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(Original Article)

Genetic Analysis of Grain Yield and its Components Under Heat Stress Conditions in Bread Wheat (*Triticum aestivum* L.)

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Abstract

This investigation aimed to study the genetic system of grain yield and related traits in a half diallel cross of bread wheat, involving eight parents and their 28 F_1 hybrids, under optimal and heat-stressed field conditions. The traits assessed included plant height (PLH), spike length (SPL), grain yield per plant (GYP), number of tillers (NOT), number of spikelets per spike (NSP), and 1000-kernel weight (TKW). Under heat stress, significant variation was observed among genotypes for all traits except TKW. Heat stress caused substantial reductions in the performance of parental lines and F_1's. Several hybrids exhibited notable heterosis. The general combining ability (GCA) was significant for all traits, whereas specific combining ability (SCA) was significant for SPL, GYP, NOT, and NSP. The predominance of GCA over SCA effects observed suggested a major role in additive gene action. These findings are further supported by the significance of both additive (a) and non-additive (b) gene actions, with a predominance of additive gene action under heat stress. Regression analysis supported the adequacy of the additive-dominance model for PLH, SPL, and TKW, while the model was non-adequate for NOT and NSP, and partially adequate for GYP. CIMMYT-9 (P4), followed by CIMMYT-10 (P5) exhibited the highest and significantly positive (P<0.01) GCA for GYP and most traits. The hybrid P4×P8, followed by P5×P7 and P3×P6, exhibited the largest and significantly positive (P<0.01) SCA for GYP. Cluster analysis using SSR markers successfully distinguished between parents based on heat tolerance. These results highlight the potential of identified superior genotypes for developing heat-tolerant wheat varieties.

Keywords: *Bread wheat, Combining ability, Diallel analysis, Grain yield, Heat stress.*

Introduction

Heat stress is a major abiotic factor that significantly reduces grain yield across various wheat-growing regions worldwide, including Egypt (Hassan and El-Rawy, 2021). The reduction caused by high temperature is primarily attributed to decreased photosynthesis, enzyme inactivation, inhibiting starch biosynthesis, elevated respiration rates, protein denaturation, membrane damage, and accelerated leaf senescence (Shah and Paulsen, 2003; Howarth, 2005). In addition, prolonged high temperature shortens crop life cycles, leading to fewer and smaller organs (Stone, 2001). The negative effects

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of heat stress are particularly severe during the grain-filling stage, by shortening the grain-filling duration, leading to a significant reduction in kernel weight, and thereby a notable decrease in grain yield (Kumar *et al*., 2016; Saha *et al*., 2020).

Breeding for heat tolerance is complicated, as it is a quantitative trait controlled by multiple genes and strongly influenced by genotype-by-environment interactions. Moreover, plants frequently encounter multiple abiotic stresses simultaneously, further complicating breeding efforts (Fleury *et al*., 2010). Therefore, selecting high-yielding genotypes under heat stress conditions remains a primary objective of wheat breeding programs. Strategies adopted in breeding programs depend on the genetic analysis of interest traits. Understanding the genetic basis of heat tolerance traits is crucial for advancing wheat breeding efforts (Kumar *et al*., 2017). In this regard, the diallel analysis method, originally proposed by Hayman (1954 a,b), offers in-depth insight into the inheritance patterns of key quantitative traits. It helps breeders differentiate between additive and non-additive gene effects. Additionally, the half-diallel mating scheme serves as a practical approach for identifying genotypes with strong combining abilities, making them valuable candidates for the development of enhanced wheat varieties (Jinks, 1954). In addition, diallel analysis is useful for predicting the best parental combinations (Baldissera *et al*., 2012). These insights are essential for improving selection efficiency and accelerating genetic gains.

The genetic diversity found among wheat germplasm for important traits is crucial for the development of improved wheat varieties in breeding programs (Khan *et al*., 2015). In this context, the use of simple sequence repeat (SSR) markers to assess genetic diversity has received considerable attention in plant breeding (El-Rawy and Hassan, 2021). SSR markers are valuable tools in wheat breeding, particularly for marker-assisted selection (MAS) and genetic diversity assessment. Their high level of polymorphism, co-dominant inheritance, and wide distribution across the wheat genome make them especially effective for identifying desirable traits and distinguishing among wheat varieties. Additionally, the level of genetic diversity assessed between parental genotypes using molecular markers can be an effective tool for predicting hybrid performance (Perenzin *et al*., 1997).

In the present study, eight bread wheat genotypes (*Triticum aestivum* L.) with contrasting levels of heat tolerance, along with their 28 F_1 hybrids, were evaluated to investigate the genetic system underlying grain yield and its components using a half-diallel analysis conducted under both favorable and heat-stressed field conditions. The objectives were to test the adequacy of an additive-dominance model, evaluate general and specific combining abilities, which reflect additive and non-additive gene effects, for the traits under investigation, identify high-yielding genotypes with heat stress tolerance, and to assess the genetic diversity among parental lines using SSR markers.

Materials and Methods

Plant materials

The initial plant materials utilized in the present study consisted of eight bread wheat genotypes (*Triticum aestivum* L.), varying in their performance under heat stress conditions. Five genotypes were provided by the International Maize and Wheat

Improvement Center (CIMMYT), Mexico, while the other three are Egyptian cultivars (Table 1).

Field experiments were carried out at the Genetics Department's research farm, Faculty of Agriculture, Assiut University, Egypt. During the 2020/2021 winter season, eight genotypes were planted on two different sowing dates, November 15 and November 30, 2020, spaced two weeks apart to align their flowering times for hybridization. An 8-parent half-diallel mating design (excluding reciprocals) was employed to generate 28 F_1 hybrids.

Table 1. Names, Pedigree, description and origin of bread wheat genotypes used in the study.

Code	Name	Pedigree	Description	Origin
P1	CIMMYT-1	NELOKI//SOKOLL/EXCALIBUR	Heat tolerant	Mexico
P2	CIMMYT-4	NADI/COPIO//NADI#2	Heat tolerant	Mexico
P3	CIMMYT-5	SBAVIS/NAVJ07//BORL14	Heat tolerant	Mexico
P4	CIMMYT -9	MACE/5/TILILA/JUCHI/4/SERI.1B//KAUZ/HEVO/3/AMAD/6/KACHU/BECARD//WBLL1*2/BRAMBLING	Heat tolerant	Mexico
P5	CIMMYT-10	KENYASUNBIRD/2*KACHU/3/WBLL1*2/BRAMBLING*2//BAVIS	Heat tolerant	Mexico
P6	GEMMEIZA-7	CMH74A.630/5X//SERI82/3/AGENT	Heat susceptible	Egypt
P7	MISR-2	SKAUZ/BAV 92	Heat susceptible	Egypt
P8	SAKHA-8	CNO67//SN64/KLRE/3/8156	Moderate heat tolerant	Egypt

Field evaluation of the diallel cross

During the 2021/2022 season, seeds of the eight parent genotypes and their 28 F_1 hybrids were sown on two different dates: November 17, 2021, representing optimal conditions, and January 15, 2022, to simulate heat stress through late sowing. The experiments followed a randomized complete block design (RCBD) with three replications. In each environment, every genotype was planted in a single-row plot within each block, consisting of 10 plants per row. Rows were spaced 30 cm apart, with 50 cm spacing between plants within rows. Field observations were recorded at maturity for plant height (cm), spike length (cm), grain yield per plant (g), number of fertile tillers, number of spikelets per spike, and 1000-kernel weight (g) on individual plants of the two environments.

The recorded maximum daily air temperatures (°C) at the experimental site during March and April 2022 are presented in Fig. 1 (Weather reports in Assiut, https://www.wunderground.com). In March, several daytime heat waves were recorded, with temperatures occasionally exceeding 33 °C. In April, heat events became more intense, with daily maximum temperatures reaching up to 37 °C and peaking at 41 °C. These extreme temperature episodes coincided with the post–ear emergence stage of wheat, thereby exposing the plants to substantial heat stress. Detailed environmental data for the experimental site during March and April 2022 are provided in the supplementary materials (Tables 1S and 2S).

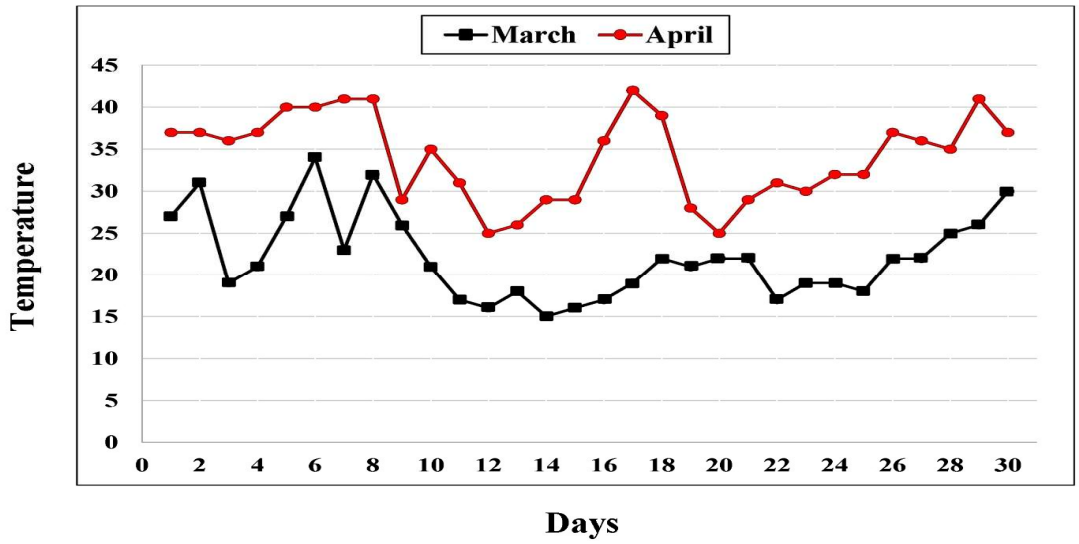

Fig 1. Maximum daily temperatures (°C) during March and April 2022 at the experimental site in Assiut Governorate, Egypt.

Biometrical analysis

The significance of differences among the means of the traits studied was tested by Fisher's Least Significant Difference (LSD) at 5% and 1% probability. To test for the significance of differences due to genotypes, general (GCA) and specific (SCA) combining ability, as well as additive (a) and non-additive gene action (b) items, an analysis of variance was performed for each environment separately. To calculate the percentage reduction due to heat stress compared to a favorable environment for a trait, the following formula was used:

Reduction (%) = [(Value in Favorable Environment–Value in Heat Stress Environment)/Value in Favorable Environment] × 100.

Heat tolerance index of each genotype, adjusted based on grain yield under favorable and heat stress conditions, was calculated following Fernandez (1992) as follows:

$$\textbf{Heat tolerance index (HTI)} = (Yp \times Ys) / (\bar{Y}p)^2$$

Where, Yp and Ys are grain yield of a genotype under favorable and heat stress conditions, respectively. Whereas $\bar{Y}p$ represents mean grain yield of all genotypes under favorable environment.

The phenotypic data of parental genotypes and their F_1 hybrids were analyzed using the half diallel analysis as described by Hayman (1954a,b), Mather and Jinks (1971), and Jones (1965) using the "DIAL98" software. GCA and SCA effects as measures of additive and non-additive gene actions, respectively, were estimated for each of the traits studied under heat stress conditions.

SSR markers analysis

SSR marker analysis was carried out to assess the genetic diversity between parental genotypes. The eight parental genotypes were screened with twelve SSR markers (Table 2). Genomic DNA was extracted from fresh leaves using the CTAB

method (Murray and Thompson, 1980). SSR primer sequences and PCR conditions were obtained from the GrainGenes Database (http://wheat.pw.usda.gov). PCR was conducted with a SensoQuest LabCycler, and amplified products were separated on 2.5% agarose gels in 0.5× TBE buffer using a 100 bp DNA ladder for size estimation. The percentage of polymorphism per marker was calculated to assess the suitability of each marker for evaluating genetic diversity among the wheat genotypes studied. Polymorphic information content (PIC) and marker index (MI) were determined following Roldan-Ruiz *et al.* (2000) and Powell *et al.* (1996), respectively.

Table 2. Names, chromosomal locations (CL), sequences of forward (F) and reverse (R) primers and annealing temperature (T) of twelve SSR markers used in the present study.

No.	Name	CL	Sequence (5' - 3')	T (°C)
1	Xgwm95	2A	F: GATCAAACACACACCCCTCC R: AATGCAAAGTGAAAAACCCG	60
2	Xgwm155	3A	F: CAATCATTTCCCCCTCCC R: AATCATTGGAAATCCATATGCC	60
3	Xgwm165	4D	F: TGCAGTGGTCAGATGTTTCC R: CTTTTCTTTCAGATTGCGCC	60
4	Xgwm186	5A	F: GCAGAGCCTGGTTCAAAAAG R: CGCCTCTAGCGAGAGCTATG	60
5	Xgwm293	5A	F: TACTGGTTCACATTGGTGCG R: TCGCCATCACTCGTTCAAG	55
6	Xgwm294	2A	F: GGATTGGAGTTAAGAGAGAACCG R: GCAGAGTGATCAATGCCAGA	55
7	Xgwm339	2A	F: AATTTTCTTCCTCACTTATT R: AAACGAACAACCACTCAATC	50
8	Xgwm356	2A	F: AGCGTTCTTGGGAATTAGAGA R: CCAATCAGCCTGCAACAAC	55
9	Xgwm458	1D	F: TTCGCAATGTTGATTTGGC R: TTCGCAATGTTGATTTGGC	60
10	Xgwm566	3B	F: TCTGTCTACCCATGGGATTTG R: CTGGCTTCGAGGTAAGCAAC	60
11	Xwmc273	7A	F: AGTTATGTATTCTCTCGAGCCTG R: GGTAACCACTAGAGTATGTCCTT	50
12	Xwmc398	6B	F: GGAGATTGACCGAGTGGAT R: CGTGAGAGCGGTTCTTTG	60

Cluster analysis of parental genotypes

Cluster analysis of the parental genotypes based on phenotypic data under heat stress was done using Standardized Euclidean's coefficient and Unweighted Pair Group Method with Arithmetic Mean (UPGMA) by MVSP version 3.22 (Kovach Computing Services). Genetic similarity estimates between parental genotypes based on twelve SSR markers were computed and UPGMA-dendrogram was performed according to Nei and Li's coefficient using MVSP version 3.22.

The Mantel test (Mantel, 1967) was performed to evaluate the correlation between distance matrices derived from phenotypic data using Euclidean's coefficient and from SSR marker data using the Nei and Li's coefficient.

Results

Performance of genotypes

Means of the parents and their F_1 hybrids for the traits studied under favorable and heat stress conditions are presented in Tables 3 and 4, respectively. The result showed

that the parental genotypes as well as their F_1's responded differentially under both favorable and heat stress conditions. Several hybrids exhibited notable heterosis across all studied traits. Due to heat stress, overall means of PLH, SPL, GYP, NOT, NSP and TKW were reduced by 35.62, 10.25, 45.71, 59.78, 10.74, and 49.25 % in parental genotypes, and by 31.89, 6.73, 77.03, 52.62, 12.88, and 51.71 % in F_1 hybrids, respectively (Fig. 2).

Table 3. Mean performance of the eight parental genotypes and their 28 F_1 hybrids for all studied traits under favorable conditions.

	Favorable					
Traits	**PLH**	**SPL**	**GYP**	**NOT**	**NSP**	**TKW**
P1	115.45±2.15	14.15±0.57	51.75±3.20	19.75±0.70	21.42±0.95	61.65±0.21
P2	115.25±2.90	14.54±0.58	46.19±3.31	16.49±0.98	21.05±0.40	60.49±0.10
P3	102.24±7.50	14.79±0.12	44.03±0.59	16.18±1.29	20.43±0.41	60.78±0.04
P4	91.53±0.33	14.05±0.32	36.64±1.47	13.56±1.39	20.47±0.06	55.81±0.08
P5	113.91±9.95	14.28±0.35	60.37±1.79	19.34±1.07	21.25±0.52	59.55±0.18
P6	91.51±11.11	14.53±0.23	37.65±5.95	13.81±1.52	20.58±0.34	62.60±0.08
P7	100.81±6.27	14.42±0.14	43.52±1.19	16.57±0.29	21.45±0.14	56.81±0.04
P8	85.04±3.92	13.95±0.03	35.87±5.69	15.16±1.19	20.15±0.28	57.74±0.21
Mean	**101.97**	**14.34**	**44.50**	**16.36**	**20.85**	**59.43**
P1×P2	134.69±3.78	14.13±0.65	54.95±4.42	21.46±3.27	20.62±0.95	61.54±0.16
P1×P3	114.82±0.61	14.10±0.27	62.47±6.77	21.58±2.12	20.36±0.89	60.95±0.32
P1×P4	112.94±1.27	14.33±0.47	49.22±6.96	17.58±2.28	21.00±0.37	62.21±0.34
P1×P5	109.06±4.65	14.92±0.30	47.13±5.49	19.81±1.30	22.53±0.36	58.51±0.44
P1×P6	98.76±0.69	14.18±0.48	45.38±1.53	16.30±2.82	21.08±0.29	63.74±0.15
P1×P7	99.23±2.58	15.09±0.30	42.81±3.84	13.79±0.93	21.59±0.49	65.00±0.09
P1×P8	98.77±2.48	14.28±0.12	40.98±4.32	14.23±1.23	22.13±0.26	58.51±0.25
P2×P3	91.00±6.96	14.28±0.12	41.61±1.52	15.21±1.24	21.79±0.34	60.79±0.13
P2×P4	87.98±3.73	14.15±0.65	46.80±0.46	13.58±1.67	20.74±1.06	62.44±0.34
P2×P5	105.77±4.81	14.28±0.54	48.20±4.26	19.08±0.57	21.79±0.41	61.20±0.05
P2×P6	94.26±2.45	15.10±0.36	57.90±3.38	18.79±1.33	21.56±0.25	54.56±0.17
P2×P7	103.01±1.50	14.84±0.42	55.40±1.49	19.53±0.99	21.99±0.10	57.16±0.58
P2×P8	102.63±1.84	14.98±0.30	54.51±4.47	18.98±2.17	21.35±0.40	62.87±0.18
P3×P4	105.77±1.63	14.19±0.47	43.56±1.77	18.57±1.28	19.96±1.65	56.23±0.06
P3×P5	106.06±2.35	14.82±0.40	46.86±3.90	16.68±2.16	22.63±0.61	53.14±0.29
P3×P6	100.34±0.95	14.62±0.61	43.41±2.04	16.41±0.71	21.64±1.09	54.43±0.04
P3×P7	107.37±1.63	14.29±0.12	49.18±0.60	17.42±1.44	19.36±0.21	54.00±0.37
P3×P8	103.77±2.00	14.60±0.35	38.41±6.90	13.84±1.22	20.01±0.39	52.44±0.16
P4×G5	103.71±3.00	16.82±0.07	49.40±8.70	16.44±1.17	23.37±0.66	53.88±0.03
P4×P6	96.80±1.44	13.71±0.21	41.71±2.83	15.28±0.14	22.87±0.34	56.75±0.13
P4×P7	99.55±2.07	14.28±0.53	44.89±2.35	17.47±1.66	21.96±0.49	53.11±0.23
P4×P8	99.90±1.74	14.80±0.46	42.58±2.22	14.99±1.08	21.11±0.85	59.28±0.16
P5×P6	97.67±1.38	14.00±0.47	40.11±2.29	16.54±2.42	19.87±1.84	57.26±0.30
P5×P7	95.27±0.96	13.79±0.02	49.46±2.42	15.39±2.36	18.42±1.05	57.83±0.30
P5×P8	107.22±0.27	14.44±0.24	40.61±4.47	14.11±1.48	21.97±0.15	56.60±0.06
P6×P7	101.20±1.15	13.84±0.39	35.91±0.70	14.17±1.93	20.64±0.55	55.17±0.11
P6×P8	94.38±2.09	13.92±0.06	37.75±1.46	16.75±1.47	18.86±0.22	55.06±0.14
P7×P8	90.46±2.60	12.59±0.54	38.47±5.64	22.25±3.26	19.88±0.49	52.53±0.12
Mean	**102.23**	**14.41**	**46.06**	**17.01**	**21.11**	**57.76**
$LSD_{(0.05)}$	**9.99**	**1.04**	**10.87**	**4.68**	**1.92**	**1.21**
$LSD_{(0.01)}$	**13.27**	**1.38**	**14.43**	**6.22**	**2.54**	**1.63**

PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight (g).

Table 4. Mean performance of the eight parental genotypes and their 28 F_1 hybrids for all studied traits under heat stress conditions, as well as heat tolerance index (HTI) based on GYP.

	Heat stress						
Traits	**PLH**	**SPL**	**GYP**	**NOT**	**NSP**	**TKW**	**HTI**
P1	61.13±1.73	12.42±0.58	13.82±1.00	7.91±0.58	18.88±0.88	34.92±0.46	0.34
P2	66.78±1.89	12.71±0.25	10.53±1.72	6.53±0.20	18.84±1.58	32.28±0.16	0.23
P3	61.14±2.14	12.63±0.23	10.26±1.63	5.89±0.35	16.38±0.94	23.94±0.08	0.22
P4	65.36±3.45	12.62±0.27	9.82±1.53	7.90±0.22	18.29±1.21	24.86±0.10	0.17
P5	64.21±1.60	13.13±0.30	9.30±1.73	6.07±0.42	19.58±1.54	30.63±0.08	0.27
P6	69.56±165	13.81±0.35	8.91±1.63	5.67±0.45	20.85±1.53	31.44±0.46	0.16
P7	69.99±1.55	12.95±0.45	10.42±1.55	6.42±0.58	19.19±0.51	32.48±0.08	0.22
P8	67.03±1.62	12.67±0.20	9.66±1.65	6.28±0.59	16.87±0.78	30.77±0.42	0.17
Mean	**65.65**	**12.87**	**24.16**	**6.58**	**18.61**	**30.16**	**0.22**
P1×P2	70.30±173	13.62±0.45	9.86±1.73	6.28±0.30	19.78±1.58	39.27±0.20	0.26
P1×P3	69.75±1.50	12.82±0.28	12.89±1.71	5.02±0.37	18.59±1.22	39.93±0.05	0.39
P1×P4	72.17±1.54	12.94±0.33	13.21±1.66	8.86±0.58	19.08±1.27	34.39±0.09	0.31
P1×P5	72.94±1.57	13.13±0.29	9.90±1.55	7.68±0.43	19.70±0.89	28.03±0.34	0.22
P1×P6	65.74±1.00	12.47±0.27	8.25±1.70	7.07±0.47	17.70±1.00	28.05±0.05	0.18
P1×P7	72.99±1.30	13.97±0.25	11.17±1.68	5.88±0.51	18.76±1.24	19.75±0.12	0.23
P1×P8	70.70±2.10	13.24±0.24	6.47±1.87	11.31±0.20	16.92±1.44	27.44±0.47	0.13
P2×P3	67.26±2.84	12.89±0.22	9.73±0.99	4.72±0.31	19.56±1.05	34.40±0.38	0.19
P2×P4	61.38±2.59	12.50±0.21	8.19±0.44	5.65±0.30	16.75±0.99	29.77±0.12	0.18
P2×P5	69.82±2.45	13.82±0.20	8.95±0.63	8.26±0.20	19.67±1.54	39.32±0.48	0.21
P2×P6	64.79±2.58	12.86±0.58	13.58±0.84	4.55±0.30	19.14±1.22	33.91±0.15	0.38
P2×P7	67.87±3.89	12.60±0.35	12.94±0.64	10.60±0.43	18.13±1.57	30.61±0.10	0.34
P2×P8	67.75±2.58	11.50±0.39	12.56±1.11	8.45±0.49	15.36±1.47	25.83±0.18	0.33
P3×P4	105.77±2.65	12.80±0.31	14.72±0.92	9.72±0.42	18.50±1.68	23.28±0.22	0.31
P3×P5	70.44±3.22	12.67±0.29	12.72±1.25	12.65±1.21	18.67±1.74	29.11±0.41	0.29
P3×P6	60.48±2.85	13.42±0.40	11.48±0.14	8.74±0.54	17.06±0.87	23.20±0.51	0.24
P3×P7	68.33±3.66	12.42±0.32	9.36±0.37	9.89±0.32	17.17±1.87	21.75±0.28	0.22
P3×P8	68.00±2.89	14.60±0.26	16.44±1.54	8.61±0.54	17.86±0.95	24.72±0.11	0.30
P4×G5	67.92±3.88	16.82±0.33	14.07±1.55	13.30±0.41	20.11±0.68	25.06±0.34	0.33
P4×P6	68.23±1.55	13.71±0.23	10.14±1.36	11.23±0.87	18.93±1.42	26.95±0.55	0.20
P4×P7	69.87±3.88	14.28±0.27	15.91±2.10	7.53±0.41	18.88±1.68	30.79±0.10	0.34
P4×P8	74.36±2.89	14.80±0.58	12.49±0.87	10.33±0.63	19.17±1.58	31.24±0.23	0.25
P5×P6	61.70±2.85	14.00±0.44	7.16±1.22	8.99±0.74	18.56±1.87	22.20±0.01	0.14
P5×P7	64.37±2.11	13.79±0.48	8.00±0.24	6.45±0.35	17.30±0.65	25.39±0.39	0.19
P5×P8	78.14±2.85	14.44±0.34	8.10±1.85	6.31±0.54	19.40±1.87	24.46±0.42	0.16
P6×P7	70.92±2.54	13.84±0.41	4.62±0.25	6.63±0.68	18.75±1.57	18.80±0.02	0.08
P6×P8	66.69±2.87	13.92±0.56	7.40±0.47	4.92±0.57	18.11±0.99	23.20±0.10	0.13
P7×P8	61.00±2.39	12.59±0.55	6.02±0.83	6.38±0.85	17.31±1.35	20.01±0.11	0.11
Mean	**69.63**	**13.44**	**10.58**	**8.06**	**18.39**	**27.89**	**0.24**
$LSD_{(0.05)}$	**6.94**	**0.39**	**1.21**	**1.36**	**1.35**	**0.81**	**-**
$LSD_{(0.01)}$	**9.21**	**0.53**	**1.63**	**1.82**	**1.79**	**1.08**	**-**

PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight (g).

Under favorable conditions, the parents P5 (CIMMYT-10) showed the highest GYP (60.37 g) followed by P1 (51.75 g). In addition, P1 (CIMMYT-1) and P5 (CIMMYT-10) showed the greatest NOT 19.75 and 19.34, respectively. The largest PLH (115.45, 115.25 and 113.91 cm) was recorded for P1 (CIMMYT-1), P2 (CIMMYT-4), and P5 (CIMMYT-10), respectively. The largest TKW (62.60 and 61.65 g) was recorded for P6 (Gemmeiza-7) and P1 (CIMMYT-1), respectively (Table 3).

Under heat stress, P1 (CIMMYT-1) showed the largest GYP (13.82 g) and TKW (34.92 g). In addition, P1 (CIMMYT-1) and P4 (CIMMYT-9) exhibited greater NOT (7.91 and 7.90, respectively). whereas the Egyptian cultivar Gemmeiza-7 (P6) exhibited the lowest GYP (8.91 g) and NOT (5.67). The highest PLH was recorded for P6 (CIMMYT-7), P7 (Misr-2) with 69.56 and 69.99 cm, respectively. The longest SPL (13.81 and 13.13 cm) was observed for the Egyptian cultivar P6 (Gemmeiza-7) followed by P5 (CIMMYT-10), respectively. In addition, largest NSP values (20.85 19.58) were also recorded for P6 (Gemmeiza-7), followed by P5 (CIMMYT-10), respectively (Table 4). As for F_1 hybrids, the cross combinations P1×P3 followed by P2×P6 showed the largest GYP (62.47 and 57.90 g, respectively), whereas P1×P7 followed by P1×P6 showed the highest TKW (65.00 and 63.74 g, respectively) under favorable conditions (Table 3). Under heat stress, the crosses P3×P8, followed by P4×P7 and P3×P4, showed greater GYP (16.44, 15.91, and 14.72 g, respectively). The longest SPL (16.82 cm) and highest NSP (20.11) were recorded in P4×G5. The largest TKW (39.27, 39.93, and 39.32 g) was found in P1×P2, P1×P3 and P2×P5, respectively (Table 4).

Regarding heat tolerance index (HTI) adjusted based on GYP under favorable and heat stress environments, the parent P1 exhibited the largest HTI (0.34) followed by P5 (0.27), whereas P6 showed the lowest HTI (0.16), with an average of 0.22. A wide range of HTI was observed in F_1 hybrids, ranging from 0.08 (P6×P7) to 0.39 (P1×P3), with an average of 0.24 (Table 4).

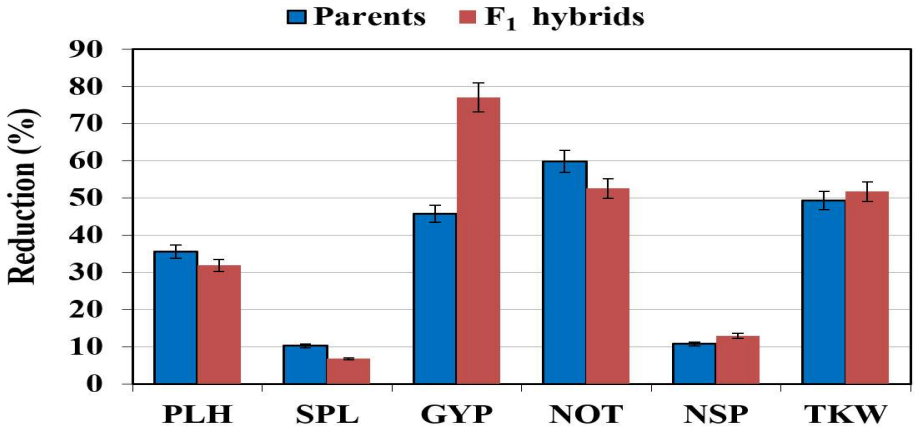

Fig 2. The reduction (%) resulted in the studied traits due to heat stress for the parents and their F_1 hybrids. PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight.

Diallel analysis

Under optimal growing conditions, genotypes exhibited highly significant differences (P<0.01) for PLH, and significant differences (P< 0.05) for GYP and TKW. Analysis of variance for GCA revealed highly significant mean squares (P<0.01) for PLH, SPL, and GYP, while significant GCA effects (P<0.05) were observed for NOT and TKW. While, SCA effects showed significant mean squares (P<0.01) for PLH, GYP, and TKW. Under heat stress, highly significant differences (P<0.01) were observed among genotypes for all traits, except TKW. The mean squares due to GCA

were highly significant (P<0.01) for PLH, SPL, GYP, and NOT, while they were significant (P<0.05) for NSP and TKW. Highly significant (P<0.01) SCA mean squares were observed for all traits except PLH and TKW. Obviously, GCA mean squares were much higher than SCA, indicating a predominance of GCA over SCA (Table 5).

Table 5. Mean square due to genotypes as well as general (GCA) and specific (SCA) combining ability for studied traits under favorable and heat stress conditions.

Traits		PLH	SPL	GYP	NOT	NSP	TKW
S.O.V.	**d.f**			**Favorable**			
Replicates	**2**	314,29**	2.037**	119.615	11.392	1.605	1.218**
Genotypes	**35**	275.37**	1.187	141.939*	17.788	3.660	0.372*
GCA	**7**	629.100**	4,121**	138.73**	25.917*	4.411	0.388*
SCA	**28**	184.82*	0.448	146.259*	14.746	3.566	0.375*
a	**7**	647.247**	1.862*	246.140**	13.968	7.029**	1.013**
b	**28**	182.404*	1.019	115.888	18.743	2.818	0.212
b1	**1**	244.180**	0.619	47.749	43.025**	0.962	0.191
b2	**7**	124.869*	1.463**	103.960	22.997	1.278	0.057
b3	**20**	199.453**	0.883	123.471	16.040	3.450	0.268
Error	**70**	37.68	0.405	44.593	8.272	1.394	0.119
				Heat stress			
Replicates	**2**	40.111	17.361**	156.250**	0.054	0.490	0.016
Genotypes	**35**	171.274**	2.704**	23.445**	15.208**	4.172**	0.921
GCA	**7**	649.864**	6.047**	45.59**	25.765**	2.353*	1.804*
SCA	**28**	48.949	1.831**	18.250**	12.962**	4.521**	0.711
a	**7**	249.440**	6.739**	33.641**	26.005**	7.636**	2.416*
b	**28**	151.732**	1.696**	20.896**	12.509**	3.305*	0.547
b_1	**1**	123.902**	2.891**	8.646**	1.958	7.479**	0.395
b_2	**7**	289.386**	1.460**	14.320**	9.317**	1.119	2.032*
b_3	**20**	104.945**	1.719**	23.810**	14.154**	3.862**	12.882**
Error	**70**	18.168	0.061	0.550	0.706	0.694	0.249

PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight. * and ** stand for significant differences at 0.05 and 0.01 probability, respectively.

Highly significant (P<0.01) additive gene action (a) was observed for all traits under heat stress, except significant (P<0.05) additive gene action (b) for TKW. Highly significant (P<0.01) non-additive gene action (b) was recorded for PLH, SPL, GYP, and NOT, and significant (P<0.05) non-additive gene action (b) was recorded for NSP. When the non-additive gene effect (b) was partitioned into its components, the significance of the (b_1) component for PLH, SPL, GYP, and NSP suggested the presence of directional dominance. In contrast, the non-significant (b_1) values for NOT and TKW indicated a lack of directional dominance for these traits. The significant (b_2) component observed in all traits except NSP reflected an unequal distribution of genes among the parental lines. Additionally, the significant (b_3) component across all traits provided further evidence of dominance effects.

The Wr/Vr relationship

The joint regression analysis of covariance (Wr) on variance (Vr) for the traits evaluated under both environmental conditions (Table 6). Under favorable conditions, the regression slopes for PLH (b= 0.72 ± 0.14) and SPL (b= 1.10 ± 0.28) significantly differed from zero but not from unity, indicating that the additive-dominance model was fully adequate for these traits. In contrast, the model was non-adequate for GYP (b= 0.56 ± 0.38), NOT (b= 0.35 ± 0.14), NSP (b= 0.37 ± 0.21), and was partially adequate

for TKW (b= 0.90 ± 0.22). Significant or highly significant mean squares for (Wr + Vr) in PLH and SPL suggested the presence of considerable dominance variance. Meanwhile, the non-significant (Wr − Vr) mean squares across all traits confirm the absence of epistatic interactions.

Table 6. Joint regression analysis and mean squares of (Wr+Vr) and (Wr–Vr) for the traits studied under favorable and heat stress conditions.

Traits	Joint regression (b ± se)	Test for b = 0	Test for b = 1	Mean squares of (Wr+Vr)	Mean squares of (Wr–Vr)	Fitness of the model
Favorable						
PLH	0.72±0.14	4.97**	1.98	41545**	4053.9	Fully adequate
SPL	1.10±0.28	3.95**	0.35	1.1543*	0.1435	Fully adequate
GYP	0.56±0.38	1.46	1.15	2207.80	970.42	Non adequate
NOT	0.35±0.14	2.56*	4.63**	106.83	60.791	Non adequate
NSP	0.37±0.21	1.80	2.95**	7.8058	2.2537	Non adequate
TKW	0.90±0.22	3.95**	0.50	0.0164	0.0105	Partially adequate
Heat stress						
PLH	0.72±0.27	2.67*	1.04	65643**	2354.3	Fully adequate
SPL	0.82±0.24	3.39**	0.73	3.503**	0.3632	Fully adequate
GYP	1.04±0.43	2.39*	0.09	238.92**	50.92*	Partially adequate
NOT	0.61±0.46	1.31	0.85	44.008**	16.1644**	Non adequate
NSP	0.14±0.19	0.74	4.53**	2.6701*	1.9854**	Non adequate
TKW	0.72±0.27	2.67*	1.04	0.0212*	0.0159	Fully adequate

PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight. * and ** stand for significant differences at 0.05 and 0.01 probability, respectively.

Under heat stress, the regression analysis supported full adequacy of an additive-dominance model for PLH (b= 0.72±0.27), SPL (b= 0.82±0.24), and TKW (b= 0.72±0.27), while the model was inadequate for NOT (b= 0.61±0.46) and NSP (b= 0.14±0.19), and partially adequate for GYP (b= 1.04±0.43). Significant or highly significant mean squares for (Wr + Vr) across all traits indicated the presence of substantial dominance variance. Meanwhile, significant (Wr − Vr) mean squares observed for GYP, NOT, and NSP confirmed the involvement of epistatic interactions. Based on Wr/Vr graphical analysis under heat stress (Fig. 4), GYP showed duplicate non-allelic gene interaction, while NOT and NSP exhibited complementary non-allelic gene interactions.

The Wr/Vr graphical analysis under favorable conditions (Fig. 3) revealed that, for all traits except NSP, the regression lines intersected the Wr axis below the origin, suggesting the presence of overdominance. In contrast, the regression line for NSP passed near the origin, indicating complete dominance. Under heat stress (Fig. 4), similar overdominance patterns were observed for PLH, GYP, NOT, and TKW, while complete dominance was found for SPL, and partial dominance for NSP.

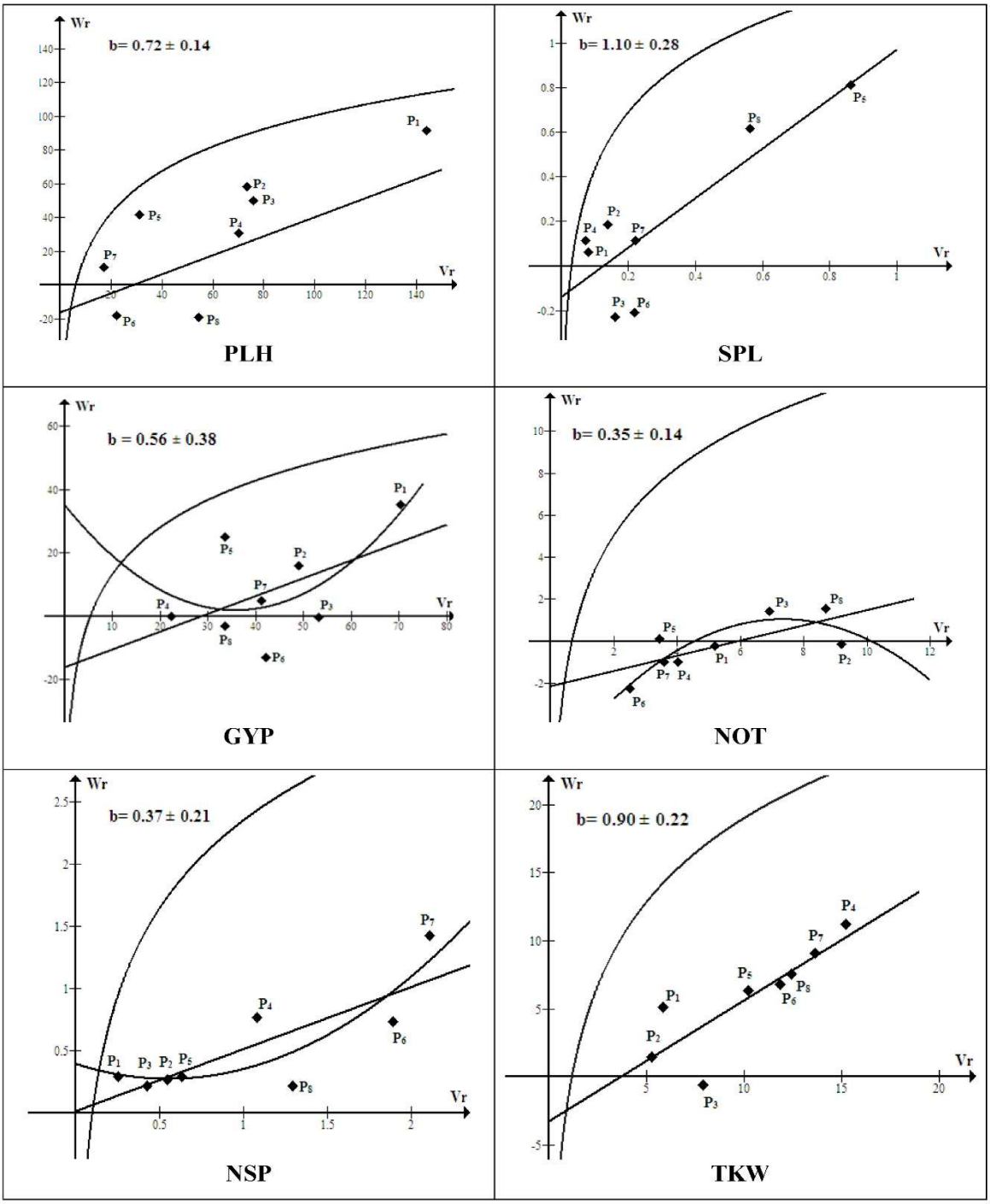

Fig 3. The Wr/Vr graphs of PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight (g) under favorable conditions.

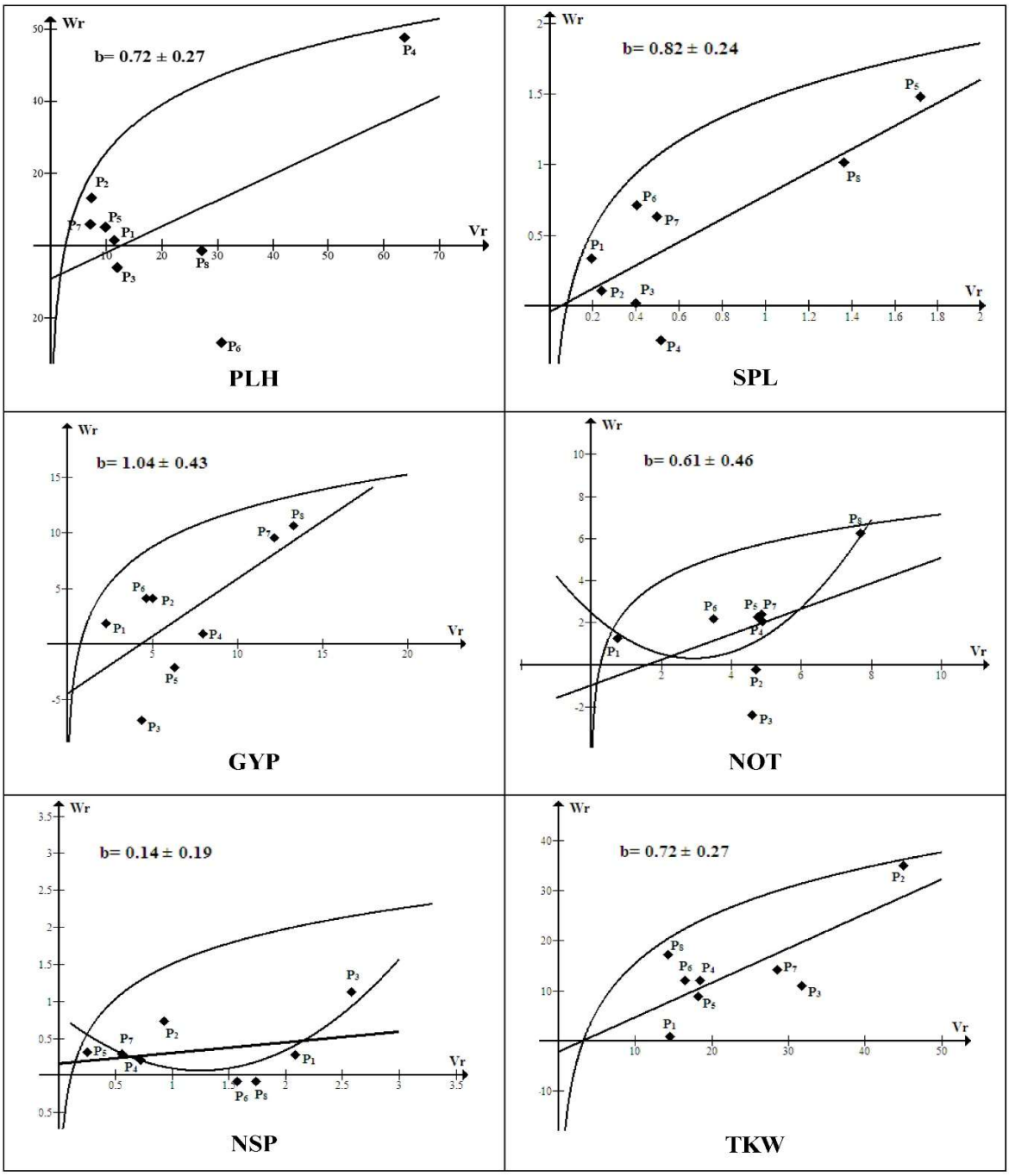

Fig 4. The Wr/Vr graphs of PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight (g) under heat stress conditions.

The GCA and SCA effects

Under heat stress, the parent P4 (CIMMYT-9), followed by P5 (CIMMYT-10), exhibited the highest and significantly positive (P<0.01) GCA effects for GYP and most agronomic traits. Meantime, the cross combination P4×P8, followed by P5×P7 and P3×P6, exhibited the largest and significantly positive (P< 0.01) SCA effects for GYP.

Table 7. Estimates of GCA effects of parental genotypes and SCA effects of the F_1 hybrids for the traits studied under heat stress conditions.

Traits	PLH	SPL	GYP	NOT	NSP	TKW
GCA effects						
P1	-3.240**	-0.449**	0.177	-0.902**	0.182	0.207*
P2	1.296	-0.133**	-0.261*	-0.752**	0.321*	0.329**
P3	-2.170**	-0.533**	0.405**	-0.196	-0.281*	0.365**
P4	5.898**	-0.308**	1.590**	2.009**	-0.408**	-0.212*
P5	0.701	0.933**	1.279**	0.613**	0.885**	0.105
P6	-2.401**	0.266**	-1.198**	-0.421**	0.155	-0.178*
P7	0.323	0.174**	-1.032**	-0.197	-0.090	-0.340**
P8	-0.406	0.049	-0.959**	-0.155	-0.764**	-0.277**
SD (Gi)	**0.73**	**0.04**	**0.13**	**0.14**	**0.14**	**0.09**
SCA effects						
P1×P2	0.55	0.06	-0.06	0.37	0.04	-0.18
P1×P3	-1.62	0.38**	-1.00*	-0.82	-1.82**	-1.05**
P1×P4	-5.47*	0.15	-2.62**	-1.01*	0.21	-0.38
P1×P5	-1.43	-0.59**	-2.84**	-1.45**	0.22	-0.12
P1×P6	7.02*	0.77**	-0.75	-0.82	2.22**	0.24
P1×P7	4.74	-0.01	0.60	-0.29	0.81	0.51
P1×P8	2.50	-0.16	-0.24	-0.47	-0.85	0.27
P2×P3	2.45	0.25	2.07**	2.00**	0.25	0.42
P2×P4	-3.20	0.16	1.20**	-1.38**	0.87	0.45
P2×P5	2.77	-0.90**	-1.79**	-0.60	0.20	-0.50
P2×P6	-1.33	-0.89**	-0.97*	-0.75	-1.07*	-0.22
P2×P7	3.20	0.70**	1.78**	4.45**	0.23	-0.88**
P2×P8	1.64	0.09	-2.99**	-2.18**	-0.93	-0.18
P3×P4	-10.53**	0.11	-4.49**	-1.36**	-0.86	-0.05
P3×P5	3.11	0.20	-3.41**	-3.67**	0.77	0.59*
P3×P6	1.18	-0.10	3.69**	3.41**	0.97*	0.33
P3×P7	1.54	-0.27	2.88**	1.04*	0.21	0.16
P3×P8	2.15	-1.24**	2.43**	2.27**	-1.89**	-0.38
P4×P5	-4.33	-1.19**	-0.83*	-1.69**	-0.11	0.15
P4×P6	-11.19**	0.24	0.40	0.50	-0.99**	-0.16
P4×P7	-6.06*	-0.68*	-1.87**	-1.01*	-0.63	-0.15
P4×P8	-5.67*	1.63**	5.13**	3.64**	0.73	0.09
P5×P6	1.76	-0.72**	-0.62	-0.47	-0.41	-0.10
P5×P7	0.67	-0.06	4.98**	2.11**	-0.22	0.44
P5×P8	5.89*	0.59**	1.49**	0.73	0.75	0.42
P6×P7	-1.73	0.12	-0.45	-0.88	-1.06*	0.18
P6×P8	12.77**	0.89**	-0.42	-0.60	1.72**	0.03
P7×P8	-1.40	0.464**	-1.292**	-1.078*	0.66	0.06
SD (Sij)	**2.46**	**0.14**	**0.43**	**0.49**	**0.48**	**0.29**

PLH: Plant height (cm), SPL: Spike length (cm), GYP: Grain yield per plant (g), NOT: No. of tillers, NSP: No. of spikelets per spike and TKW: 1000-kernel weight (g). * and ** stand for significant differences at 0.05 and 0.01 probability, respectively.

Genetic diversity based on SSR markers

The DNA amplification profiles of the parental genotypes using twelve SSR markers are presented in Figs. 5 and 6. Across the eight wheat parents, these markers produced a total of 100 DNA bands, with the number of bands per marker ranging from 4 (Xgwm293) to 13 (Xgwm186), with an average of 8.33 bands per marker. Of the 100 amplified bands, 40 were polymorphic, averaging 3.33 polymorphic bands per marker. Among the twelve SSR markers used, eleven markers were polymorphic across the parental lines. The lowest polymorphism (16.67%) was recorded for Xgwm294, while

the highest (63.64%) was for Xwmc273, located on chromosome 7A. The overall average polymorphism across markers was 38.32%. Polymorphic information content (PIC) values ranged from 0.04 (Xgwm294) to 0.27 (Xwmc398 on chromosome 6B), with Xwmc273 showing a PIC value of 0.26. The marker index (MI) varied between 0.08 (Xgwm294) and 1.82 (Xwmc273), with an average MI of 0.62 (Table 8).

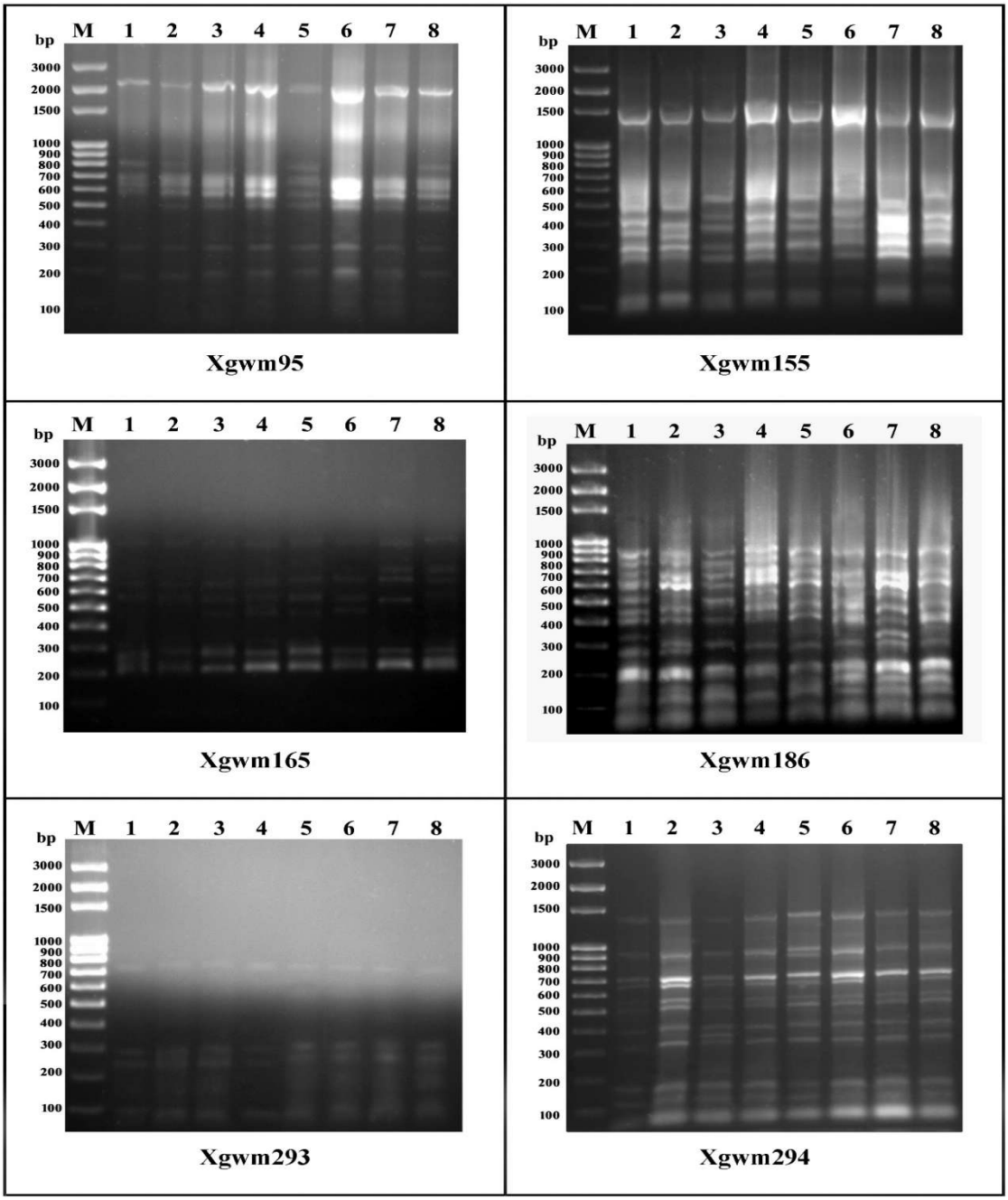

Fig. 5. DNA amplification patterns of the parents obtained using Xgwm95, Xgwm155, Xgwm165, Xgwm186, Xgwm293 and Xgwm294markers. M: the 100 bp DNA ladder.

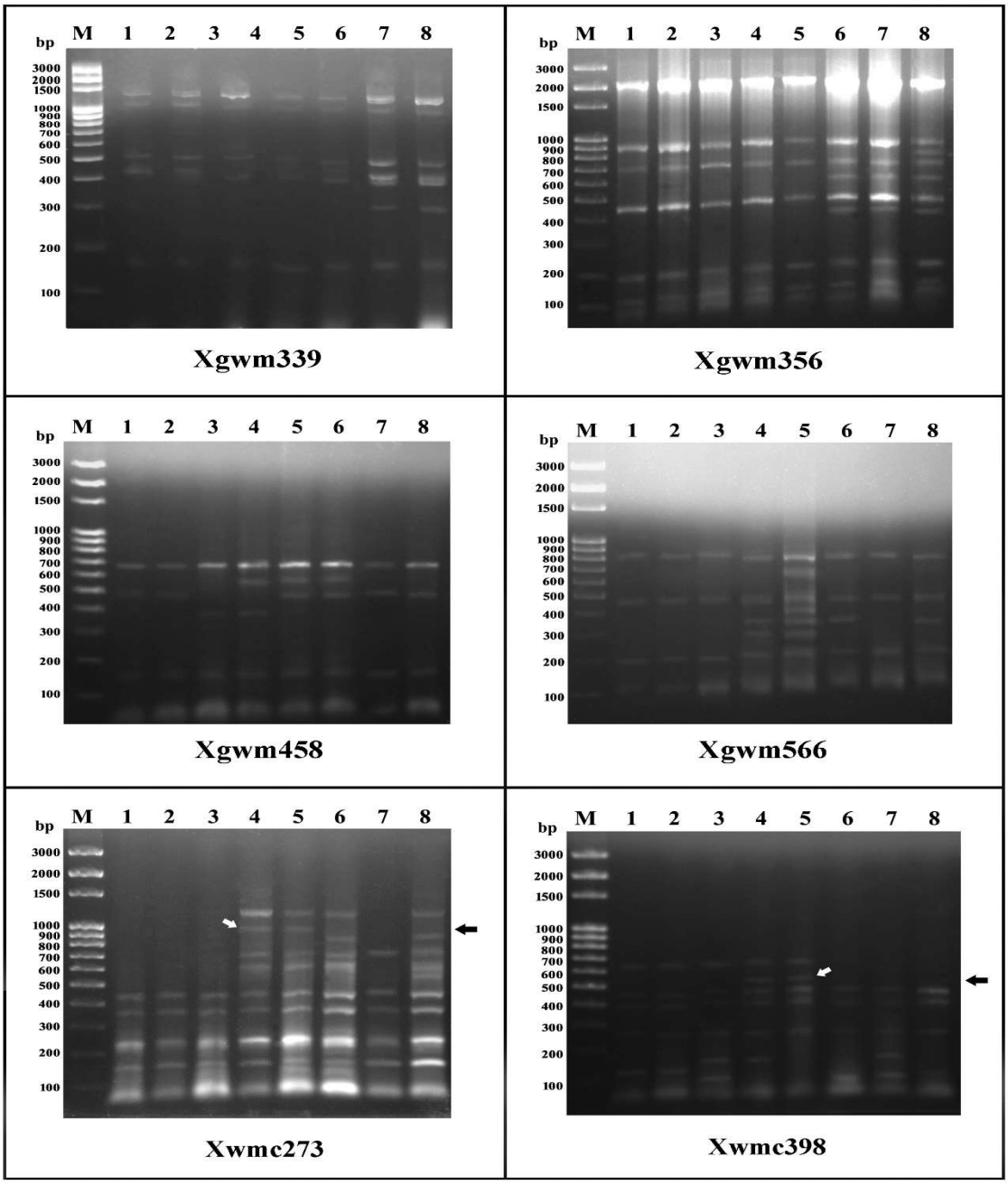

Fig. 6. DNA amplification patterns of the parents obtained using Xgwm339, Xgwm356 Xgwm458, Xgwm566, Xwmc273 and Xwmc398 markers. M: the 100 bp DNA ladder. Arrows indicate bands specific to P4 and P5, amplified by Xwmc273 (975 bp) and Xwmc398 (540 bp).

Two distinct DNA bands amplified by the SSR markers Xwmc273 (975 bp), located on chromosome 7A, and Xwmc398 (540 bp), located on chromosome 6B, as shown in Fig. 6, were exclusively present in the parental genotypes P4 (CIMMYT-9) and P5 (CIMMYT-10).

Table 8. The polymorphism detected among parental wheat genotypes using twelve SSR markers used in the study.

Name	CL	TB	PB	%P	PIC	MI
Xgwm95	2A	7	2	28.57	0.10	0.21
Xgwm155	3A	8	3	37.50	0.16	0.48
Xgwm165	4D	7	2	28.57	0.13	0.26
Xgwm186	5A	13	7	53.85	0.19	1.33
Xgwm293	5A	4	0	0.00	0.00	0.00
Xgwm294	2A	12	2	16.67	0.04	0.08
Xgwm339	2A	7	2	28.57	0.11	0.22
Xgwm356	2A	10	3	30.00	0.12	0.36
Xgwm458	1D	5	3	60.00	0.24	0.72
Xgwm566	3B	8	4	50.00	0.16	0.64
Xwmc273	7A	11	7	63.64	0.26	1.82
Xwmc398	6B	8	5	62.50	0.27	1.35
Total		**100**	**40**			
Average		**8.33**	**3.33**	**38.32**	**0.15**	**0.62**

CL: Chromosol location of a marker, TB: Number of total bands, PB: Number of polymorphic bands, %P: Percentage of polymorphism and PIC: Polymorphic information content, and MI: Marker index.

Cluster analysis of parental genotypes

Cluster analysis of the parental genotypes based on SSR markers grouped the eight parental genotypes into two distinct clusters, where cluster I included the CIMMYT genotypes P1, P2, P3, P4, and P5, whereas cluster II comprised the Egyptian cultivars P6, P7, and P8. However, cluster analysis based on phenotypic data grouped the eight parental genotypes into two clusters with six genotypes in cluster I (P1, P2, P5, P6, P7 and P8), and two genotypes gathering in cluster II (P3 and P4). Meantime. cluster I was split into two sub-clusters, where P1 which showed the highest HTI was gathered in a sub-cluster, and the remaining five genotypes were grouped together in a second sub-cluster (Fig. 7).

Table 9. Genetic distances calculated among parental wheat genotypes based on SSR markers (down diagonal), and phenotypic distances based on phenotypic data (above diagonal).

	P1	P2	P3	P4	P5	P6	P7	P8
P1	**0**	0.07	0.12	0.12	0.07	0.11	0.10	0.09
P2	0.04	**0**	0.10	0.08	0.03	0.04	0.03	0.03
P3	0.12	0.10	**0**	0.05	0.08	0.12	0.13	0.09
P4	0.15	0.12	0.08	**0**	0.06	0.09	0.09	0.07
P5	0.15	0.12	0.13	0.05	**0**	0.06	0.06	0.04
P6	0.15	0.14	0.12	0.09	0.09	**0**	0.03	0.05
P7	0.12	0.11	0.12	0.15	0.17	0.09	**0**	0.04
P8	0.15	0.13	0.16	0.13	0.13	0.06	0.08	**0**

Genetic distances (dissimilarity) calculated between each two of the eight parental wheat genotypes based on Nei and Li's coefficient (SSR markers), and phenotypic distance calculated based on Euclidean's coefficient (phenotypic data) are presented in Table 8. The phenotypic distance based on phenotypic data ranged from 0.03 (between P2 and P5, P2 and P7, P2 and P8, P6 and P7) to 0.13 (P3 and P7), with an average of 0.07. While the genetic distance calculated based on SSR markers ranged from 0.04 (P1 and P2) to 0.17 (P5 and P7), with an average of 0.12. The Mantel test revealed that there was nonsignificant correlation between the genetic distances calculated based on SSR markers and phenotypic distances based on phenotypic data (r= 0.292, P> 0.05).

Moreover, there was a highly significant difference between their means (t= 5.92, P< 0.01).

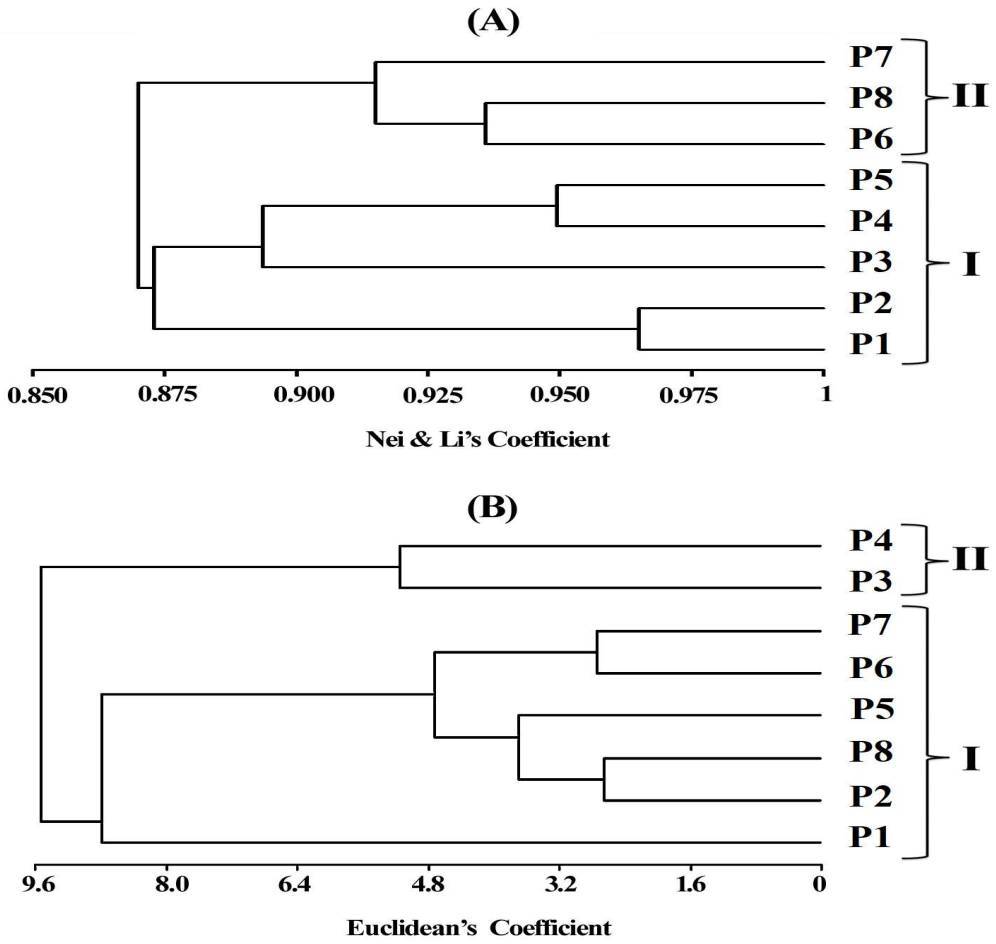

Fig 7. Dendrograms show the relationships among parental genotypes based on SSR markers (A) and phenotypic data (B). P1: CIMMYT-1, P2: CIMMYT-4, P3: CIMMYT-5, P4: CIMMYT -9, P5: CIMMYT-10, P6: Gemmeiza-7, P7: Misr-2 and P8: Sakha-8.

Discussion

Terminal heat stress is a major factor contributing to yield reduction in many wheat-growing regions worldwide, including the Mediterranean basin such as Egypt (Hassan and El-Rawy, 2021). The results demonstrated that late sowing, which exposed plants to heat stress, led to significant reductions in PLH, SPL, GYP, NOT, NSP and TKW by 35.62, 10.25, 45.71, 59.78, 10.74 and 49.25% in the parental genotypes, and by 31.89, 6.73, 77.03, 52.62, 12.88 and 51.71 % in F_1 hybrids, respectively. These findings are consistent with previous reports indicating that GYP, TKW, and various agronomic traits are significantly reduced in response to heat stress caused by delayed sowing (Suleiman *et al.*, 2014; El-Rawy, 2015; Hassan, 2016; Hassan *et al.*, 2016; Sihag *et al*., 2023). Prolonged exposure to elevated temperatures shortens the crop life cycle, leading to fewer and smaller plant organs (Stone, 2001).

The negative impact of heat stress is particularly pronounced during the grain-filling stage, as it shortens the grain-filling duration and decreases grain growth rate, leading to reduced kernel weight and, consequently a significant decline in grain yield (Garg *et al*., 2013; Kumar *et al*., 2016; Saha *et al*., 2020). In wheat, the grain-filling period may be shortened by up to 12 days with a 5°C rise above the optimal temperature of 20°C (Yin *et al*., 2009).

Plant responses to heat stress vary considerably depending on the intensity and duration of elevated temperatures, as well as the developmental stage at which stress occurs (Ruelland and Zachowski, 2010). In the present study, temperature records from the experimental site indicated that several heat waves occurred in March, with daily maximum temperatures exceeding 33 °C. More intense heat waves were recorded in April, when temperatures rose above 37 °C and occasionally reached up to 40 °C. These elevated temperatures, particularly in April, coincided with the post-ear emergence stage of wheat, subjecting the plants to significant heat stress and thereby explaining the severe reductions observed in their growth and productivity.

Understanding the genetic basis of agronomic traits under heat stress assists wheat breeders in applying suitable breeding strategies (Moustafa *et al*., 2021). Diallel analysis is a useful method to assess GCA, SCA, and underlying gene action. In the present study, significant GCA and SCA effects observed under heat stress indicated that both additive and non-additive gene effects influence the studied traits. However, the predominance of GCA effects for GYP and related traits suggests a major role of additive gene action under heat stress. This is further supported by the predominance of additive (a) over non-additive (b) gene actions, emphasizing the importance of GYP and related traits in identifying heat-tolerant, high-yielding genotypes. In accordance, Fouad *et al*. (2022) found that the magnitude of GCA variance was greater than the SCA variance, suggesting a greater additive gene action. Similar results for the importance of GCA compared to SCA were found by El Hanafi *et al.* (2022) and Kumari and Sharma (2022). In addition, Sareen *et al.* (2018) reported that grain yield, thousand-grain weight, and grain weight/spike were mainly controlled by additive gene action. Fouad *et al*. (2022) found that grain yield/plant and grains per spike under late date were controlled by additive gene action. Irshad *et al*. (2014) found mainly additive effects for thousand-grain weight, while Muhammad *et al.* (2012) observed additive gene action with partial dominance for grain yield and kernels per spike. Predominant additive gene action indicates that early-generation selection will be effective in breeding programs targeting improved heat tolerance in wheat.

Evidently, in early-generation wheat breeding for heat tolerance, additive genetic effects are crucial because they contribute predictably and cumulatively to the phenotype. Additive effects represent the sum of individual allele contributions and are reliably transmitted across generations, enabling breeders to select individuals with superior tolerance traits at early generations, even under variable heat stress conditions (Kumar and Sharma, 2022). Furthermore, additive gene action facilitates the accumulation of favorable alleles for heat tolerance through recurrent selection, leading to steady genetic gains (Sareen *et al*., 2018). In contrast, non-additive effects, such as dominance and epistasis, while important for heterosis and hybrid vigor, tend to be less

stable under heat stress due to genotype-by-environment interactions and the complex nature of these genetic interactions, leading to less efficient early generation selection for heat tolerance in wheat. Therefore, early-generation selection for heat tolerance in wheat benefits greatly from emphasizing additive genetic effects because of their stability, predictability, and direct relationship to breeding values.

The performance of genotypes under heat stress serves as a reliable indicator of heat tolerance. Moreover, heat tolerance index (HTI) is a good indicator of both yield potential and stability under heat stress (Li *et al*., 2019). Additionally, GCA and SCA analyses have long been used to identify superior parents and promising crosses for improving heat tolerance (Al-Ashkar *et al*., 2020; Riaz *et al*., 2021; Kamara *et al*., 2021). The results of the present study demonstrated that parental genotypes exhibited differential responses to heat stress. Similarly, previous studies have reported that the severity of high-temperature effects varies depending on crop species and genotype (Asseng *et al.*, 2011; Akter and Islam, 2017). Notably, P1 (CIMMYT-1) showed the highest GYP (13.82 g) and TKW (34.92 g), as well as the highest HTI (0.34). Moreover, P1 (CIMMYT-1) and P4 (CIMMYT-9) exhibited the greatest NOT (7.91 and 7.90, respectively), while the Egyptian cultivar Gemmeiza-7 (P6) showed the lowest GYP (8.91 g) and NOT (5.67). In addition, P4 (CIMMYT-9), followed by P5 (CIMMYT-10), exhibited the highest and significantly positive (P<0.01) GCA effects for GYP and most agronomic traits. Similarly, the crosses P4×P8, P5×P7, and P3×P6 showed the largest and significantly positive (P<0.01) SCA effects for GYP. These findings suggest that the CIMMYT parental genotypes P1, P4, and P5 could possess key adaptive traits, making their incorporation into crosses with Egyptian cultivars a potentially effective strategy for enhancing heat tolerance in wheat.

SSR marker-based clustering clearly separated the CIMMYT lines (P1, P2, P3, P4, and P5) from the Egyptian cultivars (P6, P7, and P8), reflecting their distinct genetic backgrounds. Cluster I, comprising the CIMMYT genotypes, exhibited the highest general combining ability (GCA) for grain yield and most agronomic traits under heat stress. In contrast, Cluster II included the Egyptian cultivars, which were identified as heat-susceptible or moderately heat tolerant. These findings demonstrate that SSR marker-based clustering effectively distinguished genotypes according to their heat tolerance levels.

Phenotypic clustering, however, grouped some Egyptian cultivars with CIMMYT lines, likely due to environmental effects and convergent trait selection. This pattern of divergence between molecular and phenotypic clustering is consistent with recent studies showing a non-significant association, based on mantel test, between the genetic and phenotypic data among the Egyptian bread wheat landraces (Almarri *et al*., 2023). Phenotypic distances, based on phenotypic data, were generally lower and less variable (0.03–0.13, mean 0.07) than those from SSR markers (0.04–0.17, mean 0.12), highlighting the greater resolution of molecular markers. The Mantel test in this study showed a non-significant correlation ($r = 0.292$, $P > 0.05$) between phenotypic and SSR distance matrices, echoing findings by Almarri *et al*. (2023) who reported no significant Mantel correlation in durum wheat landraces. The significant difference between mean distances ($t = 5.92$, $P < 0.01$) further indicates these datasets capture different aspects of

diversity. These findings emphasize the importance of integrating molecular and phenotypic data into breeding programs. SSR markers reveal underlying genetic variation, while phenotypic traits reflect environmental influences and agronomic relevance. Relying on only one data source may provide an incomplete picture of genetic relationships (Mammadova *et al.*, 2025).

Compared to other types of molecular markers, SSRs have shown higher efficiency and are widely regarded as one of the most appropriate marker systems for wheat (Sharma *et al.,* 2021). Consequently, numerous SSR markers have been developed across the three wheat genomes and are frequently employed to evaluate genetic diversity (Landjeva *et al.*, 2006). In line with this, genetic variation in wheat has been extensively analyzed using both phenotypic characteristics and SSR markers (Salem *et al*., 2015; Hassan, 2016; Gurcan *et al*., 2017; Phougat *et al*., 2018; Slim *et al*., 2019; Yang *et al*., 2020; Haque *et al*., 2021; El-Rawy and Hassan, 2021).

In conclusion, heat stress significantly affected all studied traits, with notable genetic diversity among genotypes. Additive gene action played a key role in grain yield and related traits, supporting early-generations selection. Heat-tolerant parents and crosses identified in this study offer valuable resources for wheat breeding. Cluster analysis with twelve SSR markers effectively grouped parental genotypes based on their heat tolerance. Specific bands amplified by Xwmc273 on 7A and Xwmc398 on 6B were found only in the most heat tolerant genotypes (P4 and P5), suggesting a possible association with heat tolerance. Further marker analysis is still needed for validation the usefulness of these markers in wheat selection programs.

References

Akter, N. and Islam, M.R. (2017). Heat stress effects and management in wheat. A review. Agron. Sustain. Dev. 37:37.

Al-Ashkar, I., Alotaibi, M., Refay, Y., Ghazy, A., Zakri, A. and Al-Doss, A. (2020). Selection criteria for high-yielding and early-flowering bread wheat hybrids under heat stress. PLoS ONE 15, e0236351.

Almarri, N.B., Alghamdi, S.S., ElShal, M.H. and Afzal, M. (2023). Estimating genetic diversity among durum wheat (Triticum durum desf.) landraces using morphological and SRAP markers. J. Saudi Soc. Agric. Sci., 22: 273–282.

Asseng, S., Foster, I. and Turner, N.C. (2011). The impact of temperature variability on wheat yields. Glob. Chang. Biol. 17: 997–1012.

Baldissera, J.N., Valentini, G., Coan, M.M., Almeida, C.B., Guidolin, A.F. and Coimbra, J.L. (2012). Combining ability and reciprocal effect on agronomical traits of bean. Semina: Ciências Agrárias, 33(2): 471–480.

El Hanafi, S., Cherkaoui, S., Kehel, Z., Sanchez-Garcia, M., Sarazin, J.B., Baenziger, S. and Tadesse, W. (2022). Hybrid seed set in relation with male floral traits, estimation of heterosis and combining abilities for yield and its components in wheat (*Triticum aestivum* L.). Plants, 11(4): 1–19

El-Rawy, M.A. (2015). Divergent phenotypic selection and molecular marker analysis for heat tolerance in bread wheat (*Triticum aestivum* L). J Agric Chem Biotechnol, 6(9): 301–319.

El-Rawy, M.A. and Hassan, M.I. (2021). Assessment of genetic diversity in durum and bread wheat genotypes based on drought tolerance and SSR markers. Plant Breed Biotechnol, 9(2): 89–103.

Fernandez, G.C.J. (1992). Effective selection criteria for assessing plant stress tolerance. Proceedings of International Symposium on Adaptation of Food Crops to Temperature and Water Stress, Taiwan, Aug 13-18, 1992.

Fleury, D., Jefferies, S., Kuchel, H. and Langridge, P. (2010). Genetic and genomic tools to improve drought tolerance in wheat. J Exp Bot, 61: 3211–3222

Fouad, H., Mohamed, M., Salim, M., Mohiy, M. and Abd El-Mageed, M. (2022). Half Diallel Analysis and Heat Stress Tolerance Indices for Grain Yield in Bread Wheat. J Plant Prod 13: 763–773.

Garg, D., Sareen, S., Dalal, S., Tiwari, R. and Singh, R. (2013). Grain filling duration and temperature pattern influence the performance of wheat genotypes under late planting. Cereal Res Commun 41: 500–507.

Gurcan, K., Demirel, F., Tekin, M., Demirel, S. and Akar, T. (2017). Molecular and agro-morphological characterization of ancient wheat landraces of Turkey. BMC Plant Biol, 17: 171.

Haque, M.S., Saha, N.R., Islam, M.T., Islam, M.M., Kwon, S., Roy, S.K. and Woo, S. (2021). Screening for drought tolerance in wheat genotypes by morphological and SSR markers. J Crop Sci Biotechnol, 24: 27–39.

Hassan, M.I. (2016). Assessment of genetic diversity in bread wheat genotypes based on heat tolerance and SSR markers. Assiut J Agric Sci, 47 (5): 37–55.

Hassan, M.I. and El-Rawy, M.A. (2021). Phenotypic selection and bulked segregant analysis for 1000-kernel weight under heat stress in durum wheat. J Agric Chem Biotechnol, 12(2): 37–47.

Hassan, M.I., Mohamed, E.A., El-Rawy, M.A. and Amein, K.A. (2016). Evaluating interspecific wheat hybrids based on heat and drought stress tolerance. J Crop Sci Biotechnol, 19 (1): 85–98.

Hayman, B.I. (1954a). The analysis of variance of diallel tables. Biometrics 10: 235–244.

Hayman, B.I. (1954b). The theory and analysis of diallel crosses. Genetics 39: 789–809.

Howarth, C.J. (2005). Genetic improvement of tolerance to high temperature. In Ashraf, M and Harris, PJC (eds), Abiotic stresses: plant resistance through breeding and molecular approaches. Howarth Press Inc, New York, pp 277–300.

Irshad, M., Khaliq, I., Iqbal, J., Hussain, N., Aslam, M., Hussain, K. and Din, N. (2014). Genetics of some polygenic traits in hexaploid bread wheat in high temperature stress. J Animal Plant Sci, 24(4): 1212–1219.

Jinks, J.L. (1954). The analysis of continuous variation in diallel cross in Nicotiana rustica varieties. Genetics, 39: 767–788.

Jones, RM. (1965). Analysis of variance of the half diallel table. Heredity, 20: 117–121.

Kamara, M.M., Ibrahim, K.M., Mansour, E., Kheir, A.M., Germoush, M.O., Abd El-Moneim, D., Motawei, M.I., Alhusays, A.Y., Farid, M.A. and Rehan, M. (2021). Combining ability and gene action controlling grain yield and its related traits in bread wheat under heat stress and normal conditions. Agronomy, 11(8): 1450.

Khan, A.A., Shamsuddin, A.K., Barma, N.C., Alam, M.K. and Alam, M.A. (2015). Screening for heat tolerance in spring wheat (*Triticum aestivum* L.). Trop Agric Res Extension, 17: 26–37.

Kumar, S., Singh, S.K., Gupta, S.K., Vishwanath, Yadav, P., Kumar, S., Kumar, J., Bind, H.N. and Singh, L. (2017). Combining ability in relation to wheat (*Triticum aestivum* L.), breeding program under heat stress environment. Int J Curr Microbiol App Sci, 6(10): 3065-3073.

Kumar, V.P., Rao, V.U., Bhavani, O., Dubey, A.P., Singh, C.B., and Venkateswarlu, B. (2016). Sensitive growth stages and temperature thresholds in wheat (*Triticum aestivum* L.) for index-based crop insurance in the Indo-Gangetic Plains of India. J Agric Sci, 154: 321–333.

Kumari, A. and Sharma, H. (2022). Combining ability analysis in bread wheat (*Triticum aestivum* L.) under different environmental conditions. Ann Plant Soil Res, 24(1): 69-73.

Landjeva, S., Korzun, V. and Ganeva, G. (2006). Evaluation of genetic diversity among Bulgarian winter wheat (*Triticum aestivum* L.) cultivars during the period 1925–2003 using microsatellites. Genet Resour Crop Evol, 53: 1605–1614.

Li, Q., Meng, X.H., Li, D., Zhao, M.H., Sun, S.L., Li, H.M., Li, W. and Qiao, W.C. (2019). Evaluation of heat tolerance index, susceptibility index of canopy temperature and leaf chlorophyll content of wheat (*Triticum aestivum* L.). Appl Ecol Environ Res, 17(4): 7357-7369.

Mammadova, R., Akparov, Z., Amri, A., Bakhsh, A., Alo, F., Alizade, S., Amrahov, N. and Yunisova, F. (2025). Genetic diversity analysis of Azerbaijani bread wheat (*Triticum aestivum* L.) genotypes with simple sequence repeat markers linked to drought tolerance. Genet Resour Crop Evol, 72: 315–323.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. Cancer Res, 27: 209–220.

Mather, K. and Jinks, J.L. (1971). Biometrical genetics, 2nd ed. Chapman and Hall Limited, London.

Moustafa, E.S., Ali, M., Kamara, M.M., Awad, M.F., Hassanin, A.A. and Mansour, E. (2021). Field screening of wheat advanced lines for salinity tolerance. Agronomy, 11: 281.

Muhammad, A.R., Salam, A. and Iftikhar, I.R. (2012). Genetic Studies for yield and yield related parameters in bread wheat. American-Eurasian J Agric Environ Sci, 12 (12): 1579-1583.

Murray, M.G. and Thompson, W.F. (1980). Rapid isolation of high molecular weight plant DNA. Nucleic Acids Res, 8(19): 4321–4325.

Perenzin, M., Corbellini, M., Accerbi, M., Vaccino, P. and Borghi, B. (1997). Bread wheat: F1 hybrid performance and parental diversity estimates using molecular markers. In: Braun, HJ., Altay, F., Kronstad, W.E., Beniwal, S.P.S., McNab, A. (eds) Wheat: Prospects for Global Improvement. Developments in Plant Breeding, vol 6. Springer, Dordrecht.

Phougat, D., Panwar, I.S., Punia, M.S. and Sethi, S.K. (2018). Microsatellite markers-based characterization in advance breeding lines and cultivars of bread wheat. J Environ Biol, 39: 339–346.

Powell, W., Morgante, M., Andre, C., Hanafey, M., Vogel, J., Tingey, S. and Rafalski, A. (1996). The comparison of RFLP, RAPD, AFLP and SSR (microsatellite) markers for gemplasm analysis. Mol Breed, 2: 225-238.

Riaz, M.W., Yang, L., Yousaf, M.I., Sami, A., Mei, X.D., Shah, L., Rehman, S., Xue, L., Si, H. and Ma, C. (2021). Effects of heat stress on growth, physiology of plants, yield and

grain quality of different spring wheat (*Triticum aestivum* L.) genotypes. Sustainability, 13: 2972.

Roldan-Ruiz, I., Dendauw, J., Vanbockstaele, E., Depicker, A. and De Loose, M. (2000). AFLP markers reveal high polymorphic rates in ryegrasses (*Lolium spp*.). Mol Breed, 6: 125–134.

Ruelland, E. and Zachowski, A. (2010). How plants sense temperature. Environ Exp Bot, 69(3): 225-232.

Saha, N.R., Islam, T., Islam, M. and Haque, M.S. (2020). Morpho-molecular screening of wheat genotypes for heat tolerance. African J Biotechnol, 19(2): 71-83.

Salem, K.F., Roder, M.S. and Borner, A. (2015). Assessing genetic diversity of Egyptian hexaploid wheat (*Triticum aestivum* L.) using microsatellite markers. Genet Resour Crop Evol, 62: 377–385.

Sareen, S., Bhusal, N., Singh, G. and Sharma, I. (2018) Genetics of grain yield and its components in wheat under heat stress. Cereal Res Commun, 46: 448–459.

Shah, N.H. and Paulsen, G.M. (2003). Interaction of drought and high temperature on photosynthesis and grain-filling of wheat. Plant Soil, 257(1): 219–226.

Sharma, P., Mehta, G., Shefali, Muthusamy, S. K., Singh, S. K., Singh, G. P. (2021). Development and validation of heat-responsive candidate gene and miRNA gene based SSR markers to analysis genetic diversity in wheat for heat tolerance breeding. Mol Biol Rep, 48(1): 381–393.

Sihag, P., Kumar, U., Sagwal, V., Kapoor, P., Singh, Y. Mehla, S., Balyan, P., Mir, R.R, Varshney, R.K., Singh, K.P. et al. (2023). Effect of terminal heat stress on osmolyte accumulation and gene expression during grain filling in bread wheat (*Triticum aestivum* L.). Plant Genome, e20307.

Slim, A., Piarulli, L., Chennaoui, H., Rouaissi, M., Robbana, C., Chaabane, R., Pignone, D., Montemurro, C. and Mangini, G. (2019). Genetic structure analysis of a collection of Tunisian durum wheat germplasm. Int J Mol Sci, 20: 3362.

Stone P. (2001). The effects of heat stress on cereal yield and quality In: A.S. Basra (Ed.) crop responses and adaptations to temperature stress, Food Products Press, Binghamton, NY, pp. 243–291.

Suleiman A.A., Nganya J.F. and Ashraf A. (2014). Effect of cultivar and sowing date on growth and yield of wheat (*Triticum aestivum* L.) in Khartoum. Sudan J Forest Prod Indust 3: 198-203.

Yang, X., Tan, B., Liu, H., Zhu, W., Xu, L., Wang, Y., Fan, X., Sha, L., Zhang, H., Zeng, J., Wu, D., Jiang, Y., Hu, X., Chen, G., Zhou, Y. and Kang, H. (2020). Genetic diversity and population structure of Asian and European common wheat accessions based on genotyping-by-sequencing. Front Genet, 11: 580782.

Yin, X.Y., Guo, W. and Spiertz, J.H. (2009). A quantitative approach to characterize sink-source relationships during grain filling in contrasting wheat genotypes. Field Crop Res, 114: 119–126.

التحليل الوراثي لمحصول الحبوب ومكوناته تحت ظروف الإجهاد الحراري في قمح الخبز

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الملخص

هدفت الدراسة إلى تحليل النظام الوراثي لمحصول الحبوب والصفات المرتبطة به في تهجين نصف دائري لقمح الخبز، شمل ثمانية آباء و28 هجينًا من الجيل الأول، تحت ظروف الحقل المثلى وظروف الإجهاد الحراري. شملت الصفات المدروسة: ارتفاع النبات، طول السنبلة، محصول الحبوب للنبات، عدد الخلفات، عدد السنابل في السنبلة، ووزن الألف حبة. تحت الإجهاد الحراري، لوحظ تباين معنوي بين الطرز الوراثية لجميع الصفات باستثناء وزن ألف حبة. أدى الإجهاد الحراري إلى انخفاض ملحوظ في أداء السلالات الأبوية وهجن الجيل الأول. لوحظ وجود قوة هجين في بعض الهجن. كانت القدرة العامة على الائتلاف معنوية لجميع الصفات، وكانت القدرة الخاصة على الائتلاف معنوية لصفات طول السنبلة، محصول الحبوب للنبات، عدد الخلفات وعدد السنابل في السنبلة. تشير هيمنة آثار القدرة العامة على الائتلاف على نظيرتها الخاصة على الائتلاف إلى الدور الأساسي للفعل الجيني المضيف. وقد دعمت هذه النتائج كذلك من خلال معنوية الفعل الجيني المضيف وغير المضيف، مع هيمنة الفعل الجيني المضيف تحت الإجهاد الحراري. أظهر تحليل الانحدار ملاءمة نموذج الإضافة-السيادة لصفات ارتفاع النبات، طول السنبلة، ووزن الألف، بينما لم يكن ملائمًا لصفات عدد الخلفات وعدد السنابل في السنبلة، وكان الانطباق جزئيا لصفة محصول الحبوب للنبات. أظهر الأب P4 يليه P5 أعلى قدرة عامة على الائتلاف موجبة ومعنوية لصفة محصول الحبوب ومعظم الصفات المدرسة، بينما أظهر الهجين P4×P8، يليه الهجينان P5×P7، P3×P6، أعلى قدرة خاصة على الائتلاف لصفة محصول الحبوب. وقد نجح التحليل العنقودي باستخدام واسمات SSR في التمييز بين الآباء بناءً على تحمل الإجهاد الحراري. تشير هذه النتائج إلى إمكانية الاستفادة من الطرز الوراثية المتفوقة في تطوير أصناف قمح متحملة للإجهاد الحراري.

الكلمات المفتاحية: *التحليل الدائري (الديالليل)، القدرة على الائتلاف، الإجهاد الحراري، قمح الخبز، محصول الحبوب.*