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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 ($p \leq 0.01$) 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.

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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 F_1 hybrids during 2010-11. All the experiments were carried out at the Cereal Crops Research Institute (CCRI), Nowshera, Pakistan. Parental genotypes and their F_1 hybrids were sown during 2011-2012 while parents and their F_2 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 F_1 and F_2 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 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 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.

— H_1: 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.

— 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 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: $4(ML_1-ML_o)2-4(n-1)E/n2$; 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;

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

$F_1 = \sqrt{4DH_1+F}$ / $\sqrt{4DH_1-F}$, $F_2 = \frac{1}{4}\sqrt{4DH_1+1/2F}$ / $\frac{1}{4}\sqrt{4DH_1-1/2F}$: 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).

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

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

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

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

Where;

       D = Variation due to additive effect.

       H_1 = Component of variation due to dominance effect of genes.

$H_2 = H_1[1-(u-v)^2]$ [u = positive and v = negative genes].

F = The mean of "Fr" over the arrays.

E = The expected environmental component of variation.

Results

Analysis of variance displayed highly significant (p≤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 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≤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≤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≤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_1s (p≤0.01) and F_2s (p≤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 [$\sqrt{4DH_1 + F}$ / $\sqrt{4DH_1 - F}$ = 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 ($\sqrt{\frac{1}{4}H_1 / D}$ = 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 '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 [$1/4\sqrt{4DH_1 + 1/2F}$ / $1/4\sqrt{4DH_1 - 1/2F}$ = 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≤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≤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≤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≤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 F_2 generation endorsed residual dominance due to specific genes/genes complexes for the said trait.

Genetic components of variance i.e. D, H_1, H_2, h^2, F and E were significant in F_1 generation whereas in F_2 generation, the H_1, H_2 and E were significant while D, h^2 and F were non-significant (Table 5). Additive component (D) was greater than H_1 and H_2 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 F_1 generation. In F_2 generation, the value of average degree of dominance (1.51) was greater than unity, and component D was smaller than H_1 and H_2, suggesting over dominant type of gene action. The H_1 and H_2 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 $H_2/4H_1$ (0.33, 0.23) in F_1 and F_2 generations, respectively. The genetic component H_2 was less than H_1 for plant height in F_2 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 F_1 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 F_2 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 F_1 and F_2 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 F_1 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 F_1 generation. However, due to negative intercept of regression line, over-dominant type of gene action was observed for F_2 generation (Fig. 2b). These results were supported by greater value of dominant genetic component than additive. In case of F_2 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 F_1 and F_2 generation, respectively. However, narrow sense heritability values were high (0.70) and moderate (0.44) in F_1 and F_2 generation, respectively which illustrated the major role of environment for plant height in F_2 populations (Table 5).

Tillers per plant

Analysis of variance exhibited significant ($p \leq 0.01$) values for 'a' and 'b' genetic components in F_1 and F_2 populations (Table 4). The 'b1' and 'b3' components exhibited significant ($p \leq 0.01$, $p \leq 0.05$, 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 F_1 and significant ($p \leq 0.01$) in F_2 populations, which proposed symmetrical and asymmetrical distribution of genes, respectively for said trait.

Analysis of genetic components of variance revealed that D, H_1, H_2 and E were significant for tillers per plant in F_1 and F_2 generations (Table 5). The H_1 and H_2 were greater than D and E components in F_1 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 F_1 generation. The value of D was greater than dominance components (H_1, H_2) in F_2 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 F_2 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 F_1 and F_2 generations. Significance of h^2 indicated the primary role of dominance in F_1 generation whereas non-significant h^2 in F_2 generation suggested the greater role of additive than dominance. The values of H_1 were greater than H_2 which indicated unequal proportion of positive and negative genes and the ratios of $H_2/4H_1$ (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 F_1 hybrids supported by the greater value of H_1 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 F_1 generation. Positive intercept of regression line indicated additive gene action for tillers per plant in F_2 generation supported by the greater value of D than H_1 (Fig. 3b). In F_2 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 F_1 and F_2 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 F_1 generation while significant (p≤0.01) value revealed asymmetrical distribution in F_2 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, H_1, h^2, F were non-significant while H_2 and E were significant for spike length in F_1 generation (Table 5). However, in F_2 generation, all the genetic components of variance (D, H_1, H_2, F, h^2 and E) were significant for spike length (Table 5). Additive component (D) was less than H_1 and H_2 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 F_1s and F_2s which also specified over-dominance type of gene action in both generations. Dominance component H_1 was greater than H_2 which specified the asymmetrical distribution of positive and negative alleles, and same also confirmed by the ratios of $H_2/4H_1$ (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 F_1 and F_2 generations. In both F_1s and F_2s, 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 F_1 generation. Positive intercept of regression line indicated additive gene action for spike length in F_2 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 F_2 generation. Moderate to high broad (0.56, 95) and low narrow sense (0.13, 0.33) heritability values were recorded in F_1 and F_2 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 F_1 and F_2 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 F_1 and F_2 generations.

Genetic components of variance i.e. D, H_1, H_2 and E were significant while F and h^2 were non-significant in F_1 generation (Table 5). In F_2 generation, all the genetic components of variance (D, H_1, H_2, h^2) and E were significant except F (Table 5). Greater values of H_1 and H_2 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 F_1 and F_2 generations for grain yield also authenticated over-dominance type of gene action. Unequal values of H_1 and H_2 genetic components and the ratios of $H_2/4H_1$ (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 h^2 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 F_1 generation. In F_2 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 F_1 and F_2 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 F_1 and F_2 generations (Table 4). The component 'b1' was significant (p≤0.01) in both F_1 and F_2 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 F_1 (p≤0.01) and F_2 (p≤0.05) populations, respectively.

Genetic components of variance (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 greater than unity (1.452) in F_1 hybrids, which indicated over-dominance type of gene action whereas it was less than unity (0.98) in F_2 populations, which specified additive type of gene action. Greater value of H_1 than H_2 indicating that positive and negative alleles were different among parental genotypes, and it was confirmed by ratios of $H_2/4H_1$ (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 h^2 in F_1 and F_2 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 F_1 generation (Fig. 6a). In F_2 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 F_1 and F_2 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 F_1 and F_2 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 F_1 and F_2 generations. However, in magnitude the values of dominance components were less than additive component in F_1 generation, while the case was in reverse in F_2 generation. Average degrees of dominance also revealed that earliness was controlled by additive and nonadditive gene actions in F_1 and F_2, 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 F_1 generation for plant height, while in F_2 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 F_1 generation, while in F_2 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 F_1 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 F_1 and F_2 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; Ljubičić 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 F_2 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 F_1 and F_2 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 F_1 and F_2 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 F_1 generation, while tiller per plant and grain yield per plant in F_2 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

Ahmad, I., Mahmood, N., Khaliq, I., and Khan, N. 2016. Genetic analysis for five important morphological attributes in wheat (*T. aestivum* L.). J. Anim. Plant Sci. **26**(3): 725-730.

Aghamiri, S.M.M.S., Mostafavi, K., and Mohammadi, A. 2012. Genetic study of agronomic traits in barley based diallel cross analysis. Adv. Environ. Biol. **6**(1): 62-68.

Ahmad, F., Khan, S., Ahmad, S.Q., Khan, H., Khan, A., and Muhammad, F. 2011. Genetic analysis of some quantitative traits in bread wheat across environments. Afr. J. Agric. Res. **6**(3): 686-692.

Ahmad, I., Mohammad, F., Aurangzeb, Noorka, I.R., Farhatullah, and Jadoon, S.A. 2013a. Determination and inheritance of phytic acid as marker in diverse genetic group of bread wheat. Am. J. Mol. Biol. **3**: 158-164.

Ahmad, I., Muhammad, F., and Aurangzeb. 2013b. Breeding bread wheat for low phytic acid using full diallel crosses. Sarhad J. Agric. **29**(1): 33-42.

Ahmed, N.C.M., and Khaliq, I.M.M. 2007. The inheritance of yield and yield components of five wheat hybrid populations under drought conditions. Indonesian J. Agric. Sci. **8**(2): 53-59.

Akhtar, N., and Chowdhry, M.A. 2006. Genetic analysis of yield and some other quantitative traits in bread wheat. Int. J. Agric. Biol. **4**: 523-527.

Akram, Z., Ajmal, S.U., Shabbir, G., Munir, M., and Cheema, N.M. 2009. Inheritance mechanism of some yield components in bread wheat. Pakistan J. Agric. Res. **22**:1-2.

Allah, S.U., Khan, A.S., Raza, A., and Sadique, S. 2010. Gene action analysis of yield and yield related traits in spring wheat (*T. aestivum* L.). Int. J. Agric. Biol. **12**: 125-128.

Allard, V., Martre, P., and Le Gouis, J. 2013. Genetic variability in biomass allocation to roots in wheat is mainly related to crop tillering dynamics and nitrogen status. Eur. J. Agron. **46**: 68-76.

Al-Layla, M.J. 2015. Genetic analysis of yield and its components for wheat. Jordan J. Agric. Sci. **11**(2): 507-524.

Asif, M., Khaliq, I., and Chowdhry, M.A. 2000. Genetic analysis for some metric traits in hexaploid wheat. Pakistan J. Biol. Sci. **3**: 525-527.

Aycicek, M., and Yildirim, T. 2006. Heritability of yield and some yield components in bread wheat (*T. aestivum* L.) genotypes. Bangladesh J. Bot. **35**: 17-22.

Badieh, M.M.S., Farshadfar, E., Haghparast, R., Rajabi, R., and Zarei, L. 2012. Evaluation of gene actions of some traits contributing in drought tolerance in bread wheat utilizing diallel analysis. Ann. Biol. Res. **3**(7): 3591-3596.

Ejaz-ul-Hassan, S., and Khaliq, I. 2008. Quantitative inheritance of some physiological traits for spring wheat under two different population densities. Pakistan J. Bot. **40**: 581-587.

El-Rahman, M.E.A. 2013. Estimation of some genetic parameters through generation mean analysis in three bread wheat crosses. Alex. J. Agric. Res. **58**(3): 183-195.

Eshghi, R., and Akhundova, E. 2010. Inheritance of some important agronomic traits in hulless barley. Int. J. Agric. Biol. **12**: 73-76.

Farooq, J., Khaliq, I., Kashif, M., Ali, Q., and Mahpara, S. 2011. Genetic analysis of relative cell injury percentage and some yield contributing traits in wheat under normal and heat stress conditions. Chilean J. Agric. Res. **71**(4): 511-520.

Farooq, J., Khaliq, I., Khan, A.S., and Pervez, M.A. 2010. Studying the genetic mechanism of some yield contributing traits in wheat (*T. aestivum* L.). Int. J. Agric. Biol. **12**: 241- 246.

Farshadfar, E., Rafiee, F., and Hasheminasab, H. 2013. Evaluation of genetic parameters of agronomic and morpho-physiological indicators of drought tolerance in bread wheat (*T. aestivum* L.) using diallel mating design. Aust. J. Crop Sci. **7**(2): 268-27.

Gurmani, R., Khan, S.J., Saqib, Z.A., Khan, R., Shakeel, A., and Ullah, M. 2007. Genetic evaluation of some yield and yield related traits in wheat. Pakistan J. Agric. Res. **44**: 6-11.

Hayman, B.I. 1954. The theory and analysis of diallel crosses. Genet. **39**: 789-809.

Irshad, M., Khaliq, I., Khan, A.S., and Ali, A. 2012. Genetic studies for some agronomic traits in spring wheat under heat stress. Pakistan J. Agric. Sci. **49**(1): 11-20.

Jadoon, S.A., Mohammad, F., Ullah, H., and Khalil, I.H. 2012. Gene actions for pre and post-harvest traits in F_2 wheat populations, QSci. Connect. 2-5.

Jatoi, W.A., Baloch, M.J., Kumbhar, M.B., and Keerio, M.I. 2012. Heritability and correlation studies of morpho-physiological traits for drought tolerance in spring wheat. Pakistan J. Agric. Agric. Engg. Vet. Sci. **28**(2): 100-114.

Jinks, J.L., and Hayman, B.I. 1953. The analysis of diallel crosses, Maize Genet. Coop. News **1**: 48-54.

Joshi, S.K., Sharma, S.N., Singhania, D.L., and Sain, R.S. 2002. Genetic analysis of quantitative and quality traits under varying environmental conditions in bread wheat. Wheat Info. Serv. **95**: 5-10.

Joshi, S.K., Sharma, S.N., Singhaniad, L., and Sain, R.S. 2004. Combining ability in the F_1 and F_2 generations of diallel cross in hexaploid wheat (*T. aestivum* L.). Hereditas **141**: 115-121.

Kandil,A.A., Sharief, A.E., and Gomaa, H.S.M. 2016. Estimate of gene action for yields and its components in bread wheat (*T. aestivum* L.). Int. J. Agro. Agric. Res. **8**(1): 34-40.

Kaukab, S., Saeed, M.S., and Rehman, A.U. 2014. Genetic analysis for yield and some yield traits in spring wheat. Universal J. Agric. Res. **2**(7): 272-277.

Khan, M.A., Ahmad, N., Akbar, M., Rehman, A., and Iqbal, M.M. 2007. Combining ability analysis in wheat. Pakistan J. Agric. Sci. **44**: 1-5.

Khattab, S.A.M., Esmail, R.M., EL-Rahman, A., and AL-Ansary, M.F. 2010. Genetical analysis of some quantitative traits in bread wheat (*T. aestivum* L). New York Sci. J. **3**(11): 152-157.

Khiabani, B.N., Aharizad, S., and Mohammadi, S.A. 2015. Genetic analysis of grain yield and plant height in full diallel crosses of bread wheat. Biol. Forum - An Int. J. **7**(1): 1164-1172.

Ljubičić, N., Petrović, S., Dimitrijević, M., Hristov, N., Vukosavljev, M., and Srećkov, Z. 2014. Diallel analysis for spike length in winter wheat. Turk. J. Agric. Nat. Sci. **2**: 1455-1459.

Mather, K., and Jinks, J.L. 1982. Biometrical Genetics (3rd Ed.) Chapman and Hall Ltd. London, UK. 396 pp.

Mishra, P.C., Singh, T.B., Kurmvanshi, S.M., and Soni, S.N. 1996. Gene action in diallel cross of bread wheat under late sown conditions. J. Soils and Crops **6**: 128-131.

Mohammadi, H., Emami, M.K., and Rezai, A. 2007. Estimation of genetic parameters for wheat grain yield and its components using diallel crosses. J. Water Soil Sci. **11**(40): 157-165.

Munis, M.F.H., Bano, A., Chowdhry, M.A., Ahmad, A., Chaudhary, H.J., Muhammadi, Rasul, F., Ahmad, S., Khaliq, T., and Nasim, W. 2012. Inheritance pattern of vital post-emergence morphometric and meristic traits of spring wheat. J. Med. Plants Res. **6**(16): 3246-3253.

Munns, R., and Richards, R.A. 2007. Recent advances in breeding wheat for drought and salt stresses. In: Jenks MAP, Hasegawa M, Jain SM (eds.). Advances in molecular breeding toward drought and salt tolerant crops. Springer-verlag, Dordrecht, The Netherlands. 565-586 pp.

Nawaz, R., Inamullah, Ahmad, H., Din, S., and Iqbal, M.S. 2013. Agro-morphological studies of local wheat varieties for variability and their association with yield related traits. Pak. J. Bot. **45**(5): 1701-1706.

Nazir, A., Khaliq, I., Farooq, J., Mahmood, K., Mahmood, A., Hussain, M., and Shahid, M. 2014. Pattern of inheritance in some yield related parameters in spring wheat (*T. aestivum* L.). Am. J. Biol. Life. Sci. **2**(6): 180-186.

Pal, D., and Kumar, S. 2009. Genetic analysis of forage yield and other traits in barley (*H. vulgare* L.). Barley Genet. Newsletter **39**: 13-19.

PBS (2014-15,) Year Book. Pakistan Bureau of Statistics (PBS), Govt. of Pakistan, Islamabad, Pakistan.

Poodineh, M., and Rad, M.R.N. 2015. Genetic components for physiological parameters estimates in bread wheat (*T. aestivum* L.). Annu. Res. Rev. Biol. **7**(3): 163-170.

Potla, K.R., Bornare, S.S., Prasad, L.C., Prasad, R., and Madakemohekar, A.H. 2013. Study of heterosis and combining ability for yield and yield contributing traits in barley (*H. vulgare* L.). The Bioscane **8**(4): 1231-1235.

Salehi, S., Gholami, S., Rahmati, A., and Golparvar, A.R. 2014. Combining ability of biological yield and harvest index in diallel cross of wheat cultivars under drought and non-drought Stress conditions. Agric. Conspec. Sci. **79**(4): 221-226.

Sener, O., Arslan, M., Soysal, Y., and Erayman, M. 2009. Estimates of relative yield potential and genetic improvement of wheat cultivars in the Mediterranean region. J. Agric. Sci. Cambridge **147**: 323-332.

Singh, R.K., and Chaudhary, B.D. 1985. Biometrical Methods in Quantitative Genetic Analysis. Kalyani Publishers Ludhiana & New Delhi, India. 102-142 pp.

Singh, S.P., Singh, M., and Yadav, H.K. 2006. Diallel analysis for seed yield and its component traits in Cuphea procumbens. Genetika **38**(1): 9-22.

Solomon, K.F., and Abuschagne, M.L. 2004. Inheritance of evapotranspiration and transpiration efficiencies in diallel F_1 hybrids of durum wheat (*T. turgidum* L. var. durum). Euphytica **136**: 69-79.

Steel, R.G.D., Torrie, J.H., and Dickey, D.A. 1997. Principles and Procedures of Statistics: A Biometrical Approach, 3rd edition. Mc Graw Hill Book Co., Inc., New York.

Verhalen, L.M., and Murray, J.C. 1969. A diallel analysis of several fiber properties traits in upland cotton (*G. hirsutum* L.). Crop Sci. **9**: 311-315.

Zare-Kohan M., and Heidari, B. 2012. Estimation of genetic parameters for maturity and grain yield in diallel crosses of five wheat cultivars using two different models. J. Agric. Sci. **4**(8): 74-85.

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

Cultivars	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 F_1 and F_2 half diallel crosses in 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 heading	F_1	11.95**	19.88**	9.94**	0.29	0.43	0.51
	F_2	15.79**	24.86**	9.37**	60.36**	3.46	1.52
Plant height	F_1	117.02**	173.75**	74.4*	430.06**	25.6	4.99
	F_2	117.45**	120.2**	71.83**	742.52**	12.15	3.68
Tillers plant[-1]	F_1	3.52**	4.6**	2.25*	16.01*	0.81	6.7
	F_2	4.15**	7.81**	2.85**	3.921*	0.57	5.53
Spike length	F_1	1.08**	0.76**	0.33*	13.07**	0.13	2.95
	F_2	2.52**	1.99**	2.52**	5.14**	0.19	3.42
Biological yield plant[-1]	F_1	11991.89**	12962.74**	3.104**	115.61**	11.86	9.51
	F_2	320.64**	290.73**	197.53**	2193.71**	47.07	9.90
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

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 F_1 and F_2 half diallel crosses in wheat.

Variables	F_1/F_2	t^2 test	Regression analysis		Conclusion
			b_0	b_1	
Days to heading	F_1	-0.0035^{NS}	0.1500^{NS}	-0.1722^{NS}	Partially adequate
	F_2	-0.0781^{NS}	4.5486^{NS}	-8.980^{NS}	Partially adequate
Plant height	F_1	-0.0015^{NS}	0.0280^{NS}	-0.0350^{NS}	Partially adequate
	F_2	-0.0008^{NS}	0.0840^{NS}	-0.1267^{NS}	Partially adequate
Tillers plant^{-1}	F_1	-1.2292^{NS}	2.2465^{S}	-3.0605^{NS}	Fully adequate
	F_2	-0.0615^{NS}	1.2913^{NS}	-1.7890^{NS}	Partially adequate
Spike length	F_1	-0.1493^{NS}	0.3147^{NS}	-0.5551^{NS}	Partially adequate
	F_2	4.5546^{NS}	-111.16^{NS}	249.1114^{NS}	Partially adequate
Biological yield plant^{-1}	F_1	-0.5076^{NS}	0.0698^{NS}	-0.1271^{NS}	Partially adequate
	F_2	-1.2565^{NS}	0.1559^{NS}	-0.3339^{NS}	Partially adequate
Grain yield plant^{-1}	F_1	-0.0159^{NS}	0.1626^{NS}	-0.2420^{NS}	Partially adequate
	F_2	-0.0283^{NS}	0.2220^{NS}	-0.3788^{NS}	Partially adequate

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 6×6 F_1 and F_2 half diallel crosses in wheat.

Genetic components	d.f.		Days to heading		Plant height		Tillers plant[-1]		Spike length		Biological yield plant[-1]		Grain yield 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	F_1	F_2
Replications	1	2	0.08	5.82	0.62	43.31*	7.71**	1.45	0.13	2.27**	1.17	29.76	13.71	26.79
a	5	5	47.77**	28.91**	357.29**	211.82**	4.6**	11.48**	1.57**	3.39**	206.34**	464.48**	66.37**	182.28**
b	15	15	1.37**	11.42**	36.94	85.99**	3.17**	1.84**	1.29**	2.24**	61.95**	272.69**	31.83**	41.97**
b1	1	1	0.00	60.36**	430.06**	742.53**	16.01**	4.71**	8.89**	5.16**	105**	2193.71**	159.72**	182.32**
b2	5	5	1.90**	7.6	7.29	36.82*	2.19	1.67*	0.38	1.84**	24.34	94.78	11.27	19.6
b3	9	9	1.22**	8.1*	9.72	40.36**	2.28*	1.61*	0.94**	2.13**	78.06**	158.08**	29.05**	38.81*
Error	20	40	0.12	3.46	25.6	12.15	0.81	0.62	0.17	0.18	12.67	47.07	8.31	13.62

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

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

Genetic components	Days to Heading		Plant height		Tillers plant⁻¹		Spike length		Biological yield plant⁻¹		Grain yield 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	10.90*	7.18*	74.24*	35.85*	1.93*	2.41*	0.34	0.61*	52.77*	81.84*	21.49*	42.41*
	±0.77	±2.69	±30.91	±11.98	±0.85	±2.41	±0.49	±0.18	±19.15	±35.64	±10.16	±12.97
H_1	2.97*	11.16*	17.91	81.37*	5.21*	2.00*	1.26	2.92*	91.35*	256.20*	45.33*	40.33*
	±0.4	±3.55	±25.13	±16.17	±1.31	±0.64	±0.76	±0.36	±23.94	±55.96	±13.77	±12.78
H_2	2.17*	9.71*	23.79	73.59*	4.50*	1.65*	1.33*	2.41*	88.51*	239.00*	43.56*	37.71*
	±0.29	±2.81	±21.54	±13.54	±1.05	±0.47	±0.65	±0.28	±21.03	±48.22	±11.83	±10.70
F	-0.76	4.84	-17.68	8.91	1.90	1.03	0.06	0.46*	0.59	26.96	10.28	20.40
	±0.65	±3.35	±26.69	±13.10	±1.11	±0.74	±0.6	±0.25	±18.83	±42.75	±11.68	±14.44
h^2	-0.04	12.48*	132.94*	158.27*	5.00*	0.92	2.71	1.09*	37.64	466.28*	49.48*	37.14
	±0.05	±5.82	±63.58	±37.22	±2.12	±0.67	±1.56	±0.36	±25.62	±126.79	±22.54	±19.43
E	0.07*	1.11*	12.63*	4.22*	0.37*	0.20*	0.34*	0.06*	6.93*	15.07*	4.49*	4.42*
	±0.02	±0.18	±3.03	±0.72	±0.09	±0.03	±0.08	±6.26	±1.59	±2.55	±1.04	±0.708
$F_1 = \sqrt{H_1/D}$, $F_2 = \sqrt{\frac{1}{4}H_1/D}$	0.52	1.25	0.49	1.51	1.64	0.91	1.92	2.2	1.32	1.769	1.45	0.98
$H_2/4H_1$	0.18	0.22	0.33	0.23	0.22	0.21	0.26	0.21	0.24	0.23	0.24	0.23
F_1: $\sqrt{4DH_1+F}$ / $\sqrt{4DH_1-F}$ F_2: $\frac{1}{4}\sqrt{4DH_1+1/2F}$ / $\frac{1}{4}\sqrt{4DH_1-1/2F}$	0.87	1.31	0.61	1.09	1.86	1.27	1.10	1.19	1.01	1.1	1.39	1.28
h^2/H_2	-0.02	1.54	6.71	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 F2 parameter value is tested by «t» test at n-2 d.f after dividing it by its standard error.
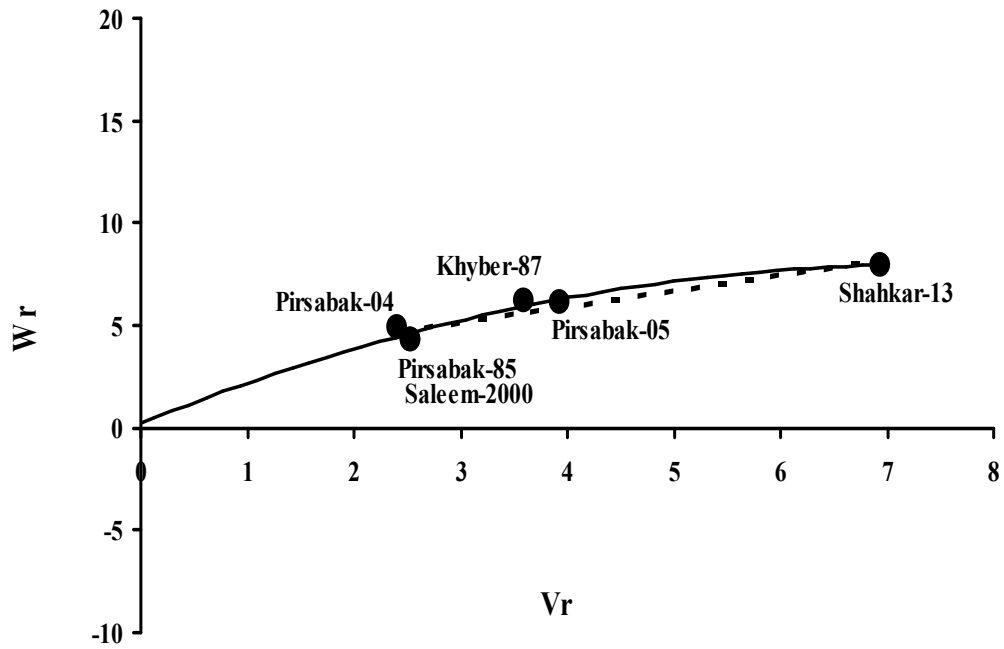
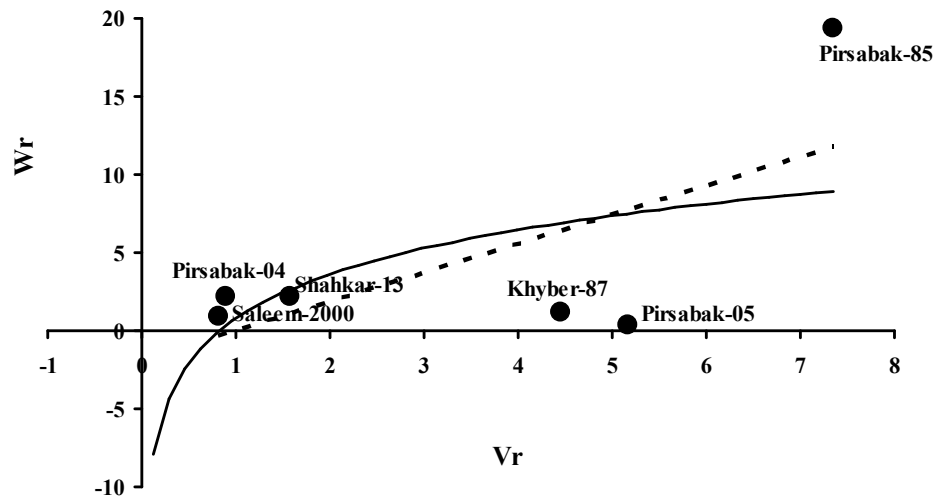**Fig. 1a.** Vr-Wr graph for days to heading in 6×6 F_1 half diallel crosses of wheat

Fig. 1b. Vr-Wr graph for days to heading in 6×6 F_2 half diallel crosses of wheat
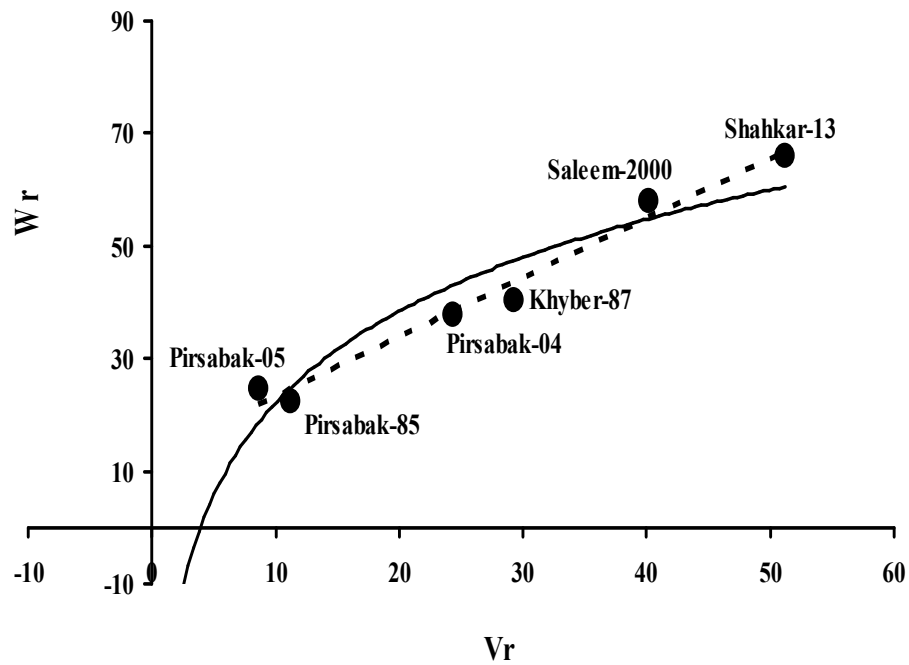
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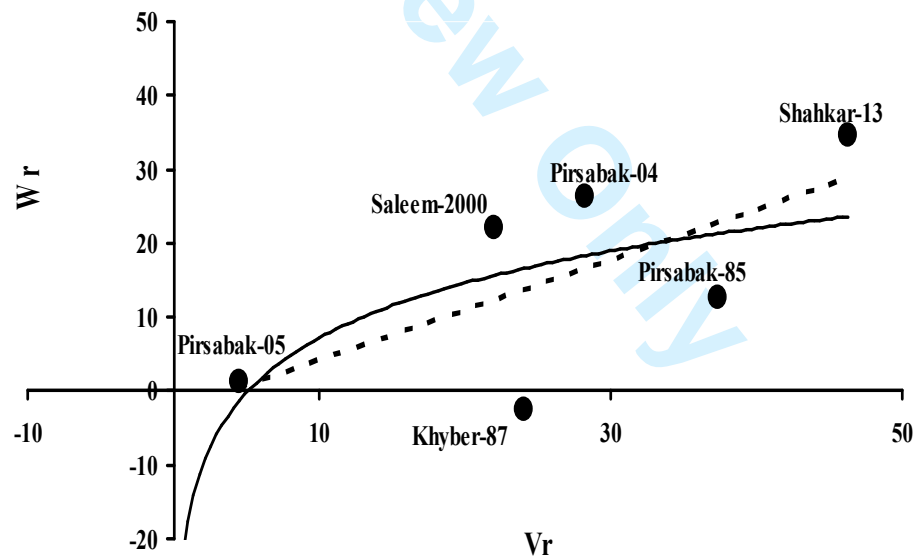**Fig. 2a.** Vr-Wr graph for plant height in 6×6 F_1 half diallel crosses of wheat

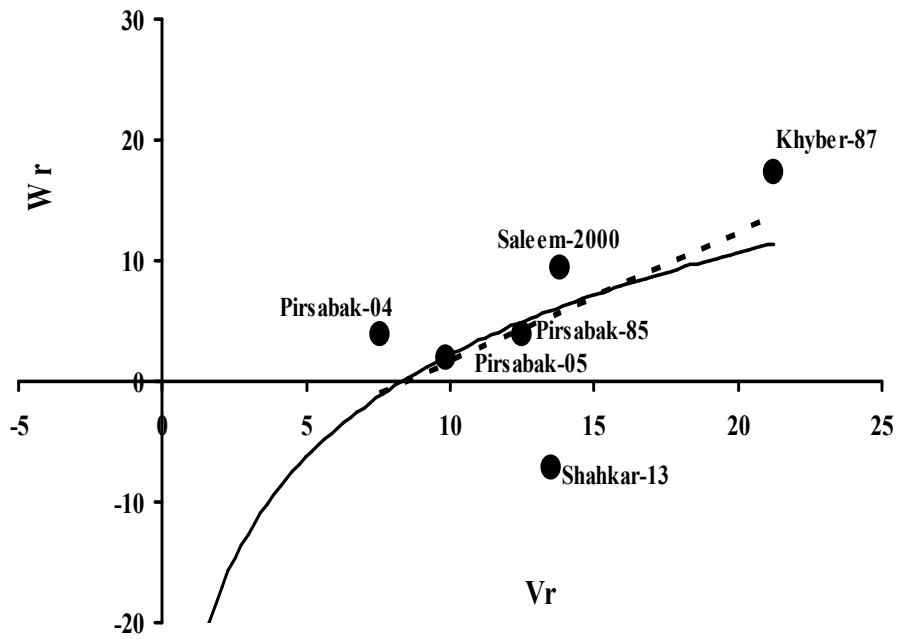**Fig. 2b.** Vr-Wr graph for plant height in 6×6 F_2 half diallel crosses of wheat

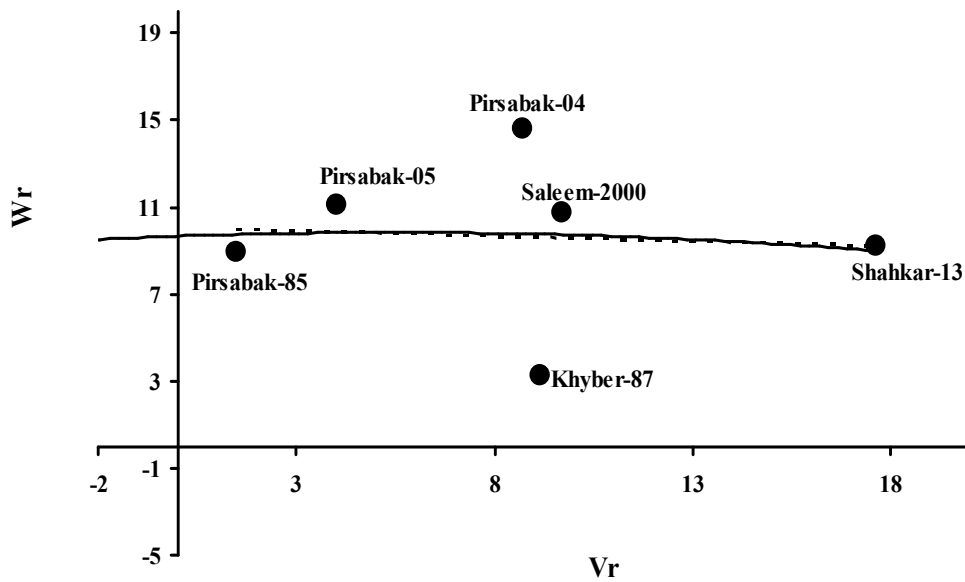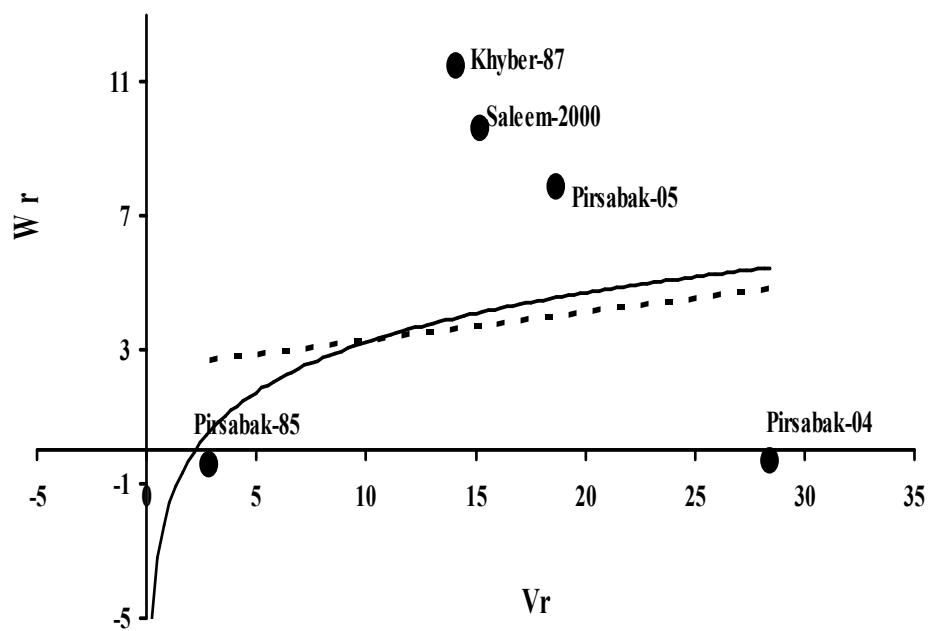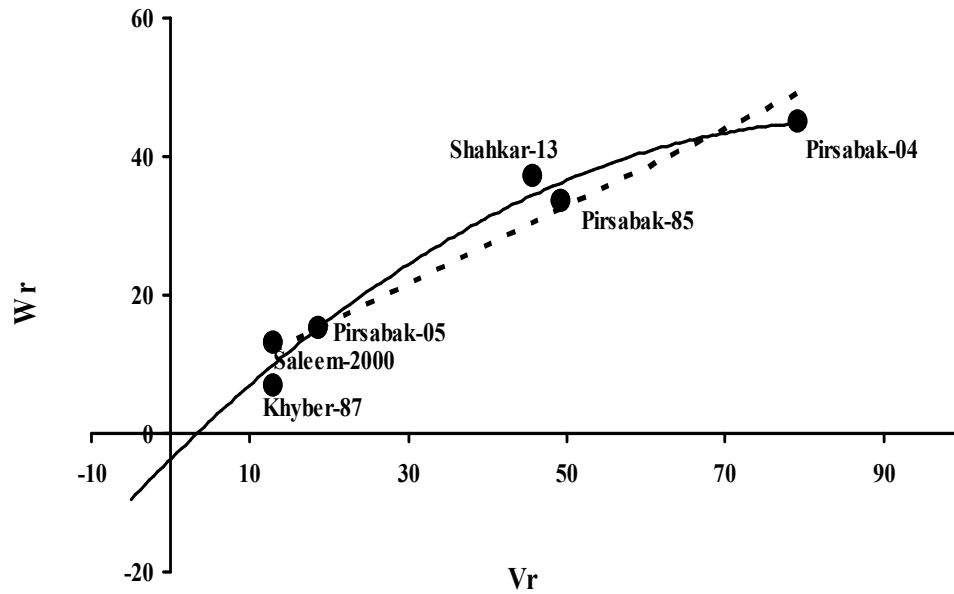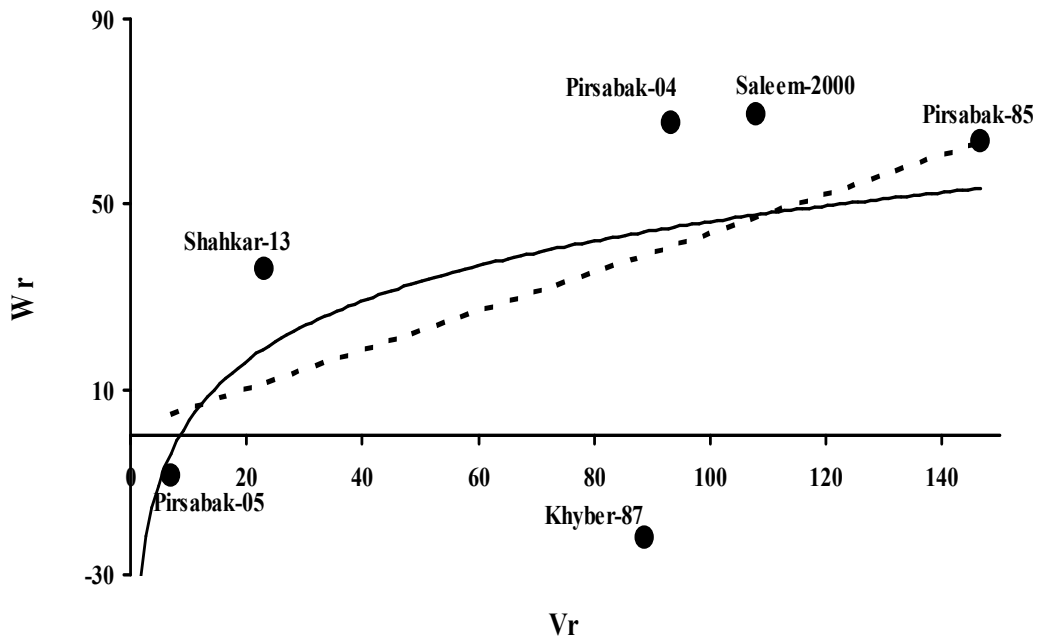**Fig. 3a.** Vr-Wr graph for tiller per plant in 6×6 F_1 half diallel crosses of wheat

Fig. 3b. Vr-Wr graph for tiller per plant in 6×6 F_2 half diallel crosses of wheat

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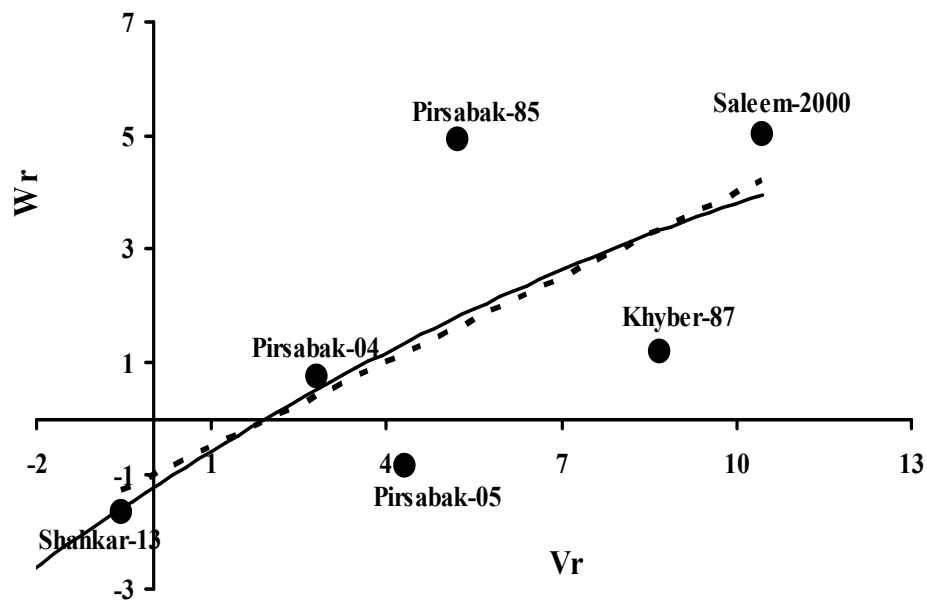
Fig. 4a. Vr-Wr graph for spike length in 6×6 F_1 half diallel crosses of wheat

Fig. 4b. Vr-Wr graph for spike length in 6×6 F_2 half diallel crosses of wheat

Fig. 5a. Vr-Wr graph for biological yield per plant in 6×6 F_1 half diallel crosses of wheat

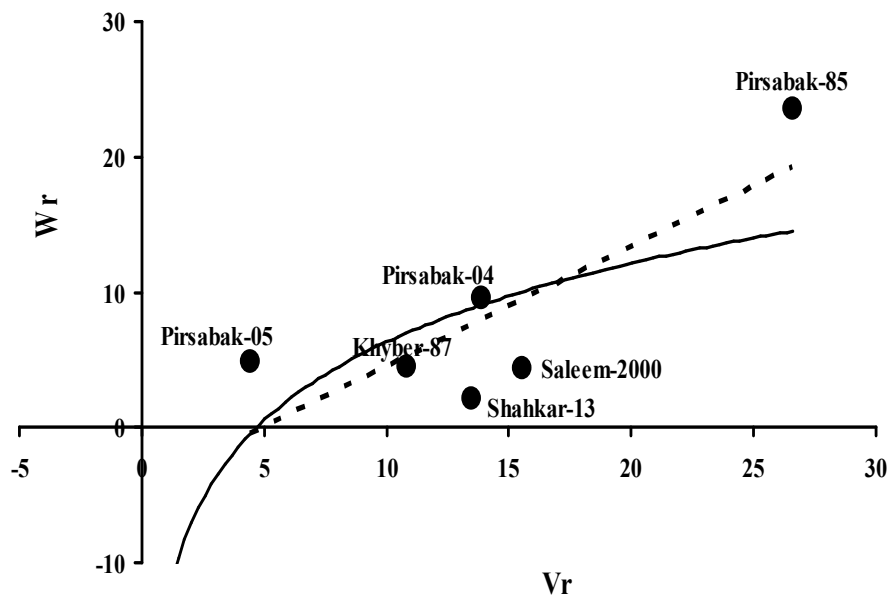**Fig. 5b.** Vr-Wr graph for biological yield per plant in 6×6 F_2 half diallel crosses of wheat

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Fig. 6a. Vr-Wr graph for grain yield per plant in 6×6 F_1 half diallel crosses of wheat
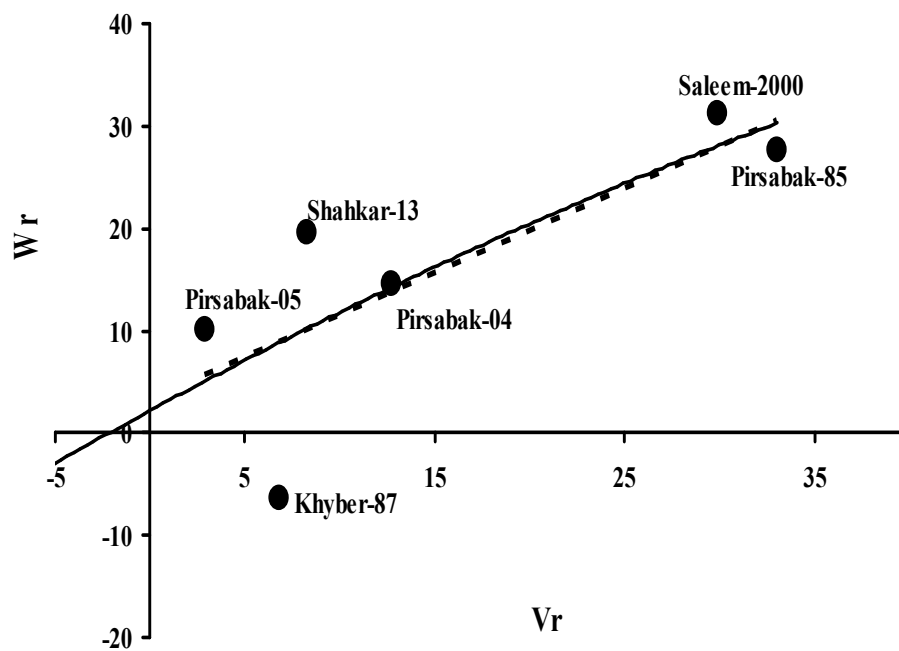

Fig. 6b. Vr-Wr graph for grain yield per plant in 6×6 F_2 half diallel crosses of wheat