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RESEARCH ARTICLE

Genetic model analysis on seedling and maturity traits in wheat under rainfed conditions

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Abstract An experiment was conducted to access the genetic variability among early vigour and quantitative traits under limited moisture in F_2 generation of a 5 × 5 diallel cross of bread wheat. The results indicated that there was significant genotypic variation among the genotypes. Additive dominance model revealed full fitness of the data for RL, DSW, FRW, DRW, spike length, and 1000-grain weight but was partially fit for SL, FSW, R/S, tillers per seedling, plant height, tillers per plant, spikelets per spike, and grain yield per plant. The partially adequate models for these plant characters might be due to the presence of non-allelic interaction, linkage, and non-independent distribution of the genes in the parents. Additive genes coupled with moderate to high narrow sense heritability were involved in the heritage of all the traits, which indicated a higher scope of selection in early generations.

Keywords wheat, seedling trait, maturity trait, genetic model, rainfed condition

Introduction

Semi-arid areas are characterized by their low and erratic rainfall, especially during the early phase of plant development. Lower rainfall results in insignificant soil moisture. Injury is caused when the tender, newly emerged seedlings are exacerbated with drought stress, which results in stunted seedlings with weaker shoots and roots and lesser plants per unit area with fewer tillers. Eventually, the plants are destabilized to such an extent that they never recover utterly from early setbacks. Hardy, physiologically efficient, and vigorous seedlings are required to handle these initial shocks. Early vigour is a genetic character that can be improved, maintained, and incorporated into the newer genotypes. Early vigour is considered an essential component of crop plant development under most environmental conditions (Ludlow and Muchow, 1990; Khan et al., 2002). Crop varieties with early seedling vigour and good stand establishment tend to maximize the use of available soil water, resulting in an increase in dry matter accumulation and the improvement of grain yield (Awan et al., 2005).

Sometimes, the traits selected for drought tolerance may be inappropriate for the target region. For example, unless the trait conditioning survival at the seedling stage also conditions response to drought at later stages, breeding for survival during drought at the seedling stage may be totally inappropriate if drought only occurs around flowering or grain filling (Reynolds et al., 2001). The most appropriate way to identify traits that may limit wheat yields in dry environments is to use the framework proposed by Passioura (1977). This framework is based on grain yield, not on drought protection or survival under drought, which was popular in the past but largely unsuccessful. Highly heritable traits in this context are easy to select and maintain their stability ranking across a wide range of environments. There are some reports about the linear relationship between early vigour and grain yield (Turner and Nicolas, 1987; Subhani, 2000; Hosseini et al., 2004). Hybridization systems, such as biparental mating and/or diallel selective mating, could be useful for the improvement of these traits, which could help in isolating drought tolerant progenies (Kumar and Sharma, 2005). Gene action following diallel cross analysis was also

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reported for various seedling, yield, and related parameters in wheat by Lonts (1986); Chowdhry et al. (2001); Mahmood and Chowdhry (2002); and Rahim et al. (2006). Hence, this genetic umbrella of different seedling and yield-related traits should be proceeded further in order to isolate drought tolerant lines with high yield potential.

The objective of this research was to access the magnitude of variability, to investigate the nature of gene action, and to predict the behavior of various early vigour and yield contributing traits in succeeding generations in bread wheat genotypes and their respective F_2 populations in a moisture stress environment.

Materials and methods

Plant material

Five varieties of spring wheat approved for cultivation in Pakistan viz., Barani-83, Pirsabak-91, Bahawalpur-95, Kohsar-95, and Bhakkar-2002 were crossed in a complete diallel fashion. Twenty F_2 populations along with five parents were sown in randomized complete block design with three replications. Plant and row spacing were kept at 30 and 60 cm, respectively.

Soil analysis

To access the soil moisture status, samples from 0–6 and 6–12 cm depth was taken when sowing. The seeds were sown in silt loam soil with pH 7.64, EC 0.68 ds/m, organic matter 1.02%, and soil moisture 11.14% (0–15 cm) and 11.31% (15–30 cm). The seedlings were uprooted after 60 days of drought. Soil samples were taken again from 0–6 and 15–30 cm soil depth before harvesting the seedlings. The soil moisture was reduced to 6.43% (0–15 cm) and 11.55% (15–30 cm) at the time of harvesting seedlings. Crop received only 6 mm of rainfall until harvesting seedlings, whereas 73 mm of rainfall was recorded after harvesting seedlings until the maturity of the crop.

Seedling traits

Ten seedlings per unit were uprooted and washed carefully in tap water to remove soil particles. Soil was watered at the spot of seedling harvesting to facilitate uprooting. Rests of the seedlings were allowed to grow in the field to reach maturity. Data were recorded for root length (cm), seedling length (cm), fresh shoot weight (g), dry shoot weight (g), fresh root weight (g), dry root weight (g), root shoot ratio, and tillers per seedling at seedling stage.

Quantitative traits

At maturity, quantitative parameters such as plant height (cm), number of tillers per plant, spike length (cm), number of spikelets per spike, 1000-grain weight (g), and grain yield per plant (g) were recorded.

Statistical analysis

Ten plants of each cultigen were randomly chosen to evaluate 13 seedling quantitative traits. The data for each measurement were tabulated and analyzed by analysis of variance technique (Steel et al., 1997) using plot means with the help of statistical program MSTAT-C (MSTAT-C Development Team, 1989). Significant differences in the arrays of means were determined. Diallel analysis of the selected measurements was used to determine how they are inherited. The diallel analysis was used to evaluate traits that had significant variation among the parents. Significant differences in phenotypes were assumed to imply that genetic differences were present. The diallel analysis, as developed by Jinks (1954) and Hayman (1954) for parental and F_2 data, was used.

Results and analysis

Preliminary analysis of variance indicated significant differences ($P < 0.01$) for all the traits among genotypes (Table 1). The mean squares for the traits displayed high significance of the '*F*' test for all the characters under study.

Table 1 Mean squares for various yield-related parameters

Source of variation	Replications	Genotypes	Error
Root length (cm)	0.07^{NS}	2.53**	0.073
Shoot length (cm)	0.16^{NS}	5.75**	0.271
Fresh shoot weight (cm)	0.04^{NS}	2.40**	0.15
Dry shoot weight (cm)	0.01^{NS}	0.28**	0.007
Fresh root weight (cm)	0.04^{NS}	0.25**	0.012
Dry root weight (cm)	0.001^{NS}	0.03**	0.001
Root shoot ratio (cm)	0.001^{NS}	0.02**	0.001
Tillers per seedling	0.07^{NS}	2.21**	0.069
Plant height (cm)	18.7^{NS}	35.1**	7.515
Tillers per plant	0.21^{NS}	2.10**	0.342
Spike length (cm)	0.08^{NS}	0.65**	0.113
Spikelets per spike	0.86^{NS}	10.5**	1.521
1000-grain weight (g)	3.35^{NS}	13.3**	3.09
Grain yield per plant (g)	213.8^{NS}	899.1**	329.2

** is significant at $P\leqslant 0.01$. * is significant at $P\leqslant 0.05$. ^{NS} means non-significant at $P > 0.05$.

Assessment of the data for additive-dominance model

The data were assessed for additive-dominance model by exploiting various adequacy parameters (Table 2). According to Mather and Jinks (1982), the data will only be valid for genetic interpretation if the value of regression coefficient (*b*) deviate significantly from zero but not from the unity. The value of *b* was significantly varying from zero but not from

Table 2 Adequacy test of additive dominance-model for yield related traits

Parameters	Test for $b = 0$	Test for $b = 1$	Mean squares of $Wr + Vr$	Mean squares of $Wr - Vr$	Fitness
Root length (cm)	11.53*	0.81^{NS}	8.44**	3.28^{NS}	Full
Shoot length (cm)	10.12*	0.15^{NS}	1.47^{NS}	0.25^{NS}	Partial
Fresh shoot weight (cm)	8.42*	-0.78^{NS}	2.29^{NS}	0.38^{NS}	Partial
Dry shoot weight (cm)	7.68*	1.20^{NS}	6.88**	0.53^{NS}	Full
Fresh root weight (cm)	23.63*	-0.69^{NS}	3.92*	0.07^{NS}	Full
Dry root weight (cm)	8.23*	0.19^{NS}	4.91*	0.47^{NS}	Full
Root shoot ratio (cm)	7.64*	-0.18^{NS}	2.22^{NS}	0.29^{NS}	Partial
Tillers per seedling	8.59*	0.85^{NS}	1.81^{NS}	0.58^{NS}	Partial
Plant height (cm)	5.97*	0.34^{NS}	0.15^{NS}	0.09^{NS}	Partial
Tillers per plant	4.29*	0.37^{NS}	1.15^{NS}	0.36^{NS}	Partial
Spike length (cm)	5.56*	-0.15^{NS}	5.71*	1.46^{NS}	Full
Spikelets per spike	7.27*	0.07^{NS}	2.93^{NS}	2.52^{NS}	Partial
1000-grain weight (g)	8.62*	-0.86^{NS}	5.57*	0.63^{NS}	Full
Grain yield per plant (g)	16.02*	-0.28^{NS}	0.90^{NS}	0.79^{NS}	Partial

** is significant at $P \leqslant 0.01$. * is significant at $P \leqslant 0.05$. ^{NS} means non-significant at $P > 0.05$.

one for all the characters under study to fulfill this criterion. The test for '*t*' square indicated its non-significant value, which proved the absence of non-allelic interactions in genetic behavior of all traits that in turn attested the data valid for AD model for all the characters. The appropriateness of the model data analysis was also verified by the analysis of variance of ($Wr + Vr$) and ($Wr - Vr$). In this test, the mean squares for ($Wr + Vr$) should be significantly different between the arrays, while the mean squares for ($Wr - Vr$) should be non-significant (Mather and Jinks, 1982). The lack of significant variation in the ($Wr - Vr$) arrays over replications for all the characters suggested that any kind of epistasis was not involved in the phenotypic expression of the traits. The value of regression coefficient (b) proved the fitness of the data for root length (0.93±0.08), DSW (0.86±0.11), FRW (1.03±0.04), DRW (0.96±0.12), spike length (1.02±0.18), 1000-grain weight (1.11±0.13), and mean square value of ($Wr + Vr$) for these traits showed significant deviation, and ($Wr - Vr$) mean squares showed non-significant deviation, thus emphasizing full validity of these characters for further genetic analysis. The value of regression coefficient (b) proved fitness of the data as it deviated significantly from zero but not from unity for the remaining traits, such as tillers per seedling (0.91±0.11), seedling length (0.99±0.09), FSW (1.10±0.13), R/S (1.02±0.13), plant height (0.95±0.16), tillers per plant (0.92±0.21), spikelets per spike (1.01±0.07), and grain yield (1.02±0.06), and for AD model, mean square value of ($Wr + Vr$) for the traits indicated no significant deviation, thus emphasizing partial validity of these characters for further genetic elaboration.

Estimation of genetic components and graphical representation of the results

Root length

Components of variation showed that, for root length D, H_1 and H_2 were positive and significant, indicating that the additive and non-additive effects were equally important in controlling root length, but the magnitude of H_1 and H_2 was lesser than D, indicating the importance of additive effects in the genetic control of root length (Table 3). The values of H_1 and H_2 were not equal to each other, thus indicating unequal distribution of positive and negative genes in the parents. Negative value of 'F' indicated the lower frequency of dominant genes in the parents. Significant value of h^2 indicated the presence of overall dominance effect due to heterozygous loci affecting the expression of this trait. The mean degree of dominance was less than 1, indicating the presence of partial dominance with heritability of 85%. The Vr/Wr graph showed that the regression line cut the Wr axis above the origin showing additive gene action with partial dominance and revealed that Bahawalpur-95 possesses maximum dominant genes as it was closest to the origin (Fig. 1). However, the maximum recessive genes were shown by the Kohsar-95 as it was farthest from the origin.

Seedling length

For seedling length, D was positive and significant, indicating the importance of additive effects for this trait. Similarly, the magnitude of H_1 and H_2 was lesser than D, thus indicating the importance of additive effects in the genetic control of seedling length. The values of H_1 and H_2 were not equal to each other, indicating unequal distribution of positive and negative genes in the parents. Negative value of F indicated the lower frequency of dominant genes in the parents. Significant value of h^2 indicated the presence of overall dominance effect due to heterozygous loci affecting the expression of this trait. The mean degree of dominance was less than 1, indicating the presence of partial dominance with heritability of 92%. The Vr/Wr graph showed that the regression line cut the Wr axis above the origin showing partial dominance and revealed that Bahawalpur-95 possesses

Table 3 Estimation of the components of genetic variation

Components of variation	D	H_1	H_2	F	h^2	E	$\sqrt{H_1/D}$	$H_2/4H_1$	$(\sqrt{4DH_1}+F)/(\sqrt{4DH_1}-F)$	h^2 (n.s.)
Root length (cm)	1.27±0.05	0.55±0.13	0.46±0.12	−0.30±0.12	0.47±0.08	0.03±0.01	0.65	0.21	0.69	0.85
Shoot length (cm)	2.27±0.04	0.01±0.10	0.006±0.09	−0.15±0.09	0.15±0.06	0.10±0.02	0.08	0.11	0.41	0.92
Fresh shoot weight (cm)	1.58±0.067	0.41±0.15	0.32±0.14	0.45±0.14	0.20±0.09	0.05±0.02	0.51	0.2	1.79	0.82
Dry shoot weight (cm)	0.14±0.006	0.05±0.01	0.04±0.01	0.04±0.01	0.004±0.009	0.003±0.002	0.59	0.21	1.64	0.8
Fresh root weight (cm)	0.19±0.002	0.009±0.004	0.008±0.003	0.03±0.004	0.01±0.003	0.004±0.006	0.21	0.24	1.99	0.93
Dry root weight (cm)	0.015±0.002	0.0056±0.026	0.0039±0.024	0.0014±0.013	−0.004±0.016	0.0002±0.001	0.61	0.18	1.17	0.87
Root shoot ratio (cm)	0.011±0.003	0.001±0.007	0.001±0.007	0.003±0.007	0.0002±0.004	0.0003±0.001	0.34	0.22	2.11	0.88
Tillers per seedling	1.78±0.02	0.06±0.04	0.05±0.04	0.35±0.04	0.01±0.03	0.03±0.007	0.19	0.21	3.22	0.95
Plant height (cm)	12.4±0.33	−5.15±0.90	−4.11±0.81	−4.93±0.83	−1.91±0.55	3.02±0.14	0.65	0.2	0.53	0.8
Tillers per plant	1.14±0.80	0.22±0.86	0.14±0.79	0.69±0.40	−1.43±0.53	0.11±0.03	0.43	0.17	5.67	0.63
Spike length (cm)	0.41±0.02	−0.003±0.04	−0.006±0.04	0.11±0.04	−0.02±0.03	0.04±0.007	0.08	0.58	−4.19	0.79
Spikelets per spike	7.83±0.14	−0.15±0.38	0.07±0.34	0.99±0.35	0.95±0.23	0.57±0.06	0.14	−0.11	2.68	0.85
1000-grain weight (g)	6.18±0.21	−1.46±0.57	−1.22±0.51	1.61±0.52	−0.53±0.35	1.17±0.09	0.49	0.21	1.73	0.71
Grain yield per plant (g)	428.23±6.2	−1335.8±67.5	−1033.3±61.2	162.52±30.9	−1320.3±41.3	109.72±2.5	1.77	0.19	1.24	0.75

* means the value is significant when it exceeds 1.96 after dividing with its standard error. E = environmental variance, D = additive variance, H_1 = dominance variance, H_2 = proportion of positive and negative genes in the parents, F = relative frequency of dominant and recessive alleles in the parent, h^2 = dominance effect (over all loci in heterozygous phase), $\sqrt{H_1/D}$ = mean degree of dominance, $H_2/4H_1$ = proportion of genes with positive and negative effects in the parents, $(\sqrt{4DH_1}+F)/(\sqrt{4DH_1}-F)$ = proportion of dominant and recessive genes in the parents, and h^2 = heritability (n.s.).

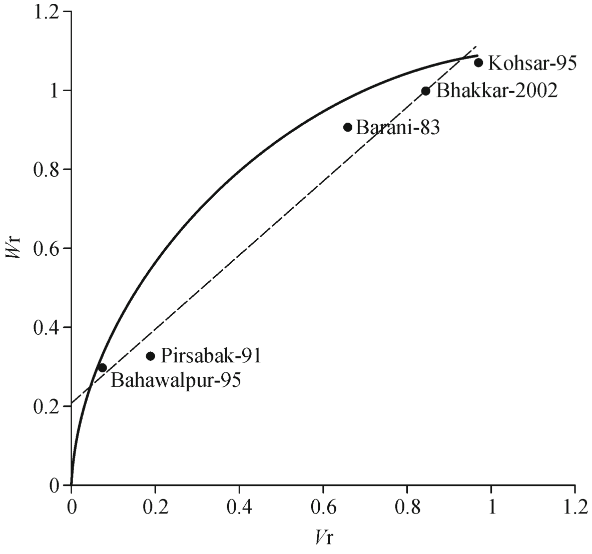

Figure 1 *W*r/*V*r graph for root length.

maximum dominant genes as it was nearest to the origin (Fig. 2). However, Kohsar-95 had the maximum recessive genes as it was farthest from the origin.

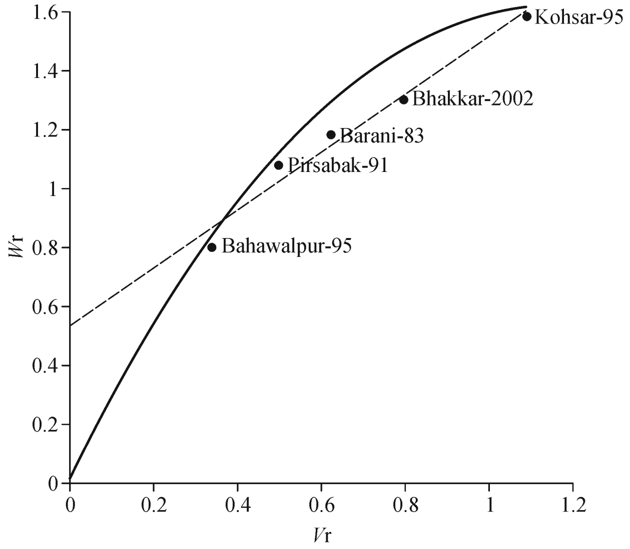

Figure 2 *W*r/*V*r graph for seedling length.

Fresh shoot weight

For FSW, the relative values of components of H_1 and H_2 were unequal in magnitude and D value was positive and significant, which indicated the importance of additive effects for the control of this trait. H_1 and H_2 were unequal, indicating the unequal distribution of genes. The value of $H_2/4H_1$ ratio was less than 0.25, which indicated unequal distribution of genes for the trait among the parents. Negative F value signified the important role of recessive genes. The positive value of h^2 was noted. The degree of dominance was less than 1, suggesting the presence of partial dominance, which was supported by the slope on the regression line (Fig. 3). The estimate of narrow sense heritability was 82%. The graphical representation of this trait (Fig. 3) indicated that the parent Pirsabak-91 contained the maximum number of dominant genes for this trait. However, Bhakkar-2002 possessed the maximum recessive genes for controlling this trait.

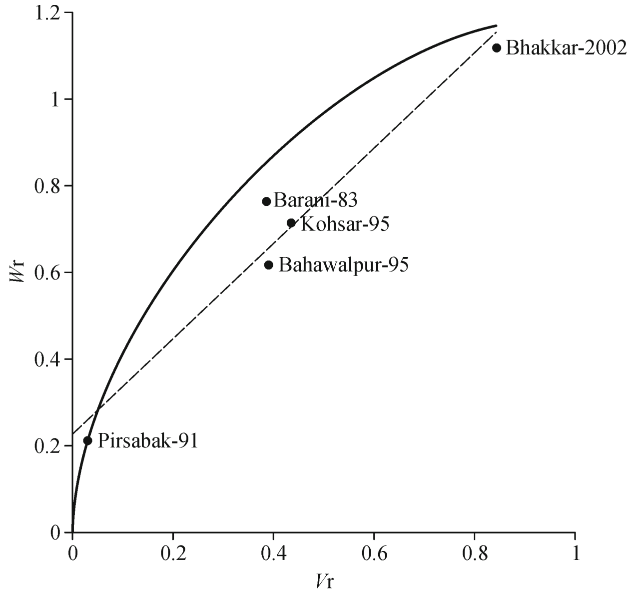

Figure 3 *W*r/*V*r graph for FSW.

Dry root weight

The significant value of D for dry shoot weight (DSW) showed that this trait was under the control of additive gene and it was more than that of H_1 and H_2, which were almost equal revealing nearly equal contribution of dominant genes for the expression of DSW. The value of $H_2/4H_1$ ratio was less than 0.25, which indicated unequal distribution of genes for the trait among the parents. Positive and significant value of 'F' indicated the presence of dominant genes in parents and it was supported by low value of $(\sqrt{4DH_1}+F)/(\sqrt{4DH_1}-F)$ = 1.64. The value of h^2 was positive, which indicated that dominance effect of genes was considerable. The degree of dominance was less than 1, indicating the presence of partial dominance type of gene action with heritability 93%. The *V*r/*W*r graph indicated that the variety Pirsabak-91 possessed the maximum dominant genes responsible for inheritance of DSW (Fig. 4). However, the maximum recessive genes were exhibited by the variety Kohsar-95 followed by Barani-83. The regression line intercepted the *W*r axis above the point of origin, showing the presence of partial dominance type of gene action along with an effective additive control for this character.

Fresh root weight

The relative values of components of H_1 and H_2 were almost

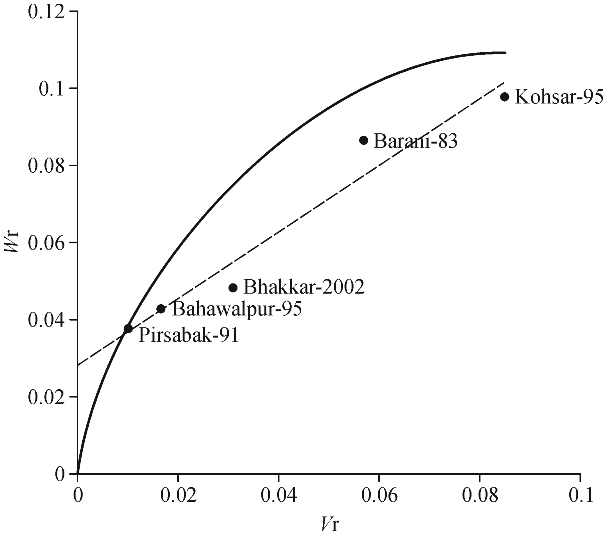

Figure 4 *Wr*/*Vr* graph for DSW.

equal in magnitude and D value was positive and significant for FRW, indicating the importance of additive effects for the control of this trait. H_1 and H_2 were nearly equal, indicating the almost equal distribution of genes. The value of $H_2/4H_1$ ratio was near to 0.25, which indicated equal distribution of genes for the trait among the parents. Positive F value signified the important role of dominant genes, which was supported by low value of $(\sqrt{4DH_1}+F)/(\sqrt{4DH_1}-F)$ (1.99). The positive value of 'h^2' was noted. The degree of dominance was less than 1, suggesting the presence of partial dominance supported by the slope on the regression line (Fig. 5). The estimate of narrow sense heritability was 93%. The regression line in case of FRW intercepted above the point of origin depicted the involvement of partial dominance (Fig. 5). The graphical representation of this trait indicated that Barani-83 contained the maximum number of dominant genes for the trait. Genotype Bhakkar-2002 possessed the maximum recessive genes controlling this trait as it was farthest from the origin.

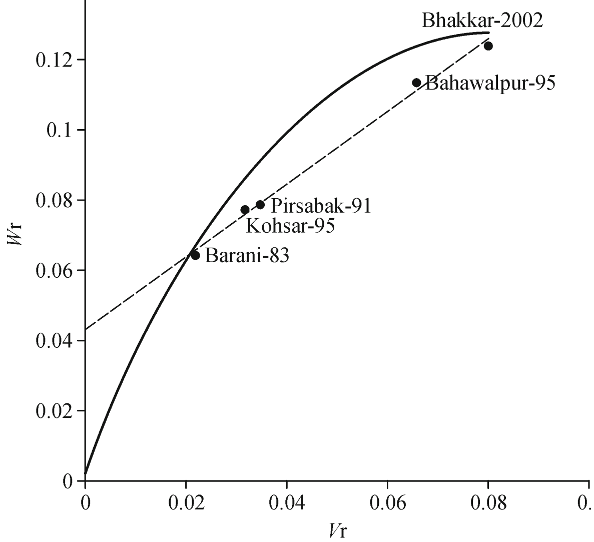

Figure 5 *Wr*/*Vr* graph for FRW.

Dry root weight

The genetic components for DRW showed that H_1 and D components were positive and significant. There were more components of D than of H_1 and H_2, showing the presence of additive genetic effects in controlling DRW. H_1 and H_2 were unequal, indicating the uneven distribution of genes. The value of $H_2/4H_1$ ratio was less than 0.25, which also indicated unequal distribution of genes for the trait among the parents. Positive F value signified the important role of dominant genes. The negative value of 'h^2' was noted. The degree of dominance was less than 1, suggesting the presence of partial dominance supported by the regression slope (Fig. 6). The estimate of narrow sense heritability was 87%. Placement of array points displayed that Kohsar-95 had the maximum number of dominant genes for DRW. However, Barani-83 had the maximum recessive genes controlling DRW. The regression line for this trait also cut the *Wr* axis above the origin, showing partial dominance for this trait.

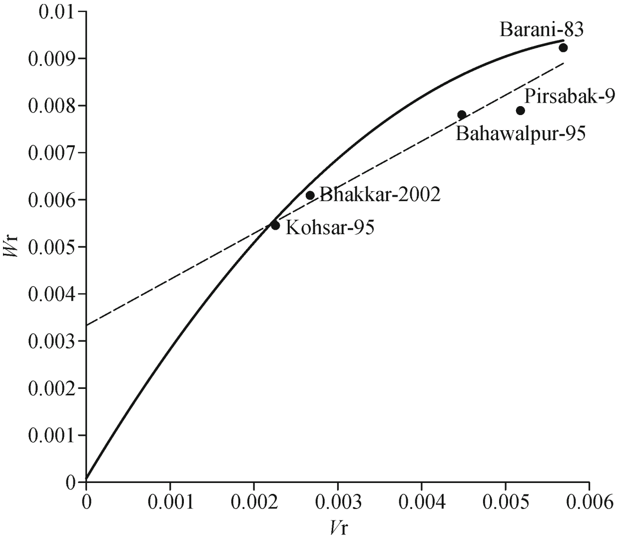

Figure 6 *Wr*/*Vr* graph for DRW.

Root shoot ratio

For root shoot ratio, D component was more than H_1 and H_2, showing the importance of additive genetic effects. H_1 and H_2 were equal, indicating the equal distribution of genes. The value of $H_2/4H_1$ ratio was less than 0.25, indicating unequal distribution of genes for the trait among the parents. Positive F value signified the important role of dominant genes. The positive value of 'h^2' was noted. The degree of dominance was less than 1, which suggested the presence of partial dominance supported by the regression slope (Fig. 7). The estimate of narrow sense heritability was 88%. Placement of

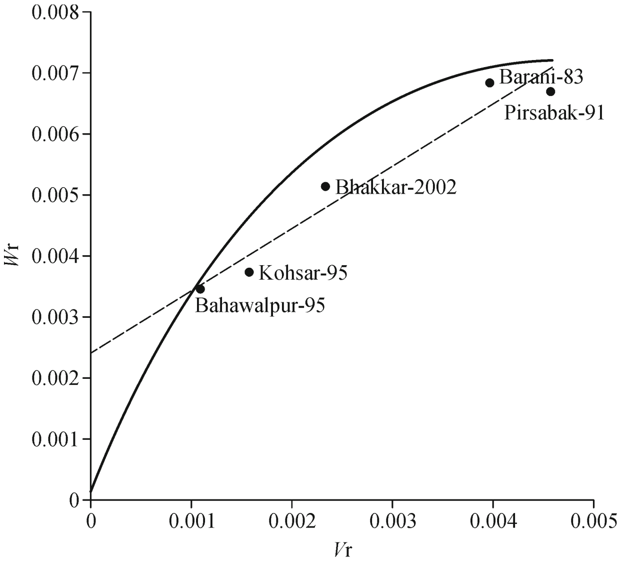

Figure 7 *Wr*/*Vr* graph for R/S.

array points displayed that Bahawalpur-95 had the maximum number of dominant genes for root shoot ratio. However, Pirsabak-91 had the maximum recessive genes controlling the root shoot ratio. The regression line for this trait also cut the *Wr* axis above the origin, showing partial dominance for this trait.

Number of tillers per seedling

When genetic components of variation for tillers per seedling were computed, it was revealed that additive D component was significant and more than the dominance components of H_1 and H_2, showing the importance of additive effects for controlling tillers per seedling. H_1 and H_2 values were necessarily equal in magnitude, displaying uniformity of distribution of positive and negative alleles among the parents. The average degree of dominance was less than 1, showing presence of partial dominance. High narrow sense heritability of 95% was also recorded, indicating considerably large additive proportion in the total heritable genetic variation. The placement of array points displayed showed that genotype Bhakkar-2002 had the least dominant genes being the farthest from the origin (Fig. 8), while Bahawalpur-95 was the nearest to the origin and had the maximum dominant genes.

Plant height

Components of genetic variation for plant height depicted significant additive (D) variation, while dominance was found absent. Unequal values of H_1 and H_2 indicated unequal distribution of positive and negative alleles in the parents. F component was negative and significant, showing lower frequency of dominant genes. The average degree of dominance was less than 1, showing the presence of partial dominance. High narrow sense heritability of 80% was also recorded, indicating considerably large additive proportion in the total heritable genetic variation. The placement of array points displayed that genotype Bhakkar-2002 had the least dominant genes being the farthest from the origin (Fig. 9), while Pirsabak-91 had the maximum dominant genes.

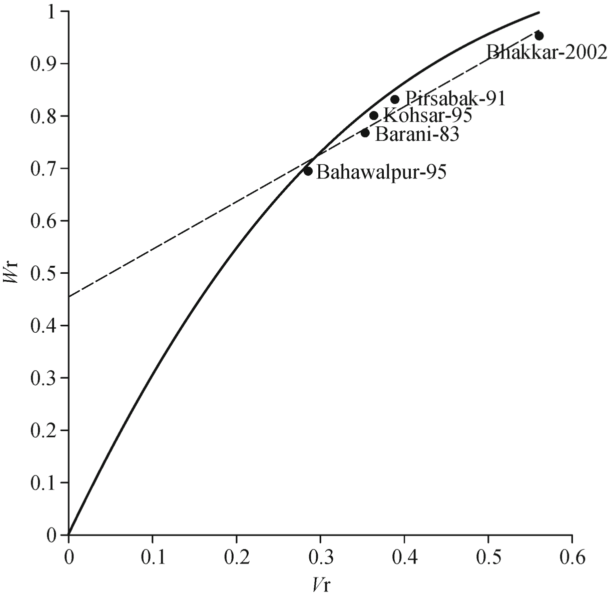

Figure 8 *Wr*/*Vr* graph for tillers per seedling.

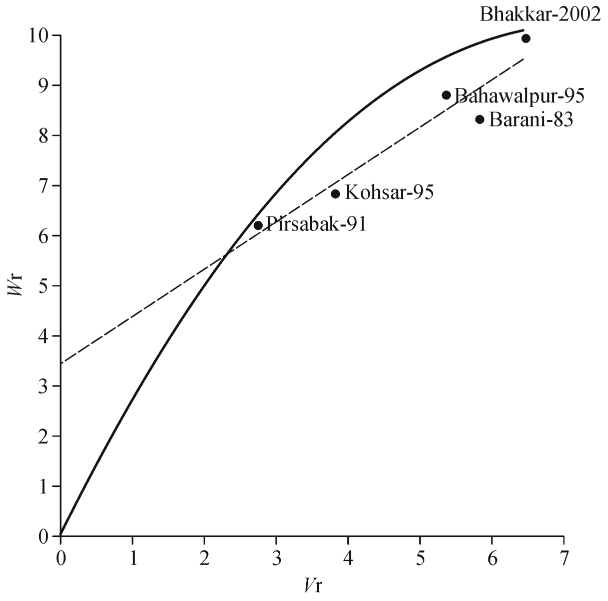

Figure 9 *Wr*/*Vr* graph for plant height.

Number of tillers per plant

When the genetic components of variations for tillers per plant were computed, it was revealed that additive component D was more than the values of H_1 and H_2, thus showing the importance of additive effects for the control of this trait.

Unequal values of H_1 and H_2 showed the unequal distribution of genes. Positive F value indicated the importance of dominant genes. The average degree of dominance was less than 1 and displayed the absence of complete dominance. The heritability for this trait was 63%. The placement of array points displayed that genotype Barani-83 was the nearest to the origin with the maximum dominant genes and the genotype Kohsar-95 had the least dominant genes being the farthest from the origin (Fig. 10).

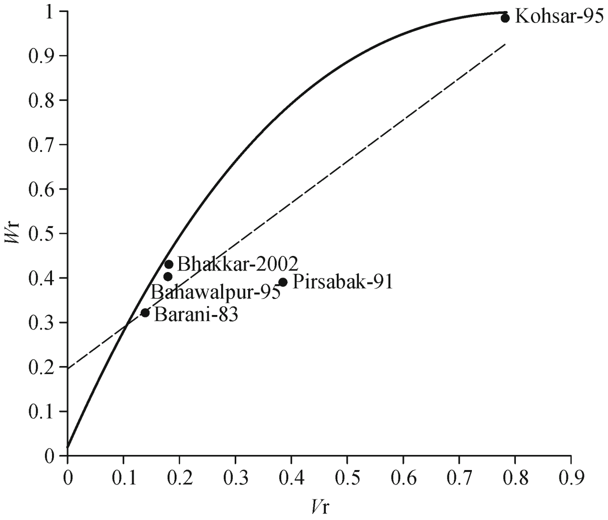

Figure 10 *Wr*/*Vr* graph for tillers per plant.

Spike length

For spike length, the additive component D was positive and significant and more than the values of H_1 and H_2, thus showing the importance of additive effects for the control of spike length. Positive F value indicated the importance of dominant genes for the control of this trait. The negative value of 'h^2' was noted. The dominance degree of less than 1, suggesting the presence of partial dominance, which was supported by regression line intercepted above the point of origin. The narrow sense heritability was 79%. The graphical representation of this trait indicated that Pirsabak-91 contained the maximum number of dominant genes for this trait as it was the nearest to the origin (Fig. 11). Genotype Kohsar-95 held the maximum recessive genes controlling this trait as it was the farthest from the origin.

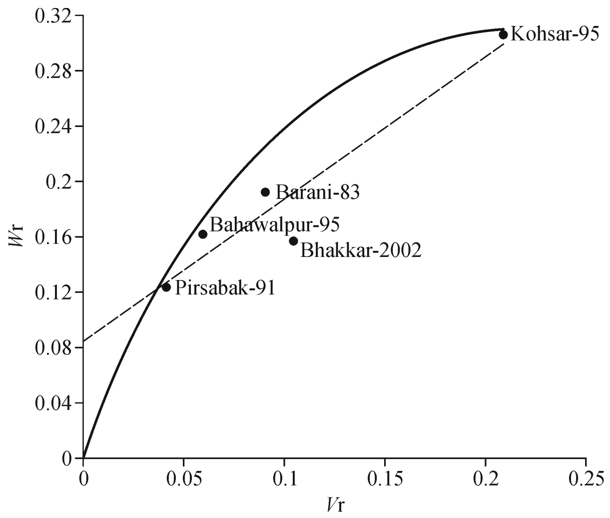

Figure 11 *Wr*/*Vr* graph for spike length.

Number of spikelets per spike

Genetic components of variations for spikelets per spike revealed that the additive component (D) was significant and more than the values of H_1 and H_2, thus confirming the importance of additive effects. F value was positive, showing the importance of dominant genes for spikelets per spike. Significant E value depicted the influence of environment on the expression of this trait. Partial dominance type of gene action for spikelets per spike was found as the degree of dominance was less than 1, which was further confirmed by the regression line intercepted above the point of origin. High narrow sense heritability estimates of 85% were recorded. The placement of array points displayed that genotype Bahawalpur-95 contained the maximum dominant genes placed the nearest to the origin (Fig. 12). However, genotype Barani-83 had the maximum recessive genes being the farthest from the origin.

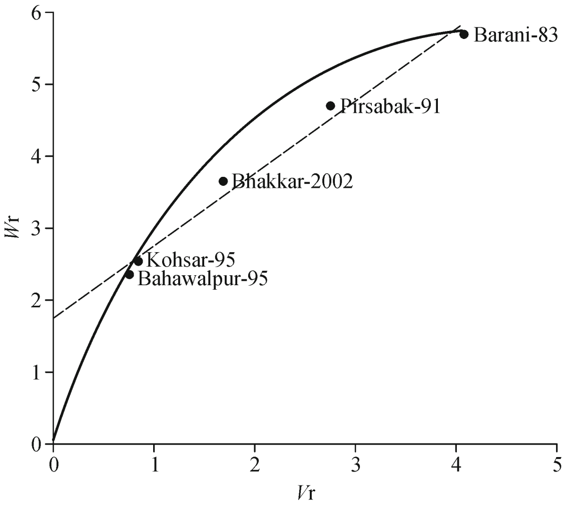

Figure 12 *Wr*/*Vr* graph for spikelets per spike.

1000-grain weight

The additive component D was positive, significant, and more than the values of H_1 and H_2 for 1000-grain weight, indicating the importance of additive effects for the control of this trait. The components H_1 and H_2 were not equal to each other, showing unequal distribution of genes. The value of $H_2/4H_1$ ratio was less than 0.25, indicating unequal distribution of genes for the trait among the parents. Positive

F value signified the important role of dominant genes, which was supported by low value of $(\sqrt{4DH_1}+F)/(\sqrt{4DH_1}-F)$ (1.73). The negative value of 'h^2' was noted. The degree of dominance was less than 1, suggesting the presence of partial dominance in F_2 progenies, which was supported by the slope on the regression line (Fig. 13). The estimate of narrow sense heritability was 71%. The regression line in case of 1000-grain weight intercepted above the point of origin showed the involvement of partial dominance (Fig. 13). The graphical representation of this trait indicated that Bhakkar-2002 contained the maximum number of dominant genes for this trait. However, genotype Kohsar-95 occupied the maximum recessive genes controlling this trait as it was the farthest from the origin.

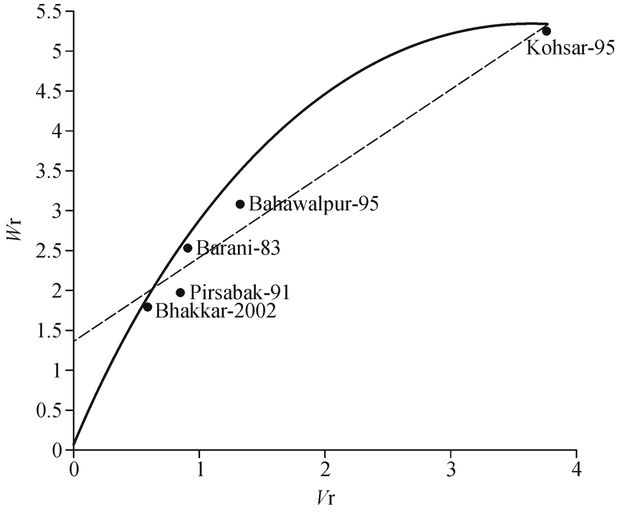

Figure 13 *W*r/*V*r graph for 1000-grain weight.

Grain yield per plant

The positive and significant additive component D showed the importance of additive effects for the control of this trait. The components H_1 and H_2 were not equal to each other, showing unequal distribution of genes. The value of $H_2/4H_1$ ratio was less than 0.25, which indicated unequal distribution of genes for the trait among the parents. Positive F value signified the important role of dominant genes, which was supported by low value of $(\sqrt{4DH_1}+F)/(\sqrt{4DH_1}-F)$ (1.73). The negative value of 'h^2' was noted. The degree of dominance was less than 1, suggesting the presence of partial dominance in F_2 populations, which was supported by the slope on the regression line (Fig. 14). The estimate of narrow sense heritability was 75%. The regression line in case of grain yield intercepted above the point of origin showed the involvement of partial dominance (Fig. 14). The graphical representation of this trait indicated that Bahawalpur-95 contained the maximum number of dominant genes for this trait being the closest to the origin. However, the genotype Kohsar-95 held the maximum recessive genes controlling this trait as it was the farthest from the origin.

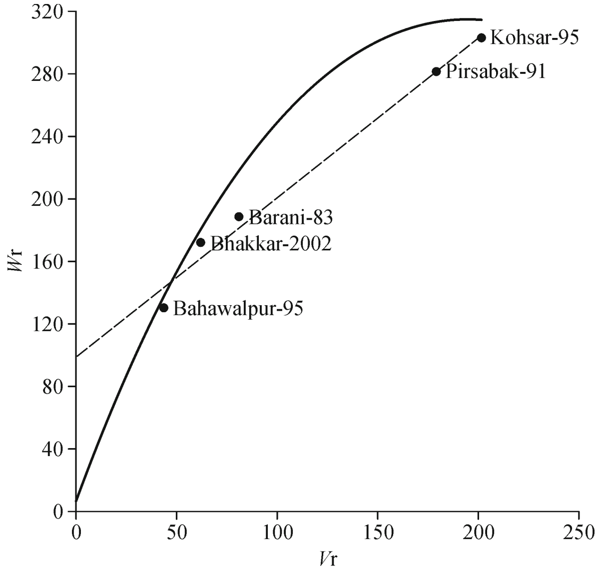

Figure 14 *W*r/*V*r graph for grain yield per plant.

Discussion and conclusions

Development of wheat varieties with consistent yields under diverse environments has been a major objective of wheat breeding. Hence, the availability of genetically based variation for various traits in breeding population is of acute importance. Present sample of genetic material was used to generate such information on various seedling and maturity traits in F_2 populations of wheat. The genotypic differences were significant for all the traits. Similar findings for grain yield and related traits in different varieties of wheat were reported by Ambreen et al. (2002) and for seedlings traits by Awan et al. (2005). The additive dominance model revealed full fitness of the data used for RL, DSW, FRW, DRW, spike length, and 1000-grain weight but was partially fit for SL, FSW, R/S, tillers per seedling, plant height, tillers per plant, spikelets per spike, and grain yield per plant. The partially adequate model for these plant characters might be due to the presence of non-allelic interaction, linkage, and non-independent distribution of the genes in the parents as suggested by Mather and Jinks (1982). However, several partial adequacies of the simple genetic model to the data set never the less analyzed the diallel cross data in wheat (Hussain, 1991).

Significant differences for genetic components, additive and dominant for all the traits studied, indicated the efficient creation of genetic variability. The breeding value of a line is a function of the additive gene action. All the seedling yield and yield contributing traits were under the control of additive genetic effects, which was evident from the significant and higher value of D than the dominance variance H_1 and H_2. Additive effects are transferable to the offspring progenies; hence, they are important for selection of high yielding drought-tolerant pure lines in this breeding program. The existence of additive effects indicated that there was a genetic basis for improving yield and seedling traits. Additive gene action with partial dominance was involved in controlling spike length (Chowdhry et al., 2005) and non-additive genetic effects (Rahim et al., 2006). However, over-dominance was involved in spike length and spikelets per spike (Habib and Khan, 2003; Rahman et al., 2003). Additive type of gene action was important for spikelets per spike (Siddique et al., 2004; Malik et al., 2005). Partial dominance was also reported by some researchers (Habib and Khan, 2003; Rahman et al., 2003). Additive gene action with partial dominance was earlier reported by Esmail (2002), Iqbal (2004), Chandrashekhar and Kerketta (2004), and Kumar and Sharma (2005). The values of H_1 and H_2 were unequal in all the traits studied, indicating unequal distribution of dominant alleles, except R/S, and equal distribution of dominant alleles. F value indicated that the relative frequency of dominant and recessive alleles in the parents was negative for RL, SL, and plant height, which showed the importance of recessive alleles in these characters. However, positive values of F in the rest of the traits showed the important role of dominant genes in the parents.

Degree of dominance was less than 1 for all the traits; hence, partial dominance type of gene action was predominated for these traits, which was confirmed from the regression line cutting the Wr axis above the origin, except grain yield. Preponderance of partial dominance in these traits revealed the importance of early-generation selection, which would be helpful in future breeding endeavors. Partial dominance with additive effects for these traits was also reported by Khan et al. (1982), Mishra et al. (1996), Aziz and Chowdhry (1999), Chowdhry et al. (2001), Esmail, (2002), Hamada et al. (2002), Joshi et al. (2002), Joshi et al. (2003), Khan et al. (2003), Hakizimana et al. (2004), Joshi et al. (2004), and Chandrashekhar and Kerketta (2004).

The value of 'h^2' showing net dominance effect was positive for RL, SL, FSW, DSW, FRW, R/S, tillers per seedling, and spikelets per spike, which indicated considerable dominance effect of genes, but negative for DRW, plant height, tillers per plant, spike length, 1000-grain weight, and grain yield. The narrow sense heritability estimates were high for all the traits but moderate for tillers per plant, suggesting that they can be readily modified by selection procedures. These results are in conformity with those of Joshi et al. (2004) and Chandrashekhar and Kerketta (2004).

Additive effects with high narrow sense heritability indicated a lesser environmental influence in the expression of these traits and were transferable to the offspring progenies. Additionally, these F_2 populations can be used for pure line selection in early generations. This study provided a strong evidence that crosses between these cultivars can produce progenies with improved early vigour and good yields.

Abbreviations used

RL: Root length; SL: Shoot length; FSW: Fresh shoot weight; DSW: Dry shoot weight; FRW: Fresh root weight; DRW: Dry root weight; R/S: Root shoot ratio

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