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Full Length Research Paper

Diallel analysis to study the genetic makeup of spike and yield contributing traits in wheat (*Triticum aestivum* L.)

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Five wheat genotypes were crossed in complete diallel fashion for gene action studies of spike length, spikelets per spike, grains per spike, grain weight per spike and grain yield per plant. Analysis of variance reveals significant differences for all the traits. The significant deviation of joint regression value “b” from zero and non significance of “t” square value, suggested the absence of epistasis for all traits which in turn attested fitness of the data for simple additive dominance model. Additive genetic component (D) proved to be significant for all traits under consideration except grain weight spike per spike, but dominant component H_1 and H_2 was higher in magnitude than additive (D) for spike length and grain yield per plant, illustrating the prevalence of dominance genetic effects. The additive genetic component was more imperative for genetic manipulation of number of spikelets per spike and number of grains per spike. Dominant genes at most of the loci were in excess than recessive genes for spike length and grain yield per plant which was firmly supported by the positive value of F and further strengthened by the value of $(4DH_1)^{0.5}+F/(4DH_1)^{0.5}-F$ which was greater than unity for these two traits. The component that was strongly influenced by the environment was spikelets per spike. High magnitude of narrow sense heritability ($h^2_{n.s}$) was noticed for spikelets per spike (79%), and grains per spike (88%) thus illustrated fixable and additive heritable variation for these traits. The operation of over dominance was observed for spike length, grain weight per spike and grain yield per plant, whereas, spikelets per spike and grains per spike were under additive type of gene action with partial dominance, implying that spikelets per spike and grains per spike can significantly be improve by pursuing pedigree method while heterosis can be exploited for spike length, grain weight per spike and grain yield per plant.

Key words: Wheat, gene action, genetic parameters, heritability, yield.

INTRODUCTION

Bread wheat is one of the most consumed cereals in Pakistan. Due to its multiple uses, wider adaptation and high nutritive value, it is the staple food for about one third of the world population. It occupies a vital position in agriculture policies of the country, as it is the main source of starch and protein. Worldwide wheat covers an area of about 225.56 million ha followed by corn (158.19 million ha) and rice (157.83 million ha) (Anonymous, 2010). In 2008/2009, world production of wheat was 683.13 million metric tons, making it the second most-produced cereal after maize (784.2 million metric tons) (Anonymous, 2010). It is cultivated on an area of 9.062 M ha with a production of 23.5 M tones and contributed 13.1% to the value added in agriculture and 2.8% to GDP of Pakistan (GOP, 2008). Wheat also plays a key role in

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terms of food security and economic permanence of the country. For a rapidly growing population in Pakistan, we need to increase the grain yield with all the upcoming biotic and abiotic factors. Though Pakistan made significant progress by attaining the 6th position in major wheat producing countries of the world in the year 2007 (FAO, 2007), there is still room for improvement in terms of overall yields. Its production can be improved through the development of genotypes proficient of producing better yield under various agro climatic conditions.

Wheat breeding, in its fundamental form, had many priorities, of which yield potential gain has been given a lot of attention. Progress in this endeavor is dependent on the understanding of the structure of genetic diversity in the wheat gene pool and the understanding of the relationship between genotypic and phenotypic variation. A large number of new genetic combinations are therefore essential for the construction of high-resolution genetic maps, for implementation of efficient breeding methods and rapid development of superior varieties. For this purpose, diallel mating design is extensively used in crop improvement programs because it offers crossing of selected parents in all possible combinations and creates variability within the breeding material and helps in selection which is the basic step of every breeding program. Moreover, the potential variability is released due to segregation and recombination after such inter mating. The diallel analysis advocated by Hayman (1954a) and Mather and Jinks (1982) provides reliable method particularly in autogamous crops like wheat to review the genetic system and gene action involved in the expression of plant attributes, right in the F_1 generation. To understand the mode of expression of genes that are present in these segregants/ recombination, gene action studies is helpful because it aids in selection of parents to be used in hybridization as well as appropriate breeding procedures for genetic improvement of various polygenically controlled characters.

The wheat inflorescence is known as a spike. The main constituent of yield in wheat is spike and it ultimately contributes a lot to the grain yield. The main objective of wheat breeding is to improve yield and related parameters by selecting and improving yield components including spike characteristics like, spike length, spikelets per spike, grains per spike, spike weight. Additive gene action is involved in controlling spike length (Chowdhry et al., 2002; Malik et al., 2005), but non-additive genetic effects were reported by Rahim et al. (2006). However, according to some researchers, over-dominance is involved in spike length and spikelets per spike (Rahman et al., 2003; Habib and Khan, 2003). But additive type of gene action with partial dominance was found for spikelets per spike (Malik et al., 2005; Khan et al., 2003; Habib and Khan, 2003). For grains per spike and grain yield per plant, over dominance was observed by Khan et al. (2003) and Riaz and Chowdhry (2003). While partial dominance was observed by Habib and Khan (2003) for controlling grains per spike.

Therefore, this study was undertaken to generate information about nature of gene action and magnitude of its contribution to various characters in a 5 × 5 diallel cross. Information derived may be effectively exploited in developing and formulating an efficient breeding program for the evolution of better quality and high yielding varieties.

MATERIALS AND METHODS

The plant material involved in this study comprised 5 wheat varieties/lines viz., Chenab-2000, Rohtas-90, SH-2002, Uqab-2000, 243-1, having broad genetic base and varied by date of release, pedigree and yield components and was crossed in a complete diallel fashion at experimental farm area of University of Agriculture, Faisalabad, during crop season 2006/2007. Seeds of F_1 hybrids along with their parents were sown in the field in a randomized complete block design with three replications. The entries were assigned randomly to experimental units in each block having row to row and plant to plant distance of 30 and 15 cm respectively. Two seeds per hole were sown with the help of a dibbler and later thinned to one seedling per hole after germination. All recommended cultural practices and inputs like hoeing, manuring and irrigation, etc., were kept uniform for all entries from sowing till harvesting to minimize environmental variation to the maximum extent. For data collection, ten guarded plants for each parent and crosses were tagged at random in each replication, and data was recorded for spike length of mother shoot of selected plants in centimeters, from base to the tip of spike, excluding awns and finally average spike length was obtained. Spikelets were counted from the mother spike of selected plants and were averaged. For grain weight, mother shoot of each selected plant was weighed on electronic balance (Compax- Cx-600). Similarly, the spike of the mother shoot was threshed manually and grains per spike were counted for each genotype and for grain yield, all spikes of individual selected plants were threshed manually and weighed using electric balance (Compax- Cx-600).

Statistical analysis

The data collected for all afore-mentioned characters were subjected to analysis of variance as proposed by Steel et al. (1997) for determining variability. In case where significant differences were found, the data were subjected to regression covariance/variance (Wr/Vr) analysis and analysis of variance of Wr +Vr and Wr-Vr arrays. The diallel crossing system as suggested by Hayman (1954a, 1958) and Jinks (1954, 1955), modified by Mather and Jinks (1982) and adopted by Singh and Chaudhary (1985) and was used for analysis of genetic parameters.

The diallel analysis was carried out on the following assumptions: (1) diploid segregation, (2) no reciprocal effects, (3) homozygous parents, (4) no epistasis, (5) no multiple allelism, and (6) independent genes distribution among parents. *Triticum aestivum* L. is an allohexaploid but it segregates in diploid manner. So, the research material executes first assumption. For removing reciprocal differences, the entries in the off diagonal cells of the diallel table were replaced by their means of cross and reciprocal prior to analysis. The parental lines were selfed for three generations to maintain true to type. For 4th, 5th and 6th assumptions, the data were subjected to two tests. Failure of any combination of these tests invalidates the additive dominance model for these parameters, which shows complete inadequacy of additive dominance model. Their further analysis was stopped, however, the genetic analysis was extended for those traits having sufficient variability and their Wr-Vr does not vary significantly from array at 0.01 probability levels. But according to Jinks (1954), the estimates were less eliable than when all assumptions have been fulfilled. The direct and derived genetic components were computed according to Hayman (1954a) and used by Hayman (1958). Heritabilities in narrow sense were worked out following Mather and Jinks (1982).

The genetic parameters studied included: D (variation due to additive genetic effects), H_1 (variation due to dominant genetic effects), H_2 (variation attributed dominant effects corrected for gene distribution), F (the relative frequencies of dominant to recessive alleles in the parental populations, which is positive when dominant alleles are more than recessive alleles), h_2 (variation due to dominance effects of heterozygous loci). The dominance additive ratio $(H_1/D)^{1/2}$ indicates the degree of dominance, which is equal to one, when dominance is complete, while greater than one refers to over dominance, and less than one in case of partial dominance gene effects, and E (variation attributed to environmental effects).

RESULTS AND DISCUSSION

Genotypic differences among parents

Analyses of variance for all characters prove to be significant (Table 1) and reveal that adequate genetic variability existed among genotypes. Hence, improvement can be made successfully through selection. Genetic parameters were therefore estimated for each of these characters. The mean squares for the traits are represented in array means (Table 2) which showed that all genotypes varied significantly, regarding yield and yield components. Genotype SH-2002 had the highest values for spikelets per spike (19.75), grain weight per spike (2.34) and grain yield per plant (22.60), while utmost values for spike length (13.05) and grains per spike (64.26) were present in genotype Uqab-2000. Lowest values for spike length (12.39) grains spike (60.36) and grain weight per spike (2.33) were found in Chenab-2000. The data also reveal that the same kind of order for highest values did not follow in each genotype (Table 2).

Additive dominance model

The validity of additive dominance model to each data set was assessed using joint regression co-efficient (b) analysis and analysis of variance of (Wr+Vr) and (Wr-Vr) arrays (Hayman1954a, b). To qualify the data for additive dominance model, the data should qualify these criteria: (a) the Wr/Vr regression slope should deviate significantly from zero but not from unity, which indicates non-allelic interaction, and; (b) the non-significant values of Wr+Vr and Wr-Vr arrays showed the presence of dominant genetic effects and absence of non-allelic interaction, respectively (Mather and Jinks, 1982; Singh and Chaudhary, 1985). For complete adequacy of additive dominance model, the data set should qualify both mentioned tests. However, for partial adequacy, at least one of them is considered adequate (Azhar and McNeilly, 1988; Johnson and Aksel, 1964). In case of partial adequacy, the most divergent Wr +Vr and parental values were removed from the analysis to obtain complete adequacy. The value of regression co-efficient (b) deviated significantly from zero (Table 3) for all traits, suggesting the absence of non allelic interaction and adequacy of the data fit for additive dominance model.

The non significance of “t” square value also attested the absence of epistasis. The fitness of the data for additive dominance model was also verified by mean squares of Wr+Vr and Wr-Vr. In this test, the mean squares of Wr+Vr should be significantly different between the arrays while the mean squares Wr-Vr should be non significant (Mather and Jinks, 1982; Singh and Chaudhary, 1985). The lack of significance for Wr-Vr determined the lack of epistasis and suggested the allelic interaction was not involved in the inheritance of all traits. The mean squares of Wr+Vr for spikelets per spike (7.956), grains per spike (3250.64) and grain weight per spike (0.29) prove no significant deviation, however, it was significant for grain yield per plant. But joint regression ‘b’ varied significantly from zero for all these attributes, which implied the partial adequacy of these traits for further genetic analysis. The spike length was the only character that fulfills all the criteria of adequacy test. The value of ‘b’ for spike length (0.78) differ from zero but not from unity, non significance of t^2 (3.93), highly significant value of mean squares for (Wr+Vr) between arrays (54.17) and non significance of (Wr-Vr) mean squares (2.12) revealed full fitness of the data for further genetic analysis (Table 4).

Illustration of genetic parameters for yield components

Genetics of yield components was estimated by analysis of genetic components of variation, that is, D, H_1, H_2 and F (Table 4). Additive (D) and dominance components (H_1, H_2) were significant for spike length and grain yield per plant, while spikelets per spike and grains per spike exhibited significance for additive variance (D) only. On the other hand, grain weight per spike indicated non significant value for both additive and dominance variance. These results elucidate that genetic control of spikelets per spike and grains per spike was completely advocated by genes that have additive effects. Riaz and Chowdhry (2003) pondered additive effects for these traits. However, Habib and Khan (2003) and Gurmani et al. (2007) reported over dominance for inheritance of spikelets per spike and Asif et al. (1999) and Chowdhry et al. (2002) for grains per spike. Since additive genes are directly inherited from parents to offspring, and resemblance among parents and progenies is the result of additive genes, additive genes determine the breeding value of plant material, therefore, spikelets per spike and

Table 1. Mean squares of some spike related traits in 5 × 5 diallel cross.

SOV	DF	Spike length	Spikelets per spike	Grains per spike	Grain weight per spike	Grain yield per plant
Replication	2	0.13 n.s.	0.15 n.s.	0.52 n.s.	0.37 n.s.	5.90 n.s.
Genotypes	24	2.02**	1.40**	29.12**	0.15**	26.59**
Error	48	0.24	0.46	9.97	0.07	3.28
C.V. %age		1.11	1.65	2.46	6.46	8.24

P* < 0.01; n.s (not significant).

Table 2. Array means for various morphological traits in 5 × 5 diallel cross in wheat.

Parent	Spike length (cm)	Spikelet per spike	Grain per spike	Grain weight per spike (g)	Grain yield per plant (g)
Chenab 200	12.39	18.93	60.36	2.33	22.27
Rohtas-90	13.01	18.85	62.93	2.27	21.87
SH-2002	12.62	19.75	62.23	2.34	22.60
Uqab-2000	13.05	19.54	64.26	2.32	21.16
243-1	12.66	19.09	60.40	2.21	21.93

Table 3. Analysis of variance-covariance arrays for traits qualifying the additive-dominance model adequacy test.

Parameter	Spike length (cm)	Spikelet per spike	Grain per spike	Grain weight per spike (g)	Grain yield per plant (g)
Joint regression (b)	0.78±0.15	0.58±0.15	0.73±0.17	0.73±0.19	0.68±0.14
Test for b=o	3.858 *	3.858 *	4.18 *	3.84 *	4.41 *
Test for b=1	2.795 $^{\text{n.s.}}$	2.795 $^{\text{n.s.}}$	1.561 $^{\text{n.s.}}$	1.383 $^{\text{n.s.}}$	2.25 $^{\text{n.s.}}$
Test for t^2	3.937 $^{\text{n.s.}}$	3.93 $^{\text{n.s.}}$	1.183 $^{\text{n.s.}}$	0.835 $^{\text{n.s.}}$	2.82 $^{\text{n.s.}}$
Mean squares of array difference Wr-Vr	2.127$^{\text{n.s.}}$	0.959 $^{\text{n.s.}}$	473.177 $^{\text{n.s.}}$	0.013 $^{\text{n.s.}}$	303.65 $^{\text{n.s.}}$
Mean squares of array difference Wr+Vr	54.179 **	7.956 $^{\text{n.s.}}$	3250.643 $^{\text{n.s.}}$	0.286 $^{\text{n.s.}}$	7.76 *

P* < 0.01; n.s (not significant).

grains per spike could significantly be improved by pursuing pedigree method right from F_2.

The phenotypic expression of spike length and grain yield per plant is a compound effect of both additive and non additive components. However, higher magnitude of dominance genetic component H_1 and H_2 over D for spike length (1.814 and 1.478 > 0.559) and grain yield per plant (30.478 and 26.103 > 3.957) represented the preponderance of non-additive genetic component for genetic manipulation of these traits. Some researchers like Rahman et al. (2003) and Farooq et al. (2010) also investigated over dominance for inheritance of these traits. For genetic manipulation of the parents for spike length and grain yield per plant, heterosis breeding could be exploited for improving the traits.

The magnitude of dominance values H_1 and H_2 was approximately equal to each other for characters like spike length, spikelets per spike and grains per spike (Table 4). It confirms the existence of approximately equal proportion of positive and negative alleles in the parents while grain weight per spike and grain yield per plant had unequal positive and negative alleles in the parents to influence these two traits.

The value of F, which is the measure of relative frequency of dominant to recessive alleles in the parents, was non significant (Table 4) for all characters under question, but spike length and grain yield per plant represented positive value while F value proved to be negative for spikelets per spike, grains per spike and grain weight per spike, implying that excess of dominant

Table 4. Estimates of components of variance for traits qualifying the additive-dominance model adequacy test.

Components of variance	Spike length(cm)		Spikelet per spike		Grains per spike		Grain weight per spike(g)		Grain yield per plant(g)	
	Estimate	**S.E.**	**Estimate**	**S.E.**	**Estimate**	**S.E.**	**Estimate**	**S.E.**	**Estimate**	**S.E.**
D	0.559 *	±0.150	0.617*	±0.948	7.944*	±0.757	-0.0059 $^{n.s.}$	±0.0058	3.957*	±1.912
H1	1.814*	±0.405	0.201 $^{n.s.}$	±0.256	1.971 $^{n.s.}$	±0.044	-0.0096 $^{n.s.}$	±0.0159	30.478*	±5.165
H2	1.478*	±0.367	0.259 $^{n.s.}$	±0.232	1.648 $^{n.s.}$	±0.323	-4.9 *	±0.027	26.103*	±4.684
F	0.617 $^{n.s.}$	±0.374	-0.201 $^{n.s.}$	±0.236	-1.735 $^{n.s.}$	±1.891	-0.0194 $^{n.s.}$	±0.014	7.644 $^{n.s.}$	±4.778
h^2	2.798 *	±0.247	-0.096 $^{. n.s.}$	±0.156	-1.319*	±1.252	0.098 $^{n.s.}$	±0.190	51.842*	±3.163
E	0.08 $^{n.s}$	±0.611	0.152 *	±0.038	3.202 $^{n.s.}$	±0.309	0.029 $^{n.s.}$	±0.002	1.128 $^{n.s.}$	±6.78
$(H_1/D)^{0.5}$	1.801		0.693		0.498		1.277		2.768	
$(h^2_{n.s})$	0.235		0.793		0.880		0.51		0.49	
$H_2/4H_1$	0.258		0.323		0.209		0.0125		0.249	
$\frac{(4DH_1)^{0.5}+F}{(4DH_1)^{0.5}-F}$	1.883		0.483		0.640		-0.125		2.063	
h^2/H_2	1.89		-0.372		-0.800		1.84		1.98	

P*<0.01; n.s. (not significant).

alleles was present in the parents for spike length and grain yield per plant and recessive alleles for spikelets per spike, grains per spike and grain weight per spike.

The claim was strengthened by value of $(4DH_1)^{0.5}$+F/$(4DH_1)^{0.5}$-F which was greater than unity for spike length and grain yield per plant and less than unity for spikelets per spike, grains per spike and grain weight per spike.

The measurement of net dominance (h^2) was positive and significant for spike length and grain yield per plant and indicated that the direction of dominance was toward a greater side and substantial contribution to dominance was due to heterogeneity of loci. Hence, utilization of heterosis breeding could be rewarding for these traits.

The significant environment component (E) for spikelets per spike indicates that this trait was strongly persuaded by the environment (Table 4). Such might lead to discrepancy because environment had its contribution to the variation, while all other characters had not been significantly influenced by this factor.

The estimates of frequencies at non-additive loci can be obtained from $H_2/4H_1$. This ratio between the genes with positive and negative effects was somewhat equal to 0.25 for spike length (0.258) and grain yield per plant (0.249), indicating the distribution of positive and negative alleles at the loci exhibiting dominance (Mather and Jinks, 1982; Singh and Chaudhary, 1985). However, $H_2/4H_1$ ratio deviated from 0.25 for spikelets per spike (0.323), grains per spike (0.209) and grain weight per spike (0.012) which confirmed the asymmetrical distribution of these alleles among the parents.

The number or group of genes that control the character and exhibited dominance (h^2/H_2) were 1.89, 0.37, 0.8,1.84 and 1.98 for spike length, spikelets per spike, grains per spike, grain weight per spike and grain yield per plant with values of 1.89, -0.37, -0.800,1.840 and 1.980, respectively.

Narrow sense heritability ($h^2_{(n.s)}$) measures the magnitude of genotypic variation in the breeding material, which is mainly responsible for changing the genetic composition of the population via selection (Dabholkar, 1992; Falconer, 1989). Moreover, narrow sense heritability is directly proportional to additive genetic variance and is maximum in additively controlled characters, and lower in non-additive genetic components. So, spikelets per spike and grains per spike coupled with significant additive variance showed relatively

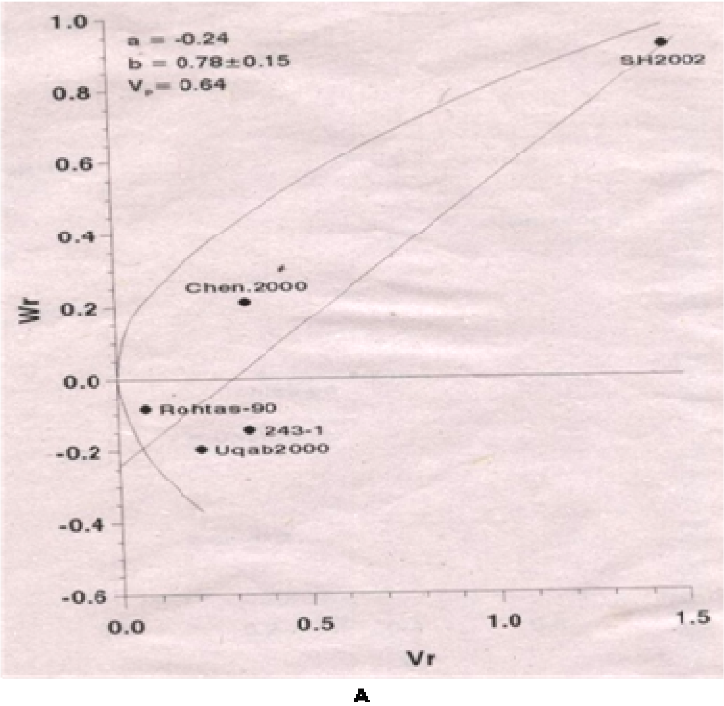


Figure 1. Vr/Wr graph for (A) spike length, (B) spikelets per spike, (C) grains per spike, (D) grain weight per spike, (E) grain yield per plant.

high heritability (79 and 88%, respectively) value for these character and prove the importance of additive gene action in the expression of these character and could be useful in selection of elite genotypes from segregating material while other character that were under the influence of dominance namely spike length, grain weight per spike and grain yield per plant had lower heritability value, that is, 23, 51 and 49%, respectively.

From these results, it was concluded that spikelets per spike and grains per spike should be significantly exploited through selection in early generations. These inferences were also reflected and pronounced by values of additive genetic effects (D) which were greater than dominance components (H_1 and H_2) and supported the conclusion.

The degree of dominance $(H_1/D)^{0.5}$ greater than 1, for spike length (1.801), grain weight per spike (1.270) and grain yield per plant (2.768) in Table 4 indicated these traits were governed by over dominance type of gene action, while spikelets per spike (0.698) and grains per spike (0.493) were under partial dominance type of gene action. Complete dominance was found to be absent for all characters.

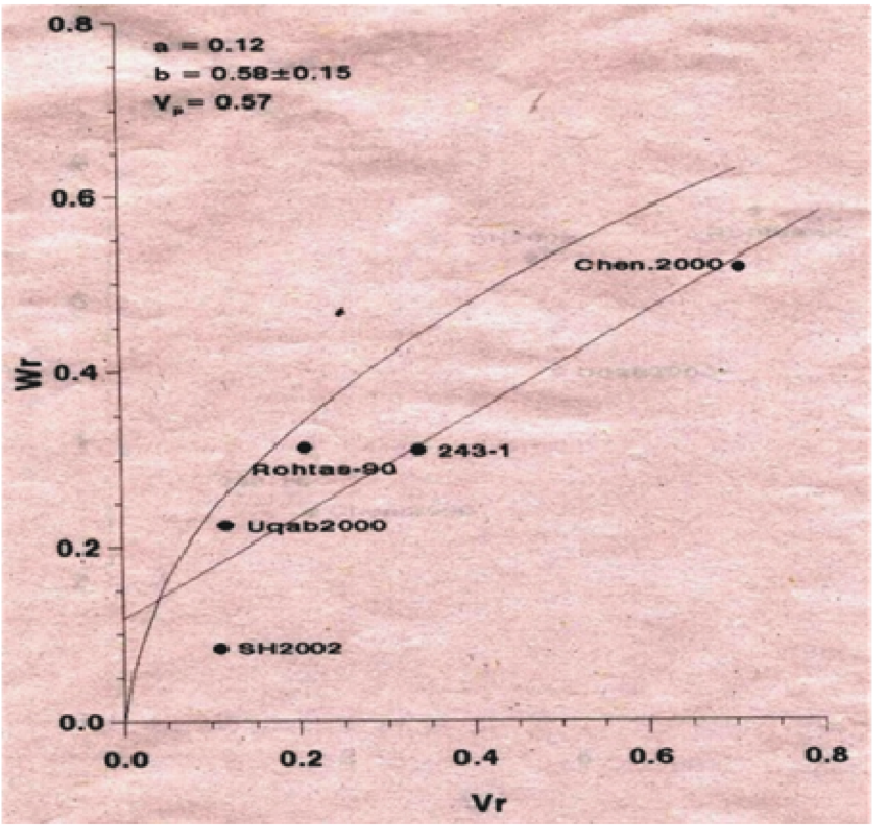
Graphical representation

The graphical representation of Vr/ Wr graph (Figure 1a to e) illustrates the absence of epistasis for all traits under consideration, as estimated, regression line did not deviate significantly from unit slope. Genes regulating the inheritance of spike length, grain weight per spike and grain yield per plant were governed by over dominance type of gene action as regression line intercepted the Y-axis below the point of origin. The same kind of results, as reflected in Table 4, was also supported by greater value of “H_1 and H_2” than “D” (Flintham et al., 1997; Walia et al., 1995; Chowdhry et al., 2002). The inheritance of spikelets per spike and grains per spike confirmed the contribution of additive genetic effects as regression line cut the vertical axis well above the point of origin (Asif et al., 1999; Habib and Khan, 2003).

The varietals distribution along the regression line showed that maximum dominant genes for spike length and grains per spike were present in Chenab-2000, while SH-2002 had maximum dominant genes for spikelets per spike and grain weight per spike being closer to the point of origin. Genotype Uqab-2000 was located near the origin and carried most dominant genes for grain yield per plant while Rohtas-90 had most recessive genes for grains per spike and grain weight per spike. In contrast, genotypes SH-2002, Chenab-2002 and 243-1 had most recessive genes for spike length, spikelets per spike and grain yield per plant respectively.

Conclusion

The results from this study determine that all genotypes



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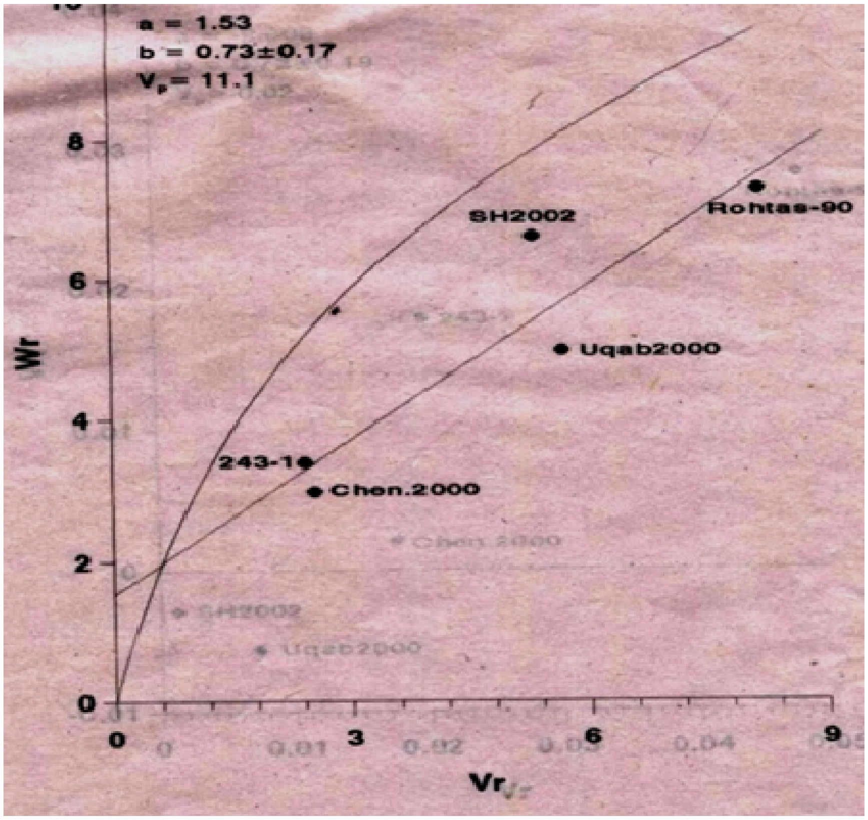

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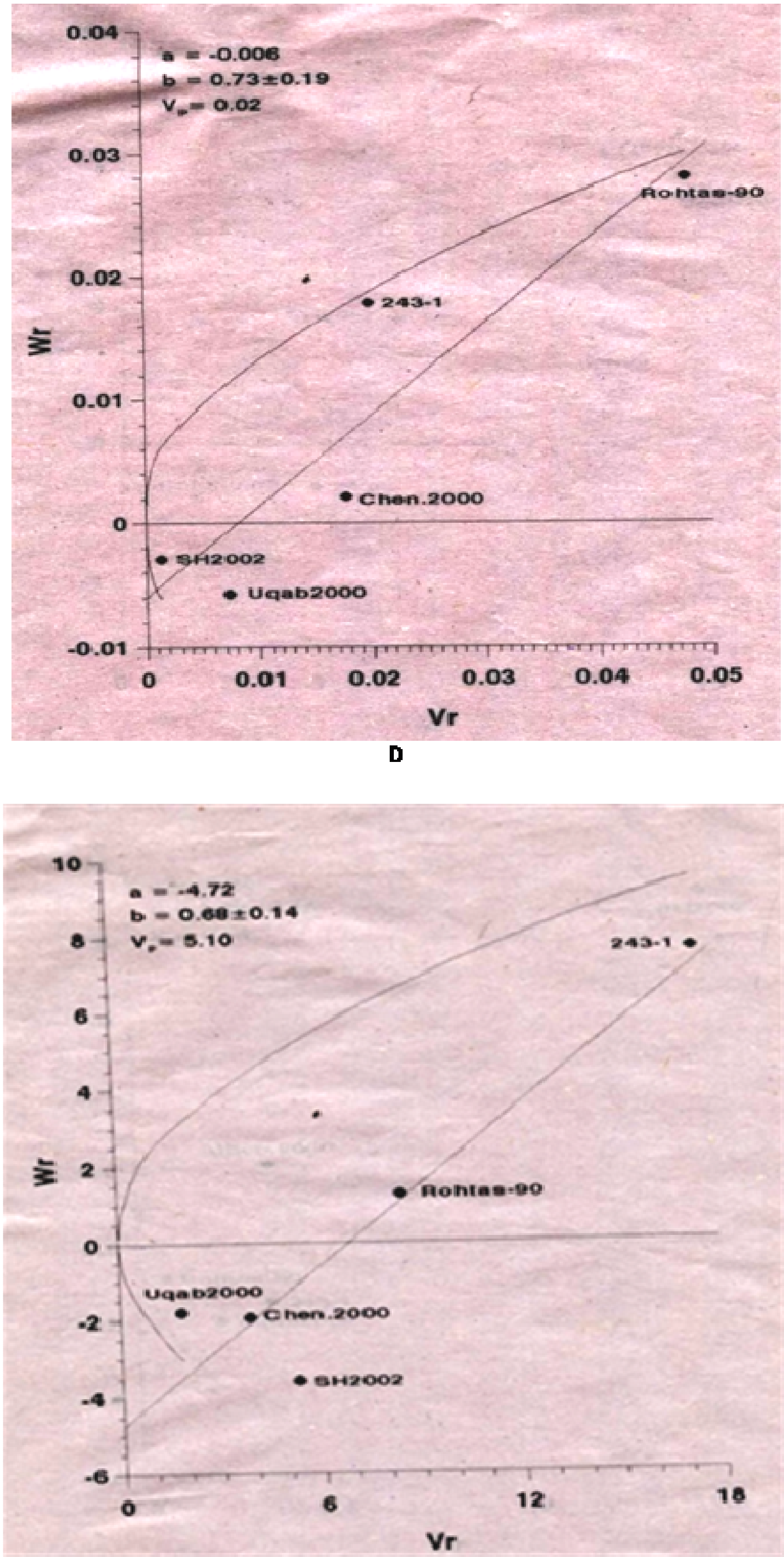
Figure 1. Contd.



D

E

Figure 1. Contd.

had substantial genotypic distinction among themselves. Additively, controlled character provides a more reliable selection mechanism in early segregating generation. So, spikelets per spike and grains per spike coupled with high heritability value suggested that significant improvement can be made through selection by pursuing pedigree method. Pervasiveness of dominance phenomenon as depicted by genetic components was further verified by graphs which demonstrate over dominance for spike length, grain weight per spike and grain yield per plant called for prudent and more cautious selection exercise for exploitation of these attributes and suggested that manipulation of the parents might be useful through heterosis.

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