

Original Research

Insights into the Combining Ability Analysis for Yellow Rust Resistance, Grain Yield Per Plant, and Yield Components in Bread Wheat

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Abstract

Understanding the inheritance of traits is critical for developing sustainable and environmentally friendly plant breeding programs. Six wheat genotypes, viz., Galaxy-13, Inqilab-91, Ghaznavi-98, Khaista-17, Benazir-13, and Parula, were crossed using a Griffing's half-diallel scheme, producing 15 F_1 hybrids. These hybrids and their parental lines were assessed using a randomized complete block design with three replications at Cereal Crops Research Institute (CCRI), Pirsabak, and The University of Agriculture, Peshawar (UAP), during 2016-17. The same pattern was observed in F_2 population studies conducted in 2017-18. Significant genotype and genotype \times environment interaction effects were observed for all traits. The F_1 hybrids generally outperformed their parental lines, highlighting the potential for superior hybrid performance. This study aimed to investigate the genetic mechanisms underlying yellow rust resistance, flag leaf area, 1000-grain weight, and grain yield per plant using Griffing's combining ability analysis. Analysis revealed that combining ability effects were significant for all traits. Maximum and significant GCA effects were observed in parental cultivars, i.e., Benazir-13 at CCRI, followed by Inqilab-91 at UAP and Inqilab-91 for 1000-grain weight and grain yield per plant at the CCRI and UAP, respectively. However, in the case of SCA effects, the F_1 hybrids Inqilab-91 \times

Galaxy revealed significant SCA effects for grain yield per plant at CCRI and UAP, suggesting non-additive gene action. These promising populations hold potential for further improvement in yellow rust resistance and grain yield in future breeding efforts. Furthermore, these findings underscore the potential of hybridization in reducing reliance on fungicides by developing yellow rust-resistant varieties. Such environmentally friendly approaches not only minimize chemical inputs but also offer cost-effective and sustainable solutions for wheat production, contributing to ecological conservation and economic benefits for farmers.

Keywords: combining ability, yellow rust resistance, *Triticum aestivum* L. F₁ hybrids, F₂ populations, fungicides, non-additive gene action, genotype × environment interaction

Introduction

Wheat (*Triticum aestivum* L.), commonly known as bread wheat, is a highly essential crop due to its multiple uses, supplying approximately one-fifth of the kilocalories to the global population for survival [1]. The twenty-first century is facing a challenge in managing food for the rapidly growing population without harming the ecosystem [2]. Worldwide, wheat is cultivated on approximately 240.8 million hectares of land [3]. The global population is expected to increase by more than a quarter billion, reaching 9.2 billion by 2050, leading to a 60% increase in food demand [4]. High-yielding and disease-resistant wheat varieties from the available germplasm are the only solution to ensure food security in the face of uncontrolled population growth [5].

During 2022-23, an area of 9.60 million hectares was cultivated, producing 31.40 million tons of wheat with an average yield of 3117 kg/ha [6]. This production is attributed to multiple factors, including the introduction of new high-yielding wheat cultivars and the application of cutting-edge production technology. However, heat, drought, and unpredictable precipitation caused by climate change have substantial impacts on wheat yield [7]. In this scenario, high-yielding varieties with early maturity need to be introduced by agricultural research to confer resistance against lodging and other biotic and abiotic stresses.

Grain yield and its components may vary unexpectedly due to unanticipated genotype by environment interaction. These types of interactions between genotypes and environment make it complicated for breeders to tackle this problem [8]. Genotypes (G) and environment (E) interact, and how the genotypes respond to the new environment is an integral part of wheat breeding research programs. These findings substantially facilitate the search for superior genotypes that maintain performance and stability over the final rounds of selection for the traits of interest [9]. The use of G × E in plant breeding makes it more challenging to connect phenotypic and genotypic characteristics in progeny, hence retarding genetic progression [10]. To develop stable and high-yielding wheat genotypes, it is imperative to use high-quality grains utilized in different ranges of environmental conditions. Phenotype

is determined by the interactions between their genes and environment [11].

Fungal infections are the most prevalent form of biotic stress that reduces wheat yield, and they occur nearly anywhere wheat is produced [12]. The most destructive fungus is *Puccinia* spp., which causes leaf, stem, and stripe rusts [13]. Yellow/stripe rust could threaten up to 70% of the wheat-growing regions in Pakistan. Yellow/stripe rust, the most devastating of the three wheat rust types, will be a great problem in the future regarding costs of production; therefore, a strategy should be used to develop wheat varieties that are not only high-yielding but also resistant to the prevailing diseases [14]. This strategy of wheat cultivar development through hybridization is eco-friendly because it reduces the judicious use of rusticides to control yellow rust.

In Pakistan, rust disease epidemics were between 20 and 30% severe in 1972 and 1973, and between 40 and 50% severe in 1974 and 1975. In contrast, outbreaks in 1976 and 1978 caused 30 to 40% yield losses and were 50 to 80% severe. From 1995 to 2005, yellow rust caused major crop yield losses [15]. It has been estimated that 0.10 to 25% yield losses in wheat have occurred due to yellow rust [16]. To maximize yield, it is necessary to keep these diseases below a threshold level. There are multiple ways to control wheat rust, including rusticides and inbuilt mechanisms against the prevalent rust races, but the former one is detrimental to health, leading to serious health complications. Developing wheat cultivars through breeding is the safest and cheapest method [17]. Nowadays, molecular markers are being used to facilitate the process of identification of parental cultivars for hybridization against strip rust [18].

Grain yield in crops is determined by a variety of factors, including genetic potential, management practices, and environmental conditions. Environmental factors, such as temperature, precipitation, soil quality, sunlight, and pest or disease pressures, play a critical role in influencing how well a crop performs. Therefore, various techniques, including diallel studies, line tester analyses, and generation mean analysis, are employed to investigate the mode of action of genes and their inheritance patterns from parental cultivars to their subsequent filial generations [19]. In all the aforementioned techniques, diallel analysis is essential

Table 1. Environmental conditions at CCRI and UAP during 2017-18.

Environments	Growing season	Geographical Position		Altitude (m.a.s.l)	Average rainfall (mm)	Temperature (°c)	
		Latitude	Longitude			Min.	Max.
E-I (UAP)	2017-18	34.0150° N	71.5805° E	359	189	17.8	38.2
E-II (CCRI)	2017-18	34.0159° N	71.9755° E	288	112	16.3	35.9

to comprehend the nature of inheritance for quantitative traits, and therefore is a frequently used tool to assess the parents for breeding by investigating the mode of gene action by carrying out cross-breeding in all possible combinations [20].

Combining ability refers to a genotype's capacity to transmit desirable traits to its hybrids, determining its potential to produce superior offspring when crossed with other genotypes. It has two types, i.e., General Combining Ability (GCA), which refers to the average performance of a line across hybrids and is governed by additive gene action, and Specific Combining Ability (SCA), representing the deviation of a hybrid's performance from the average GCA of its parents, influenced by non-additive gene action like dominance and epistasis. The distinction between GCA and SCA is vital for understanding the genetic mechanisms of trait inheritance, aiding breeders in selecting appropriate strategies to enhance desired traits. Research by [21] highlights the significance of both GCA and SCA in impacting growth, yield, and related traits, emphasizing the importance of this knowledge for developing superior hybrids and achieving sustainable crop improvement.

Few studies have assessed the inheritance of yellow rust resistance and yield traits using both F_1 and F_2 generations, and combining ability across rust-prone environments remains underexplored. Additionally, there has been limited evaluation of local germplasm for the development of stable, high-yielding, and rust-resistant wheat genotypes. As CIMMYT, Mexico, has stopped sending stable wheat lines, a trend of initiating local crossing and developing breeding programs has emerged in Pakistan to address this critical gap. The mutating nature of yellow rust, coupled with unpredictable climate conditions, further complicates wheat production, as a variety typically remains effective for only 4–5 years. Therefore, continuous breeding efforts are essential to develop resilient and sustainable wheat cultivars capable of withstanding evolving biotic stresses and environmental variability.

This study aimed to evaluate the genetic components and the relative contributions of general and specific combining abilities for key traits, including resistance to yellow rust, flag leaf area, 1000-grain weight, and grain yield, through the analysis of $6 \times 6 F_1$ and F_2 half diallel crosses in wheat.

Materials and Methods

The study on wheat breeding was conducted during 2016-17 at the University of Agriculture, Peshawar, Pakistan, using six diverse wheat genotypes: Benazir-13, Khaista-17, Inqilab-91, Ghaznavi-98, Galaxy-13, and Parula. These genotypes were selected for traits such as early maturity, grain yield, and yellow rust resistance. A half-diallel crossing scheme was employed to produce 15 F_1 hybrids through direct crosses. Standard agricultural practices were applied uniformly across all genotypes. During 2017-18, the parental genotypes and their F_1 hybrids were evaluated in a randomized complete block design (RCBD) with three replications at two locations: The University of Agriculture, Peshawar, and the Cereal Crops Research Institute (CCRI), Pirsabak, Nowshera. In 2018-19, the same F_1 hybrids and parental genotypes were grown as F_2 populations using RCBD with three replications at the same locations. Details of environmental conditions are provided in Table 1 whereas, ANOVA in Table 2. Uniform cultural practices and agronomic inputs were applied across all wheat genotypes and experimental sites to minimize field variability. Standardized procedures included land preparation, sowing, weed management, fertilizer application, and irrigation. A recommended fertilizer dose of 120 kg N, 90 kg P_2O_5 , and 60 kg K_2O per hectare was applied, with nitrogen applied in two splits (half at sowing and half at first irrigation). Irrigation was provided at five critical growth stages: crown root initiation, tillering, booting, flowering, and grain filling.

Data Measurement

Yellow Rust Scoring

Wheat cultivar Morocco (highly susceptible to all rusts) was sown around the experimental materials in two rows to create inoculum pressure. The yellow rust inoculum was collected from cultivar Morocco, and then the urediospore suspension was prepared in sterile distilled water with 2-3 drops of Tween-20. Parental cultivars, F_1 , F_2 populations, and spreader lines were inoculated uniformly at the booting stage in the evening by spraying a suspension of 0.1 g spore in 1-l water using a hand sprayer. The yellow rust data was recorded following the Cobb Scale. The host reaction (HR) types in order of Immune (I), traces

Table 2. Mean squares and percentages of total variation of G, E, G × E interaction, and experimental error (replications) for various traits in bread wheat in F1 and F2 at the CCRI and UAP.

Variables	S.O.V.	D.F.	M.S.		% Total variation		C.V. (%)	
	-		F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
Flag leaf area	G	20	63.81*	28.58**	66.72	39.9	6.18	-
	E	1	18.92**	306.02**	0.99	21.4		-
	G × E	20	12.52**	22.89**	13.09	32.0		3.34
	Replications	4	1.61	5.71	0.34	1.6		-
	Error	80	4.51	0.91	18.87	5.1		-
1000-grain weight	G	20	62.4**	57.27**	55.39	41.0	4.40	-
	E	1	137.4**	1.43**	6.10	0.1		-
	G × E	20	28.12**	63.02**	24.96	45.2		5.69
	Replications	4	5.61	7.79	1.00	1.1		-
	Error	80	3.54	4.4	12.56	12.6		-
-	G	20	34.19**	22.52**	43.02	38.9	-	-
Grain yield per plant	E	1	371.74**	36.15**	23.38	3.1	-	-
-	G × E	20	8.25**	17.26**	10.38	29.8	6.39	7.12
-	Replications	4	7.56	12.26	1.90	4.2	-	-
-	Error	80	4.24	3.46	21.31	23.9	-	-
-	G	20	71.59**	153.65**	72.3	67.6	-	-
-	E	1	69.44**	471.46**	3.5	10.4	-	-
Yellow rust resistance	G × E	20	21.57**	47.05**	21.8	20.7	24.21	14.65
-	Replications	4	0.47	1.17	0.1	0.1	-	-
-	Error	80	0.58	0.68	2.3	1.2	-	-

(T), resistance (R), resistance to moderately resistance (RMR), moderately resistant (MR), moderately resistant to moderately susceptible (M), moderately susceptible (MS), moderately susceptible to susceptible (MSS) and susceptible (S) were then converted into HR values through assigning values of 0.0, 0.1, 0.2, 0.3, 0.4, 0.6, 0.8, 0.9 and 1.0 for each host reaction, respectively [22].

$$\text{Coefficient of infection (C.I.)} = \text{Severity} \times \text{Value of host reaction}$$

whereas; Severity (%): 0-100

Traits Measurement

Flag Leaf Area (cm²)

Flag leaves were selected from the main tillers of the 10 randomly selected plants in F₁ and 20 plants in F₂ at post anthesis. Flag leaf area was measured according to following formula:

$$\text{Flag leaf area} = \text{Maximum width} \times \text{length} \times 0.75.$$

1000-Grain Weight (g)

After manual threshing, a representative sample of 1000 grains was draw out from each entry in each replication and weighed with the help of an electronic balance to record data on 1000-grain weight.

Grain Yield Per Plant (g)

Grain yield per plant was taken by weighing the grains of 10 randomly selected plants in gram in each sub-plot in F₁ and 20 in F₂ population in each replication after threshing with a single plant thresher.

Griffing's Combining Ability Analysis

In wheat breeding programs, it is crucial to identify and select parents with desirable traits for successful hybridization. This practice will lead to desirable traits

Table 3. Mean performance of F1 hybrids and F2 populations at CCRI and UAP.

Genotypes	Flag leaf area (cm ²)						1000-grain weight (g)						Grain yield per plant (g)						Yellow rust resistance						
	F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		
	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	
Benazir-13	35.74	36.00	29.90	26.03	44.9	42.40	37.90	32.20	34.50	30.70	25.60	20.80	34.50	30.70	25.60	20.80	0.06	0.00	0.06	0.00	0.03	0.00	0.03	0.00	
Khaista-17	37.30	33.48	29.00	32.10	47.5	44.90	41.20	36.30	36.90	31.80	29.80	25.70	36.90	31.80	29.80	25.70	0.02	0.00	0.02	0.00	0.00	0.00	0.00	0.00	
Inqilab-91	29.70	29.47	21.23	31.70	43.4	37.50	34.10	34.30	32.00	27.70	24.70	23.30	32.00	27.70	24.70	23.30	13.51	11.95	13.51	11.95	21.18	21.18	0.17	0.17	
Ghaznavi-98	31.54	27.63	18.63	24.61	39.7	40.20	37.20	33.80	28.80	28.10	24.90	21.90	28.80	28.10	24.90	21.90	17.03	0.07	17.03	0.07	18.05	18.05	3.95	3.95	
Galaxy-13	33.21	35.55	28.57	27.02	41.8	44.40	37.50	37.40	31.70	30.20	26.50	25.50	31.70	30.20	26.50	25.50	10.17	8.67	10.17	8.67	21.52	21.52	12.60	12.60	
Parula	34.36	31.54	26.90	28.98	38.6	38.80	33.90	36.70	30.20	26.40	23.60	24.20	30.20	26.40	23.60	24.20	0.40	0.23	0.40	0.23	0.00	0.00	0.00	0.00	
Benazir-13 × Khaista-17	39.25	36.81	31.03	31.33	48.1	46.20	38.80	39.70	38.10	35.20	28.60	27.70	38.10	35.20	28.60	27.70	0.03	0.00	0.03	0.00	0.58	0.58	0.50	0.50	
Benazir-13 × Inqilab-91	36.98	35.43	27.53	30.79	45.2	40.90	35.90	36.60	32.30	31.60	26.60	23.20	32.30	31.60	26.60	23.20	6.85	2.69	6.85	2.69	9.47	9.47	2.42	2.42	
Benazir-13 × Ghaznavi-98	28.73	29.78	30.03	29.63	36.9	36.40	46.30	37.60	32.90	28.60	29.90	25.70	32.90	28.60	29.90	25.70	2.61	3.82	2.61	3.82	2.56	2.56	2.49	2.49	
Benazir-13 × Galaxy-13	39.15	35.36	29.00	29.03	42.9	42.90	24.30	40.80	35.40	31.30	22.60	32.80	35.40	31.30	22.60	32.80	5.60	2.33	5.60	2.33	7.69	7.69	5.42	5.42	
Benazir-13 × Parula	36.91	37.29	26.90	32.92	45.6	41.50	36.30	39.70	35.30	30.00	27.50	26.60	35.30	30.00	27.50	26.60	1.84	0.00	1.84	0.00	1.37	1.37	0.00	0.00	
Khaista-17 × Inqilab-91	35.85	37.71	26.20	32.62	42.4	44.90	41.50	38.30	33.90	31.70	29.70	28.10	33.90	31.70	29.70	28.10	5.38	4.76	5.38	4.76	6.06	6.06	5.96	5.96	
Khaista-17 × Ghaznavi-98	33.59	34.60	24.47	29.42	47.3	43.30	38.00	36.90	35.20	29.90	27.70	25.60	35.20	29.90	27.70	25.60	2.55	2.46	2.55	2.46	2.74	2.74	1.65	1.65	
Khaista-17 × Galaxy-13	39.10	40.20	27.70	26.78	46.1	50.40	27.60	40.10	37.60	37.80	24.70	28.50	37.60	37.80	24.70	28.50	0.00	0.00	0.00	0.00	0.40	0.40	0.17	0.17	
Khaista-17 × Parula	39.61	33.14	29.93	31.95	47.8	44.30	52.50	38.10	37.30	29.90	30.70	25.50	37.30	29.90	30.70	25.50	0.14	0.00	0.14	0.00	2.59	2.59	0.00	0.00	
Inqilab-91 × Ghaznavi-98	33.13	27.49	23.37	33.48	45.2	35.00	31.60	32.10	35.20	28.90	23.20	22.30	35.20	28.90	23.20	22.30	0.58	2.35	0.58	2.35	9.73	9.73	9.73	9.73	
Inqilab-91 × Galaxy-13	36.59	38.08	22.60	29.53	44.2	44.80	37.10	34.30	34.80	31.60	25.80	25.60	34.80	31.60	25.80	25.60	2.95	3.12	2.95	3.12	15.62	15.62	8.23	8.23	
Inqilab-91 × Parula	29.13	31.28	26.00	31.35	42.9	32.10	33.60	37.80	32.60	26.30	27.10	29.70	32.60	26.30	27.10	29.70	3.48	2.77	3.48	2.77	10.16	10.16	0.59	0.59	
Ghaznavi-98 × Galaxy-13	33.69	35.35	27.23	27.44	45.2	37.30	35.90	35.90	33.80	28.40	26.60	24.20	33.80	28.40	26.60	24.20	2.58	2.19	2.58	2.19	12.23	12.23	11.29	11.29	
Ghaznavi-98 × Parula	28.06	31.98	28.07	33.97	37.4	41.90	37.10	35.50	29.80	31.20	25.50	23.90	29.80	31.20	25.50	23.90	1.24	0.36	1.24	0.36	5.93	5.93	3.96	3.96	
Galaxy-13 × Parula	37.71	34.87	30.53	29.59	45.4	45.70	38.10	37.90	34.50	33.50	28.80	26.9	34.50	33.50	28.80	26.9	4.52	2.57	4.52	2.57	11.04	11.04	8.57	8.57	
LSD _{0.05} Genotypes	2.44		1.09		2.16		2.41		2.36		2.14		2.36		2.14		1.62		1.62		1.76		1.76		1.76
LSD _{0.05} Environments	0.75		0.34		0.67		0.74		0.73		0.66		0.73		0.66		0.27		0.27		0.29		0.29		0.29
LSD _{0.05} GEI	3.45		1.55		3.56		3.41		3.34		3.02		3.34		3.02		2.52		2.52		2.74		2.74		2.74

Table 4. Mean squares and Griffing's analysis of variance for yield traits under investigation in F₁'s of bread wheat at CCRI.

Traits	-	Mean squares			Variance components		
		GCA	SCA	Error	σ^2 GCA	σ^2 SCA	σ^2 GCA/ σ^2 SCA
Flag leaf area	CCRI	14.87**	12.94**	1.83	0.48	11.11	0.04
-	UAP	22.30**	8.59**	1.18	3.43	7.41	0.46
1000-grain weight	CCRI	5.32**	12.83**	0.97	-1.88	11.86	-0.16
-	UAP	23.05**	17.94**	1.39	1.28	16.55	0.08
Grain yield plant ⁻¹	CCRI	6.11**	5.56**	1.17	0.14	4.39	0.03
-	UAP	9.44**	6.93**	1.57	0.63	5.36	0.12
Yellow rust resistance	CCRI	11.96**	24.90**	0.24	-3.23	24.66	-0.13
-	UAP	6.21**	10.44**	0.15**	-1.05	10.29	-0.10

Note: ** shows significance@P≤0.01

in filial generations. Knowledge about combining ability, accompanied by gene actions and genetic variance, is important for the breeder in selecting the best lines with high-potential segregants. For this very purpose [23] is the best tool for the assessment of general and specific combining ability. It helps in analysing inheritance patterns of diverse traits in bread wheat speed up the selection process by predicting progeny performance across generations [24]. Results are discussed herein;

Mean Performance and Combining Ability Analysis

Flag Leaf Area

At CCRI, the F₁ hybrids Khaista-17 × Parula (39.61 cm²) and Benazir-13 × Khaista-17 (39.25 cm²) revealed maximum flag leaf area, and was found at par with other F₁ hybrids ranging from 35.85 to 37.71 cm². The minimum flag leaf area was recorded for the

Ghaznavi-98 × Parula (28.06 cm²), which was at par with several other hybrids ranging from 28.73 to 33.13 cm². In F₂ generation at the same experimental site, flag leaf area varied from 24.47 to 31.03 cm² (Table 3). The maximum flag leaf area was noted for the F₂ population Benazir-13 × Khaista-17 (31.03 cm²), which was at par with other populations viz., Ghaznavi-98 × Parula (28.07 cm²) and Khaista-17 × Parula (29.93 cm²). The minimum flag leaf area was recorded for the F₂ population at UAP was Inqilab-91 × Galaxy-13 (22.60 cm²), which was at par with other populations ranging from 23.37 to 24.47 cm². However, the maximum flag leaf area was observed for F₁ hybrid Khaista-17 × Galaxy (40.20 cm²) and F₂ population i.e., Ghaznavi-98 × Parula (33.97 cm²).

Significant ($P \leq 0.01$) GCA and SCA effects for flag leaf area were observed at CCRI and UAP, highlighting the roles of additive and non-additive genetic actions (Table 4). SCA variance exceeded GCA, with σ^2 GCA/ σ^2 SCA ratios below unity. GCA effects ranged from -2.16 to 1.81 at CCRI and -2.67 to 1.77 at UAP. Khaista-17 (1.81, CCRI) and Galaxy-13 (1.77, UAP) exhibited the

Table 5. Estimates of GCA effects (\hat{g}_i) for studied traits in F₁'s bread wheat parents at CCRI and UAP.

Variables	Benazir-13		Khaista-17		Inqilab-91		Ghaznavi-98		Galaxy-13		Parula		S.E. (Gj)	
	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP	CCRI	UAP
Flag leaf area	-0.69	-1.00	1.81	0.91	0.94	1.32	-2.16	-2.67	0.05	1.77	0.05	-0.34	0.437	0.350
1000-grain weight	-0.67	-0.25	1.03	0.93	1.06	1.70	-0.60	-3.11	-0.42	0.93	-0.39	-0.20	0.318	0.380
Grain yield plant ⁻¹	-1.31	-1.00	1.25	1.26	0.40	0.84	-0.55	-1.43	0.27	0.67	-0.06	-0.34	0.349	0.405
Yellow rust resistance	1.76	0.52	-1.27	-0.99	0.83	1.23	0.32	0.02	-0.26	0.26	-1.38	-1.03	0.157	0.124

Note: S.E. (Gj) = Standard error

highest positive GCA effects (Table 5). SCA effects ranged from -6.77 to 3.97 at CCRI and -4.81 to 5.01 at UAP. The cross Ghaznavi-98 × Galaxy-13 showed the highest positive SCA effects (3.97, CCRI; 5.01, UAP) (Table 6). These results identify promising genotypes and hybrids for improving flag leaf area.

1000-Grain Weight

In F_1 generation at CCRI, the maximum 1000-grain weight was recorded for the F_1 hybrid Benazir-13 × Khaista-17 (48.10 g), which was found at par with two other hybrids including Khaista-17 × Parula (47.80 g) and Khaista-17 × Ghaznavi-98 (47.30 g) (Table 3). The minimum 1000-grain weight was observed for the F_1 hybrids Benazir-13 × Ghaznavi-98 (36.90 g) and Ghaznavi-98 × Parula (37.40 g). In F_2 generation at CCRI, the 1000-grain weight varied from 24.30 to 52.50 g. The F_2 population Khaista-17 × Parula (52.50 g), followed by Benazir-13 × Ghaznavi-98 (46.30 g) and Khaista-17 × Ghaznavi-98 (47.30 g), manifested a maximum 1000-grain weight at CCRI. However, at UAP the F_1 hybrid Khaista-17 × Galaxy-13 (50.40 g) and the F_2 population Benazir × Galaxy-13 (40.13 g) were high-yielding genotypes. Overall, genotypes involving Khaista-17 and Galaxy-13 consistently exhibited superior performance in both F_1 and F_2 generations, highlighting its potential as a parental line for enhancing grain weight. Additionally, the CCRI location provided more favorable conditions for TGW expression as compared to UAP, emphasizing the role of environment in trait performance.

The analysis of 1000-grain weight revealed significant genetic variability, as indicated by the mean squares for GCA and SCA at two locations, CCRI and UAP (Table 4). Significant differences ($P \leq 0.01$) were observed for both GCA and SCA effects, highlighting the influence of both additive and non-additive gene actions. However, the SCA variance was more prominent, as evidenced by the GCA-to-SCA variance ratio consistently below unity in both environments. This trend emphasizes the dominance of non-additive gene effects in governing 1000-grain weight inheritance. GCA effects ranged from -4.36 to 3.29 at CCRI and from -3.11 to 1.70 at UAP (Table 5). Three cultivars at each location displayed favorable GCA effects, while an equal number showed negative effects. Among the parental genotypes, Khaista-17 exhibited the highest positive GCA effect (3.29) at CCRI, whereas Inqilab-91 showed a notable GCA effect (1.70) at UAP, marking them as key contributors to favorable additive effects for this trait. SCA effects varied from -7.25 to 3.42 at CCRI and -6.60 to 6.16 at UAP (Table 6). Seven F_1 hybrids at each location demonstrated positive SCA effects. Among these, the cross Benazir-13 × Khaista-17 showed the highest SCA effect (3.42) at CCRI, while Inqilab-91 × Galaxy-13 exhibited the maximum SCA effect (6.16) at UAP. These combinations emerged as the most promising for enhancing 1000-grain weight,

signifying their potential for hybrid development. The predominance of non-additive gene action, coupled with the identification of superior hybrids and parental genotypes, underscores the importance of SCA effects and specific cross combinations for improving 1000-grain weight in wheat.

Grain Yield Plant⁻¹

In F_1 generation, the maximum grain yield plant⁻¹ was recorded for Benazir-13 × Khaista-17 (38.1 g). Among F_1 hybrids, Benazir-13 × Khaista-17 demonstrated superior grain yield across two environments, reaching 38.1 g at CCRI and 35.2 g at UAP (Table 3). In F_2 generation, grain yield plant⁻¹ varied from Benazir-13 × Galaxy-13 (22.60 g) to Khaista-17 × Inqilab-91 (29.90 g). Other notable F_2 crosses at UAP were Benazir-13 × Galaxy-13 (32.8 g) and Inqilab-91 × Parula (29.71 g). F_2 crosses involving Khaista-17 consistently outperformed other parental cultivars, emphasizing its role in improving grain yield. However, F_2 crosses generally exhibited lower grain yield than their corresponding F_1 hybrids.

The grain yield per plant, a critical trait in wheat breeding, exhibited substantial genetic variability as reflected by the mean squares for GCA and SCA across two contrasting environments, CCRI and UAP (Table 4). Significant differences ($P \leq 0.01$) were noted in the GCA and SCA mean squares, underscoring the effects of both additive and non-additive gene actions. Notably, SCA contributed more prominently to the observed variation, as evidenced by the GCA-to-SCA variance ratios consistently falling below unity in both environments. This highlights the dominance of non-additive gene action in governing the inheritance of grain yield per plant. The GCA effects ranged from -1.31 to 1.25 at CCRI and from -1.43 to 1.26 at UAP (Table 5). Among the parental genotypes, three cultivars from each location demonstrated positive GCA effects, while an equal number displayed negative effects. Khaista-17 emerged as the most promising general combiner, exhibiting the highest and statistically significant GCA effects (1.25) at both CCRI and UAP, indicating its superior potential for enhancing grain yield per plant. SCA effects varied from -3.51 to 2.83 at CCRI and -2.81 to 5.79 at UAP (Table 6). Five F_1 hybrids at CCRI and four F_1 hybrids at UAP displayed positive SCA effects, signifying their potential for yield improvement. Among the hybrids, Inqilab-91 × Parula exhibited the highest positive SCA effect (2.83) at CCRI, while Inqilab-91 × Galaxy-13 demonstrated the highest SCA effect (5.79) at UAP. These specific hybrid combinations are identified as the most effective for improving grain yield per plant, underscoring their relevance in hybrid development programs. The findings emphasize the predominance of non-additive gene action in controlling grain yield per plant and highlight the importance of identifying superior parental lines and specific hybrid combinations for yield enhancement.

Yellow Rust Resistance

At CCRI, the minimum and at par ACI values (Average coefficient of infection) were recorded for F_1 hybrids Khaista-17 \times Galaxy-13, Benazir-13 \times Khaista-17, Khaista-17 \times Parula, Khaista-17 \times Ghaznavi-98. Similarly, at UAP, the lowest ACI values were observed for the F_1 hybrids Benazir-13 \times Khaista-17, Benazir \times Parula, Khaista \times Galaxy-13 and Khaista \times Parula (Table 3). In F_2 populations at CCRI, the lowest and at-par ACI values were noted for Khaista \times Galaxy-13, followed by Benazir-13 \times Khaista-17. Whereas at UAP, Benazir \times Parula and Khaista-17 \times Parula exhibited the desirable ACI values for yellow rust.

The GCA effects for yellow rust resistance in F_1 hybrids ranged from -1.27 to 1.76 at CCRI and -1.03 to 1.23 at UAP. At CCRI, significant negative GCA effects were observed in parental cultivars Khaista-17 (-1.27), Parula (-1.38), and Galaxy-13 (-1.38), while the remaining three parental cultivars exhibited positive GCA effects (Table 4). At UAP, Parula (-1.03) and Khaista-17 (-0.99) displayed the most significant negative GCA effects, indicating their potential as poor combiners for yellow rust resistance (Table 5). The SCA effects, which assess the specific hybrid combinations, ranged from -4.45 to 11.00 at CCRI and -3.89 to 7.81 at UAP (Table 6). At both locations, a notable proportion of F_1 hybrids exhibited negative SCA effects, suggesting the involvement of non-AGA for yellow rust resistance. At CCRI, the hybrid Inqilab-91 \times Galaxy-13 (-4.45) showed the most significant negative SCA effects, followed by Benazir-13 \times Khaista-17 (-4.35) and Benazir-13 \times Parula (-3.86). Similarly, at UAP, the hybrids Inqilab-91 \times Galaxy-13 (-3.89) and Benazir-13 \times Khaista-17 (-2.86) displayed significant negative SCA effects, indicating their superior performance in conferring yellow rust resistance. The observed non-additive gene action at both sites is further supported by the GCA/SCA ratio, which was consistently less than unity, reinforcing the dominance of non-additive gene effects for yellow rust resistance in the studied genotypes. This emphasizes the importance of specific hybrid combinations rather than individual parental effects in improving yellow rust resistance in wheat.

Discussion

The genotypes exhibited highly significant differences in traits such as yellow rust resistance, flag leaf area, and yield, highlighting substantial genetic variability among them. This variability offers potential for developing high-yielding wheat hybrids. The significant mean squares for both GCA and SCA confirmed the validity of the diallel analysis in the breeding material studied. Significant mean squares for genotypes, GCA, and SCA were observed for all

traits across F_1 and F_2 wheat populations, aligning with previous findings [25, 26].

In both generations, Khaista-17 and Parula displayed higher resistance to yellow rust at CCRI and UAP, though the said location is a hotspot for yellow rust, evidenced by their minimal ACI values. Conversely, Benazir at CCRI and Inqilab-91 at UAP exhibited higher susceptibility, as reflected by their maximum ACI values. Cultivars such as Khaista-17 and Galaxy-13 were individually resistant and susceptible, respectively. However, the F_2 progeny (Khaista-17 \times Galaxy-13) showed resistance to current yellow rust strains, potentially due to the accumulation or interaction of resistance genes from the male parent in the F_1 generation, both at CCRI and UAP. Similarly, the same genotype resistance against rust at CCRI was observed in the F_2 generation. The F_2 populations Benazir-13 \times Parula and Khaista-17 \times Parula revealed the minimum ACI value at UAP and hence were considered to be the best resistant F_2 populations. Most Pakistani bread wheat cultivars resist stripe rust through the incorporation of Yr genes such as Yr-A, Yr-2, Yr-4, Yr-6, Yr-7, Yr-18, Yr-9, Yr-22, and Yr-27. Among these, Yr-6, Yr-7, and Yr-9 occur more frequently, either alone or in combination. Reports from Mexican wheat cultivars like Opata (Yr-27 + Yr-18) and Super Kauz (Yr-9, Yr-27, and Yr-18) highlighted virulence for Yr genes under natural conditions in diverse environments [27]. Such genetic resistance, being inherited and durable, offers an ecologically sustainable and environmentally friendly approach to disease management by minimizing dependence on chemical fungicides.

The flag leaf and its orientation play a critical role in determining the photosynthetic efficiency of wheat plants, directly impacting grain yield [28]. Modifying the architecture of the flag leaf to enhance photosynthate production during the grain-filling period is a key objective in wheat breeding efforts. This study found that genotypes with larger flag leaf areas consistently produced higher grain yields across both generations and experimental sites [29]. A positive correlation between flag leaf area and yield has been reported, indicating its utility as a selection criterion for high-yielding wheat lines [30, 31]. However, in durum wheat genotypes, flag leaf size did not show a direct association with grain yield. Similarly, some studies reported non-significant differences in flag leaf area and yield among wheat cultivars [32, 33].

Results also demonstrated that genotypes with a maximum 1000-grain weight produced the highest grain yield in both generations and experimental sites. For instance, Khaista-17 in the F_1 generation at CCRI and UAP, and in the F_2 generation at CCRI, exhibited the maximum 1000-grain weight, and at UAP, the parental cultivar Galaxy-13 in the F_2 generation excelled in performance. The F_2 populations Khaista-17 \times Parula and Benazir-13 \times Galaxy-13 showed the maximum 1000-grain weight. Grains with greater 1000-grain weight are known to exhibit superior quality required for processing in flour mills and have better germination

percentage [34]. A positive correlation between grain yield and 1000-grain weight has also been reported in earlier studies [35, 36].

The F_1 hybrids (Benazir-13 \times Khaista-17) and (Khaista-17 \times Galaxy-13) revealed the maximum grain yield at CCRI and UAP, respectively. Whereas, the F_2 populations (Khaista-17 \times Parula) at CCRI and Benazir-13 \times Galaxy-13 at UAP manifested the maximum grain yield per plant, and cultivars such as Khaista-17 and Benazir-13 achieved the highest grain yields in both locations and generations due to their resistance to yellow rust and adaptation to other environmental fluctuations. Similar findings have shown that cultivars grown in diverse environments demonstrate superior adaptability with minimal yield fluctuations [37]. The F_1 hybrids and F_2 populations in wheat have revealed significant differences confirmed by the earlier studies in bread wheat for yield and yield components [38].

For the cross combination Inqilab-91 \times Galaxy-13, parental genotypes with positive GCA effects produced F_2 populations with negative, desirable SCA effects for yellow rust resistance, indicating the role of non-additive gene action such as dominance or epistasis. Parents with high GCA effects often produced hybrids with low SCA effects, potentially due to a lack of gene complementation between them [39]. Variances due to GCA were lower than those for SCA, with their ratios below unity, indicating a predominance of non-additive gene effects for yellow rust resistance in F_1 hybrids at CCRI and UAP. Previous studies identified genotypes with low GCA effects for traits such as pustule density, latent period, pustule size, infection type, and as suitable parents for breeding programs aimed at improving yellow rust resistance [40].

Crosses involving low \times high GCA parents, such as Benazir-13 \times Khaista-17 and Inqilab-91 \times Galaxy-13 in the F_1 generation, exhibited the highest SCA effects for 1000-grain weight at CCRI and UAP, respectively. These combinations complemented epistatic effects, enhancing overall performance. Thousand-grain weight and grain yield per plant showed significant combining ability effects with additive effects [41]. Ratios greater than unity suggested an additive gene action for 1000-grain weight across both locations. Conversely, some studies reported non-additive gene effects for this trait [42], while others suggested additive gene action [43].

For grain yield, the cross Benazir-13 \times Khaista-17, involving low \times high GCA effects, yielded the F_1 hybrids with the highest specific combining ability effects at both experimental sites. In contrast, Inqilab-91 \times Galaxy-13, with high \times high GCA parents, resulted in F_1 hybrids with maximum SCA effects. These findings emphasize the potential of heterosis breeding and transgressive segregation to enhance yield traits. Although non-additive gene effects predominated for grain yield, some studies reported additive effects [44].

Conclusions

Analysis of variance revealed significant differences among the wheat genotypes and their interaction with environments for all studied traits. The F_1 hybrids had generally higher mean performance than their parental cultivars for all the traits, indicating the presence of better hybrids than parental cultivars. Analysis of combining ability revealed significant results for all traits. Maximum and significant GCA effects were observed in parental cultivars, i.e., Khaista-17 and Inqilab-91, for 1000-grain weight and grain yield per plant at CCRI and UAP. However, in the case of SCA effects, the F_1 hybrids Inqilab-91 \times Galaxy revealed the significant SCA effects for grain yield per plant at CCRI and UAP. Hence, the utilization of these hybrids and F_2 populations offers a sustainable and cost-effective solution for developing yellow rust-resistant wheat varieties, reducing fungicide use, and supporting environmental conservation. Moreover, multi-location field trials under diverse climatic conditions, coupled with molecular validation of resistance genes, are needed to confirm the stability and genetic basis of the observed resistance.

Aknowlegment

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Conflict of Interest

The authors declare no conflict of interest.

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