Full Length Article

Genetic Characterization of Stripe Rust and Yield Traits in Bread Wheat

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Abstract

The insight into the nature of gene action, involved in the expression of a trait of interest, is essential to a plant breeder for deploying a judicious breeding program. The objective of this study was to study the inheritance (additive vs. dominance) of stripe rust resistance and yield traits in wheat through diallel analysis. Six wheat cultivars, i.e., Pirsaabak-85, Khyber-87, Saleem-2000, Pirsaabak-04, Pirsaabak-05 and Shahkar-13 were crossed in a half diallel fashion during 2014-2015, and advanced to F2 generation during 2015-2016. Parental genotypes along with their F1 and F2 populations were evaluated during 2016-2017 through randomized complete block design with three replications. Genotypes differed significantly (p ≤ 0.01) for all the traits in F1 and F2 generations. Additive-dominance model was partially adequate for resistance to stripe rust and yield-related traits. Greater values of additive (D) than dominance (H1, H2) components of genetic variance, average degree of dominance and Vr/ Wr graphs revealed that stripe rust resistance and yield traits were primarily controlled by additive gene action except for grain yield in F1 and area of flag leaf in the F2 generation which governed by overdominance. In loci, unequal proportions of positive (H1) and negative (H2) alleles revealed the asymmetrical distribution of genes in parental genotypes for stripe rust resistance and yield traits. The preponderance of additive gene action suggested that selection could be made in early segregating generations for improving resistance against stripe rust to enhance wheat yield. © 2019 Friends Science Publishers

Keywords: Diallel cross; Gene action; Genetic variance; Heritability; Stripe rust; Yield traits

Introduction

Wheat (Triticum aestivum L.) is one of the dominant crops and serves as a major source of staple food worldwide. In Pakistan, it contributes about 9.1% to the value added in agriculture and 1.7% to the gross domestic product (GDP) (ESP, 2017-2018). During 2016-2017, wheat was grown on an area of 8.73 million hectares, which produced 25.49 million tons of grains with average yield of 2919 kg ha⁻¹ in Pakistan (PBS, 2017-2018). Nevertheless, our national yields are still far below by comparing with other countries like USA, China and even with our immediate neighbor – India (Ahmed, 2015). Late planting, weeds infestation, drought stress, imbalance use of fertilizers and disease epidemics etc., are among the major reasons of low average yield (Hussain et al., 2012a, 2016a; Shahzad et al., 2016; Afridi et al., 2017b).

Food security risks increased due to current circumstances of climatic revolution and its impact on some susceptible crops like wheat. However, during this year, shortfall in wheat production is attributed to decline in area sown, less and uneven rainfall, delayed and lengthy sugarcane crushing season, delayed harvesting of rice fine cultivars, acute water shortages and heat stress (ESP, 2017-2018; PBS, 2017-2018). During past half decade, the incidence of rainfall amplified during peak growth stage of wheat which made climate conducive for occurrence of different diseases i.e., stripe rust, fusarium head blight, powdery mildew, black point (kernel smudge) and Karnal bunt (Tilletia indica). Stripe rust (Puccinia striiformis f. spp. tritici) mainly expands in moist and cool weather conditions (Afridi et al., 2017b). Theurediospores of the said fungus are lengthened and lay down in linear rows between leaf veins and it produces black teliospores in late season (Chen et al., 2014).

During 2017, most important disease of wheat was stripe rust, following a trend of recent years (Hollandbeck et al., 2017; Waqar et al., 2018). Percent yield loss during 2017 was 8.6%, which was lower than 2016 (9.1%) and 2015 (15.4%) but still well above the last 05, 10 and 20-year averages (6.63, 4.92 and 3.77%, respectively). The continued slight decrease in yield loss due to stripe rust might be due to continued foliar spray of fungicide used by growers in response to the very high yield losses occurred during 2015. This may have managed to keep the fungus at bay and minimize losses for a second year in a row.
In Pakistan, during mid 1990s severe epidemics have been caused by *Puccinia striiformis* causing economic losses in wheat cultivars Pirsaabak-85 and Pak-81 which were grown on a larger area in Khyber Pakhtunkhwa, Pakistan (Afridi *et al*., 2017b). The rust resistance of these cultivars was overcome by a new race during 1994-1995 and caused rust epidemic in this province, with 40% losses in grain yield (Morgounov *et al*., 2004; Afzal *et al*., 2007). Wheat cultivars Pirsaabak-85 and Pak-81 were replaced by cultivar Inqalab-91 and cultivated on 80% of the area, posing a high-risk crop loss due to new races of stripe rust (Afridi *et al*., 2017a, b). Development of new rust races (stripe rust) and favorable environmental conditions played a key role in rust epidemics during 2004-2005 and caused yield losses up to 70% especially in Inqalab-91 sown areas (Ahmad *et al*., 2006).

Wide range of variation in wheat lines response to stripe rust proposed the development of new wheat cultivars with durable rust resistance and high grain yield (Chen, 2013). To control stripe rust of wheat, the only option is to develop disease resistant cultivars through cost-effective, environment friendly, efficient and sustainable approach (Paillard *et al*., 2012; Afridi *et al*., 2017b). However, a resistant cultivar does not remain resistant for a longer period (De-Vallavieille-Pope *et al*., 2012). Wheat cultivars with a uniform genetic background of rust resistance put severe selection pressure on the pathogen and therefore, new pathotypes of stripe rust develop which break the resistance of cultivars (Chen *et al*., 2014). A resistant cultivar is at 'Boom' when it produced more yield and 'bust' when the resistance is broken down after few years of release and severely reduced grain yield (Farahani *et al*., 2014).

For developing wheat genotypes with good yield potential, it is crucial to study the genetic architecture of distinct wheat populations, legacy configuration of yield attributing traits and correlation of yield with yield contributing traits under present environmental conditions. Bolder wheat grains with high 1000-grain weight have better quality traits and ensure healthier germination during sowing (Afridi *et al*., 2017b).

Different biometrical approaches like diallel and line × tester analyses are designed by Hayman (1954a, b), Griffling (1956) and Kempthorne (1957) for genetic analysis of various traits in different crops. Based on diallel analysis, the nature of gene action has been reported in several studies (Cheruiyot *et al*., 2014; Farahani *et al*., 2014; Afridi, 2016; Afridi *et al*., 2017a, b; Ahmed *et al*., 2017, 2018; Würschum *et al*., 2018), however most of the times the results remained discordant. Hence, the present study was designed with the aim to study the inheritance of stripe rust resistance and yield traits in wheat.

**Materials and Methods**

**Experimental Site and Crop Seasons**

The said study was carried out during three consecutive growing seasons i.e., 2014-2015, 2015-2016 and 2016-2017 at Cereal Crops Research Institute (CCRI), Pirsaabak - Nowshera, Pakistan.

**Breeding Material and Procedure**

The breeding material comprised of three diverse bread wheat cultivars for earliness and yield traits i.e., Pirsaabak-85, Khyber-87, Saleem-2000, Pirsaabak-04, Pirsaabak-05 and Shahkar-13 (Table 1). These six wheat cultivars were crossed in a half-diallel fashion to develop 15 F1 hybrids during 2014-2015. During 2015-2016, the F1 hybrids were sown and selfed to advance the generation. During 2016-2017, parental cultivars and F1 hybrids with two replications, and parental cultivars + F2 populations with three replications were grown in a randomized complete block design (RCBD) in same field. The sub-plot size was 3 × 0.9 m².

**Crop Husbandry**

Before sowing the file was well irrigated to create conditions conducive for seedbed preparation. The field was ploughed with deep plough then harrowed with planking each time to make the soil loose, fine, leveled and pulverized. The fertilizer was applied at the rate of 120:90:60 kg ha⁻¹ of NPK, respectively. All P₂O₅, K₂O and half N were applied at sowing time and the remaining half N was applied in two split doses with first and second irrigations. Sowing was carried out during 2nd week of November. In F1 generation, single seed per hill was planted while in F2 populations and parental genotypes the seed rate was maintained as 120 kg ha⁻¹ (25.5 g per sub-plot). Overall, four irrigations have been given to the crop every year. The dominant weeds were *Avena fatua*, *Chenopodium album*, *Chenopodium murale*, *Convolvulus arvensis*, *Cynodon dactylon*, *Malva parviflora*, *Melilotus indica*, *Medicago denticulata*, *Phalaris minor* and *Rumex dentatus*. The broad and narrow-leaved weeds were controlled with Buctril Super (750 mL ha⁻¹) and Puma Super (1250 mL ha⁻¹), respectively, however, the left over weed plants were removed manually. The randomly selected plants were harvested on single plant basis and used for data recording separately after threshing.

**Data Collection**

**Scoring of stripe rust:** To create inoculum pressure of *Puccinia striiformis* f. sp. *tritici* (PST), the wheat cultivar ‘Morocco’ which is highly susceptible to all races of rusts, was grown in two spreader rows around the experimental material. For artificial inoculation the spores of stripe rust were collected from cultivar Morocco and the suspension of urediospores was made in sterile distilled water with 2-3 drops of tween-20. In the evening time and at the booting stage of crop, the suspension of 0.1 g spore in 1-1 water was sprayed with hand sprayer to uniformly inoculate the parental genotypes, and F1 and F2 populations.
Table 1: Parental genotypes with local names, parentage, origin, Yr genes and yield traits

<table>
<thead>
<tr>
<th>Parental cultivars</th>
<th>Pedigree</th>
<th>Resistance to Yr*</th>
<th>Yr genes**</th>
<th>Plant Color$</th>
<th>Grains spike's</th>
<th>Potential yield (kg ha') €</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pirsaabak-85</td>
<td>KVV/BSUH/KAL/BB (CIMMYT)</td>
<td>Susceptible</td>
<td>Yr7, Yr9</td>
<td>Green</td>
<td>73</td>
<td>6000</td>
</tr>
<tr>
<td>Pirsaabak-04</td>
<td>KAUZSTAR (CIMMYT)</td>
<td>Moderately Susceptible</td>
<td>Yr18</td>
<td>Waxy green</td>
<td>75</td>
<td>6000</td>
</tr>
<tr>
<td>Pirsaabok-05</td>
<td>MUNIA/SHTO/AMSEL (CIMMYT)</td>
<td>Resistant</td>
<td>-</td>
<td>Dark green</td>
<td>63</td>
<td>5500</td>
</tr>
<tr>
<td>Shakkar-13</td>
<td>CMH84.339/C9M7H8.578/MILAN (CIMMYT)</td>
<td>Resistant</td>
<td>Yr17</td>
<td>Waxy green</td>
<td>69</td>
<td>5500</td>
</tr>
<tr>
<td>Saleem-2000</td>
<td>CHAM-6/KITE/PGO (CIMMYT)</td>
<td>Moderately Susceptible</td>
<td>Yr18</td>
<td>Waxy green</td>
<td>64</td>
<td>6000</td>
</tr>
<tr>
<td>Khyber-87</td>
<td>KVV/TRM/PTM/ANA-CM 4390 (CIMMYT)</td>
<td>Susceptible</td>
<td>Yr9+</td>
<td>Green</td>
<td>71</td>
<td>4500</td>
</tr>
</tbody>
</table>

CIMMYT: International Maize and Wheat Improvement Center

* Cultivars Pirsaabok-05 and Shakkar-2013 are rusts resistant cultivars while Pirsaabak-85, Khyber-87, Saleem-2000 and Pirsaabok-04 are rust susceptible genotypes. Crop Disease Research Institute NARC, 2014-15, 2015-16


¥ Afridi, K., 2016. Inheritance of yellow rust resistance and glutenin content in wheat. Ph.D Dissertation, Department of Plant Breeding and Genetics, The University of Agriculture, Peshawar – Pakistan

$ Phenotypic observations

€ Respective varietal proposal

The data on stripe rust was documented on flag leaves at the peak stage of epidemic development of rust on the leaves following modified Cobb’s scale (Ali et al., 2014) while host response was recorded according to Cheruiyot et al. (2014) (Table 2).

Yield Traits

The area of flag leaf, 1000-grain weight and grain yield was recorded using randomly selected 10 plants in F1 hybrids and 20 plants in F2 populations and parental genotypes. Area on flag leaf was determined at post-anthesis stage (Francis et al., 1969). All the individual plants were thinned with single plant thrasher. A descriptive sample of 1000 grains was used in each entry/replication and weighed with an electric balance to record the 1000-grain weight. By weighing the grains of 10 plants in F1 hybrids and 20 plants in F2 populations and parental cultivars in each genotype/replication, and then averaged for getting grain yield per plant.

Biometrical Analyses

Collected data were subjected to analysis of variance (ANOVA) according to Steel et al. (1997). After getting significant mean differences, the diallel analysis was further carried out (Hayman, 1954a, b; Mather and Jinks, 1982; Singh and Chaudhary, 1985). In F2 populations, the formulae were modified to calculate the components of genetic variance as proposed by Verhaelen and Murray (1969).

Results

Mean differences among parental genotypes and their F1 and F2 populations for stripe rust resistance, area of flag leaf, 1000-grain weight, and grain yield were significant (p<0.01) (Table 3). Adequacy of the additive-dominance model was tested through three scaling tests (t² test, regression, and arrays analysis), and the model was found partially adequate for all the traits in both generations (Table 4). Results pertaining to genetic analysis for studied traits are provided as follows.

### Table 2: Scale for scoring of data on stripe rust

<table>
<thead>
<tr>
<th>Host response</th>
<th>Abbreviated sign</th>
<th>Host reaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immune</td>
<td>T</td>
<td>0.0</td>
</tr>
<tr>
<td>Traces</td>
<td>T</td>
<td>0.1</td>
</tr>
<tr>
<td>Resistant</td>
<td>R</td>
<td>0.2</td>
</tr>
<tr>
<td>Resistant to moderately resistant</td>
<td>RMR</td>
<td>0.3</td>
</tr>
<tr>
<td>Moderately resistant</td>
<td>MR</td>
<td>0.4</td>
</tr>
<tr>
<td>Moderately resistant to moderately susceptible</td>
<td>M</td>
<td>0.6</td>
</tr>
<tr>
<td>Moderately susceptible</td>
<td>MS</td>
<td>0.8</td>
</tr>
<tr>
<td>Moderately susceptible to susceptible</td>
<td>MSS</td>
<td>0.9</td>
</tr>
<tr>
<td>Susceptible</td>
<td>S</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Coefficient of infection (C.I) = Severity × Value of host reaction, Severity (%): 0-100 (Cheruiyot et al., 2014)

### Table 3: Mean square for various traits in 6 × 6 F1 and F2 half diallel crosses of wheat

<table>
<thead>
<tr>
<th>Variables</th>
<th>F1/F2</th>
<th>Mean squares</th>
<th>CV%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genotypes</td>
<td>Parents</td>
<td>F1 × F2</td>
<td>Parents vs. Error</td>
</tr>
<tr>
<td>d.f.</td>
<td>F1</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>F1</td>
<td>20</td>
<td>5</td>
<td>14</td>
</tr>
<tr>
<td>Stripe rust F1</td>
<td>45.09**</td>
<td>140.33**</td>
<td>2.26**</td>
</tr>
<tr>
<td>resistance F1</td>
<td>155.77**</td>
<td>379.11**</td>
<td>58.01**</td>
</tr>
<tr>
<td>Area of flag F1</td>
<td>21.74*</td>
<td>22.67*</td>
<td>19.97*</td>
</tr>
<tr>
<td>leaf F1</td>
<td>27.97**</td>
<td>33.59**</td>
<td>14.47**</td>
</tr>
<tr>
<td>1000-grain F1</td>
<td>5.01**</td>
<td>7.88**</td>
<td>4.32**</td>
</tr>
<tr>
<td>weight F1</td>
<td>98.34**</td>
<td>193.95**</td>
<td>61.24**</td>
</tr>
<tr>
<td>Grain yield F1</td>
<td>40.29**</td>
<td>51.95**</td>
<td>27.53**</td>
</tr>
<tr>
<td>plant1 F1</td>
<td>76.98**</td>
<td>140.50**</td>
<td>46.78**</td>
</tr>
</tbody>
</table>

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

### Stripe Rust Resistance

For stripe rust resistance, significant (p≤0.01) values of genetic components i.e., ‘a’ and ‘b’ suggested the key role of additive and non-additive genes in both generations (Table 5). Significant (p≤0.01) values of ‘b1’ specified the occurrence of directional genes in the F1 and F2 generations. Significant (p≤0.01) values of ‘b2’ indicated asymmetrical gene distribution among the parental cultivars in both generations. Specific gene effects were found in F2 due to significant (p≤0.01) value of ‘b1’ whereas in F1 generation no specific gene effects were observed due its non-significant value.
The scattered positions of generations and revealed that dominant genes were acting in both generations. The values of $h^2$ authenticated by the ratios of dominant and recessive genes (0.15, 0.18). Positive $F$ values indicated the important role of dominant genes in both generations and the same was also authenticated by the ratios of dominant and recessive genes (4.17, 1.58) in the parental cultivars for stripe rust resistance in both generations. The values of $h^2$ were positive in both generations and revealed that dominant genes were acting mostly towards the susceptibility. Significant positive values of the environmental component in both generations illustrated the primary role of environment in the inheritance of said trait. Broad-sense heritability values (0.99, 0.98) were greater than narrow sense (0.38, 0.65) in $F_1$ and $F_2$ generations, respectively (Table 6). High broad-sense heritability estimates demonstrating less effect of environment on the expression of stripe rust resistance. However, narrow-sense heritability for stripe rust resistance was moderately high indicating that additive effects of genes were essential in the inheritance of said trait in $F_2$ generation.

The $\overline{Vr}$ graphs revealed that regression line intercepted the covariance line above the origin, which revealed partial dominance type of gene action in both generations (Fig. 1a, b). The scattered positions of cultivars on regression line illustrated that cultivars Pirsabak-04, Pirsabak-05, Shahkar-13 and Saleem-2000 had maximum dominant genes, whereas Pirsabak-85 had...
maximum recessive genes in F₁ generation. In the F₂ generation, parental genotype Shahkar-13 had maximum dominant while cultivar Saleem-2000 had maximum recessive genes to govern the inheritance of stripe rust resistance.

**Area of flag leaf**

The component 'a' was significant (p≤0.01) while 'b' was non-significant in F₁ generation whereas both components (a, b) were significant (p<0.01) for area of flag leaf in F₂ populations (Table 5). Hence, both additive and non-additive genetic components were important in the inheritance of area of flag leaf in segregating generation. Significant 'b₁' component specified directional dominance in F₁ (p≤0.05) and F₂ (p≤0.01) populations. However, non-significant 'b₂' component showed symmetrical gene distribution among parents in F₁ generation. Asymmetrical gene distribution was observed in F₂ generation due to significant 'b₂' (p≤0.05) component. Significant (p≤0.01) value of 'b₁' demonstrated the residual dominance effects for area of flag leaf in the F₂ generation, which indicated the involvement of dominance deviation.

All the components of genetic variation (D, H₁, H₂ and F) were non-significant whereas E was significant for area of flag leaf in the F₁ generation (Table 6). The average degree of dominance was less than unity (0.83), which confirmed that area of flag leaf was controlled by the additive type of gene action in the F₁ generation. The F value was negative for area of flag leaf, which suggested that greater number of recessive alleles were owned by the parental genotypes in the F₁ generation, and it was also authenticated by the ratio of dominant and recessive genes in the parental lines (0.105). In the F₂ populations, the components of genetic variance displayed that D, H₁, H₂, b₂ and E were significant for area of flag leaf (Table 5). Equally additive and non-additive components of genetic variance were crucial for legacy of the trait under study. However, the value of H₁ was greater than D component in F₂ population which revealed that area of flag leaf was controlled by non-additive gene action in the F₂ generation. The average degree of dominance for area of flag leaf was greater than unity, which suggested that the character was regulated by over-dominance type of gene action in the F₂ generation. The value of F was non-significant but positive for area of flag leaf, which proposed that greater number of dominant alleles were carried by the parental genotypes in the F₂ generation.
and it was also supported by the ratio of dominant and recessive genes in the parental cultivars (1.09). Unequal $H_1$ and $H_2$ components and the ratios of $H_2/4H_1$ (0.29, 0.23) exhibited an asymmetrical distribution of positive and negative genes among the parental cultivars for area of flag leaf in both generations. Results further revealed that additive and non-additive gene actions played a key role in genetic regulation of this character. Broad-sense heritability values (0.70, 0.95) were comparatively high than narrow-sense heritability (0.60, 0.53) in $F_1$ and $F_2$ generations, respectively (Table 6). Greater broad sense heritability than narrow-sense, showed the primary role of genetic variance as compared to environmental variance.

According to $Vr$-$Wr$ graph, the regression line cut off the $Wr$-axis above the point of origin and partial dominance gene action was responsible for controlling area of flag leaf in the $F_1$ generation (Fig. 2a). However, in the $F_2$ generation the inheritance of area of flag leaf was controlled by the over-dominance type of gene action as regression line touched the $y$-axis below the point of origin (Fig. 2b). The relative distribution of cultivars along the regression line revealed that $Pirsabak-05$ had maximum dominant genes and resides closer to the origin in both generations. Cultivars Saleem-2000 and Shakar-13 had a maximum number of recessive genes in $F_1$ and $F_2$ generations, respectively as both of these cultivars were farthest from the origin.

**Yield Traits**

Significant ($p\leq0.01$) mean squares were observed for component 'a' in both generations however, the value of component 'b' was non-significant and significant ($p\leq0.01$) in the $F_1$ and $F_2$ generations, respectively for 1000-grain weight (Table 5). Hence, additive and dominant components of genetic variance were imperative for inheritance of the studied trait. Additive component was significant whereas all other components were non-significant for 1000-grain weight in the $F_1$ generation (Table 6). In $F_2$ generation, all the genetic components were significant except 'F' which was non-significant. Additive component was larger than dominance components in both generations which revealed that 1000-grain weight was managed by additive gene action. Average degrees of dominance were less than unity (0.31, 0.84) for 1000-grain weight in both generations. Unequal $H_1$ and $H_2$ components and the ratios of $H_2/4H_1$ (0.42, 0.24)
exhibited the asymmetrical distribution of positive and negative genes among the parental genotypes for 1000-grain weight in F1 and F2 populations, respectively. In F1 and F2 generations, h2 and F values were negative and positive, showing more recessive and dominant genes, respectively. High broad (0.83, 0.92) and narrow-sense (0.78, 0.60) heritability values were recorded for 1000-grain weight in F1 and F2 generations, respectively (Table 6). Inheritance pattern for 1000-grain weight seemed to be of partial dominance, as the regression line cut off the Wr-axis above the point of origin in both generations (Fig. 3a, b). Cultivar Khyber-87 was near the point of origin and possessed maximum dominant genes in both generations. Parental cultivars i.e., Pirsabak-85 and Pirsabak-05 reside far away from the point of origin and possessed maximum recessive genes in F1 and F2 generations, respectively.

Significant (p≤0.01) components i.e., ‘a' and ‘b' were recorded for grain yield per plant which showed the involvement of additive and non-additive gene action in both generations (Table 5). Majority of the components of genetic variation were significant for grain yield in F1 and F2 populations (Table 6). The values of dominance components were greater than additive in the F1 generation which revealed non-additive gene action in genetic control of grain yield per plant. However, the F2 generation specified the greater role of the additive gene action. The values for average degree of dominance was greater (1.45) in F1 and lesser (0.98) in F2 than unity indicated the over-dominance type and additive type gene action, respectively. The value of h2 was significant in F1 and non-significant in F2 populations, supporting the dominant gene action in F1 and additive gene action in F2 generation. Broad-sense heritability values (0.80, 0.83) were greater than narrow-sense (0.30, 0.47) for grain yield in F1 and F2 populations (Table 6). In Vr-Wr graphical analysis, the regression line cut off the Wr-axis below the point of origin which revealed the over-dominance type of gene action for grain yield per plant in the F1 generation (Fig. 4a). In the F2 generation, the regression line intercepted Wr-axis above the origin, suggesting the additive type of gene action for grain yield per plant (Fig. 4b). Cultivars Pirsabak-05 and Pirsabak-85 had the most dominant and recessive genes, respectively in both generations.

Results of the study revealed that additive type of gene action played a major role in controlling stripe rust resistance, area of flag leaf, 1000-grain weight and grain yield in both generations except grain yield in F1 and area of flag leaf in F2 populations. Therefore, these traits could be improved through selection in early segregating generations.

Discussion

Parental genotypes and their F1 and F2 populations possessed greater genetic variability by having significant differences for all the traits. Additive-dominance model was partially adequate for all the traits including stripe rust resistance in both generations. Past studies revealed partial adequacy for area of flag leaf, 1000-grain weight and grain yield (Ahmad et al., 2016) and grains per spike (Nazir et al., 2014) in wheat. However, the additive-dominance model was fully adequate for area of flag leaf and yield traits (Nazir et al., 2014), stem rust and yield traits (Cheruiyot et al., 2014) in different wheat populations.

For stripe rust resistance, significance of genetic components suggested the key role of the additive and non-additive genes in both generations. However, additive component and average degrees of dominance suggested additive type of gene action in both generations. Therefore, desirable genotypes could be improved through simple selection in segregating populations. Similarly, Cheruiyot et al. (2014) mentioned the greater value of the additive genetic component for stripe rust resistance in advanced lines of wheat. Generation mean analysis showed that dominant effects were more important than additive for resistance to stripe rust (Farahani et al., 2014). Specified preponderance of additive and dominant genes governed the partial resistance to stripe rust in parental cultivars and F1 populations in wheat (Afridi et al., 2017b). However, complete dominance was reported for stripe rust resistance in wheat genotypes (Farahani et al., 2014). However, Afridi et al. (2017b) reported preponderance of non-additive gene effects for resistance to stripe rust in F1 and F2 populations of wheat. Such contradictory findings might be due varied genotypic and environmental differences.

Present results revealed that majority of the genetic components were non-significant for area of flag leaf in F1 generation. Similarly, non-significant components of genetic variance for area of flag leaf in wheat also supported the present results (Ahmad et al., 2013). However, in present studies the additive genetic effects were more prominent than dominance. Involvement of the additive gene action in the expression of area of flag leaf was also reported in wheat under different environmental conditions (Afridi et al., 2017b). In F2 generation, the inheritance of area of flag leaf was controlled by over-dominance type of gene action. Selections in such promising hybrids could be utilized in hybrid wheat production to increase the wheat yield. Over-dominance type of gene action was reported for area of flag leaf in different wheat populations (Nazeer et al., 2010; Nazir et al., 2014; Ahmad et al., 2016).

Additive component of variation was significant whereas other genetic components were non-significant for 1000-grain weight in F1 populations. In F2 populations, all the genetic components were significant; however, the magnitude of additive component was greater than non-additive which suggested early generation selection for 1000-grain weight. Significant of additive and dominance components for 1000-grain weight in F2 populations proposed that selection could be practiced in early generations (Afridi et al., 2017b). Past studies revealed that 1000-grain weight and other yield traits were controlled by additive type of gene action with partial dominance in different wheat populations (Nazir et al., 2014).
However, over-dominance type of gene action was specified for 1000-grain weight in spring wheat (Nazeer et al., 2010; Hussain et al., 2012b). Significant and importance of both additive and dominance genetic effects for 1000-grain weight were reported in F1 populations of wheat (Minhas et al., 2014). Contrasting views might be due to broad genetic make-up of the wheat genotypes and the genotype by environment interactions.

Components of the genetic variation were significant for grain yield in F1 and F2 populations. However, in F1 generation the inheritance of grain yield was controlled by non-additive gene action while in F2 generation the additive genetic component was responsible for inheritance of the said trait. The contradiction in genetic components of both generations might be due to residual heterozygosity in parents (Hayman, 1954a, b). The grain yield per plant could be improved in desirable genotypes by using simple selection in F2 populations. However, over-dominance in F1 generation could be used for exploitation of heterosis by selection in promising wheat F1 populations. Greater values of dominance components than additive revealed that grain yield was controlled by dominant genes in spring wheat (Zare-Kohan and Heidari, 2012). For grain yield, additive gene action was confirmed by components of genetic variation and graphical analysis in wheat (Nazir et al., 2014; Ahmad et al., 2016). However, dominance effects were also found for grain yield in genetic analysis in wheat (Nazeer et al., 2010). Contradictions in past and present findings about F1 and F2 generations might be due to different genetic make-up of the wheat genotypes and the environment. Genetic components revealed that additive genetic effects were indispensable for majority of the traits. Therefore, selection in early segregating generations would be successful.

**Conclusion**

Greater genetic variability revealed by parental genotypes and their F1 and F2 populations for stripe rust resistance and yield traits. Additive-dominance model was partially adequate for rust resistance and yield traits, which allowed further genetic analysis in both generations. Due to preponderance of additive type of gene action for yellow rust resistance, 1000-grain weight and grain yield in F2 populations, the pedigree method could be used to improve these traits. However, due to prevalence of over-dominance type of gene action for area of flag leaf in F2 generation, bulk method would be preferred to improve the trait.

**References**


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