



Full Length Article

Assessment of Genetic Effects for Earliness and Yield Traits in F₁ and F₂ Half Diallel Populations of Wheat

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Abstract

To develop high yielding wheat cultivars, it is imperative to study the genetic makeup of diverse wheat lines, and inheritance pattern of earliness and yield traits under existing environmental conditions. Inheritance of pre- and post-harvest yield-associated traits was studied in 6 × 6 F₁ and F₂ half diallel populations using Hayman's genetic analysis. Six diverse wheat genotypes were crossed in a half diallel fashion during 2010–2011. Parental genotypes along with their respective F₁ and F₂ half diallel populations were evaluated during 2011–2012 and 2012–2013 to explore the genetic basis of various traits. Genotypes differed significantly ($p \leq 0.01$) for all the traits in both generations. According to scaling tests, additive-dominance model was partially adequate for all the traits in both generations. The significance of additive (D) and dominance (H₁ and H₂) components of genetic variance revealed the involvement of both additive and non-additive gene effects for days to maturity, peduncle length, spikelets per spike, grains per spike, grain yield and harvest index. The values of H₂/4H₁ were lower than optimum value (0.25) for all the traits which indicated the asymmetrical distribution of positive and negative genes among the parental genotypes. However, according to components of genetic variance and Vr-Wr graphs, over-dominance type of gene action was predominant for the majority of the traits. Broad-sense heritability values were greater than narrow sense, which also confirms non-additive gene effects. Prevalence of over-dominance type of gene action revealed that selection could be delayed to later segregating generations to improve yield traits. © 2018 Friends Science Publishers

Keywords: Genetic components of variance; Additive and non-additive gene action; Earliness and yield traits; F₁ and F₂ half diallel populations; *Triticum aestivum* L.

Abbreviations: D — additive genetic component of variance; H₁ and H₂ — dominance genetic components of variance; F — The mean of Fr values over arrays; h₂ — dominance effect (as algebraic sum over all loci in heterozygous phase in all crosses); E — The expected environmental component of variation; b — regression coefficient; H₂/4H₁ — denotes the proportion of genes with positive and negative effects in the parents; h²/H₂ — denotes the number of gene groups/genes which control the character and exhibit dominance

Introduction

Wheat (*Triticum aestivum* L.) occupies an important position among cereals with respect to production and utilization. In Pakistan, it is used as the staple food and occupies a prominent position in economy (Saeed *et al.*, 2005). It ranks as first cereal crop with respect to utilization, nutritive value, production, storage qualities, adaptation and world trade. During 2016–2017, wheat was grown on an area of 9.052 million hectares, which produced 25.750 million tons of grains with average yield of 2845 kg ha⁻¹ in Pakistan (PBS, 2016–2017). Pakistan has made a significant progress towards increasing the grain yield per unit area

through introduction and hybridization of new high yielding wheat genotypes accompanied with new packages of production technology for various areas.

Climate change will increase the risk of food security for some vulnerable group of crops like wheat. In current scenario of climatic change, major constraints in wheat production are drought, heat, and irregular rainfall (Inamullah and Khalil, 2011; Ahmed *et al.*, 2015; Xiao *et al.*, 2017). Therefore, development of new wheat lines with early maturity and medium stature is pre-requisite to cope with environmental changes and for the genotypes to escape from onset of stress at later stages and are likely less lodging resistant. Early maturity in wheat is important for

adaptability to different environmental conditions. Early-matured cultivars/lines may also be less prone to pre-harvest sprouting, which is an end-season phenomenon happens in humid conditions (Zare-Kohan and Heidari, 2012; Pervez *et al.*, 2014; Kayan *et al.*, 2017). Maturity is delayed for few days in cooler environments, where crops get more time to produce assimilates and to transfer them to sink resulting in higher grain yield.

Warmer temperatures affect crop growth and temperature above 30°C during grain filling, not only had negative impact on grain yield but also effect days to heading and maturity, and plant stature (Mondal *et al.*, 2013). Peduncle length is an essential feature and major contributor to plant height and it differs genotype to genotype in wheat. Past studies revealed that peduncle length plays an important role in stem reserve remobilization which correlated with high grain yield (Farooq *et al.*, 2011; Kaukab *et al.*, 2013). Peduncle length was found positively correlated with plant height which contributes a great deal to plant stature in wheat (Yao *et al.*, 2011). Spikelets per spike have key role in managing the variations in grain yield and significant positive association with grain yield (Ahmad *et al.*, 2007; Ahmed *et al.*, 2015). Grains per spike and grain size showed evidence about the structure of wheat plant; however, slight about the causes of variation in grain yield in wheat. Four components *i.e.*, spikes per plant, spikelets per spike, grains per spike and individual grain weight are the key contributors to wheat grain yield (Afridi *et al.*, 2017a).

To develop high yielding wheat cultivars, it is important to study the genetic makeup of diverse wheat lines, inheritance pattern of earliness and yield contributing traits and association of various traits with yield under existing environmental conditions. Grain yield being a polygenic character shows association with numerous traits greatly influenced by different environmental conditions (Inamullah and Khalil, 2011; Afridi *et al.*, 2017a). Breeders have a great desire to identify wheat genotypes with rust resistance and greater yield potential. For exploitation of available germplasm and to determine the nature of inheritance for important traits, there are several breeding schemes like diallel analysis, line x tester analysis, and generation means analysis etc. Diallel analysis is one of the important tools used to cross the available germplasm (with desirable traits) in all possible combinations and to determine the nature of inheritance for various variables.

Hayman diallel analysis is one of the approaches used to determine genetic components of variance (D, H₁ and H₂) for classification of various traits with their gene action. Based on diallel analysis, the nature of gene action has been reported in several past studies. Over-dominance type of gene action was observed for days to maturity and grain yield in bread wheat (Ahmad *et al.*, 2007; Nazir *et al.*, 2014; Afridi *et al.*, 2017b). Ahmed *et al.* (2015) also reported over-dominance type of gene action among parental lines for spikelets per spike, grains per spike and grain yield in

spring wheat. However, additive type of gene action with partial dominance was noted for controlling earliness, peduncle length, plant height, and grain yield in wheat (Farooq *et al.*, 2011). Additive type of gene action was also reported for spikelets per spike, grains per spike and grain yield in wheat (Rabbani *et al.*, 2011). Both additive and non-additive components of genetic demonstrated the involvement of additive and non-additive gene actions; however, over-dominance was predominant for harvest index in wheat (Ahmad *et al.*, 2007; Afridi *et al.*, 2017b). Some other studies suggested over-dominance type of gene action (Farooq *et al.*, 2011) and additive type of gene action (Pervez *et al.*, 2014) for harvest index and other yield related traits in wheat.

Thus, before developing an appropriate breeding program it is essential that genetic mechanism controlling various characteristics using available populations must be studied. Keeping in view the importance of wheat yield in current scenario of climatic change, the current study was undertaken using 6 × 6 half diallel crosses to estimate gene action and inheritance patterns (additive vs. dominance) for various traits through Hayman's approach in F₁ and F₂ populations in wheat.

Materials and Methods

Breeding Material and Procedure

This study was conducted at Cereal Crops Research Institute (CCRI), Pirsabak, Nowshera, Pakistan during three consecutive years/growing seasons *i.e.*, 2010–2011, 2011–2012 and 2012–2013. The genetic material was consisted of six bread wheat cultivars (Pirsabak-85, Khyber-87, Saleem-2000, Pirsabak-04, Pirsabak-05 and Shahkar-13) representing a wide range of diversity for earliness and yield traits (Table 1). All the six genotypes were crossed in 6 × 6 half diallel fashion during 2010–2011 to produce 15 F₁ hybrids. Parental genotypes and their F₁ hybrids were sown during 2011–2012, while parents and their F₂ populations were grown during 2012–2013 in a randomized complete block (RCB) design with two and three replications, respectively. The sub-plot size was 5 × 2.1 m² having seven rows with five meters length. Similarly, recommended cultural practices and inputs including land preparation, sowing, weed control, fertilizer application, and irrigation were applied same to all the wheat genotypes in both experiments.

Traits Measurement

In both experiments, all the data were recorded on twenty randomly selected plants in parental genotypes, their F₁ and F₂ populations and then averaged. The studied traits were days to maturity, peduncle length, spikelets per spike, grains per spike, grain yield and harvest index per plant, and then averaged before analysis.

Statistical Analyses

Data were subjected to analysis of variance (ANOVA) according to Steel *et al.* (1997). After getting the significant mean differences, the diallel analysis was carried out according to Hayman (1954).

Diallel Analysis

Hayman's diallel approach (1954) and Mather's concept of D, H components of genetic variation for additive and dominance variances, respectively (as D used for additive variance instead of A, and H_1 and H_2 for dominance genetic components of variance instead of D) were used to study the genetic effects for various traits in both generations. Mather and Jinks (1982) have also made the recent development about this technique and components of genetic variation were estimated following that method of diallel analysis (Singh and Chaudhary, 1985). In F_2 populations, the formulae were modified to calculate the components of variance as proposed by Verhalen and Murray (1969).

Assumptions of Diallel Analysis and Tests of Adequacy

The validity of information from a group of genotypes obtained from diallel method is based on following assumptions, diploid segregation of chromosomes, homozygosity of parents, absence of reciprocal effects, absence of epistasis, no multiple allelism and independent distribution of genes among parents. Homozygous inbred lines of wheat were used in a diallel crossing program. The entries in the off diagonal cells of the diallel table were replaced by their means of direct cross and reciprocal prior to analysis for removing the reciprocal differences. The remaining three assumptions of non-allelic interaction, multiple allelism and independent assortment of genes were satisfied through scaling tests. Significant "F values" in the analysis of variance revealed their heterogeneity, which invalidates any one of these assumptions. In order to test the adequacy of the additive-dominance model and validity of diallel assumptions underlying the genetic model for data sets of various traits were tested through three scaling tests i.e., t^2 test, regression analysis and arrays analysis of variance ($W_r + V_r$ and $W_r - V_r$).

According to Mather and Jinks (1982), non-significant value of t^2 test also confirms presence of no non-allelic interaction. The regression coefficient is expected to be significantly different from zero ($b = 0$) but not from unity ($b = 1$). Failure of this test indicates presence of epistasis and the data will be unfit for further genetic analysis. Significant differences between the arrays ($W_r + V_r$) and non-significant differences within the arrays ($W_r - V_r$) show the presence of dominance and absence of epistasis, and therefore, the genes will be independent in their action for random association. If all the three tests are found in favor of assumptions, the genetic model is declared fully

adequate, partially adequate if at least one test fulfills the assumptions. Failure of all the three tests completely invalidates the additive-dominance model.

Estimation of Genetic Components of Variance

The genetic components of variance, their ratio along with standard error and correlation coefficient were estimated as follows:

— D: additive genetic variance; $F_1 = [D = V_{DLO} - E]$ (V_{DLO} = Variance of the parents), $F_2 = V_{DLO} - E$, where E is the expected environmental component of variation.

— H_1 : dominance variance [$H_1 = V_{DLO} - 4W_{DLO} + 4V_{DLO} - (3n-2)E/n$, (W_{DLO} = Mean covariance between the parents and the arrays)], where V_{DLO} is mean variance of arrays, and n is number of parental cultivars.

— H_2 : $H_1 [1 - (u-v)^2]$, where u and v are the proportions of positive and negative genes, in the parents.

— F: mean of F_r values over arrays = $2V_{DLO} - 4W_{DLO} - 2(n-2)E/n$, where F_r is the covariance of additive and dominance effects in a single array. F is positive where dominant genes are more frequent than recessive.

— h^2 : $4(ML_1 - ML_0)^2 - 4(n-1)E/n^2$; dominance effect (as algebraic sum over all loci in heterozygous phase in all crosses). When frequency of dominant and recessive alleles is equal, then $H_1 = H_2 = h_2$. Significance of h_2 confirms that dominance is unidirectional.

— E: expected environmental component of variation.

$$F_1 = \sqrt{H_1 / D}, F_2 = \sqrt{1/4 H_1 / D}$$

: denotes average degree of dominance, If the value of this ratio is zero, there is no dominance; If it is greater than zero but less than 1, there is partial dominance; and if it is greater than 1, it denotes over-dominance.

$H_2/4H_1$: denotes the proportion of genes with positive and negative effects in the parents, and if the ratio is equal to 0.25, indicates symmetrical distribution of positive and negative genes.

$$F_1 = \sqrt{4DH_1 + F} / \sqrt{4DH_1 - F}$$

$$F_2 = 1/4 \sqrt{4DH_1 + 1/2F} / 1/4 \sqrt{4DH_1 - 1/2F}$$

: denotes the ratio of dominant and recessive genes in the parents, If the ratio is 1, the dominant and recessive genes in the parents are in equal proportion; if it is less than 1, it indicates an excess of recessive genes; but being greater than 1, it indicates excess of dominant genes.

h^2/H_2 : denotes the number of gene groups/genes, which control the character and exhibit dominance.

Heritability

In F_1 generation, the broad and narrow sense heritability values were calculated for each character according to Mather and Jinks (1982).

$$\text{Broad sense heritability (F}_1\text{)} = \frac{\left(\frac{1}{2}\right)D + \left(\frac{1}{2}\right)H_1 - \left(\frac{1}{4}\right)H_2 - \left(\frac{1}{2}\right)F}{\left(\frac{1}{2}\right)D + \left(\frac{1}{2}\right)H_1 - \left(\frac{1}{4}\right)H_2 - \left(\frac{1}{2}\right)F + E}$$

$$\text{Narrow sense heritability (F}_1\text{)} = \frac{\left(\frac{1}{2}\right)D + \left(\frac{1}{2}\right)H_1 - \left(\frac{1}{2}\right)H_2 - \left(\frac{1}{2}\right)F}{\left(\frac{1}{2}\right)D + \left(\frac{1}{2}\right)H_1 - \left(\frac{1}{4}\right)H_2 - \left(\frac{1}{2}\right)F + E}$$

In F₂ generation, the narrow sense heritability values were calculated as follows (Verhalen and Murray, 1969; Singh and Chaudhary, 1985).

$$\text{Narrow sense heritability (F}_2\text{)} = \frac{\left(\frac{1}{4}\right)D}{\left(\frac{1}{4}\right)D + \left(\frac{1}{16}\right)H_1 - \left(\frac{1}{8}\right)F + E}$$

Where;

D = Variation due to additive effect

H₁ = Component of variation due to dominance effect of genes

H₂ = H₁[1-(u-v)²] [u = positive and v = negative genes]

F = The mean of "Fr" over the arrays

E = The expected environmental component of variation

Results

Highly significant ($p \leq 0.01$) differences were observed among F₁ and F₂ populations and their parental cultivars for days to maturity, peduncle length, spikelets per spike, grains per spike, grain yield and harvest index (Table 2). Adequacy of additive-dominance model was tested through three scaling tests *i.e.*, t^2 test, regression analysis and arrays analysis of variance (Wr + Vr and Wr - Vr). In present studies, the additive-dominance model was found partially adequate for all the traits in both generations (Table 3).

Days to Maturity

Components of genetic variance *i.e.*, 'a' and 'b' were significant ($p \leq 0.01$) for days to maturity in F₁ and F₂ generations (Table 4). Both components 'b₁' and 'b₂' were also significant ($p \leq 0.01$) for the said trait in F₁ generation, and significant 'b₁' illustrated dominance deviation in one direction in F₁ generation. Significance of component 'b₂' showed asymmetrical distribution of genes affecting the said trait at loci whereas non-significant 'b₃' illustrated the absence of specific genes for days to maturity in F₁ generation. In F₂ generation, significance ($p \leq 0.01$) of component 'b₁' displayed dominance deviation in one direction whereas significance ($p \leq 0.01$) of component 'b₃' exhibited specific gene effects for days to maturity. Non-significant value of component 'b₂' suggested symmetrical gene distribution among parents for days to maturity in F₂ generation.

Components of genetic variance (D, H₁ and H₂), F, h² and environmental (E) components were significant for days to maturity in F₁ generation (Table 5). However, in F₂ generations, H₁, H₂ and E were significant while D, F and h² were non-significant. In both generations, dominance components (H₁ and H₂) were found greater than D and E components which suggested that non-additive gene action played important role in the inheritance of days to maturity. These results were also justified by the high values of the average degrees of dominance than unity (1.23, 1.679) in both generations, respectively. Unequal H₁ and H₂ components and the ratios of H₂/4H₁ (0.19, 0.22) in both generations also exhibited irregular distribution of positive and negative genes among the parental cultivars. The value of F was positive for both generations and significant in F₁ generation, indicated greater frequency of dominant alleles in the parental genotypes, which also confirmed by positive values of h² (6.94, 4.915) and proportion of dominant and recessive genes in the parental cultivars (2.45, 1.09) in both generations. Broad-sense heritability estimate were high in F₁ (0.82) and F₂ (0.75) generations for days to maturity. Narrow-sense heritability estimate were low in both F₁ (0.30) and F₂ (0.35) generations for said trait (Table 5).

In Vr-Wr graphical analysis, inheritance for days to maturity was regulated by over-dominance type of genes as the regression line transected the co-variance axis below the point of origin in F₁ and F₂ generations (Fig. 1a and b). According to array analysis on the regression line, cultivar Pirsabak-05 was being nearest to origin and had most dominant genes for days to maturity while cultivar Khyber-87 being farthest from origin having recessive genes in F₁ generation. In F₂ generation, cultivar Khyber-87 was being nearest to the origin had the most dominant genes while cultivar Pirsabak-05 was being far away from origin had recessive genes.

Peduncle Length

Genetic components 'a' and 'b' were significant ($p \leq 0.01$) in both generations, which demonstrated the role of additive and non-additive gene effects in controlling peduncle length (Table 4). The value of component 'b₁' was also significant ($p \leq 0.01$) in both generations, presented the existence of directional genes for peduncle length. The value of component 'b₂' was significant for F₁ ($p \leq 0.05$) and F₂ ($p \leq 0.01$) populations, which indicated asymmetrical distribution of genes among the parental genotypes. The component 'b₃' was non-significant in F₁ which revealed the absence of particular gene effects for the said trait. However, component 'b₃' was significant ($p \leq 0.01$) for F₂ populations indicating residual dominance for peduncle length.

Analysis of genetic components illustrated that D, H₁, H₂ and E were significant in F₁ and F₂ generations for peduncle length (Table 5).

Table 1: Local name, parentage and origin of the six parental cultivars

Genotype	Pedigree	Origin
Pirsabak-85	KVZ/BUSHS/KAL/BB	CIMMYT
Pirsabak-04	KAUZ/STAR	CIMMYT
Pirsabak-05	MUNIA/SHTO//AMSEL	CIMMYT
Shahkar-13	CMH84.339/CMH78.578//MILAN	CIMMYT
Saleem-2000	CHAM-6//KITE/PGO	CIMMYT
Khyber-87	KVZ/TRM//PTM/ANA-CM-43930	CIMMYT

Table 2: Mean square for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Variables	F ₁ /F ₂	Mean squares					CV %
		Genotypes	Parents	F ₁ /F ₂	Parents vs. F ₁ & F ₂	Error	
d.f.	F ₁	20	5	14	1	20	
	F ₂	20	5	14	1	40	
Days to maturity	F ₁	4.11**	7.6**	1.59*	21.94**	0.63	0.46
	F ₂	10.31**	11.02**	8.99**	25.20**	3.05	1.04
Peduncle length	F ₁	14.31**	25.04**	10.21**	17.94**	1.29	3.23
	F ₂	28.90**	32.90**	14.86**	205.51**	1.48	3.59
Spikelets spike ⁻¹	F ₁	5.27**	2.8*	3.10*	48.00**	1.18	5.12
	F ₂	5.03**	9.72**	3.48**	3.16*	0.72	3.94
Grains spike ⁻¹	F ₁	29.18**	42.28**	22.5**	57.2**	2.6	2.25
	F ₂	18.69**	30.15**	15.42**	7.14 ^{NS}	5.49	3.62
Grain yield plant ⁻¹	F ₁	40.29**	51.95**	27.53**	160.7**	8.32	9.2
	F ₂	76.98**	140.50**	46.78**	182.11**	13.62	15.31
Harvest index plant ⁻¹	F ₁	32.24*	43.02*	23.58*	99.72*	11.76	9.13
	F ₂	44.77**	99.92**	27.84*	6.05 ^{NS}	11.09	9.65

*, ** = Significant at $P \leq 0.05$ and $P \leq 0.01$, NS = Non-significant

Table 3: Scaling test for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Variables	F ₁ /F ₂	t ² test	Regression analysis		ANOVA of Arrays		Conclusion
			b0	b1	Wr + Vr	Wr - Vr	
Days to maturity	F ₁	1.4270 ^{NS}	-0.2735 ^{NS}	1.2853 ^{NS}	0.4266 ^{NS}	0.2437 ^{NS}	Partially adequate
	F ₂	0.3913 ^{NS}	-1.1187 ^{NS}	2.4668 ^{NS}	0.7598 ^{NS}	1.0912 ^{NS}	Partially adequate
Peduncle length	F ₁	-0.0225 ^{NS}	0.2008 ^{NS}	-0.2511 ^{NS}	1.8257 ^{NS}	0.6677 ^{NS}	Partially adequate
	F ₂	-0.0034 ^{NS}	0.3256 ^{NS}	-0.4895 ^{NS}	1.4302 ^{NS}	0.4025 ^{NS}	Partially adequate
Spikelets spike ⁻¹	F ₁	2.0397 ^{NS}	-0.0831 ^{NS}	2.9959 ^{NS}	0.4474 ^{NS}	0.8233 ^{NS}	Partially adequate
	F ₂	-0.0068 ^{NS}	0.7065 ^{NS}	-1.1497 ^{NS}	1.7218 ^{NS}	0.2427 ^{NS}	Partially adequate
Grains spike ⁻¹	F ₁	-0.1493 ^{NS}	0.3147 ^{NS}	-0.5551 ^{NS}	1.2759 ^{NS}	0.6361 ^{NS}	Partially adequate
	F ₂	-0.0283 ^{NS}	0.2220 ^{NS}	-0.3788 ^{NS}	1.0321 ^{NS}	0.5442 ^{NS}	Partially adequate
Grain yield plant ⁻¹	F ₁	-0.0159 ^{NS}	0.1626 ^{NS}	-0.2420 ^{NS}	1.1571 ^{NS}	0.7899 ^{NS}	Partially adequate
	F ₂	-0.0249 ^{NS}	1.0822 ^{NS}	-1.4096 ^{NS}	1.1864 ^{NS}	1.1848 ^{NS}	Partially adequate
Harvest index plant ⁻¹	F ₁	2.5162 ^{NS}	-0.4991 ^{NS}	0.9176 ^{NS}	0.9291 ^{NS}	0.1507 ^{NS}	Partially adequate
	F ₂	-0.1642 ^{NS}	0.1168 ^{NS}	-0.1481 ^{NS}	1.5666 ^{NS}	1.6400 ^{NS}	Partially adequate

Table 4: Genetic analysis for various traits in 6 × 6 F₁ and F₂ half diallel crosses of wheat

Source of variation	d.f.	Days to maturity		Peduncle length		Spikelets spike ⁻¹		Grains spike ⁻¹		Grain yield plant ⁻¹		Harvest index plant ⁻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	
Replications	1	2	0.41	0.90	36.21**	8.67**	3.43	3.90**	22.87*	8.27	13.71	26.79	29.13	21.75
a	5	5	7.6**	18.08**	43.12**	58.38**	4.72*	10.2**	59.47**	39.3**	66.37**	182.28**	35.85*	135.93**
b	15	15	2.94**	7.74**	4.29*	18.99**	5.46**	3.37**	18.69**	11.82*	31.83**	41.97**	31.04*	14.41
b ₁	1	1	21.94**	25.2**	18.02**	204.69**	48.01**	2.99*	25.75*	6.75	159.72**	182.32**	99.65**	6.04
b ₂	5	5	3.43**	5.63	4.05*	5.83**	4.32*	3.27**	4.97	10.52	11.27	19.6	30.86	9.87
b ₃	9	9	0.56	5.63*	2.89	5.67**	1.37	3.47**	25.52**	13.11*	29.05**	38.81*	23.51	17.86
Error	20	40	0.63	5.63	1.41	1.49	1.18	0.72	3.68	5.42	8.31	13.62	11.75	11.12

*, ** = Significant at $P \leq 0.05$ and $P \leq 0.01$, NS = Non-significant

The F values were non-significant in both generations while h² was significant in F₂ generation. Additive effects were found to be larger than dominance and environmental components, which specified that additive type of gene action played primary role in

inheritance of peduncle length in F₁ generation. Average degree of dominance was also less than unity (0.75) which authenticated additive type of gene action for peduncle length. In F₂ generation, dominance components effects were larger than additive, which

Table 5: Genetic components of variance for various traits in 6×6 F_1 and F_2 half diallel crosses of wheat

Genetic Components	Days to maturity		Peduncle length		Spikelets spike ⁻¹		Grains spike ⁻¹		Grain yield plant ⁻¹		Harvest index plant ⁻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
D	3.46 [±] 1.02	2.64 [±] 1.89	11.9 [±] 2.85	10.26 [±] 2.26	0.91 [±] 0.80	3.05 [±] 0.79	22.69 [±] 5.88	8.46 [±] 3.69	21.49 [±] 10.16	42.41 [±] 12.97	15.17 [±] 11.38	29.92 [±] 10.01
H ₁	5.25 [±] 1.32	7.43 [±] 3.04	6.49 [±] 2.43	16.90 [±] 2.91	7.90 [±] 1.95	4.24 [±] 0.97	32.3 [±] 6.56	12.70 [±] 4.74	45.33 [±] 13.77	40.33 [±] 12.78	46.49 [±] 19.31	11.43 [±] 8.16
H ₂	3.97 [±] 0.95	6.51 [±] 2.39	5.23 [±] 1.76	15.64 [±] 2.51	6.33 [±] 1.46	3.44 [±] 0.73	31.38 [±] 5.97	10.77 [±] 3.61	43.56 [±] 11.83	37.71 [±] 10.70	37.35 [±] 14.37	10.95 [±] 6.47
F	3.59 [±] 1.35	0.75 [±] 2.39	2.84 [±] 2.93	2.01 [±] 2.35	1.076 [±] 1.33	2.53 [±] 1.01	12.09 [±] 6.28	4.88 [±] 4.64	10.28 [±] 11.68	20.40 [±] 14.44	18.57 [±] 16.70	11.87 [±] 10.55
h ²	6.94 [±] 2.24	4.92 [±] 3.60	5.46 [±] 3.13	43.90 [±] 8.13	15.31 [±] 4.14	0.53 [±] 0.60	7.44 [±] 5.88	0.62 [±] 2.76	49.48 [±] 22.54	37.14 [±] 19.43	29.07 [±] 24.16	-42 [±] 4.50
E	0.34 [±] 0.08	1.04 [±] 0.17	0.75 [±] 0.12	0.62 [±] 0.11	0.49 [±] 0.12	0.24 [±] 0.04	1.78 [±] 0.43	1.64 [±] 0.27	4.49 [±] 1.04	4.42 [±] 0.708	6.34 [±] 1.49	3.38 [±] 0.56
F ₁ : $\sqrt{H_1/D}$	1.23	1.68	0.74	1.28	2.95	1.18	1.19	1.23	1.45	0.98	1.75	0.618
F ₂ : $\sqrt{1/4H_1/D}$												
H ₂ /4H ₁	0.19	0.22	0.20	0.23	0.20	0.20	0.24	0.21	0.24	0.23	0.20	0.24
KD / KR	2.45	1.09	1.39	1.08	1.50	1.43	1.57	1.27	1.39	1.28	2.07	1.38
h ² /H ₂	2.1	0.91	1.25	3.37	2.90	0.18	0.28	0.07	1.36	1.18	0.93	-0.05
Heritability (bs)	0.82	0.75	0.90	0.93	0.82	0.87	0.88	0.77	0.80	0.83	0.66	0.78
Heritability (ns)	0.30	0.35	0.72	0.51	0.25	0.38	0.38	0.39	0.30	0.47	0.16	0.60

* In F₁ parameter value is significant when it exceeds 1.96 after dividing it by its standard error

specified the dominant gene action for inheritance of peduncle length. Average degree of dominance was more than unity (1.283) which also suggested non-additive type of gene action in F₂ populations. Unequal values of H₁ and H₂ and ratios of H₂/4H₁ (0.20, 0.23) exhibited the asymmetrical distribution of positive and negative genes among the parental genotypes for peduncle length in both generations. Positive values of F demonstrated important role of dominant alleles in the parental genotypes for peduncle length in both generations which also authenticated by ratios of dominant and recessive genes in the parental genotypes (1.385, 1.08). Broad-sense heritability estimates were high (0.90, 0.93) for F₁ and F₂ generations, respectively for peduncle length. Narrow-sense heritability estimate were high to moderate *i.e.*, 0.72 and 0.51 in F₁ and F₂ generations, respectively (Table 5).

Peduncle length was controlled by additive type of gene action with partial dominance as the regression line cut the W_r-axis above the origin in F₁ generation (Fig. 2a). Varietal positions along the regression line indicated that Pirsabak-85 had the most dominant genes and Shahkar-13 had the most recessive genes for peduncle length in F₁ hybrids. In F₂ generation, regression line intersected the covariance axis below the point of origin for peduncle length, demonstrated over-dominance gene action for said trait (Fig. 2b). On the regression line, Pirsabak-05 being was found nearest to origin and comprised of the dominant genes while Shahkar-13 was being far away from origin which owned maximum recessive genes.

Spikelets per Spike

Genetic analysis displayed significant ($p \leq 0.01$) components 'a' and 'b' in both generations, which indicated the involvement of both additive and non-additive gene action for spikelets per spike (Table 4). Significant values of component 'b1' in F₁ ($p \leq 0.01$) and F₂ ($p \leq 0.05$) populations specified the occurrence of directional genes for said trait. Asymmetrical genes distribution among the parental genotypes was supported by significant value of component 'b₂' in F₁ ($p \leq 0.05$) and F₂ ($p \leq 0.01$) generations. Specific gene effects were identified due to significant ($p \leq$

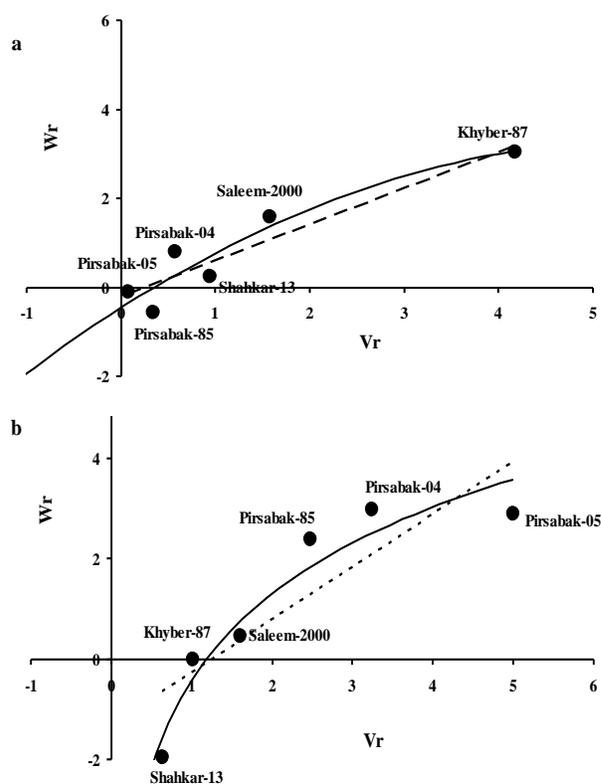


Fig. 1: Vr-Wr graph for days to maturity in 6×6 (a) F₁ and (b) F₂ half diallel populations of wheat

0.01) value of component 'b₃' in F₂ generation; however, no such gene effect was found in F₁ generation due to non-significant value of said component.

According to analysis, all the components of genetic variance were significant in both generations except components D and F in F₁s and h² in F₂ generation (Table 5). Dominant components were greater than additive and showing important role of non-additive type of gene action for spikelets per spike in both generations. Average degrees of dominance were greater than unity (2.95, 1.179) which also suggested over-dominance for said trait in both generations.

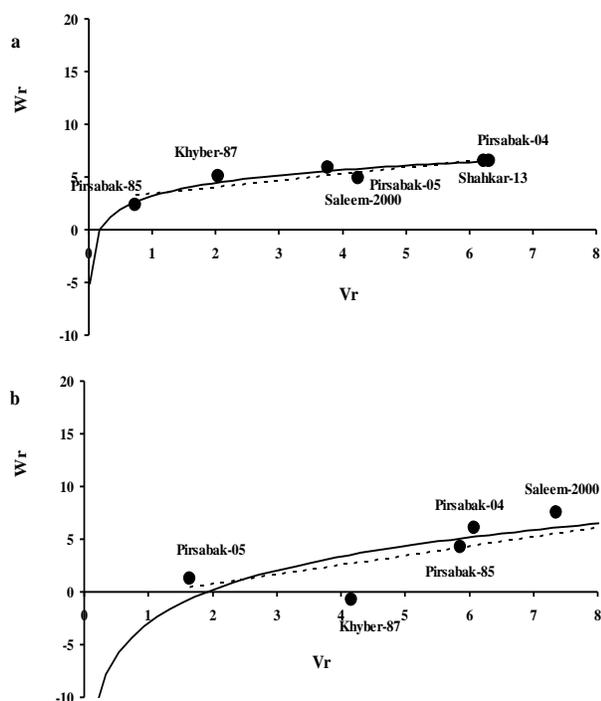


Fig. 2: Vr-Wr graph for peduncle length in 6×6 (a) F_1 and (b) F_2 half diallel populations of wheat

The H_2 value was less than H_1 in both generations, which signified that positive and negative genes were not in proportion at all loci, and it was confirmed by the ratios of $H_2/4H_1$ (0.20, 0.20). The component F was positive for spikelets per spike in both generations which demonstrated unequal distribution of dominant and recessive genes in the parental genotypes, and said findings also verified by ratios of dominant and recessive genes in the parental cultivars (1.50, 1.43). Heritability provides the essential information for the transfer of characters from parents to their progeny, hastens the evaluation of genetic and environmental effects on phenotype diversity, and helps in selection. High broad-sense (0.82, 0.87) and low narrow (0.25, 0.38) heritability values were recorded for F_1 and F_2 generations, respectively which specified that dominant gene action was responsible for controlling spikelets per spike in wheat (Table 5).

For spikelets per spike, the Vr-Wr graph showed that regression line intercepted Wr-axis on the negative side and revealed over-dominance type of gene action in both generations (Fig. 3a and b). The parental genotypes along the regression line revealed that maximum dominant genes were observed for cultivars Pirsabak-04 in F_1 and Shahkar-13 in F_2 generation, as these cultivars were closer to the point of origin. Cultivars Pirsabak-85 and Pirsabak-05 received maximum recessive genes being on distant positions from the origin in F_1 and F_2 generations, respectively.

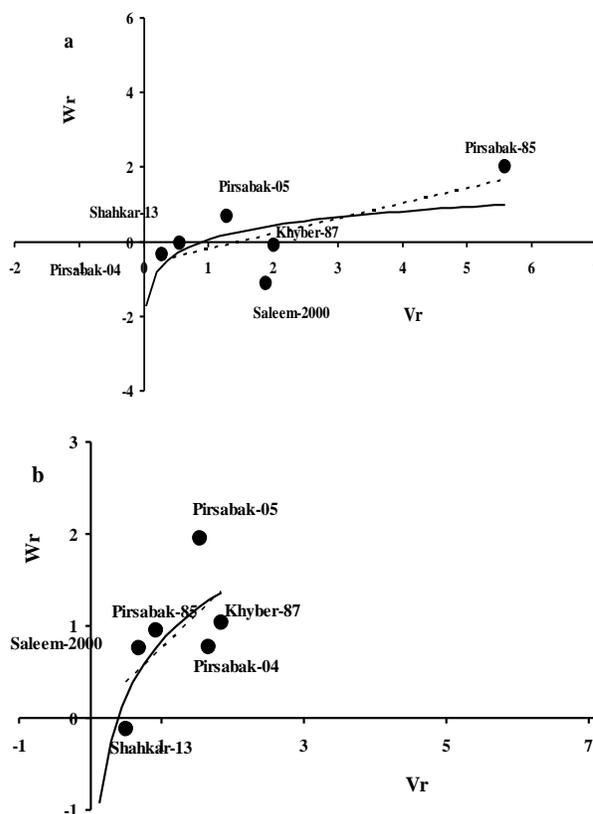


Fig. 3: Vr-Wr graph for spikelets per spike in 6×6 (a) F_1 and (b) F_2 half diallel populations of wheat

Grains per Spike

Analysis of variance displayed that components 'a' and 'b' were significant ($p \leq 0.01$) for grains per spike in F_1 and F_2 generations, which indicated the involvement of both additive and non-additive gene action (Table 4). Significant ($p \leq 0.05$) component 'b₁' in F_1 s and non-significant in F_2 s showing directional dominance genes and absence of directional dominance genes, respectively for grains per spike. Symmetrical genes distribution among the parental genotypes was supported by non-significant values of component 'b₂' in both generations. Specific gene effects were observed due to significant values of component 'b₃' in F_1 ($p \leq 0.01$) and F_2 ($p \leq 0.05$) generations.

Components of genetic variation (D, H_1 and H_2) and E were significant whereas covariance of additive and dominance effects (F) and h^2 were non-significant in both generations (Table 5). Significant positive value of E displayed important role of environment in the phenotypic expression of the said trait in both generations. However, dominance components were greater in magnitude than additive variance, suggesting dominant type of gene action for controlling grains per spike in both generations. Average degrees of dominance were greater than unity (1.19, 1.225) which also confirms over-dominance in both generations.

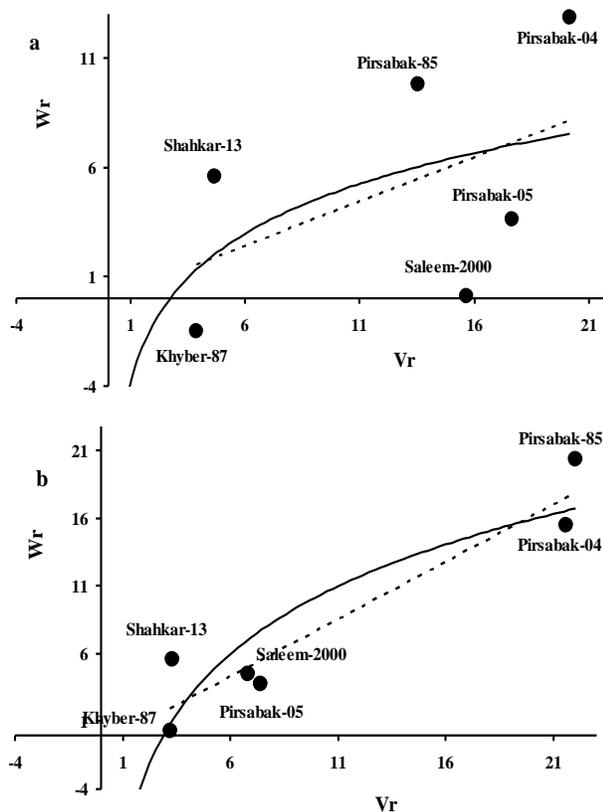


Fig. 4: Vr-Wr graph for grains per spike in 6×6 (a) F_1 and (b) F_2 half diallel populations of wheat

The values of H_1 and H_2 were different from each other, which indicated that positive and negative alleles were different among parental cultivars for grains per spike in both generations, and it was also authenticated by the ratios of $H_2/4H_1$ (0.24, 0.21). In both generations, the F value was positive for grains per spike which demonstrated unequal distribution of dominant and recessive genes, and the same was also confirmed by the ratios of dominant and recessive genes in the parental cultivars (1.57, 1.27). High broad (0.88, 0.77) and low narrow sense (0.38, 0.39) heritability values were observed for grains per spike in F_1 and F_2 generations, respectively (Table 5).

Graphical analysis showed that over-dominance type of gene action was observed as the regression line intercepted the Wr-axis below the point of origin for grains per spike in both generations (Fig. 4a and b). Arrays of parental cultivars on the regression line revealed that parental cultivars were genetically diverse for grains per spike. Cultivar Khyber-87 had more dominant genes as it was nearest the origin while genotype Pirsabak-85 was away from the origin with more recessive genes in F_1 generation. Cultivars Pirsabak-85 and Khyber-87 were being nearest the origin had more dominant genes while cultivar Pirsabak-05 was far away from the origin and had more recessive genes for grains per spike in F_2 generation.

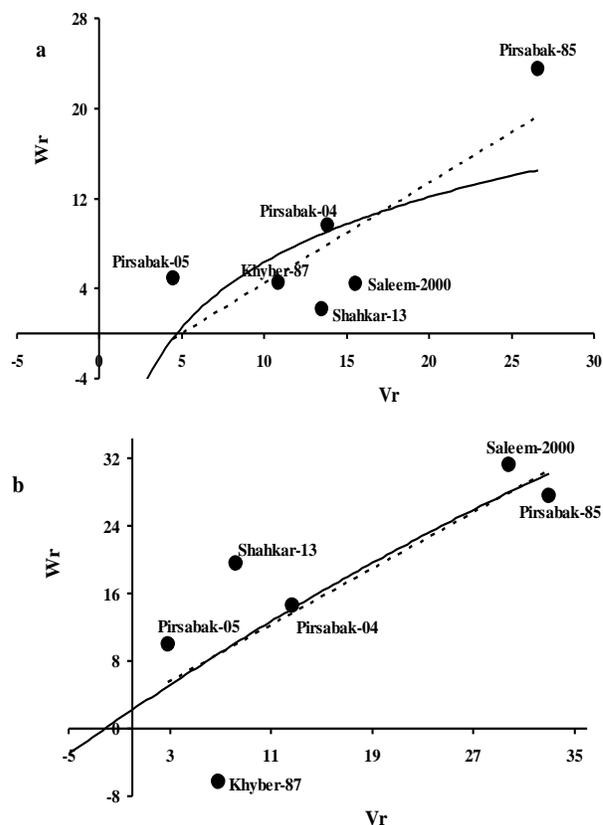


Fig. 5: Vr-Wr graph for grain yield per plant in 6×6 (a) F_1 and (b) F_2 half diallel populations of wheat

Grain Yield

The components *i.e.*, 'a' and 'b' were significant ($p \leq 0.01$) for grain yield per plant which showed the involvement of additive and non-additive gene action in both generations (Table 4). Significant ($p \leq 0.01$) component 'b₁' in F_1 and F_2 generations specified the occurrence of directional genes for grain yield per plant. Non-significant component 'b₂' indicated asymmetrical distribution of genes among parental genotypes in both generations. Specific gene effects were observed due to significant values of component 'b₃' in F_1 ($p \leq 0.01$) and F_2 ($p \leq 0.05$) generations.

Components of genetic variation (D, H_1 and H_2) and E were significant while F was non-significant for grain yield per plant in both generations (Table 5). The values of H_1 and H_2 were greater than D in F_1 generation which revealed non-additive gene action in genetic control of grain yield per plant. However, the value of D was greater than H_1 and H_2 in F_2 generation which specified the greater role of additive gene action. Average degree of dominance was also greater than unity (1.452) in F_1 hybrids, while it was less than unity (0.98) in F_2 populations. Greater value of H_1 than H_2 indicating that positive and negative alleles were different among parental lines, and it was confirmed by ratios of $H_2/4H_1$ (0.24, 0.23) for grain yield in both generations.

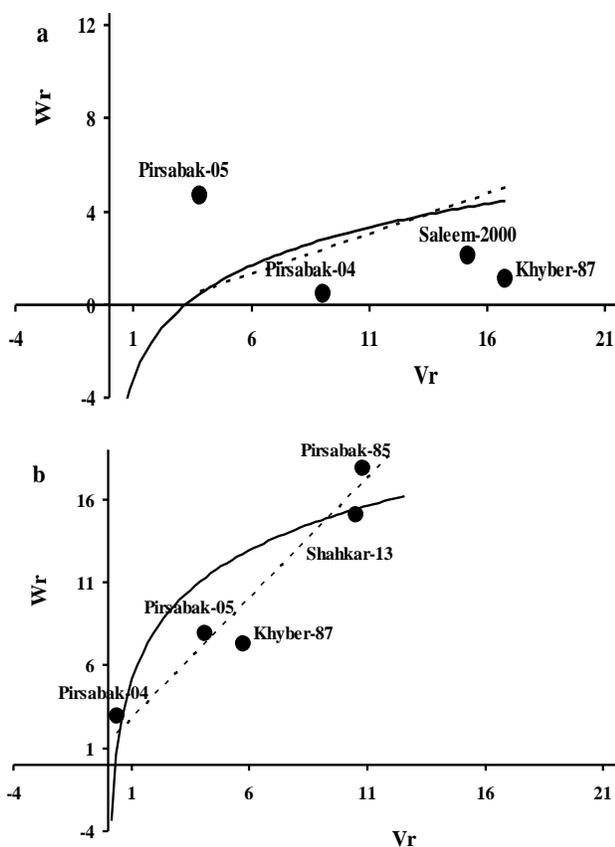


Fig. 6: Vr-Wr graph for harvest index per plant in 6×6 (a) F_1 and (b) F_2 half diallel populations of wheat

Positive value of F for grain yield demonstrating unequal distribution of dominant and recessive genes in parental cultivars for both generations. Significant and non-significant h^2 in F_1 and F_2 generations, respectively supporting the dominant and additive gene action, however, ratios of dominant and recessive genes confirmed excess of dominant genes in the parental cultivars (1.39, 1.28). Significant environmental variance (E) specified the primary role of environment in controlling grain yield in wheat. Broad-sense heritability (0.80, 0.83) were greater than narrow-sense (0.30, 0.47) for grain yield per plant in F_1 and F_2 generations, respectively (Table 5).

In Vr-Wr graphical analysis, the regression line cut off the Vr-axis below the point of origin which revealed over-dominance type of gene action for grain yield in F_1 generation (Fig. 5a). In F_2 generation, the regression line intercepted the Vr-axis above the origin and suggesting additive type of gene action for grain yield (Fig. 5b). Parental cultivars on the regression line revealed that cultivar Pirsabak-05 had the most dominant genes, while cultivar Pirsabak-85 had the most recessive genes in both generations.

Harvest Index

The components 'a' and 'b' were significant for harvest index per plant in F_1 generation ($p \leq 0.05$), which suggested the involvement of both additive and non-additive gene effects (Table 4). In F_2 generation, significant ($p \leq 0.01$) components 'a' and non-significant 'b' suggested that additive type of gene action was involved in genetic control of harvest index per plant. The component 'b₁' was significant ($p \leq 0.01$) which specified the occurrence of directional genes in F_1 generation. However, component 'b₁' was non-significant in F_2 generation and indicating absence of directional genes. In both generations, the component 'b₂' was non-significant which revealing asymmetrical distribution of genes among the parental genotypes. Non-specific gene effects were recorded due to non-significant values of component 'b₃' in both generations.

Additive component was non-significant while dominant components were significant in F_1 s, which indicated the primary role of non-additive genes in genetic control of harvest index (Table 5). However, in F_2 generation, additive component was significant while dominant genetic components were non-significant which specified the greater role of additive gene action for harvest index. Average degree of dominance was greater than unity (1.751) in F_1 s while less than one (0.618) in F_2 s which confirming the non-additive and additive gene action in F_1 and F_2 generations, respectively for harvest index. Unequal values of H_1 and H_2 components and the ratios of $H_2/4H_1$ (0.20, 0.24) exhibited the irregular distribution of positive and negative genes among the parental cultivars for harvest index in both generations. Positive value of F showed that dominant genes were more active among parental cultivars for harvest index in both generations, and it was confirmed by ratios of dominant and recessive genes in the parental cultivars (2.07, 1.38). Positive and negative values of h^2 in F_1 and F_2 generations indicating the high level of dominant genes in F_1 s and low level in F_2 populations. Broad-sense heritability (0.66, 0.78) values were greater than narrow sense (0.16, 0.60) for harvest index per plant in F_1 and F_2 generations, respectively which specified non-additive gene effects for harvest index per plant in both generations (Table 5).

In Vr/Wr graph, the regression line intercepted the covariance line below the origin and mentioned over-dominance type of gene action (Fig. 6a). In F_2 generation, the regression line cut the covariance line above the origin, which demonstrated partial dominance for harvest index (Fig. 6b). The genotypes along the regression line illustrated that cultivars Pirsabak-05 and Pirsabak-04 had the maximum dominant genes for harvest index in both generations whereas Saleem-2000 and Khyber-87 had the maximum recessive genes in F_1 and F_2 generation, respectively.

Discussion

After knowing the inheritance pattern of various variables and nature of genetic components, the breeders could better decide about the future use of the developed and improved populations after hybridization. The mode of inheritance of different characters can be investigated following Hayman (1954) diallel analysis in full and half diallel crosses. These investigations revealed that F_1 and F_2 populations and their parental genotypes have greater genetic variability, and thus the said data was further for genetic analysis. In previous studies, different wheat populations with diverse genetic makeup also revealed significant differences for days to maturity, spikelets per spike, grains per spike, grain yield and harvest index (Ahmad *et al.*, 2007; Afridi *et al.*, 2017a). Adequacy of additive-dominance model was found partially adequate for all the traits in both generations. In past studies, additive-dominance model was partially adequate for days to maturity, yield traits and harvest index in wheat (Farooq *et al.*, 2011; Afridi *et al.*, 2017b). Additive-dominance model was partially adequate for spikelets per spike, grains per spike and grain yield in different wheat populations with diverse genetic makeup (Nazir *et al.*, 2014; Ahmed *et al.*, 2015; Afridi *et al.*, 2017b). However, Yao *et al.* (2011) observed that the model was fully adequate for earliness and yield traits in bread wheat genotypes.

Significance of both additive and dominance components of genetic variance revealed the involvement of both additive and dominance genetic effects for days to maturity, peduncle length, spikelets per spike, grains per spike, grain yield and harvest index. Previous studies also revealed that both additive and dominance components were involved in the inheritance of earliness and yield traits in different wheat populations under diverse environments (Farooq *et al.*, 2011, 2015). Dominance components were predominant and greater in magnitude than additive component which suggested that non-additive gene action played primary role in the inheritance of days to maturity in both generations. Present results further revealed that according to Vr-Wr graph, the inheritance for days to maturity was regulated by over-dominance type of gene action in F_1 and F_2 generations. Farshadfar *et al.* (2012) reported that average degree of dominance was greater than unity for earliness which demonstrated the greater role of over-dominance in bread wheat. However, additive component excelled dominance components for earliness traits in diallel crosses of five wheat cultivars using two different models (Zare-Kohan and Heidari, 2012). Contradiction between present and past findings might be due varied genetic makeup of the wheat genotypes and the environment where studied.

According to components of genetic variance and Vr/Wr graph, additive gene action played an important role in the inheritance of peduncle length in F_1 generation. However, in F_2 generation, the said trait was controlled by

non-additive gene action as authenticated by components of genetic variance, average degree of dominance and Vr/Wr graph. In past studies, components of genetic variance and average degree of dominance confirmed that peduncle length showed the involvement of additive genes for inheritance in bread wheat (Ajmal *et al.*, 2011; Rabbani *et al.*, 2011). In graphical analysis, additive type gene action was found responsible for management of peduncle length in bread wheat (Pervez *et al.*, 2014). However, over-dominance type of gene action was reported for peduncle length in graphical analysis for yield and yield related traits in spring wheat (Kaukab *et al.*, 2013).

Greater values of dominance components and average degrees of dominance suggested over-dominance type of gene action for spikelets per spike, grains per spike and grain yield in both generations. Past studies also revealed that according to genetic components, average degree of dominance and Vr-Wr graphs, the spikelets per spike, grains per spike and grain yield were controlled by non-additive gene action in spring wheat (Farooq *et al.*, 2011; Asadabadi *et al.*, 2012). Key role of dominance components was observed for spikelets per spike, grains per spike and grain yield in spring wheat and triticale (Grebennikova *et al.*, 2011; Nazir *et al.*, 2014; Ahmed *et al.*, 2015). According to graphical analysis, over-dominance type of gene action was noted for various yield traits in wheat (Ojaghi and Akhundova, 2010). However, Ajmal *et al.* (2011) findings revealed that according to components of genetic variance and average degree of dominance, additive type of genes were found responsible for inheritance of spikelets per spike, grains per spike and grain yield in wheat. Graphical analysis for grain yield and its components showed additive type of gene action in spring wheat (Allah *et al.*, 2010). The inconsistent findings might be due to varied genetic make-up of the wheat genotypes and the environment.

For harvest index, dominance genetic components were significant and larger than additive in F_1 s, which indicated the primary role of non-additive genes in inheritance of the said trait. However, after segregation in F_2 generation, the harvest index was controlled by additive gene action. Significant additive and non-additive components of genetic demonstrated the involvement of both additive and non-additive gene actions for harvest index in wheat (Ahmad *et al.*, 2007). In past studies, average degree of dominance and graphical analysis suggested over-dominance type of gene action for harvest index in wheat (Farooq *et al.*, 2011). However, additive type of gene action was responsible for inheritance of various yield traits including harvest index in spring wheat (Rabbani *et al.*, 2011; Pervez *et al.*, 2014).

For all the pre- and post-harvest traits, the broad-sense heritability values were greater than narrow sense which confirms the over-dominance type of gene action. High broad and low narrow-sense heritability values were

recorded for various yield traits in F₁ and F₂ generations of bread wheat (Ahmad *et al.*, 2007). High broad and low narrow-sense heritability values were recorded for spike traits and grain yield in bread wheat, suggesting non-additive genes control in the inheritance of these traits (Nazir *et al.*, 2014; Ahmed *et al.*, 2015).

Overall, both additive and dominance components of genetic variance were significant for days to maturity, peduncle length, spikelets per spike, grains per spike, grain yield and harvest index in both generations which revealed important role of both additive and non-additive gene action in controlling these traits. However, prevalence of dominance type of gene action was noted for inheritance of various traits in F₁ and F₂ wheat half diallel populations. Broad-sense heritability values were greater than narrow sense which also specified preponderance of non-additive gene effects for inheritance of these traits. Selection for these traits in early segregating generation will might be not effective and delayed selection in later segregating generations is recommended for fruitful results (Afridi *et al.*, 2017a, b).

Conclusion

Additive and dominance components were found significant for all the traits which revealed the primary role of both additive and non-additive gene action in controlling days to maturity, peduncle length, spikelets per spike, grains per spike, grain yield and harvest index in F₁ and F₂ populations. However, components of genetic variance, Vr-Wr graphs and greater values of broad sense heritability revealed preponderance of over-dominance type of gene action which suggested that selection should be delayed to later segregating generations for improving yield associated traits.

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