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Combining Ability Analysis and Genetic Studies of Stripe Rust Resistance in Bread Wheat Genotypes

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Abstract

A set of eighteen F1 and F2 experimental crosses were grown in a randomized complete block design (RCBD) with three replications. From lines, TD-1 was on top by showing greater and significant general combining ability (GCA) effects for maximum number characters including grain yield in both (F1 and F2) populations, while tester Benazir remained exceptional by showing higher and significant specific combining ability (GCA) effects for majority traits including grain yield in F1 and F2 populations, as a result, both parents would contribute significantly to the improvement of the bread wheat. Regarding the SCA effects in F1 population, the hybrids TD-1 × Pakistan-2013, TJ-83 × Benazir, and NIA-Sundar × NIA-Sarang and from F2 populations, the crosses TD-1 × Benazir, TJ-83 × Benazir, Kiran-95 × NIA-Sarang and NIA-Amber × Pakistan-2013 expressed desirable and maximum SCA effects for number of traits including grain yield, thus may be preferred in future wheat breeding programs. Disease reaction on selected 18 F2 populations was performed, the introgression stripe rust resistance showed single dominant gene. The genetic analysis reported the involvement of major genes for stripe rust resistance. These findings could be used to grow high-yielding wheat lines that could have a profitable yield in stripe rust-prone areas.

Keywords: Bread wheat, combining ability, stripe rust, yield traits.

Introduction

Wheat is Pakistan's most common food crop, and its products are widely used. As the staple food, wheat dominates over all crops in acreage and production. The value added in agriculture for wheat is 8.7% and the value of gross domestic product is 1.7% (GOP, 2020). Bread wheat is a major cereal crop threatened by several biotic and abiotic restrictions (Afzal *et al.*, 2015). Biotic stresses, such as rusts, caused by various fungus, have remained a serious threat to the production of global wheat (Grover *et al.*, 2019). Two approaches have been used to control rust diseases: chemical and genetic management. Genetic resistance is the most economical and environmentally friendly to defend crops against damage caused by biotic factors, such as stripe rust (Chen, 2005). Growing resistant cultivars is the most economical and environmentally friendly approach to stripe rust protection (Line & Chen, 1995). To ensure genetic tolerance, new resistance genes must be identified in various wheat germplasms (Sumikova & Hanzalova, 2010). Durable resistance provides resistance over a long period during the extensive cultivation of a variety in environments with favorable disease spread conditions (Johnson *et al.*, 1975). Therefore, plant pathologists and breeders have given priority to producing high-yielding disease-resistant varieties by pyramiding successful and long-lasting resistance genes because it is difficult to track the expression of individual resistance genes in this field (Pedersen *et al.*, 1988). Nevertheless, durable resistance is based on various genetic tools, such as, backcross breeding and marker assisted selection (Wellings, 2011). Rust diseases are one of the economically significant wheat diseases because they cause substantial worldwide loss of yield. In global wheat production, leaf rusts are very common among rust diseases, and losses above 50% are recorded in susceptible cultivars (Zaman *et al.*, 2017).

Over the past 15 years, wheat stripe rust has become the main biotic stress to wheat production and poses a danger to the global food supply. About 88% of the world's wheat supply is now prone to rust, leading to global losses of more than 5 million tons of wheat with an estimated US$ 1 billion in annual market value (Beddow *et al.*, 2015). Yellow rust is another name for stripe rust because owing to the spore color during its asexual period of infection. However, the obligate biotrophic fungus emerged this disease, called *Puccinia striformis* f. sp. *Tritici* (*Pst*). This fungus is a threat to agriculture production because of its immense genetic diversity, mainly in the Himalayan region, the distant dispersal of this fungus through the continents by natural means, and its rapid adaptation to the local area through development (Hovmøller *et al.*, 2011).

Stripe rust resistance may be divided into two categories: seedling (all stages) or complete resistance and adult plant resistance. The resistance expressed at the seedling stage typically remains successful for a virulent pathogen pathotype during the plant growth cycle (McIntosh *et al.,* 1995). According to many pathologists, the seedling resistance is like non-durable, vertical, race-specific and major gene resistance (McIntosh & Brown, 1997). Nevertheless, in post-seedling growth phases, plants sensitive to seedling may develop adult plant resistance (McIntosh *et al.,* 1995). Many seedling and adult plant resistance genes are now ineffective because of virulence in the pathogen in different geographic areas of the world (Sharma-Poudyal *et al.,* 2013). An understanding of the genetic basis for stripe rust resistance in commercial wheat crops and selected elite genotypes is an important goal for wheat breeding programs (McIntosh & Brown, 1997). Inheritance studies have generally demonstrated that rust disease resistance is simply an inherited process (Roelfs *et al.,* 1992). According to McIntosh *et al.*(1995), resistance may be single or major gene (regulated by a single Mendelian gene), oligogene (regulated by fewer genes with visible effects) or polygene (controlled by multiple genes or minor genes, each with minor effects).To date, 82 Yr genes have been formally described, of which about 25 confer resistance to adult plants or high temperature adult plant resistance, whereas the rest offer all stage resistance (Gebreslasie *et al.,* 2020).

The development of disease resistant and competitive varieties is a major priority for wheat breeding. That involves understanding the combining ability and the nature of gene action involved in expressing desired traits of its progenies by crossing parents in a hybridization program. The parents with significant GCA and SCA effects for desirable characteristics is important for successful breeding (Desale *et al.,* 2014). GCA is described as a line's mean performance in hybrid combinations. SCA is the deviation in performance of a cross from its theoretical performance predicted based on GCA (Schlegel, 2010). Many researchers (Hayman, 1954; Griffing, 1956; Singh & Chuadhary, 1979; Mather & Jinks, 1982) established biometrical techniques for analysis of GCA and SAC effects of parents and crosses, respectively. For the analysis of combining ability via line × tester was proposed by (Singh & Chuadhary, 1979), a biostatistical method used widely to evaluate parents' ability to transfer their desired characteristics to their descendants and compare the parental success in hybrid combinations. Therefore, the current study evaluated the genetic basis of wheat genotypes for combining ability and stripe rust resistance.

Materials and Methods

Development of breeding materials: The current investigation was conducted at Botanical Garden, Sindh Agriculture University, Tandojam during the Rabi season of 2017-18. A total of six female lines including TD-1, TJ-83, Kiran-95, Khirman, NIA-Amber and NIA-Sundar tagged as susceptible to stripe rust were crossed through line × tester mating design with three male testers, such as, Benazir, Pakistan-2013 and NIA-Sarang, which recognized as resistant to stripe rust. During 2018-19, the obtained 18 F_1 hybrids were grown in respect to produce F_2 populations. Moreover, six female lines (susceptible to stripe rust) were also crossed with three male testers (resistant to stripe rust) to produce 18 F_1 hybrids for genetic analysis of stripe rust resistance. Inthird year (2019-20), the experiment regarding genetic analysis having three generations of genetic materials (parents, F_1 hybrids and F_2 progenies) were also grown. The current experiment was also done to analyze the genetic basis of stripe rust resistance in three abovementioned populations in an RCBD with four replications.

Inoculation of stripe rust: Using a hand sprayer, urediospores suspension of stripe rust was used to artificially infect the wheat experimental materials. Spores were counted using a hemocytometer; however, the final concentration of 10^6 spores/ml was roughly adjusted. Additionally, tween-20 (0.05%) was added to the suspension to increase the rust spores' ability to stick. Hence, all the parents, F_1 and F_2crosses and spreader (Morocco)were artificially inoculated with mixture of stripe rust spores of prevailing races by spraying at adult plant stage under field conditions.

Disease assessment: The plots were irrigated after artificial inoculation to provide a more favorable environment for disease development. Rust intensities based on the modified Cobbs Scale for rust (Peterson *et al.,* 1948) were recorded for 70 individual plants per replication with one-week intervals. The first data recording date and stage were jointing and booting, and data collection was completed when spreader showed a maximum rust intensity, and the plants began to reach maturity. At maturity, the plants from each parental line and their respective F_1 and F_2 generations were also randomly selected to measure different agronomic traits.

Phenotypic characterization: Days to 75% heading and days to 90% maturity were visually recorded in the field. Plant height and spike length were measured in centimeters. Tillers plant^{-1} and grains spike^{-1} were counted. The grain weight of main spike, grain yield plant^{-1} and biological yield plant^{-1} were weighed in grams, while 1000-grain weight also weighed in grams and termed as seed index.

Fertilizer, irrigation, weedicide, and statistical analysis: The recommended amount of fertilizer was given to the experimental field with 134N: 67 P_2O_5 kg/ha. The nitrogen(N) was applied in three stages, while the phosphorus(P) was applied before cultivation. During the cropping season, the experiment was irrigated six times. Weeds were removed from the experimental field using the weedicide Loughran (160 grams/acre). All statistical analysis were carried out through RStudio software.

Results and discussion

Analysis of variances: The current study showed significant differences ($P \leq 0.05$) of mean squares for genotypes, parents, crosses, parents versus crosses for majority of the studied characters in F_1 and F_2 generations (Tables 1 and 2). This indicates that these wheat genotypes have a high potential to be used in a variety of breeding experiments for genetic improvement of wheat crop. In this context, (Farooq *et al.,* 2019) also carried out line × tester analysis for assessing the genetic efficiency in wheat genotypes and reported that on mean squares of parents and F_1 showed significant differences for all the traits under investigation. Similarly, in Pakistani wheat germplasm, the suitable amount of variability in parents, crosses and parents versus crosses was reported by (Khokhar *et al.,* 2019). In another study, (Bajaniya *et al.,* 2019) reported that for all the yield attributing traits, the mean squares due to the lines × tester interaction showed substantial hybrids' contribution to different components of combining ability. The mean squares due to GCA (lines and testers) and SCA (lines × tester) were found significantly different ($p \leq 0.05$) for most of the studied characters in $F_1$and F_2 generations, demonstrating the role of both additive and non-additive gene effects (Tables1 and 2). However, GCA mean squares of lines and testers in F_1 and F_2 generations were greater in magnitude than SCA. Combining ability effects due to GCA and SCA are used as main indicators for the identification and selection of potential inbred lines in most of the crops including wheat for the development of commercial cultivars. Significant mean squares for GCA and SCA effects among various wheat populations for earliness, morphological, and yield traits were reported by (Hama-Amin & Towfiq, 2019; Sharma *et al.,* 2019; and Ayoob, 2020). Contrary to our results, the non-significant GCA mean squares of testers for all agronomical parameters were also reported by (Din *et al.,* 2020).

Combining ability variances: Knowledge of combining ability is useful in identifying genotypes for promising cross combinations as well as recognizing the inheritance involved in different quantitative wheat traits (Din *et al.,* 2020).Combining ability has been carried out by breeders in recent past for different field crops, including cotton (Reddy *et al.,* 2017; Bilwal *et al.,* 2018; Noor & Qayyum, 2020), maize (Zakiullah *et al.,* 2019), rice (Rahimi *et al.,* 2010), millet (Jeeterwal *et al.,* 2017), sorghum (Chikuta *et al.,* 2017), sunflower (Rizwan *et al.,* 2020), rapeseed (Channa *et al.,* 2018; Gul *et al.,* 2018; Gul *et al.,* 2019), mustard (Lal *et al.,* 2012; Chaurasiya *et al.,* 2018) and chickpea (Amadabade *et al.,* 2014).

Early maturity is desired hence negative combining ability effects benefit wheat crop development. In present work (Table3a), the line TD-1 showed negative GCA effects for earliness. The GCA effects of line TD-1 were -4.33 (F_1) and -4.31(F_2) for days to 70% heading and -14.60 (F_1) and -12.71 (F_2) for days to 90% maturity, while two other lines (NIA-Amber and NIA-Sundar) also revealed negative GCA effects for only days to 70% heading in both genetic populations (F_1 and F_2). From testers, only Benazir displayed negative GCA effects (-1.59) in F_2 for days to 90% maturity, while Pakistan-2013 reported maximum negative GCA effects (-1.12) in F_1 for days to 70% heading. The negative and desirable SCA effects for days to 70% heading ranged between -0.19 and -3.99 in F_1 and ranged from -0.10 and -6.86 in F_2 generation. Similarly, the desirable SCA effects for days to 90% maturity varied from -0.42 to -2.58 in F_1 and in $F_{2,}$ the range were from-0.03 to -2.13. Out of 18 F_1 and F_2 populations (Table4a), three populations (Kiran-95 × NIA-Sarang, Khirman × Pakistan-2013 and NIA-Sundar × NIA-Sarang) showed negative SCA effects for heading and maturity. These genotypes (parents and crosses) would be considered as reliable breeding materials in the development of early matured wheat genotypes. Bajaniya *et al.* (2019) reported similar results for heading by revealing that five lines and three testers were negative for GCA effects and four lines and one tester were negative for maturity. While Dedaniya *et al.* (2019) also reported that four lines and two testers registered negative GCA effects for heading and five lines and two testers also marked negative GCA effects for maturity. However, Bajaniya *et al.* (2019) and Dedaniya *et al.* (2019) also reported that more than 10 F_1 hybrids disclosed negative and useful SCA effects for both the maturity characters. In wheat, the negative combining ability effects are desirable for plant height. From lines (Table 3a), TD-1(-26.97 and -20.60) and TJ-83 (-12.66 and -1.86) showed negative GCA effects in F_1 and F_2 populations and from testers, NIA-Sarang disclosed negative GCA effects in both breeding populations ($F_{1=}$-1.744 and $F_{2=}$ -0.46). From 18 F_1 and F_2 crosses (Table 4a), 10 crosses of F_1 and 8 crosses of F_2 revealed negative and desirable SCA effects, however, only 2 crosses, such as, NIA-Amber × Pakistan-2013 (-1.74 and -1.90) and NIA-Sundar × Benazir (-2.92 and -1.56) had negative GCA effects in both populations (F_1 and F_2). These parents and crosses may prove useful in developing dwarf or medium tall wheat crop plants when used in a specific hybridization program. Because of the lodging resistance and high yielding ability, the bread wheat varieties of short or medium height tend to have a prominent place in breeding programs. However, excessive shortening of plant height has a negative impact on machine harvestability, photosynthesis area, and adaptation to barren conditions (Altinkut *et al.,* 2001). Short cultivars are more yielding, especially in irrigated areas, while tall cultivars are better suited to arid-marginal areas (Kutlu & Siren, 2019). By using line × tester mating design, (Farooq *et al.,* 2019) also found negative GCA effects for lines and testers, and also reported negative SCA effects for maximum number of F_1 crosses. Another study (Parveen *et al.,* 2019) also showed negative combining ability effects of parents and crosses for plant height.

For tillers plant^{-1}, three lines, such as, TD-1 (2.39 and 0.62), TJ-83 (0.77 and 0.11) and Kiran-95 (1.74 and 1.23) in F_1 and F_2 generations, while tester Pakistan-2013 (0.46) in F_1 and Benazir (1.01) in F_2 generation exhibited maximum positive GCA effects (Table 3a). For SCA effects, nine crosses from each population (F_1 and F_2) recorded positive SCA effects (Table 4a), regarding spike length, same three lines including TD-1 (0.73 and 0.48), TJ-83(1.94 and 0.36) and Kiran-95 (1.00 and 0.47) in F_1 and F_2 generations. In contrast, tester Benazir in both generations (F_1= 1.06 and F_2= 0.88) unveiled maximum positive GCA effects (Table 3a). The range of positive SCA effects were from 0.05 to 1.50 in F_1 and from 0.01 to 1.70 in F_2 generation. Eleven crosses from F1 and nine from F_2 generation recorded positive SCA effects. However, seven crosses (TD-1 × Benazir, Kiran-95 × Benazir, Khirman × Pakistan-2013, NIA-Amber × Pakistan-2013, NIA-Amber × NIA-Sarang, NIA-Sundar × Pakistan-2013 and NIA-Sundar × NIA-Sarang) showed positive SCA effects in both generations (Table 4a). The described genotypes may have excellent genetic resources for agronomically important characters.

Mentioning the combining ability effects of spikelets spike^{-1} (Table 3a), TD-1 (1.08 and 1.20) and TJ-83 (0.08 and 0.69) as line and Benazir (0.15 and 0.47) as tester recorded positive GCA effects, while four crosses such as TD-1 × Benazir (1.46 and 2.31), TJ-83 × Benazir (1.30 and 0.75), Kiran-95 × NIA-Sarang (1.49 and 1.69) and Khirman × NIA-Sarang (1.11 and 1.54) also showed positive SCA effects in F_1 and F_2 generations, respectively for spikelets spike^{-1} (Table 4a). For grains spike^{-1}, three lines namely TD-1 (0.34 and 3.83), TJ-83 (1.40 and 2.60) and Kiran-95 (1.67 and 7.04), whereas tester Benazir (2.15 and 6.08) also registered positive GCA effects in F_1 and F_2 generations, respectively (Table 3b). Nonetheless, eight crosses (TD-1 × Benazir, TJ-83 × Benazir, Kiran-95 × Pakistan-2013, Khirman × Pakistan-2013, Khirman × NIA-Sarang, NIA-Amber × Pakistan- 2013, NIA-Amber × NIA-Sarang and NIA-Sundar × NIA-Sarang) showed positive SCA effects in F_1 and F_2 populations (Table 4b). The maximum positive SCA effects in F_1 (5.48) were observed in NIA-Amber × NIA-Sarang and F_2 (12.75) was recorded in TD-1 × Benazir. For grain weight spike^{-1}, TJ-83 from F_1(0.22) and lines TD-1 (0.53) and NIA-Amber (0.49) from F_2 populations remained on top for positive GCA effects, while testers Pakistan-2013 (0.07) and NIA-Sundar (0.06) from F_1 and Benazir (0.69) from F_2 were topper in positive GCA effects (Table 3b). Four crosses viz., TD-1 × Benazir (0.37 and 0.03), Kiran-95 × Benazir (0.14 and 0.19), Khirman ×Benazir (0.11 and 0.11) and NIA-Amber × NIA-Sarang (0.41 and 0.78) showed positive SCA effects in F_1 and F_2 generations, respectively (Table 4b). These genotypes can be used to produce high-yielding wheat varieties by pedigree and progeny selection, as well as mass selection in later generations from promising segregating populations. Present findings are in confirmation with (Aslam *et al.,* 2014; Kalhoro *et al.,* 2015; Kandil *et al.,* 2016; Rajput & Kandalkar, 2018; Parveen *et al.,* 2019; and Dedaniya *et al.,* 2019).

The most significant goal of all breeding programs is to increase grain yield. GCA and SCA results are important indicators of plant breeding for identifying possible parental accessions in hybrid combinations (Channa *et al.,* 2018). For grain yield plant^{-1}, two lines, such as, TD-1 (2.22 and 1.03) and TJ-83 (0.62 and 0.72) and tester Benazir (1.84 and 1.01) disclosed positive GCA effects in F_1 and F_2 populations, respectively (Table 3b). Four crosses including TD-1 × Benazir (0.53 and 3.78), TJ-83 × Benazir (2.16 and 3.42), Kiran-95 × NIA-Sarang (1.43 and 3.96) and NIA-Sundar × NIA-Sarang (3.45and 0.52) were positive for SCA effects in F_1 and F_2 populations, respectively (Table 4b). Positive GCA and SCA effects for grain yield were also obtained in wheat genotypes by (Patel, 2017; Saeed & Khalil, 2017;Tiwari *et al.,* 2017; Uddin *et al.,* 2017; Ali *et al.,* 2018; Ishaq *et al.,* 2018; Rajput & Kandalkar, 2018; Abdelkhalik *et al.,* 2019; Ali *et al.,* 2019; Bajaniya *et al.,* 2019; Dedaniya *et al.,* 2019; Hama-Amin & Towfiq, 2019; Sharma *et al.,* 2019; Thakur *et al.,* 2019; and Younas *et al.,* 2020).

Taking the GCA effects of lines for seed index, the lines TD-1 with maximum GCA effects of 3.29 and 5.83 and NIA-Amber with maximum positive GCA effects of 1.19 and 0.26 were ranked as promising in F_1 and F_2 generations, respectively. At the same time, tester Benazir was also reported as promising one in F_1 (2.89) and F_2 (4.60) generations for GCA effects in positive direction (Table 3b). The cross TD-1 × Benazir was recorded as superior one with maximum positive SCA effects in F_1(5.28) and F_2(13.39) generations (Table 4b), reflecting the importance in hybrid development program of wheat crop. Hence, such F_1 hybrids are being considered as best specific cross combinations with a remarkable mean performance and involve high × high GCA parents. Describing the combining ability effects for biological yield plant^{-1}, the lines TJ-83 (0.24) and NIA-Amber (0.26) in F_1 and TD-1 (6.37), TJ-83 (3.96) and Kiran-95 (3.81) were top in F_2 by showing the positive GCA effects. At the same time, tester NIA-Sarang (0.15 and 0.16) depicted positive GCA effects in both generations (Table 3b). These parents could be used as parents in a hybridization program aimed at improving and increasing the biomass of wheat crops. The highest positive SCA effects in both generations (F_1= 1.64 and F_2= 2.99) were noted in NIA-Sundar × Benazir (Table 4b). The high SCA effects of this cross involve low × low general combiners and that may be due to over dominance or dominance × dominance type of gene action. Such crosses may be exploited for heterosis breeding. However, if a cross combination with a high SCA and high *per Su*performance has at least one parent, a decent general combiner for a particular phenotype, it is supposed to produce favorable transgressive segregants in subsequent generations (Rajput & Kandalkar, 2018).

Introgression of stripe rust resistance: The availability of resistance sources, which can be used to grow cultivars resistant to major diseases and pests, is the first criterion for breeding programs (Li *et al.*, 2018). Similarly, the current research also included a set of resistant and susceptible wheat genotypes to highlight the genetic bases of stripe rust resistance in breeding materials. The results of scoring of parental lines and their F_1 and F_2 populations in different cross combinations indicated that all resistant parents showed resistance to the prevailing race of stripe rust whereas susceptible parents displayed susceptibility in the field. In each F_2 progenies of TD-1 × Benazir, TD-1 × Pakistan-2013 and TD-1 × NIA-Sarang, from 200 plants, 144, 143 and 153 were resistant and 56, 57 and 47 were susceptible, respectively (Table 5). In each F_2 progenies of TJ-83 × Benazir, TJ-83 × Pakistan-2013 and TJ-83 × NIA-Sarang, out of 200 plants, 145, 149 and 144 were considered as resistant and 55, 51 and 46 were reported as susceptible, respectively (Table5). In each F_2 progenies of Kiran-95 × Benazir, Kiran-95 × Pakistan-2013 and Kiran-95 × NIA-Sarang, out of 200 plants, 131, 139 and 145 were marked as resistant and 69, 41 and 55 were testified as susceptible, respectively (Table 5).In each F_2 progenies of Khirman × Benazir, Khirman × Pakistan-2013 and Khirman × NIA-Sarang, from 200 plants, 133, 132 and 150 were found as resistant and 67, 68 and 50 were noted as susceptible, respectively (Tables 5). In each F_2 progenies of NIA-Amber × Benazir, NIA-Amber × Pakistan-2013 and NIA-Amber × NIA-Sarang, from 200 plants, 154, 163 and 143 were found as resistant and 46, 37 and 57 were noted as susceptible, respectively (Table 5). In each F_2 progenies of NIA-Sundar × Benazir, NIA-Sundar × Pakistan-2013 and NIA-Sundar × NIA-Sarang, from 200 plants, 147, 140 and 138 were found as resistant and 53, 60 and 62 were noted as susceptible, respectively (Table 5). The 3:1 ratio based on field reaction patterns indicates the presence of a single dominant gene for resistance to stripe rust. These resistant genes may be useful in producing new resistant cultivars in wheat breeding programs in Southeast Asia, especially in Sindh province, to meet the new challenges posed by the rust problem. Similarly, (Olivera *et al.*, 2008) also reported that all F_2 populations from crosses between resistant and susceptible accessions segregated in their response to leaf rust. The number of resistant susceptible plants were found in a 3:1 ratio at both the seedling and adult plant stages. (Wu *et al.*, 2016) analyzed 352 plants for stripe rust along with parents and F_1 generations at adult plant stage, the obtained results indicated that resistance was conferred by a single dominant gene. Recently, (Li *et al.*, 2018) observed 212 F_2 plants, which segregated into 158 resistant and 54 susceptible, fitting the ratio of 3:1, indicating that resistance under field conditions was also controlled by a single-dominant gene.

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Table 1. The obtained mean squares of different characters for various source of variances in F_1 generation

Source of variances	**Replications D.F. (02)**	**Genotypes D.F. (26)**	**Parents D.F. (08)**	**Crosses D.F. (17)**	**P vs C D.F. (01)**	**Lines (GCA) D.F. (05)**	**Tester (GCA) D.F. (02)**	**Lines x Tester (SCA) D.F. (08)**	**Error D.F. (52)**
Days to 70% heading	11.14	86.37^{**}	$124.8^{**}0$	37.10^{**}	616.40^{**}	65.98^{**}	35^{**}	25.60^{**}	2.60
Days to 90% maturity	1676.76	190.24^{**}	200.90^{**}	190.95^{*}	92.98^{*}	613.06^{**}	17^{ns}	16.25^{ns}	86.18
Plant height	220.35	828.78^{**}	413.79^{**}	907.97^{**}	2802.51^{**}	2764.44^{**}	47.68^{*}	168^{**}	19.73
Tillers plant^{-1}	0.23	9.21^{**}	5.91^{**}	10.83^{**}	8.09^{**}	31.47^{**}	2.92^{**}	2.33^{**}	0.37
Spike length	0.19	37.90^{**}	0.06^{ns}	12.84^{**}	766.58^{**}	19.81^{**}	29.7^{**}	6.63^{**}	0.32
Spikelets spike	0.16	21.88^{**}	0.10^{ns}	5.09^{**}	481.53^{**}	3.29^{**}	5.10^{**}	6.66^{**}	0.23
Grains spike	7.56	344.47^{**}	72.41^{**}	55.48^{**}	7433.87^{**}	67^{**}	65.16^{**}	52.76^{**}	5.79
Grain weight spike^{-1}	0.01	0.56^{**}	0.00^{ns}	0.33^{**}	8.89^{**}	0.36^{**}	0.27^{**}	0.36^{**}	0.02
Grain yield plant^{-1}	5.26	60.35^{**}	2.13^{*}	21.23^{**}	1191.26^{**}	19.02^{**}	45.8^{**}	19.36^{**}	1.20
Seed index	6.66	250.25^{**}	4.18^{*}	54.10^{**}	5553.41^{**}	66.63^{**}	122.13^{**}	38.04^{**}	3.19
Biological yield plant^{-1}	0.98	31.15^{**}	2.19^{*}	1.76^{*}	795.56^{**}	0.69^{*}	1.25^{**}	2.78^{*}	0.68

** represents significant at 1% and * shows significant at 5% of the probability level, while ns refers non-significant
D.F. = Degree of Freedom
P vs C = Parents versus Crosses

Table 2. Analysis of variances of various traits in F_2 generation

Source of variances	**Replications D.F. (02)**	**Genotypes D.F. (26)**	**Parents D.F. (08)**	**Crosses D.F. (17)**	**P vs C D.F. (01)**	**Lines (GCA) D.F. (05)**	**Tester (GCA) D.F. (02)**	**Lines x Tester (SCA) D.F. (10)**	**Error D.F. (52)**
Days to 70% heading	3.94	81.63^{**}	124.80^{**}	63.75^{**}	40.30^{**}	143^{**}	38.48^{**}	31.90^{**}	2.63
Days to 90% maturity	4.64	134.10^{*}	203.63^{**}	109.12	2.44^{ns}	361^{**}	0.54^{ns}	5.44	4.09
Plant height	82.52	381.52^{**}	436.04^{**}	349.63^{**}	487.41^{**}	1055^{**}	4.07	73.2^{**}	7.74
Tillers plant^{-1}	0.87	3.76^{**}	0.67^{**}	4.96^{**}	8.00^{**}	7.20^{**}	14.10^{**}	2.23^{**}	0.16
Spike length	0.68	2.90^{**}	0.06^{ns}	4.40^{**}	0.18	3.01^{**}	10.45^{**}	4.33^{**}	0.15
Spikelets spike	0.48	5.68^{**}	0.10^{ns}	7.39^{**}	21.13^{**}	7.77^{**}	5.87^{**}	8.34^{**}	0.51
Grains spike	4.96	177.23^{**}	2.02^{ns}	251.98^{**}	308.07^{**}	238^{**}	524^{**}	227^{**}	1.15
Grain weight spike^{-1}	0.02	1.51^{**}	0.00^{ns}	1.93^{**}	6.57^{**}	1.75^{**}	6.41^{**}	1.25^{**}	0.04
Grain yield plant^{-1}	0.68	12.48^{**}	0.87	18.27^{**}	7.01^{**}	8.23^{**}	13.87^{**}	26.86^{**}	0.26
Seed index	0.18	115.15^{**}	0.63^{ns}	165.63^{**}	173.19^{**}	131^{**}	288.01^{**}	175.75^{**}	0.82
Biological yield plant^{-1}	1.25	73.16^{**}	40.57^{**}	93.29^{**}	-8.31^{ns}	284.86^{**}	0.45^{ns}	37.87^{**}	11.88
Harvest index	122.38	141.54^{*}	199.03^{**}	120.54^{*}	38.64^{ns}	318.48^{**}	105.70^{*}	27.26^{ns}	39.23

** represents significant at 1% and * shows significant at 5% of probability level, while ns refers non-significant
D.F. = Degree of Freedom
P vs C = Parents versus Crosses

Table 3a. Estimation of general combining ability in F_1 and F_2 generations for agro-morphological traits

Parents	**Days to 70% heading**		**Days to 90% maturity**		**Plant height**		**Tillers plant^{-1}**		**Spike length**		**Spikelets spike^{-1}**	
Lines	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
TD-1	-4.33	-4.31	-14.60	-12.71	-26.97	-20.60	2.39	0.62	0.73	0.48	1.08	1.20
TJ-83	3.80	7.49	1.70	2.29	-12.66	-1.86	0.77	0.11	1.94	0.36	0.08	0.69
Kiran-95	1.29	-0.52	8.53	3.17	16.30	5.43	1.74	1.23	1.00	0.47	-0.35	-0.55
Khirman	0.60	0.20	-3.68	3.36	-1.03	2.03	-1.94	-0.54	-1.45	-0.90	0.20	-0.69
NIA-Amber	-1.18	-0.76	2.34	3.52	5.66	5.01	-1.46	-0.09	-1.87	-0.52	-0.49	-1.17
NIA-Sundar	-0.18	-2.10	5.72	0.36	18.70	9.99	-1.50	-1.33	-0.35	0.12	-0.51	0.52
S.E. (si)	0.54	0.54	3.09	0.67	1.48	0.93	0.20	0.13	0.19	0.13	0.16	0.24
Testers												
Benazir	1.57	-1.59	0.93	-0.20	1.48	-0.024	-0.24	1.01	1.06	0.88	0.15	0.47
Pakistan-2013	-1.12	0.30	0.10	0.09	0.27	0.49	0.46	-0.34	0.37	-0.49	-0.59	0.16
NIA-Sarang	-0.444	1.289	-1.023	0.106	-1.744	-0.46	-0.224	-0.661	-1.431	-0.389	0.443	-0.635
S.E. (gi)	0.38	0.38	2.19	0.48	1.05	0.66	0.14	0.09	0.13	0.09	0.11	0.17

Table 3b. Estimation of general combining ability in F_1 and F_2 generations for agro-morphological traits

Parents	**Grains spike^{1}**		**Grain weight spike^{1}**		**Grain yield plant^{1}**		**Seed index**		**Biological yield plant^{1}**	
Lines	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
TD-1	0.34	3.83	-0.05	0.53	2.22	1.03	3.29	5.83	-0.20	6.37
TJ-83	1.40	2.60	0.22	-0.14	0.62	0.72	-0.34	2.71	0.24	3.96
Kiran-95	1.67	7.04	0.04	-0.03	-2.05	0.64	-3.32	-3.72	-0.05	3.81
Khirman	1.90	-4.80	0.13	-0.25	0.36	-1.47	2.17	-3.23	0.17	-1.00
NIA-Amber	0.09	-4.99	-0.36	0.49	-0.24	-0.38	1.19	0.98	0.26	-6.29
NIA-Sundar	-5.39	-3.69	0.02	-0.61	-0.91	-0.53	-2.99	-2.57	-0.43	-6.85
S.E. (gi)	0.80	0.36	0.05	0.07	0.36	0.17	0.60	0.30	0.08	1.15
Testers										
Benazir	2.15	6.08	-0.14	0.69	1.84	1.01	2.89	4.60	0.15	-0.15
Pakistan-2013	-0.69	-1.84	0.07	-0.33	-0.86	-0.57	-0.73	-2.66	-0.30	-0.01
NIA-Sarang	-1.45	-4.24	0.06	-0.36	-0.98	-0.44	-2.16	-1.93	0.15	0.16
S.E. (gi)	0.57	0.25	0.03	0.05	0.26	0.12	0.42	0.21	0.19	0.81

Table 4a. Estimation of specific combining ability of F_1hybrids and F_2progenies for agro-morphological traits

Hybrids/progenies	**Days to 70% heading**		**Days to 90% maturity**		**Plant height**		**Tillers plant ^{1}**		**Spike length**		**Spikelets spike ^{1}**	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
TD-1 × Benazir	2.32	-6.86	1.03	-2.13	-5.59	7.80	0.02	0.33	0.52	0.28	1.46	2.31
TD-1 × Pakistan-2013	-3.99	2.59	-1.47	1.57	3.96	-3.49	-0.69	-0.29	1.27	-0.29	0.94	-0.45
TD-1 × NIA-Sarang	1.67	4.27	0.43	0.56	1.63	-4.31	0.67	-0.04	-1.79	0.01	-2.40	-1.85
TJ-83 × Benazir	-2.34	1.78	-1.42	-0.03	-2.46	0.06	-1.23	0.81	-0.86	1.53	1.30	0.75
TJ-83 × Pakistan-2013	3.08	-0.41	-2.58	-0.19	-2.51	0.45	0.24	-1.01	-0.91	-0.13	-0.10	0.16
TJ-83 × NIA-Sarang	-0.73	-1.37	4.00	0.23	4.97	-0.51	0.99	0.21	1.76	-1.40	-1.20	-0.91
Kiran-95 × Benazir	3.37	-0.18	-0.54	0.22	-6.52	0.77	0.67	-0.52	0.35	0.92	-1.01	-0.55
Kiran-95 × Pakistan-2013	-1.61	-1.07	1.20	0.56	4.62	-1.18	-0.06	0.60	0.90	-0.58	-0.48	-1.14
Kiran-95 × NIA-Sarang	-1.76	1.24	-0.66	-0.78	1.90	0.40	-0.61	-0.08	-1.26	-0.34	1.49	1.69
Khirman × Benazir	-2.28	1.97	1.45	-0.67	3.43	-8.16	-0.71	0.63	-1.10	-0.38	-0.83	-1.24
Khirman × Pakistan-2013	-0.19	-0.86	-1.03	-0.16	-1.69	2.76	0.85	-0.59	0.05	0.69	-0.29	-0.30
Khirman × NIA-Sarang	2.47	-1.11	-0.42	0.83	-1.74	5.40	-0.13	-0.04	1.05	-0.31	1.11	1.54
NIA-Amber × Benazir	-1.30	1.66	0.09	0.74	14.06	1.09	0.51	-0.19	-0.41	-1.06	0.06	-0.53
NIA-Amber × Pakistan-2013	1.12	-0.10	1.15	-0.95	-4.00	-1.90	-0.30	0.99	0.34	0.71	0.17	-0.15
NIA-Amber × NIA-Sarang	0.18	-1.56	-1.24	0.21	-10.06	0.81	-0.21	-0.79	0.08	0.34	-0.23	0.68
NIA-Sundar × Benazir	0.23	1.63	-0.62	1.87	-2.92	-1.56	0.74	-1.05	1.50	-1.30	-0.98	-0.75
NIA-Sundar × Pakistan-2013	1.59	-0.16	2.73	-0.83	-0.38	3.36	-0.03	0.30	-1.65	-0.40	-0.24	1.89
NIA-Sundar × NIA-Sarang	-1.82	-1.48	-2.11	-1.04	3.30	-1.80	-0.71	0.75	0.15	1.70	1.22	-1.14
S.E. (si)	0.93	0.94	5.36	1.17	2.56	1.61	0.35	0.23	0.33	0.23	0.28	0.41

Table 4b. Estimation of specific combining ability of F$_1$hybrids and F$_2$progenies for agro-morphological traits

Hybrids/progenies	**Grains spike^{1}**		**Grain weight spike^{1}**		**Grain yield plant^{-1}**		**Seed index**		**Biological yield plant^{-1}**	
	F$_1$	F$_2$	F$_1$	F$_2$	F$_1$	F$_2$	F$_1$	F$_2$	F$_1$	F$_2$
TD-1 × Benazir	4.05	12.75	0.37	0.03	0.53	3.78	5.28	13.39	-0.13	0.69
TD-1 × Pakistan-2013	-0.84	-8.64	-0.21	0.85	2.39	-1.61	0.59	-6.62	-0.14	-0.29
TD-1 × NIA-Sarang	-3.21	-4.10	-0.16	-0.88	-2.92	-2.17	-5.87	-6.77	0.27	-0.40
TJ-83 × Benazir	3.79	8.40	0.00	0.43	2.16	3.42	1.71	7.14	0.09	-3.40
TJ-83 × Pakistan-2013	-1.20	-5.39	0.13	-0.25	-0.64	-1.50	-2.27	-3.16	0.15	1.15
TJ-83 × NIA-Sarang	-2.60	-3.01	-0.13	-0.18	-1.52	-1.92	0.56	-3.98	-0.24	2.25
Kiran-95 × Benazir	1.35	-1.73	0.14	0.19	-2.00	-3.20	-2.98	-4.80	-0.35	1.21
Kiran-95 × Pakistan-2013	2.66	8.41	-0.14	-0.16	0.57	-0.76	-0.63	2.63	-0.43	2.16
Kiran-95 × NIA-Sarang	-4.01	-6.68	0.00	-0.03	1.43	3.96	3.61	2.17	0.78	-3.37
Khirman ×Benazir	-1.61	-6.16	0.11	0.11	1.96	-0.99	-1.40	-5.06	-0.37	1.09
Khirman × Pakistan-2013	0.07	1.88	-0.01	-0.04	-1.57	0.56	2.35	2.84	0.08	-0.76
Khirman × NIA-Sarang	1.54	4.29	-0.10	-0.07	-0.39	0.43	-0.95	2.22	0.29	-0.33
NIA-Amber × Benazir	-6.03	-6.68	-0.71	-0.07	0.63	-1.88	-0.29	-7.73	0.34	-1.22
NIA-Amber × Pakistan- 2013	0.55	1.77	0.30	-0.72	-0.57	2.70	0.26	2.29	0.26	-1.54
NIA-Amber × NIA-Sarang	5.48	4.91	0.41	0.78	-0.05	-0.82	0.03	5.44	-0.60	2.76
NIA-Sundar × Benazir	-1.55	-6.58	0.09	-0.70	-3.27	-1.13	-2.31	-2.94	0.43	1.64
NIA-Sundar × Pakistan-2013	-1.24	1.97	-0.08	0.32	-0.17	0.61	-0.30	2.02	0.08	-0.74
NIA-Sundar × NIA-Sarang	2.79	4.61	-0.01	0.38	3.45	0.52	2.61	0.93	-0.51	-0.91
S.E. (si)	1.39	0.62	0.08	0.12	0.63	0.29	1.03	0.52	0.18	1.99

Table 5. Introgression of stripe rust in wheat populations

Crosses	**Parents/ Generations**	**The total number of plants observed**	**Infection type**					**Expected ratio**	**X^2**	**P value**
			0	**1**	**2**	**3**	**4**			
TD-1 × Benazir	TD-1	20				13	07			
	Benazir	20	12	06						
	F$_1$	16	15	01						
	F$_2$	200	80	27	37	14	42	3:1	0.27	0.45
TD-1 × Pakistan-2013	TD-1	20				13	07			
	Pakistan-2013	20	17	03						
	F$_1$	18	18							
	F$_2$	200	92	32	19	18	39	3:1	0.67	0.39
TD-1 × NIA-Sarang	TD-1	20				13	07			
	NIA-Sarang	20	17	03						
	F$_1$	22	20	02						

	F_2	200	67	52	34	11	38	3:1	0.56	0.28
TJ-83 × Benazir	TJ-83	20				09	11			
	Benazir	20	12	06						
	F_1	19	17	02						
	F_2	200	73	44	28	07	48	3:1	0.43	0.03
TJ-83 × Pakistan-2013	TJ-83	20				09	11			
	Pakistan-2013	20	17	03						
	F_1	17	17							
	F_2	200	53	83	13	24	27	3:1	045	0.78
TJ-83 × NIA-Sarang	TJ-83	20				09	11			
	NIA-Sarang	20	17	03						
	F_1	25	23	02						
	F_2	200	43	70	31	15	41	3:1	0.11	0.30
Kiran-95 × Benazir	Kiran-95	20				12	08			
	Benazir	20	12	06						
	F_1	21	21							
	F_2	200	37	90	14	22	37	3:1	0.65	0.12
Kiran-95 × Pakistan-2013	Kiran-95	20				12	08			
	Pakistan-2013	20	17	03						
	F_1	27	26	01						
	F_2	200	41	77	21	25	36	3:1	0.77	0.24
Kiran-95 × NIA-Sarang	Kiran-95	20				12	08			
	NIA-Sarang	20	17	03						
	F_1	19	18	1						
	F_2	200	39	71	35	26	29	3:1	0.78	0.18
Khirman × Benazir	Khirman	20				07	13			
	Benazir	20	12	06						
	F_1	23	20	03						
	F_2	200	33	45	43	15	52	3:1	0.73	0.88
Khirman × Pakistan-2013	Khirman	20				07	13			
	Pakistan-2013	20	17	03						
	F_1	29	23	04						
	F_2	200	56	51	23	14	54	3:1	0.67	0.28
Khirman × NIA-Sarang	Khirman	20				07	13			
	NIA-Sarang	20	17	03						
	F_1	22	20	2						
	F_2	200	33	67	40	33	27	3:1	0.68	0.34
NIA-Amber × Benazir	NIA-Amber	20				13	07			
	Benazir	20	12	06						
	F_1	31	27	04						
	F_2	200	47	70	29	15	31	3:1	0.87	0.54
NIA-Amber× Pakistan-2013	NIA-Amber	20				13	07			
	Pakistan-2013	20	17	03						

	F_1	23	20	03						
	F_2	200	56	52	53	17	22	3:1	0.39	0.68
NIA-Amber × NIA-Sarang	NIA-Amber	20				13	07			
	NIA-Sarang	20	17	03						
	F_1	14	13	01						
	F_2	200	43	56	54	18	39	3:1	0.28	0.89
NIA-Sundar × Benazir	NIA-Sundar	20				10	10			
	Benazir	20	12	06						
	F_1	38	37	01						
	F_2	200	52	62	33	23	30	3:1	0.10	0.60
NIA-Sundar × Pakistan-2013	NIA-Sundar	20				10	10			
	Pakistan-2013	20	17	03						
	F_1	27	27							
	F_2	200	33	80	27	31	39	3:1	0.25	0.92
NIA-Sundar × NIA-Sarang	NIA-Sundar	20				10	10			
	NIA-Sarang	20	17	03						
	F_1	33	31	02						
	F_2	200	45	56	37	31	31	3:1	0.73	0.38

Conclusions

From lines/female inbreds, TD-1 was on top by showing greater and significant GCA effects for maximum number characters including grain yield in both (F_1 and F_2) populations. In contrast, tester/male inbred Benazir remained exceptional by showing higher and significant GCA effects for majority of the studied traits including grain yield in F_1 and F_2 populations. Regarding the SCA effects in F_1 population, the hybrids TD-1 × Pakistan-2013, TJ-83 × Benazir, and NIA-Sundar × NIA-Sarang and from F_2 populations, the crosses TD-1 × Benazir, TJ-83 × Benazir, Kiran-95 × NIA-Sarang and NIA-Amber × Pakistan-2013 expressed desirable and maximum SCA effects for number of traits including grain yield, thus may be preferred in future wheat breeding programs. Disease reaction on selected 18 F_2 populations was performed, the introgression stripe rust resistance showed single dominant gene.

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