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Exploring the genotype-environment interaction of bread wheat in ambient and high-temperature planting conditions: a rigorous investigation

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The current study is carried out to find out the stable wheat genotype in ambient and high temperature planting conditions. The objective was to estimate the genotype x environment interactions through various univariates and multivariate techniques. Twenty wheat genotypes were evaluated at Jabalpur, Narmadapuram, and Sagar districts of Madhya Pradesh, India, across cropping years 2019–20 and 2021–21, considering both timely and late planting conditions. The univariate and multivariate stability analysis were performed based on per-plant grain yield and grain filling rate. Our result revealed that environment, genotype, and GEI effects were significant ($P < 0.001$) across all the environments. The wheat genotypes JW3288, L8, and L13 have been discerned as top performers, exhibiting remarkable stability in grain yield per plant. Similarly, for grain filling rate, genotypes L11 and L13 have emerged as superior and consistently stable performers. Notably, the AMMI and GGE models demonstrated superior effectiveness and accuracy compared to the linear regression model. In conclusion, based on thorough univariate and multivariate stability analyses, L13 emerges as the most stable genotype across all environments under both planting conditions. Consequently, L13 holds promise for inclusion in future breeding programs. It's noteworthy that Jabalpur stands out as the most discriminating and representative environment among all the conditions assessed.

Wheat (*triticum aestivum* L.) is a most widely consumed cereal crop in the world¹. It undergoes widespread cultivation on a global scale, with India assuming a pivotal role as a primary region where it serves as an indispensable staple food. In the prevailing circumstances, high temperatures have been identified as a foremost determinant in the reduction of wheat yield^{2–7}. Predictable wheat yield nearly suffers from 6 to 10 percent per one °C increase in temperature at the grain-filling stage^{8–10}. Rao et al.¹¹ described 0.28 °C and 0.32 °C per decade increase in the least and extreme temperatures, respectively over wheat-growing parts of India. The central zone of India is determined as the most heat-prone area¹². Nearly ~42%, wheat cultivating area has suffered by heat stress in the central zone of India¹³.

In earlier studies, researchers predominantly identified wheat genotypes demonstrating stable yield in the North Plain Zone of India^{14–16}. Nevertheless, the exigency for a stable, heat-tolerant wheat variety is notably urgent in Central India¹⁶. While specific research has historically focused on the stability of wheat grain yield, recent studies have appropriately shifted their focus towards elucidating the genotype-environment interaction (GEI) for grain yield^{17,18}. The meticulous control of grain yield involves a substantial number of genes with a heritability ranging from low to moderate¹⁹. The analysis of multi-environmental data under both heat stress and

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non-stress conditions, researchers sought to unravel the intricate interactions between genotype and environment for heat stress and non-stress conditions^{14,20–22}.

The elucidation of genotype by environment interaction (GEI) patterns is facilitated through the application of two principal methodological approaches: regression-based models, as showcased by the frameworks established by Eberhart and Russell; and advanced multivariate stability prediction methods, exemplified by additive main effects and multiplicative interaction (AMMI), as well as genotypic main effects plus genotype by environment interaction (GGE) biplot analysis^{20,23,24}. A biplot is like a special chart that helps show information from a table in two directions. It lets us see how things in rows are related and how things in columns are related at the same time. This helps us understand the connections between both rows and columns in a simple picture^{25,26}. The first-time people used biplots to study farm data and pick the best model, when they looked at information from a multilocation trials of cotton²⁷. After that, biplots were used to study tables that show how different types of plants interact with different environments²⁸. Many plant breeders and agricultural researchers using the biplot tool because it's helpful in evaluating crop plants in different environments. Its popularity grew after it was successfully used for these purposes^{29,30}. The additive main effects and multiplicative interaction (AMMI) model, characterized by its multiplicative nature, effectively gauges genotype by environment interaction (GEI) components through sophisticated multidimensional methodologies, demonstrating high discriminatory power in the estimation of such components^{31,32}. Concurrently, the genotypic main effects plus genotype by environment interaction (GGE) biplot analysis serves as a valuable tool for delineating mega-environments, establishing stable genotype rankings, and pinpointing ideal varieties with consistent performance over the heat stress and non-stress conditions^{16,33}. The GGE biplot was evaluated by Gauch et al.³⁴ for decomposing $G + G \times E$, while they still appealed that GGE biplots interpret $G + G \times E$ more exactly than AMMI stability^{35–37}. The GGE biplot studies have been extensively used to describe macro environments, aspect genotype ranks, and correspondingly to find environments that are representative and discriminative⁷. By incorporating both main effects and interaction effects, AMMI and GGE biplots provide a comprehensive understanding of how wheat varieties respond in different climatic regimes of Central India. However, the primary objective of current study was to organize different places where plants experience stress into specific large categories called mega-environments. This helps us decide which locations affect plants in similar ways, and we can then exclude certain places from future testing. Additionally, we aim to find the best places for future tests and figure out which plant types are stable and superior in heat stress and non-stress environment. These high-quality plant types can be used as different varieties or sources for a particular mega-environment or even for adapting to a wide range of environments with heat stress tolerance.

Materials and methods

Experimental material

A set of 240 recombinant inbred lines was meticulously bred at the Indian Institute of Wheat and Barley Research in Karnal. This was accomplished through a meticulous crossing of the heat-susceptible parent (MACS2496) and the heat-tolerant parent (WH730), a contrast pairing that has been confirmed and validated by many researchers^{5,38–41}. Among the 240 recombinant inbred lines fifteen-heat tolerant recombinant inbred lines were recognised by Department of Plant Breeding and Genetics JNKVV Jabalpur based on their performance and heat susceptibility index. Hence the identified stable recombinant inbred lines were still not registered anywhere. To further identification of stable performing recombinant inbred lines for ambient and high-temperature planting conditions. The analysis of genotype-environment interaction was meticulously conducted. To performing the analysis the selected heat tolerant recombinant inbred lines along with two parents (WH730 and MACS2496) and three commercial checks (GW322, JW3382, and JW3288), were planted at three locations (Jabalpur, Narmadapuram and Sagar), two cropping years (2019–20 and 2020–21) and two planting conditions (timely and late) of Madhya Pradesh (Table 1 and Supplemental Table s1 and s2).

Testing environment

Selected heat-tolerant recombinant inbred lines, their parents and commercial checks were tested into timely sown and late sown planting conditions. Timely sown environments designated as NSE (normal sown environment) and late sown environment designated as HSE (heat stressed environment). Under NSE the experimental material was screened in two cropping years (2019–20 and 2020–21) at three locations (Jabalpur, Sagar and Narmadapuram) on the other hand under HSE the experimental material was screened in two cropping years (2019–20 and 2020–21) at two locations (Jabalpur and Narmadapuram). The maximum and minimum day–night temperatures during two cropping years (2019–20 and 2020–21), under NSE, 36.8/16.7–21.4/4.8 °C, 39.1/22.8–23.1/02.1 °C and 39.1/22.8–23.1/02.1 °C, were recorded at Jabalpur, Sagar and Narmadapuram, respectively while under HSE, 39.3/23.2–22/4.8 °C and 41.5/12.2–20.5/2.9 °C, were recorded at Jabalpur and Narmadapuram, respectively (Supplemental Table s5, s6 and s7). Geographically the experimental field of Jabalpur, Sagar and Narmadapuram were located at 23.21, 23.83, and 21.50, latitudes (N) 79.95, 78.71, and 76.43, longitudes (E) and heights from mean sea level were recorded 392, 433, and 229 m, respectively. Geographically, JNKVV's College of Agriculture Jabalpur, Regional Agriculture Research Centre Sagar, and College of Agriculture Narmadapuram were located at latitudes (N) of 23.21, 23.83, and 21.50, longitudes (E) of 79.95, 78.71, and 76.43, and heights(m) from mean sea level of 392, 433, and 229, respectively (Table 2). For the experimental fields in Jabalpur, Sagar, and Narmadapuram, the soil pH values were 7.61, 6.96, and 8.10, respectively (Table 2). Throughout the cropping period, adherence to recommended packages and practices, coupled with the implementation of an optimal number of irrigations, was rigorously maintained.

Genotypes	$Y_{(hsi)}$	Pedigree	Origin
<i>Heat tolerant recombinant inbred lines</i>			
L1	0.03	MACS2496/WH730	IWBR, Karnal
L2	0.12	MACS2496/WH730	IWBR, Karnal
L3	0.21	MACS2496/WH730	IWBR, Karnal
L4	0.23	MACS2496/WH730	IWBR, Karnal
L5	0.25	MACS2496/WH730	IWBR, Karnal
L6	0.28	MACS2496/WH730	IWBR, Karnal
L7	0.28	MACS2496/WH730	IWBR, Karnal
L8	0.37	MACS2496/WH730	IWBR, Karnal
L9	0.38	MACS2496/WH730	IWBR, Karnal
L10	0.38	MACS2496/WH730	IWBR, Karnal
L11	0.41	MACS2496/WH730	IWBR, Karnal
L12	0.42	MACS2496/WH730	IWBR, Karnal
L13	0.43	MACS2496/WH730	IWBR, Karnal
L14	0.44	MACS2496/WH730	IWBR, Karnal
L15	0.44	MACS2496/WH730	IWBR, Karnal
<i>Parents</i>			
WH730	0.45	CPAN2092/Improved Lok 1	HAU, Hisar
MACS2496	1.7	SERI "S"	ARI, Pune
<i>Commercial checks</i>			
GW322	1.69	GW173/GW196	SDAU, VIJAPUR
JW3382	0.66	CHOIX/STAR/3/HE1/3*CNO79//2*SERI/4/GW273	JNKVV, Jabalpur
JW3288	1.24	DOVE/BUC/DL 788-2	JNKVV, Jabalpur

Table 1. Pedigree and heat susceptibility indices of studied wheat genotypes. $Y_{(hsi)}$ = heat susceptibility index based on grain yield.

General detail of experimental locations					
Environment	Locations	Planting year	Planting Date	Day night temperature range (°C)	
NSE1	Jabalpur	2019–20	2 nd Dec	36.8/20.4—21.0/6.3	
NSE2	Sagar	2019–20	2 nd Dec	39.1/22.8—19.5/5.8	
NSE3	Narmadapuram	2019–20	2 nd Dec	37.6/14.6—17.1/3.1	
NSE4	Jabalpur	2020–21	2 nd Dec	36.3/16.7—21.4/4.8	
NSE5	Sagar	2020–21	2 nd Dec	38.1/23.5—23.1/2.1	
NSE6	Narmadapuram	2020–21	2 nd Dec	36.1/22.5—12.5/4.2	
HSE1	Jabalpur	2019–20	4 th Jan	39.3/24.0—22.0/7.5	
HSE2	Narmadapuram	2019–20	4 th Jan	41.5/12.2—20.2/2.9	
HSE3	Jabalpur	2020–21	4 th Jan	38.8/23.2—21.4/4.8	
HSE4	Narmadapuram	2020–21	4 th Jan	40.3/24.5—20.5/4.2	
Geographical detail of experimental locations					
Latitude (N)	Longitude (E)	Altitude (a.m.s.l.)	Soil Colour	Soil pH	Locations
23.21	79.95	392	Dark grey	7.61	Jabalpur
23.83	78.71	433	Black soils	6.96	Sagar
21.5	76.43	229	Deep black soil	8.1	Narmadapuram

Table 2. Experimental details. *N* = North, *E* = East, *a.m.s.l.* = Above mean sea level, *NSE* = normal sown environment, *HSE* = Heat stress environment, *Dec* = December, *Jan* = January.

Design of experiment and data collections

Each experimental trial was conducted in randomised block design with three replications. Numerous component traits were observed manually, including days to heading, days to maturity, thousand kernel weight, grain filling duration, grain filling rate and grain yield per plant. Grain filling rate and grain yield per plant were subjected to the current study. As per Dias and Lidon's⁴² methodology, the comprehensive span from anthesis to maturity was considered as the grain filling duration. This duration was subsequently utilized to calculate the grain filling rate in grams per day using the formula (total grain yield per plant/grain filling duration).

Statistical analysis

Analysis of variance and association study

Fischer and Maurer's⁴³ method, $1 - (y_s/y_p) / 1 - (x_s/x_p)$, was used to estimate the heat susceptibility index (HSI). Y_s stands for yield under stress, Y_p for yield without stress, and X_s and X_p stand for mean yields across all cultivars under stress and non-stress circumstances, respectively. "Stress intensity" is the definition of the expression $(1 - X_s/X_p)$. To ascertain the variance among grain yield per plant and grain filling rate, a combined ANOVA was performed through various packages of R software version 4.2. Whereas genotypes were measured as fixed factors, environments were measured as random variables. The "corroplot" package of R software was used to perform the Pearson association between studied traits and heat susceptibility index, and the resulting model is given as: $rG = \text{cov}(A, B) / \sqrt{\text{var}(A) \text{var}(B)}$, where $\text{cov}(A, B)$ designates the covariance present among traits, and $\text{var}(A)$, and similarly, $\text{var}(B)$, displays the genetic alteration of trait⁴⁴.

Regression based stability analysis

Initially genotype \times environment interactions were estimated through regression-based stability models. Eberhart and Russell's model⁴⁵, the regression coefficient (b_i), and the deviation from regression (S^2d_i) are all stability indicators based on regression. These parameters collectively govern the performance of a genotype across a variety of contexts⁴⁶. The Eberhart and Russell's stability model⁴⁵ is given as: $Y_{ij} = \mu_i + \beta_i I_j + \delta_{ij}$, where the Y_{ij} designates the assessment of i th ($i = 1, 2, 3, \dots, x$) genotype across the j th ($1, 2, 3, \dots, n$) environment, μ_i is the genotype mean, β_i designates the regression coefficient, δ_{ij} demonstrates the deviation from the regression coefficient, and I_j is the environmental index acknowledged by deducting the total mean from each environmental mean⁴⁷.

AMMI and GGE biplot analysis

Additionally, the multivariate method for stability analysis were directed rendering to AMMI and GGE biplot by means of different statistical packages obtainable in R studio. The "metan" package of R studio was practical for AMMI analysis, while the GGE Biplot GUI package was working for GGE biplot based analysis. In the AMMI model, the ANOVA and PCA are compound collected into an individual statistical package. Therefore, GEI exposed to PCA investigation only when key authentication has already been accomplished by means of ANOVA⁴⁸. The equation for AMMI model is specified as below: $Y_{ge} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge}$, where in circumstance of the additive factors, Y_{ge} is display the grain yield and grain filling rate for a specific (g) genotype in an (e) environment, where μ stand for grand mean, α_g designates deviation of genotype from the mean, β_e is deviation of environment from the mean, λ_n stands for singular value of n component, γ_{gn} designates the value of eigenvector for genotype (g) and δ_{en} is the value of eigenvector for e and ρ_{ge} ; which is known as residual⁴⁹. The AMMI stability values (ASV) were estimated as per Rad et al.⁴⁹, $ASV = \sqrt{[(SSIPCA1/SSIPCA2) + (IPCA1)^2 + (IPCA2)^2]}$, Where, SSIPCA1 and SSIPCA2 are sum of squares of IPCA1 and IPCA2, respectively and IPCA1 and IPCA2 are the genotypic scores in the AMMI model. Moreover, the equation for GGE biplot model is characterized as: $P_{ij} = (y_{ij} - \mu - \delta_j) / \lambda_j = (\beta_i + \epsilon_{ij}) / \lambda_j$, where P_{ij} is the matrix for genotype i and environment j , μ denotes the grand mean, δ_j is the column (environment) main effect, λ_j is an evaluating factor, β_i is the row (genotype) main effect, and ϵ_{ij} characterizes genotype \times environment interaction, and y_{ij} is genotype and environment, two-way table⁵⁰. The GGE biplot also includes a group of biplot-based platforms for interpreting interactions between the environment and the genotype. In a general context, for addressing inquiries related to Genotype by Environment (G \times E), both GGE biplot and AMMI utilize graphical representations⁵¹. In total, the results of both biplot analyses are further interpreted based on the standards established by Khan et al¹⁵. The Genomic Selection Index (GSI) was computed following Farshadfar's methodology⁴³, where GSI is defined as the sum of the rank of ASV (R_{ASV}) and the mean grain yield rank of the genotype (R_{gm}).

Bioethical statement

The seed material remains unregistered and has not been submitted to any publicly accessible herbarium. It was acquired from IIWBR, Karnal, through a legally binding agreement, without any associated costs. We emphasize our unwavering commitment to strict adherence to all local, national, and international guidelines and legislation governing the use of plants in this study, as delineated in the editorial policies for research involving plants (<https://www.nature.com/srep/journal-policies/editorialpolicies#research-involving-plants>).

Results

Combined analysis of variance

The pooled analysis of variance (ANOVA) was used to identify interactions between and within the sources of variation that were examined in this investigation. Table 3 contains the results of the combined ANOVA for grain yield and grain filling rate. Under normal and heat stress environment, omitting the year for grain filling rate under heat stress, replication for grain yield under normal and heat stress environment, the variation owing to genotype (G), location (L), year (Y), G \times Y, G \times L, and G \times Y \times L interactions for all two characters was significant, either at 0.001% or 0.05% level of significance. For grain yield and grain filling rate, wheat genotypes shown a considerable degree of heterogeneity.

Association study

Supplemental Figure s1 illustrates a highly significant correlation ($P = 0.001\%$) between grain filling rate and heat susceptibility index with grain yield. The strong positive and negative correlation originated among grain yield in normal sown environment ($r = 0.80$) and heat stress environment ($r = -0.82$) with heat susceptibility index,

Sources	Normal sown environment (NSE)			Heat stress environment (HSE)		
	DF	YLD	GFR	DF	YLD	GFR
Genotype (G)	19	57.81***	0.078***	19	42.97***	0.014***
Replication (R)	2	0.82 ^{ns}	0.001*	2	0.0001 ^{ns}	0.006*
Location (L)	2	23.78***	0.281***	1	34.77***	0.059***
Year (Y)	1	55.36***	0.005*	1	13.45***	0.001 ^{ns}
G x L	38	16.81***	0.579***	19	15.89***	0.014***
G x Y	19	15.55***	0.013***	19	26.57***	0.007***
L x Y	2	14.78***	0.043***	1	33.89***	0.041***
G x L x Y	38	15.44***	0.012***	19	22.84***	0.008***
Residual	120	0.851	0.111	80	0.317	0.001

Table 3. Combined analysis of variances for wheat genotypes under normal and heat stress environment. *DF*= degree of freedom, *YLD*= grain yield, *GFR*= grain filling rate, *G x L*= Genotype x Location, *G x Y*= Genotype x Year, *L x Y*= Location x Year, *G x L x Y*= Genotype x Location x Year, **P*<0.05, ****P*<0.001, *ns*= non-significant.

respectively. The grain filling rate ($r=0.79$) was found significance ($P=0.001\%$) strong and positive correlation with grain yield.

Regression based stability analysis

The slope of linear regression (b_i) and deviation from regression (S^2d_i) displayed a vast range, for heat tolerant wheat genotypes (Tables 4 and 5). Across normal sown environments, b_i for grain yield ranged from 0.22 (L2) to 1.76 (L5), and absolute values of S^2d_i ranged from 0.35 (L12) to 11.20 (WH730) while for grain filling rate b_i range from 0.05 (L9) to 2.65 (WH730), and absolute value of S^2d_i ranged from zero (L11) to 0.027 (WH730)

Genotype	Grain yield							Grain filling rate						
	G_m	R_{gm}	b_i	S^2d_i	ASV	R_{ASV}	GSI	G_m	R_{gm}	b_i	S^2d_i	ASV	R_{ASV}	GSI
<i>Heat tolerant recombinant inbred lines</i>														
L1	11.38	16	0.64	2.95	1.31	7	23	0.30	16	0.18	0.001	0.05	1	17
L2	10.75	19	0.22	4.88	2.32	11	30	0.29	17	0.33	0.006	0.47	13	30
L3	10.65	20	0.29	8.71	1.87	9	29	0.31	14	0.88	0.012	0.62	17	31
L4	12.37	12	0.63	0.89	0.46	2	14	0.28	19	0.87	0.002	0.27	9	28
L5	12.98	7	1.76	9.42	3.90	17	24	0.41	4	1.98	0.006	0.79	18	22
L6	12.13	13	0.98	4.11	1.70	8	21	0.29	18	0.69	0.004	0.20	6	24
L7	11.18	17	1.57	5.16	2.53	12	29	0.31	13	1.49	0.004	0.25	8	21
L8	12.63	9	0.30	7.34	3.52	16	25	0.31	12	0.20	0.003	0.55	14	26
L9	10.91	18	0.45	10.3	4.21	19	37	0.30	15	0.05	0.009	0.83	19	34
L10	11.93	15	0.85	5.17	2.65	13	28	0.32	11	0.83	0.004	0.43	12	23
L11	13.74	6	1.42	2.96	1.18	5	11	0.39	6	1.14	0.000	0.07	2	8
L12	12.57	10	1.44	0.35	0.41	1	11	0.33	10	1.47	0.001	0.21	7	17
L13	12.92	8	1.48	0.84	0.74	3	11	0.39	7	1.55	0.005	0.28	10	17
L14	12.38	11	0.91	6.35	2.68	15	26	0.36	9	0.73	0.007	0.58	16	25
L15	11.96	14	0.75	6.11	2.68	14	28	0.27	20	0.84	0.001	0.20	5	25
<i>Parents</i>														
WH730	19.10	1	1.74	11.20	5.95	20	21	0.62	1	2.65	0.027	1.55	20	21
MACS2496	15.67	2	1.65	10.60	3.98	18	20	0.44	2	1.62	0.006	0.31	11	13
<i>Commercial checks</i>														
GW322	14.47	5	1.33	3.73	1.26	6	11	0.40	5	1.47	0.001	0.18	4	9
JW3382	14.83	3	1.07	8.67	1.96	10	13	0.38	8	0.97	0.005	0.11	3	11
JW3288	14.59	4	0.51	3.58	1.10	4	8	0.43	3	0.06	0.009	0.56	15	18

Table 4. Stability parameters for grain yield and grain filling rate under normal sown environment. G_m = Grand mean, R_{gm} = Rank of genotypes based grand mean, b_i = Regression coefficient of Eberhart and Russell model, S^2d_i = Deviation form regression of Eberhart and Russel model, ASV = AMMI stability value, R_{ASV} = Stability rank based on AMMI stability value, GSI = Genomic selection index.

Genotypes	Grain yield							Grain filling rate						
	G_m	R_{gm}	b_i	S^2d_i	ASV	R_{ASV}	GSI	G_m	R_{gm}	b_i	S^2d_i	ASV	R_{ASV}	GSI
<i>Heat tolerant recombinant inbred lines</i>														
L1	11.29	10	2.44	0.97	0.498	4	14	0.366	17	0.61	0.002	0.2	7	24
L2	10.45	17	-0.7	1.34	0.911	12	29	0.352	18	-1.58	0.001	0.5	17	35
L3	9.76	18	0.79	0.18	0.323	2	20	0.423	9	2.76	0.003	0.42	15	24
L4	11.66	5	1.8	6.4	1.458	17	22	0.424	8	2.04	0.001	0.16	5	13
L5	11.88	3	0.52	12.4	2.214	20	23	0.469	2	0.64	0.006	0.24	9	11
L6	11.01	14	0.61	3.51	1.017	13	27	0.382	16	0.85	0.007	0.06	1	17
L7	10.48	16	1.83	1.03	0.778	11	27	0.456	5	1.95	0.001	0.27	11	16
L8	11.99	2	0.72	1.29	0.66	7	9	0.347	20	0.61	0.001	0.06	2	22
L9	9.7	20	1.75	0.25	0.499	5	25	0.351	19	1.9	0.001	0.21	8	27
L10	11.19	13	-1.91	3.14	0.726	9	22	0.476	1	1.29	0.02	0.51	18	19
L11	12.29	1	-0.41	6.47	1.47	18	19	0.429	7	-0.82	0.004	0.34	12	19
L12	11.5	7	-0.31	6.18	1.61	19	26	0.461	4	-1.54	0.003	0.54	20	24
L13	11.54	6	1.48	1.49	0.693	8	14	0.454	6	0.51	0.003	0.11	3	9
L14	11.2	12	2.27	0.92	0.607	6	18	0.467	3	2.66	0.004	0.25	10	13
L15	11.4	9	0.04	-0.05	0.115	1	10	0.385	14	-1.29	0.001	0.44	16	30
<i>Parents</i>														
WH730	11.84	4	2.59	3.35	1.31	16	20	0.414	11	3.33	0	0.4	14	25
MACS2496	9.71	19	3.13	1.81	1.056	14	33	0.39	13	3.97	0	0.52	19	32
<i>Commercial checks</i>														
GW322	11.23	11	-0.87	0.89	0.426	3	14	0.414	12	-1.46	0	0.39	13	25
JW3382	11.44	8	1.36	1.33	0.75	10	18	0.416	10	1.46	0.002	0.15	4	14
JW3288	10.53	15	2.85	3.63	1.291	15	30	0.385	15	2.09	0.004	0.2	6	21

Table 5. Stability parameters for grain yield and grain filling rate under heat stress environment. G_m = Grand mean, R_{gm} = Rank of genotypes based grand mean, b_i = Regression coefficient of Eberhart and Russell model, S^2d_i = Deviation from regression of Eberhart and Russell model, ASV = AMMI stability value, R_{ASV} = Stability rank based on AMMI stability value, GSI = Genomic selection index.

(Table 4). On the other hand, across heat stress environments for grain yield, b_i ranged from -1.91 (L10) to 3.13 (MACS2496), with the absolute values of S^2d_i ranging from -0.05 (L15) to 12.4 (L5) (Table 5). Among the wheat genotypes for grain yield, L12 ($S^2d_i = 0.35$) and L13 ($S^2d_i = 0.84$) under normal sown environment, L15 ($S^2d_i = -0.05$) and L9 ($S^2d_i = 0.25$) under heat stress environment showed lower S^2d_i value (Tables 4 and 5). Similarly, for grain filling rate, L11 ($S^2d_i = 0.0$) under normal sown environment while under heat stress environment WH730, MACS2496 and GW322 (0.0) showed lower S^2d_i value (Tables 4 and 5). Under normal sown environments (NSE) L12 ($b_i = 1.44$, $S^2d_i = 0.35$) for grain yield and L11 ($b_i = 1.14$, $S^2d_i = 0.0$) for grain filling rate were identified as most stable genotypes (Table 4). For grain yield L3 ($b_i = 0.79$, $S^2d_i = 0.18$) and for grain filling rate L6 ($b_i = 0.85$, $S^2d_i = 0.007$) were identified as most stable wheat genotype under heat stress environments (HSE) (Table 5). Across all the environments, good levels of stability for grain yield were exhibited by WH730 ($b_i = 0.78$, $S^2d_i = 0.05$), while for grain filling rate L6 ($b_i = 0.97$, $S^2d_i = 0.0$) followed by JW3382 ($b_i = 0.93$, $S^2d_i = 0.0$) were found most stable genotype (Supplemental Table s3).

Additive main effect and multiplicative interactions (AMMI) analysis

AMMI based ANOVA

The AMMI-based analysis of variance (ANOVA) results for the current study's evaluations of grain yield and grain filling rate are shown in Table 6 and supplemental table s4. The results showed that G, E, and GEI significantly influenced by grain yield and grain filling rate. The first two interaction principal component analysis (IPCA) axes explained about 68.9, 78.2 and 68.9% of the GEI across normal sown, heat stressed and across all the environments for grain yield, respectively while 68.9, 78.2 and 59.5% of GEI were explained by first two IPCA for grain filling rate in normal sown, heat stress and across all the environments, respectively (Table 6 and supplemental table s4). Across all the environments proportion of total variation contributed by G, E, and GEI were executed for grain yield was 12.8, 12.3, and 35.8, percentage, respectively while for grain filling rate 15.4, 14.5 and 33.7 percentage, respectively (Supplemental table s4).

Stable genotypes identified based on AMMI-ASV and GSI value

The AMMI, additive main effects and multiplicative interaction stability value (ASV) is presented for grain yield and grain filling rate under normal sown, heat stress and across all the environments in the Tables 4, 5 and supplemental table s3. The range of ASV value from 0.41 (L12) to 5.95 (WH730) and 0.05 (L1) to 1.55 (WH730) were observed for grain yield and grain filling rate respectively, in normal sown environments (Table 4). Similarly, the range of ASV value from 0.115 (L15) to 2.21 (L5) and 0.06 (L6) to 0.54 (L12) were observed for grain yield and

Source	DF	Grain yield			Grain filling rate		
		MSS	Percent explained	p value	MSS	Percent explained	p value
<i>Under normal sown environment</i>							
Environment	5	132.08	15.4	<0.001	0.131	13.54	<0.001
Block	6	1.14	0.2	0.234	0	0.03	0.941
Genotype	19	49.17	21.8	<0.001	0.079	30.97	<0.001
G x E	95	13.61	30.2	<0.001	0.014	26.58	<0.001
PC1	23	32.3	57.4	<0.001	0.029	52.2	<0.001
PC2	21	13.37	21.7	<0.001	0.01	16.7	<0.001
PC3	19	10.07	14.8	<0.001	0.01	14.2	<0.001
PC4	17	4.62	6.1	<0.001	0.008	10.2	<0.001
PC5	15	0	0	<0.001	0.006	6.7	<0.001
Residuals	114	0.84	-	-	0.001	-	-
Total	334	12.82	-	-	0.014	-	-
<i>Under heat stress environment</i>							
Environment	3	12.219	9.74	<0.001	0.033	6.5	0.02
Block	4	0.806	0.42	0.082	0.003	0.77	0.009
Genotype	19	4.677	19.5	<0.001	0.014	17.35	<0.001
G x E	57	5.401	39.83	<0.001	0.01	35.69	<0.001
PC1	21	6.722	45.9	<0.001	0.014	54.3	<0.001
PC2	19	5.635	34.8	<0.001	0.007	23.9	<0.001
PC3	17	3.508	19.4	<0.001	0.007	21.8	<0.001
Residuals	76	0.374	-	-	0.001	-	-
Total	216	3.578	-	-	0.007	-	-

Table 6. AMMI-based ANOVA for grain yield and grain filling rate. *DF*= Degree of freedom, *MSS*= Means of sum square, *G x E*= Genotype x Environment and *PC*= Principal component.

grain filling rate respectively, in heat stress environments (Table 5). For grain yield L12 (ASV = 0.41) in normal sown, L15 (ASV = 0.41) in heat stress and WH730 (ASV = 0.20) across all the environments while for grain filling rate L1 (ASV = 0.05) in normal sown, L6 (ASV = 0.06) in heat stress and L1 (ASV = 0.02) across all the environments were observed as most stable genotypes (Tables 4, 5 and supplemental table s3). The genomic selection index was estimated and presented for grain yield and grain filling rate in Table 4, 5 and supplemental table s3. Genotype with the lowest stability parameter was deemed stable, and that with a lower GSI value had higher mean yield and higher stability. For grain yield the JW3288 (GSI rank = 8) in normal sown, L8 (GSI rank = 9) in heat stress and L13 (GSI rank = 9) in all the environments while for grain filling rate L11 (GSI rank = 8) in normal sown, L13 (GSI rank = 9) in heat stress and GSI rank = 9 was achieved by L11 and L13 in all the environments, suggested that high stable and well performed genotypes (Table 4, 5 and supplemental table s3).

AMMI 1

The AMMI biplots of 20 (Supplemental table s1 and s2) heat stress tolerance wheat genotypes across normal sown, heat stress sown and across both the environmental conditions are presented in Figs. 1, 2, supplemental fig. s2 and s3. In the current study, IPCA1 for grain yield explained 57.4, 45.9, and 46.2% while for grain filling rate 52.2, 54.3 and 39.6% of the variation attributed to GEI in normal sown, heat stress and across both the environmental conditions, respectively (Fig. 1 and supplemental fig. s2). Based on AAMI1, for grain yield NSE4 and HSE3 (Fig. 1a and c) while for grain filling rate NSE1 and HSE3 (Fig. 1b and d) are high-potential environments under normal sown and heat stress environments, respectively. Similarly for grain yield NSE3 and HSE1 (Fig. 1a and b) while for grain filling rate NSE3 and HSE4 (Fig. 1c and d) are low-potential environments under normal sown and heat stress environments, respectively. Similarly, for grain yield and grain filling rate, WH730 are specifically adapted to high-potential environments in normal sown environments while respectively, for grain yield and grain filling rate L11 and L10 are specifically adapted to high-potential environments in heat stress environments, (Fig. 1). With an almost zero IPCA1 score, the cultivar is said to have a poor interaction with its environment it means the cultivar have high stability. For grain yield and grain filling rate NSE3 (Fig. 1a and b) across normal sown environments while HSE2 (Fig. 1b and d) across heat stress environments had a PCA1 score or vector nearer to zero compared to other environments, specifies lower interaction effect which nearly ensures the better performance of all genotypes in that environment. Hence, for grain yield L1, L13 and GW322 (Fig. 1a) while for grain filling rate L6, L12, L11 and GW322 (Fig. 1b) might be the utmost stable genotypes among the normal sown environments based on IPCA1. Similarly, for grain yield L3, L1 and L15 (Fig. 1c) while for grain filling rate L8, L6, L4 and L13 (Fig. 1d) identified as most stable genotype among heat stress environment. Across all the environments for grain yield and grain filling rate, NSE3 and NSE6 identified as most stable environment

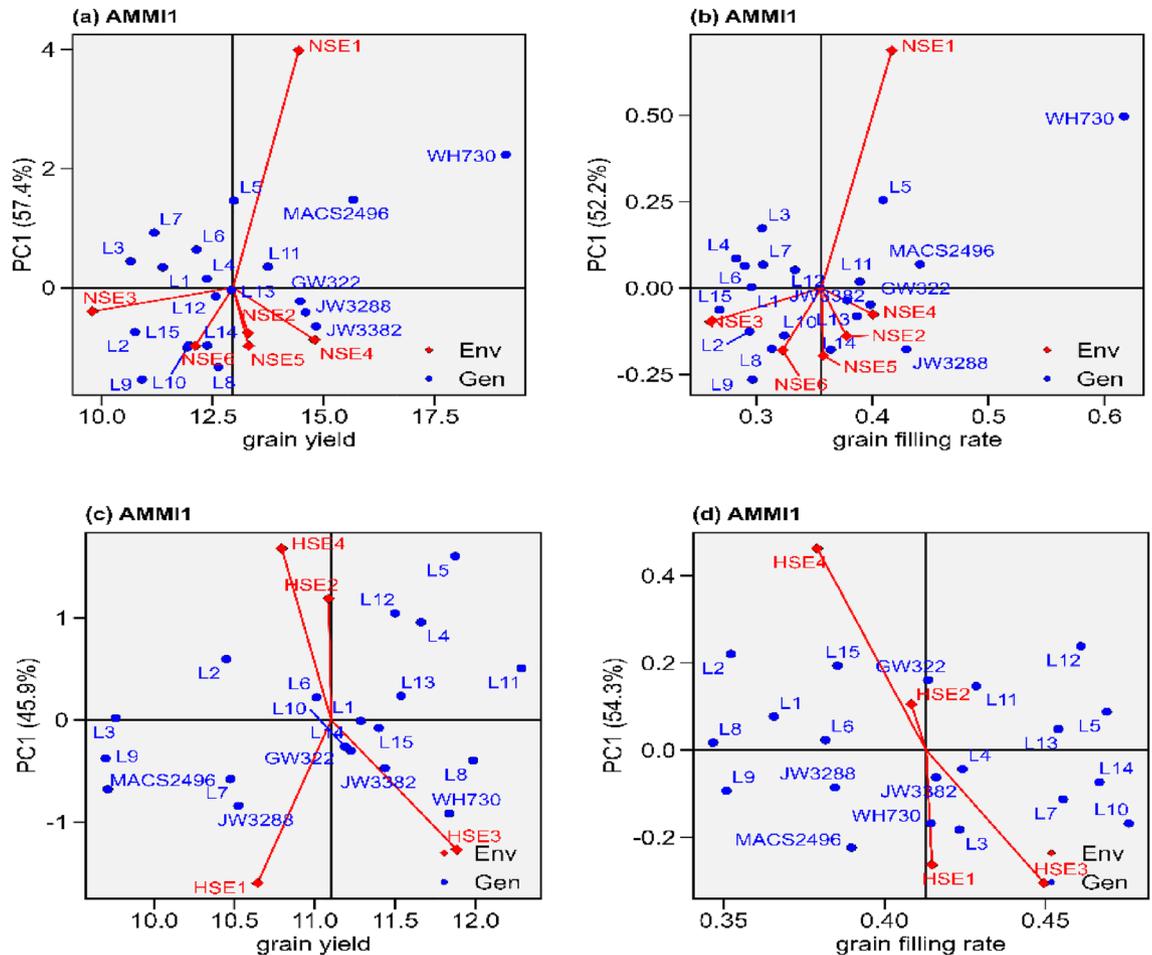


Figure 1. The “AMMI1” graphs displays the main effect and IPC1 effect values describing relationship among examined wheat genotypes and environments. (a) grain yield under normal sown environment, (b) grain filling rate under normal sown environment, (c) grain yield under heat stress environment (d) grain filling rate under heat stress environment.

respectively, on the other hand, for grain yield L13, L1, L12, L13 and GW322 while for grain filling rate L1, L6, JW3382 and GW322 identified as most stable genotype across all the environments (Supplemental fig. s1).

AMMI 2

The AMMI2 expose and inferring the difficult GEI that comprises significant multi-environments and finding of genotypes with also broad or narrow spectrum adaptability. For grain yield and grain filling rate under normal sown environments, NSE1 (Fig. 2a and b) while under heat stressed environments, HSE4 for grain yield and HSE1 for grain filing rate was farthest from the origin, suggesting that the best discriminatory ability but was not stable. In contrast, for grain yield NSE4 (Fig. 2a) and for grain filling rate NSE6 (Fig. 2b), across normal sown environments while for grain yield HSE3 (Fig. 2c) and for grain filling rate HSE2 (Fig. 2d) was nearest to the origin, suggesting that was the most stable environment across heat stressed environments. Across all the tested environments NSE3 and NSE4 were very closer to the origin suggested as most stable environments for grain yield and grain filling rate, respectively (Supplemental fig. s2). In contrast to genotypes that are placed apart from one another, genotypes that assemble together on the biplot origin suggested that genotypes have identical response to all tested environment. Also, compared to genotypes that are near positioned to the biplot origin, those that are located away are more vulnerable to environmental interactions.

GGE Biplot analysis

The GGE biplots for grain yield and grain filling rate of 20 selected heat tolerant wheat genotypes are shown in Figs. 3, 4, 5, and 6. As the x axis and y axis, the first and second principal component scores, respectively.

“Which-Won-Where” approaches

A “which-won-where” polygon view of the biplot showing which wheat genotype did best in which environment is shown in Fig. 3a to d and supplemental fig. s4. For grain yield and grain filling rate, respectively the biplots accounted variation approximately 83.75% and 82.03% (Fig. 3a and b) across normal sown environments, 68.17%

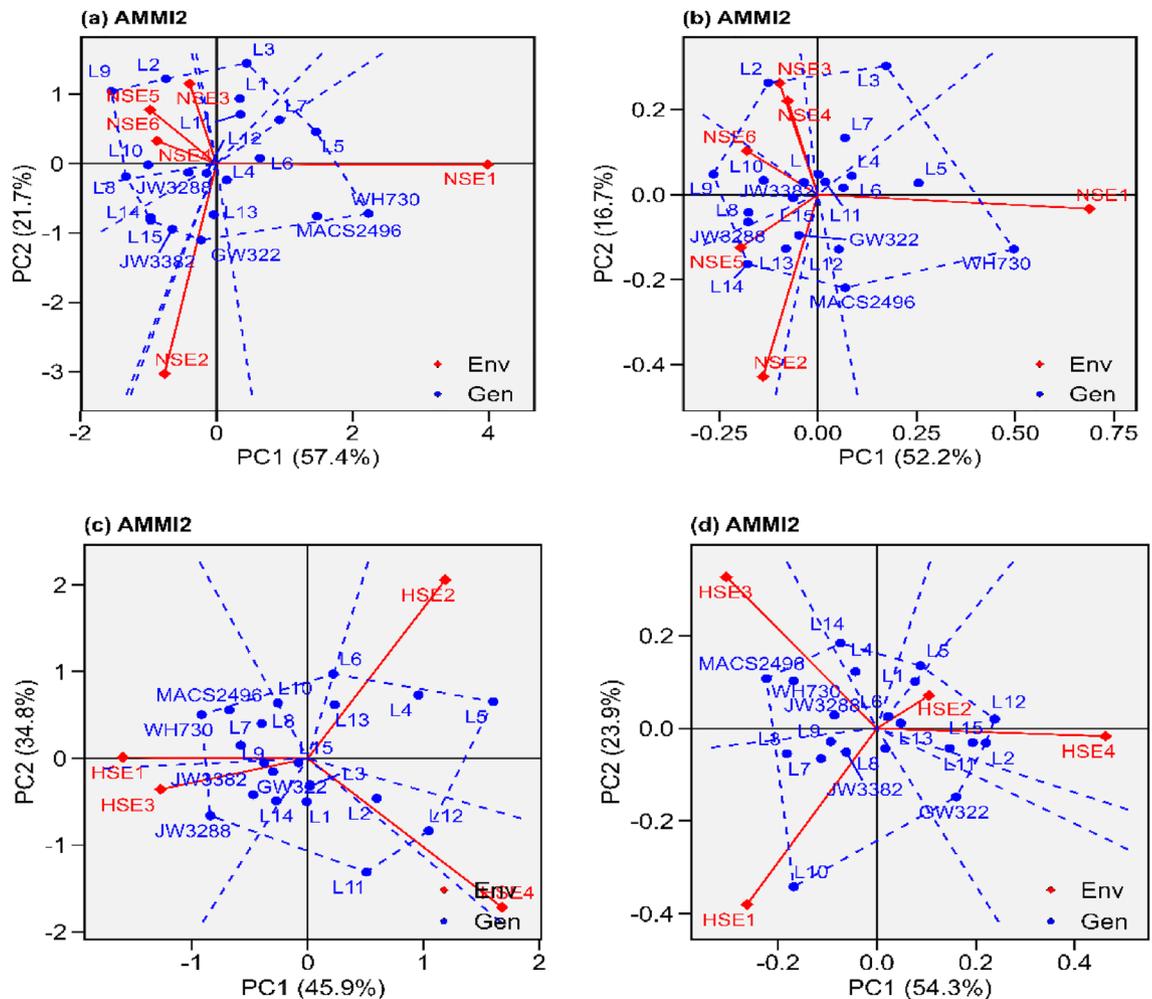


Figure 2. “AMMI2” graphs displays both the axes of interaction (IPCA1 and IPCA2) values for genotype effect and genotype by environment interaction effect. (a) grain yield under normal sown environment, (b) grain filling rate under normal sown environment, (c) grain yield under heat stress environment (d) grain filling rate under heat stress environment.

and 69.43% (Fig. 3c and d) across heat stressed environments, 73.42% and 66.19% (Supplemental fig. s4) across all the environments from total variation related to genotype and GEI. The vertex wheat genotypes in each sector of the biplots represented the top-performing wheat genotypes in the environments that fell within that sector. Wheat genotypes that were positioned nearer the biplot's origin were more stable than vertex genotypes. The genotypes that formed the corners of the polygon for grain yield in the normal sown (L3, L5, WH730, GW322, L14, L9 and L2) (Fig. 3a) and in heat-stressed environments (L5, L6, MACS2496, JW3288, L11 and L12) (Fig. 3c) were utmost responsive genotypes to environments in their corresponding directions compared with the other genotypes. Similarly, for grain filling rate in normal sown environment (L3, WH730, JW3288, L9 and L15) (Fig. 3b) and in heat stressed environment (L2, L8, L9, MACS2496, L10 and L12) (Fig. 3d) genotypes were outmost responsive genotypes compared with other genotypes. The biplot was divided into several sectors by a line drawn perpendicular to the sides of the polygon and extending from the biplot's origin. For grain yield under normal sown environments, WH730 was the highest performing genotype at NSE1; JW3382 was the best genotype at NSE2, NSE3, NSE4, NSE5 and NSE6 (Fig. 3a), similarly for grain filling rate WH730 was the highest performing genotype at NSE1, NSE3 and NSE4; JW3288 was best at NSE2, NSE5 and NSE6 (Fig. 3b). Under heat stressed environments for grain yield, L5 at HSE2, L11 at HSE4, W3288 at HSE3 and MACS2496 at HSE1 were the winner genotypes (Fig. 3c) while for grain filling rate L10 was at HSE1, HSE2 and HSE3; L12 was at HSE4 identified as best performing genotypes, nevertheless L2, L8, L9 and MACS2496 did not win in any of the environments (Fig. 3d). Across all the environments for grain yield L5 was at HSE2; WH730 was at NSE1 and NSE3; L2 was at HSE4; JW3382 was at NSE4, HSE3, HSE1, NSE6, NSE2 and NSE5 while for grain filling rate L3 was at HSE2; WH730 was at NSE5, NSE2, NSE6 and NSE3; L15 was at HSE4; L5 was at HSE3 and NSE1 identified as best performing genotypes (Supplemental fig. s4).

Mean vs. stability and ranking of genotypes

If single value partitioning or $SVP = 1$, the biplot's origin is intersected by the average environment coordinate (AEC) line (single value partitioning). The “Mean vs. stability” view often referred to as AEC and SVP, helps to

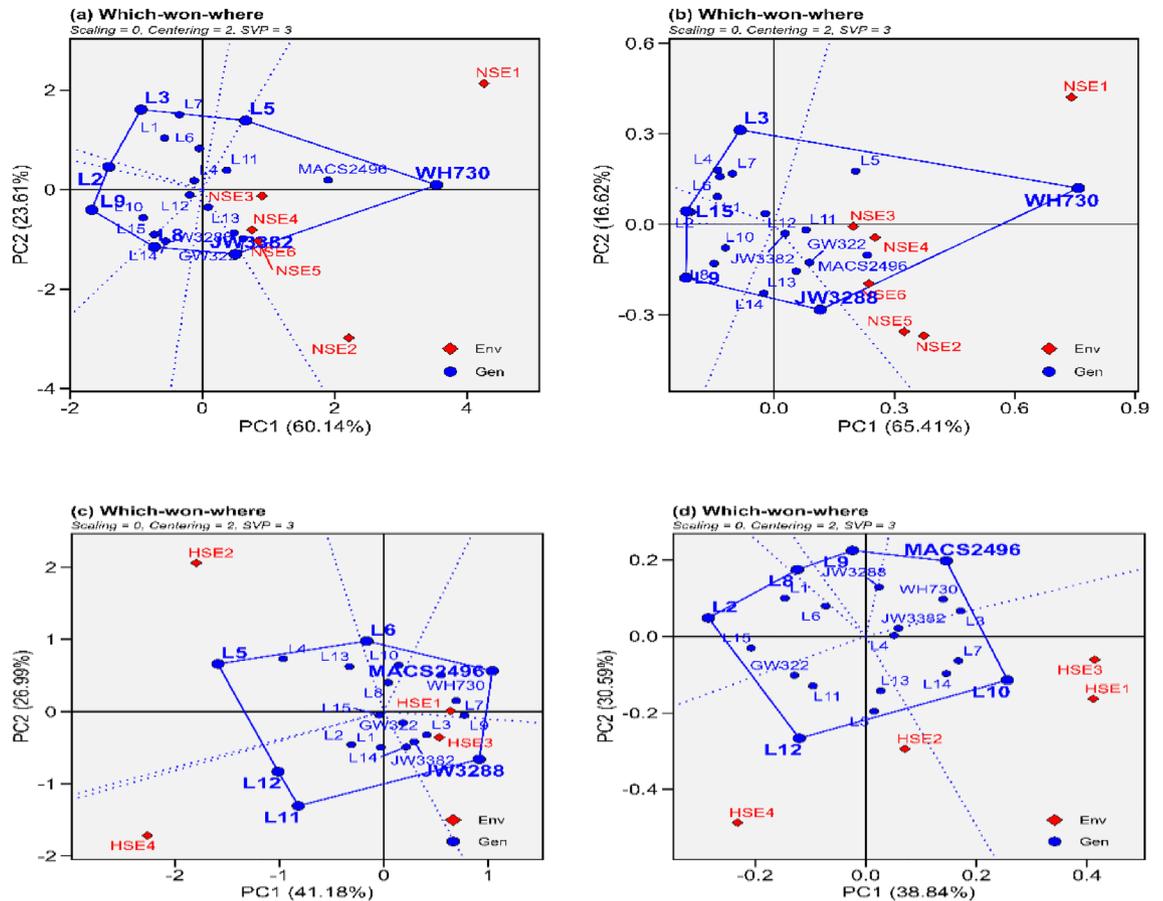


Figure 3. The polygon view of “Which-won-where” model of GGE biplot representing the performance of wheat genotypes and their interactions with environment. (a) grain yield under normal sown environment, (b) grain filling rate under normal sown environment, (c) grain yield under heat stress environment (d) grain filling rate under heat stress environment.

simplify genotype assessment by focusing on mean performance and stability over different environmental conditions (Fig. 4). The biplot graph is made up of two straight lines: I the AEC ordinate (horizontal) and (ii) the AEC abscissa (vertical). The arrow on line one of Fig. 4 indicated in the direction of higher mean performance for the characteristic under this study. It can be seen that for grain yield and grain filling rate in normal sown environments WH730 (Fig. 4a and b) had the highest performing ability while L3 (Fig. 4a and b) had the lowest performing ability. Moreover, MACS2496 (Fig. 4a and b) had the highest performing stability, while L3 (Fig. 4a and b) had the lowest performing stability, and other cultivars had general stability in normal sown environments. In heat stressed environments for grain yield L5 (Fig. 4c) had the highest performing ability while MACS2496 (Fig. 4c) had the lowest performing ability. Whereas, for grain yield L2 (Fig. 4c) had the highest performing stability, while JW3288 (Fig. 4c) had the lowest performing stability in heat stress environments. Similarly, for grain filling rate L10 (Fig. 4d) had the highest performing ability while L2 (Fig. 4d) had the lowest performing ability in heat stress environments. Additionally, L4 (Fig. 4d) had the highest performing stability, while L2 (Fig. 4d) had the lowest performing stability. Across all the environments MACS2496 and L13 (Supplemental fig. s5) had the highest performing stability, while L3 and L9 (Supplemental fig. s5) had the lowest performing stability for grain yield and grain filling rate, respectively. The most stable genotypes for grain yield and grain filling rate were identified as JW3288 and L11 (Fig. 5a and b) in environments where seeds were sown timely, L15 and L13 (Fig. 5c and d) in heat-stressed environments, and L13 and L11 (Supplemental fig. s6) in both of these environmental conditions, respectively. These genotypes had above-average yields and were located on the AEC abscissa with zero (very low) projection onto the AEC ordinate. In contrast, L5 and L10 under heat stressed environment for grain yield and grain filling rate respectively (Fig. 5c and d), while for grain yield and grain filling rate WH730 under normal sown and across all the environmental conditions was identified as highest performing but less stable (Fig. 5a, b and supplemental fig. s6), as evident from greater projection onto the AEC ordinate.

Relationships, discrimination and representativeness of the test environments

Figure 6a to d and Supplemental fig. s7 present a vector view of the GGE biplot, elucidating the relationships between environmental interactions and the biplot origin through depicted vectors. All of the normal sown environments showed positive correlation ($<90^\circ$) for grain yield and grain filling rate (Fig. 6a and b). On the other hand, under heat stressed environments HSE1 and HSE3; HSE2 and HSE4 were positively correlated (Fig. 6c) for

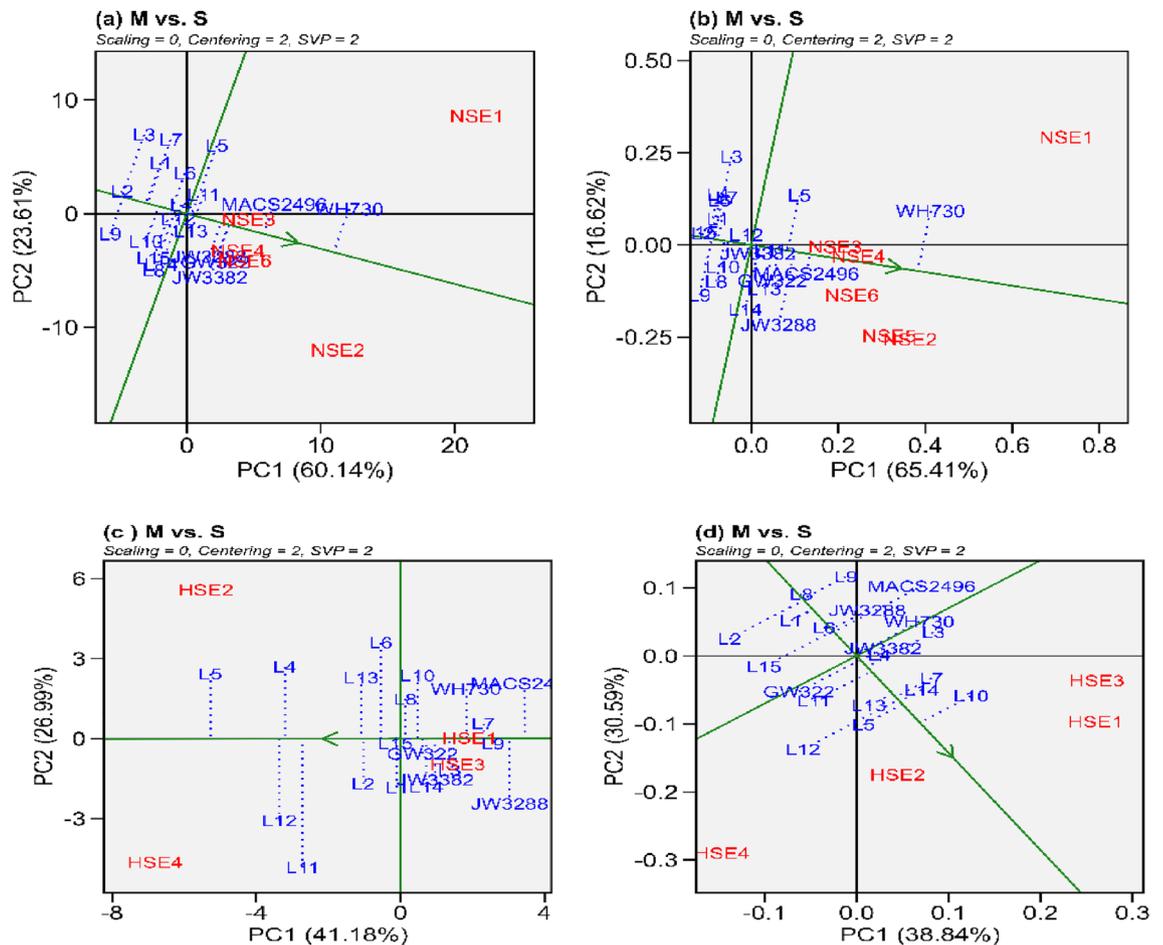


Figure 4. The “mean versus stability” model describe the interaction effect of wheat genotypes. (a) grain yield under normal sown environment, (b) grain filling rate under normal sown environment, (c) grain yield under heat stress environment (d) grain filling rate under heat stress environment.

grain yield while for grain filling rate excluding HSE4 all the tested environments associated positively (Fig. 6d). Across all the environments for grain yield excluding HSE1 and HSE4 all the environments associated positively (Fig. S6) while for grain filling rate excluding HSE2 and HSE4 all the environments associated positively (Supplemental fig. s7). The “ideal environment” in Fig. 6 is represented by the circle at the centre of the concentric circle; it is a virtual environment with the longest vector (most discriminating) of all environments and is fully representative (i.e., it has no significant contribution to GEI and thus is positioned on the AEC abscissa). Similarly, for grain yield and grain filling rate, a cultivar closer to the centre has more stability, as shown in Fig. 6a to d, for grain yield L4 and L12, for grain filling rate L10 and L11 under normal sown environments while for grain yield L15 and GW322, for grain filling rate L4 and JW3382 in heat stressed environments had relatively high performing ability with good stability. Similarly, L12 for grain yield and grain filling rate has high performing ability and stability across all the environments (Supplement fig. s7).

Discussion

In central India, a region heavily reliant on wheat for daily dietary needs, the identification of heat-tolerant, high-performing wheat varieties surpassing commercial checks is crucial for advancing nutritional security. Numerous studies have previously shown the potential for concurrent enhancement of wheat grain yield and grain filling rate under both heat stress and nonstress conditions^{7,16,52}. The observed variations in grain yield and grain filling rate among the experimental genotypes, under both heat-stressed and non-stressed conditions, imply the possibility of identifying preferred genotypes that exhibit favourable traits across both environments. Prior investigations have documented significant variances among tested wheat genotypes concerning the examined traits in both heat-stressed and non-stress environments^{40,53,54}. The discernible interactions observed between wheat genotype and environment, coupled with stability estimates derived from the univariate and multivariate stability analysis, imply the existence of a GEI interaction⁵⁵. This suggests a dynamic alteration in the response patterns and ranking of wheat genotypes in response to diverse environmental conditions. Consistent findings were observed in prior research concerning wheat genotypes, encompassing both heat-stressed and non-stressed environments^{40,56,57}. As indicated by the outcomes of preceding research, the environmental influences were notably significant across diverse environmental conditions^{7,16,52,58}. As anticipated, environments subjected to

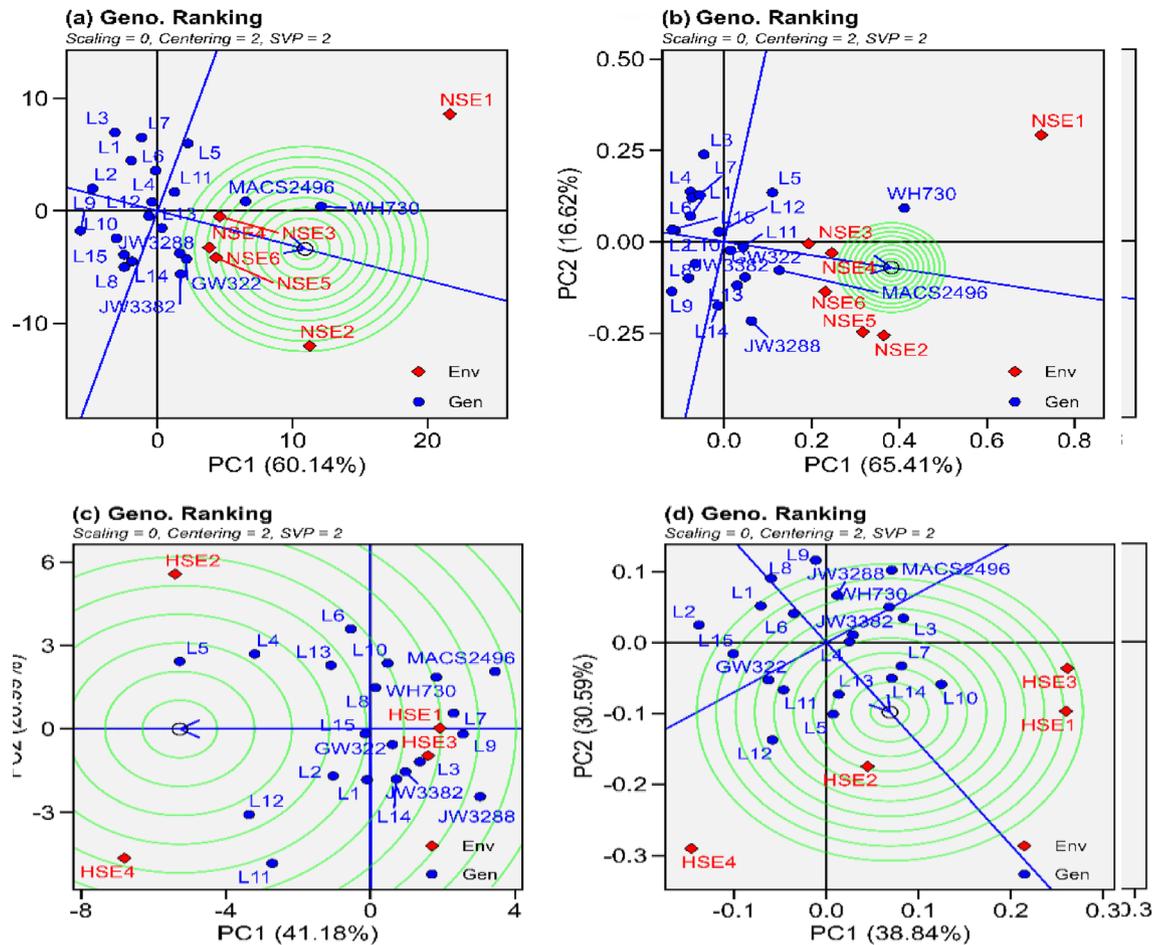


Figure 5. “Ranking of genotypes” model of biplot assess other wheat genotypes against the ideal genotype conferring genotype interaction and genotype x environment interactions. (a) grain yield under normal sown environment, (b) grain filling rate under normal sown environment, (c) grain yield under heat stress environment (d) grain filling rate under heat stress environment.

heat stress demonstrated a diminished mean grain yield compared to non-stressed environments^{2,4,41}. Previous reports in India have documented the grain yield superiority of newly developed recombinant lines over commercial checks^{16,40,59}. This suggested that the newly created recombinant lines outperformed over the commercial checks under heat stress situations.

Elevated *bi* values observed in the majority of high-yielding and fast grain-filling wheat genotypes in this study suggest their heightened adaptability to high-yield environments⁴⁵. As per Betrán et al.⁶⁰, a positive correlation was observed between high mean performance and regression coefficient across diverse environmental conditions. According to univariate stability analysis, L12 and L11 exhibited the highest stability (low $S^2_{d_i}$ values) for grain yield and grain filling rate, respectively, under normal sown conditions. For both traits under heat stress, L3 and L6 displayed superior stability, while WH730 and L6 were identified as the most stable across all environments.

The predominance of genotype-environment interaction (GEI) over genotype suggests that the AMMI biplot is effective for visualizing genotype evaluation. Similar investigations were conducted in other crops to explore genotype-environment interaction (GEI) through the AMMI model^{61–63}. Efficient selection of genotypes excelling in both stability and performance can be achieved through the Genomic Selection Index (GSI), calculated from AMMI stability values. Hence, JW3288, L8, and L13 emerged as superior genotypes for grain yield under normal sowing conditions, heat stress, and across all environments, respectively. This approach has been efficiently employed in other crops^{64,65}. While AMMI can aid in selecting stable cultivars achieving both high and low yields, it often overlooks numerous high-yielding cultivars with poor stability^{34,66}.

By segmenting the biplot, the GGE biplot provides a polygonal perspective, facilitating a clearer examination of ‘which-won-where’ patterns. “When diverse test environments cluster into distinct segments, it signifies the presence of diverse high-performing genotypes for those segments, indicating the existence of genotype-environment interaction (GEI)⁶⁶. The polygonal view divided the biplot into two sectors: one represented by NSE1 and the other by all remaining environments, consistently observed across normal sown conditions for both grain yield and grain filling rate. In grain yield under heat stress, four sectors were identified across different environments, and for grain filling rate, two sectors represented by HSE3 and HSE4. Across all environments,

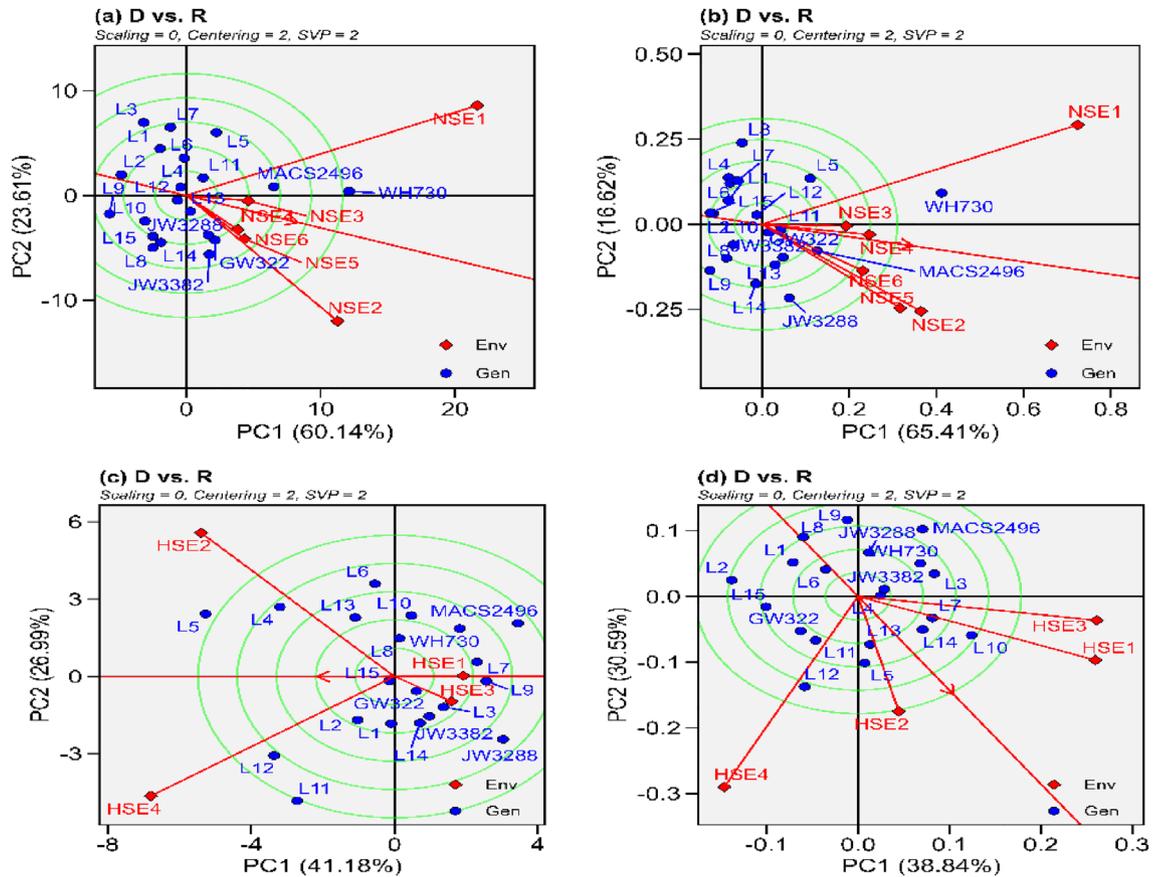


Figure 6. The “Discrimitiveness vs. Representiveness” model of biplot evaluate the wheat genotypes against the ideal genotypes, conferring genotype interaction and genotype x environment interactions. (a) grain yield under normal sown environment, (b) grain filling rate under normal sown environment, (c) grain yield under heat stress environment (d) grain filling rate under heat stress environment.

both grain yield and grain filling rate exhibited two sectors represented by NSE1 and HSE. This data is essential for categorizing environments into distinct mega-environments and recommending specific wheat genotypes for each environment^{21,67,68}. An optimal genotype, defined by Yan and Kang⁶⁹ as one that excels in performance while maintaining stability. The most desired genotypes in this study were those that were closest to the ideal genotype in each environment. Across all of the test environments genotype L12 as the best genotype, telling this genotype’s inherent capacity for superior performance and added adaptability. Yan^{70,71}, declares that the association among the vectors of binary test environments is resolute via the cosine of the angle among them. Angles > 90° advised a negative association of genotype presentation among these environments, whereas lesser angles (< 90°) designated resemblance in genotype presentation among these environments. Right angles (90°) designated orthogonality and absence of association. It was obvious after the GGE biplot’s vector interpretation that convinced environments had positive relationships while others showed negative relationships. While negative or low associations indicate considerable dissimilarity among environments resultant strongly influenced by Genotype-Environment Interaction (GEI) however, positive relationships suggest similarity in genotype performance across various environments^{72,73}. When assessing crops, environments with long vectors and modest angles with the AEC abscissa are beneficial^{66,74}.

Conclusion

The present study identified the most promising stable heat tolerant wheat genotypes for the central India. Under various heat stress regimes L8, L15 and L1 were identified as most stable recombinant lines for grain yield while for grain filling rate L13, L5 and L4 identified as most stable lines based on univariate stability analysis. Whereas, across heat stress and non-stressed environments GW322, L11, L12, and L13 were identified as most stable lines for both the traits. When choosing outstanding wheat genotypes in terms of stability, the multivariate stability analysis performed better than the univariate stability model. The NSE3 and HSE2 identified as most stable environments. In heat stress regimes, L8 was identified as the most stable recombinant inbred line, determined through comprehensive analyses encompassing both univariate and multivariate stability assessments. The recombinant inbred line, L8, could be further tested and utilized in future breeding programs.

Data availability

The datasets of the current study can be requested from corresponding author with strong reason.

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Competing interests

The authors declare no competing interests.

Additional information

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