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RESEARCH ARTICLE

Genetic architecture and combining ability of agronomic and nutritional traits in bread wheat (*Triticum aestivum* L.): A half diallel analysis using Griffing and Hayman approaches

Vikas Verma[1,2*], Deepak Saran[3], Yashowardhan Singh[4] & Vikrant Khare[1]

[1]Department of Plant Breeding and Genetics, Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur 482 004, Madhya Pradesh, India
[2]Department of Genetics and Plant Breeding, Central Agricultural University, Imphal 795 004, Manipur, India
[3]Department of Genetics and Plant Breeding, Indira Gandhi Krishi Vishwavidyalaya, Raipur 492 012, Chhattisgarh, India
[4]Department of Plant Pathology, Jawaharlal Nehru Krishi Vishwa Vidyalaya, Jabalpur 482 004, Madhya Pradesh, India

*Correspondence email - vikasvermagpb@outlook.com

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Abstract

Wheat plays a pivotal role in global food and nutritional security, supplying a significant proportion of calories, protein and essential micronutrients such as iron (Fe) and zinc (Zn). However, breeding efforts focused on yield enhancement have often compromised grain nutritional quality, exacerbating micronutrient deficiencies in populations reliant on wheat as a staple. This study aimed to dissect the genetic architecture of key agronomic and nutritional traits in bread wheat using a comprehensive diallel mating design, combining Griffing's combining ability analysis, Hayman's graphical approach and Vr-Wr regression. Significant general combining ability (GCA) and specific combining ability (SCA) effects indicated the involvement of both additive and non-additive gene actions across agronomic and nutritional traits. Traits such as total protein content (TPC), grain iron content (GFeC) and grain zinc content (GZnC) exhibited high heritability and predictability, supporting the feasibility of selection-based breeding. In contrast, yield-related traits like grain yield per plant (GYPP) and grains per spike (GPS) were predominantly governed by non-additive effects, favoring heterosis breeding. Graphical analysis further confirmed overdominance and epistasis for complex traits, while additive effects dominated micronutrient traits. Promising parental lines, including JW 1203, HI 1633 and HI 1634, along with superior hybrids such as WB02 × HI 1633, were identified for their potential in combined yield and nutritional improvement. These findings highlight the necessity of dual breeding strategies, integrating selection-based approaches for micronutrient enhancement with heterosis breeding for yield improvement, to achieve sustainable gains in wheat productivity and nutritional quality. The insights generated provide a robust genetic framework for advancing biofortification and climate-resilient wheat breeding programs.

Keywords: biofortification combining ability; diallel; Griffing; Hayman; heritability; heterosis

Introduction

Wheat is a cornerstone of global food security, contributing approximately 30 % of the world grain production and constituting half of the grain traded internationally (1). It serves as a staple food in over 40 countries, providing a major share of dietary calories and protein worldwide (1). With the global population projected to reach 9.1 billion by 2050, the demand for wheat is expected to rise significantly, necessitating enhanced productivity and production to meet future food demands (1, 2).

Whole-grain wheat products are particularly beneficial, as they contain fiber and bioactive compounds that help reduce the risk of chronic diseases such as cardiovascular disease and type 2 diabetes (3). Additionally, wheat is a major source of micronutrients like zinc (Zn) and iron (Fe), which are essential for human health, particularly in developing regions where dietary diversification is limited (4–6). Phytic acid, a compound found in wheat grains, chelates minerals like Zn, Fe and P, reducing their bioavailability. Low phytic acid (LPA) wheat genotypes have been developed to improve mineral bioavailability; however, these lines often exhibit reduced grain yield and kernel size, creating a trade-off between nutritional quality and productivity (7). Wheat is also limited by its protein content and quality. While some progress has been made in improving grain protein concentration through breeding, these efforts often conflict with yield improvement goals. Additionally, the gluten composition of wheat can vary, affecting its suitability for different end-use applications (8, 9). Wheat breeding has historically prioritised yield improvement, often at the expense of nutrient content. Studies have shown that selecting for higher grain yield can lead to a decline in mineral content, such as zinc (Zn) and iron (Fe), due to negative correlations between yield and micronutrient concentration (10, 11). For instance, high-yielding wheat cultivars often exhibit lower grain Zn and Fe levels, exacerbating micronutrient malnutrition in populations reliant on wheat as a staple food (12).

Given the magnitude of global micronutrient malnutrition, especially in resource-limited settings, there is an urgent need to enhance the concentration and bioavailability of essential micronutrients in wheat grains. Current recommended dietary allowances (RDA) for adults highlight the importance of these elements: Fe (10–15 mg/day), Zn (9–15 mg/day), Se (0.055 mg/day) and Cu (1.0–1.6 mg/day) (13). Biofortification, the process of increasing nutrient density through genetic improvement, thus emerges as a sustainable and impactful strategy. As wheat serves as the primary ingredient in a wide variety of staple foods-ranging from bread and chapatti to pasta and breakfast cereals-biofortified wheat varieties have the potential to deliver significant health benefits and help address the "hidden hunger" of micronutrient deficiencies. Once fully integrated into the food system, biofortified wheat could serve as a cornerstone of future nutritional security.

Breeding wheat for improved nutritional quality alongside agronomic performance requires the identification of genetically superior parental lines and a clear understanding of the genetic control of yield and grain quality traits, including protein, Fe and Zn content. Combining ability analysis offers a robust framework to elucidate the relative importance of additive and non-additive gene effects and to identify promising parental combinations for both hybrid development and selection-based improvement. Diallel mating designs are particularly effective in evaluating general combining ability (GCA), specific combining ability (SCA), heterosis and the genetic architecture of trait inheritance (14, 15). Although prior studies have explored combining ability and heterosis in wheat for yield and yield-related traits in wheat (16, 17), information on genetic architecture of nutritional traits, particularly in self-pollinated crops remains limited. To address this gap, we employed a comprehensive diallel mating design (18, 19) with the objectives (i) to assess the extent of genetic variability for key agronomic and nutritional traits, (ii) estimate general and SCA effects for yield, protein, iron and zinc content, (iii) evaluate heterosis and the nature of gene action governing these traits using diallel analysis and (iv) identify superior parents and cross combinations suitable for simultaneous improvement of grain yield and nutritional quality. The findings are expected to provide valuable genetic insights to support wheat biofortification and the development of nutritionally enriched, high-yielding cultivars.

Materials and Methods

Experimental site and plant material

The field experiment was conducted at the Breeder Seed Production Unit of Jawaharlal Nehru Krishi Vishwa Vidhyalaya (JNKVV), Jabalpur, Madhya Pradesh, India (23°10′N latitude, 79° 56′E longitude; elevation: 306.06 m above sea level). The experimental site is characterized by medium to deep black soils (Vertisols) with clayey texture, high moisture-holding capacity and neutral to slightly alkaline pH, which are well suited for wheat cultivation. The region experiences a subtropical climate, with wheat sown in November under optimum temperatures of 20–25 °C for germination and early growth, followed by cool winter conditions (10–20 °C) during tillering and grain filling. The area receives an average annual rainfall of 1300–1400 mm, largely concentrated during the monsoon season and wheat cultivation during the Rabi season relies on residual soil moisture supplemented by irrigation. Six agronomically well-adapted bread wheat (*Triticum aestivum* L.) genotypes-JW-1203, WB-02, GW-322, HI-1633, HI-1634 and MP-3382-were selected as parental lines based on their regional adaptability and genetic diversity. During the Rabi season of 2020–2021, these genotypes were sown in a staggered planting schedule to synchronise flowering and facilitate hybridisation. A half-diallel mating design (6 × 6), excluding reciprocals, was used to generate 15 F_1 hybrids.

Experimental design and crop management

In the subsequent Rabi season (2021–2022), the 15 F_1 hybrids along with their six parental genotypes were evaluated using a randomised complete block design (RCBD) with three replications. Each plot consisted of a single row of 1 m in length, with seeds sown manually by dibbling at a spacing of 25 cm × 25 cm. Standard agronomic practices were applied uniformly across all plots to ensure optimal plant growth and minimise environmental variation.

Phenotypic data collection

Data were recorded from five randomly selected plants per plot excluding the border rows for the following traits: Days to 50 % heading (DH 50 %), Plant height (PH) (cm), Days to maturity (DM), Spike length (SL)(cm), Number of spikelets per spike (SPS), Number of grains per spike (GPS), Thousand kernel weight (TKW) (g), Grain yield per plant (GYPP) (g).

Grain protein content estimation

Protein content was estimated using the Kjeldahl method. One gram of finely ground wheat flour was digested in concentrated sulfuric acid (H_2SO_4), using a digestion catalyst to convert organic nitrogen into ammonium sulphate. The digested material was then subjected to distillation and titration and nitrogen content was calculated. The protein percentage was derived using the nitrogen-to-protein conversion factor:

Total Protein Content (TPC)(%) = Nitrogen content (%) × 5.70

Estimation of grain iron (GFeC) (Fe) and zinc (GZnC) (Zn) content

Fe and Zn concentrations were measured using wet acid digestion followed by Atomic Absorption Spectrophotometry (AAS). One gram of flour was digested with a diacid mixture of nitric acid and perchloric acid (HNO_3:$HClO_4$, 4:1 v/v) until a clear solution formed. The digest was diluted to 50 mL with double glass distilled water containing 1 % HCl and filtered. The final filtrate was analyzed using a PERKIN-ELMER 2380 AAS. Concentrations were expressed in mg kg^{-1}.

Statistical analysis

Combining ability and genetic analysis

Combining ability effects were assessed following Griffing's Method II, Model I (20), which considers both parents and F_1 hybrids (excluding reciprocals) and treats genotypes as fixed effects. The statistical model used is:

$$Yij = \mu + gi + gj + sij + eij$$

Where:

Yij = Observed value of the cross between parent i and parent j

μ = General mean

gi, gj = General combining ability (GCA) effects of parent i and j respectively

sij = Specific combining ability (SCA) effect for the cross between parent i and j

eij = Random error associated with the observation.

GCA and SCA mean squares were extracted from the analysis of variance (ANOVA) and their significance was tested using the F-test. A higher GCA/SCA ratio indicates the predominance of additive gene action, while a lower ratio suggests dominance or non-additive effects.

Estimation of heterosis

Heterosis was calculated as follows:

$$\text{Mid-parent heterosis (\%)} = \left(\frac{F_1 - MP}{MP}\right) x100$$

$$\text{Economic heterosis (\%)} = \left(\frac{F_1 - BP}{BP}\right) x100$$

Where:

F_1 = Mean performance of the hybrid

MP = Mean of the two parental genotypes

BP = Performance of the Better parent

In the present experiment, the better parent refers to the superior genotype among the six parental lines used.

Hayman's analysis

To investigate the genetic basis of variation in the studied traits, Hayman's diallel analysis method (19, 21) was applied to a half diallel mating design (without reciprocals). The method assumes diploid inheritance, homozygous parental lines, independent gene segregation and absence of maternal or epistatic effects.

Regression analysis (Vr–Wr graph)

A regression of Wr (covariance of a parent with its offspring) on Vr (variance of the same parent's array) was performed to assess the nature of gene action.

A slope (b) ≈ 1 suggests purely additive gene action

A slope between 0 < b < 1 indicates partial dominance

A slope = 0 suggests complete dominance

A slope < 0 indicates overdominance, where heterozygotes outperform homozygotes

A slope > 1 may suggest epistatic interaction

The significance of the regression was evaluated using the t-test for the slope (b) and the coefficient of determination (r) was computed to assess the linear association between Vr and Wr.

Interpretation of Vr-Wr graph

The intersection point of the regression line on the Wr axis was used to infer gene action:

Above the origin: Partial dominance

At the origin: Complete dominance

Below the origin: Overdominance

The position of parental points along the regression line was used to estimate the relative proportion of dominant and recessive alleles:

Parents near the origin: More dominant alleles

Parents farther from origin: More recessive alleles

Estimation of genetic components

Hayman's approach was used to partition genetic variance into its components:

D: Additive genetic variance

H_1 and H_2: Dominance variance components

F: Covariance of additive and dominance effects

h^2: Contribution of heterozygous loci to dominance

E: Environmental error variance

Additional derived parameters included:

$H_2/4H_1$: Proportion of genes with positive and negative effects distributed among parents

$(4DH_1)^{0.5} + F / (4DH_1)^{0.5} - F$: Degree of dominance and gene distribution

All statistical analyses were performed using INDOSTAT software (version 8.1) and significance was assessed at standard probability thresholds ($P < 0.05$ and $P < 0.01$).

Results

Analysis of variance and genetic components

The analysis of variance (ANOVA) revealed significant variability across all studied traits, indicating the presence of substantial genetic diversity among the evaluated genotypes (Table 1). The total variation was partitioned into components due to replication, treatments, parents, hybrids, parents vs. hybrids and error. Further genetic dissection was conducted through GCA and SCA analyses. Significant replication effects were observed for DH50, DM, SL, SPS, GFeC and GZnC, suggesting minor but consistent environmental variation within the experimental setup for these traits. This underscores the importance of replication in minimizing environmental noise and enhancing experimental reliability. Highly significant treatment effects were detected across all traits, encompassing both agronomic traits (e.g., PH, GYPP) and nutritional traits (e.g., GFeC, GZnC, TPC). These results confirm the presence of considerable genetic variability, which forms the foundation for effective selection and breeding strategies.

Table 1. Analysis of variance for yield and quality traits

Source of Variation	DF	DH50	PH	DM	SL	SPS	GPS	TKW	TPC	GFeC	GZnC	GYPP
Replication	2	12.333*	7.522	21.333*	1.917***	2.103*	25.75	1.307	0.132	10.405*	10.98*	17.026
Treatments	20	18.605***	103.137***	24.652***	0.876***	4.032***	72.518***	4.008*	1.891***	56.063***	34.145***	147.082***
Parents	5	27.3***	72.081***	37.467***	1.005**	3.149***	126.87***	4.348	1.756**	42.767***	45.727***	107.839***
Hybrids	14	15.276***	119.22***	20.657***	0.886***	4.620***	58.196***	4.166*	2.054***	61.789***	32.363***	95.618***
Parents vs Hybrids	1	21.729**	33.244**	16.514	0.101	0.221	1.269	0.085	0.288	42.38***	1.195	1063.79***
Error	40	2.417	2.774	5.1	0.206	0.568	10.122	1.923	0.422	3.029	2.627	12.823
Total	62	7.959	35.302	11.931	0.477	1.735	30.754	2.576	0.886	20.374	13.064	56.268

Where, ***, ** and * represent significant values at 0.01, 0.1 and 0.5 % level of significance.

The comparison between parents and hybrids revealed statistically significant differences for traits such as DH50, PH, GFeC and GYPP, indicating the superior expression of these traits in hybrids relative to parental lines. This provides clear evidence of heterosis (hybrid vigour), particularly for traits associated with early flowering, plant height, micronutrient content and yield potential. Partitioning the treatment sum of squares into parents, hybrids and parents vs. hybrids provided additional genetic insights. The parental component exhibited highly significant mean squares for all traits except TKW, indicating predominant additive genetic variation. Hybrids showed significant variation for all traits, confirming the role of non-additive gene action. Traits such as GPS, GFeC, GZnC and GYPP displayed particularly high F-values, reflecting strong hybrid performance for both grain yield and nutritional traits.

Combining ability analysis (Table 2) further clarified the genetic architecture. General combining ability effects (additive gene action) were highly significant for all traits except TKW, suggesting that additive effects largely govern these traits. High GCA variances for PH, GFeC, GZnC and GYPP indicate promising potential for improvement through recurrent selection and other additive-based breeding approaches. SCA effects (non-additive gene action) were also significant for most traits, especially GPS, SPS, SL and GYPP, pointing to the involvement of dominance and epistatic interactions. The pronounced SCA variance for GYPP reinforces the relevance of hybrid breeding for maximizing grain yield. Finally, low error mean squares across all traits confirm the precision and reliability of the experimental data. Traits such as GYPP, GFeC and GZnC exhibited minimal experimental error, lending strong credibility to the observed genetic differences.

General combining ability, genetic parameters and heritability estimates

Table 3 and supplementary Table 1 provides critical insights into the genetic control of agronomic and nutritional traits in a set of wheat genotypes, elucidating the role of additive and non-additive gene actions, heritability estimates and predictability parameters for devising effective selection strategies. The GCA effects for each parent across traits indicate their average performance in hybrid combinations. Notably, HI 1633 and MP 3382 exhibited significantly negative GCA effects for early heading (DH50), while MP 3382 also demonstrated a significantly negative effect for early maturity, identifying it as a strong general combiner for both traits. HI 1633, HI 1634 and MP 3382 contributed negatively to plant height (PH), indicating their utility in developing semi-dwarf wheat genotypes. In terms of nutritional traits, HI 1633 showed a significant positive GCA effect for grain iron (GFeC) and zinc (GZnC) contents. HI 1634 exhibited significant positive effects for total protein content (TPC) and micronutrients (GFeC and GZnC), while MP 3382 showed significant positive effects for TPC and GZnC, highlighting their potential in biofortification breeding programs.

Critical DDfferences (CD) and GCA Significance**:** The Gi ≠ 0 and Gi – Gj values at both 5 % and 1 % significance levels indicate that most parents exhibited significant differences in combining ability for key traits, reflecting substantial genetic variability. Traits such as GYPP, PH, GPS, GFeC and GZnC displayed highly significant Gi values, underscoring their importance in targeted parental selection.

Additive (σ^2⊠) and Dominance (σ^2_d) Variances: Both additive and dominance variances were substantial across most traits. High dominance variance was recorded for PH, GFeC and GYPP, suggesting a predominant role of non-additive gene action. Moderate additive variance observed for DH50, GPS and TPC suggests that selection could be effective for early flowering and nutritional quality traits.

Heritability estimates: Broad-sense heritability (H^2) was high for nearly all traits, with the highest values reported for GFeC, PH and GYPP, indicating a strong genetic contribution to phenotypic expression. Narrow-sense heritability (h^2), which reflects additive genetic variance, was moderate for GFeC (0.553) and GZnC, implying that selection for micronutrient content could be moderately effective. However, traits like GYPP and GPS had low narrow-sense heritability, indicating a greater influence of dominance or epistatic effects and therefore favoring hybrid development approaches over conventional selection.

Table 2. Analysis of variance for combining ability among yield and quality traits

Source of Variation	DF	DH50	PH	DM	SL	SPS	GPS	TKW	TPC	GFeC	GZnC	GYPP
GCA	5	11.083***	71.237***	14.967***	0.275**	2.186***	27.255***	1.837*	1.446***	46.918***	32.043***	50.614***
SCA	15	4.574***	22.093***	5.968***	0.298***	1.064***	23.145***	1.169	0.358**	9.277***	4.495***	48.498***
Error	40	0.806	0.925	1.7	0.069	0.189	3.374	0.641	0.141	1.01	0.876	4.274

Table 3. Genetic parameters, general combining ability and variance components for agronomic and nutritional traits in bread wheat parental lines

Parameter	DH50	PH	DM	SL	SPS	GPS	TKW	TPC	GFeC	GZnC	GYPP
JW1203	2.042***	3.001***	2.667***	0.001	0.302*	-1.372*	0.540*	-0.154	-0.155	0.519	4.734***
WB 02	-0.083	1.349***	-0.458	-0.081	-0.138	-2.887***	-0.557*	-0.163	-0.125	0.237	-1.754*
GW 322	0.583	3.387***	-0.042	0.186*	0.840***	1.114	-0.572*	-0.634***	-4.413***	-4.002***	-2.240**
HI 1633	-0.917**	-3.521***	-0.792	-0.052	-0.656***	0.643	0.002	0.001	2.370***	0.743*	-0.904
HI 1634	-0.458	-2.797***	-0.208	0.224*	-0.346*	2.259***	0.445	0.466***	2.026***	1.219***	-0.303
MP 3382	-1.167***	-1.418***	-1.167**	-0.278**	-0.002	0.243	0.143	0.484***	0.297	1.284***	0.468
Genetic Variance (σ^2g)	1.285	8.789	1.658	0.026	0.250	2.985	0.149	0.163	5.739	3.896	5.792
Specific Variance (σ^2s)	3.769	21.168	4.268	0.229	0.874	19.771	0.528	0.218	8.268	3.619	44.224
Error Variance (σ^2e)	0.806	0.925	1.700	0.069	0.189	3.374	0.641	0.141	1.010	0.876	4.274
Additive Variance (σ^2a)	2.569	17.578	3.317	0.052	0.499	5.970	0.299	0.326	11.477	7.792	11.585
Dominance Variance (σ^2D)	3.769	21.168	4.268	0.229	0.874	19.771	0.528	0.218	8.268	3.619	44.224
Phenotypic Variance (σ^2p)	7.144	39.671	9.284	0.349	1.563	29.115	1.468	0.685	20.755	12.287	60.083
Heritability (Narrow Sense)	0.360	0.443	0.357	0.148	0.319	0.205	0.204	0.477	0.553	0.634	0.193
Heritability (Broad Sense)	0.887	0.977	0.817	0.804	0.879	0.884	0.563	0.795	0.951	0.929	0.929
GCA/SCA Ratio	0.341	0.415	0.389	0.113	0.285	0.151	0.283	0.750	0.694	1.076	0.131
Predictability Ratio	0.405	0.454	0.437	0.184	0.363	0.232	0.362	0.600	0.581	0.683	0.208

Where, ***, ** and * represent significant values at 0.01, 0.1 and 0.5 % level of significance.

General combining ability/specific combining ability ratio and predictability: The low GCA/SCA ratio for most traits, particularly for GYPP, GPS and SPS, reinforces the predominance of non-additive gene action, supporting the use of hybrid breeding strategies. Conversely, high predictability ratios for TPC, GFeC and GZnC suggest that these traits can be effectively predicted from parental performance, favouring recurrent selection or pedigree-based breeding approaches.

Specific combining ability and mean performance (Per Se) of wheat hybrids for agronomic and nutritional traits

The analysis of variance for SCA and per se performance among 15 wheat hybrids revealed significant genetic variability for most of the traits studied (Table 4 and 5 respectively). These included agronomic parameters such as days to 50 % heading (DH50), plant height (PH), days to maturity (DM), spike length (SL), spikelets per spike (SPS), grains per spike (GPS) and thousand kernel weight (TKW), as well as nutritional traits such as total protein content (TPC), grain iron content (GFeC), grain zinc content (GZnC) and grain yield per plant (GYPP). The hybrids JW 1203 × WB 02 and GW 322 × MP 3382 exhibited significantly negative SCA effects for DH50, indicating early heading. GW 322 × MP 3382 and GW 322 × HI 1634 also showed significantly negative SCA for DM, suggesting their potential as early maturing hybrids. JW 1203 × HI 1633 displayed a highly significant negative SCA value, indicating reduced plant height, which is desirable in semi-dwarf wheat ideotypes.

Conversely, hybrids such as JW 1203 × MP 3382 and HI 1633 × MP 3382 recorded highly positive SCA values for PH, suggesting their utility in improving biomass. For GPS, WB 02 × HI 1633 showed a highly significant positive SCA effect (8.448***), indicating superior yield potential. JW 1203 × MP 3382 also emerged as a top performer for GYPP. On the other hand, hybrids like JW 1203 × HI 1634 and HI 1634 × MP 3382 exhibited significantly negative SCA effects for GPS, indicating poor SCA for this trait.

JW 1203 × HI 1634 and WB 02 × HI 1634 exhibited significantly positive SCA effects for GFeC, while WB 02 × GW 322 and HI 1633 × HI 1634 showed significantly positive SCA effects for GZnC, highlighting their potential in iron and zinc biofortification programs. Among all hybrids, WB 02 × HI 1633 recorded the highest GFeC (7.005***) along with a high per se value (51.74), making it ideal for micronutrient enrichment.

Hybrids such as JW 1203 × GW 322 and HI 1634 × MP 3382 exhibited high positive SCA values for TPC, indicating their potential in enhancing protein content in wheat. Based on superior performance for GYPP, TPC and micronutrient traits, JW 1203 × MP 3382 and JW 1203 × GW 322 are particularly promising. The $S_{ij} - S_{kl}$ and $S_{ij} - S_{ik}$ values (Supplementary Table 2) revealed considerable variation among cross combinations, reaffirming the presence of significant non-additive gene action, particularly for GYPP, GPS and DM. Traits with high $S_{ij} - S_{kl}$ values, such as GYPP (2.53) and GPS (2.24), suggest considerable potential for exploitation through heterosis breeding.

Heterosis estimates

The evaluation of heterosis for eleven agronomic and quality traits across various wheat hybrids revealed distinct patterns of hybrid vigour and parent-specific contributions (Table 6). Both mid-parent (MP) and better-parent heterosis were analyzed to identify superior hybrid combinations suitable for breeding programs

Table 4. Specific combining ability of wheat hybrids for agronomic and nutritional traits

Hybrid Combination	DH50	PH	DM	SL	SPS	GPS	TKW	TPC	GFeC	GZnC	GYPP
	Sca	sca	sca	sca	sca	Sca	sca	sca	sca	sca	sca
JW 1203 x WB02	-1.720*	-2.282*	-0.685	0.065	-0.162	4.363*	-0.949	-0.044	-2.084*	-0.66	-5.812**
JW 1203 x GW322	1.946*	1.937*	1.565	0.365	0.126	1.252	0.6	0.784*	-0.432	2.108*	-10.220***
JW 1203 x HI 1633	3.446***	-11.412***	1.315	-0.917**	-1.738***	-1.49	-1.761*	-0.921*	0.198	1.203	0.102
JW 1203 x HI 1634	-3.345***	4.364***	-0.268	-0.15	0.049	-4.226*	1.463	-0.21	5.588***	-0.74	-2.683
JW 1203 x MP 3382	0.696	5.001***	1.024	0.099	0.871*	3.184	0.005	-0.117	-1.415	0.043	6.766**
WB02 x GW 322	0.738	2.179*	0.024	-0.467	0.946*	-0.309	1.961*	-0.887*	0.971	2.784**	.04.672*
WB02 x HI 1633	1.905*	1.566	4.440**	1.375***	1.752***	8.448***	-1.094	0.181	7.005***	-3.014**	-3.14
WB02 x HI 1634	2.780**	-3.667***	-1.476	0.175	-0.067	3.532*	0.786	0.549	1.912*	-2.297*	-5.495**
WB02 x MP 3382	1.488	-1.117	0.149	0.291	-0.852*	-8.105***	0.212	-0.625	-0.862	1.589	-9.419***
GW 322 x HI 1633	-1.762*	-0.578	-0.643	-0.142	-1.246**	-1.189	0.191	0.146	-2.294*	-3.445***	1.325
GW 322 x HI 1634	0.446	-1.109	-2.560*	0.005	0.008	-0.505	-1.398	0.1	-2.187*	-1.539	0.518
GW 322 x MP 3382	-2.179*	1.942*	-3.601**	0.247	0.45	4.345*	-1.039	0.496	1.363	-1.006	-1.604
HI 1633 x HI 1634	0.28	-2.124*	2.857*	0.236	-1.313**	1.249	0.264	0.319	0.937	4.117***	-2.815
HI 1633 x MP 3382	1.321	4.976***	0.482	-0.171	1.106*	-1.741	0.953	-0.032	-1.46	0.519	-2.859
HI 1634 x MP 3382	-0.47	-6.568***	2.232	-0.631*	-0.491	-7.461***	-0.543	0.902*	0.541	-0.967	-8.320***

Table 5. Mean performance (*Per Se*) of wheat hybrids for agronomic and nutritional traits

Hybrid Combination	DH50	PH	DM	SL	SPS	GPS	TKW	TPC	GFeC	GZnC	GYPP
	per se	per se	per se	per se	per se	per se	per se	per se	per se	per se	per se
JW 1203 x WB02	66.33	94.54	118.67	9.56	17.52	45	41.65	12.06	40.13	40.42	20.45
JW 1203 x GW322	70.67	100.8	121.33	10.13	18.79	45.89	43.18	12.41	37.49	38.95	15.55
JW 1203 x HI 1633	70.67	80.54	120.33	8.61	15.43	42.68	41.39	11.34	44.9	42.79	27.21
JW 1203 x HI 1634	64.33	97.04	119.33	9.65	17.53	41.56	45.06	12.52	49.95	41.32	25.03
JW 1203 x MP 3382	67.67	99.06	119.67	9.4	18.69	46.95	43.3	12.63	41.22	42.17	35.25
WB02 x GW 322	67.33	99.39	116.67	9.22	19.17	42.81	43.44	10.73	38.92	39.34	23.96
WB02 x HI 1633	67	91.87	120.33	10.82	18.48	51.1	40.96	12.44	51.74	38.29	17.48
WB02 x HI 1634	68.33	87.36	115	9.9	16.97	47.8	43.29	13.27	46.3	39.48	15.73
WB02 x MP 3382	66.33	91.29	115.67	9.51	16.53	34.15	42.41	12.11	41.8	43.43	12.57
GW 322 x HI 1633	64	91.76	115.67	9.57	16.46	45.46	42.23	11.93	38.15	33.62	21.46
GW 322 x HI 1634	66.67	91.95	114.33	9.99	18.02	47.76	41.09	12.35	37.92	36	21.25
GW 322 x MP 3382	63.33	96.38	112.33	9.73	18.81	50.6	41.14	12.76	39.74	36.6	19.9
HI 1633 x HI 1634	65	84.03	119	9.99	15.21	49.05	43.32	13.2	47.82	46.4	19.26
HI 1633 x MP 3382	65.33	92.51	115.67	9.08	17.97	44.04	43.71	12.87	43.7	42.87	19.98
HI 1634 x MP 3382	64	81.69	118	8.89	16.68	39.94	42.66	14.27	45.35	41.86	15.12

Table 6. Summary of mid-parent and better-parent heterosis estimates for agronomic and nutritional traits in wheat hybrids, including range, mean, number of superior crosses and best performing hybrid

Trait	Type of Heterosis	Min. Heterosis (%)	Max. Heterosis (%)	Mean Heterosis (%)	No. of Suitable Hybrids	Best Performing Hybrid (Cross)	Heterosis Value (%)
DH50 %	MP (Mid-parent)	-4.69	7.61	2.04	1	JW 1203 × HI 1634	-4.69
	EV (Better-parent)	-9.09	1.44	-3.29	10	GW 322 × MP 3382	-9.09
DM	MP (Mid-parent)	-4.13	6.33	1.17	2	GW 322 × MP 3382	-4.13
	EV (Better-parent)	-7.16	0.28	-2.90	7	GW 322 × MP 3382	-7.16
PH	MP (Mid-parent)	-14.72	5.84	-1.01	5	JW 1203 × HI 1633	-14.72
	EV (Better-parent)	-19.19	1.13	-6.56	11	JW 1203 × HI 1633	-19.19
SL	MP (Mid-parent)	-10.00	20.36	1.34	1	WB02 x HI 1633	20.36
	EV (Better-parent)	-15.67	5.97	-4.97	0		
SPS	MP (Mid-parent)	-13.03	10.77	-0.40	2	WB02 x HI 1633	10.77
	EV (Better-parent)	-20.22	0.58	-8.21	0		
GPS	MP (Mid-parent)	-22.75	29.86	1.92	2	WB02 x HI 1633	29.86
	EV (Better-parent)	-35.72	-3.80	-14.99	0		
TKW	MP (Mid-parent)	-5.23	5.51	-0.14	1	WB02 x GW 322	5.51
	EV(Better-parent)	-6.93	2.38	-3.34	0		
TPC	MP (Mid-parent)	-9.02	11.51	1.35	1	HI 1634 x MP 3382	11.51
	EV (Better-parent)	-17.90	9.15	-3.76	1	HI 1634 x MP 3382	9.15
GFeC	MP (Mid-parent)	-4.60	23.47	4.99	4	WB02 x HI 1633	23.47
	EV (Better-parent)	-16.76	14.88	-4.38	2	WB02 x HI 1633	14.88
GZnC	MP(Mid-parent)	-10.34	8.42	-0.31	1	HI 1634 x HI 1634	8.42
	EV (Better-parent)	-22.67	6.73	-6.80	1	HI 1634 x HI 1634	6.73
GYPP	MP (Mid-parent)	-58.98	-0.16	-27.51	0		
	EV (Better-parent)	-67.49	-8.85	-44.16	0		

targeting specific traits.

Several traits exhibited positive MP heterosis of up to 7.61 % and better-parent heterosis of up to 1.44 %, while some hybrids also showed desirable negative heterosis for earliness. The best-performing hybrid for early maturity was JW 1203 × HI 1634, which recorded an MP heterosis of -4.69 %, while GW 322 × MP 3382 showed the highest better-parent heterosis in the desirable negative direction (-9.09 %). These results suggest that both combinations are promising candidates for early-maturing wheat breeding.

Early maturity is advantageous across various agro-climatic regions. The hybrid GW 322 × MP 3382 consistently recorded desirable negative heterosis values for both MP (-4.13 %) and better-parent heterosis (-7.16 %), reinforcing its potential as a superior early-maturing hybrid. Reduced plant height contributes to lodging resistance. The cross JW 1203 × HI 1633 exhibited the most negative MP heterosis (-14.72 %) and better-parent heterosis (-19.19 %), making it an ideal candidate for developing semi-dwarf wheat ideotypes.

Among the hybrids, WB 02 × HI 1633 showed the highest positive MP heterosis (20.36 %) for spike length, indicating promise for enhanced spike architecture. However, none of the hybrids exhibited significant positive better parent heterosis for this trait. The same hybrid, WB 02 × HI 1633, also showed the highest positive MP heterosis (10.77 %) for SPS. However, better-parent heterosis values were mostly negative, indicating limited improvement over the superior parent.

For GPS, WB 02 × HI 1633 demonstrated outstanding heterosis with an MP heterosis of 29.86 %, identifying it as the most prolific hybrid in terms of grain number per spike. However, better-parent heterosis was negative for all hybrids, indicating that none surpassed the better parent in this trait. Positive MP heterosis was observed in WB 02 × GW 322 (5.51 %) for thousand kernel weight (TKW), indicating potential for improving seed size. However, no hybrids showed favorable better parent heterosis for this trait.

In terms of nutritional traits, HI 1634 × MP 3382 showed superior MP heterosis (11.51 %) and better-parent heterosis (9.15 %) for total protein content (TPC), indicating its potential for protein enrichment in wheat. The hybrid WB 02 × HI 1633 emerged as the best-performing cross for grain iron content (GFeC), with MP heterosis of 23.47 % and better-parent heterosis of 14.88 %, showing strong potential for biofortified wheat breeding.

Positive heterosis for grain zinc content (GZnC) was observed in HI 1634 × HI 1634, with MP heterosis of 8.42 % and better-parent heterosis of 6.73 %, identifying it as a promising cross for enhancing zinc concentration in wheat grains. Unfortunately, all hybrids exhibited negative heterosis for grain yield per plant (GYPP). The highest MP heterosis was -0.16 % and better-parent heterosis was -8.85 %, indicating the need for a broader genetic base or further selection from advanced segregating generations to achieve yield improvement.

Hayman's analysis results (Vr-Wr graphs)

Days to 50 % heading (DH50): The Vr-Wr graph (Fig. 1) suggests the presence of overdominance or epistatic gene interactions for the trait studied. The negative regression slope and its significance indicate that non-additive gene action plays a substantial role. Moreover, the variation in Vr positions implies differential gene expression among parents, with some being more dominant or recessive.

Plant height (PH): The Vr-Wr graph (Fig. 2) shows that plant height is controlled by partial dominance gene action, as indicated by a regression slope (b = 0.2199) less than 1, with the line intersecting above the origin. This suggests both additive and dominance effects are involved. Parents closer to the origin carry more dominant alleles, while those farther carry more recessive alleles, reflecting genetic diversity among parents. The non-significant t-value (t = 0.6375, p = 0.5585) and a low correlation (r = 0.3037) imply the possible presence of epistatic or non-allelic gene interactions. Therefore, both additive and non-additive genetic variances are important in determining plant height and selecting parents with dominant alleles could benefit breeding programs targeting this trait.

Days to maturity (DM): The Vr-Wr graph (Fig. 3) indicates that days to maturity is controlled by partial dominance gene action, as shown by a regression slope of 0.8052 (<1) and the line intersecting above the origin. The regression is statistically significant (t = 2.815, p = 0.0481), suggesting a valid additive-dominance model with

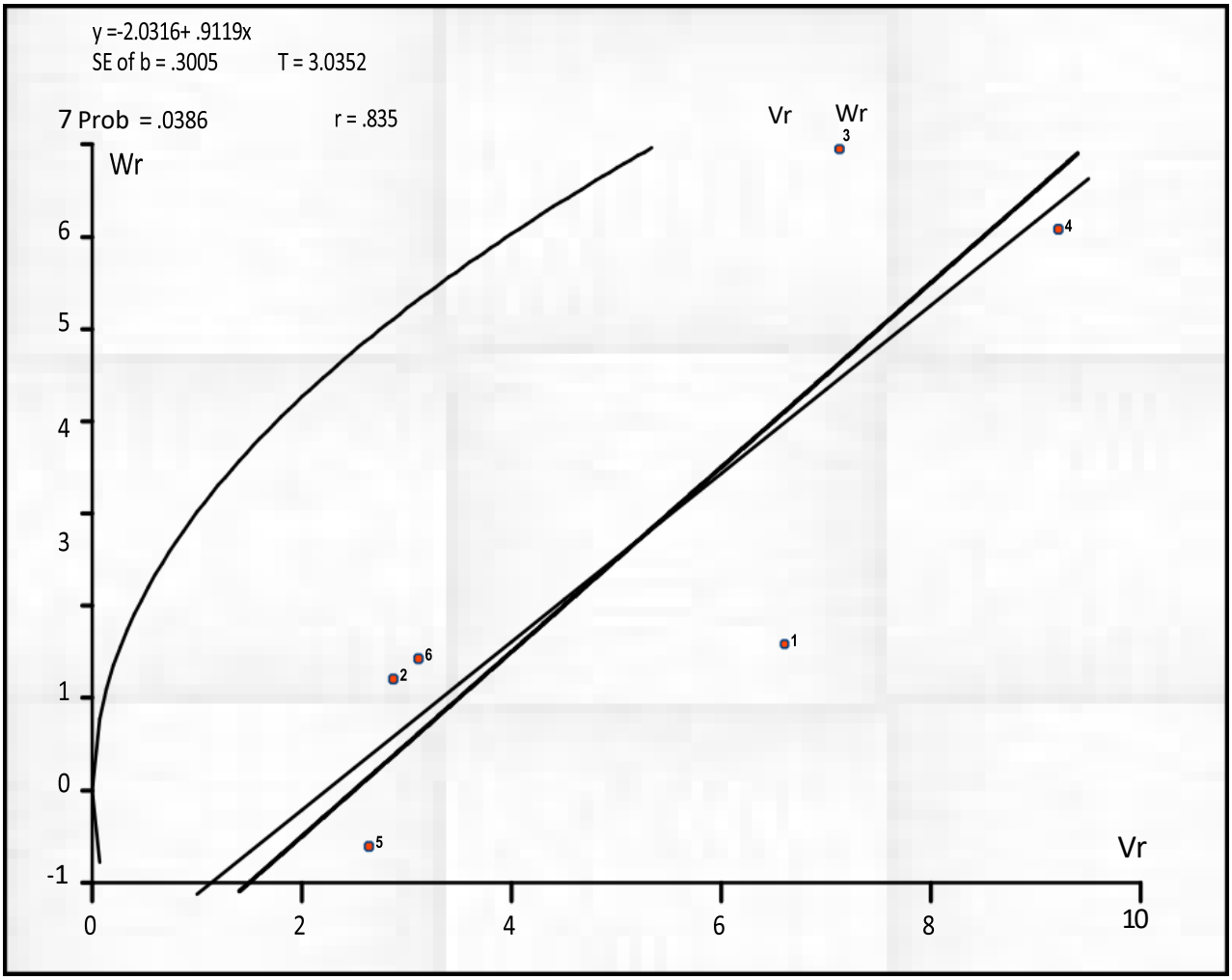

Fig. 1. Vr-Wr graph representing days to 50 % heading.

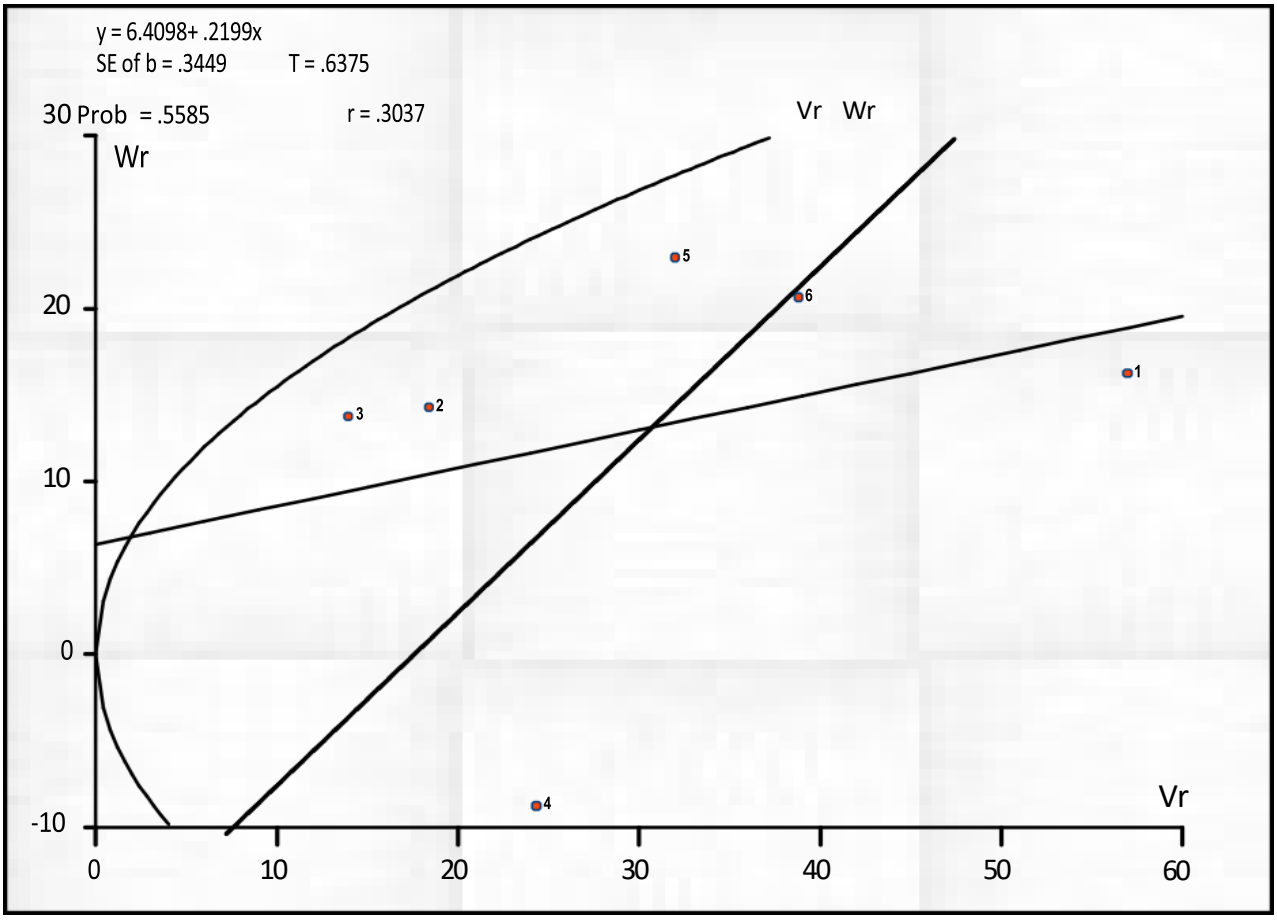

Fig. 2. Vr-Wr graph representing plant height.

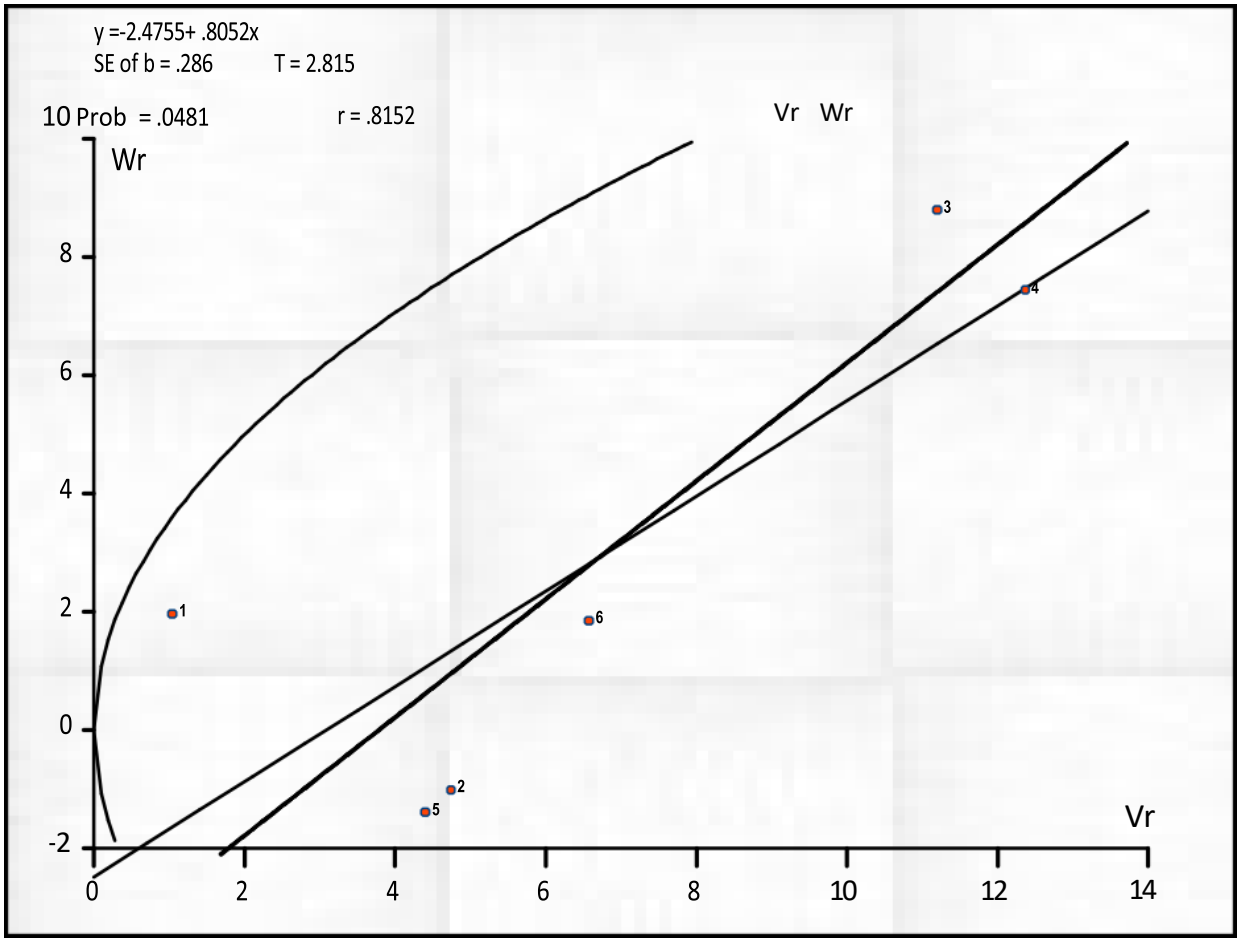

Fig. 3. Vr-Wr graph representing days to maturity.

minimal epistasis. A high correlation (r = 0.8152) confirms the presence of additive genetic effects. Parents near the origin carry dominant alleles for days to maturity, while those farther possess recessive alleles, indicating genetic variability useful for breeding early maturing lines.

Spike length (SL): The Vr-Wr graph (Fig. 4) shows that spike length is governed by overdominance gene action, indicated by a negative regression slope (-0.3118) and the line intersecting below the origin. The negative t-value (t = -1.2183) and non-significant p-value (p = 0.29) suggest that the regression is not statistically significant, implying potential epistatic interactions or deviation from the additive-dominance model. The negative correlation (r = -0.5202) further confirms the strong role of non-additive effects. Parents differ in dominance, with some carrying more dominant alleles. Thus, heterosis breeding can be effectively utilized to enhance spike length.

Spikelet per spike (SPS): The Vr-Wr graph (Fig. 5) shows that SPS is primarily governed by overdominance gene action, as indicated by the negative regression slope (-1.3754) and the line intersecting below the origin. The regression is not statistically significant (t = -1.691, p = 0.1601), suggesting possible epistatic interactions. The moderately strong negative correlation (r = -0.6456) further supports the presence of non-additive gene effects. Parental distribution reflects variability in dominance, making heterosis breeding a suitable approach for improving SPS.

Grains per spike (GPS): The Vr-Wr graph (Fig. 6) indicates that GPS is primarily governed by partial dominance gene action, as reflected by the positive regression slope (b = 0.2326) and the line intersecting above the origin. The non-significant t-value (t = 1.1741, p = 0.3055) suggests that the additive-dominance model may not fully explain the trait, possibly due to epistatic interactions. The moderate positive correlation (r = 0.5063) indicates the presence of both additive and non-additive genetic effects. Overall, the trait is influenced by partial dominance and selection strategies should focus on parents carrying favorable dominant alleles for improving GPS.

Thousand kernel weight (TKW): The Vr-Wr graph (Fig. 7) indicates that TKW is governed by partial dominance gene action, as shown by the positive regression slope (b = 0.4012) and the line intersecting above the origin**.** The non-significant t-value (t = 0.698, p = 0.5526) and low correlation (r = 0.3303) suggest possible epistatic interactions and a weaker additive effect. Parental distribution reflects genetic diversity, with some carrying dominant alleles. Overall, both additive and non-additive effects influence TKW and a combination of selection and hybrid breeding may be effective.

Total protein content (TPC): The Vr-Wr graph (Fig. 8) shows that TPC is governed by partial dominance, as indicated by the positive regression slope (b = 0.9602) and intersection above the origin. The regression is statistically significant (t = 3.4209, p = 0.0251), validating the additive-dominance model. A strong positive correlation (r = 0.8678) suggests a predominant additive genetic effect. Parental distribution reveals genetic variability, with some carrying dominant alleles. Overall, additive effects are important and selection breeding can effectively improve TPC.

Grain iron content (GFeC): The Vr-Wr graph (Fig. 9) indicates that GFeC is controlled by partial dominance gene action, as shown by the positive regression slope (b = 0.3090) and the line intersecting above the origin. The regression is approaching statistical significance (t = 2.3420, p = 0.0792), suggesting the additive-dominance model is reasonably valid but may include some epistatic effects. A strong

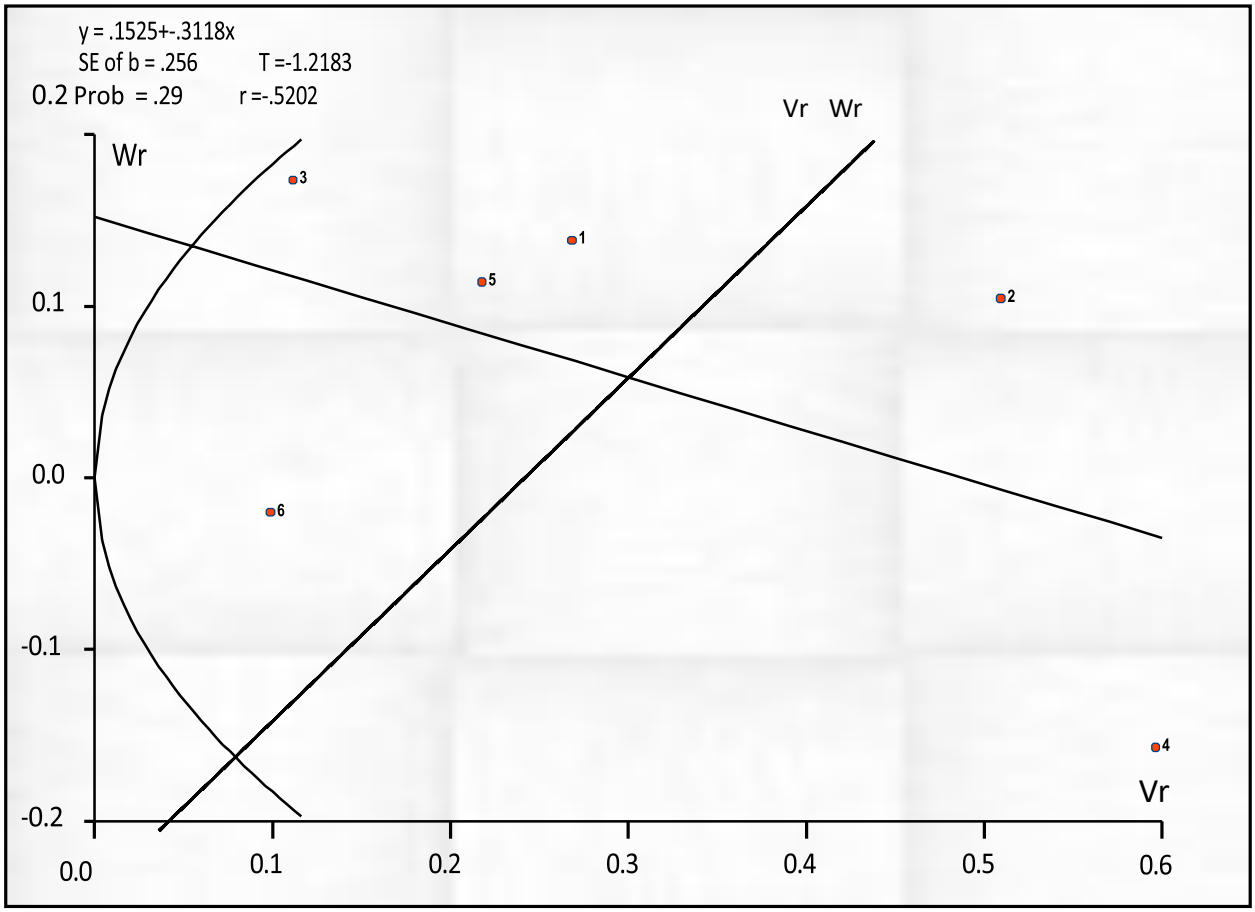

Fig. 4. Vr-Wr graph representing spike length.

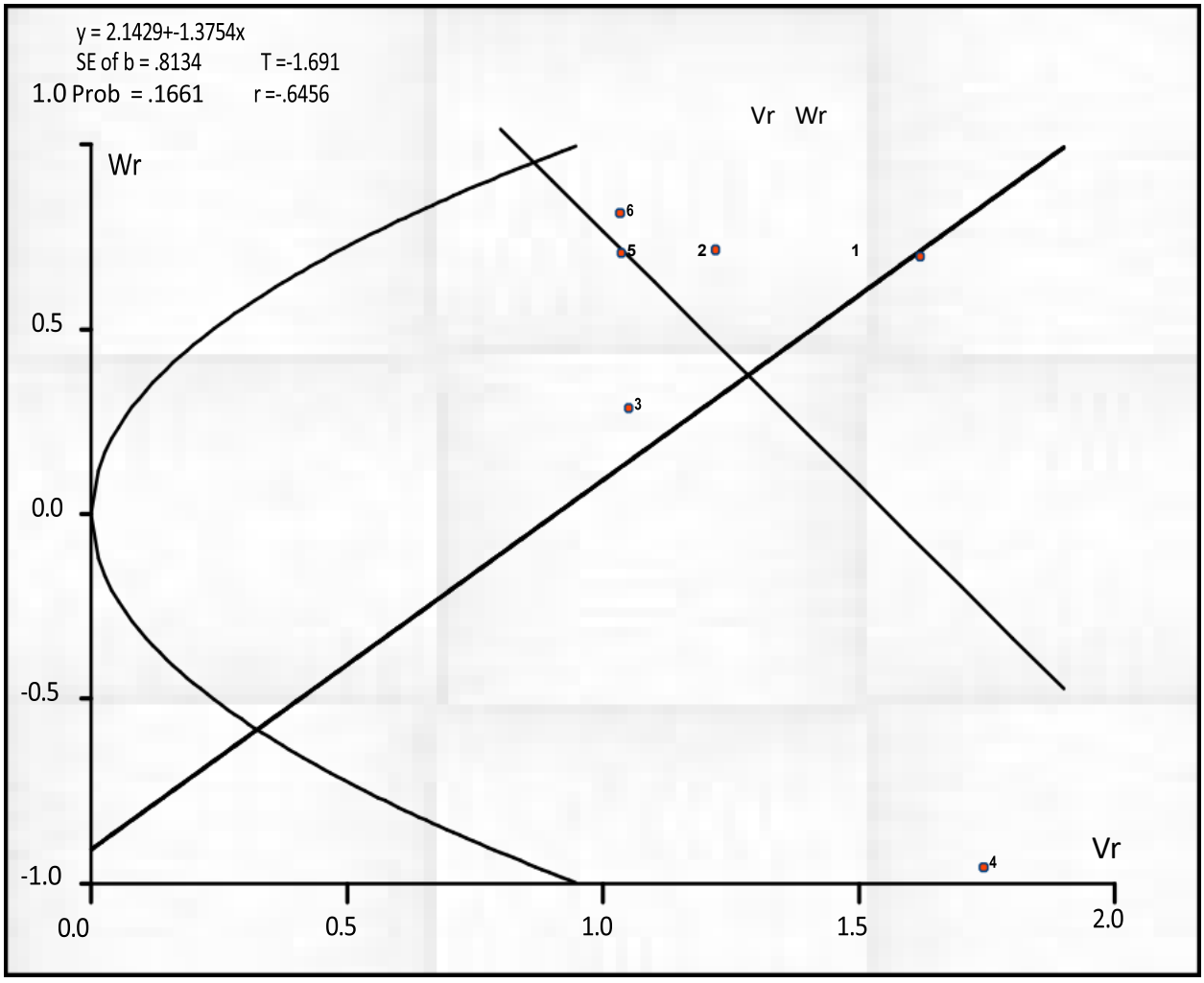

Fig. 5. Vr-Wr graph representing spikelet per spike.

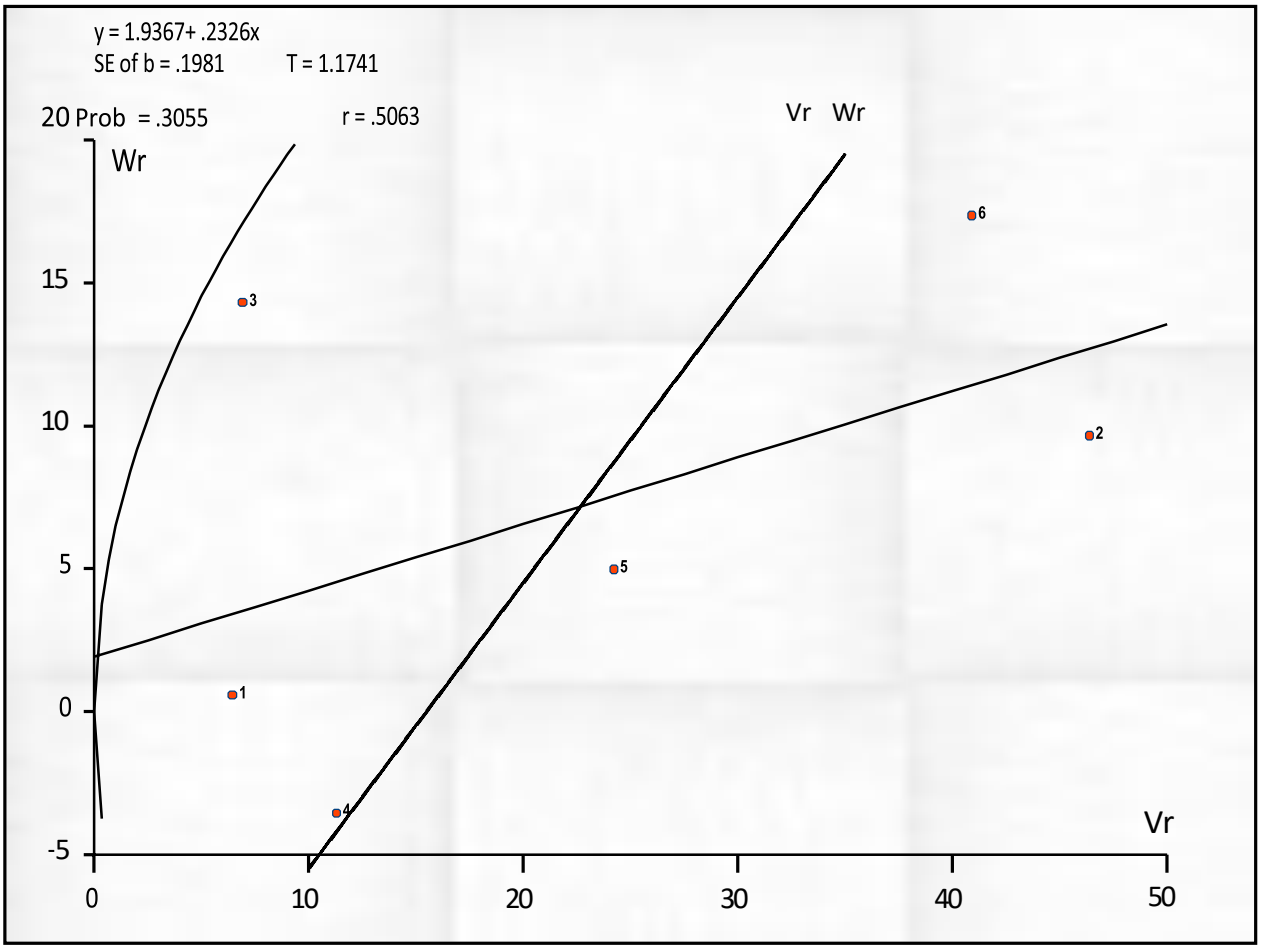

Fig. 6. Vr-Wr graph representing grain per spike.

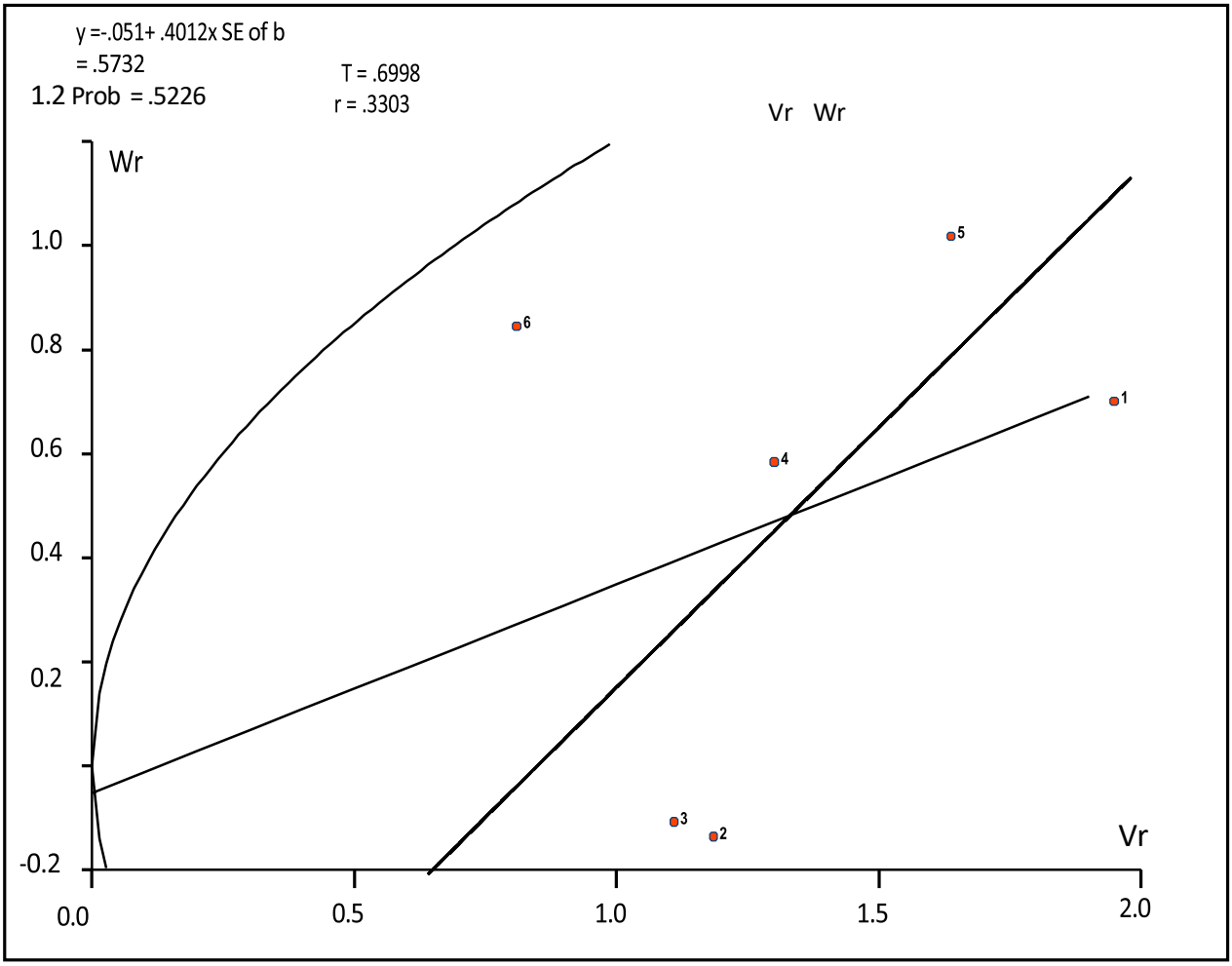

Fig. 7. Vr-Wr graph representing thousand kernel weight.

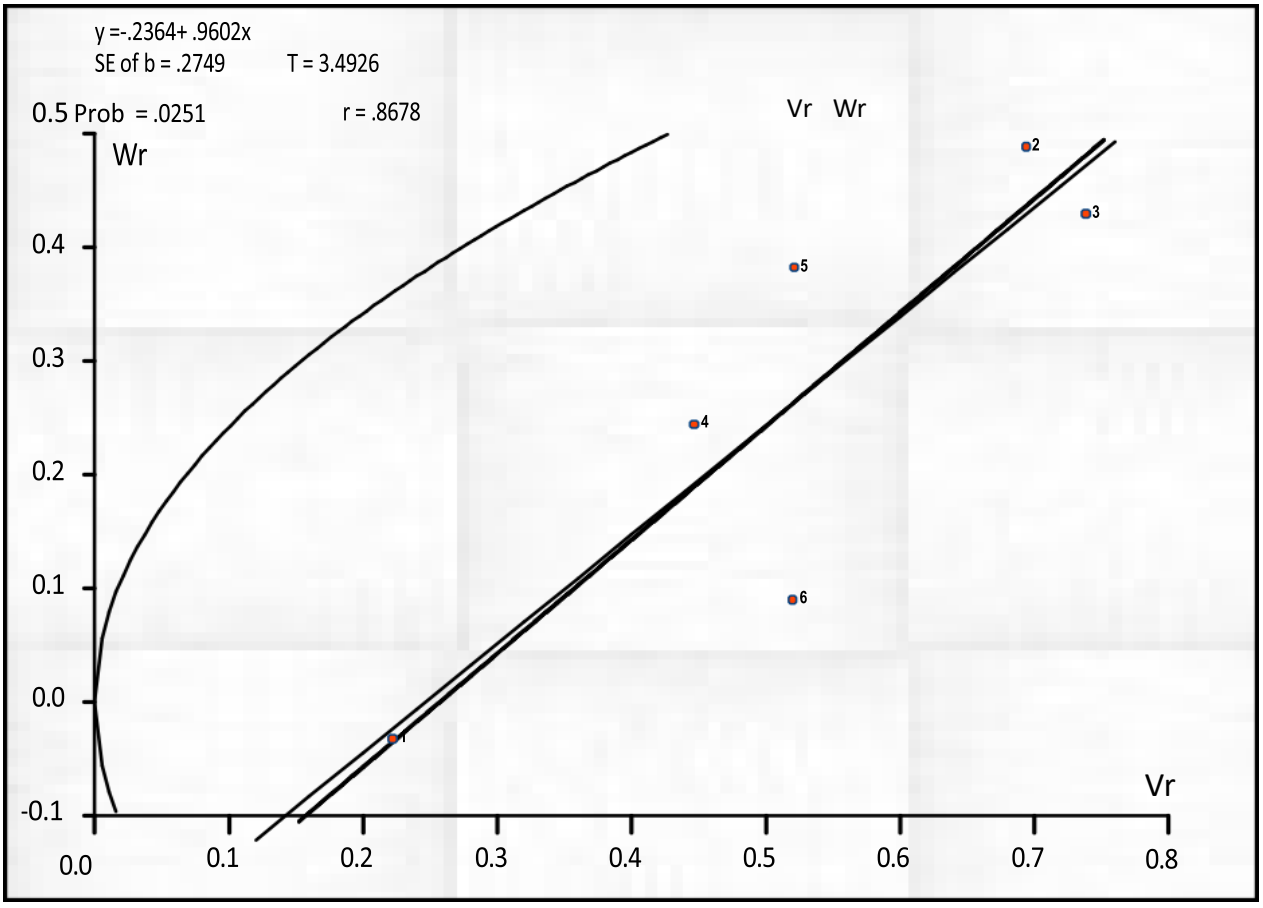

Fig. 8. Vr-Wr graph representing total protein content.

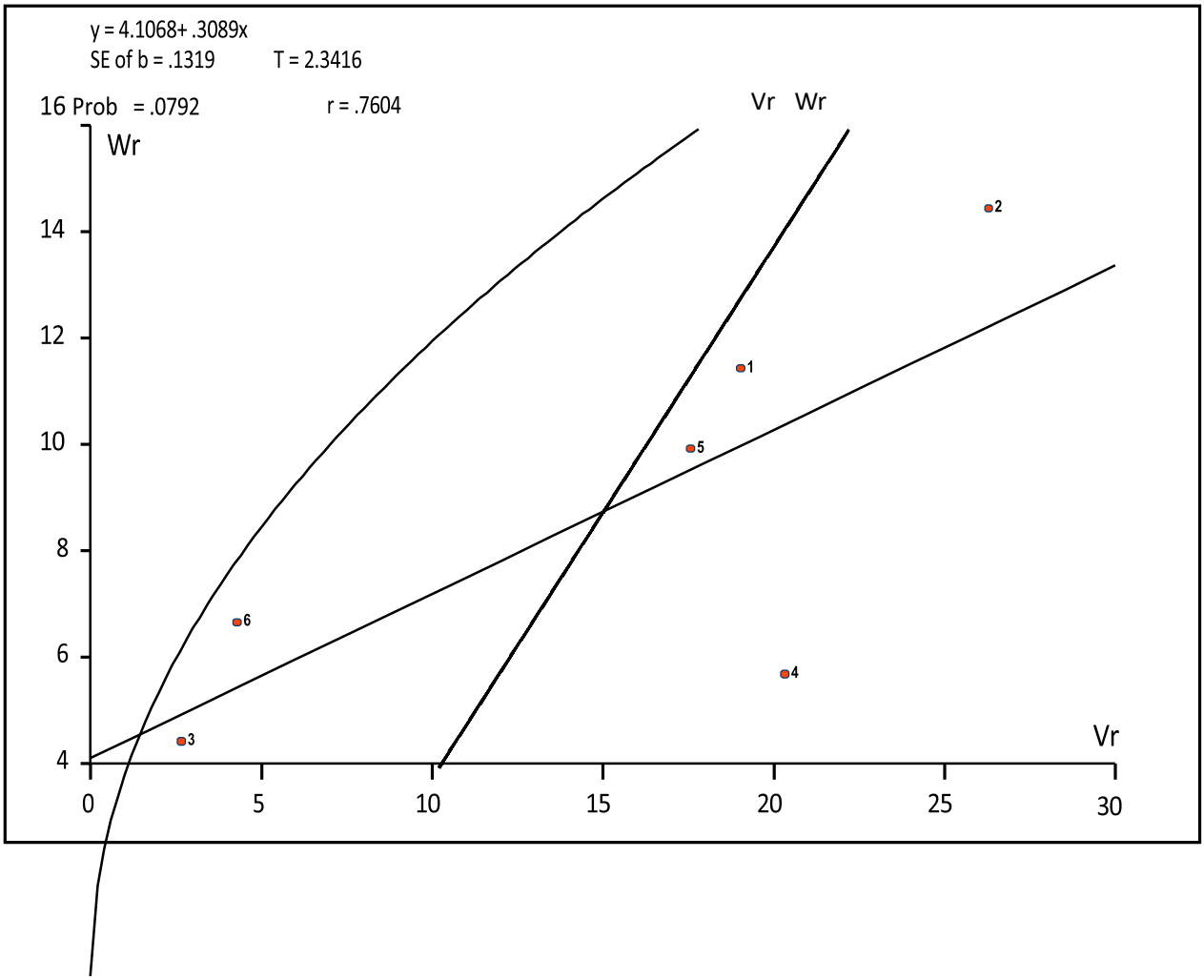

Fig. 9. Vr-Wr graph representing grain iron content.

positive correlation (r = 0.7600) points to a substantial additive genetic component. Overall, both additive and non-additive effects influence GFeC and selection-based breeding can be effective for improving iron content in grains.

Grain zinc content (GZnC): The Vr-Wr graph (Fig. 10) indicates that GZnC is governed by partial dominance gene action, as shown by the positive regression slope (b = 0.6741) and the line intersecting above the origin. The regression is highly significant (t = 4.7124, p = 0.0092), validating the additive-dominance model. The very strong positive correlation (r = 0.9205) suggests a dominant role of additive genetic effects. The wide distribution of parents shows genetic variability, with some possessing more dominant alleles. Overall, additive and partial dominance effects influence GZnC and selection-based breeding is a promising strategy for improving zinc content in grains.

Grain yield per plant (GYPP): The Vr-Wr graph (Fig. 11) indicates that GYPP is governed by partial dominance gene action, as shown by the positive regression slope (b = 0.6020) and the intersection above the origin. The regression is statistically significant (t = 3.4940, p = 0.025), confirming the adequacy of the additive-dominance model. A strong positive correlation (r = 0.8680) suggests a major role of additive genetic effects. The distribution of parents reflects genetic variability, with some carrying dominant alleles. Overall, selection and hybrid breeding strategies can effectively enhance grain yield by exploiting both additive and partial dominance effects.

Genetic parameters in diallel analysis of wheat for agronomic and nutritional traits

The diallel analysis based on Hayman's approach provided valuable insights into the inheritance pattern, gene action and parental contributions for key agronomic and nutritional traits in wheat (Table 7). Below is a trait-wise summary of the major findings:

Additive and dominance effects

1. Additive gene effects (D) were substantial for most traits like PH (23.03), GFeC (13.13), GZnC (14.23) and GYPP (31.60), indicating the scope for improvement through recurrent selection.
2. Dominance effects (H1 and H2) were higher than additive for traits such as PH, GPS and GYPP, suggesting the prevalence of non-additive gene action.
3. H1 > H2 across most traits confirms asymmetric distribution of dominant and recessive alleles among parents.

Degree of dominance and nature of gene action

1. The mean degree of dominance > 1 for all traits, particularly for SL (2.09), SPS (2.22) and GYPP (2.18), confirms overdominance.
2. The ratio of dominant to recessive genes exceeded unity for traits like DM (2.05) and GPS (2.45), further supporting the role of dominant alleles in trait expression.
3. For GFeC (0.691) and GZnC (0.887), the ratio indicates a greater frequency of recessive genes, suggesting additive effects are still important in these traits.

Heritability estimates

1. Narrow-sense heritability (h^2) was moderate to high for GFeC (0.62), GZnC (0.62) and TPC (0.52), suggesting potential for selection-based improvement in nutritional traits.
2. Traits with low h^2, like GPS (0.16) and GYPP (0.23), indicate the dominance variance predominates, necessitating hybrid breeding approaches.

Environmental effects

1. Environmental variance (E) was generally low across traits, especially for SL (0.09), suggesting greater genetic control.
2. TPC (0.13) and GFeC (1.12) also showed low environmental influence, favoring stable expression under different environments.

Genetic advance and selection potential

1. Additive genetic variance (Va) was appreciable for PH (21.37) and GFeC (14.03), indicating that additive gene action can be effectively utilized in breeding programs.
2. Dominance deviations (Vd) exceeded Va in traits like GPS (18.40) and GYPP (34.59), supporting hybrid exploitation.

Parental influence and genetic control

1. The number of gene groups (h^2/H2) was highest for GYPP (1.64), indicating a polygenic control.
2. Traits like SPS, GPS and SL showed negative h^2/H2, indicating epistasis or non-allelic interaction.
3. Parental estimates identified asymmetry in dominance and recessiveness, with GFeC and GZnC showing closer estimation

Table 7. Genetic parameters in diallel analysis of wheat for agronomic and nutritional traits

Parameters	DH50	PH	DM	SL	SPS	GPS	TKW	TPC	GFeC	GZnC	GYPP
D (Additive Effect)	8.1370	23.0272	10.5312	0.2391	0.8359	38.6679	0.8182	0.4493	13.1289	14.2342	31.6052
F (Mean Fr over arrays)	5.8420	-5.9663	10.6185	0.3070	0.3078	50.8865	0.1237	-0.0777	-7.9977	-1.7902	19.7228
H_1 (Dominance Effect)	16.5120	91.6885	22.4082	1.0462	4.1099	94.5412	3.1612	1.2516	36.3861	15.6416	150.5679
H_2	13.9790	77.9257	14.9736	0.8814	3.3853	73.6237	3.2388	0.9589	29.4361	15.5235	138.3616
h^2 (Heritability)	4.1590	6.6269	2.4803	-0.0314	-0.0710	-1.7380	-0.3322	-0.0134	8.5303	-0.3019	227.4196
E (Environmental Component)	0.9630	0.9999	1.9577	0.0958	0.2138	3.6222	0.6312	0.1360	1.1267	1.0082	4.3410
Mean Degree of Dominance	1.4250	1.9950	1.4590	2.0920	2.2170	1.5640	1.9660	1.6690	1.6650	1.0480	2.1830
Proportion of genes with +/- effects in parents	0.2120	0.2120	0.1670	0.2110	0.2060	0.1950	0.2560	0.1920	0.2020	0.2480	0.2300
Ratio of dominant/recessive genes in parents	1.6740	0.8780	2.0560	1.8860	1.1810	2.4530	1.0800	0.9020	0.6910	0.8870	1.3340
Va (Additive gene effects)	2.4140	21.3780	3.6740	0.0480	0.6260	4.3490	0.3080	0.4100	14.0380	8.0710	12.0440
Vd (Dominance deviations)	3.4950	19.4810	3.7430	0.2200	0.8460	18.4060	0.8100	0.2400	7.3590	3.8810	34.5900
h^2 / H2 (No. of gene groups)	0.2980	0.0850	0.1660	-0.0360	-0.0210	-0.0240	-0.1030	-0.0140	0.2900	-0.0190	1.6440
h^2 (Narrow Sense Heritability)	0.3510	0.5110	0.3920	0.1330	0.3710	0.1650	0.1760	0.5220	0.6230	0.6230	0.2360
Estimation of most dominant parent	60.1170	87.8290	111.6030	9.5520	18.9740	41.3140	42.2830	11.7980	35.7860	30.1130	10.4550
Estimation of most recessive parent	69.2790	88.0220	121.9130	9.5460	18.6520	49.7800	42.4820	12.1800	38.7610	48.6780	15.8150
T^2	0.1030	0.4760	0.0020	1.5670	4.7300	3.9630	0.1720	0.1660	10.0130	2.6270	2.2660
a (Intercept)	-2.0320	6.4100	-2.4760	0.1520	2.1430	1.9370	-0.0510	-0.2360	4.1070	2.0000	-14.3780
b (Slope)	0.9120	0.2200	0.8050	-0.3120	-1.3750	0.2330	0.4010	0.9600	0.3090	0.6740	0.6020
T (t-stat)	3.0350	0.6380	2.8150	-1.2180	-1.6910	1.1740	0.7000	3.4930	2.3420	4.7120	3.4940
Correlation (r)	0.8350	0.3040	0.8150	-0.5200	-0.6460	0.5060	0.3300	0.8680	0.7600	0.9210	0.8680

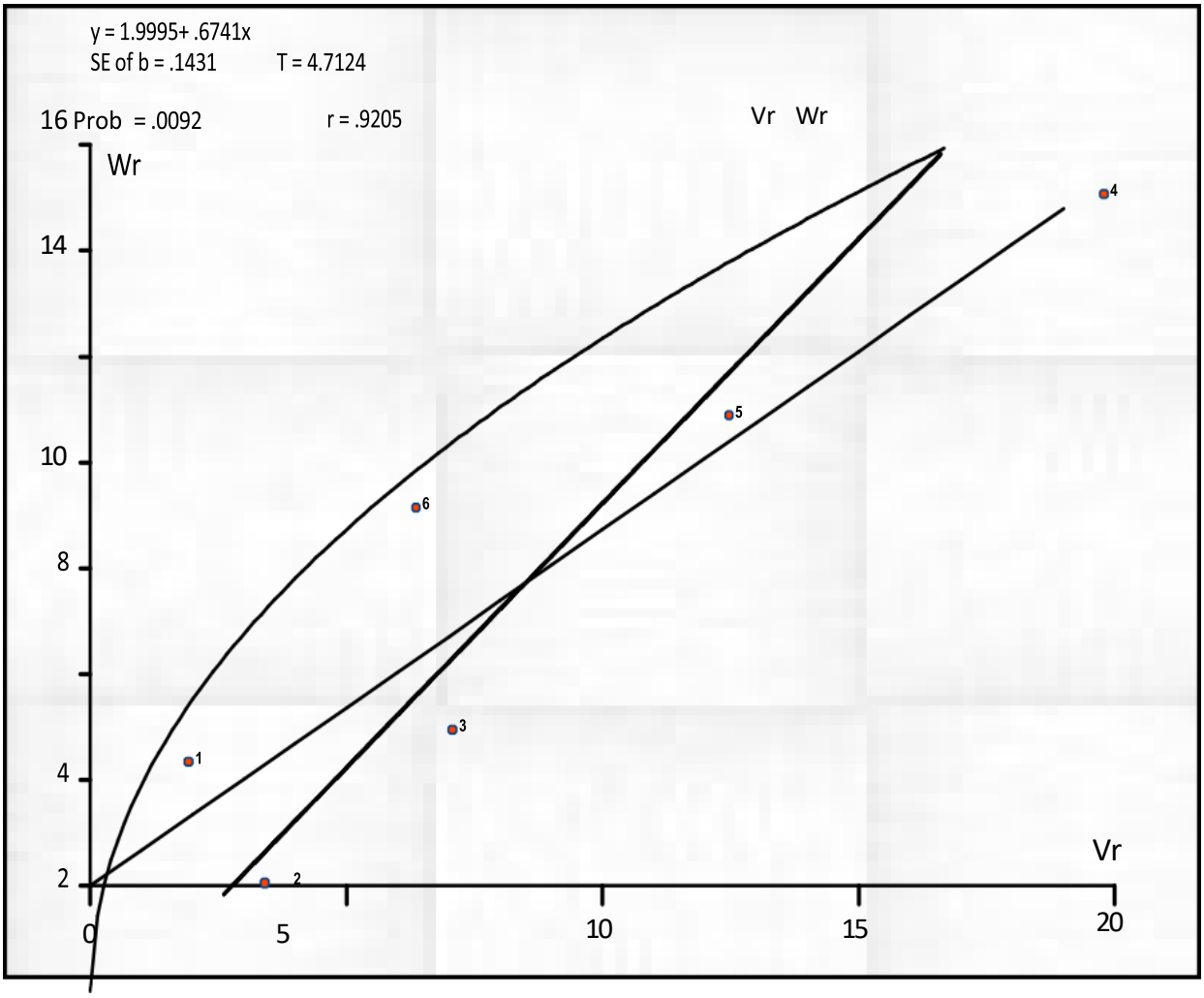

Fig. 10. Vr-Wr graph representing grain zinc content.

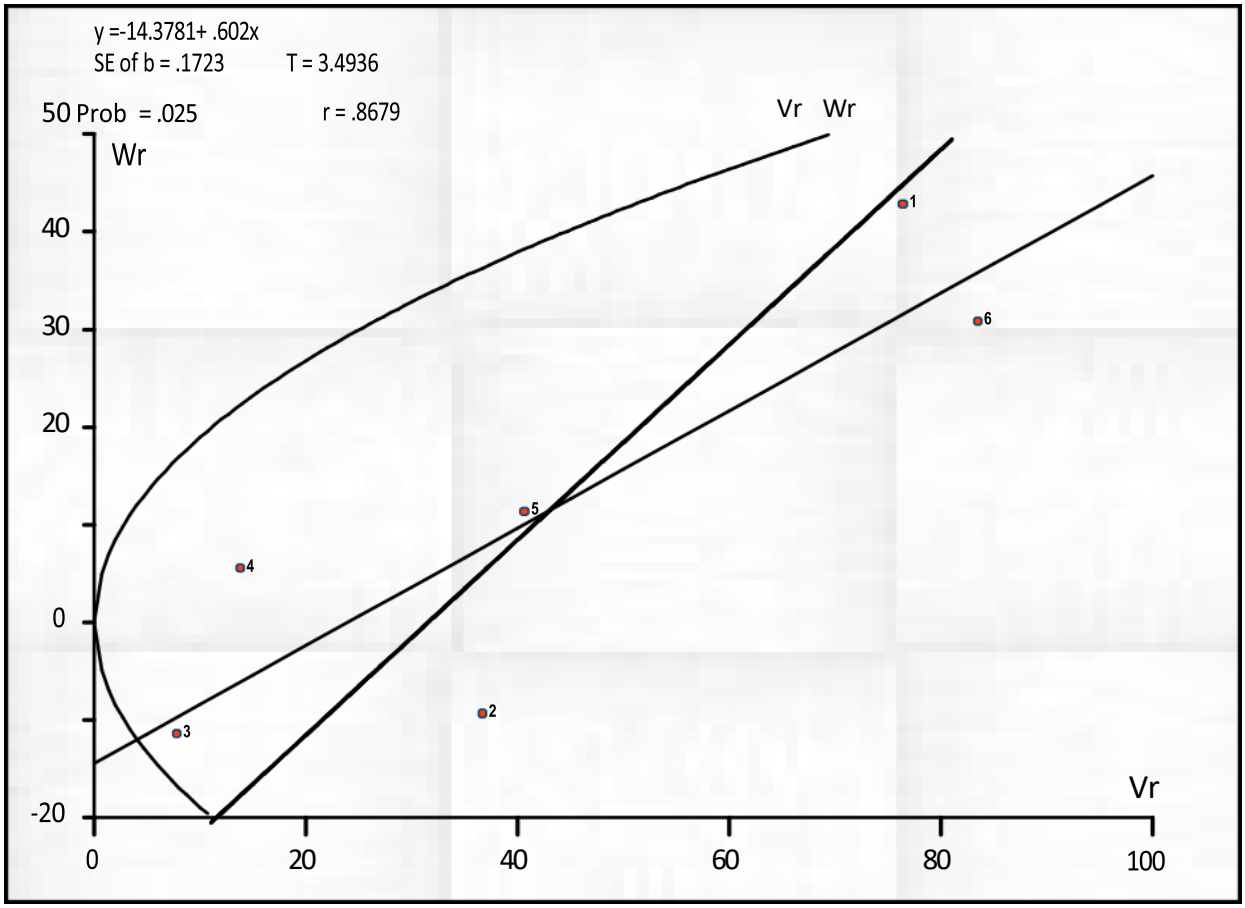

Fig. 11. Vr-Wr graph representing grain yield per plant.

between dominant and recessive groups.

Graphical and statistical indicators

1. High correlation coefficients (r) for DH50 (0.83), DM (0.81), TPC (0.86) and GYPP (0.86) validate the reliability of the analysis.
2. Significant t-values (T) for DH50, DM, TPC, GFeC and GZnC suggest linear regression and additive-dominant model fit is appropriate for these traits.
3. Slope values (b) around 1 (especially for TPC = 0.96) confirm partial dominance, whereas deviations from unity suggest non-allelic interaction or epistasis.

Understanding the genetic mechanisms underlying complex traits in bread wheat is essential for developing cultivars combining improved yield and nutritional quality, as demonstrated in the present diallel analysis. The combined application of Griffing's diallel approach and Hayman's graphical analysis in the current study provided comprehensive insights into the gene action controlling yield-contributing and micronutrient traits. These findings are further supported by variance component analysis, regression-based Vr-Wr plots and trait-specific genetic parameters.

Discussion

Genetic architecture and combining ability analysis

The analysis of variance indicated significant GCA and SCA effects for most traits, confirming the involvement of both additive and non-additive gene actions. Similar trends have been reported in earlier diallel studies in wheat across environments, where both GCA and SCA effects were significant for yield and related traits (22, 23). However, the relative contribution of these components differed markedly between nutritional and yield traits.

Grain iron (GFeC) and zinc content (GZnC) exhibited moderate-to-high narrow-sense heritability ($h^2 \approx 0.62$) along with higher predictability ratios, indicating a greater role of additive gene action and confirming their suitability for selection-based breeding. In contrast, grain yield per plant (GYPP), grains per spike (GPS) and spikelets per spike (SPS) showed low narrow-sense heritability and low GCA/SCA ratios (<0.5), suggesting the predominance of non-additive gene effects and supporting the use of heterosis-oriented breeding approaches (24, 25).

Estimates of genetic components further supported these observations. Additive variance (D) was substantial for plant height (PH), GFeC, GZnC and GYPP, indicating the potential effectiveness of recurrent selection. However, dominance components (H_1 and H_2) exceeded additive variance for several yield-related traits, highlighting the importance of non-additive gene action. These results are consistent with previous reports emphasizing the role of dominance and interaction effects in wheat improvement (26, 27). Although the mean degree of dominance exceeded unity for several traits, this should be interpreted cautiously, as the presence of epistasis may inflate dominance estimates rather than indicate true overdominance.

The $H_1 > H_2$ relationship for most traits suggested an asymmetrical distribution of dominant and recessive alleles. A dominance-to-recessive gene ratio greater than unity for DM and GPS indicated a higher frequency of dominant alleles, whereas ratios below unity for GFeC and GZnC implied a greater contribution of recessive alleles, reinforcing the additive nature of micronutrient inheritance. Negative estimates of gene group numbers for SPS, GPS and SL further pointed toward epistatic interactions and non-allelic gene action. Although some nutritionally superior hybrids expressed reduced yield, these genotypes remain valuable as donor parents for improving micronutrient density in elite backgrounds.

Graphical analysis (Vr–Wr Regression)

Hayman's Vr–Wr graphical analysis largely corroborated the combining ability results and provided additional insight into gene action. For days to 50 % heading (DH50), a significant negative regression slope suggested the involvement of overdominance or epistasis, supported by a high correlation and significant t-value, validating the additive–dominance model. Similar observations have been reported earlier, highlighting the importance of epistatic interactions in wheat (28).

Plant height (PH) and days to maturity (DM) predominantly exhibited partial dominance. The relatively low correlation for PH suggested possible epistatic interference, whereas the strong correlation and significant regression for DM supported a valid additive–dominance relationship. Traits such as spike length (SL) and spikelets per spike (SPS) showed apparent overdominance; however, non-significant regression and poor model fit indicate that these traits are more likely governed by partial dominance with substantial epistatic effects.

For grains per spike (GPS) and thousand kernel weight (TKW), regression parameters suggested partial dominance, although epistasis could not be excluded. Total protein content (TPC) showed a regression slope close to unity, a significant t-value and strong correlation, confirming the predominance of additive gene action. Micronutrient traits (GFeC and GZnC) also followed partial dominance models, with GZnC showing a highly significant regression and strong correlation, validating the additive–dominance hypothesis. Similar inheritance patterns for these traits have been reported earlier (29), reinforcing their amenability to selection-based breeding. Grain yield per plant (GYPP) exhibited partial dominance with significant regression parameters, indicating the involvement of both additive and dominance components, but also underscoring the complexity of yield improvement through direct selection. Nutritional traits such as grain iron, zinc and protein content are genetically more stable and selection-responsive than yield-related traits**.** Yield attributes are influenced by complex dominance and epistatic interactions, reducing predictability under selection. Therefore, breeding strategies should prioritize selection for nutritional traits while utilizing nutritionally superior genotypes as donor parents in yield-focused breeding programs, rather than relying on direct yield improvement from these crosses.

Parental selection and hybrid recommendations

The asymmetrical distribution of dominant genes, observed through Vr-Wr curves and gene ratio estimates, reinforces the complexity of gene action and the importance of strategic parental selection. Like earlier findings (30), certain genotypes in the current study showed favorable dominant alleles for nutritional traits and kernel weight. Parents such as JW1203, HI 1633 and HI 1634 were identified as promising donors for yield and nutritional enhancement. Among hybrids, WB02 × HI 1633 stood out for its consistent superior performance across key agronomic and nutritional traits (SL, SPS, GPS and GFeC), making it ideal for hybrid wheat development. Previous studies have also highlighted heterotic combinations like GW 451 × GW 173 and GW 322 × MP 3382 as effective crosses for enhancing Fe and Zn content and earliness (8, 29). The occurrence of

significant negative heterosis for grain yield per plant indicates that the F_1 hybrids yielded less than the superior parent, suggesting unfavorable allelic interactions for yield expression. However, when considered alongside enhanced grain iron, zinc and protein content, this response reflects a likely trade-off between grain yield and nutritional quality. Such antagonistic relationships are commonly observed in biofortification-oriented breeding, where increased micronutrient accumulation may occur at the expense of biomass partitioning or grain number, resulting in reduced yield.

Conclusion

The integrated application of Griffing's combining ability model, Hayman's diallel analysis and Vr-Wr graphical interpretation in this study provided a robust understanding of the genetic control of key agronomic and nutritional traits in bread wheat. The presence of both additive and non-additive gene effects across most traits underlines the importance of adopting a dual breeding strategy that combines selection-based improvement for traits like grain Fe, Zn and protein content with heterosis breeding for complex traits such as grain yield, grains per spike and plant height. The low GCA/SCA ratios and mean degree of dominance > 1 for several traits confirmed the dominance of non-additive gene action, emphasising the potential of hybrid development to exploit heterosis. Simultaneously, traits with high additive variance, predictability ratios and heritability estimates, such as TPC, GFeC and GZnC, validate the effectiveness of recurrent selection and pedigree breeding. Promising parental genotypes such as JW 1203, HI 1633 and HI 1634 and superior hybrids like WB02 × HI 1633, emerged as potential candidates for the development of high-yielding, nutrient-rich wheat cultivars. Future research should prioritize the evaluation of segregating generations to identify recombinants combining acceptable yield levels with elevated grain iron, zinc and protein content. Detailed correlation and path coefficient analyses among yield and nutritional traits are required to quantify trade-offs and identify favorable indirect selection criteria. Additionally, genetic dissection through combining ability and gene action studies will help clarify whether micronutrient traits are predominantly governed by additive effects. Multi-location trials are essential to assess the stability of micronutrient expression under diverse environments. Integration of marker-assisted or genomic selection approaches targeting iron, zinc and protein-related loci would further enhance the efficiency of developing nutritionally enriched, high-yielding wheat cultivars.

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Authors' contributions

VV designed the experiment. VV and DS were involved in conceptualization and writing the original draft. YS and VK carried out compilation, editing and preparation of the final draft of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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