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Diallel analysis using graphical & numerical approach for grain yield & its attributes in bread wheat (*Triticum aestivum* L.)

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Abstract

Ten wheat (*Triticum aestivum* L.) genotypes are crossed in half diallel fashion. Components of gene effect revealed that most of the characters were governed by both additive and dominance gene effect across the environments with greater influence of dominance gene effect except for days to 50% heading, days to maturity and grain yield per main spike. The estimated ' t^2 ' values were found significant for all the character except days to 50% heading, which indicates the failure of assumptions of diallel analysis. The over dominance behaviour was observed for days to 50% heading, days to maturity, no. of effective tillers per plant, length of main spike, no. of spikelets per main spike, no. of grains per main spike, grain yield per main spike and 1000 grain weight. The array points on the Wr-Vr graph expected to fall on the line of unity (450) and the value of regression 'b' was unity for days to 50% heading and 1000 grain weight which revealed an absence of digenic interactions for these characters and rest of the characters had non-random distribution of genes at different loci among the parents and/ or presence of inter allelic interaction at different loci.

Key words

Half diallel, t^2 value, Wr-Vr graph, Regression value (b), Additive gene and Non-additive gene, genetic variance

INTRODUCTION

Wheat (*Triticum aestivum* L.) is the world's most important cereal being the chief source of staple food for about one third of global population¹. To cope with the problem of ever-increasing population in the country, it appears to be a dire need to enhance the productivity of this cereal grain. So, in bread wheat, breeding based on economic traits had been receiving maximum attention for a long time and this factor, has been fully exploited². Hence an estimate of gene action is important in launching a successful breeding programme. During

breeding of high yielding varieties of crop plants, breeders are continually challenged with the problem of parent selection. Though elimination of poor crosses on the basis of their performance in initial generation has been suggested; but information on the genetic architecture of yield and its components will help to sort out the improved crosses more competently³. Several reports in the past indicate that the diallel analysis is the easiest method of understanding the genetic nature of quantitatively inherited traits and to ascertain the prepotency of parents. Diallel analysis helps in understanding the genetic control of the trait, which guides the breeder to advance and select segregating populations. There are several approaches available for analysis of diallel crosses but the two main approaches being followed are Griffing's and Hayman's approaches. These two approaches are often used together for complementary data interpretation⁴.

The nature of gene action involved in the inheritance of various characters is very important to decide any breeding methodology for crop improvement. This can be determined by graphical approach (Vr-Wr graph). The Vr-Wr statistic provides an estimate of the relative number of dominance to recessive genes present in the common arrays of the parents, with the Vr and Wr statistics, calculated from diallel tables, graphs can be drawn and the geometric representation of these statistics can be interpreted. The position of the regression line in the graph indicates the degree of dominance and we can construct parabola limits in this graph. The interpretation of the results of this analysis is easy and straight forward if the main assumptions of the diallel analysis are fulfilled⁴. Kearsey⁵ noted that Hayman and Jink's diallel analysis⁶ deliver more evidence than other methods, but has more necessary assumptions. Diallel analysis by Griffing⁷ do not afford any test to detect epistasis or linkage but Hayman and Jink's analysis do provide such test. When using Griffing's analysis to estimate variance components, it has been suggested that simple tests, such as the Wr-Vr evaluation found in Hayman⁸ model, may be used to ascertain the presence of epistasis and/or linkage disequilibrium^{9,10}. This analysis is based on simple additive-dominance model of gene effects with certain assumptions. The validity of the hypothesis of additive-dominance model was tested by confirming unit slope of regressions of Wr and Vr and by non-significant value of t^2 as prescribed by Hayman⁸.

In the present Study the diallel analysis given by Jinks and Hayman⁶ and Hayman¹¹ was employed to find out the genetic constitution of the parents with respect to various traits and to assess the gene action in all the ways for different quantitative characters in bread wheat that could be utilized in specific breeding programme for achieving fruitful results.

Sr. No.	Genotypes	Pedigree	Source
1	GW 451	GW 324/4/CROC_1/AE.SQUARROSA (205) /JUP/JY/3/ SKAUZ /4/ KAUZ /5/ GW 339	Regional Research Station, Anand Agricultural University, Anand-388110
2	GW 496	HD 2285 / CPAN 1861	
3	LOK 1	S 308 / S 311	
4	GW 322	PBW 173 / GW 196	
5	GW 366	DL 802-3 / GW 232	
6	HI 1544	HIND162/BOBWHITE/CPAN 2099	
7	GW 173	TW 275 -7-6-10 / LOK1	
8	GW 11	LOK 1 / HW 1042 // LOK 1	
9	HD 2864	DL509-2/DL377-8	
10	UAS 385	GW344/UAS239/DWR162	
Standard check varieties			
1	MASC 6222 – TS	HD 2189*2//MASC 2496	
2	HD 2932 – LS	KAUZ/STAR//HD 2643	

Table 1: List of genotypes and their pedigree information

Environments	Sowing time	Season & Year
E ₁	Normal	<i>Rabi</i> 2018-19
E ₂	Late	
E ₃	Normal	<i>Rabi</i> 2019-20
E ₄	Late	

Table 2: Environments under study

Male Parents											
Female Parents		P1	P2	P3	P4	P5	P6	P7	P8	P9	P10
	P1	GW 451	P1× P2	P1 × P3	P1 × P4	P1 × P5	P1 × P6	P1 × P7	P1 × P8	P1 × P9	P1 × P10
	P2		GW 496	P2 × P3	P2 × P4	P2 × P5	P2 × P6	P2 × P7	P2 × P8	P2 × P9	P2 × P10
	P3			LOK 1	P3 × P4	P3 × P5	P3 × P6	P3 × P7	P3 × P8	P3 × P9	P3 × P10
	P4				GW 322	P4 × P5	P4 × P6	P4 × P7	P4 × P8	P4 × P9	P4 × P10
	P5					GW 366	P5 × P6	P5 × P7	P5 × P8	P5 × P9	P5 × P10
	P6						HI 1544	P6 × P7	P6 × P8	P6 × P9	P6 × P10
	P7							GW 173	P7 × P8	P7 × P9	P7 × P10
	P8								GW 11	P8 × P9	P8 × P10
	P9									HD 2864	P9 × P10
	P10										UAS 385
Standard check varieties	1.	MASC 6222 – TS									
	2.	HD 2932 – LS									

Table 3: Crossing pattern in 10 × 10 half diallel crosses in wheat

Fig 1: Plant stature of parents and checks

GW 451

GW 496

LOK 1

GW 322

GW 366

HI 1544

GW 173

GW 11

HD 2864

UAS 385

Fig 2: Spike and grain characteristics of parents

Graphical and Numerical approach

The numerical analysis was carried out as per procedures outlined by Hayman^{8,11-14} and Jinks^{15,16} as described in details by Mather and Jinks¹⁷ and Singh and Chaudhary¹⁸ and Graphical approach as per Jinks and Hayman⁶ and Hayman⁸. This analysis is based upon following assumptions: 1. Diploid segregation 2. No differences in reciprocal crosses i.e. no maternal effect. 3. Independent action of non-allelic genes in the diallel cross i.e. absence of epistasis 4. Homozygous parents 5. Genes independently distributed between the parents i.e. no linkages 6. No multiple allelism. To test failure of any of the assumptions of diallel analysis, ' t^2 ' test was applied as suggested by Hayman¹¹; however, ' t^2 ' also test the adequacy of basic assumption of additive dominance model. A non-significant value of ' t^2 ' would indicate the uniformity of the W_r-V_r , and confirms validity of hypothesis postulated, particularly adequacy of additive dominance model.

Estimation of genetic parameters

After observing adequacy of additive dominance model, the components of genetic variation viz., D, H_1 , H_2 , E, F and h^2 were estimated. The component analysis was only performed for the data which fitted the additive dominance model. These genetic components of variation were calculated from the diallel table following the methods given by Hayman¹¹.

COMPONENTS OF GENETIC VARIANCE

Numerical Approach

The estimated ' t^2 ' values for different characters in each individual environment are presented in **Table 4**. Out of twelve characters studied, the estimated ' t^2 ' values were found significant for two characters viz., plant height, grain yield per plant and biological yield per plant over all the environments; however, the estimates were non-significant over all the environments for one character i.e., days to 50% heading. Moreover, for rest of the characters, ' t^2 ' value was significant either in E_1 , E_2 , E_3 and E_4 in combination of either of the environments. Significance of ' t^2 ' suggested failure of certain assumptions of diallel analysis. Therefore, components of gene effect and related parameters have been presented and discussed for the characters, where ' t^2 ' estimate of uniformity of the W_r-V_r value was non-significant (**Table 5 and 6**).

Days to 50% heading

The value of “ t^2 ” was non-significant in all environments. Significance of additive (D) and dominance components (H_1 and H_2) of gene effect revealed that the character was governed by both additive as well as dominance gene actions in all the environments. The estimates of average degree of dominance suggested the existence of over dominance gene action in all environment (E_1 :1.69%, E_2 :1.20%, E_3 :1.50% and E_4 :1.23%). Asymmetrical distribution of positive and negative alleles among the parents was observed in all environments as values of $H_2/4H_1$ ratio was less than 0.25. The positive values of F and more than one ratio of KD/KR indicated that the character was indicated an excess of dominant genes in analysis except E_1 . At least one dominant gene or group of genes appeared to govern the character as h^2/H_2 ratio was less than one across the environments. The dominant gene or group of genes was not computed as h^2 values were positive or non-significant. The estimates of narrow sense heritability was low to medium in all analysis (E_1 : 24.58%, E_2 : 48.33%, E_3 : 30.33% and E_4 : 49.69%).

Days to maturity

The value of “ t^2 ” test was found to be significant in E_1 , while, for rest of environments it was non-significant. Significance of additive (D) and dominance components (H_1 and H_2) of gene effect revealed that the character was governed by both additive as well as dominance gene effects in all environments; however preponderance gene effects was noticed through magnitude of component of gene effects

The estimates of average degree of dominance suggested the existence of over dominance gene action in all environments (E_2 :1.97%, E_3 :1.55% and E_4 :1.90%). Asymmetrical distribution of positive and negative alleles among the parents was observed in all environments as value of $H_2/4H_1$ ratio was less than 0.25. The positive values of F and more than one ratio of KD/KR was observed in all the analysis which indicated the excess of dominant genes among parents. At least one dominant gene or group of genes appeared to govern the character as h^2/H_2 ratio was less than one across the environments. The dominant gene or group of genes was not computed as h^2 values were positive or non-significant. The estimates of narrow sense heritability were low in all the environments (E_1 : 19.21%, E_2 : 28.64% and E_3 : 18.35%), which also confirmed that character was under control of dominance gene effects.

SN	Characters	t^2 test				b (Regression)			
		E ₁	E ₂	E ₃	E ₄	E ₁	E ₂	E ₃	E ₄
1	Days to 50% heading	1.96	0.20	0.60	0.04	0.18++	0.87\$\$	0.15+	0.69\$
2	Days to maturity	11.63**	2.58	0.09	0.07	0.29\$++	0.27++	0.51	0.44
3	Plant height	6.21**	9.56**	10.18**	19.17**	0.19++	0.20++	0.06++	0.17++
4	No. effective tillers per plant	1.34	13.53**	0.45	18.10**	0.20++	-0.13++	0.36+	-0.11++
5	Length of main spike	3.96**	1.31	0.93	21.47**	0.13++	0.16++	0.37+	0.22\$++
6	Number of spikelets/main spike	7.07**	0.20	3.28	2.04	0.24++	0.60	0.31++	0.59
7	Number of grains per main spike	3.01	0.208	6.68**	0.24	-0.07++	0.57	0.04++	0.65
8	Grain yield per main spike	34.90**	0.004	21.91**	0.04	0.10++	0.14+	0.08++	0.20
9	Grain yield per plant	29.21**	7.32**	43.61**	7.99**	0.22\$++	0.01++	0.21\$++	0.13++
10	1000 grain weight	1.81	0.04	0.97	0.006	0.67\$\$+	0.46\$\$++	0.71\$\$	0.66\$
11	Biological yield per plant	476.05**	7.14**	88.27**	8.41**	-0.04++	0.04++	-0.06++	0.20++
12	Harvest index	0.97	11.22**	3.94*	9.71**	-0.20++	0.55\$\$++	-0.29++	0.35\$++

*,** Significant at 5% and 1% levels, respectively , \$,\$\$ Significant at 5% and 1% levels, respectively when Ho: b = 0; +, ++ Significant at 5% and 1% levels, respectively when Ho: b = 1

Table 4: “ t^2 ” value and regression coefficient for different metric characters of Wr on Vr

Days to 50% heading					Days to maturity			No. of effective tillers per plant		Length of main spike	
Genetic components	E ₁	E ₂	E ₃	E ₄	E ₂	E ₃	E ₄	E ₁	E ₃	E ₂	E ₃
$\hat{E}$	0.44	0.60*	0.64	0.54	0.91	0.54	0.82	0.28	0.30	0.14**	0.13**
$\hat{D}$	17.32**	7.37**	19.04**	7.09**	5.11**	10.15**	2.93**	0.87	0.74	0.13	0.13
$\hat{F}$	-2.16	5.22**	1.58	5.73**	2.04	1.19	0.82**	-0.08	-1.04	-0.19	0.13
$\hat{H}_1$	49.19**	10.69**	42.75**	10.74**	19.88**	24.31**	10.56**	11.18**	9.58**	1.82**	2.11**
$\hat{H}_2$	41.79**	9.36**	36.90**	8.75**	13.80**	17.58**	8.21**	8.25**	7.89**	1.45**	1.55**
$\hat{h}^2$	10.64	0.01	11.33	0.23	3.41	4.76	4.25	0.08	0.04	0.88**	1.22**
$(\hat{H}_1/\hat{D})^{0.5}$	1.69	1.20	1.50	1.23	1.97	1.55	1.90	3.59	3.59	3.79	4.01
$\hat{H}_2/4\hat{H}_1$	0.21	0.22	0.22	0.20	0.17	0.18	0.19	0.18	0.21	0.20	0.18
KD/KR	0.93	1.83	1.06	1.98	1.23	1.08	1.16	0.97	0.67	0.67	1.28
$\hat{h}^2/\hat{H}_2$	0.25	0.00	0.31	0.03	0.25	0.27	0.52	0.01	0.01	0.61	0.79
% Heritability (narrow sense)	24.58	48.33	30.33	49.69	19.21	28.64	18.35	6.53	5.91	4.69	5.01

$KD/KR = \{(4\hat{D}\hat{H}_1)^{0.5} + \hat{F}\} / \{(4\hat{D}\hat{H}_1)^{0.5} - \hat{F}\}$; *,** Significant at 5 and 1 per cent levels, respectively

Table 5: Genetic components for days to 50% heading, days to maturity, No. of effective tillers per plant and Length of main spike

No. of spikelets per main spike				No. of grains per main spike			Grain yield per main spike		1000 grain weight				Harvest index
Genetic components	E ₂	E ₃	E ₄	E ₁	E ₂	E ₄	E ₂	E ₄	E ₁	E ₂	E ₃	E ₄	E ₁
$\hat{E}$	0.49**	0.39**	0.36**	1.53	6.85**	3.14	0.02	0.01	0.63	0.64	1.01	0.79	9.34
$\hat{D}$	2.01**	0.82	2.19**	17.21	23.12**	21.02**	0.09**	0.10**	12.46**	30.12**	13.82**	30.78**	66.93
$\hat{F}$	-0.31	-0.28	0.53	12.26	2.40	4.56	0.19	0.23**	-4.71	12.56	-0.54	14.22	115.29
$\hat{H}_1$	5.26**	5.04**	4.47**	98.85**	109.88**	121.19**	0.49**	0.45**	41.62**	68.97**	37.71**	62.35**	357.26**
$\hat{H}_2$	4.81**	3.87**	3.86**	79.04**	78.17**	85.93**	0.35**	0.29**	32.99**	52.25**	30.82**	47.28**	290.10**
$\hat{h}^2$	11.25**	-0.13	5.63**	13.29	33.53**	35.67**	0.15**	0.07	77.41**	85.02**	76.95**	90.71**	59.62
$(\hat{H}_1/\hat{D})^{0.5}$	1.62	2.48	1.43	2.40	2.18	2.40	2.38	2.07	1.83	1.51	1.65	1.42	2.31
$\hat{H}_2/4\hat{H}_1$	0.23	0.19	0.22	0.20	0.18	0.18	0.18	0.16	0.20	0.19	0.20	0.19	0.20
KD/KR	0.91	0.87	1.19	1.35	1.05	1.09	2.65	3.37	0.81	1.32	0.98	1.39	2.19
$\hat{h}^2/\hat{H}_2$	2.34	-0.03	1.46	0.17	0.43	0.42	0.43	0.24	2.35	1.63	2.50	1.92	0.21
% Heritability (narrow sense)	21.06	10.58	28.99	15.65	14.62	13.99	18.27	29.12	20.31	33.80	24.63	37.49	19.32

$$KD/KR = \{(4\hat{D}\hat{H}_1)^{0.5} + \hat{F}\} / \{(4\hat{D}\hat{H}_1)^{0.5} - \hat{F}\}; *, ** \text{ Significant at 5 and 1 per cent levels, respectively}$$

Table 6: Genetic components for no. of spikelets per main spike, no. of grains per main spike, grain yield per main spike, 1000 grain weight and harvest index

No. of effective tillers per plant

The value of “ t^2 ” test was significant in E_2 and E_4 , which suggested failure of certain assumptions of diallel analysis. Significance of only both the dominance components (H_1 and H_2) of gene effect in E_1 and E_3 clearly indicated that was mainly governed by dominance gene effect. The estimate of average degree of dominance (3.59) suggested existence of over dominance. Asymmetrical distribution of positive and negative alleles among the parents was observed as value of $H_2/4H_1$ was less than expected value 0.25. The negative value of F and below one ratio of KD/KR indicated that the character was controlled by more number of recessive genes. Less than one estimate of h^2/H_2 ratio indicated that at least one dominant group of genes appear to govern this trait. The dominant gene or group of genes was not computed as h^2 values were positive or non-significant. The estimate of narrow sense heritability was extremely low in E_1 (6.53%) and E_2 (5.91%), which also confirmed that character was under control of dominance gene effect.

Length of main spike

The value of “ t^2 ” test was significant in E_1 and E_4 , which suggested failure of certain assumptions of diallel analysis. Significance of only dominance components (H_1 and H_2) of gene effect in E_2 and E_3 revealed that the character was solely governed by dominance gene action. The estimates of average degree of dominance $(H_1/D)^{0.5}$ suggested existence of over dominance gene actions. The below 0.25 values of $H_2/4H_1$ ratio indicated asymmetrical distribution of positive and negative alleles among the parental genotypes.

The negative F value and below one ratio of KD/KR observed in E_2 indicated that character was controlled by more number of recessive genes; however in E_3 , character was mainly governed by more number of dominant genes as values of F was positive and ratio of KD/KR was above unity. The estimates of h^2/H_2 ratio indicated that at least one dominant group of genes appeared of govern this trait in E_2 and E_3 . Significant and positive estimates of h^2 in both environments indicated evidence for net dominance gene effect sum over loci. The estimates of narrow sense heritability were low in both E_2 (4.69%) and E_3 (5.01%).

No. of spikelets per main spike

For number of spikelets per main spike, “ t^2 ” test was found to be significant in E_1 , while for rest of the environments it was non-significant. However, greater influence of additive gene effect in E_2 and E_4 and dominance components (H_1 and H_2) of gene effect were

significant in E_2 and E_4 with preponderance of dominant gene effect, while only dominance gene effect governed the character in E_3 . The values of average degree of dominance indicated existence of over dominance in all the three environments. The below 0.25 values of $H_2/4H_1$ ratio indicated asymmetrical distribution of positive and negative alleles among the parental genotypes. The negative F value and below one ratio of KD/KR that the character was mainly controlled by more number indicated preponderance of recessive genes in E_2 and E_3 . The positive value of F and above one ratio of KD/KR indicated that the character was controlled by excess of dominant genes in E_4 . The estimate of h^2/H_2 ratio was above two in E_2 and above one in E_4 and one dominant group of genes appeared to govern this character, respectively. The estimate of narrow sense heritability was low in E_2 (21.06%), E_3 (10.58%) and E_4 (28.99%), which also confirmed that character was largely under control of dominance gene effect.

No. of grains per main spike

The value of “ t^2 ” test was found to be significant in E_3 , while for rest of the environments it was non-significant. Additive (D) and dominance components (H_1 and H_2) of gene effect were significant in E_2 and E_4 with preponderance of dominant gene effect, while an only dominance gene effect was involved in E_1 . The values of average degree of dominance indicated existence of over dominance. The values of $H_2/4H_1$ ratio below 0.25 indicated asymmetrical distribution of positive and negative alleles among the parental lines in E_1 , E_2 and E_4 . The positive values of F and more than one values of KD/ KR indicated symmetrical distribution of dominant and recessive genes among the parental genotypes, and dominant genes were excess across the environments.

Less than one estimate of h^2/H_2 ratio indicated that at least one dominant group of genes appear to govern this trait. Significant and positive estimates of h^2 in E_2 and E_4 indicated evidence for net dominance gene effect sum over loci. The estimates of narrow sense heritability was low in E_1 (15.65%), E_2 (14.62%) and E_3 (13.99%).

Grain yield per main spike

The value of “ t^2 ” test was significant in E_1 and E_3 , which suggested failure of certain assumptions of diallel analysis. Significance of additive (D) and dominance components (H_1 and H_2) of gene effect in E_2 and E_4 revealed that the character was governed by both additive and dominance gene action. The estimate of average degree of dominance (E_2 :2.38 and E_4 :2.07) suggested existence of over dominance. Asymmetrical distribution of positive and

negative alleles among the parents was observed as value of $H_2/4H_1$ was less than expected value 0.25. The positive value of F and above one ratio of KD/KR indicated that the character was controlled by excess of dominant genes. Less than one estimate of h^2/H_2 ratio indicated that at least one dominant group of genes appear to govern this trait. Significant and positive estimate of h^2 observed in E_2 indicated evidence for net dominance gene effect sum over loci. The estimate of narrow sense heritability was low in E_2 (18.27%) and E_4 (29.12%), which also confirmed that character was under control of dominance gene effect.

1000 grain weight

The value of " t^2 " was non-significant in all the analysis. Significance of additive (D) and dominance components (H_1 and H_2) of gene effect revealed that the character was governed by both additive as well as dominance gene actions in all environments. The estimates of average degree of dominance suggested existence of over dominance gene action in all environments. The below 0.25 values of $H_2/4H_1$ ratio indicated asymmetrical distribution of positive and negative alleles among the parental genotypes in all the environments. The positive value of F and above one ratio of KD/KR indicated that the character was controlled by excess of dominant genes in E_2 and E_4 , when negative value of F and below one ratio of KD/KR indicated that that the character was controlled by more number of recessive gene in E_1 and E_3 . More than one estimate of h^2/H_2 ratio indicated that more than two and three dominant groups of genes appeared to govern this character. Significant and positive estimates of h^2 in all the environments indicated evidence for net dominance gene effect sum over loci. The estimates of narrow sense heritability were low and medium in all the analysis (E_1 : 20.31%, E_2 : 33.80%, E_3 : 24.63% and E_4 : 37.49%).

Harvest index

The value of " t^2 " test was significant in E_2 , E_3 and E_4 , which suggested failure of certain assumptions of diallel analysis. Significance of only dominance components (H_1 and H_2) of gene effect in E_1 revealed that the character was solely governed by dominance gene action. The estimate of average degree of dominance (2.31) suggested existence of over dominance. Asymmetrical distribution of positive and negative alleles among the parents was observed as value of $H_2/4H_1$ was less than expected value 0.25. The positive value of F and above one ratio of KD/KR indicated that the character was controlled by more number of dominant genes. Less than one estimate of h^2/H_2 ratio indicated that at least one dominant group of genes appear to govern this trait. The estimate of narrow sense heritability was low

(19.32%), which also confirmed that character was largely under control of dominance gene effect.

Discussion of Numerical approach

Components of gene effect revealed that most of the characters were governed by both additive and dominance gene action across the environments with greater influence of dominance gene effect except for days to 50% heading in E₁, E₂, E₃ and E₄; days to maturity in E₂, E₃ and E₄; grain yield per main spike in E₄; while, for no. of effective tillers per plant (E₁ and E₃), length of main spike (E₂ and E₃), no. of spikelets per main spike (E₃), no. of grains per main spike (E₁) and harvest index (E₁) only dominance component (H₁ and H₂) of gene effect was significant. The findings were also claimed the involvement of both additive and non-additive gene action in the inheritance of yield and related traits in bottlegourd^{19, 20}.

The values of average degree of dominance varied across the environments. The over dominance behaviour of interacting alleles was depicted for days to 50% heading (E₁, E₂, E₃ and E₄), days to maturity (E₂, E₃ and E₄), no. of effective tillers per plant (E₁ and E₃), length of main spike (E₂ and E₃), no. of spikelets per main spike (E₂, E₃ and E₄), no. of grains per main spike (E₁, E₂ and E₄), grain yield per main spike (E₂ and E₄), 1000 grain weight (E₁, E₂, E₃ and E₄) and harvest index (E₁). The higher proportions of dominant genes observed in most of the characters are in agreement with the findings²¹. Thus, the additive and dominance both the variances were pre dominance component governing the expression of yield and other yield components accordance with²². The findings were also found non-additive gene action playing important roles in controlling grain yield under both drought stress and favorable growing environments²³

Asymmetrical distribution of positive-negative and dominance-recessive genes was depicted for most of the characters. However, excess of dominant genes were exhibited for days to 50% heading (E₂, E₃ and E₄), days to maturity (E₂, E₃ and E₄), length of main spike (E₃), no. of spikelets per main spike (E₄), no. of grains per main spike (E₁, E₂ and E₄), grain yield per main spike (E₂ and E₄), 1000 grain weight (E₂ and E₄) and harvest index (E₁); whereas, excess of recessive genes were noticed for days to 50% heading (E₁), no. of effective tillers per plant (E₁ and E₃), length of main spike (E₂), no. of spikelets per main spike (E₂ and E₃) and 1000 grain weight (E₁ and E₃). The ratio (H₂/4H₁) indicated a symmetrical distribution of positive and negative dominant genes in parents in all studied characters²⁴.

The estimates of narrow sense heritability were low for days to 50% heading (E_1 and E_3), days to maturity (E_1 and E_3), no. of effective tillers per plant (E_1 and E_3), length of main spike (E_2 and E_3), no. of spikelets per main spike (E_2 , E_3 and E_4), no. of grains per main spike (E_1 , E_2 and E_4), grain yield per main spike (E_2 and E_4), 1000 grain weight (E_1 , E_2 , E_3 and E_4) and harvest index (E_1), which indicated that these characters were under greater influence of dominant gene effect. The narrow sense heritability was found moderate for days to 50% heading (E_2 and E_4), which confirmed that these characters were under genetic control of both additive and dominant genes. Narrow-sense heritability was generally of small magnitude and ranged from 0.86% to 66.67%²⁴.

Graphical Analysis

To test the validity of the basic assumptions postulated for diallel analysis (Hayman, 1954), $W_r - V_r$ homogeneity “ t^2 ” test was performed. The value of “ t^2 ” test was significant for majority of the characters either in E_1 , E_2 , E_3 and E_4 , or in their different combinations, indicating failure of any of the basic assumptions of diallel analysis. However, further verification of the validity of assumption in respect to presence or absence of epistatic gene effects could be more precisely made from W_r - V_r graph, the array points on the W_r - V_r graph expected to fall on the line of unity (45°) and thereby the value of regression “ b ” should be significantly deviated from zero, but not from one, suggesting the absence of epistatic gene effect. The regression value “ b ” was statically at par one for days to 50% heading (E_1 and E_4) and 1000 grain weight (E_3 and E_4), which revealed an absence of digenic interactions for these characters in respective environment (**Table 4**).

The graphical analyses are presented in **Figure 3 to Figure 6** and are described as follows.

Days to 50% heading

In E_2 , regression line ($Y = 0.8771x - 0.7497$) (**Figure 3**) intercepted the W_r axis below the origin indicating presence of over dominance gene action. Among the parents, HD 2864 had more frequency of dominant genes, as these parents occupied the nearest position to the origin of regression line, accordingly parents GW 366, HI 1544 and UAS 385 had more frequency of recessive genes, as those occupied the farthest position from the origin; while LOK 1, GW 322, GW 173 and GW 11 had equal proportion of dominant and recessive genes as those occupied an intermediate position on regression line. The parents GW 451 and GW 496 would be carrier of genes causing inter allelic interaction as those occupied their

positions outside truncated area of the graph. The slope of regression line of W_r - V_r graph was statistically of unity in E_4 ($Y = 0.6967x - 0.1504$) (**Figure 4**) indicating absence of digenic interactions. Similarly, the regression line intercepted W_r axis passes through the origin indicating presence of complete dominance gene action.

Among the parents, HD 2864 and GW 496 had more frequency of dominant genes, as these parents occupied the nearest position to the origin of regression line, accordingly parents GW 366 and HI 1544 had more frequency of recessive genes, as both the genotypes occupied the farthest position from the origin; parents GW 451, LOK 1, GW 322, GW 11, GW 173 and UAS 385 had equal proportion of dominant and recessive genes as those occupied an intermediate position on regression line.

1000 grain weight

Regression line ($Y = 0.711x - 2.5028$) (**Figure 5**) intercepted W_r axis below the origin, indicating over dominance gene action for the character in E_3 . The array point of parent GW 451 was nearest to the origin, and thereby it was supposed to contribute excess of dominant genes. Whereas, the parent HD 2864 occupied its position at tail of regression line indicating it as carrier of excess of recessive genes. Moreover, rest of the parents *viz.*, GW 451, GW 496, GW 322, HI 1544, GW 173, GW 11 and UAS 385 occupied intermediate positions on regression line indicating equal distribution of dominant and recessive genes with them. The parents LOK 1 and GW 366 could be carrier of genes causing inter allelic interaction as those occupied their positions outside the truncated area of the graph.

In E_4 , the slope of regression line of W_r - V_r graph was linear and probably at par to one. The regression line ($Y = 0.6615x - 1.4252$) intercepted the W_r axis below the origin indicating presence of over dominance gene action. The scattered array points of the parents on and around the regression line revealed existence of sufficient variability among the parents. The array point of LOK 1 occupied their position nearer to origin, indicating that it would likely to contribute dominant genes in high frequency; in contrast to this, parents GW 173, GW 11 and UAS 385 attained their positions at the tail of regression line indicating carrier of high frequency of recessive genes. Moreover, rest of the parents occupied intermediate positions on regression line within the truncated area indicating equal distribution of dominant and recessive genes with them (**Figure 6**).

Discussion of graphical approach

In graphical analysis, regression value “b” was unity for days to 50% heading (E_1 and E_4) and 1000 grain weight (E_3 and E_4), which revealed an absence of digenic interactions for these characters in respective environment. Based on interception of regression line on W_r axis, degree of dominance was depicted as, over dominance for days to 50% heading (E_2), 1000 grain weight (E_3 and E_4), whereas, complete dominance for days to 50% heading (E_4). The dispersion of parents around the regression line revealed that parents 3, 1 and 2 were close to the origin of the coordinate, and accordingly had > 75% of dominant genes, parents 4 and 6 had 50% dominant genes, while parent 5 was far from the origin and therefore had mostly recessive genes²⁴.

Conclusions

Components of gene effect revealed that most of the characters were governed by both additive and dominance gene action across the environments with greater influence of dominance gene effect except for days to 50% heading in E_1 , E_2 , E_3 and E_4 ; days to maturity in E_2 , E_3 and E_4 ; grain yield per main spike in E_4 ; sedimentation value in E_2 and E_4 , gluten; wet gluten in E_4 ; starch content in E_2 and iron content in E_2 . Therefore, population improvement may be followed to isolate superior recombinants for development of desired parent/s in future breeding programme.

The character grain yield per plant was influenced by over dominance gene effect. Therefore, while selecting segregants for improvement of yield attributing traits. Selection may be delayed by the time dominance will be diluted and transgressive segregants could be identified.

In graphical analysis, regression value “b” was unity for days to 50% heading (E_1 and E_4), 1000 grain weight (E_3 and E_4), protein content (E_1 and E_3), sedimentation value (E_1 , E_2 and E_3) and starch content (E_1), which revealed an absence of digenic interactions for these characters in respective environment. Rest of the characters had non-random distribution of genes at different loci among the parents and/ or presence of inter allelic interaction at different loci. The contradiction between the approaches of as genetic component of variation and V_r - W_r graph analysis could be ascribed to the presence of correlated gene distribution¹¹.

MATERIALS AND METHODS

Plant material and field performance evaluation. The experimental material comprised of 10 parents, their 45 hybrids and 2 check varieties. The crosses were made during *Rabi* 2017-18 & 2018-19 through 10 ×10 diallel mating excluding reciprocals. The parents, hybrids and

standard checks were evaluated in complete randomized block design with three replication in the Regional Research Station, Anand Agricultural University, Anand, India (22° 35' N, 72° 55' E) during normal and late sown conditions in four environments E₁ and E₂ (normal and late sown, *Rabi* 2018-19), E₃ and E₄ (Normal and late sown *Rabi* 2019-20) (**Table 2**). Each treatment consists, each female lines of 3 meter length were grown with 20 × 10 (Normal) and 18 × 10 (Late) cm inter and intra row spacing, respectively.

All the recommended package of practice followed for raising the crop. The observations were recorded on yield and its ten component traits viz., (Plant height, Days to 50% flowering, Days to maturity, No. of effective tillers per plant, Length of main spike, No. of spikelets per main spike, No. of grains per main spike, 1000 grain weight, Grain yield per main spike, Grain yield per plant and Harvest index). The details of the parental genotypes, Checks and Hybrid crosses are given in **Table 1 and 3**. None of the wheat germplasm was procured from outside of the institute since it is available with the institute or it is in the public domain. The guidelines and legislation are not applicable in this study.

Statistical analysis. The data recorded on studied traits in parents and hybrids were subjected to components of genetic variance using general linear model as implemented in SPAR01. In addition, numerical approach and graphical approach were calculated.

Estimation of numerical and graphical approach. For each parents these approaches were estimated.

Competing interests. Authors have declared that no competing interests exist.

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Fig 3: Wr- Vr graph for days to 50% heading in E₂

Fig 4: Wr- Vr graph for days to 50% heading in E₄

P₁ = GW 451; P₂ = GW 496; P₃ = LOK 1; P₄ = GW 322; P₅ = GW 366; P₆ = HI 1544; P₇ = GW 173; P₈ = GW 11; P₉ = HD 2864; P₁₀ = USA 385

■ Parabola ▲ Regression — Poly.(parabola) — Linear(Regression)

Fig. 5: W_r - V_r graph for 1000 grain weight in E_3

Fig. 6: W_r - V_r graph for 1000 grain weight in E_4

P_1 = GW 451; P_2 = GW 496; P_3 = LOK 1; P_4 = GW 322; P_5 = GW 366; P_6 = HI 1544; P_7 = GW 173; P_8 = GW 11; P_9 = HD 2864; P_{10} = USA 385

■ Parabola ▲ Regression — Poly.(parabola) — Linear(Regression)