

GENETIC EXPRESSION OF YELLOW RUST RESISTANCE, YIELD AND YIELD RELATED TRAITS IN WHEAT USING GRIFFING'S COMBINING ABILITY ANALYSIS

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Abstract

Knowledge of traits inheritance is a prerequisite for any plant breeding program. Wheat cultivars like Pirsabak-85, Khyber-87, Saleem-2000, Pirsabak-04, Pirsabak-05 and Shahkar-13 were crossed in 6 × 6 half diallel fashion during 2010-11 at the Cereal Crops Research Institute (CCRI), Pirsabak - Nowshera, Pakistan. The F₁ and F₂ half diallel hybrids in comparison with parental genotypes were studied during 2011-12 and 2012-13, respectively. The aim of the present work was to explore the genetic basis of yellow rust (*Puccinia striiformis* West. f. sp. *tritici*) resistance, flag leaf area, 1000-grain weight and grain yield in F₁ and F₂ wheat hybrids through Griffing's combining ability approach. Significant (p≤0.01) differences were observed among the genotypes for all the traits. Mean squares due to general combining ability (GCA) and specific combining ability (SCA) were significant (p≤0.01) for majority of the traits in both the generations. Genetic components of variances due to GCA and SCA revealed that SCA variances excelled the GCA for majority of the traits, thus non-additive type of gene action controlled the inheritance of such traits. However, flag leaf area and 1000-grain weight in F₁ generation showed preponderance of GCA variances and revealed additive type of gene action advocating those traits. Based on GCA effects, Pirsabak-05 was considered as the best general combiner for rust resistance and yield traits in F₁ generation. However, in F₂ generation, cultivar Shahkar-13 appeared to be the best general combiner for rust resistance and grain yield. The F₁ hybrid Pirsabak-85 × Pirsabak-04 and F₂ population Pirsabak-05 × Shahkar-13 performed better for majority of the traits. Therefore, these promising populations need to be further exploited for yellow rust resistance and grain yield in future breeding programmes.

Key words: Combining ability, GCA and SCA effects, Additive and non-additive gene action, Yellow rust resistance, Grain yield, *Triticum aestivum* L.

Introduction

Wheat is the leading food grain of Pakistan and being the staple diet of the people and occupies a central position in agricultural policies. Wheat contributes 10.3% to the value addition in agriculture and 2.2% to GDP (Anon., 2015). Pakistan is the 4th largest producer of wheat in Asia and stands 11th in world production.

Climate change increased the risk of food security for some vulnerable group of crops like wheat, rice and maize. In current situation of climatic change, major limitations in wheat production are drought, heat, and irregular rainfall. Since last few years, frequency of rainfall increased during peak growing stage of wheat development which made micro as well as macro climate conducive for development of different diseases such as yellow rust, fusarium head blight, powdery mildew, black point and karnal bunt. Yellow rust (*Puccinia striiformis* f. sp. *tritici* Westend) mainly develops in cool and moist conditions (Gocmen *et al.*, 2003). The distinguishing symptoms of this disease are yellow pustules (urediniospores) appear mostly on the leaves but in severe conditions, it can also be seen on the leaf sheaths, spikes, glumes and awns of the susceptible plants. The urediniospores are elongated and arranged in linear rows between veins of the leaf. The fungus produces linear rows of black teleospores late in the season (Chen *et al.*, 2014). Several new wheat cultivars were released after the green revolution. However, development of new pathotypes of rust breakup the resistance and caused severe yield losses (Mateen & Khan, 2014). Chemical control is neither supported by the researcher nor suitable for food

grains due to its health hazards. Therefore, the preferable and most economical approach is the deployment of genetic resistance to cope with the wheat rusts.

Grain yield is a complex character made up from interaction between yield components and environmental effects. To develop high yielding wheat cultivars, it is important to study the genetic make-up of diverse wheat lines, inheritance pattern of yield contributing traits and association of various traits with yield under existing environmental conditions. Flag leaf plays an important role in the emergence of the spikes and reproductive growth of the wheat (Ahmad *et al.*, 2013). Positive correlation between flag leaf area and yield indicating that flag leaf area might be a useful parameter for selection of high yielding genotypes (Zeuli & Qualset, 1990). Grains with higher 1000-grain weight have better milling quality and ensure better emergence (Protic *et al.*, 2007).

Combining ability is an effective technique for isolating the best combiners that may be used in crosses either to exploit heterosis or to accumulate fixable genes and obtain desirable segregates that helps to understand the genetic architecture of various characters. In previous studies, the GCA variances were higher than SCA variances for plant height, spike length, and grain yield in both the generations which revealed that inheritance of these traits was managed by additive type of gene action in different wheat populations (Verma *et al.*, 2016). The SCA variances were higher than GCA variances for all the traits which indicated the predominance of non-additive (dominant, overdominance and epistasis) type of gene action in the inheritance of the yield traits in wheat (Mandal

& Madhuri, 2016; Saeed & Khalil, 2017) and barley (Patil *et al.*, 2016). However, in some studies mean squares indicated that both additive and dominance genetic components were significant and important for inheritance of the majority of the traits in wheat (Jat *et al.*, 2016; Kandil *et al.*, 2016). These type of contradictions might be due to nature of the genotypes and the environment where studied. Such knowledge can enable the breeder to design effective strategy for development of the existing materials in future breeding program.

Therefore, the present research was planned with the objectives to study and evaluate the relative importance of general and specific combiners and the genetic components for resistance to yellow rust, flag leaf area, 1000-grain weight and grain yield in 6×6 F₁ and F₂ half diallel hybrids of wheat through combining ability analysis.

Materials and Methods

Breeding material and procedure: This study was conducted at Cereal Crops Research Institute (CCRI), Pirsabak-Nowshera, Pakistan during three consecutive growing seasons viz., 2010-11, 2011-12 and 2012-13. The genetic material consisted of six bread wheat cultivars including Pirsabak-85, Pirsabak-04, Pirsabak-05, Shahkar-13, Saleem-2000 and Khyber-87, representing a wide range of diversity for rust resistance, earliness and yield traits. All the six genotypes were crossed in a half diallel fashion to produce 15 F₁ hybrids during 2010-11. Parental genotypes and their F₁ hybrids were sown during 2011-2012 while parents and their F₂ populations were grown during 2012-2013 in a randomized complete block design (RCBD) with two and three replications, respectively. Similarly, recommended and same cultural practices and inputs including land preparation, sowing, weed control, fertilizer application, and irrigation were applied to all the wheat genotypes and experiments to avoid the field variations.

Measurement of traits

Yellow rust scoring: Wheat cultivar Morocco (highly susceptible for 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 urediospores suspension was prepared in sterile distilled water with 2-3 drops of tween-20 (Shah *et al.*, 2010). Parental cultivars, F₁, F₂ populations and spreader lines were inoculated uniformly at booting stage in the evening by spraying a suspension of 0.1 g spore in 1-l water by using hand sprayer. The yellow rust data was recorded following Cobb Scale (Peterson *et al.*, 1948; Stavely, 1985; Ali *et al.*, 2014). The host reaction (HR) types in order of Immune (I), traces (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 (Roelfs *et al.*, 1992; Cheruiyot *et al.*, 2014).

Coefficient of infection (C.I.) = Severity \times Value of host reaction

whereas; Severity (%): 0-100

In addition, data were also recorded for flag leaf area, 1000-grain weight and grain yield per plant on 10 randomly tagged plants in F₁ and 20 plants in F₂ populations and parental genotypes. Flag leaf area was measured at post anthesis according to following formula, developed by Francis *et al.* (1969).

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

After manual threshing, a representative sample of 1000 grains was taken from each entry in each replication and weighed with the help of an electronic balance to record the data on 1000-grain weight. Grain yield per plant was recorded by weighing the grains of each genotype in each replication after threshing with single plant thresher.

Statistical analyses: Data were subjected to analysis of variance according to Steel *et al.* (1997). The genotypes means for each variable were further separated and compared by using the least significant difference (LSD) test at 5% level of probability (Hayter, 1986). Data were further analyzed through combining ability analysis as outlined by Griffing (1956) following Method-II, Model-I to assess the genetic variances due to GCA and SCA effects (Singh & Chaudhary, 1985). For various traits, the variances due to σ^2 GCA and σ^2 SCA and their ratios (σ^2 GCA/ σ^2 SCA) were also calculated according to Singh & Chaudhary (1985).

Results

Highly significant ($p \leq 0.01$) differences were observed among F₁ and F₂ populations and their parental cultivars for most of the traits (Table 1). However, for flag leaf area the genotypic differences were merely significant ($p \leq 0.05$). Results revealed that these populations have greater genetic variability and suitable for further biometrical study through combining ability analysis. Results about resistance to yellow rust and yield traits for various populations are presented as follows.

Yellow rust resistance: The yellow rust resistance was estimated through average co-efficient of infection (ACI). The ACI varied from 0.00 to 20.00 among parental cultivars, and 0.00 to 3.84 among F₁ hybrids (Table 2). Minimum ACI (0.00) was observed for nine genotypes (including three parental cultivars i.e., Pirsabak-04, Pirsabak-05 and Saleem-2000, and their six F₁ hybrids (Pirsabak-85 \times Pirsabak-04, Pirsabak-85 \times Pirsabak-05, Pirsabak-04 \times Pirsabak-05, Pirsabak-05 \times Shahkar-13, Shahkar-13 \times Saleem-2000 and Shahkar-13 \times Khyber-87). However, these genotypes were at par in resistance to yellow rust with six other genotypes (one parental cultivar and five F₁ hybrids) ranging from 0.03 to 0.43. Maximum ACI was recorded for cultivar Pirsabak-85 (20.00). In F₂ generation, the ACI varied from 0.00 to 25.97 among parental cultivars, and 0.58 to 15.66 among F₂ populations (Table 2). Minimum and at par ACI was recorded for two cultivars Pirsabak-05 (0.00), Shahkar-13 (0.02) and three F₂ populations i.e. Pirsabak-05 \times Shahkar-13 (0.58), Shahkar-13 \times Saleem-2000 (2.58) and Shahkar-13 \times Khyber-87 (2.74). However, maximum severity and ACI was noted for cultivar Pirsabak-85 (25.97) and the said genotype was found highly susceptible as compared to all other cultivars and their F₁ and F₂ populations.

Table 1. Mean squares for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat.

Variables	F ₁ / F ₂	Mean squares					CV %
		Genotypes	Parents	F ₁ / F ₂	Parents vs. F ₁ / F ₂	Error	
D.F.	F ₁	20	5	14	1	20	
	F ₂	20	5	14	1	40	
Yellow rust resistance	F ₁	45.09**	140.33**	2.26**	168.52**	0.0804	15.13
	F ₂	155.77**	379.11**	58.01**	405.10**	2.92	16.96
Flag leaf area	F ₁	21.74*	22.67*	19.97*	41.77*	7.86	7.9
	F ₂	27.97**	33.59**	14.47**	188.97**	1.46	3.61
1000-grain weight	F ₁	5.01**	7.88**	4.32**	0.4 ^{NS}	1.07	2.61
	F ₂	98.34**	193.95**	61.24**	139.83**	8.03	7.69
Grain yield plant ⁻¹	F ₁	40.29**	51.95**	27.53**	160.7**	8.32	9.2
	F ₂	76.98**	140.50**	46.78**	182.11**	13.62	15.31

*, ** = Significant at p≤0.05 and p≤0.01, NS = Non-significant

Table 2. Mean performance of 6 × 6 F₁ and F₂ half diallel crosses for yellow rust resistance and flag leaf area.

Parental genotypes, F ₁ & F ₂ populations	Yellow rust resistance		Flag leaf area (cm ²)	
	F ₁	F ₂	F ₁	F ₂
Pirsabak-85	20.00	25.97	33.61	30.03
Pirsabak-04	0.00	18.91	33.17	31.08
Pirsabak-05	0.00	0.00	40.44	35.70
Shahkar-13	0.09	0.02	33.18	28.61
Saleem-2000	0.00	21.46	30.59	26.14
Khyber-87	10.17	18.19	32.55	32.98
Pirsabak-85 × Pirsabak-04	0.00	9.96	36.51	35.33
Pirsabak-85 × Pirsabak-05	0.00	11.70	37.83	34.79
Pirsabak-85 × shahkar-13	0.03	6.65	36.75	33.63
Pirsabak-85 × Saleem-2000	0.15	15.49	33.63	32.08
Pirsabak-85 × Khyber-87	3.84	10.17	32.91	36.92
Pirsabak-04 × Pirsabak-05	0.00	9.75	37.23	36.62
Pirsabak-04 × Shahkar-13	0.17	6.35	32.58	33.42
Pirsabak-04 × Saleem-2000	0.43	15.66	33.70	30.78
Pirsabak-04 × Khyber-87	1.00	10.81	32.65	35.95
Pirsabak-05 × Shahkar-13	0.00	0.58	40.56	37.48
Pirsabak-05 × Saleem-2000	0.27	10.47	41.60	33.53
Pirsabak-05 × Khyber-87	1.87	8.35	41.75	35.35
Shahkar-13 × Saleem-2000	0.00	2.58	34.51	31.44
Shahkar-13 × Khyber-87	0.00	2.74	35.52	37.97
Saleem-2000 × Khyber-87	1.37	5.93	34.20	33.59
LSD_{0.05}	0.59	2.82	5.84	1.99

Flag leaf area: Flag leaf area varied from 30.59 to 40.44 cm² and 32.59 to 41.75 cm² among parental cultivars and F₁ hybrids, respectively (Table 2). In F₁ generation, F₁ hybrids such as Pirsabak-05 × Khyber-87 (41.75 cm²) and Pirsabak-05 × Saleem-2000 (41.60 cm²) revealed maximum and similar flag leaf area, and these genotypes were at par with six other genotypes (having one parental genotype and five F₁ hybrids) ranging from 36.51 to 40.57 cm². The lowest flag leaf area of 30.59 cm² was recorded for cultivar Saleem-2000 which was at par with twelve other genotypes (having four parental cultivars and eight F₁ hybrids) ranging from 32.55 to 35.52 cm². In F₂ generation, flag leaf area varied from 26.14 to 35.70 cm² and 30.78 to 37.97 cm² among parental cultivars and F₂ populations, respectively (Table 2). Maximum flag leaf area of 37.97 cm² was noted for F₂ population Shahkar-13 × Khyber-87, which was found at par with three other populations i.e., Pirsabak-04 × Pirsabak-05, Pirsabak-85 × Khyber-87 and Pirsabak-05 × Shahkar-13 ranging from 36.62 to 37.48 cm². Minimum flag leaf area was recorded for cultivar Saleem-2000 (26.14 cm²) in F₂ generation.

1000-grain weight: The 1000-grain weight ranged from 37.00 to 43.00 g and 37.50 to 42.50 g among parental cultivars and F₁ hybrids, respectively (Table 3). In F₁ generation, highest 1000-grain weight was recorded for parental cultivar Pirsabak-05 (43.00 g) and it was found at par with four other F₁ hybrids viz., Pirsabak-04 × Shahkar-13, Pirsabak-04 × Pirsabak-05, Pirsabak-05 × Shahkar-13 and Pirsabak-85 × Pirsabak-05 ranging from 41.00 to 42.50 g. Minimum 1000-grain weight was recorded for Saleem-2000 (37.00 g) and it was at par with eight other genotypes (having two parental cultivars and six F₁ hybrids) ranging from 37.50 to 39.00 g. In F₂ generation, 1000-grain weight varied from 26.12 to 44.55 g and 27.25 to 45.97 g among parental cultivars and F₂ segregants (Table 3). Maximum 1000-grain weight was noted for F₂ population i.e., Pirsabak-05 × Shahkar-13 (45.97 g), and it was found equal in performance with three other genotypes i.e., Pirsabak-05 (44.55 g), Shahkar-13 (42.87 g) and Pirsabak-04 × Pirsabak-05 (41.83 g). Minimum and alike 1000-grain weight was noted for two parental genotypes i.e. Pirsabak-85 (26.12 g) and Saleem-2000 (26.23 g). These genotypes were found at par with two other F₂ populations i.e., Pirsabak-85 × Saleem-2000 (27.25 g) and Pirsabak-04 × Saleem-2000 (30.60 g).

Table 3. Mean performance of 6 × 6 F₁ and F₂ half diallel crosses for 1000-grain weight and grain yield per plant.

Parental genotypes, F ₁ & F ₂ populations	1000-grain weight (g)		Grain yield plant ⁻¹ (g)	
	F ₁	F ₂	F ₁	F ₂
Pirsabak-85	39.50	26.12	32.50	13.80
Pirsabak-04	39.00	31.15	32.50	16.45
Pirsabak-05	43.00	44.55	33.50	27.52
Shahkar-13	39.50	42.87	25.00	31.02
Saleem-2000	37.00	26.23	23.50	16.92
Khyber-87	38.50	36.05	22.50	22.78
Pirsabak-85 × Pirsabak-04	39.50	36.68	40.50	23.27
Pirsabak-85 × Pirsabak-05	42.50	37.82	38.50	24.88
Pirsabak-85 × Shahkar-13	40.00	39.07	30.00	25.30
Pirsabak-85 × Saleem-2000	38.50	27.25	28.50	16.18
Pirsabak-85 × Khyber-87	38.50	40.35	27.50	29.50
Pirsabak-04 × Pirsabak-05	41.00	41.83	32.10	27.95
Pirsabak-04 × Shahkar-13	41.00	36.72	33.40	22.93
Pirsabak-04 × Saleem-2000	37.50	30.60	33.00	19.30
Pirsabak-04 × Khyber-87	38.00	34.63	28.20	22.73
Pirsabak-05 × Shahkar-13	41.50	45.97	35.10	31.23
Pirsabak-05 × Saleem-2000	40.00	40.08	31.50	26.80
Pirsabak-05 × Khyber-87	40.50	36.62	32.00	25.08
Shahkar-13 × Saleem-2000	38.00	38.93	35.90	26.15
Shahkar-13 × Khyber-87	39.50	40.12	32.50	26.85
Saleem-2000 × Khyber-87	38.50	40.22	30.00	29.50
LSD_{0.05}	2.15	4.67	6.01	6.09

Grain yield per plant: In F₁ generation, grain yield per plant varied from 22.50 to 33.50 g and 27.50 to 40.50 g among parental cultivars and F₁ hybrids, respectively (Table 3). Maximum grain yield was observed in F₁ hybrid Pirsabak-85 × Pirsabak-04 (40.50 g) and it was found equal in performance with three other F₁ hybrids viz., Pirsabak-85 × Pirsabak-05 (38.50 g), Shahkar-13 × Saleem-2000 (35.90 g) and Pirsabak-05 × Shahkar-13 (35.10 g). Minimum and at par grain yield was noted for two cultivars Khyber-87 (22.50 g) and Saleem-2000 (23.50 g) and these parental cultivars were found at par with four other genotypes ranging from 25.00 g to 28.50 g. In F₂ generation, grain yield varied from 13.80 to 31.00 g among parental cultivars and 16.18 to 31.22 g among F₂ populations (Table 3). Maximum grain yield was observed for F₂ population Pirsabak-05 × Shahkar-13 (31.2 g), and it was found equal to nine other genotypes (with two parental cultivars and seven F₂ populations) ranging from 25.3 to 31.0 g. Minimum grain yield per plant was observed for three genotypes viz., Pirsabak-85 (13.80 g), Pirsabak-85 × Saleem-2000 (16.18 g) and Pirsabak-04 (16.45 g). These genotypes were also found at par with two other genotypes i.e. Saleem-2000 (16.92 g) and Pirsabak-04 × Saleem-2000 (19.30 g).

Combining ability analysis: Combining ability analysis was used to estimate the GCA effects of the parental genotypes, and SCA effects of the specific cross combinations in F₁ and F₂ populations, which could guide the breeder in selecting the desirable parental genotypes and their F₁ and F₂ populations. Variance due to GCA (σ^2 GCA) is a measure of additive gene action, while variance due to SCA (σ^2 SCA) is measure of non-additive gene action. Combining ability studies showed that mean squares due to GCA and SCA were significant ($p \leq 0.01$) for majority of the traits in F₁ and F₂ populations and their parental genotypes. However, for flag leaf area and 1000-grain weight, the SCA mean squares were nonsignificant in F₁ generation (Table 4).

For yellow rust resistance, the GCA effects ranged from -1.59 to 3.86 and -6.45 to 4.42 in F₁ and F₂ generations, respectively (Table 5). For yellow rust resistance, four parental genotypes were observed with negative GCA effects while two genotypes were recorded with positive GCA effects in F₁ generation. In F₂ generation, two parental cultivars were observed with negative while four other genotypes with positive GCA effects. Among parental cultivars, maximum negative and significant GCA effects for yellow rust resistance were recorded for cultivar Shahkar-13 (-1.59) followed by Pirsabak-04 (-1.44) and Pirsabak-05 (-1.37) in F₁ generation. In F₂ generation, cultivar Shahkar-13 (-6.45) was again the leading genotype by having maximum negative and significant GCA effects followed by Pirsabak-05 (-3.72) for yellow rust resistance. Therefore, cultivar Shakar-13 proved to be the best general combiner by having maximum resistance to yellow rust in both the generations.

The SCA effects for yellow rust resistance ranged from -4.36 to 1.36 and -7.44 to 1.51 in F₁ and F₂ generations, respectively (Table 6). For yellow rust resistance, nine F₁ and eight F₂ populations revealed negative SCA effects while six F₁s and seven F₂s showed positive SCA effects. Among F₁ hybrids, Pirsabak-85 × Pirsabak-05 (-4.36) was the best specific combination whereas in F₂ populations, Saleem-2000 × Khyber-87 (-7.44) was the best specific population for yellow rust resistance by having maximum negative and significant SCA effects. Parental genotypes with positive × negative GCA effects were involved to produce promising F₁ hybrid i.e., Pirsabak-85 × Pirsabak-05 with maximum desirable negative SCA effects. Parental cultivars of cross combination Saleem-2000 (*Yr-18*) × Khyber-87 (*Yr-9+*) were having positive × positive GCA effects to produce F₂ populations with maximum negative and desirable SCA effects for yellow rust resistance. Variances due to σ^2 GCA were less than σ^2 SCA and ratios due to σ^2 GCA/ σ^2 SCA were also less than unity, presenting predominance of non-additive gene effect for yellow rust resistance in both the generations (Table 4).

Table 4. Mean squares of general and specific combing ability for various traits in 6 × 6 F₁ and F₂ half diallel crosses in wheat.

Variables	F ₁ /F ₂	Mean squares			Variance components		
		GCA	SCA	Error	Σ ² GCA	σ ² SCA	σ ² GCA/σ ² SCA
Yellow rust resistance	F ₁	43.08**	15.70**	0.04	5.38	15.66	0.34
	F ₂	142.67**	21.67**	0.97	17.72	20.69	0.86
Flag leaf area	F ₁	30.65**	4.27 ^{NS}	3.93	3.34	0.34	9.75
	F ₂	19.72**	5.86**	0.49	2.40	5.37	0.45
1000-grain weight	F ₁	8.86**	0.39 ^{NS}	0.53	1.04	-0.14	-7.20
	F ₂	90.35**	13.59**	2.68	10.96	10.92	1.00
Grain yield plant ⁻¹	F ₁	33.31**	15.76**	4.16	3.64	11.60	0.31
	F ₂	60.68**	13.99**	4.54	7.02	9.45	0.74

*, ** = Significant at p≤0.05 and p≤0.01, NS = Non-significant

Table 5. General combing ability effects of parental genotypes for various traits in 6 × 6 F₁ and F₂ half diallel crosses in wheat.

Parental genotypes	F ₁ /F ₂ generation	Yellow rust resistance	Flag leaf area	1000-grain weight	Grain yield plant ⁻¹
Pirsabak-85	F ₁	3.86**	-0.45	0.13	1.32
	F ₂	4.42**	-0.21	-3.07**	-2.75**
Pirsabak-04	F ₁	-1.44*	-1.19	-0.25	1.60**
	F ₂	2.48**	-0.03	-1.90**	-2.45**
Pirsabak-05	F ₁	-1.37**	3.92**	-1.81**	2.10**
	F ₂	-3.72**	1.84**	4.18**	2.78**
Shakar-13	F ₁	-1.59**	-0.28	0.25	-0.31
	F ₂	-6.45**	-0.42	3.57**	3.22**
Saleem-2000	F ₁	-1.36**	-1.21	-1.31**	-1.69*
	F ₂	2.81**	-2.60**	-3.55**	-2.12**
Khyber-87	F ₁	1.91**	-0.80	-0.63*	-3.03**
	F ₂	0.48	1.41**	0.76*	1.32
S.E. (gj)	F ₁	0.06	0.64	0.24	0.66
	F ₂	0.32	0.23	0.53	0.69

*, ** = Significant at p≤0.05 and p≤0.01, NS = Non-significant, S.E. (gj) = Standard error

Table 6. Specific combing ability effects in 6 × 6 F₁ and F₂ half diallel crosses for various traits in wheat.

F ₁ and F ₂ populations	Yellow rust resistance		Flag leaf area		1000-grain Weight		Grain yield plant ⁻¹	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
Pirsabak-85 × Pirsabak-04	-4.30**	-7.01**	2.65**	2.07**	0.05	4.80**	6.23**	4.37**
Pirsabak-85 × Pirsabak-05	-4.36**	0.92*	-1.13	-0.33	1.00**	-0.15	3.73**	0.74
Pirsabak-85 × Shahkar-13	-4.11**	-1.39**	1.98*	0.75*	0.05	1.71*	-2.36*	0.72
Pirsabak-85 × Saleem-2000	-4.22**	-1.82**	-0.2	1.39**	0.12	-2.98**	-2.48**	-3.05**
Pirsabak-85 × Khyber-87	-3.81**	-4.8**	-1.34	2.22**	-0.57	5.81**	-2.14*	6.83**
Pirsabak-04 × Pirsabak-05	0.94**	0.91*	-1.00	1.31**	-0.13	2.70**	-2.94**	3.52**
Pirsabak-04 × Shahkar-13	1.33**	0.25	-1.46	0.36	1.43**	-1.81**	0.77	-1.94*
Pirsabak-04 × Saleem-2000	1.36**	0.29	0.59	-0.09	-0.51	-0.80	1.74	-0.23
Pirsabak-04 × Khyber-87	-1.34**	-2.22**	-0.86	1.07**	-0.70*	-1.08	-1.72	-0.23
Pirsabak-05 × Shahkar-13	1.09**	0.67	1.42	2.56**	-0.13	1.36	1.97*	1.13
Pirsabak-05 × Saleem-2000	1.13**	1.29**	3.39**	0.79*	-0.07	2.60**	-0.26	2.03*
Pirsabak-05 × Khyber-87	-0.54**	1.51**	3.12**	-1.40**	-0.26	-5.18**	1.58	-3.12**
Shakar-13 × Saleem-2000	1.08**	-3.86**	0.50	0.95**	-0.51*	2.06**	6.56**	0.94
Shakar-13 × Khyber-87	-2.19**	-1.37**	1.09	3.48**	0.30	-1.07	4.49**	-1.79
Saleem-2000 × Khyber-87	-1.05**	-7.44**	0.70	1.28**	0.87*	6.16**	3.37**	6.20**
S.E. (ij)	0.08	0.42	0.84	0.29	0.31	0.69	0.86	0.90

*, ** = Significant at p≤0.05 and p≤0.01, NS = Non-significant, S.E. (ij) = Standard error

For flag leaf area, the GCA effects among parental cultivars ranged from -1.21 to 3.92 and -2.60 to 1.84 in F₁ and F₂ generations, respectively (Table 5). For flag leaf area, one parental cultivar in F₁ and two in F₂ generation showed positive GCA effects while five parental cultivars in F₁ and four in F₂ generation were observed with negative GCA effects. Among parental cultivars, for flag leaf area significant and maximum positive GCA effects were recorded for cultivar Pirsabak-05 (3.92, 1.84) in F₁ and F₂ generations, respectively and identified as best general combiner in both generations.

The SCA effects for flag leaf area ranged from -1.46 to 3.39 and -1.40 to 3.48 in F₁ and F₂ generations, respectively (Table 6). For flag leaf area, nine F₁s and twelve F₂s showed positive while six F₁ hybrids and three F₂ populations revealed negative SCA effects. Significant and maximum positive SCA effects were observed for cross combinations i.e. Pirsabak-05 × Saleem-2000 (3.39) and Shahkar-13 × Khyber-87 (3.48) in F₁ and F₂ generations, respectively and ranked as the best specific combinations for flag leaf area. In cross combination Pirsabak-05 × Saleem-2000 (3.39), the parental genotypes with high × low GCA effects were involved to produce F₁ hybrids with maximum SCA effects. However, low × high GCA parents were involved to produce F₂ population i.e., Shahkar-13 × Khyber-87 with highest positive SCA effects (3.48) for flag leaf area. Estimates of $\sigma^2\text{GCA}$ were greater than $\sigma^2\text{SCA}$ and ratio due to $\sigma^2\text{GCA}/\sigma^2\text{SCA}$ was more than unity indicating additive type of gene action for flag leaf area in F₁ generation (Table 4). Variances due to GCA and SCA and ratio of $\sigma^2\text{GCA}/\sigma^2\text{SCA}$ suggested non-additive gene effects for flag leaf area in F₂ generation.

For 1000-grain weight, the GCA effects for parental cultivars varied from -1.31 to 1.81 and -3.55 to 4.18 in F₁ and F₂ generations, respectively (Table 5). Three each parental genotypes showed positive and negative GCA effects for 1000-grain weight in both generations. Maximum positive and significant GCA effects (1.81, 4.18) were recorded for parental cultivar Pirsabak-05 in F₁ and F₂ generations, respectively and ranked as best general combiner for 1000-grain weight in both generations.

Specific combining ability effects for 1000-grain weight ranged from -0.70 to 1.43 among F₁ hybrids and -5.18 to 6.16 among F₂ populations (Table 6). Seven F₁ hybrids were noted with positive and eight with negative SCA effects. Eight F₂ populations were observed with positive and seven with negative SCA effects. The highest positive and significant SCA effects (1.43) were found for F₁ hybrid Pirsabak-04 × Shahkar-13 in F₁ generation. In F₂ generation, F₂ population Saleem-2000 × Khyber-87 revealed significant and maximum positive SCA effects (6.16). Parental cultivars with low × high GCA effects were involved to produce best specific combination i.e., Pirsabak-04 × Shahkar-13 for 1000-grain weight with maximum SCA effects in F₁ generation. Similarly, in F₂ generation, low × high GCA genotypes played an important role in production of best specific combination i.e., Saleem-2000 × Khyber-87 for 1000-grain weight. Variances due to $\sigma^2\text{GCA}$ were greater than $\sigma^2\text{SCA}$ and ratio due to $\sigma^2\text{GCA}/\sigma^2\text{SCA}$ was also greater than one which suggested that 1000-grain weight was under influence of additive type of gene action in both the generations (Table 4).

For grain yield per plant, the GCA effects ranged from -3.03 to 2.10 and -2.75 to 3.22 in F₁ and F₂ generations, respectively (Table 5). Three each parental genotypes were having positive GCA effects in F₁ and F₂ generations, while with same pattern, three each parental varieties showed negative GCA effects in both generations. Among parental cultivars, for grain yield maximum positive and significant GCA effects (1.81, 4.18) were observed for cultivars Pirsabak-05 and Shahkar-13 in F₁ and F₂ generations, respectively which suggested being best general combiners for grain yield in both generations.

For grain yield, the SCA effects ranged from -2.94 to 6.56 and -3.12 to 6.83 in F₁ and F₂ generations, respectively (Table 6). Nine each F₁ and F₂ cross combinations revealed positive while six each F₁ and F₂ populations showed negative SCA effects for grain yield. Significant and highest positive SCA effects (6.56, 6.83) were recorded for Shahkar-13 × Saleem-2000 and Pirsabak-85 × Khyber-87 for grain yield per plant in F₁ and F₂ generations, respectively. The cross combination Shahkar-13 × Saleem-2000 was having parental genotypes with low × low GCA effects to produce F₁ hybrid with maximum SCA effects. However, parental cultivars of the cross combination Pirsabak-85 × Khyber-87 were low × high general combiners to produce F₂ population with maximum positive SCA effects for grain yield per plant. Variances due to $\sigma^2\text{GCA}$ were lesser than $\sigma^2\text{SCA}$ and ratios due to $\sigma^2\text{GCA}/\sigma^2\text{SCA}$ were also less than unity indicating non-additive gene effects for grain yield per plant in both generations (Table 4).

Discussion

Genotypes revealed highly significant differences for yellow rust resistance, flag leaf area and yield traits. This indicated greater genetic variability among the genotypes for the studied traits which can be exploited for the development of high yielding wheat hybrids. Mean squares due to GCA and SCA were also highly significant which validated the diallel analysis in the said breeding material. Mean squares of the genotypes and due to GCA and SCA were found highly significant for all the traits in F₁ and F₂ wheat populations (Verma *et al.*, 2016; Mandal & Madhuri, 2016; Saeed & Khalil, 2017; Kandil *et al.*, 2016).

In both generations, cultivars Pirsabak-05 and Shahkar-13 showed more resistance to yellow rust with minimum ACI values while Pirsabak-85 with greater ACI values ranked as the most susceptible genotype among parental cultivars. Cultivars Saleem-2000 (*Yr18*) and Khyber-87 (*Yr9+*) individually showed high susceptibility. However, their F₂ progeny (Saleem-2000 × Khyber-87) showed resistance to prevailing yellow rust races which might be due to accumulation of some resistance genes or combined effect of both parents with *Yr* genes. Majority of Pakistani bread wheat cultivars were protected against stripe rust by incorporating the *Yr* genes like, *YrA*, *Yr2*, *Yr4*, *Yr6*, *Yr7*, *Yr18*, *Yr9*, *Yr22* and *Yr27*; however, the genes i.e., *Yr6*, *Yr7* and *Yr9* are occurring more frequently either in combination with other *Yr* genes or alone (Qamar *et al.*, 2011). The virulence for resistant genes i.e., *YrA*, *Yr2*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr17*, *Yr27* and gene combinations was reported in Mexican wheat cultivars Opata (*Yr27 + Yr18*) and Super Kauz (*Yr9*, *Yr27*

and *Yr18*) under natural conditions over four locations with variable environments (Bux *et al.*, 2011, 2012). In F_2 populations, low ACI was mostly observed in genotypes having one of the resistant cultivars i.e., Pirsabak-05 and Shahkar-13 in their parentage.

Flag leaf area play a key role in yield of wheat during spike development, as flag leaf provide photosynthates for grain yield (Ahmad *et al.*, 2013). Finding of this study revealed that genotypes with larger flag leaf area produced more grain yield in both generations. Positive correlation was reported between flag leaf area and yield, indicating that flag leaf area might be a useful parameter for selection of high yielding plants (Zeuli & Qualset, 1990). However, crosses among durum wheat genotypes showed that the size of flag leaf was not associated with grain yield (Grignac, 1974). Non-significant mean differences were observed for flag leaf area and grain yield among wheat cultivars (Malik *et al.*, 2005; Rahim *et al.*, 2006). Results revealed that the genotypes with maximum 1000-grain weight had high grain yield in both generations. Cultivar Pirsabak-05 in F_1 generation and cross combination Pirsabak-05 \times Shahkar-13 in F_2 generation with maximum 1000-grain weight produced maximum grain yield. Similarly, grains with higher 1000-grain weight have better milling quality and ensure better emergence (Protic *et al.*, 2007). Akram *et al.* (2008) also reported that grain yield was positively correlated with 1000-grain weight.

Results revealed that F_1 hybrid (Pirsabak-85 \times Pirsabak-04), F_2 population (Pirsabak-05 \times Shahkar-13) and cultivars (Pirsabak-2005, Shahkar-13) with highest grain yield were due to their better adaptability and resistance to biotic stress i.e., yellow rust. Past studies revealed that a cultivar grown in diverse environmental conditions had shown better adaptability with low degree of fluctuation in grain yield (Amin *et al.*, 2005). Several researchers recorded significant differences among parental cultivars and F_1 hybrids for grain yield in bread wheat (Adel & Ali, 2013; Fellahi *et al.*, 2013, 2015).

Parental cultivars of cross combination Saleem-2000 (*Yr-18*) \times Khyber-87 (*Yr-9+*) were with positive \times positive GCA effects to produce F_2 populations with maximum negative and desirable SCA effects for yellow rust resistance. Parental genotypes with high GCA effects produced hybrid with low SCA effects which might be due to the absence of complementation of the parent's genes (Kumari *et al.*, 2015). Variances due to GCA were less than SCA and their ratios were also less than unity, presenting non-additive gene effect for yellow rust resistance in F_1 and F_2 populations. Past studies revealed that parental genotype (MV-17) with low GCA effects for latent period, infection type, pustule size and number of pustules was identified as suitable parent to be used in breeding programs for development of yellow rust resistance lines (Khodarahmi *et al.*, 2009). Significant GCA and SCA effects were reported for four yellow rust resistance components (latent period, infection type, pustule density and size) in bread wheat and suggested additive and non-additive effects in genetic control of yellow rust resistance (Khodarahmi *et al.*, 2014). Significant GCA and SCA effects suggested the involvement of additive and non-additive gene action for terminal yellow rust severity and area under disease progress curve (Kaur *et al.*, 2003).

In cross combination Pirsabak-05 \times Saleem-2000, parental genotypes with high \times low GCA effects were involved in production of F_1 hybrids with maximum SCA effects for flag leaf area. However, low \times high GCA parents were involved to produce F_2 population Shahkar-13 \times Khyber-87 (3.48) with highest positive SCA effects for flag leaf area. F_1 hybrid with maximum SCA effects for flag leaf area were noted with high \times low GCA parents in bread wheat (Dere, 2006). The crosses involving parents with high \times medium, medium \times medium and medium \times low general combiners, indicated non-additive type of gene actions in specific cross combinations in wheat (Singh *et al.*, 2012). Ratio due to GCA and SCA variances was more than unity indicating additive gene effect for flag leaf area in F_1 generation. However, in F_2 generation the said ratio was less than one showing non-additive gene effects for flag leaf area. Greater role of additive genes in genetic regulation of flag leaf area illustrated that genetic efficiency of selection was greater for increasing flag leaf area particularly in early generations in wheat (Golparvar, 2013). Parental cultivars with high GCA effects produced hybrids with low SCA effects which might be due to absence of complementary genes in parental genotypes (Kumari *et al.*, 2015).

Parental cultivars with low \times high GCA effects were involved to produce best specific combination i.e., Pirsabak-04 \times Shahkar-13 with maximum SCA effects for 1000-grain weight in F_1 generation. Similarly, in F_2 generation, low \times high general combiners played an important role in production of best specific combination i.e., Saleem-2000 \times Khyber-87 for 1000-grain weight. The low \times high and high \times low GCA crosses, besides exhibiting the favorable additive GCA effects of the parental genotypes, complement the epistatic effects present in the crosses, which would finally result in higher SCA effects. Significant GCA and SCA effects were observed for 1000-grain weight and grain yield in wheat, and were seen to be initiated from genotypes having high \times high, high \times low, medium \times low and low \times low GCA effects (Kamaluddin *et al.*, 2007). Present results revealed that ratios due to GCA and SCA variances were greater than one, which suggested that 1000-grain weight was controlled by additive type of gene action in both generations. Predominance of non-additive gene effects were observed for 1000-grain weight and other yield traits in wheat (Seboka *et al.*, 2009; Majeed *et al.*, 2011), however, Chandrashekhar & Kerketta (2004) reported additive type of gene action for yield traits in wheat.

The cross combination Shahkar-13 \times Saleem-2000 was having parental genotypes with low \times low GCA effects to produce F_1 hybrid with maximum SCA effects for grain yield. However, parental cultivars of the cross combination Pirsabak-85 \times Khyber-87 were low \times high general combiners to produce F_2 segregants with maximum positive SCA effects for grain yield. The F_1 hybrids demonstrating higher SCA effects for grain yield were observed to be derived from wheat genotypes having high \times high, high \times low, low \times low and medium \times low general combiners (Kamaluddin *et al.*, 2007). Results further revealed that the ratios due to GCA and SCA variances were less than unity indicating non-additive gene effect for grain yield in both generations. Similarly,

non-additive gene effects were exhibited for grain yield, suggesting possibility for improvement of this trait through transgressive segregates and heterosis breeding for developing genotypes with greater yield potential (Sanjeev *et al.*, 2005). However, additive type of gene action was observed for grain yield in bread wheat genotypes (Arshad & Chowdry, 2002).

Conclusion

Significant ($p \leq 0.01$) differences were observed among the genotypes for all the traits. Mean squares due to general and specific combining ability were significant ($p \leq 0.01$) for majority of the traits in both generations. The SCA variances were greater than GCA for majority of the traits, and non-additive type of gene action controlled the inheritance of these traits in both generations. Based on GCA effects, cultivars Pirsabak-05 and Shahkar-13 were considered to be the best general combiners for yellow rust resistance and grain yield in F_1 and F_2 generations, respectively. The F_1 hybrid Pirsabak-85 \times Pirsabak-04 and F_2 population Pirsabak-05 \times Shahkar-13 performed better for majority of the traits which could be further exploited for improvement in yellow rust resistance and grain yield.

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