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Inheritance pattern of earliness and yield traits in half diallel crosses of spring wheat

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Abstract

Half diallel mating system was used to evaluate six wheat cultivars and their F 1 and F 2 populations for inheritance of earliness, morphological and yield traits. These genotypes were crossed in a half diallel fashion during 2010-11 to get 15 cross combinations. The 6 × 6 wheat F 1 and F 2 half diallel populations and their parental cultivars were assessed through randomized complete block (RCB) design during 2011-12 and 2012-13, respectively. Genotypes revealed significant (p≤0.01) differences for all the traits in both generations. According to scaling tests, additive-dominance model was partially adequate for all the traits in F 1 and F 2 generations. Diallel analysis revealed significant values for additive (D) and dominance (H 1, H 2) genetic components of variance for majority traits in both generations, however, over dominance type of gene action was predominant for inheritance. Additive gene action was observed for days to heading and plant height in F 1, tiller per plant and grain yield per plant in F 2 generation. In the loci (H 2<H 1), majority of the traits showed unequal proportion of positive and negative genes with asymmetrical distribution among parental genotypes (H 2/4H 1<0.25). Significance of both additive and non-additive genetic variations suggested integrated breeding strategies with delayed selection for improvement in wheat populations.

Key words: additive and non-additive gene action, Additive-dominance model, genetic components of variance, Vr/Wr graph, earliness and yield traits, Triticum aestivum L.

Abbreviations: D, additive genetic component of variance; H 1 and H 2, dominance genetic components of variance; F, The mean of Fr values over arrays; h 2, dominance effect (as algebraic sum over all loci in heterozygous phase in all crosses); E, The expected environmental component of variation; b, regression coefficient; H 2/4H 1, denotes the proportion of genes with positive and negative effects in the parents; h 2/H 2, denotes the number of gene groups/genes, which control the character and exhibit dominance.
Introduction

Wheat (*T. aestivum* L.) occupies an important position among cereals with respect to production and utilization. Wheat is one of dominant crops and serve as a major source of food worldwide. In Pakistan, it contributes about 10% to the value added in agriculture and 2.1% to the GDP (PBS 2014-15). To develop high yielding wheat cultivars, it is important to study the genetic make-up of diverse wheat lines, inheritance pattern of yield contributing traits and association of various traits with yield under existing environmental conditions. Breeders are interested in desirable genes and gene complexes, while selection of desirable individuals has always been the key aspect of all breeding programs.

In current era of molecular breeding, conventional breeding has sustainable base. It is also well known fact that molecular markers application must be certified through conventional breeding. Transgressive segregation based on the classification of genotypes having the ability of transmitting genes of interest in specific genotypic combinations. Biometrical techniques used for genetic analysis of vital traits are helpful to the plant breeder in picking improved genotypes for different existing environments and production systems (Khiabani et al. 2015; Poodineh and Rad 2015). Diallel analyses are the well-known mechanisms of conventional breeding to understand allelic and non-allelic gene action, nature and amount of genetic variance utilized by genotypes in specific combinations (Hayman 1954; Mather and Jinks 1982). Parental lines and their hybrids can be assessed through diallel analysis in all possible combinations. Gene action is designated as additive, dominant and epistatic effects and interactions between them as well as with environmental factors.

Both additive and non-additive genetic components of variance were involved in controlling the inheritance of plant height, biological yield, and grain yield in wheat (Khan et al. 2007; Ahmad et al. 2016). Non-additive and overdominance type of gene action was reported by many researchers for days to heading, spike length, biological yield and grain yield in wheat (Singh et al. 2006; Akram et al. 2009; Jadoon et al. 2012; Zare-Kohan and Heidari 2012). For yield contributing traits and grain yield, over-dominance type of gene action was reported in different populations of wheat (Ljubičić et al. 2014; Al-Layla 2015; Kandil et al. 2016;). However, additive effects with partial dominance were reported for inheritance of earliness, tillers per plant, plant height, spike length and grain yield in wheat (Farooq et al. 2010; El-Rahman 2013; Kaukab et al. 2014; Nazir et al. 2014). Graphic analysis based on Jinks and Hayman (1953) make it possible to figure out average dominant degree, the ratio of distribution and dispersion of dominant and recessive alleles in parental genotypes as well as direction of dominance.
Traits such as semi dwarf stature, long coleoptiles, water use efficient leaf traits, and reduced unproductive tillers are used in trait based wheat breeding programs (Munns and Richards 2007; Allard et al. 2013). Grain yield is a complex character made up from interaction between yield components and environmental effects. Being grain yield dependency on yield contributing traits needs improvement in yield components which would eventually bring variation and improvement in grain yield (Mishra et al. 1996; Sener et al. 2009; Nawaz et al. 2013 ). The present study was conducted to draw information about genetic mechanism controlling traits i.e. days to heading, plant height, tillers per plant, spike length, biological yield, and grain yield which could be helpful to develop future breeding strategies to evolve suitable genotypes.

**Materials and Methods**

**Breeding material and experimental procedure**

The breeding material consists of six bread wheat cultivars representing a wide range of diversity for earliness and yield traits (Table 1). All the six genotypes were crossed in half diallel fashion to produce 15 F₁ hybrids during 2010-11. All the experiments were carried out at the Cereal Crops Research Institute (CCRI), Nowshera, Pakistan. 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. Similarly, all the cultural practices and inputs including sowing, fertilizer application, irrigation, and weed control were carried out as per recommended package for wheat. Data were recorded on single plant basis for days to heading, plant height, tillers per plant, spike length, biological yield and grain yield per plant in F₁ and F₂ generations.

**Statistical analyses**

**Analysis of variance**

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

**Diallel analysis**

Hayman’s diallel approach (1954) and Mather’s concept of D, H genetic components for additive and dominance variances, respectively (as D used for additive variance instead of A, and H₁ and H₂ 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 genetic components of variation were estimated following that method of diallel analysis (Singh and Chaudhary 1985).
In $F_2$ populations, the formulae were modified to calculate the genetic 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, a) diploid segregation of chromosomes, b) homozygosity of parents, c) absence of reciprocal effects, d) absence of epistasis, e) no multiple allelism, and f) independent distribution of genes among parental genotypes. Homozygous inbred lines of wheat were used in a diallel crossing programme. 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 heterogenity, 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 two scaling tests i.e. $t^2$ test and regression analysis. According to Mather and Jinks (1982), 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. Non-significant value of $t^2$ test also confirms presence of no non-allelic interaction and therefore, the genes will be independent in their action for random association. If both tests are found in favor of assumptions, the genetic model is declared fully adequate, partially adequate if one test fulfills the assumptions. Failure of both 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; $F_1 = \{D = Volo-E (Volo = Variance of the parents)\}, F_2 = Volo-E (Volo- E)$, where E is the expected environmental component of variation.

- **H1**: dominance variance $[H_1 = Volo-4Wolo1 + 4V1L1-(3n-2)E/n, (Wolo = Mean covariance between the parents and the arrays)], where V1L1 is mean variance of arrays, and n is number of parental cultivars.

- **H2**: $H_1 [1-(u-v) \ 2], where u and v are the proportions of positive and negative genes, in the parents.

- **F**: mean of Fr values over arrays $= 2Volo - 4Wolo1-2(n-2)E/n$, where Fr is the covariance of additive and dominance effects in a single array. F is positive where dominant genes are more frequent than recessive.
— $h^2$: $4(M_1-M_0)2-(n-1)E/n^2$; 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;

\[ F_1 = \frac{\sqrt{H_1}}{D}, \quad F_2 = \frac{\sqrt{H_1}}{2D} \]  

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.

$F_1 = \sqrt{6D} + \frac{1}{2}E$, $F_2 = \frac{1}{4}\sqrt{6D} + \frac{1}{2}E$: 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 according to Mather and Jinks (1982).

\[
\text{Broad sense heritability (F_1)} = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 + \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E}
\]

\[
\text{Narrow sense heritability (F_1)} = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F + E}
\]

In $F_2$ generation, the narrow sense heritability values were calculated as follows (Verhalen and Murray 1969; Singh and Chaudhary 1985).

\[
\text{Narrow sense heritability (F_2)} = \frac{\frac{1}{4}D}{\frac{1}{4}D + \frac{1}{16}H_1 - \frac{1}{8}F + E}
\]

Where;

- $D$ = Variation due to additive effect.
- $H_1$ = Component of variation due to dominance effect of genes.
\[ H_2 = H_1[1-(u-v)^2] \quad [u = \text{positive and } v = \text{negative genes}] \]

\[ F = \text{The mean of "Fr" over the arrays.} \]

\[ E = \text{The expected environmental component of variation.} \]

**Results**

Analysis of variance displayed highly significant \((p \leq 0.01)\) differences among the genotypes for days to heading, plant height, tillers per plant, spike length, biological yield, and grain yield per plant in both generations (Table 2). The adequacy of additive-dominance model was tested through two scaling tests \((t^2 \text{ test and regression analysis})\). The model was partially adequate for all the traits in both generations except tillers per plant in \(F_1\) generation where the model was fully adequate (Table 3).

**Days to heading**

Diallel analysis displayed that significance \((p \leq 0.01)\) of additive 'a' and non-additive 'b' genetic components of variance were equally important in genetic control of days to heading in \(F_1\) and \(F_2\) populations (Table 4). Additive component accounted for greater proportion than non-additive component in both generations. Non-significance of 'b1' component indicated the absence of directional dominance deviation for said trait in \(F_1\) generation. However, significance \((p \leq 0.01)\) of 'b1' component in \(F_2\) populations displayed dominance deviation in one direction. Asymmetrical gene distribution of dominant and recessive alleles was suggested by the significance \((p \leq 0.01)\) of 'b2' values in \(F_1\) generation, demonstrating that some parents had more dominant alleles for days to heading. However, symmetrical distribution of dominant and recessive alleles was suggested by the non-significance values of 'b2' in \(F_2\) populations. Moreover, residual dominance due to specific gene complexes was indicated by the significance of 'b3' values in \(F_1\)s \((p \leq 0.01)\) and \(F_2\)s \((p \leq 0.05)\) along with parents.

In \(F_1\) generation, genetic components of variance revealed that additive \((D)\), dominant components \((H_1, H_2)\) and \(E\) were significant while \(h^2\) and \(F\) values were non-significant for days to heading (Table 5). However, the values of \(H_1\) and \(H_2\) were smaller than \(D\), indicating additive type of gene action. Average degree of dominance was also less than unity \((\sqrt{H_1/D} = 0.52)\) which suggested low level of dominance of the loci effecting this trait and showing additive type of gene action with increasing pattern of additive genes as justified by non-significant negative value of \(h^2\) (-0.04). Unequal \(H_1\) and \(H_2\) genetic components and the ratio of \(H_2/4H_1\) (0.18) exhibited the irregular distribution of positive and negative genes among the parental genotypes for days to heading in \(F_1\) generation. Negative value of \(F\) (-0.76) indicated that recessive genes were more frequent than dominant genes in \(F_1\) generation, and the same also confirmed by ratio of dominant and recessive genes in the
parental genotypes \[
\sqrt{4D+4F/4D-4F} = 0.875
\]. Significant positive value of \( E \) (0.07) indicated that environment played an important role in phenotypic expression of days to heading.

In \( F_2 \) generation, genetic components of variance (\( D, H_1, H_2, h^2 \) and \( E \)) were significant while \( F \) was non-significant for days to heading (Table 5). However, the values of \( H_1 \) and \( H_2 \) were greater than \( D \), indicating non-additive type of gene action as also confirmed by average degree of dominance (\( \sqrt{4H_1/D} = 1.247 \)) for days to heading. The greater value of \( H_1 \) than \( H_2 \) component and the ratio of \( H_2/4H_1 \) (0.22) exhibited the asymmetrical distribution of positive and negative genes among the parental genotypes for days to heading in \( F_2 \) generation. Positive value of \( \hat{F} \) suggested that dominant alleles were more frequent than recessive ones for days to heading, supported by significant positive value of \( h^2 \) and ratio of dominance and recessive gene in the parental genotypes in \( F_2 \) generation \[
\sqrt{4D+4F} / \sqrt{4D-4F} = 1.31
\].

In \( F_1 \) generation, Vr-Wr graph revealed incomplete dominance for days to heading as the regression line intercepted the Wr-axis above the point of origin (Fig. 1a). The placement of array points displayed that genotypes Pirsabak-04, Saleem-2000 and Pirsabak-85 had maximum dominant genes being close to origin while genotype Shahkar-13 had more recessive genes being placed farthest from the origin for days to heading in \( F_1 \) generation. Parental genotypes Khyber-87 and Pirsabak-05 occupied the intermediary position showing equal proportion of dominant and recessive genes for said trait. In \( F_2 \) generation, Vr-Wr graph displayed over dominance type of gene action as the regression line intercepted the Wr-axis below the point of origin and was supported by the higher values of dominant genetic components (\( H_1 \) and \( H_2 \)) than \( D \) (Fig. 1b). Placement of array points revealed that genotype Saleem-2000 had maximum dominant genes followed by Pirsabak-04 while maximum recessive genes were noted in Pirsabak-85 for days to heading. High broad (0.99) and narrow sense (0.91) heritability values were recorded for days to heading in \( F_1 \) generation. However, in \( F_2 \) generation, the broad sense was also high (0.80) while narrow sense heritability was low (0.35) for days to heading (Table 5).

**Plant height**

Significance (\( p \leq 0.01 \)) of \('a'\) and non-significance of \('b'\) genetic components of variance indicated the primary role of additive genes in controlling the plant height in \( F_1 \) generation (Table 4). However, in \( F_2 \) generation, both \('a'\) and \('b'\) components were significant (\( p \leq 0.01 \)) revealing both additive and dominance effects (Table 4). Results further revealed that both additive \('a'\) and non-additive \('b'\) genetic components were equally important in the inheritance of plant height. Significance (\( p \leq 0.01 \)) of \('b1'\) component in \( F_1 \) and \( F_2 \) generations illustrated dominance deviation in one direction. In \( F_1 \) generation, the \('b2'\) and \('b3'\) were non-significant whereas in \( F_2 \) generation significance (\( p \leq 0.05 \)) of \('b2'\) proposed asymmetrical distribution of dominant and recessive
alleles. This unequal distribution of genes specified that some parental genotypes have considerably more dominant alleles than others for plant height. Moreover, significance (p≤0.01) of 'b3' value in F2 generation endorsed residual dominance due to specific genes/genes complexes for the said trait.

Genetic components of variance i.e. D, H1, H2, h2, F and E were significant in F1 generation whereas in F2 generation, the H1, H2 and E were significant while D, h2 and F were non-significant (Table 5). Additive component (D) was greater than H1 and H2 indicating additive type of gene action, and the same also confirmed by the value of average degree of dominance (\(\sqrt{H_1/D} = 0.49\)) which endorsed additive type of gene action in F1 generation. In F2 generation, the value of average degree of dominance (1.51) was greater than unity, and component D was smaller than H1 and H2, suggesting over dominant type of gene action. The H1 and H2 genetic components were not similar in both generations, which specified that positive and negative allele frequencies were not equal as confirmed by the ratios of H2/4H1 (0.33, 0.23) in F1 and F2 generations, respectively. The genetic component H2 was less than H1 for plant height in F2 segregants, which specified that favorable positive alleles were not proportional to the negative alleles at all loci among parents. Negative value of F (-17.678) in F1 indicated that recessive alleles were greater than dominant alleles as confirmed by ratio of dominant and recessive genes in the parents (0.609). Positive value of F (8.91) in F2 population showed that dominant alleles were greater than recessive, which was also supported by ratio of dominant and recessive genes in the parents (1.09). Significant positive values of E (12.6, 4.22) in F1 and F2 generations, respectively displayed the key role of environment in the expression of plant stature.

In Vr-Wr graph, the regression line intercepted the co-variance (Wr) axis above the point of origin in F1 generation, which demonstrated that plant height was controlled by additive type of gene action with partial dominance (Fig. 2a). The distribution of varietal array points on regression line revealed that cultivars Pirsabak-85 and Pirsabak-05 had maximum dominant genes, as these genotypes were closest to the origin whereas, Shahkar-13 had the most recessive genes, being farthest from the origin for plant height in F1 generation. However, due to negative intercept of regression line, over-dominant type of gene action was observed for F2 generation (Fig. 2b). These results were supported by greater value of dominant genetic component than additive. In case of F2 populations, cultivar Pirsabak-05 contained the most dominant genes and Shahkar-13 was noted with most recessive genes for plant height. For plant height, high broad sense (0.80, 0.90) heritability values were recorded in F1 and F2 generation, respectively. However, narrow sense heritability values were high (0.70) and moderate (0.44) in F1 and F2 generation, respectively which illustrated the major role of environment for plant height in F2 populations (Table 5).
Tillers per plant

Analysis of variance exhibited significant (p≤0.01) values for 'a' and 'b' genetic components in F₁ and F₂ populations (Table 4). The 'b1' and 'b3' components exhibited significant (p≤0.01, p≤0.05, respectively) values in both generations which suggested the presence of directional dominance and dominance effects of specific genes in the expression of tillers per plant. The 'b2' component was non-significant in F₁ and significant (p≤0.01) in F₂ populations, which proposed symmetrical and asymmetrical distribution of genes, respectively for said trait.

Analysis of genetic components of variance revealed that D, H₁, H₂ and E were significant for tillers per plant in F₁ and F₂ generations (Table 5). The H₁ and H₂ were greater than D and E components in F₁ generation, which signified that non-additive gene action was important for the inheritance of tillers per plant. Results were further supported by the greater value of average degree of dominance than unity (1.64) in F₁ generation. The value of D was greater than dominance components (H₁, H₂) in F₂ segregants, demonstrating additive type of gene action for the inheritance of tillers per plant. Average degree of dominance supported additive type of gene action, which was less than unity (0.91) in F₂ generation. The value of F was positive for both generations, demonstrating large number of dominant alleles in the parental lines, and the same was assured by ratios of dominant and recessive genes in the parents (1.86, 1.22), respectively in F₁ and F₂ generations. Significance of h² indicated the primary role of dominance in F₁ generation whereas non-significant h² in F₂ generation suggested the greater role of additive than dominance. The values of H₁ were greater than H₂ which indicated unequal proportion of positive and negative genes and the ratios of H₂/4H₁ (0.22, 0.21) also confirmed the asymmetrical distribution of positive and negative genes among the parental genotypes for tiller per plant in both generations.

Negative intercept of regression line indicated over-dominant gene action for tillers per plant in F₁ hybrids supported by the greater value of H₁ than D (Fig. 3a). Distribution of parental cultivars on the regression line revealed that cultivar Pirsabak-04 was nearest to origin with maximum dominant while cultivar Khyber-87 was located farthest from the origin confirming maximum recessive genes in F₁ generation. Positive intercept of regression line indicated additive gene action for tillers per plant in F₂ generation supported by the greater value of D than H₁ (Fig. 3b). In F₂ populations, cultivar Pirsabak-85 was nearest to origin with maximum dominant genes while genotype Shahkar-13 was farthest from origin with maximum recessive genes. Broad-sense heritability values were high (0.80 and 0.87) than narrow-sense (0.20 0.59) in for tillers per plant both generations, which specified higher genetic variances than environmental effects for said trait (Table 5).
Spike length

For spike length, analysis of variance displayed significant (p≤0.01) value for genetic components 'a' and 'b' in F₁ and F₂ generations, which illustrated the involvement of both additive and non-additive gene actions (Table 4). Significant (p≤0.01) 'b1' specified the occurrence of directional genes for spike length in both generations. Symmetrical genes distribution among the parental genotypes was supported by the non-significant value of 'b2' in F₁ generation while significant (p≤0.01) value revealed asymmetrical distribution in F₂ generation. Specific gene effects were noted due to significant (p≤0.01) value of 'b3' in both generations.

Genetic components of variance i.e. D, H₁, h², F were non-significant while H₂ and E were significant for spike length in F₁ generation (Table 5). However, in F₂ generation, all the genetic components of variance (D, H₁, H₂, F, h² and E) were significant for spike length (Table 5). Additive component (D) was less than H₁ and H₂ suggesting the greater role of dominance in controlling spike length in both generations. The values of average degree of dominance were more than unity (1.92, 2.196), respectively in F₁s and F₂s which also specified over-dominance type of gene action in both generations. Dominance component H₁ was greater than H₂ which specified the asymmetrical distribution of positive and negative alleles, and same also confirmed by the ratios of H₂/4H₁ (0.26, 0.21) among parental genotypes for spike length in both generations. Positive value of F showed that dominant genes were more frequent than recessive genes, and said results were also authenticated by the ratios of dominant and recessive genes in the parental genotypes (1.10, 1.19), respectively for spike length in F₁ and F₂ generations. In both F₁s and F₂s, significant positive value of E showing some role of environment in the expression of said trait.

The Vr-Wr graphical analysis showed that spike length was under the control of over-dominance gene effects as the regression line passed below the origin in F₁ generation (Fig. 4a, b). The relative scattering of array points in graph displayed that cultivar Shakar-13 occupied the closer and genotype Saleem-2000 the outermost position from the origin, which specified that these genotypes had maximum dominant and recessive alleles, respectively for spike length in F₁ generation. Positive intercept of regression line indicated additive gene action for spike length in F₂ generation. According to array points in graphical analysis, cultivar Pirsabak-85 occupied the closest and cultivar Pirsabak-04 the farthest location from the origin, which revealed that Pirsabak-85 had maximum dominant while Pirsabak-04 had maximum recessive genes for spike length in F₂ generation. Moderate to high broad (0.56, 95) and low narrow sense (0.13, 0.33) heritability values were recorded in F₁ and F₂ generations, respectively (Table 5).
Biological yield per plant

The genetic components 'a' and 'b' were significant (p≤0.01) for biological yield per plant in F₁ and F₂ generations (Table 4). Occurrence of directional dominance effects due to significant (p≤0.01) 'b1' and symmetrical distribution of genes was observed due to non-significant component 'b2'. Vital role of specific genes due to significant (p≤0.01) 'b3' was reported for biological yield per plant in F₁ and F₂ generations.

Genetic components of variance i.e. D, H₁, H₂ and E were significant while F and h² were non-significant in F₁ generation (Table 5). In F₂ generation, all the genetic components of variance (D, H₁, H₂, h²) and E were significant except F (Table 5). Greater values of H₁ and H₂ than D suggested that dominant gene action was responsible for governing biological yield in both generations. The values for average degree of dominance were also greater than unity (1.316, 1.769), respectively in F₁ and F₂ generations for grain yield also authenticated over-dominance type of gene action. Unequal values of H₁ and H₂ genetic components and the ratios of H₂/4H₁ (0.24, 0.23) exhibited the asymmetrical distribution of positive and negative genes among the parental cultivars for biological yield in both generations. Positive value of component F and h² showed that dominant genes were large in proportion than recessive among parental genotypes for biological yield, and the same was also assured by ratios of dominant and recessive genes (1.01, 1.10) in both generations. Environmental variance E was significant in both generations, which indicated the vital role of environment in expression of said trait.

Biological yield was controlled by additive type of gene action as the regression line transected the Wr-axis above the point of origin in both generations (Fig. 5a, b). Varietal positions on regression line demonstrated that cultivar Khyber-87 and cultivar Pirsabak-05 being nearest to origin had the most dominant genes for biological yield per plant. However, cultivar Pirsabak-04 was far away from origin had the most recessive genes in F₁ generation. In F₂ generation, the varietal points on regression line indicated that cultivar Pirsabak-05 being close to origin had most dominant genes while cultivar Pirsabak-85 being away from origin had the most recessive genes for biological yield. Higher broad (0.88, 0.86) and moderate narrow sense (0.49, 0.33) heritability values were observed in F₁ and F₂ generations, respectively which specified the key role of dominant gene effects in controlling the biological yield (Table 5).

Grain yield per plant

Significant (p≤0.01) genetic components i.e. 'a' and 'b' were recorded for grain yield per plant which showed the involvement of both additive and non-additive gene actions in F₁ and F₂ generations (Table 4). The component 'b1' was significant (p≤0.01) in both F₁ and F₂ generations, which specified the occurrence of
directional genes for grain yield. Non-significant ‘b2’ component indicated asymmetrical distribution of genes among parental cultivars in both generations. Specific gene effects were observed due to significant values of genetic component ‘b3’ in F₁ (p<0.01) and F₂ (p<0.05) populations, respectively.

Genetic components of variance (D, H₁ and H₂) and E were significant while F was non-significant for grain yield per plant in both generations (Table 5). The values of H₁ and H₂ were greater than D in F₁ generation which revealed non-additive gene action in genetic control of grain yield per plant. However, the value of D was greater than H₁ and H₂ in F₂ generation which specified the greater role of additive gene action. Average degree of dominance was greater than unity (1.452) in F₁ hybrids, which indicated over-dominance type of gene action whereas it was less than unity (0.98) in F₂ populations, which specified additive type of gene action. Greater value of H₁ than H₂ indicating that positive and negative alleles were different among parental genotypes, and it was confirmed by ratios of H₂/4H₁ (0.24, 0.23) for grain yield in both generations. 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 h² in F₁ and F₂ generations, respectively supporting the dominant and additive gene action, however, the ratios of dominant and recessive genes confirmed excess of dominant genes in the parental cultivars (1.39, 1.28). Significant environmental component of variance (E) specified the primary role of environment in controlling grain yield in both generations.

In Vr-Wr graphical analysis, the regression line cut off the Wr-axis below the point of origin which revealed over-dominance type of gene action for grain yield per plant in F₁ generation (Fig. 6a). In F₂ generation, the regression line intercepted Wr-axis above the origin, suggesting additive type of gene action for grain yield per plant (Fig. 6b). According to array points on regression lines, cultivar Pirsabak-05 had the most dominant genes, while cultivar Pirsabak-85 had the most recessive genes in both generations. Broad sense heritability values were high (0.80, 0.83) and greater than narrow sense (0.30, 0.47) for grain yield per plant in F₁ and F₂ generations, respectively (Table 5).

Discussion

Development of wheat cultivars with improved earliness and yield traits had been the key objective of breeders. Thus, availability of genetically based variation for traits like earliness, plant height, tillers per plant, spike length, and grain yield in breeding population is essential. Therefore, the present breeding material used here to generate information on genetic mechanism of these traits. Significant differences were observed among F₁ and F₂ hybrids along with parental genotypes for all the traits, which revealed greater genetic variability and chances of improvement in these traits. Significant differences were observed among diverse genotypes of
wheat for plant height, and yield traits (Joshi et al. 2002, 2004; Khan et al. 2007). Significant variations were observed among different wheat genotypes for days to heading and yield traits (Jadoon et al. 2012; Farshadfar et al. 2013).

Additive-dominance model was partially adequate for earliness and yield related traits in both generations. In various studies of genetic mechanism in wheat, additive-dominance model was partially adequate for earliness and yield attributing traits (Ahmad et al. 2011; Jadoon et al. 2012). However, additive-dominance model was found fully adequate for days to heading, plant height, tillers per plant, spike length and grain yield in wheat populations (Nazir et al. 2014). Khattab et al. (2010) also studied the pattern of inheritance in spring wheat and reported that additive-dominance model was fully adequate for yield related traits.

Additive and dominant genetic components of variance were significant for days to heading in F₁ and F₂ generations. However, in magnitude the values of dominance components were less than additive component in F₁ generation, while the case was in reverse in F₂ generation. Average degrees of dominance also revealed that earliness was controlled by additive and nonadditive gene actions in F₁ and F₂, respectively. Past studies revealed additive and non-additive gene actions governed the days to heading in bread wheat (Ahmad et al. 2013b; Farshadfar et al. 2013). El-Rahman (2013) noted that average degree of dominance was less than unity, and earliness traits were managed by additive gene effects in bread wheat. Additive gene action for days to heading in wheat had also been reported by Ahmad et al. (2013b). Partial dominance was reported for earliness traits which suggested that early maturing genotypes were suitable in late-sown conditions in wheat (Irshad et al. 2012). Solomon and Labuschagne (2004) reported high heritability for days to heading which might be due to involvement of few major genes in durum wheat. High heritability was reported for days to heading in genetic analysis for earliness and yield associated traits in spring wheat under normal and stress environments (Farooq et al. 2011).

Additive component was significant and greater than dominance components in F₁ generation for plant height, while in F₂ generation dominance genetic components were greater than additive. Zare-Kohan and Heidari (2012) observed additive type gene action for plant height in wheat cultivars by having average degree of dominance of less than unity. Past findings revealed that over-dominance type of gene action was recorded for plant height in various wheat populations (Mishra et al. 1996); however, in some other studies partial dominance type of gene action was observed for inheritance of plant height in wheat (Akhtar and Chowdhry 2006; Munis et al. 2012). High broad and narrow sense heritabilities were reported for plant height in bread
wheat (Jatoi et al. 2012; Khiabani et al. 2015); however, Ahmed et al. (2007) noted low heritability for plant height in wheat hybrid populations. For tiller per plant, the dominance genetic components excelled additive component in F1 generation, while in F2 generation the additive component was greater than dominance components. Nazir et al. (2014) observed significant additive and dominance components for tillers per plant with greater value of additive than dominance components in F1 generation. Average degree of dominance was less than unity for tillers per plant in barley and the inheritance of said trait was controlled by additive gene action (Potla et al. 2013). Additive type of gene action with partial dominance regulated tillers per plant in wheat as the regression line cut Wr-axis above the point of origin (Kaukab et al. 2014). High broad than narrow sense heritability values were recorded for tillers per plant and suggested greater role of non-additive gene effects in the inheritance of studied trait in barley (Eshghi and Akhundova 2010).

Spike length is an important yield contributing trait in wheat and according to genetic components of variance, the dominance components were greater than additive variance and the average degree of dominance also verified dominant type of gene action in F1 and F2 generations. Ahmad et al. (2013a) reported involvement of both additive and non-additive gene actions for spike length in genetic study of diverse bread wheat populations. Over-dominance type of gene action was reported for spike length in genetic studies of spring wheat populations (Akram et al. 2009; Al-Layla 2015). However, additive type of gene action with partial dominance was observed for spike length in wheat as regression line intercepted Wr-axis above the point of origin (Gurmani et al. 2007). Over-dominance type of gene action was reported for spike length as the regression line intercepted Wr-axis below the point of origin in bread wheat (Kaukab et al. 2014; Ljubičič et al. 2014). High broad and low narrow sense heritabilities were mentioned for spike length in bread wheat, suggesting predominance control of non-additive gene effects for spike length in wheat (Badieh et al. 2012).

Biological yield was controlled by dominant gene action as indicated by significant and greater dominant genetic components than additive in both generations. Whereas, Asif et al. (2000) and Pal and Kumar (2009) found that biological yield was managed by over-dominance type of genes in wheat and barley, respectively. Significantly higher value of additive than dominance genetic components indicated additive type gene action in controlling biological yield in wheat (Farooq et al. 2011). Greater value of average degree of dominance than unity was reported for biological yield in F2 populations of wheat (Jadoon et al. 2012). However, Salehi et al. (2014) found that average degree of dominance less than unity and suggested partial dominance type of gene action for biological yield in wheat. High broad and narrow sense heritability values
were reported that specified the involvement of both additive and non-additive gene effects in controlling the biological yield in barley (Aghamiri et al. 2012).

For grain yield, the dominance genetic components were greater than additive and revealed the predominance of non-additive gene action for the inheritance of said trait in both generations. Zare-Kohan and Heidari (2012) reported larger values of dominance genetic components than additive for grain yield in spring wheat. However, Mohammadi et al. (2007) and Allah et al. (2010) findings revealed that average degree of dominance was less than unity and proposed additive type of gene action for grain yield in wheat. Graphical diallel analysis showed additive type of gene action for grain yield in spring wheat (Farooq et al. 2011). Contradictions in presents and past findings about F₁ and F₂ generations might be due to different genetic make-up of the wheat genotypes and the environment. Low to moderate heritability estimates were reported for grain yield in quantitative inheritance of physiological traits for spring wheat (Ejaz-ul-Hassan and Khaliq 2008). However, Poodineh and Rad (2015) found greater values for broad than narrow sense heritability for grain yield in bread wheat while low heritability was reported by Aycicek and Yildirim (2006).

Conclusion

Significant differences were observed among the 6 × 6 half diallel F₁ and F₂ populations for various traits. Overdominance type of gene action was predominant for majority of the traits in both generations. However, partial dominance was observed for days to heading and plant height in F₁ generation, while tiller per plant and grain yield per plant in F₂ generation. Significance of both additive and non-additive genetic variations suggested integrated breeding strategies, and delayed selection in later segregating generations could be more effective in future wheat breeding programs.

References


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**Table 1.** Parental wheat cultivars with pedigree and origin used in the studies.

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Pedigree</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pirsabak-85</td>
<td>KVZ/BUSHS/KAL/BB</td>
<td>CIMMYT</td>
</tr>
<tr>
<td>Pirsabak-04</td>
<td>KAUZ/STAR</td>
<td>CIMMYT</td>
</tr>
<tr>
<td>Pirsabak-05</td>
<td>MUNIA/SHTO//AMSEL</td>
<td>CIMMYT</td>
</tr>
<tr>
<td>Shahkar-13</td>
<td>CMH84.339/CMH78.578//MILAN</td>
<td>CIMMYT</td>
</tr>
<tr>
<td>Saleem-2000</td>
<td>CHAM-6//KITE/PGO</td>
<td>CIMMYT</td>
</tr>
<tr>
<td>Khyber-87</td>
<td>KVZ/TRM//PTM/ANA-CM 43930</td>
<td>CIMMYT</td>
</tr>
</tbody>
</table>
### Table 2. Mean square for various traits in 6 × 6 F₁ and F₂ half diallel crosses in wheat.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Mean squares</th>
<th>CV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Genotypes</td>
<td>Parents</td>
</tr>
<tr>
<td>d.f.</td>
<td>F₁</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>20</td>
</tr>
<tr>
<td>Days to heading</td>
<td>F₁</td>
<td>11.95**</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>15.79**</td>
</tr>
<tr>
<td>Plant height</td>
<td>F₁</td>
<td>117.02**</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>117.45**</td>
</tr>
<tr>
<td>Tillers plantᵀ¹</td>
<td>F₁</td>
<td>3.52**</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>4.15**</td>
</tr>
<tr>
<td>Spike length</td>
<td>F₁</td>
<td>1.08**</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>2.52**</td>
</tr>
<tr>
<td>Biological yield plantᵀ¹</td>
<td>F₁</td>
<td>11991.89**</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>320.64**</td>
</tr>
<tr>
<td>Grain yield plantᵀ¹</td>
<td>F₁</td>
<td>40.29**</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>76.98**</td>
</tr>
</tbody>
</table>

**Note:** *, ** = Significant at P≤0.05 and P≤0.01, NS = Non-significant
Table 3. Adequacy of additive-dominance model for various traits in 6 × 6 F₁ and F₂ half diallel crosses in wheat.

<table>
<thead>
<tr>
<th>Variables</th>
<th>F₁/F₂</th>
<th>t² test</th>
<th>Regression analysis</th>
<th>Conclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>b₀</td>
<td>b₁</td>
</tr>
<tr>
<td>Days to heading</td>
<td>F₁</td>
<td>-0.0035&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.1500&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.1722&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>-0.0781&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>4.5486&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-8.980&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>Plant height</td>
<td>F₁</td>
<td>-0.0015&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.0280&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.0350&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>-0.0008&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.0840&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.1267&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td>Tillers plant&lt;sup&gt;1&lt;/sup&gt;</td>
<td>F₁</td>
<td>-1.2292&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>2.2465&lt;sup&gt;S&lt;/sup&gt;</td>
<td>-3.0605&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>-0.0615&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>1.2913&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-1.7890&lt;sup&gt;NS&lt;/sup&gt;</td>
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<tr>
<td>Spike length</td>
<td>F₁</td>
<td>-0.1493&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.3147&lt;sup&gt;NS&lt;/sup&gt;</td>
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</tr>
<tr>
<td></td>
<td>F₂</td>
<td>4.5546&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-111.16&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>249.1114&lt;sup&gt;NS&lt;/sup&gt;</td>
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<td>Biological yield plant&lt;sup&gt;1&lt;/sup&gt;</td>
<td>F₁</td>
<td>-0.5076&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.0698&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.1271&lt;sup&gt;NS&lt;/sup&gt;</td>
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<tr>
<td></td>
<td>F₂</td>
<td>-1.2565&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.1559&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.3339&lt;sup&gt;NS&lt;/sup&gt;</td>
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<td>Grain yield plant&lt;sup&gt;1&lt;/sup&gt;</td>
<td>F₁</td>
<td>-0.0159&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.1626&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.2420&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>F₂</td>
<td>-0.0283&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>0.2220&lt;sup&gt;NS&lt;/sup&gt;</td>
<td>-0.3788&lt;sup&gt;NS&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Note: Adequate: If all the scaling tests are found in favor of assumptions, the additive-dominance model is declared fully adequate. Partially adequate: if one out of tests fulfills the assumptions, the genetic model is declared partially adequate. Invalid model: Failure of all tests completely invalidates the genetic model.
Table 4. Genetic analysis for various traits in $6 \times 6$ $F_1$ and $F_2$ half diallel crosses in wheat.

<table>
<thead>
<tr>
<th>Genetic components</th>
<th>d.f.</th>
<th>Days to heading</th>
<th>Plant height</th>
<th>Tillers plant$^1$</th>
<th>Spike length</th>
<th>Biological yield plant$^1$</th>
<th>Grain yield plant$^1$</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$F_1$</td>
<td>$F_2$</td>
<td>$F_1$</td>
<td>$F_2$</td>
<td>$F_1$</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a</td>
<td>5</td>
<td>5</td>
<td>47.77**</td>
<td>28.91**</td>
<td>357.29**</td>
<td>211.82**</td>
<td>4.6**</td>
</tr>
<tr>
<td>b</td>
<td>15</td>
<td>15</td>
<td>1.37**</td>
<td>11.42**</td>
<td>36.94</td>
<td>85.99**</td>
<td>3.17**</td>
</tr>
<tr>
<td>b1</td>
<td>1</td>
<td>1</td>
<td>0.00</td>
<td>60.36**</td>
<td>430.06**</td>
<td>742.53**</td>
<td>16.01**</td>
</tr>
<tr>
<td>b2</td>
<td>5</td>
<td>5</td>
<td>1.90**</td>
<td>7.6</td>
<td>7.29</td>
<td>36.82*</td>
<td>2.19</td>
</tr>
<tr>
<td>b3</td>
<td>9</td>
<td>9</td>
<td>1.22**</td>
<td>8.1*</td>
<td>9.72</td>
<td>40.36**</td>
<td>2.28*</td>
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<tr>
<td>Error</td>
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<td>12.15</td>
<td>0.81</td>
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Note: *, ** = Significant at $P \leq 0.05$ and $P \leq 0.01$, NS = Non-significant
Table 5. Genetic components of variance for various traits in $6 \times 6 F_1$ and $F_2$ half diallel crosses in wheat.

<table>
<thead>
<tr>
<th>Genetic components</th>
<th>Days to Heading</th>
<th>Plant height</th>
<th>Tillers plant$^{-1}$</th>
<th>Spike length</th>
<th>Biological yield plant$^{-1}$</th>
<th>Grain yield plant$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F_1$</td>
<td>$F_2$</td>
<td>$F_1$</td>
<td>$F_2$</td>
<td>$F_1$</td>
<td>$F_2$</td>
</tr>
<tr>
<td>$D$</td>
<td>10.90*</td>
<td>7.18*</td>
<td>74.24*</td>
<td>35.85*</td>
<td>1.93*</td>
<td>2.41*</td>
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<tr>
<td></td>
<td>±0.77</td>
<td>±2.69</td>
<td>±30.91</td>
<td>±11.98</td>
<td>±0.85</td>
<td>±2.41</td>
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<tr>
<td>$H_1$</td>
<td>2.97*</td>
<td>11.16*</td>
<td>17.91</td>
<td>81.37*</td>
<td>5.21*</td>
<td>2.00*</td>
</tr>
<tr>
<td></td>
<td>±0.4</td>
<td>±3.55</td>
<td>±25.13</td>
<td>±16.17</td>
<td>±1.31</td>
<td>±0.64</td>
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<tr>
<td>$H_2$</td>
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<td>9.71*</td>
<td>23.79</td>
<td>73.59*</td>
<td>4.50*</td>
<td>1.65*</td>
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<tr>
<td></td>
<td>±0.29</td>
<td>±2.81</td>
<td>±21.54</td>
<td>±13.54</td>
<td>±1.05</td>
<td>±0.47</td>
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<td>$F$</td>
<td>±0.76</td>
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<td>1.90</td>
<td>1.03</td>
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<tr>
<td>$h^2$</td>
<td>±0.04</td>
<td>12.48*</td>
<td>132.94*</td>
<td>158.27*</td>
<td>5.00*</td>
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<tr>
<td></td>
<td>±0.05</td>
<td>±5.82</td>
<td>±63.58</td>
<td>±37.22</td>
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<tr>
<td>$E$</td>
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<td>12.63*</td>
<td>4.22*</td>
<td>0.37*</td>
<td>0.20*</td>
</tr>
<tr>
<td></td>
<td>±0.02</td>
<td>±0.18</td>
<td>±3.03</td>
<td>±0.72</td>
<td>±0.09</td>
<td>±0.03</td>
</tr>
</tbody>
</table>

$F_1 = \sqrt{H_1/D}$,  $F_2 = \sqrt{H_2/D}$

$H_2/4H_1$

$F_1: \sqrt[4]{4DH_1 + F_1} / \sqrt[4]{4DH_1 - F_1}$

$F_2: \sqrt[4]{4DH_2 + F_2} / \sqrt[4]{4DH_2 - F_2}$

$h^2/H_2$ -0.02 1.54 2.58 1.332 0.67 2.4357 0.54 0.51 2.34 1.36 1.1817

Heritability (bs) 0.99 0.80 0.80 0.90 0.80 0.87 0.56 0.95 0.88 0.86 0.80 0.83

Heritability (ns) 0.91 0.35 0.70 0.45 0.20 0.59 0.13 0.33 0.49 0.33 0.30 0.47

Note: * In $F_1$ parameter value is significant when it exceeds 1.96 after dividing it by its standard error, *In $F_2$ parameter value is tested by «t» test at n-2 d.f after dividing it by its standard error.
Fig. 1a. Vr-Wr graph for days to heading in 6 × 6 F₁ half diallel crosses of wheat

Fig. 1b. Vr-Wr graph for days to heading in 6 × 6 F₂ half diallel crosses of wheat
Fig. 2a. Vr-Wr graph for plant height in $6 \times 6$ F$_1$ half diallel crosses of wheat

Fig. 2b. Vr-Wr graph for plant height in $6 \times 6$ F$_2$ half diallel crosses of wheat
Fig. 3a. Vr-Wr graph for tiller per plant in 6 × 6 F₁ half diallel crosses of wheat

Fig. 3b. Vr-Wr graph for tiller per plant in 6 × 6 F₂ half diallel crosses of wheat
Fig. 4a. Vr-Wr graph for spike length in 6 × 6 F1 half diallel crosses of wheat

Fig. 4b. Vr-Wr graph for spike length in 6 × 6 F2 half diallel crosses of wheat
Fig. 5a. Vr-Wr graph for biological yield per plant in 6 × 6 F₁ half diallel crosses of wheat

Fig. 5b. Vr-Wr graph for biological yield per plant in 6 × 6 F₂ half diallel crosses of wheat
Fig. 6a. Vr-Wr graph for grain yield per plant in 6 × 6 F₁ half diallel crosses of wheat

Fig. 6b. Vr-Wr graph for grain yield per plant in 6 × 6 F₂ half diallel crosses of wheat