Research article

Heritability, genetic gain and detection of gene action in hexaploid wheat for yield and its related attributes

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Abstract: Selection of promising genotypes from a diverse genetic pool and their utilization for hybridization is an important strategy for wheat crop improvement. The data from ten parents and their F_1 progenies using line ×tester mating scheme were analyzed to assess the effects of combining ability for yield and its cognate characters using randomized complete block design with three replications. Data were taken for grain yield and its associated characters like plant height, peduncle and spike length, flag leaf area, per plant tillers, spikelets spike^{-1}, grains spike^{-1}, spike density, thousand-grain weight and grain yield plant^{-1}. Analysis of variance was used to statistically analyze the data. Line × tester analysis was used to find out association among traits and to estimate the effects of GCA and SCA. Highly significant differences were found among parents (lines, testers) and their F_1 hybrids for all the parameters under study. Among parents, Line 9796 and tester 107 manifested as best general combiners and exhibited significant GCA effects for almost all the mentioned traits. In the case of F_1 hybrids, 9793 × 118 and Punjab-2011 × 108 were recognized as best specific combiners exhibiting significant SCA effects. A higher value of SCA variance than the variance of GCA revealed the preponderance of non-additive genetic action. The degree of dominance revealed the involvement of both type of gene action for the traits under investigation. The deviations among total variation were mainly due to genotypes. Most of the yield associated traits were highly heritable with more than 80% heritability. These findings were confirmed by genetic gain. Thus, potential homozygous lines can be selected from transgressive segregants to improve yield and these crosses will be beneficial for commercial exploitation to heterosis.

Keywords: wheat; line × tester; combining ability; gene action; yield

Abbreviations: PH: Plant height (cm); FLA: Flag leaf area (cm^2); SL: Spike length (cm); PL: Peduncle length (cm); Tp^{-1}: Productive tiller plant^{-1}; Gsp^{-1}: Grains spike^{-1}; Spsp^{-1}: Spikelets spike^{-1}; SD: Spike density; 1000 Gwt: 1000 -grain weight (g); GylP: Grain yield plant^{-1}; D.F: Degree of freedom; Cov. H. S: Covariance of Half-Sib; Cov. F. S: Covariance of Full-Sib; σ^2GCA: Variance of GCA; σ^2D: Additive genetic variance; σ^2SCA: Variance of SCA; σ^2H: Dominant genetic variance; σ^2GCA/σ^2SCA: Variance ratio of GCA to SCA; Degree of dominance: sqrt(σ^2D/σ^2H); Ve: Environmental variance; Vg: Genotypic variance; Vp: Phenotypic variance; H^2: Heritability; GA: Genetic advance; CV: Coefficient of variability.

1. Introduction

Wheat belongs to family poaceae. A leading food grain regarding nutrition and production among cereals that have major importance in agricultural policies. It is being the staple food, occupies the central position in Asia. It imparts 20% calories and 55% carbohydrates of the world's requirement annually [1]. In Pakistan's agriculture during the year 2017–2018, its contribution is 9.1% to value addition and 1.7% to GDP. Its area under cultivation was reduced up to 8.734 million hectares while production stood at 25,492 thousand tonnes with a yield of 2919 kg/ha as compared with 8.972 million hectares, 26,674 thousand tonnes and 2973 kg/ha respectively during 2016–2017. Area, production and yield decreased up to 2.6%, 4.4% and 1.8% respectively in the year 2017–2018 [2]. As the environmental stress and population rate are increasing day by day, breeders should develop the new superior varieties as well as existing varieties should be improved to meet the challenges of the variable environmental conditions. It is predicted that the population of the world will increase up to 9.3 billion by the year 2050 [3]. Hence, to meet the feed requirements of such a large population, production of cereals should be improved [4]. Cereals could be biofortified with beneficial micronutrients like (organic microelements; selenium; zinc and amylose) to overcome the world's dietary needs [5,6]. In rice, the biofortification leads to accumulation of beneficial nutrients (selenium) more than 75% into the edible parts of the plants [7].

Developing high yielding, semi-dwarf, disease resistant and biofortified varieties that also have a broad range of adaptation under variable agro-climatic conditions is an alternative avenue to fulfil burning issues. To meet this objective, genetic variation based on performance and degree of dominance among parents and their hybrids should be determined. Parental lines and their superior crosses could be selected through estimation of gene action and its magnitude using combining ability analysis. The pattern of inheritance for yield and its cognate characters can be predicted using a statistical approach elaborated by Kempthorne (1957). Line × tester mating approach is a well-known mating design to evaluate parents and their hybrids, where a greater number of crosses and a fewer number of parents can be tested at a time. Hence, the present investigation was carried out to determine the genetic action and combining ability estimates, and to screen out parents and hybrids with more general and specific combining ability effects for grain yield and its cognitive traits. The particulars achieved with the help of this investigation will be worthwhile for the selection

of favourable parental lines/varieties and their superior hybrids to exploit them for an efficacious breeding program.

2. Materials and methods

This experiment was carried out in the field area of Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan during the cropping season 2013/2014–2014/2015.

2.1. Experimental material

The experimental material consisted of six different spring wheat lines/varieties, namely 9793, 9795, 9796, Galaxy-2013 (abbreviated as Glxy13 in short), Millat-2011 (abbreviated as Mlt11 in short) and Punjab-2011 (abbreviated as PB11 in short) and material taken from ESWYT (Elite Spring Wheat Yield Trial) namely 107, 117, 118 and 108 were used as testers. This material was crossed in line × tester mating fashion in the crop season (2013–2014). At maturity, seeds were harvested and saved separately for each cross.

2.2. Sowing method and data collection

F_1 hybrid seeds along their ten parents were sown in the field using triplicated RCBD (randomized complete block design) during crop season in 2014. In each block of the experimental unit, varieties were assigned randomly. At maturity ten well-guarded plants from each line were taken and data were recorded for the characters: plant height (cm), flag leaf area (cm^2), spike and peduncle length (cm), number of tillers per plant, grains spike^{-1}, spikelets spike^{-1}, spike density, thousand-grain weight (g), per plant grain yield (g). Production technology and other data collection practices were the same as our previous report [8] for the mentioned traits. The data presented for parents was the pooled data of two years (when crosses made and later sown year) and presented as mean average data of 2 years while the data presented for F_1 were 1-year triplicate mean average data. Moreover, triplicate experimental repeats of material at different places made the results statistically more significant and reduced the experimental error.

2.3. Statistical analysis

The data collected for the above-mentioned parameters were expressed as mean with least significant differences (LSD$_{0.05}$), then subjected to analysis of variance as given by [9] to find out significant differences among hybrids and parents. Data were then analyzed using line × tester analysis [10] to compute GCA and SCA effects. Significance for GCA and SCA effects was determined using t-test as determined by [11]. Taking the expectations of mean squares for line × tester analysis, GCA and SCA variances were computed taking the inbreeding coefficient (F) equal to one as both parents (lines and testers) were inbred [12]. The predominance of gene action (additive or non-additive) in the expression of the characters was determined by comparing the ratio of GCA and SCA then computing the degree of dominance by using this formula.

$$\text{Degree of dominance} = \text{Sqrt} (\sigma^2 H/\sigma^2 D) \tag{1}$$

Different variances (V_g, V_p and V_e), heritability, genetic gain and coefficient of variability (CV) were computed following formula [13]. Figures and Radar graph were built using software Origin version 8.0 and Microsoft Excel 2016.

3. Results and discussion

3.1. Estimates of mean square values

For all the morphometric traits under study, mean square values were observed using line × tester analysis, presented in Table 1. Results of analysis of variance revealed that all the treatments were highly significant ($p < 0.01$) for all the characters under study while non-significant differences were observed among replications. Differences were highly significant among parents for all the parameters excluding peduncle length and number of spikelets spike^{-1}. Testers showed highly significant differences for all the characters while significant for peduncle length and non-significant for spike density. Highly significant differences were found in all crosses for all the characters. Significant differences were observed for three traits viz. 1000-grain weight, plant height and the flag leaf area in interaction (parents vs crosses) while non-significant for all the other traits. Interaction (line × tester) depicted differences that were significant for spikelets spike^{-1}, flag leaf area and peduncle length while differences were highly significant for the other traits. Significant differences among wheat genotypes for yield and its cognate characters were also demonstrated in various previous studies [14–16]. So, it is justifiable to estimate effects of GCA and SCA for those parameters which exhibited significant differences among genotypes.

3.2. Comparison of mean performances of parents and crosses

Mean values and average mean between different parental lines and testers can be seen under Figure 1 (Table S1). Among parents, highest mean values were depicted by line Punjab-2011 for spike length (14.02 cm), peduncle length (30.50 cm), per plant tillers (13.2) and grains spike^{-1} (75.93). While tester 107 performed best for spike density (1.76) and grain yield plant^{-1} (28.3 g). Lines 9795, 9796 and Galaxy-2013 contributed more for spikelets spike^{-1} (20.86), flag leaf area (51.74 cm^2) and 1000-grain weight (47.35 g) respectively. Mean values for hybrids can be evaluated at Figure 2 (Table S2). Among crosses, Punjab-2011 × 108 contributed more in average mean performance for most of the traits viz. plant height (105.83 cm), peduncle length (30.33 cm), number of grains spike^{-1} (76.76) and grain yield plant^{-1} (28.43 g). For 1000-grain weight (50.66 g) and flag leaf area (50.09 cm^2), 9796 × 118 showed highest mean values. 9796 ×117, 9795 ×107 and Millat-2011 ×117 showed the highest mean values for spike length (14.29 cm), tillers plant^{-1} (13.86) and spikelets spike^{-1} (21.26) respectively. For spike density (1.71), Galaxy-2013 × 107 performed better. However, mean performances are not a valid measure to assess variation between parents and hybrids. The data should be subjected to mean square values for differences among lines, testers and their interaction in order to assess GCA and SCA estimates.
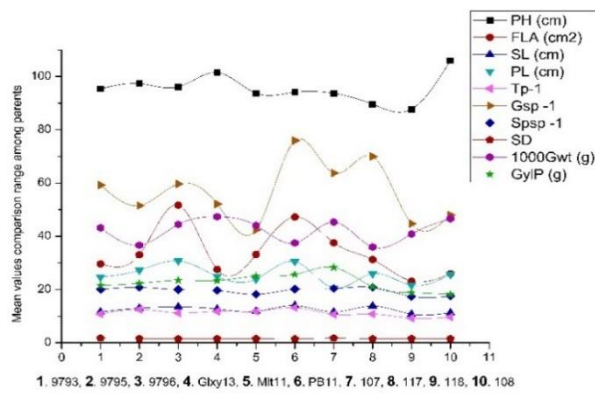
Figure 1. Mean performance for 10 parents (6 lines and 4 testers) compared at least significant difference (LSD) 0.05. Figure's data can be found in Table S1.
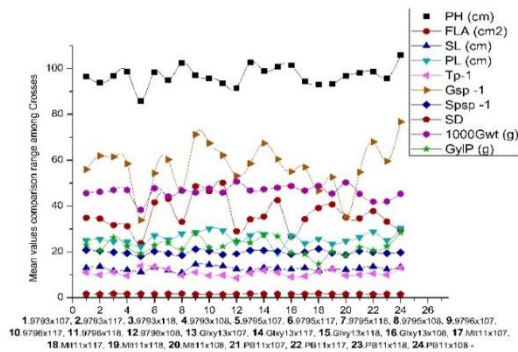

Figure 2. Mean performance for 24 crosses compared at least significant difference (LSD) 0.05. Figure's data can be found in Table S2.

3.3. Estimates of general combining ability (GCA) effects

Based on mean square analysis of variance for combining abilities, GCA effects were estimated for all yield cognate traits (Table 2). Among parents, significant and negative GCA effects for the plant height were observed in three lines (9793, 9795 and Millat-2011) and one tester 117. While other parental lines possess negative and non-significant GCA effects for this trait (Table 2). Thus, these four parents were good general combiners for dwarfness. About 40% of parental lines showed significant GCA effects in a negative desirable direction and can be utilized for wheat improvement for plant height. Nazir S, et al. [17] also supported similar results and found a strong positive association of dwarfness with yield. Line 9796 was prominent for most of the characters under study. During grain filling, flag leaf fixes a huge amount of photosynthates to the grains in cereals and have a major role towards grain yield [18]. For flag leaf area, line 9796 and tester 118 manifested as good general combiners showing significant and positive GCA effects. Similar results were found by [19], [20] and [21] while the findings of [22] were in contradiction to the present study. For spike length, grains spike^{-1} and peduncle length, spikelets spike^{-1}, thousand-grain weight and grain yield plant^{-1}, positive and significant GCA estimates were revealed by line 9796, while most of the parental lines had negative undesirable GCA effects for this character. Positive effects of GCA are also reported in [22–27] for these traits. While [28] and [29] had a contradiction with the present results. Tester 107 exhibited significant positive GCA effects for tiller plant^{-1}, spikelets spike^{-1}, spike length, spike density and yield plant^{-1} [30–32]. Many researchers found deviated results for spikelets spike^{-1} and 1000-grain weight [33,34].

3.4. Estimates of specific combining ability (SCA) effects

All cross combinations manifested considerable variation for specific combining ability effects (Table 3). Among crosses, Millat-2011 × 118 revealed as the best specific combiner for the plant height which had shorter plant height than the mean values of parents involved in each cross combination and can be utilized in wheat improvement program as reported by [35]. Out of all cross combinations, Punjab-2011 × 108 was evinced as the best specific combiner for the maximum characters under study, e.g., spike length, tillers plant^{-1}, grains spike^{-1} and per plant grain yield. 9795 × 108 had good SCA effects for flag leaf area. These findings were in concurrence with [21,24,25,29,36]. Millat-2011 × 117 was good specific combiner for spikelets spike^{-1} and spike density while 9793 × 118 for peduncle length and thousand grain-weight. Similar results were predicted by [37]. It was observed that at least one of the parents that contributed in SCA effects, appeared as a good general combiner for that specific trait so selection from the transgressive segregants of these crosses probably will be fruitful for genetic improvement [38] and pure lines can be developed due to additive gene action even when SCA effects showed non-significant values as mentioned by [39]. Likewise, some parents involved in crosses were good general combiners while proved poor specific combiners. Thus, parents with high GCA effects were not always showed high SCA effects indicating that negative direction was taken as a favourable SCA effect for traits like grain filling, maturity and plant height [15,35].

3.5. Contribution to the total variance, gene action, degree of dominance, heritability and genetic gain

The paternal influence was not so obvious among all the traits except for spikelets spike[-1] (Figure 3). The results depicted that maternal and maternal × paternal interaction contributed more to genetic variation of cognate traits. Plant height, flag leaf area, tillers plant[-1], peduncle length, spike density and yield plant[-1] were contributed by interaction (maternal × paternal), while spike length, 1000 grain -weight and grains spike[-1] had more maternal influence (Table S3). These findings were in concurrence with [13] while in contradiction with [12] where paternal influence was more dominant for studied traits.
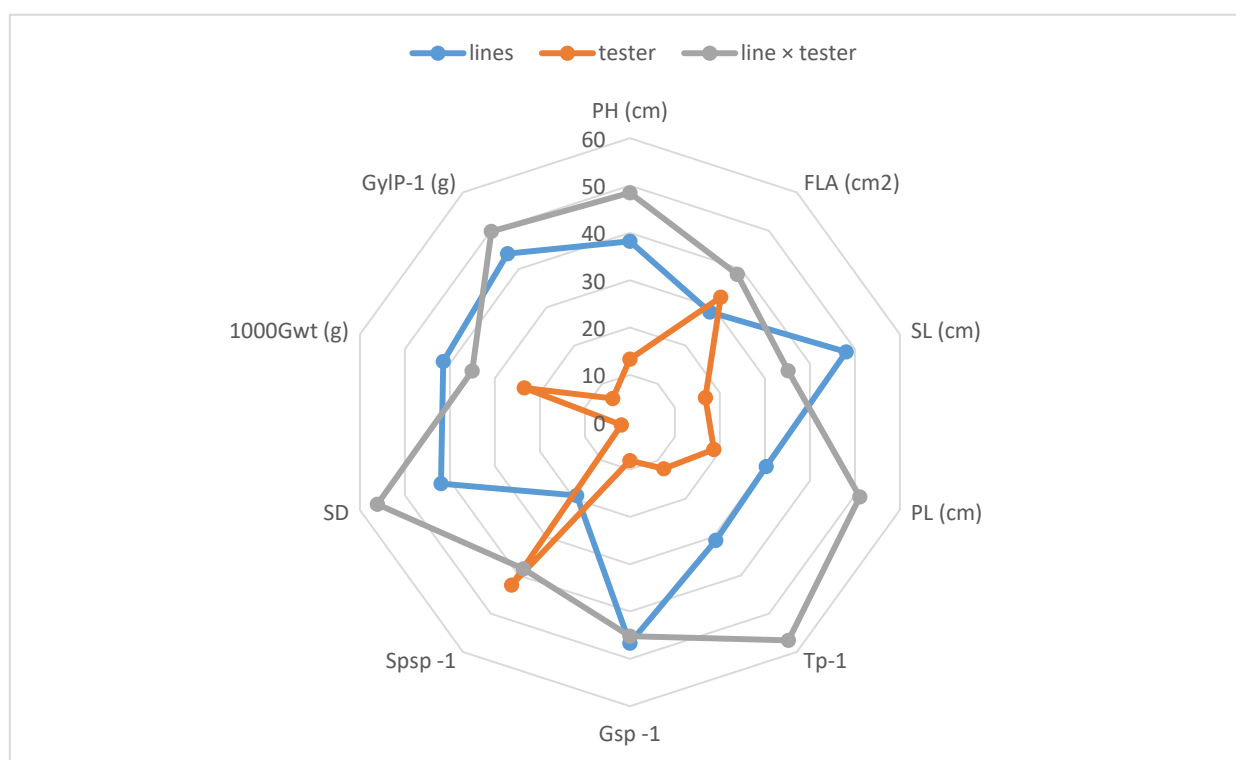
Figure 3. Proportional contribution of material under study towards total genetic variation. Figure's data can be found in Table S3.

It was noticed that SCA variance was dominant over GCA variance for all the characters. Non-additively controlled gene action was found prominent than additive for most of the traits as escorted by additive and dominant genetic variances while confirmed by the degree of dominance results (Table 4). Spike length, spikelets spike[-1] and 1000grain weight were conditioned by additive genetic effect while all the other parameters were under the control of non-additive gene action. The result was strengthened by the variance ratio of GCA to SCA as found less than unity while the dominant genetic variance was more than additive variance for all traits except for spike length, 1000 grain- weight and spikelets spike[-1]. Ratios of genetic variances exhibited that all the yield cognate characters were non-additively controlled showing the preponderance of dominant gene action for them that was also demonstrated by [12,40] and [24]. While [41] and [42] confirmed additive genetic action for all the yield cognate traits.

Major involvement in phenotypic variation was due to genotypes, as environmental variance seems to influence a little for total phenotypic variability (Table 5). The results implied that the major proportion of variability and gene action was due to genotypes. While the coefficient of variability (C.V) disclosed the experiment was successfully conducted in field conditions. As C.V was below 15 for all the studied parameters. Experimental results indicate the involvement of the non-additive type of gene action for traits inheritance. These results were further subjected to estimate heritability and genetic gain to confirm at what proportion inheritance of traits takes place, and what are the probabilities of the estimated trait to be transferred into the next generation. As can be seen from Table 5, the traits like plant height, flag leaf area, grains spike^{-1}, 1000- grain weight and grain yield plant^{-1} disclosed more than 80% heritability into next generation while spikelets spike^{-1} and spike length were heritable with 53.2% and 74.8% probability to next generation. However, traits like peduncle length and spike density were computed with low heritability. These findings were confirmed by the expected genetic gain into next generation [43]. All the yield cognate traits were highly heritable with maximum genetic gain than other metric characters. A similar trend for grain yield and 1000 -grain weight was observed by [8,13] while the result obtained by Fellahi and Hussain for yield-related traits [12,44] were in contradiction with the present study. Hence, short stature and high yielding varieties can be developed by controlling the favourable genes for plant height, peduncle length and spike related traits. Additionally, this study indicated the involvement of gene action particularly additive in the present scenario for the inheritance of spike length especially spikelets spike^{-1} with highly heritable features.

Table 1. Mean square values from analysis of variance (ANOVA).

Source of Variation	D.F	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
Replication	2	2.104 ns	1.832 ns	0.046 ns	4.376 ns	1.327 ns	5.771 ns	1.854 ns	0.0061 ns	3.789 ns	2.501 ns
Genotypes	33	61.296**	164.881**	5.358**	22.716**	5.495**	307.328**	2.929**	0.031**	39.838**	31.017**
Parents	9	84.346**	251.437**	3.949**	33.057**	4.383*	360.510**	5.189**	0.032**	52.955**	28.453**
Crosses	1	53.183**	133.497**	2.534**	19.538**	6.036**	299.398**	2.119**	0.032**	21.588**	33.293**
Parents vs Crosses	23	40.455**	107.436**	1.249 ns	2.746 ns	3.0713 ns	11.088 ns	1.217 ns	0.0021 ns	341.558**	1.744 ns
Lines	5	93.515**	176.565**	5.603**	27.211*	8.571**	642.934**	1.868*	0.063**	41.182**	67.396**
Testers	3	54.298**	334.081**	3.262**	27.918*	5.623*	186.239**	6.911**	0.0047 ns	38.845**	15.754**
Lines × Testers	15	39.517**	79.021*	1.366**	15.303*	5.273**	207.519**	1.244*	0.028**	11.605**	25.435**
Error	66	2.05121	2.027878	0.538281	8.294102	1.828286	4.496943	0.662793	0.011033	1.918604	1.743431

Different values derived from ANOVA indicate significant differences at probability; ** = $p \leq 0.01$; * = $p \leq 0.05$; ns = Non-significant.

Table 2. General combining ability effects of parents.

Lines	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
9793	−0.444*	−3.238*	−0.104*	−1.127*	−0.379*	1.984	0.306	0.037	0.23	0.59
9795	−1.440*	−0.910*	−0.899*	−0.306*	1.537	−8.606*	−0.759*	0.053	−1.978*	−0.709*
9796	−2.386	7.250*	1.121*	2.058*	−1.012	6.018*	0.090*	−0.125	1.297*	1.773*
Glxy13	4.14	−1.585*	−0.093*	−0.703*	−0.129*	2.893	0.306	0.03	1.494	1.915
Mlt11	−2.565*	0.976	−0.363*	−1.578*	−0.112*	−9.590*	0.065	0.051	1.567	−4.434*
PB11	0.413	0.411	0.211	0.831	0.39	0.612	0.235	0.03	0.399	0.381
Testers										
107	−1.093	−1.239	0.063*	−0.46	0.204*	−2.251	0.351*	0.021*	−1.445	0.068*
117	−0.465*	2.85	0.564	1.482	0.315	3.481	0.651	−0.015*	0.381	−1.165*
118	−1.012	3.923*	−0.205	−1.439	0.315*	1.943*	−0.276	0.001	−0.823	1.123*
108	2.571	−5.534*	−0.422*	0.417	−0.834*	−3.173*	−0.726*	−0.007*	1.887	−0.026*

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Lines	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
S.E Lines	0.413	0.411	0.211	0.831	0.39	0.612	0.235	0.03	0.399	0.381
S.E Tester	0.337	0.335	0.172	0.678	0.318	0.499	0.191	0.024	0.326	0.311

S.E = Standard Error; * = $p \leq 0.000$.

Table 3. Specific combining ability effects of crosses.

Crosses	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
9793 × 107	1.240*	3.098*	0.274*	0.610*	0.379*	−1.223	0.315*	−0.004	0.581*	−0.084
9793 × 117	−2.234*	−1.460*	0.446	−0.827*	−0.798*	−1.023*	−0.384*	−0.090*	−0.618*	−1.251*
9793 × 118	1.319*	−5.293	−0.696	1.116*	0.401*	0.048*	0.009*	0.093*	1.367*	2.059*
9793 × 108	−0.324*	3.656	−0.023*	−0.899*	0.018	2.198	0.059	0.002	−1.330*	−0.723*
9795 × 107	−8.436*	−10.38*	−0.690*	−2.869*	1.329	−12.77*	−1.284*	−0.020*	−4.435*	−2.584*
9795 × 117	3.521	3.326	0.875	−0.085*	0.684	1.968	0.548	−0.076*	3.134	2.248
9795 × 118	0.469	3.837	0.225	1.075	−0.248*	9.473	0.543	0.01	0.766	0.959
9795 × 108	4.445*	3.218*	−0.411	1.879*	−1.765	1.323*	0.193*	0.086*	0.535*	−0.623
9796 × 107	3.676	6.304	0.668	0.951	1.079	9.976	0.931	−0.008*	−0.161*	3.731
9796 × 117	1.734*	0.126*	−0.059	0.636*	−0.431	0.476*	−0.168	−0.004	−0.235	−1.301
9796 × 118	0.105*	2.619*	0.204*	2.704*	−0.298	−3.284	−0.773	−0.079	−0.862	−3.09
9796 × 108	−5.515	−9.05	−0.812	−4.292	−0.348	−7.168	0.009*	0.092*	1.259*	0.659*
Glxy13 × 107	2.768	0.71	−0.603*	2.326	−0.137*	0.434	0.181	0.097	0.527	−0.476*
Glxy13 × 117	−1.546	−2.153	−0.037	0.821*	0.884*	3.568*	−0.118	−0.011	−0.765	4.023*
Glxy13 × 118	0.9	3.885	0.479	−4.274*	0.018	−1.826*	0.409	−0.026*	1.099	1.234
Glxy13 × 108	−2.123	−2.443	0.162*	1.126*	−0.765	−2.176	−0.473	−0.059	−0.861	−4.781
Mlt11 × 107	1.051*	−1.786	0.593*	−0.171	−1.554	11.351*	−0.376	−0.106	0.385*	0.840*
Mlt11 × 117	−0.893	−1.002	−1.201	−0.22	0.334*	−4.748	0.790*	0.228*	0.595*	−2.159
Mlt11 × 118	−0.026*	−0.500*	0.269	0.514	1.401	2.756	−0.048*	−0.043*	−1.566*	0.951
Mlt11 × 108	−0.130*	3.289	0.338	−0.122*	−0.181*	−9.359*	−0.365*	−0.077*	0.586	0.368

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Crosses	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
PB11 ×107	−0.299*	2.055	−0.241*	−0.848*	−1.095*	−7.773*	0.231	0.042	3.103	−1.426*
PB11 ×117	−0.581*	1.163	-0.022*	−0.323*	−0.673*	−0.240*	−0.668*	−0.044*	−2.11*	−1.559*
PB11 ×118	−2.767*	−4.548*	−0.482*	−1.135*	−1.273*	−7.168*	−0.140*	0.045	−0.804*	−2.115*
PB11 ×108	3.648*	1.329*	0.747*	2.307*	3.043*	15.181*	0.576*	−0.043	−0.188	5.101*
S.E Crosses	0.826	0.822	0.423	1.662	0.78	1.224	0.47	0.06	0.799	0.762

* = $p \leq 0.000$.

Table 4. Genetic component variations (additive, dominance genetic effects and degree of dominance).

Genetic components	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
Cov. H. S. lines	4.4994	8.1281	0.353	0.9922	0.2748	36.2845	0.0519	0.0028	2.4647	3.4966
Cov. H. S. testers	0.8211	14.1697	0.1052	0.7008	0.0194	−1.1821	0.3147	−0.0012	1.5132	-0.5378
Cov. H. S. (Av.)	1.4967	4.8186	0.0985	0.5084	0.1283	9.2129	0.077	0.0007	0.841	0.9003
Cov. F. S.	20.6297	66.4495	0.9898	5.2306	1.5964	116.76	0.9184	0.007	9.8221	11.784
σ^2GCA	1.4967	4.8186	0.0985	0.5084	0.1283	9.2129	0.077	0.0007	0.841	0.9003
When F = 0, σ^2D	23.9482	77.099	1.5762	8.1356	2.054	147.4073	1.232	0.0113	13.4562	14.4063
When F = 1, σ^2D	5.987	19.2747	0.394	2.0339	0.5135	36.8518	0.308	0.0028	3.364	3.6015
σ^2SCA	49.9572	102.665	1.1033	9.3458	4.5935	270.6958	0.7758	0.0222	12.9154	31.5893
When F = 0, σ^2H	49.9572	102.665	1.1033	9.3458	4.5935	270.6957	0.7758	0.0222	12.9154	31.5893
When F = 1, σ^2H	12.4893	25.6662	0.2758	2.3364	1.1483	67.6739	0.1939	0.0055	3.2288	7.8973
σ^2GCA/σ^2SCA	0.02996	0.046935	0.089278	0.054399	0.027931	0.034034	0.099252	0.031532	0.065116	0.0285
Degree of dominance	1.444317	1.15395	0.836645	1.071799	1.495449	1.355131	0.793541	1.401643	0.979699	1.480791

Table 5. Heritability, genetic gain and coefficient of variability.

	PH (cm)	FLA (cm2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	$Spsp^{-1}$	SD	1000 Gwt (g)	$GylP^{-1}$ (g)
V_e	2.0	2.0	0.5	8.3	1.8	4.5	0.7	0.0110	1.9	1.7
V_g	19.74896767	54.28190733	1.604433	4.807209333	1.222427	100.9439523	0.755481	0.006679333	12.640002	9.758163
V_p	21.79826467	56.30978533	2.142714	13.10131133	3.050713	105.4408953	1.418274	0.017712333	14.558606	11.501594
H^2	0.905988067	0.963987112	0.748785419	0.366925815	0.400702065	0.957351054	0.532676338	0.377100702	0.86821513	0.848418315
GA	7.444681218	12.73139027	1.929088492	2.337482233	1.23178504	17.30168617	1.116493357	0.088329932	5.830420984	5.064093545
CV %	1.5	4.0	5.8	11.1	12.4	3.7	4.1	6.7	3.1	5.8

Table S1.

Lines	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	$Spsp^{-1}$	SD	1000 Gwt (g)	$GylP^{-1}$ (g)
9793	95.4	29.6	11.6	24.7	10.8	59.2	20.1	1.7	43.2	21.6
9795	97.3	33.1	13.0	27.3	12.5	51.5	20.9	1.6	36.7	22.3
9796	96.2	51.7	13.5	30.8	11.2	59.7	20.0	1.5	44.5	23.4
Glxy13	101.5	27.6	12.7	24.9	11.8	52.1	19.7	1.5	47.4	23.4
Mlt11	93.7	33.2	11.8	23.9	11.8	42.4	18.2	1.5	44.1	25.0
PB11	94.1	47.3	14.0	30.5	13.2	75.9	20.2	1.4	37.5	25.7
Mean	96.379	37.074	12.787	27.011	11.888	56.816	19.833	1.557	42.206	23.561
Testers										
107	93.7	37.6	11.6	20.6	10.7	63.7	20.4	1.8	45.4	28.3
117	89.6	31.3	13.8	26.0	10.8	70.0	20.8	1.5	36.0	21.1
118	87.8	23.2	10.8	21.6	9.3	44.7	17.4	1.6	40.9	18.8
108	106.0	25.9	11.3	25.7	9.7	48.0	17.5	1.6	46.6	18.2
Mean	94.268	29.506	11.877	23.457	10.108	56.608	19.051	1.611	42.206	21.608

Table S2.

Crosses	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
9793 ×107	96.6	34.9	12.9	25.0	11.0	56.0	20.7	1.6	45.6	23.1
9793 ×117	93.8	34.5	13.6	25.5	9.9	61.9	20.3	1.5	46.2	20.7
9793 ×118	96.8	31.7	11.7	24.5	11.1	61.4	19.8	1.7	47.0	26.3
9793 ×108	98.7	31.2	12.1	24.3	9.6	58.5	19.4	1.6	47.0	22.3
9795 ×107	85.9	23.8	11.1	22.3	13.9	33.8	18.1	1.6	38.4	19.3
9795 ×117	98.5	41.6	13.2	27.0	13.3	54.3	20.2	1.5	47.8	22.9
9795 ×118	94.9	43.2	11.8	25.3	12.4	60.3	19.3	1.6	44.2	23.9
9795 ×108	102.5	33.1	10.9	27.9	9.7	47.0	18.5	1.7	46.7	21.1
9796 ×107	97.1	48.6	14.5	28.5	11.1	71.2	21.1	1.5	45.9	28.1
9796 ×117	95.8	46.5	14.3	30.1	9.7	67.4	20.3	1.4	47.7	21.8
9796 ×118	93.6	50.1	13.8	29.3	9.8	62.1	18.8	1.4	45.8	22.3
9796 ×108	91.6	29.0	12.6	24.1	8.6	53.1	19.1	1.5	50.7	24.9
Glxy13 ×107	102.7	34.2	12.0	27.1	10.7	58.5	20.6	1.7	46.8	24.0
Glxy13 ×117	99.0	35.4	13.1	27.6	11.9	67.4	20.6	1.6	47.3	27.3
Glxy13 ×118	100.9	42.5	12.8	19.5	11.0	60.5	20.2	1.6	48.0	26.8
Glxy13 ×108	101.5	26.7	12.3	26.8	9.1	55.0	18.9	1.5	48.7	19.6
Mlt11 ×107	94.3	34.3	13.0	23.7	9.3	57.0	19.8	1.5	46.7	19.0
Mlt11 ×117	93.0	39.1	11.7	25.6	11.3	46.6	21.3	1.8	48.8	14.7
Mlt11 ×118	93.3	40.7	12.4	23.4	12.4	52.6	19.5	1.6	45.4	20.1
Mlt11 ×108	96.8	35.0	12.2	24.7	9.7	35.3	18.7	1.5	50.3	18.4
PB11 ×107	98.2	34.6	12.8	26.3	10.0	54.7	20.3	1.6	45.3	22.0
PB11 ×117	98.6	37.8	13.5	28.8	10.5	68.0	19.7	1.5	41.9	20.6
PB11 ×118	95.8	33.2	12.3	25.0	9.9	59.5	19.3	1.6	42.0	22.4
PB11 ×108	105.8	29.6	13.3	30.3	13.1	76.8	19.6	1.5	45.3	28.4
Mean	96.917	36.299	12.666	25.949	10.795	57.456	19.759	1.568	46.222	22.492

Table S3.

Proportional Contribution	PH (cm)	FLA (cm^2)	SL (cm)	PL (cm)	Tp^{-1}	Gsp^{-1}	Spsp^{-1}	SD	1000 Gwt (g)	GylP^{-1} (g)
lines	38.22357	28.75209	48.06333	30.27737	30.86987	46.68298	19.15755	41.98285	41.47044	44.00507
tester	13.31699	32.64147	16.78264	18.63865	12.15196	8.113644	42.53734	1.899425	23.47004	6.171885
line × tester	48.45944	38.60644	35.15402	51.08398	56.97817	45.20338	38.30512	56.11772	35.05953	49.82305
Total variability	100	100	100	100	100	100	100	100	100	100

4. Conclusions

It could be deliberated from this study that all lines, testers and their cross combinations had significant variations. SCA variance was greater than variance computed for GCA explicated that an inheritance of studied parameters was prominent with the non-additive type of gene action. Among parents, line 9796 and tester 107 appeared as best general combiner while Punjab-2011 × 108 and 9793 × 118 were the cross combinations that manifested as best specific combiners for most of the mentioned parameters. Thus, parental genotypes with good GCA and specific cross combinations scored good SCA should be involved in multiple crosses to make tangible improvement of yield and its cognate characters in spring wheat. Moreover, the involvement of both types of gene actions opens a new chapter of discussion. As dominant type of gene action was prominent for yield-related traits, the selection of paternal and maternal lines proved to be best specific combiners should be utilized for yield enhancement in the next generation while the heritability and genetic gain for these traits indicated a broader spectrum of acclimatization of yield-related traits in the next generation as non-additive gene action was prominent.

Conflict of interest

All authors declare no conflicts of interest in this paper.

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