choudhary¹, M K Poonia³, S K Sharma¹, S Choudhary⁴ & A S Kharbas¹

¹Division of Genetics and Plant Breeding, Sri Karan Narendra Agriculture University, Jobner, Jaipur 303 328, Rajasthan, India

²Division of Agronomy, Sri Karan Narendra Agriculture University, Jobner, Jaipur 303 328, Rajasthan, India

³Division of Genetics and Plant Breeding, Swami Keshwanand Rajasthan Agricultural University, Bikaner 334 006, Rajasthan, India

⁴Division of Genetics and Plant Breeding, Maharana Pratap University of Agriculture and Technology, Udaipur 313 001, Rajasthan, India

*Correspondence email - bdhaka707@gmail.com

Received: 11 July 2025; Accepted: 18 June 2026; Available online: Version 1.0: 30 July 2026

Cite this article: Dhaka BL, Gothwal DK, Shivran AC, Rajput SS, Choudhary RR, Poonia MK, Sharma SK, Choudhary S, Kharbas AS. Assessment of heterosis for grain yield and component traits in bread wheat (*Triticum aestivum* L. em Thell). Plant Science Today. 2026; 13(sp5): 1-10.

<https://doi.org/10.14719/pst.10592>

Abstract

The present study was conducted under two environments created by different sowing dates, namely normal and late sowing (heat stress environment). During rabi 2022–23, eight genetically diverse parents were crossed in a half diallel mating design. These eight parents, along with their 28 F₁ progenies, were evaluated in a randomised block design (RBD) with 3 replications during rabi 2023–24 at the Instructional Farm of Sri Karan Narendra College of Agriculture, Jobner, Rajasthan, India. A substantial degree of heterosis and heterobeltiosis was observed for all the traits studied. Among the significant and desirable heterobeltiosis crosses, HD 2932 × Raj 4238, HD 2864 × Raj 4238, MP 3336 × Raj 4238, MP 3336 × HD 2932, HD 2864 × HD 2932, MP 3336 × CG 1029, Raj 4238 × CG 1029 and Raj 4238 × HI 1634 were identified as promising in the normal environment (E₁). In the heat stress environment (E₂) the crosses, MP 3336 × HI 1634, Raj 4238 × Raj 3777, HD 2932 × HI 1634 and HD 2864 × Raj 3765 exhibited desirable heterobeltiosis. Notably, HD 2864 × CG 1029 performed well in both environments. Overall, these crosses emerge as promising candidates for achieving significant improvement in wheat (*Triticum aestivum* L.) grain yield and its component traits under both normal and heat stress conditions.

Keywords: heat stress; heterobeltiosis; heterosis; wheat

Introduction

Wheat (*Triticum aestivum* L.) belonging to family Poaceae is one of the major and the most consumed cereals of the world (1). Wheat is one of the world's most valuable and widely grown crops, used primarily for human consumption and supports nearly 35 % of the world's population (2). Wheat development is as old as humanity and the first crop mentioned in BIBLE is considered to be this. Earlier studies reported that the wheat originated in the Euphrates and Tigris valley (3). Durum wheat is believed to have originated in Abyssinia and soft wheat groups found in the area of Western Pakistan, South West Afghanistan and South Mountainous Babshara sections (4).

The genus *Triticum* is composed of diploid, tetraploid and allohexaploid species. So, polyploidy has played a major role in wheat evolution. The diploid species (2n = 2 (x) = 14) (commonly known as 'einkorn wheats') as *Triticum monococcum* L. and *Triticum urartu* Thumanjan ex Gandiljan is usually found in the wild and its grains are hulled. *Triticum monococcum* is also grown in small quantities for consumption in some areas. The tetraploid species (2n = 4 (x) = 28) contain both hulled and hullless. The wild species *Triticum turgidum* subsp. *dicoccoides* and domesticated *Triticum turgidum* subsp. *dicoccum* (now designated as

Triticum dicoccum or *Triticum dicoccon*) is hulled, commonly referred to as emmer wheat and *Triticum turgidum* subsp. *durum* (now designated as *Triticum durum*) is hullless and commonly referred as macaroni wheat. The hexaploid hulled wheat (2n = 6 (x) = 42) species are *Triticum aestivum* subsp. *spelta* and *Triticum aestivum* subsp. *macha*. *Triticum aestivum* subsp. *aestivum* presently referred as bread wheat (5).

Heterosis breeding has long been recognised as a potential method for increasing yield in cross-fertilised crops. However, the commercial exploitation of heterosis in self-pollinated crops such as wheat has been limited due to the technical and practical difficulties associated with hybrid seed production. Therefore, the early identification of superior crosses is essential for handling breeding material efficiently and effectively in the advanced generations. Hybrid vigour or heterosis, has been known in wheat for a long time, but its utilisation has been constrained by the self-pollinating nature of the crop. Several methods have been developed for producing wheat hybrids, including hand emasculatation, the use of chemical hybridising agents and male sterility systems. Among these, hand emasculatation is highly laborious and is therefore used primarily for research purposes or for developing breeding materials.

Heat stress during post-anthesis and grain-filling stages may reduce availability and translocation of photosynthates to the developing kernels and starch synthesis and deposition within the kernel, thus resulting in lower grain weight and altered grain quality. It has been observed that each degree rise in ambient temperature reduces the yield by 3–4 %.

In the development of new genotypes with desirable traits, the selection of suitable parents is one of the most critical steps in any breeding programme. It has now become evident that self-pollinated crops can exhibit levels of heterosis comparable to those observed in cross-pollinated crops (6). Economic heterosis, also known as standard or useful heterosis, refers to the superiority of an F_1 hybrid over a standard commercial variety or check. Hybrid performance is typically assessed in terms of the percentage increase or decrease in heterosis and heterobeltiosis. However, from a breeder's perspective, heterobeltiosis is more valuable than heterosis, particularly in self-pollinating crops where the primary objective is to identify superior hybrids (7–8).

Therefore, the present study was conducted to identify superior genotypes and their crosses, assess the magnitude and extent of heterosis in hybrid and evaluate heat stress tolerance. The study aimed to better understand the genetic architecture and mode of inheritance of yield-related traits, heat tolerance and their associated characteristics.

Materials and Methods

Location, climate and weather condition

The research experiment was conducted during rabi 2022–23 and 2023–24 at the Instructional Farm of Sri Karan Narendra College of Agriculture, Jobner (Rajasthan) which is situated at an altitude of 435 m above mean sea level, at a latitude of 26°5' N and longitude of 75°20' E. It falls under agro-climatic zone III-A (semi-arid eastern plain zone) and is characterised by loamy-sandy soils. The average annual rainfall in the region is approximately 400 mm, most of which is received from the Southwest monsoon, typically from the last week of June to the end of September. The climate of this zone is typically semi-arid, with extreme temperatures in both summer and winter. Summer temperatures may rise as high as 46°C, while winter temperatures can drop below the freezing point. Weather parameters play a crucial role in influencing plant growth and the overall development of crops.

Experimental material

Eight genetically diverse wheat genotypes were selected based on a broad range of genetic diversity for major yield components from the germplasm maintained under the All India Coordinated Wheat and Barley Improvement Project (AICW and BIP) at the Rajasthan Agricultural Research Institute, Durgapura. These eight parents

HD 2864, MP 3336, Raj 3765, HD 2932, Raj 4238, Raj 3777, CG 1029 and HI 1634 were crossed in a half diallel fashion (excluding reciprocals) using hand emasculatation. The pedigrees of the parents used in the study are given in Table 1.

During rabi 2022–23, crossing blocks were established and direct F_1 crosses were produced with sufficient seed following a half diallel mating design. The experimental material, consisting of 8 parents and 28 F_1 crosses, was planted during rabi 2023–24 under two environments: normal (E_1) and heat stress (E_2). All genotypes were evaluated in a randomised block design (RBD) with three replications in both environments. Each plot for the non-segregating generations (parents and F_1 's) consisted of two rows, each 2 m long, with a row spacing of 30 cm and an inter-plant spacing of 10 cm in both environments.

Design of the environments

In order to create heat stress condition at post anthesis, the sowing in the E_2 was delayed by about 30 days later than the E_1 during rabi 2023–24. Thus, late sowing created post anthesis E_2 as it exposed the crop to heat stress after anthesis. The detail of each environment and date of sowing was as follows:

E_1 (Normal environment) - November 11, 2023

E_2 (Heat stress environment) - December 11, 2023

Observations recorded

Observations were recorded on days to 75 % heading, days to maturity, flag leaf area (cm^2), effective tillers per plant, grains per spike, 1000-grain weight (g), biological yield per plant (g), grain yield per plant (g), harvest index (%), protein content (%), proline content ($\mu\text{g}/100$ mg fresh weight), total chlorophyll content (mg/g fresh weight) and membrane stability index (%) on 10 randomly selected plants in each of the F_1 's progenies along with each parent from each replication except days to 75 % heading, days to maturity and 1000-grain weight which were observed on plot basis.

Heterosis (Heterosis over mid parent)

Heterosis is expressed as per cent deviation from mid parent, whereas heterobeltiosis expressed as per cent deviation toward desirable direction over better parent. Heterosis and heterobeltiosis were calculated according to the method suggested from some previous studies (9, 10)

Per cent heterosis of a cross was calculated by the following formula:

$$\text{Heterosis in per cent} = \frac{\bar{F}_1 - \overline{\text{MP}}}{\overline{\text{MP}}} \times 100$$

where,

$\bar{F}_1$ = Mean value of hybrid

Table 1. The pedigrees of the parents used in the study

Sl. No.	Name of genotype	Special characteristic	Parent	Parentage
1.	HD 2864	Highly resistance to brown rust, suitable for late sown condition and high yielding	DL 509-2/ DL 377- 8	
2.	MP 3336	Resistance to brown and black rust, late sown and high yielding	HD 2402/GW 173	
3.	Raj 3765	Tolerance to terminal heat stress, very late sown and high yielding	HD 2402/VL639	
4.	HD 2932	Resistance to brown rust, high Zn content, late sown and high yielding	KAUZ/STAR//HD 2643	
5.	Raj 4238	Good for chapatti making quality and high yielding	HW 2021/RAJ 3765	
6.	Raj 3777	Tolerance to terminal heat stress, LS/IR/RF and high yielding	RAJ3160/HD2449	
7.	CG 1029	Suitable for irrigated late sown condition and high yielding	HW 2004/ PHS 725	
8.	HI 1634	Good chapatti quality, high grain hardness and high yielding	GW 322/PBW 498	

LS – Late Sown, IR – Irrigated, RF – Rainfed.

$\overline{MP}$ = Mean of the two parents involved in the particular cross

Heterobeltiosis (Heterosis over better parent)

Per cent heterobeltiosis of a cross was calculated by the following formula (10).

$$\text{Heterobeltiosis in per cent} = \frac{\bar{F}_1 - \overline{BP}}{\overline{BP}} \times 100$$

where,

$\bar{F}_1$ = Mean value of hybrid

$\overline{BP}$ = Mean value of the better parent over replications

Significance of heterosis and heterobeltiosis estimates was done using 't' test. The standard error (SE) for testing the significance was calculated using the following formula:

$$SE_{(\bar{F}_1 - \overline{MP})} = \left(\frac{3 \times EMS}{2 \times r} \right)^{1/2}$$

$$SE_{(\bar{F}_1 - \overline{BP})} = \left(\frac{2 \times EMS}{r} \right)^{1/2}$$

The 't' value was estimated by the following formula,

$$t_{(r-1)(g-1)} = (\bar{F}_1 - \overline{MP}) / SE_{(\bar{F}_1 - \overline{MP})}$$

$$t_{(r-1)(g-1)} = (\bar{F}_1 - \overline{BP}) / SE_{(\bar{F}_1 - \overline{BP})}$$

where,

$\bar{F}_1$ = Mean value of hybrid

$\overline{MP}$ = Mean of the two parents involved in the particular cross

$\overline{BP}$ = Mean value of the better parent over replications

r = Number of replications

g = Number of genotypes

EMS = Error mean square from analysis

The calculated 't' value was compared with table value at error degree of freedom that is (r-1) (g-1). To calculate heterobeltiosis, parent with higher mean values were considered desirable for all the characters except for days to 50 % flowering and days to maturity where negative direction was considered desirable.

Results and Discussion

The present experiment, conducted using eight diverse wheat (*Triticum aestivum* L.) genotypes, was carried out to assess heterosis and heterobeltiosis for yield and its contributing traits under both normal and heat stress conditions.

Analysis of variance for individual environments revealed significant differences among the genotypes for all traits under both normal and heat-stress conditions, except for effective tillers per plant in E_1 (Table 2). Furthermore, partitioning of genotypes into parents and F_1 's showed significant differences for all traits in both environments, except for effective tillers per plant in E_1 and harvest index in E_1 for the F_1 's and biological yield per plant in E_2 for both parents and F_1 's. Significant differences between parents and F_1 's were observed for all traits except effective tillers per plant in E_1 and harvest index and protein content in both environments.

Heterosis and heterobeltiosis analyses for various characters revealed that some cross combinations exhibited

desirable heterosis for more than one trait, while others showed desirable heterosis for only a single trait. Under E_1 and E_2 conditions, the magnitude of heterosis also varied among different crosses. The extent of heterosis provides valuable information on the degree of genetic diversity among the parents and aids in selecting superior parental combinations to exploit hybrid vigour in the F_1 generation. Heterosis results from allelic or non-allelic gene interactions influenced by specific environmental conditions. Wheat, being a self-pollinated crop, lacks an efficient commercial-scale hybrid seed production system. Consequently, heterosis itself may not have direct economic value at present. However, understanding the degree and magnitude of heterosis is crucial for designing future breeding programmes and identifying promising crosses that may yield superior segregants in advanced generations, ultimately contributing to the improvement of grain yield in wheat. The range of heterosis and the number of crosses exhibiting significant desirable heterosis and heterobeltiosis for all traits are presented in Table 3.

Higher grain yield is the primary objective of any breeding programme; therefore, positive and significant heterosis and heterobeltiosis for this trait are desirable. In E_1 , heterosis ranged from -6.30 HD 2864 × MP 3336 to 50.26 HD 2864 × Raj 4238, while in E_2 it ranged from -5.44 % HD 2864 × HI 1634 to 33.95 MP 3336 × HI 1634. Heterobeltiosis varied from 0.51 MP 3336 × HI 1634 to 32.33 HD 2932 × Raj 4238 in E_1 and from 1.35 Raj 3765 × CG 1029 to 33.87 MP 3336 × HI 1634 in E_2 . Out of the 28 crosses, 17 in E_1 and 14 in E_2 exhibited significant positive heterosis over the mid-parent, while 9 crosses in E_1 and 5 in E_2 showed significant positive heterobeltiosis. These crosses were therefore considered the most desirable for improving grain yield (Table 4).

Maximum desirable heterosis was exhibited by the cross HD 2864 × Raj 4238 (50.26 %) followed by HD 2932 × Raj 4238 (44.38 %) in E_1 and MP 3336 × HI 1634 (33.95 %) followed by Raj 3765 × HD 2932 (17.56 %) in E_2 . The maximum desirable heterobeltiosis was exhibited by the cross HD 2932 × Raj 4238 (32.33 %) followed by HD 2864 × Raj 4238 (29.71 %) in E_1 and MP 3336 × HI 1634 (33.87 %) followed by HD 2864 × CG 1029 (14.33 %) in E_2 .

Comparison across the environments revealed that the crosses HD 2864 × CG 1029 in both environments and HD 2864 × HD 2932, HD 2864 × Raj 4238, MP 3336 × HD 2932, MP 3336 × Raj 4238, MP 3336 × CG 1029, HD 2932 × Raj 4238, Raj 4238 × CG 1029 and Raj 4238 × HI 1634 in E_1 and HD 2864 × Raj 3765, MP 3336 × HI 1634, HD 2932 × HI 1634 and Raj 4238 × Raj 3777 in E_2 showed significant positive heterosis and heterobeltiosis, hence these crosses were considered most desirable for improvement of grain yield per plant in each environment. Therefore, the crosses which showed positive significant heterosis and heterobeltiosis under specific environment may be considered suitable material for environment specific breeding.

The level of heterosis in a crop depends on how effectively it has been exploited and on the feasibility of producing hybrid seeds. In crop breeding, heterosis is particularly valuable when it can be successfully utilised for hybrid development. Its true utility is realised in advanced generations, where it helps identify desirable crosses and obtain superior segregants. This approach ultimately aims to enhance

Table 2. Analysis of variance showing mean squares in normal (E₁) and heat stress environment (E₂) for parents and F₁'s for yield and its contributing traits in bread wheat

Characters	Environments		Source of variations				
		Replications (2)	Genotypes (35)	Parents (7)	F ₁ 's (27)	Parents vs F ₁ 's (1)	Error (70)
Days to 75 % heading	E ₁	1.56	11.77**	13.76**	10.53**	31.14**	3.24
	E ₂	7.34	44.12**	30.67**	43.69**	149.85**	5.57
Days to maturity	E ₁	10.48	21.03**	28.74**	12.72*	191.43**	7.33
	E ₂	3.79	16.92**	49.50**	7.74*	36.84**	4.26
Flag leaf area (cm ²)	E ₁	0.97	51.54**	69.80**	44.14**	123.47**	9.20
	E ₂	8.12	87.45**	172.00**	67.51**	33.89*	8.63
Effective tillers per plant	E ₁	1.88	0.48	1.55**	0.21	0.09	0.45
	E ₂	0.24	1.88**	0.99**	1.24**	25.25**	0.17
Grains per spike	E ₁	3.95	48.10**	111.79**	25.70**	206.89**	7.07
	E ₂	5.83	62.15**	63.39**	29.08**	946.36**	4.78
1000-Grain weight (g)	E ₁	8.56	18.84**	17.37**	17.81**	57.03**	4.23
	E ₂	8.91	20.81**	35.92**	16.95*	19.38**	8.72
Biological yield per plant (g)	E ₁	12.51	71.30**	65.61*	47.24*	760.71**	24.10
	E ₂	11.38	25.37*	30.01	22.68	65.70*	15.89
Grain yield per plant (g)	E ₁	4.02	20.93**	31.17**	11.69**	198.90**	3.26
	E ₂	1.26	6.26**	5.99**	5.19**	36.94**	1.00
Harvest index (%)	E ₁	10.64	17.60*	27.73*	14.34	34.80	10.70
	E ₂	9.66	41.12**	63.81**	34.09*	72.22	20.11
Protein content (%)	E ₁	1.74	0.59**	0.73**	0.57**	0.23	0.07
	E ₂	1.72	0.53**	0.73**	0.50**	0.06	0.08
Proline content (µg/100 mg fresh weight)	E ₁	15.70	1005.88**	1124.46**	967.73**	1205.63**	19.93
	E ₂	14.40	1036.70**	554.23**	1194.42**	155.86*	22.97
Total chlorophyll content (mg/g fresh weight)	E ₁	0.01	1.35**	0.72**	1.44**	3.08**	0.01
	E ₂	0.00	0.98**	0.55**	1.06**	1.68**	0.01
Membrane stability index	E ₁	1.43	118.54**	81.65**	130.82**	45.38**	4.41
	E ₂	4.04	86.22**	78.26**	89.79**	45.59**	5.12

*, ** Significant at 5 % and 1 % respectively.

Table 3. Range of heterosis, heterobeltiosis and desirable crosses for grain yield and its component traits under normal and heat stress environment

Character	Range of heterosis						No. of crosses showing heterosis					
	Heterosis (over mid -parent)			Heterobeltiosis			Heterosis (over mid -parent)			Heterobeltiosis		
	E ₁	E ₂	E ₁	E ₂	E ₁	E ₂	E ₁	E ₂	E ₁	E ₂	E ₁	E ₂
Days to 75 % heading	-3.14 - 5.61	-5.49 - 13.85	-2.75 - -1.05	-2.27 - -1.54	2	1	0	0	0	0		
Days to maturity	-3.37 - 6.41	-2.71 - 8.59	-2.76 - -0.26	-2.18 - -0.01	1	2	0	0	0	0		
Flag leaf area (cm ²)	-18.05 - 52.18	-39.04 - 39.97	1.94 - 49.17	2.21 - 33.69	10	4	4	4	1	1		
Effective tillers per plant	-12.86 - 16.41	0.39 - 65.74	1.36 - 14.07	0.01 - 65.08	1	23	0	0	14	14		
Grains per spike	-15.77 - 28.63	-9.43 - 44.52	0.41 - 27.19	2.36 - 65.03	12	23	8	8	17	17		
1000-Grain weight (g)	-7.83 - 14.49	-6.80 - 21.45	1.29 - 14.25	0.74 - 19.65	9	4	3	3	1	1		
Biological yield per plant (g)	-4.94 - 32.83	-11.57 - 21.12	1.84 - 24.18	0.38 - 15.43	15	5	6	6	0	0		
Grain yield per plant (g)	-6.30 - 50.26	-5.44 - 33.95	0.51 - 32.33	1.35 - 33.87	17	14	9	9	5	5		
Harvest index (%)	-9.09 - 21.43	-9.75 - 28.28	0.32 - 15.62	0.25 - 24.30	4	5	1	1	1	1		
Protein content (%)	-9.24 - 9.34	-10.03 - 8.34	0.79 - 7.87	0.15 - 7.30	9	8	4	4	2	2		
Proline content (µg/100 mg fresh weight)	-58.53 - 61.96	-35.94 - 42.29	0.57 - 51.80	0.23 - 27.27	5	9	1	1	5	5		
Total chlorophyll content (mg/g fresh weight)	-28.27 - 55.09	-27.11 - 44.34	0.71 - 46.76	0.19 - 38.05	17	16	11	11	10	10		
Membrane stability index (%)	-24.23 - 24.37	-20.77 - 22.67	0.39 - 16.05	3.77 - 13.90	7	7	3	3	3	3		

Table 4. Estimates of heterosis and heterobeltiosis for grain yield per plant under normal (E_1) and heat stress environment (E_2)

Crosses	E_1		E_2	
	H	HB	H	HB
HD 2864 × MP 3336	-6.30	-	3.07	-
HD 2864 × Raj 3765	2.91	-	10.59**	9.95*
HD 2864 × HD 2932	28.98**	20.73**	13.54**	5.73
HD 2864 × Raj 4238	50.26**	29.71**	2.09	-
HD 2864 × Raj 3777	9.40	2.68	7.91*	5.64
HD 2864 × CG 1029	27.61**	20.94**	14.40**	14.33**
HD 2864 × HI 1634	-4.39	-	-5.44	-
MP 3336 × Raj 3765	20.45**	9.60	6.18	-
MP 3336 × HD 2932	27.91**	21.88**	0.07	-
MP 3336 × Raj 4238	41.83**	24.42**	-0.48	-
MP 3336 × Raj 3777	1.95	-	14.96**	5.91
MP 3336 × CG 1029	22.73**	18.44*	11.89**	5.21
MP 3336 × HI 1634	4.61	0.51	33.95**	33.87**
Raj 3765 × HD 2932	15.76**	0.87	17.56**	8.89
Raj 3765 × Raj 4238	23.48**	-	5.28	2.83
Raj 3765 × Raj 3777	-2.76	-	-0.41	-
Raj 3765 × CG 1029	-2.14	-	2.00	1.35
Raj 3765 × HI 1634	9.90	3.84	6.21	-
HD 2932 × Raj 4238	44.38**	32.33**	14.24**	3.54
HD 2932 × Raj 3777	12.20*	-	14.06**	4.15
HD 2932 × CG 1029	13.21*	11.73	11.69**	4.07
HD 2932 × HI 1634	18.08**	8.32	12.28**	11.26*
Raj 4238 × Raj 3777	18.54**	-	13.03**	12.11**
Raj 4238 × CG 1029	29.59**	17.36*	2.35	-
Raj 4238 × HI 1634	34.46**	13.98*	7.37	-
Raj 3777 × CG 1029	0.72	-	-0.52	-
Raj 3777 × HI 1634	-1.65	-	2.51	-
CG 1029 × HI 1634	15.89*	7.61	15.55**	8.59

*, ** Significant at 5 % and 1 % respectively.

grain yield and improve overall productivity in wheat breeding programs. Therefore, the present experiment was conducted to investigate the genetic architecture of yield and its related traits in wheat using a half diallel mating design involving eight parents.

The mean values for all the 13 characters of F_1 hybrids were compared with the values of mid parent (heterosis) and over better parent (heterobeltiosis) expressed as percentage increase or decrease. Similar findings in different environments for different characters were also reported from previous studies (11–17). The superiority of hybrids particularly over better parent (heterobeltiosis) is more important and useful in determining the feasibility of commercial exploitation of heterosis and also indicating the parental combinations capable of producing the highest level of transgressive segregants.

Significant heterobeltiosis crosses for grain yield per plant are presented in Table 5. Examination of the data indicates that the crosses HD 2932 × Raj 4238, HD 2864 × Raj 4238, MP 3336 × Raj 4238, MP 3336 × HD 2932, HD 2864 × HD 2932, MP 3336 × CG 1029, Raj 4238 × CG 1029 and Raj 4238 × HI 1634 in E_1 , as well as MP 3336 × HI 1634, Raj 4238 × Raj 3777, HD 2932 × HI 1634 and HD 2864 × Raj 3765 in E_2 , exhibited significant heterobeltiosis. In addition, HD 2864 × CG 1029 showed significant heterotic effects across both environments. These crosses emerged as strong candidates for grain yield and related component traits. Therefore, they may be considered promising for further improvement of wheat yield under both normal sown and heat stress conditions.

Assessment of Table 5 revealed an interesting relation between heterobeltiosis for grain yield per plant and its

attributes. The parental crosses that exhibited desirable heterobeltiosis for one or more yield attributes were identified. Heterobeltiosis for grain yield per plant were mainly contributed with higher grains per spike, 1000-grain weight, biological yield per plant and harvest index in both environments. Results of this study supported the contentions of a previous study, which suggested that there could be no separate gene system for yield per se as yield is an end product of the multiplicative interactions among its various contributing characters (18). The results from the present study in varying environments for different characters is in agreement with the findings some earlier experiments (19–22).

An overall assessment of parents indicated that HD 2864, Raj 4238 and CG 1029 were found to be desirable for grain yield and its attributes on the basis of heat susceptibility index. The crosses namely, HD 2864 × MP 3336, MP 3336 × Raj 3777, MP 3336 × HI 1134, Raj 3765 × CG 1029, HD 2932 × CG 1029, Raj 4238 × Raj 3777, Raj 4238 × CG 1029 and Raj 3777 × CG 1029 showed the superiority under E_2 for grain yield and more than two characters (Table 6).

Low value of heat stress intensity (D-value) that is less than 0.20, indicated that the parameters viz., days to 75 % heading (0.08), days to maturity (0.10), flag leaf area (0.07), grains per spike (0.06), 1000-grain weight (0.16), harvest index (-0.01), protein content (0.01), proline content (-0.15), total chlorophyll content (0.12) and membrane stability index (0.10) showed more tolerance whereas effective tillers per plant (0.34), biological yield per plant (0.25) and grain yield per plant (0.24) with high D-value that is 0.21–0.35, suffered more under E_2 . The greater heat tolerance value indicated the larger yield reduction under heat

Table 5. Crosses showing significant desirable heterobeltiosis for grain yield per plant and its contributing traits under normal (E₁) and heat stress environment (E₂)

Environments	Crosses	Heterobeltiosis	Days to 75 % heading	Days to maturity	Flag leaf area	Effective tillers per plant	Grains per spike	1000-Grain weight	Biological yield per plant	Harvest index	Protein content	Proline content	Total chlorophyll content	Membrane stability index
E ₁	HD 2932 x Raj 4238	32.33**	-	-	-	-	+	-	+	-	-	-	-	-
	HD 2864 x Raj 4238	29.71**	-	-	-	-	-	-	+	-	-	-	-	-
	MP 3336 x Raj 4238	24.42**	-	-	-	-	+	-	-	+	-	-	-	-
	MP 3336 x HD 2932	21.88**	-	-	-	-	+	+	-	-	-	-	+	-
	HD 2864 x CG 1029	20.94**	-	-	-	-	-	-	-	-	-	-	+	-
	HD 2864 x HD 2932	20.73**	-	-	-	-	-	-	+	-	-	-	+	+
	MP 3336 x CG 1029	18.44*	-	-	+	-	+	+	-	-	-	-	+	-
	Raj 4238 x CG 1029	17.36*	-	-	-	-	+	-	-	-	-	-	-	-
	Raj 4238 x HI 1634	13.98*	-	-	-	-	-	-	+	-	-	-	+	-
	MP 3336 x HI 1634	33.87**	-	-	-	-	-	-	-	+	-	+	-	-
E ₂	HD 2864 x CG 1029	14.33**	-	-	-	+	+	-	-	-	-	+	+	-
	Raj 4238 x Raj 3777	12.11**	-	-	-	-	+	-	-	-	-	-	-	-
	HD 2932 x HI 1634	11.26*	-	-	-	+	+	-	-	-	-	+	+	-
	HD 2864 x Raj 3765	9.95*	-	-	-	-	-	-	-	-	-	-	-	+

+ indicate significant desirable.

Table 6. Heat susceptibility index (HSI) and heat tolerance (TOL) for grain yield per plant

Parents	HSI	TOL
HD 2864	0.83	4.37
MP 3336	1.12	5.68
Raj 3765	1.29	7.99
HD 2932	0.87	3.99
Raj 4238	0.69	3.30
Raj 3777	1.11	6.67
CG 1029	0.45	2.10
HI 1634	1.36	7.49
F ₁ Crosses		
HD 2864 × MP 3336	0.65	3.16
HD 2864 × Raj 3765	0.85	5.01
HD 2864 × HD 2932	1.25	7.92
HD 2864 × Raj 4238	1.46	9.98
HD 2864 × Raj 3777	1.02	6.31
HD 2864 × CG 1029	1.01	6.46
HD 2864 × HI 1634	1.14	5.85
MP 3336 × Raj 3765	1.56	10.60
MP 3336 × HD 2932	1.69	10.44
MP 3336 × Raj 4238	1.48	9.31
MP 3336 × Raj 3777	0.73	4.10
MP 3336 × CG 1029	1.09	6.56
MP 3336 × HI 1634	0.43	2.36
Raj 3765 × HD 2932	1.06	6.64
Raj 3765 × Raj 4238	1.07	6.58
Raj 3765 × Raj 3777	1.13	6.71
Raj 3765 × CG 1029	0.79	4.21
Raj 3765 × HI 1634	1.42	9.12
HD 2932 × Raj 4238	0.99	6.02
HD 2932 × Raj 3777	0.95	5.67
HD 2932 × CG 1029	0.70	3.69
HD 2932 × HI 1634	1.29	7.66
Raj 4238 × Raj 3777	0.58	3.37
Raj 4238 × CG 1029	0.82	4.54
Raj 4238 × HI 1634	1.25	7.84
Raj 3777 × CG 1029	0.86	4.64
Raj 3777 × HI 1634	1.11	6.26
CG 1029 × HI 1634	0.95	5.62

Table 7. Mean of all genotypes under normal (E₁) and heat stress environment (E₂) and heat stress intensity (D-value) for different characters

Characters	Mean of all genotypes in		D-value
	E ₁	E ₂	
Days to 75 % heading	94.31	87.07	0.08
Days to maturity	129.64	116.99	0.10
Flag leaf area (cm ²)	27.71	25.84	0.07
Effective tillers per plant	7.04	4.62	0.34
Grains per spike	45.31	42.67	0.06
1000-Grain weight(g)	48.70	40.84	0.16
Biological yield per plant (g)	54.45	40.88	0.25
Grain yield per plant (g)	23.33	17.64	0.24
Harvest index (%)	41.72	41.93	-0.01
Protein content (%)	11.03	10.93	0.01
Proline content (µg/100mg fresh weight)	65.36	75.37	-0.15
Total chlorophyll content (mg/g fresh weight)	1.87	1.64	0.12
Membrane stability index (%)	58.23	52.26	0.10

stress conditions and the higher heat sensitivity. Therefore, a smaller value of heat tolerance is favoured (Table 7).

Perusal of Table 7 revealed that among the parents in general, HD 2864, HD 2932, Raj 4238, Raj 3765 and CG 1029 were found to be desirable for grain yield and most of its attributes on the basis of heat tolerance. The crosses viz., HD 2864 × MP 3336, MP 3336 × Raj 3777, MP 3336 × HI 1134, Raj 3765 × CG 1029, HD 2932 × CG 1029, Raj 4238 × Raj 3777, Raj 4238 × CG 1029 and Raj 3777 × CG 1029 showed superiority under E₂ for seed yield and more than two characters.

Conclusion

The observed levels of heterosis and heterobeltiosis were sufficient across all the traits studied. Among the significant and desirable heterobeltiosis crosses, HD 2932 × Raj 4238, HD 2864 × Raj 4238, MP 3336 × Raj 4238, MP 3336 × HD 2932, HD 2864 × HD 2932, MP 3336 × CG 1029, Raj 4238 × CG 1029 and Raj 4238 × HI 1634 performed well in E₁. In E₂, the crosses MP 3336 × HI 1634, Raj 4238 × Raj 3777, HD 2932 × HI 1634 and HD 2864 × Raj 3765 showed significant heterobeltiosis. Additionally, HD 2864 × CG 1029 exhibited desirable heterobeltiosis effects in both

environments. These crosses emerged as promising candidates for enhancing grain yield and related component traits in wheat. Therefore, they may be considered potential contenders for achieving significant yield improvement under both normal and heat stress conditions.

The overall ranking based on the heat susceptibility index and heat tolerance revealed that the crosses HD 2864 × MP 3336, MP 3336 × Raj 3777, MP 3336 × HI 1134, Raj 3765 × CG 1029, HD 2932 × CG 1029, Raj 4238 × Raj 3777, Raj 4238 × CG 1029 and Raj 3777 (x) CG 1029 were the most desirable for heat stress tolerance.

Research consistently shows that non-additive gene action plays a significant role in the inheritance of traits such as yield, grain quality and other agronomic characteristics in wheat. The present study also revealed a strong influence of non-additive gene action. Therefore, it is recommended that, alongside conventional breeding methods, non-conventional approaches such as diallel selective mating, bi-parental mating in early segregating generations and multiple crossing strategies be considered, as they may offer effective alternatives for enhancing grain yield in wheat. Furthermore, intermating superior segregants from hybrids, followed by cyclic selection, can help increase the frequency of desirable alleles in subsequent generations, ultimately improving grain yield and its contributing traits in wheat.

Acknowledgements

We are deeply indebted to Sri Karan Narendra College of Agriculture, Jobner, Jaipur (SKNAU, Jobner) for providing the field and laboratory facilities essential for the successful execution of this research, which formed part of the Ph.D. thesis work.

Authors' contributions

BLD contributed to the conceptualisation and design of the experiments, provided experimental materials, carried out field and laboratory work, collected and analysed data, interpreted the results and prepared the manuscript. DKG, ACS and SSR contributed to the conceptualisation and design of the experiments, provided experimental materials and participated in data analysis. RRC contributed to the conceptualisation and design of the experiments, provided experimental materials, collected and analysed data, interpreted the results and assisted in manuscript preparation. MKP contributed experimental materials and was involved in the execution of field and laboratory work. SKS contributed to the conceptualisation and design of the experiments, provided experimental materials and participated in data interpretation and manuscript preparation. SC and ASK contributed experimental materials and assisted in the execution of field and laboratory work. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

1. United States Department of Agriculture, World Agricultural Outlook Board. World Agricultural Supply and Demand Estimates (WASDE). Washington (DC): United States Department of Agriculture; 2021.
2. Mohammadi-Joo S, Mirasi A, Saeidi-Aboeshaghi R, Amiri M. Evaluation of bread wheat (*Triticum aestivum* L.) genotypes based on resistance indices under field conditions. *Int J Biosci.* 2015;6 (2):331–7. <https://doi.org/10.12692/ijb/6.2.331-337>
3. de Candolle A. Origin of cultivated plants. New York: Appleton; 1885.
4. Vavilov NI, Dorofeev VF. Origin and geography of cultivated plants. Cambridge: Cambridge University Press; 1992.
5. Gustafson P, Raskina O, Ma X, Nevo E. Wheat evolution, domestication and improvement. In: Carver BF, editor. Wheat: Science and Trade. Ames (IA): Wiley-Blackwell; 2009. p. 3–30.
6. Larik AS, Mahar AR, Hafiz HM. Heterosis and combining ability estimates in diallel crosses of six cultivars of spring wheat. *Wheat Inf Serv.* 1995;80:12–9.
7. Hassan GH, Gull RA. Evaluation of the heterotic and heterobeltiotic potential of wheat genotypes for improved yield. *Pak J Bot.* 2006;38 (4):1159–67.
8. Hochholdinger F, Hoecker N. Towards the molecular basis of heterosis. *Trends Plant Sci.* 2007;12(9):427–32. <https://doi.org/10.1016/j.tplants.2007.08.005>
9. Shull GH. Duplicate genes for capsule-form in *Bursa bursa-pastoris*. *Z Indukt Abstamm Vererbungsl.* 1914;12:97–149. <https://doi.org/10.1007/BF01837282>
10. Fonseca S, Patterson FL. Hybrid vigor in a seven-parent diallel cross in common winter wheat (*Triticum aestivum* L.). *Crop Sci.* 1968;8(1):85–8. <https://doi.org/10.2135/cropsci1968.0011183X000800050032x>
11. Singh H, Sharma SN, Sain RS. Heterosis studies for yield and its components in bread wheat over environments. *Hereditas.* 2004;141(2):106–14.
12. Lal C, Kumar V, Maloo SR. Heterosis and inbreeding depression for some quantitative and heat tolerance characters in bread wheat (*Triticum aestivum* L.). *J Cereal Res.* 2014;5(2):84–90.
13. Barot HG, Patel MS, Sheikh WA, Patel LP, Allam CR. Heterosis and combining ability analysis for yield and its component traits in wheat (*Triticum aestivum* L.). *Electron J Plant Breed.* 2014;5(3):350–9.
14. Kumar J, Singh SK, Singh L, Kumar M, Srivastava M, Singh J, et al. Combining ability analysis for yield and its components in bread wheat (*Triticum aestivum* L.) under abiotic stress. *Int J Curr Microbiol Appl Sci.* 2017;6(3):24–39. <https://doi.org/10.20546/ijcmas.2017.603.003>
15. Thomas N, Marker S, Lal GM, Dayal A. Study of heterosis for grain yield and its components in wheat (*Triticum aestivum*) over normal and heat stress condition. *J Pharmacogn Phytochem.* 2017;6(4):824–30.
16. Kajla SL, Sharma AK, Singh H. Heterosis analysis in F1 hybrids of bread wheat (*Triticum aestivum* L. em. Thell.) over environments. *Int J Curr Microbiol Appl Sci.* 2020;9(5):2052–7. <https://doi.org/10.20546/ijcmas.2020.905.234>
17. Burdak A, Prakash V, Kakralya BL, Gupta D, Choudhary R. Heterotic performance and inbreeding depression for yield and component traits in bread wheat (*Triticum aestivum* L. em. Thell.). *J Cereal Res.* 2023;13(3):56–64.
18. Grafius JE. Heterosis in barley. *Agron J.* 1959;51(9):551–4. <https://doi.org/10.2134/agronj1959.00021962005100090013x>
19. Akbar M, Anwar J, Hussain M, Iqbal MM, Sabir W. Heterosis and heterobeltiosis for grain yield improvement in bread wheat. *J Agric Res.* 2010;48(1):15–23.
20. Bajaniya NA, Pansuriya AG, Vekaria DM, Singh C, Patel JM. Estimation of heterosis in different crosses of durum wheat (*Triticum durum* L.). *Int J Chem Stud.* 2019;7(3):3833–9.

21. Kumar P, Singh H, Lal C, Choudhary R. Heterosis analysis for yield and its component traits in bread wheat (*Triticum aestivum* L.) over different environments. J Environ Biol. 2021;42:438–45.
22. Kumari A, Sharma H, Dashora A. Heterosis in bread wheat (*Triticum aestivum* L.) for earliness and heat tolerant traits over the environments. Int J Plant Soil Sci. 2022;34(3):36–40. <https://doi.org/10.9734/ijpss/2022/v34i330844>

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonpublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is

covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc

See https://horizonpublishing.com/journals/index.php/PST/indexing_abstracting

Copyright: © The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution and reproduction in any medium, provided the original author and source are credited (<https://creativecommons.org/licenses/by/4.0/>)

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.