

DIALLEL ANALYSIS OF HEADING DATA AND PLANT HEIGHT IN WHEAT*

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Abstract

Detailed genetic retrospect, with respect to degree of dominance, nature of dominance, proportion of positive to negative effects of genes at the loci exhibiting dominance, proportion of dominant to recessive genes in the parents and the number of groups of genes controlling the particular character was studied for onset-of-heading, 75%-heading, heading-span and plant height in a five-parent diallel cross of common wheat (*Triticum aestivum* L.) for four generations at two locations in the University of Alberta, Edmonton, Canada. The parents involved were Marquis, Chinook (both Canadian), Khushhal (Pakistan), Ciano-67 and Inia-66 (of Mexican origin) and the generations considered were F1, F2, Backcross and selfed backcross in a complete diallel matrix fashion.

For each generation diallel and at each location the analysis for genetic components of variation was supplemented by graphical representation of variance-covariance and standardized deviation graphs of parental measurements and order of dominance with reference to individual character.

Summarily, onset-of-heading and 75%-heading were partially dominant in their inheritance in all the diallel-generations at both locations. Heading-span was over dominant in F1 (both locations), F2 (at one location and at the other dominance was complete), backcross (at one location, partial at the other) and selfed backcross (at one location, nearly complete at the other). Plant height inherited as a partial dominant trait for all the four generations of diallel at both locations. Complete heading data suggested that early-heading genes were dominant over late-heading ones. For plant height, usually shortness was found to be dominant over tallness. The varying exceptions in all the four characters with respect to diallel-generations and locations, were analysed in the form of genotype-environment interaction.

Introduction

In a polygenic system underlying a quantitative character, the allelic and non-allelic interactions are the most common forms of manifestation of gene effects in inheritance. The interaction of alleles at a given locus is known as dominance, while non-allelic interaction, viz., interaction between genes at different loci, may take the form of complementary-gene, duplicate-gene or other classical relationship. All these effects are generally referred to as 'epistasis' in biometrical genetics. Different genotypes, defined with reference to a metrical character, do not react alike to a given change in environment. This means that genotype and environment are not independent in their action in producing the phenotype. Consequently, variation in the degree of expression of a character is assumed to consist of genotypic, environmental and genotype-environment interaction components which may respectively be partitioned in a biometrically defined experimental design.

The evaluation of these components of variation in diallel cross becomes quite efficient and informative since a number of parental strains can be assessed together

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with their hybrid generations. Diallel cross technique is one of the conventional approaches used in biometrical genetics to obtain adequate information regarding the inheritance of quantitative character. The procedure, first introduced by Schmidt (1919), involves crossing a set of parental lines in all possible combinations, including their reciprocals, in order to obtain an estimation of the magnitude of genetic variability ascribable to the differences among the parental lines. The quantitative genetic analysis of a diallel cross, based on a set of postulated assumptions, is presented and discussed in detail by Jinks & Hayman (1953), Hayman (1954a, 1954b, 1958, 1960), Jinks (1954, 1956), Kempthorne (1956) and Mather & Jinks (1971). By means of pertinent parameters obtainable from the analysis of diallel cross, the mean degree of dominance, the proportion of positive to negative alleles at loci exhibiting dominance, the proportion of dominant to recessive genes in the parents and the correlation between parental order of dominance and parental measurements, can be determined. In addition, the graphical analysis of the regression of array covariances (W_r) on array variances (V_r) permits the separation of true dominance from the spurious one caused by non-allelic interaction and categorizes the parents according to their degree of dominance.

The work reported in this article deals with such type of analysis of genotype-environment interaction with respect to components of variation in a five-parent diallel cross of common wheat (*Triticum aestivum* L.) for four generations and at two locations. The purpose of the investigation was to obtain information regarding an extent to which the genetic components of variation are affected by respective generations of diallel cross at different locations.

Material and Methods

Five cultivars of common wheat (*Triticum aestivum* L.); Marquis and Chinook from Canada, Khush-hal from Pakistan and Ciano-67 and Inia-66 from Mexico, were used in diallel study. All possible F1 combinations were made during 1970's summer at Parkland farm of the University of Alberta. Following winter, some of the F1's together with their parents were sown in growth chambers to make backcrosses, reciprocal backcrosses, further F1 combinations and to provide F2 seed. During 1971's spring, same procedure was repeated to have sufficient number of seed for every combination. In the fall of 1971, the backcrosses and their reciprocals were seeded in growth chambers to have their first selfed generation.

The whole of the experimental material, consisting of 5 parents, 20 F1's, 20 F2's, 80 backcrosses and 80 selfed backcrosses (amounting to 205 different entries), was sown in a 15 x 15 partially balanced lattice design with three replications at two locations, viz., Department of Genetics Eilerslie Field Lab and Department of Plant Science, Parkland Farm of the University of Alberta. To meet the requirements of the design, 20 more entries were needed and since F2 is the maximum segregating generation, each F2 combination was represented twice in each replication to complete the required 205 entries. Each of the fifteen (15' x 15') blocks in a replication was space-seeded with 15 rows of 30 seeds each at a spacing of 30.4 cms between rows and 15.2 cms between seeds within a row. Observations on heading date and plant height, at each of the location, were recorded in the following manner:

- (1) *Onset-of-heading*, expressed in number of days between seeding date and the date of appearance of first head in the row or entry.

- (2) *Final-heading*, recorded in number of days from the date of seeding to the day when 75% of the plants have headed in a particular row.
- (3) *Heading-span*, measured by the difference between (1) and (2).
- (4) *Plant height*, measured in centimeters from the surface of the soil to the tip of the spike on the highest tiller (excluding awns). Ten consecutive plants per row were recorded for height irrespective of their growth performance, leaving the first plant as border effects except in those rows where the number of surviving plants were reduced to ten or less.

STATISTICAL ANALYSIS: Entry means were calculated and then treated as independent variables for further analyses. Missing entries were calculated according to Cochran & Cox's (1957) formula for the randomized block design except at Parkland. Here, since the missing entries were less than three, the recommended procedure for partially balanced lattice design was used. The complete set of data was subjected to analysis of variance for partially balanced lattice design. This provided a single set of adjusted treatment means at each location. However, unadjusted treatment means (original entry means as treated in randomized block) were used in diallel analysis. These were categorized into four diallel sets, viz., F1's, F2's, backcrosses and selfed backcrosses.

Diallel analysis was performed in two steps, i.e., diallel analysis for genetic components of variation and graphical analysis of W_r (parent offspring covariance of the rth. array) on V_r (Variance of the rth. array) to complement the former via graphical representation. In the diallel analysis for genetic components of variation, each diallel table was subjected to tests of validity of the following assumptions (Hayman, 1954b):

1. homozygous parents.
2. normal diploid segregation.
3. no difference between reciprocal crosses.
4. no multiple allelism.
5. independent action of non-allelic genes.
6. uncorrelated gene distribution.

The condition of 'homozygous parents' in the present case could be satisfied as the parent material was sown preceding crossing and found to be true-to-type. 'Normal diploid segregation' may be assured from the pedigree record of the organism used as experimental material. Wheat, though an amphi-diploid derivative of *Triticum monococcum* for the 'A' genome (Melburne & Thompson, 1927; Zohary & Feldman, 1962), *Aegilops speltoides* for the 'B' genome (Sarkar & Stebbins, 1956; Riley *et al.* 1958; Sears & Okamoto, 1958) and *Aegilops squarrosa* for the 'D' genome (Kihara, 1944; McFadden & Sears, 1944, 1946; Kihara & Lilienfeld, 1949) behaves cytogenetically as a normal diploid (Sears, 1948; Riley *et al.* 1961). It follows, therefore, that the assumption of normal diploid segregation could be considered valid. 'No reciprocal differences' were checked after Hayman's (1954a) procedure of analysis of

variance for diallel tables, where significance of the component 'c' indicates failure of this hypothesis. The remaining three conditions of 'no multiple allelism', 'independent action of non-allelic genes' and 'uncorrelated gene distribution' were checked through the analysis of variance of $W_r - V_r$ values for arrays of each diallel table. Heterogeneity of $W_r - V_r$ variances will reveal non-validity of these assumptions.

After validity checks for above mentioned conditions, the diallel analysis for genetic components of variation (Hayman, 1954b, 1958; Jinks, 1954, 1956) was performed on each of the diallel tables by replacing the off-diagonal cells of the diallel table with the common mean of the relevant cross and its reciprocal irrespective of the significance of Hayman's 'c' component. In the F₂ generation diallel, the estimation of genetic components of variation from second degree statistics were computed after Johnson & Aksel's (1959) notation describing the average effect of heterozygote in different filial generation. In case of backcross diallel, since the expected mean of a pair of reciprocal backcross is the same as that of the F₂ generation of a cross between two parents provided the differential loci are independent in their action (Jinks, 1956), the expected statistics for the analysis of backcross family means in a diallel set, assuming no non-allelic interaction, are the same as those for F₂ family means. A complete diallel table of backcrosses therefore requires an amalgamation of four backcrosses to compute the appropriate means of each of the off-diagonal cells in the diallel matrix. Denoting Marquis, Chinook, Khush-hal, Ciano and Inia as (M), (CH), (K), (C) and (I) and taking any two parents, the appropriate backcross combinations can be shown to be equivalent to the mean of the corresponding F₂ hybrid. Thus the mean of M (MxCH), (MxCH)M, CH(MxCH) and (MxCH) CH means is equivalent to the (MxCH) F₂ mean, while the mean of M(CHxM), (CHxM)M, CH(CHxM) and (CHxM)CH means is equivalent to the mean of its reciprocal, i.e., (CHxM) F₂ hybrid. Consequently, a complete diallel table can be constructed which will correspond statistically to the F₂ diallel table and may therefore be used for the analysis of genetic components of variation as described by Jinks (1956). Such a table may be termed as synthetic F₂ diallel table. Similarly, a synthetic F₃ diallel table was constructed from selfed backcross family means. From the estimates of genetic components of variation, various parameters such as mean degree of dominance, proportion of positive to negative alleles, ratio of dominant to recessive genes in the parents and number of groups of genes controlling the particular character were estimated.

The graphical analysis of regression of W_r on V_r was performed after Hayman (1954b) by plotting the regression line and the limiting parabola constructed by calculating its points ($W_r^2 = V_r \times V_0 L_0$) and plotting the V_r , $(W_r \times V_0 L_0)^{1/2}$ points. The W_r , V_r graphs were supplemented with Johnson & Aksel's (1959) standardized deviation graphs of parental measurements (Y_r) and parental order of dominance ($W_r + V_r$) where the deviations of the Y_r 's and $W_r + V_r$'s from their respective means were standardized by dividing them by their respective standard deviations. An abscissa (Y_r) and an ordinate ($W_r + V_r$) intersecting each other produce four quadrants of the graph classified as (+, +), (-, +), (-, -) and (+, -). The plus and minus signs for ($W_r + V_r$) denote 'recessive' and 'dominant' and for Y_r , they refer to 'high' and 'low' performances respectively.

Experimental Results and Discussion

Table 1 shows the results of the analysis of variance of partially balanced lattice design and its efficiency as compared to the analysis as a randomised block.

TABLE 1. Mean square values from the analysis of variance of partially balanced tripple lattice design with respect to four characters at two locations.

Character	Replication	Blocks within replication	Treatments (adjusted)	% efficiency over randomized block
+ D.F.	2	42	224	—
Onset-of-heading	5.7305	4.9140**	10.3581**	119.205
	19.8980	18.1369**	18.2897**	127.013
Final-heading	14.4640	8.0242**	17.2218**	118.699
	204.9375	14.7080**	19.2502**	108.332
Heading-span	24.0635	2.8539*	3.1996*	95.829
	137.0770	6.6719**	4.6495**	107.162
Plant height	273.8125	566.9384**	543.1385**	121.334
	1017.5480	524.6927**	738.0608**	99.301

First reading under each column refers to Ellerslie and the second to Parkland.

*Corresponding to missing values for different characters, the number of D.F. have been subtracted from error D.F. in calculating mean squares.

*Significant at 5% level.

**Significant at 1% level.

The mean squares of the adjusted treatments showed significant differences among the entries. The relative efficiency of the balanced lattice design at Parkland over randomized block was greater than that at Ellerslie.

Before proceeding to analysis for genetic components of variation, the F₁, F₂, backcross and selfed backcross diallel tables were respectively subjected to Hayman's (1954a) analysis of variance. The results are presented in Table 2.

In this table, component 'a' tests the significance of additive effects and 'b' the dominance effects of genes, while 'b1' tests the mean deviation of hybrids from their mid-parent values. The dominance-deviations, if predominately in one direction, may result in significant 'b1' in the analysis of variance. Component 'b2' indicates the extent to which the mean dominance deviations within a given array of the diallel table differ from those of the other arrays. A significant 'b2' thus implies that some of the parents contain an excess of dominant alleles. Component 'b3' tests the portion of dominance-deviations attributable to individual particular hybrid. The difference between reciprocal crosses is assessed by the significance of 'c' and the maternal effects not ascribable to 'c' are reflected by 'd'. In Table 2, each of the component has been tested for significance against its own block-interaction mean-squares. 'c' was not significantly different from zero in case of F₁ diallel but for plant height at both locations in F₂ diallel. In backcross diallel table, 'c' was significant for heading-span at Ellerslie and for plant height at Parkland. Heading-span at Parkland and plant height at both locations also showed significant reciprocal differences in selfed backcross diallel set. Thus the assumption of no differences between reciprocal crosses was considered valid after replacing the off-diagonal cells of each diallel table with the common mean of the relevant crosses. Substantial differences among the parents are suggested by the significance of 'a' for all the characters in all the diallel sets except for heading-span at both locations in F₁ and F₂ diallel and at Parkland in

TABLE 2. Mean squares from the analysis of variance of 5 x 5 four diallel tables for four characters at two locations.

Source of variation	D.F.	F ₁ diallel table				F ₂ diallel table			
		Onset-of-heading	Final heading	Heading-span	Plant height	Onset-of-heading	Final heading	Heading-span	Plant height
a	4	79.171**	109.687**	4.107	4228.00**	68.093**	73.125	4.095	3510.500**
		125.875**	192.250**	7.860	4191.00**	117.093**	138.179	4.582	4245.500**
b	10	5.775	8.525**	1.485	68.40	6.381**	61.243	1.582	53.000**
		6.712	21.381**	13.744*	67.700	12.068**	17.012**	5.875	75.700*
b1	1	16.333	38.163	5.880	67.594	36.749	79.567	0.020	6.482
		20.803	66.270	12.403	31.191	51.667	82.687	3.740	10.083
b2	4	2.421	4.437*	1.882	112.56	4.140	44.921	0.952	59.703
		4.795	1.046	5.128	93.17*	4.260	5.109	7.609	93.125*
b3	5	6.362**	5.850**	0.288	33.01	2.100**	70.650**	2.399	56.900**
		5.450*	28.675**	20.106*	54.86**	10.375**	13.425**	4.915	74.612*
c	4	2.133	0.616	1.433	11.15	2.254	71.754	0.537	239.153**
		4.183	0.583	2.466	6.60	1.162	0.554	2.029	141.637**
d	6	0.855	0.894	0.711	63.19**	0.497	56.643	0.801	75.935**
		3.572*	1.194	2.105	38.98**	0.440	1.318	0.820	44.511*

	Backcross diallel table		Selfed backcross diallel table						
a	4	66.531** 96.390**	110.609** 117.453**	7.044** 8.804*	3790.00** 4037.00**	75.781** 107.812**	104.078** 133.281**	4.381* 7.777	3675.750** 3919.750**
b	10	7.662** 7.193**	5.306 11.537**	1.626 3.715	41.50* 79.30*	4.581** 3.175	3.187** 11.556**	1.211 5.714	40.800* 40.900
b1	1	27.451 45.435	19.380* 69.841	0.130 3.000	4.84 5.69	14.851 12.100	6.526 41.255	0.653 8.670	25.477 10.266
b2	4	4.593* 3.892	1.343 7.843	2.821 6.303	33.01 120.17	2.546 1.140	2.312 5.796	1.229 4.684	22.500 61.609
b3	5	6.150* 2.187	5.625** 2.837	0.971 1.789*	55.61 61.60**	4.137** 3.000	3.162** 10.250**	1.308** 5.949**	58.200* 30.637*
c	4	0.236 1.106	0.254 0.757	0.486* 0.841	46.96 18.14*	0.632 0.451	2.443 0.286	0.805 0.662*	124.927** 111.706**
d	6	0.371 0.639	0.561 1.406	0.156 0.612	19.80 22.05	0.705 1.492	2.834 0.709	1.404 0.520	13.147 5.609

First reading under each column refers to Ellerslie and the second to Parkland.

Error D.F. comprises of block-interaction with D.F. of (a+b+c+d).

Each component has been tested against its own block-interaction.

*Significant at 5% level and **Significant at 1% level.

selfed backcross diallel. Similarly, item 'b' which measures over-all dominance effects of the genes can also be interpreted accordingly keeping in view the significant mean squares for particular character at particular location and in particular diallel set. 'b1' was significant only for final-heading at Ellerslie in backcross diallel indicating directional dominance for the particular character. Significance of 'b2' confirms the preponderance of dominant genes in some of the parents for particular character in particular diallel set (Table 2) and significant 'b3' implies that specific combining ability for the concerned characters is comparatively more important than general combining ability when pedigree selection procedure is followed in breeding program (Mather & Jinks, 1971).

The assumptions of no non-allelic interaction, no multiple allelism and uncorrelated gene distribution were checked by the analysis of variance of W_r-V_r . The test of homogeneity of W_r-V_r is given in Table 3. None of the characters, except plant height at Parkland in F₂ and backcross diallel generations and onset-of-heading at both locations in backcross diallel, showed heterogeneity and these assumptions, may therefore, be considered valid. The exceptions of plant height and onset-of-heading in the particular generation of diallel will be considered later.

For analysis of genetic components of variation, array variances (V_r) and parent-offspring covariances (W_r) over five arrays of each diallel table provided the basis for calculating other second degree statistics presented in Table 4. The estimates of genetic components of variation obtained from second degree statistics (Hayman, 1954b; Jinks, 1956) are presented in Table 5. Table 5 supplied 35 statistics (15 V_r of five arrays and three replications, 15 W_r , V_0L_0 , W_0L_0 , V_1L_1 and $(ML_1-ML_0)_2$ for each of the diallel set and 10 constants were fitted to them (5 Fr values, D, H₁, H₂, h, and E; E was not considered as it is the mean of five Fr's) leaving 25 D.F. for error to test the significance of genetic components of variation. The proportional estimates of the genetic parameters from Table 5 are given in Table 6. The results shown in tables 5 and 6 supported by the graphical analysis of regression of W_r upon V_r are interpreted under separate diallel-set headings.

F₁ diallel set

At both locations, onset-of-heading was inherited as a partially dominant trait as shown by the mean degree of dominance $((H_1-D)_{\frac{1}{2}}=0.48)$ and the regression line which cuts the limiting parabola above its origin (Fig. 1a). The proportion of genes with positive and negative effects in the parents $(H_2 \div 4H_1)$ is 0.23 at Ellerslie and 0.21 at Parkland, suggesting a slight asymmetry of alleles at the loci exhibiting dominance. The proportion of dominant to recessive genes in the parents $[(4DH_1)_{\frac{1}{2}}+F] \div [(4DH_1)_{\frac{1}{2}}-F]$ is 1.92 at Ellerslie and 0.86 at Parkland, suggesting a preponderance of dominant genes in the parents at Ellerslie and equal proportion of dominants to recessives at Parkland. The coefficient of correlation between the parental order of dominance, i.e., $(W_r \cdot V_r)$ and the parental measurements (Y_r) are 0.96 and 0.66 at Ellerslie and Parkland respectively. High positive correlation suggests the dominance of early heading genes over the late heading ones. This situation is reflected in the standardized deviation graph (Fig. 2a) where all the Y_r , (W_r+V_r) parental intercepts occupy (+,+) and (-,-) quadrants, except Khush-hal at Parkland. Fig. 1a classifies Marquis as the highly recessive and Inia as the highly dominant parents at both locations, since they lie, respectively, farthest and nearest to the point of intersect of regression line and limiting parabola. Fig 2a

TABLE 3. Analysis of variance of Wr-Vr differences from four diallel tables for four characters at two locations.

Character	F1 diallel set		F2 diallel set		Error M.S.
	Block M.S.	Entry M.S.	Block M.S.	Entry M.S.	
Onset-of heading	9.2560 18.9050	0.5815 0.0396	7.3843 8.3904	0.2675 2.4463	0.4078 0.8015
Final heading	5.1354 73.2777	1.4540 11.9745	2.3424 35.5057	0.7644 5.2120	0.2218 3.7671
Heading-span	0.9138 31.5321	0.1887 18.5786	0.0046 8.1741	0.1472 4.4720	0.2028 2.0416
Plant height	17021.1562 4453.5938	344.3281 180.5625	10448.0312 4912.7812	150.1719 427.7812**	157.5544 38.5703
		Backcross diallel set		Selfed backcross diallel set	
Onset-of-heading	4.9320 16.4215	1.5831* 1.6003*	9.6481 3.6885	0.3595 0.5320	0.3829 0.2390
Final heading	0.2722 38.3562	0.7335* 2.5496	0.6643 34.1073	0.1281 1.1282	0.1925 1.2708
Heading-span	0.5333 1.1121	0.0653 0.7220	3.3027 4.9299	1.7202 0.4529	0.6324 1.3684
Plant height	12060.9687 9119.5000	309.5469 303.1406*	967.5663 6449.6875	139.6562 166.1875	55.6016 194.0000

The first reading under each column refers to Ellerslie and the second to Parkland.

*Significant at 5% level.

**Significant at 1% level.

supplements this conclusion by revealing that at both locations the highly recessive parent contributes towards late heading (+,+ quadrant) and the highly dominant one towards early heading (-,- quadrant). As far as the other parents are concerned, Chinook and Ciano, lying in (+,+) and (-,-) quadrants, may be classified as recessive late headers and dominant early headers. Khush-hal's order of dominance seems to be affected by the environmental influence, being dominant early header at Ellerslie (-,- quadrant) and a recessive medium-early header (-,+ quadrant) at Parkland. The number of groups of genes ($h^2 \div H_2$)=1 at both locations suggests that atleast one group of genes control the inheritance of onset-of-heading and exhibit dominance.

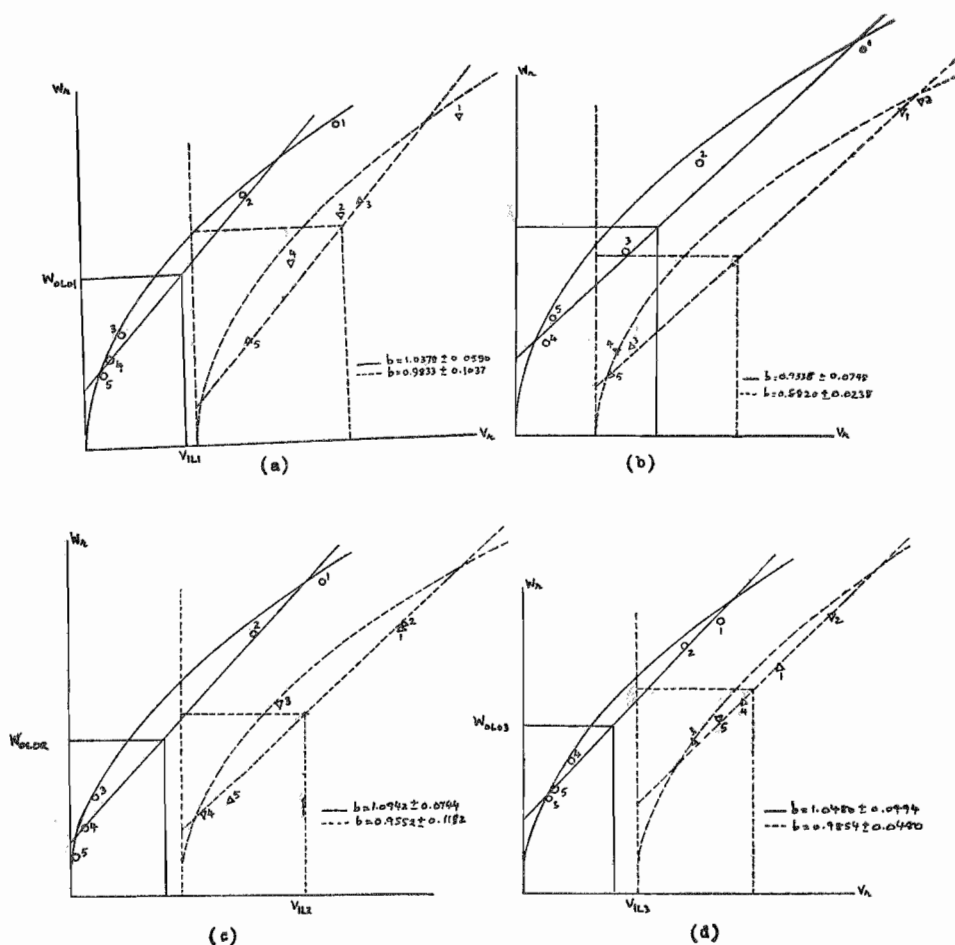


Fig. 1. W_r, V_r graph for onset-of-heading from (a) F1 (b) F2 (c) Backcross and (d) selfed backcross diallel sets.

—○ = W_r, V_r intercepts at Ellerslie.
△ = W_r, V_r intercepts at Parkland.

TABLE 5. Estimates of genetic components of variation for four characters from four diallel sets at two locations.

Character	D	F	H1	H2	h2
F₁ diallel					
Onset-of-heading	14.684 ± 0.319** 14.935 ± 0.405**	4.544 ± 0.798** -1.043 ± 1.012	3.524 ± 0.863** 3.447 ± 1.094**	3.243 ± 0.782** 2.947 ± 0.992**	3.282 ± 0.528** 3.949 ± 0.670**
Final heading	16.616 ± 0.520** 26.203 ± 1.094**	2.800 ± 1.301* 0.573 ± 2.734	5.670 ± 1.406** 12.002 ± 2.956**	4.977 ± 1.275** 12.374 ± 2.681**	7.917 ± 0.861** 13.530 ± 1.810**
Heading-span	0.274 ± 0.132* 2.393 ± 1.199*	0.040 ± 0.330 2.218 ± 2.749	0.549 ± 0.356 6.987 ± 2.972**	0.361 ± 0.323 6.546 ± 2.696**	1.053 ± 0.218** 1.808 ± 1.820
Plant height	480.034 ± 4.665** 511.074 ± 6.758**	-62.619 ± 11.654** -30.582 ± 16.882	50.573 ± 12.599 44.636 ± 18.252*	32.025 ± 11.428** 30.440 ± 16.554	10.105 ± 7.715 1.938 ± 11.177
F₂ diallel					
Onset-of-heading	14.670 ± 0.206** 15.191 ± 0.674	6.449 ± 0.516** 0.322 ± 1.683	4.467 ± 0.558** 7.567 ± 1.820**	3.780 ± 0.506** 7.011 ± 1.650**	7.687 ± 0.341** 10.697 ± 1.114**
Final heading	16.750 ± 0.374** 28.387 ± 0.531**	4.868 ± 0.935** 8.825 ± 1.326**	4.800 ± 1.011* 10.404 ± 1.433**	4.180 ± 0.917** 9.838 ± 1.300**	6.212 ± 0.619** 17.151 ± 0.878**
Heading-span	0.338 ± 0.160** 2.701 ± 0.733**	-0.067 ± 0.401 3.430 ± 1.832	0.593 ± 0.433 3.073 ± 1.981	0.553 ± 0.393 2.097 ± 1.797	-0.156 ± 0.265 0.215 ± 1.213
Plant height	482.276 ± 5.340** 510.702 ± 11.483**	25.269 ± 13.340 -38.325 ± 28.686	35.643 ± 14.422** 48.948 ± 31.013	26.426 ± 13.081* 34.904 ± 28.129	-1.496 ± 8.831 -2.803 ± 18.991

TABLE 6. Estimates of genetic parameters for four characters from four diallel sets at two locations.

Character	$(H_1 \div D)^{\frac{1}{2}} (H_2 \div 4H_1)$		$\frac{(4DH_1)^{\frac{1}{2}} + F}{(4DH_1)^{\frac{1}{2}} - F}$		(h^2/H_2)		$(H_1/D)^{\frac{1}{2}} (H_2/4H_1)$		$\frac{(4DH_1)^{\frac{1}{2}} + F}{(4DH_1)^{\frac{1}{2}} - F}$		(h^2/H_2)	
	F1 diallel set						F2 diallel set					
Onset-of-heading	0.4899	0.2301	1.9232	1.0119	0.5501	0.2116	2.3175	2.0336				
	0.4804	0.2137	0.8645	1.3400	0.7058	0.2316	1.0305	1.5257				
Final heading	0.5842	0.2195	1.3372	1.5907	0.5354	0.1277	1.7451	1.4862				
	0.6768	0.2578	1.0329	1.0934	0.6279	0.2364	1.7279	1.7432				
Heading-span	1.4144	0.1644	1.1093	2.9160	1.3249	0.2330	0.8596	-0.2818				
	1.7419	0.2342	1.7646	0.2763	1.0666	0.1706	3.9415	0.1028				
Plant height	0.3246	0.1583	0.6654	0.3156	0.2719	0.1854	1.2131	-0.0566				
	0.2955	0.1705	0.8161	0.0637	0.3096	0.1783	0.7838	-0.0803				
	Backcross diallel set						Selfed backcross diallel set					
Onset-of-heading	0.6057	0.2135	2.2149	1.2334	0.4432	0.2119	2.2715	1.1839				
	0.5492	0.2227	1.2557	2.5016	0.2957	0.2487	1.2719	1.7521				
Final heading	0.4446	0.2377	1.3539	1.2729	0.3557	0.2079	1.7689	0.7248				
	0.5409	0.2108	2.4173	2.2741	0.5220	0.2229	2.0905	1.3030				
Heading-span	1.7077	0.1500	0.9305	-0.1699	1.1562	0.1909	0.9939	0.0116				
	0.7829	0.1366	4.3292	0.1636	0.9908	0.2064	2.7079	0.5912				
Plant height	0.2086	0.2079	0.8343	-0.1293	0.2043	0.2276	0.9584	0.1418				
	0.3369	0.1653	0.9738	-0.0899	0.2185	0.1596	1.0099	-0.0982				

First reading under each column refers to Ellerslie and the second to Parkland.

The results of final heading (Figures 1b, 2b) and heading-span (Figures 1c, 2c) are subject to same kind of interpretations as for onset-of-heading except for changes in the relative positions of the parents with respect to their ranking order for dominance, and therefore they are not discussed separately.

For plant height, the mean degree of dominance of 0.3 at both locations shows that height is inherited as a partially dominant character. The W_r V_r graph (Fig. 1d) with a regression line intersecting the limiting parabola above its origin supports the above conclusion. The proportion of genes with positive and negative effects

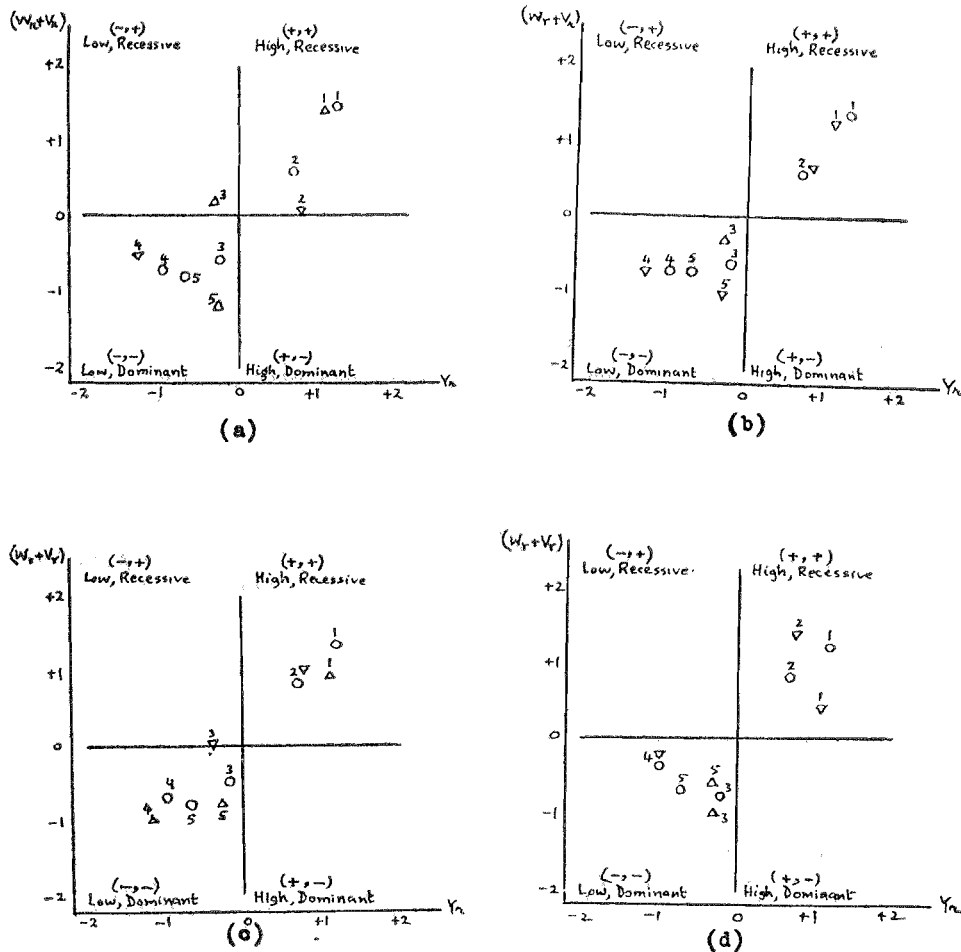


Fig. 2. Standardized deviation graph of parental order of dominance ($W_r + V_r$) and parental measurements (Y_r) for onset-of-heading from (a) F1 (b) F2 (c) backcross and (d) selfed backcross diallel sets.

—○ = Y_r , $W_r + V_r$ intercepts at Ellerslie.
△ = Y_r , $W_r + V_r$ intercepts at Parkland.

in the parents is approximately the same for both locations (0.158 at Ellerslie and 0.170 at Parkland), indicating asymmetry in the distribution of alleles at loci exhibiting dominance. The ratio of dominant to recessive genes in the parents is approximately equal to one at both locations, suggesting that the parents contain equal number of dominants and recessives. The coefficient of correlation between the parental order of dominance and parental measurements is 0.17 at Ellerslie and 0.07 at Parkland, indicating weak association between the measurements of the parents and the order of their dominance. Fig. 1d indicates that Marquis at Ellerslie and Khush-hal at Parkland are the most recessive parents while Inia at both locations is the most dominant parent. Fig. 2d classifies the parental order of dominance together with their height performance. It places highly recessive parents Marquis (at Ellerslie) and Khush-hal (at Parkland) into (+, +) and (-, +) quadrants, showing that the recessiveness of the former is responsible for tallness, while the recessive genes of the latter carry effects decreasing height. The position of Inia in the (-, -) quadrant at both locations suggests that it contains a preponderance of dominant genes contributing towards shortness. The ranking order of Ciano appears to be influenced by location effects. At Ellerslie, it is highly dominant, contributing towards reduced height while at Parkland, it has an excess of recessive genes, again responsible for shortness.

F₂ Diallel set

The mean degree of dominance (0.55 at Ellerslie and 0.75 at Parkland) indicates that the character is partially dominant at both locations. This is also shown by the regression line in Fig. 3a which intersects the limiting parabola above the origin. The proportion of positive to negative alleles in the parents at loci exhibiting dominance is approximately 0.25, indicating equal proportions at both locations. The proportion of dominant to recessive genes in the parents is 2.3 and 1.03 for Ellerslie and Parkland, suggesting a preponderance of dominants in the parents. Fig. 3a shows that Marquis is highly recessive at both locations. Ciano at Ellerslie and Inia at Parkland rank as the two most dominant parents. The coefficient of correlation between Y_r and $(W_r + V_r)$ is 0.96 at Ellerslie and 0.87 at Parkland suggesting that most of the negative genes (for early maturing) are dominant. The distribution of parents with respect to order of dominance is shown in standardized deviation graph of Fig. 4a. Marquis and Chinook at both locations fall into the (+, +) quadrant indicating that they contain mostly recessive genes responsible for lateness while Khush-hal, Ciano and Inia fall into the (-, -) quadrant and are therefore early heading dominant parents. The number of groups of genes controlling onset-of-heading has been estimated as 2.303 for Ellerslie and 1.52 for Parkland indicating at least two groups of genes, exhibiting dominance, control this character.

The results of the analyses for final heading (Tables 5, 6; Figures 3b, 4b) and heading-span (Figures 3c, 4c) can also be interpreted accordingly keeping in mind the relative ranking orders of the parents for dominance or recessiveness. Any change in the distribution of dominants and recessives would be attributed to environmental effect of inter-location type.

For plant height, the components of variation, D, H₁, H₂ and E were significant for Ellerslie but none except D were significant at Parkland. Heterogeneity of $W_r - V_r$ values (Table 3) implies either non-allelic interaction, multiple allelism or correlated gene distribution. In case of correlated gene distribution, the W_r, V_r curve is convex upwards and the mean degree of dominance is seriously inflated.

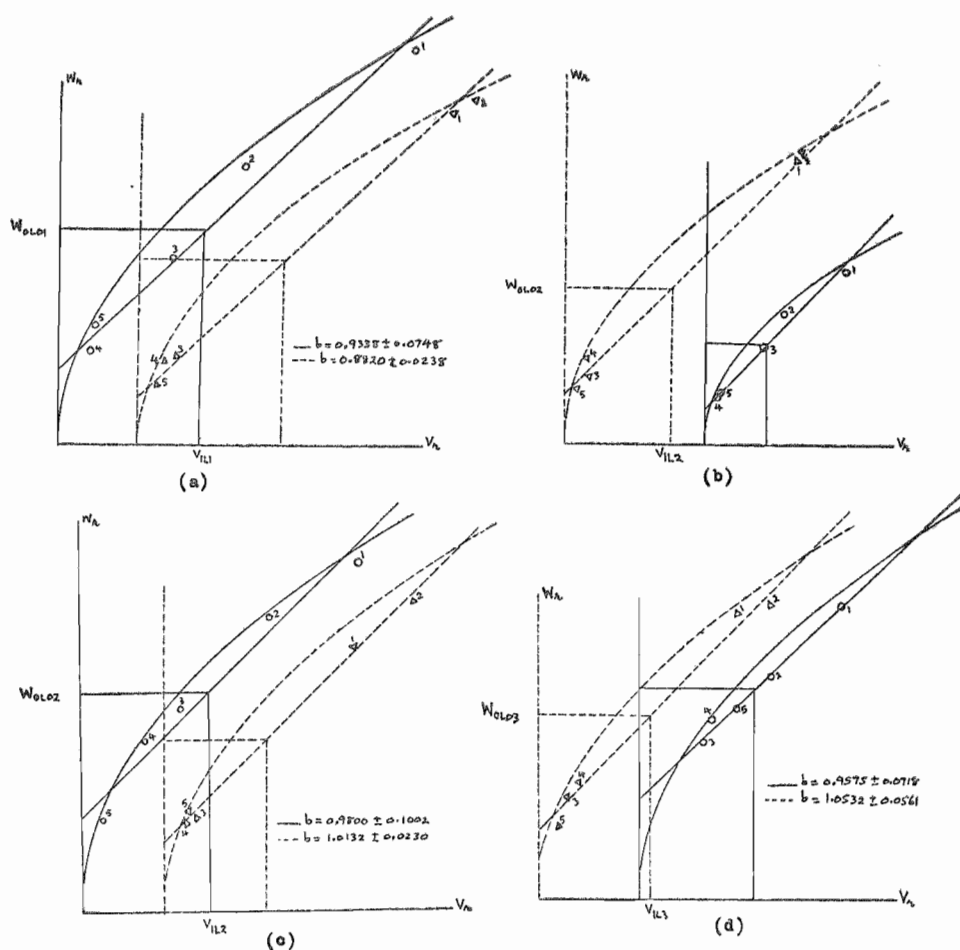


Fig. 3. W_r , V_r graph for final heading from (a) F1 (b) F2 (c) backcross and (d) selfed backcross diallel sets.

—○ = W_r , V_r intercepts at Ellerslie.
△ = W_r , V_r intercepts at Parkland.

giving an impression of apparent over-dominance (Hayman, 1954b) in a situation where, in fact, partial dominance exists. In the case of multiple allelism, the effects are extremely complicated. Models to explain the consequences in terms of W_r , V_r graph are awaiting. It might show spurious dominance (Hayman, 1954b) by scattering the W_r , V_r points and thus causing their mean (V_{1L2} , W_{0L02}) to lie inside and not on the limiting parabola. Non-allelic interaction of the complimentary type distorts the W_r , V_r graph, inflates the $(H_1 \div D)_{\frac{1}{2}}$ and depresses (h_2/H_2) but has very little effect on the estimator of gene frequency. A duplicate type of gene interaction depresses (n_2/H_2) by increasing the proportion of dominants but does not alter $(H_1/D)_{\frac{1}{2}}$, $(H_2/4H_1)$ and the W_r , V_r graph.

Considering the various effects of three above mentioned conditions, and examining the W_r , V_r graph for plant height at Parkland (Fig. 3d) we come to the conclusion that there is actually no non-validity of any of the above mentioned hypotheses. This is because the regression of W_r upon V_r is not significantly different from unity, the array W_r , V_r intercepts do not show any convexity upwards or downwards and there are no serious effects on the estimates of genetic parameters (Table 6). Our conclusion is supported by the fact that all the estimates of genetic components of variation at Parkland except D are non-significant (Table 5). The only reason we might give for the heterogeneity of W_r — V_r over the arrays is a strong environmental effect.

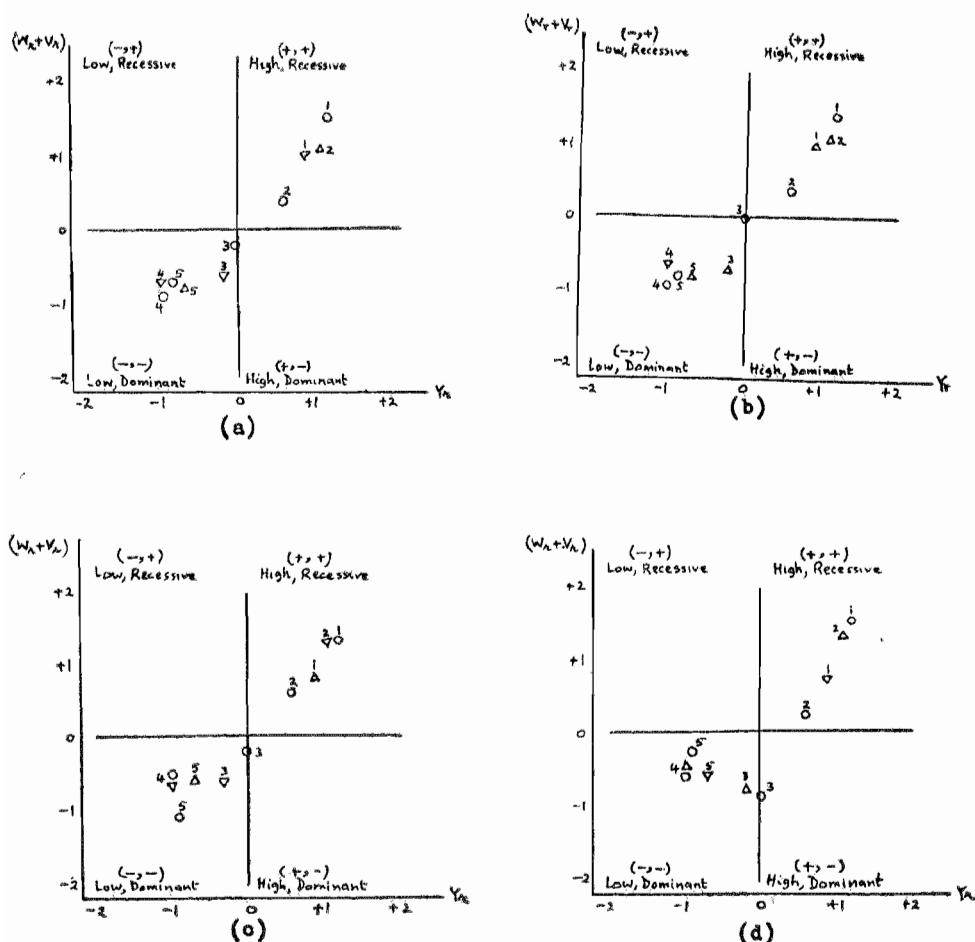


Fig. 4. Standardized deviation graph of parental order of dominance ($W_r + V_r$) and parental measurements (Y_r) for final heading from (a) F1 (b) F2 (c) backcross (d) selfed backcross diallel sets.

- = Y_r , $W_r + V_r$ intercepts at Ellerslie.
Δ = Y_r , $W_r + V_r$ intercepts at Parkland.

At Ellerslie, plant height is inherited as a partially dominant trait since the mean degree of dominance is 0.27 (see also fig. 3d). The proportion of positive to negative alleles at loci exhibiting dominance is 0.18 indicating asymmetry while the proportion of dominant to recessive genes in the parents is 1.2, i.e., close to equality. The coefficient of correlation between the parental order of dominance and parental measurements is 0.75 at Ellerslie and 0.08 at Parkland indicating that the genes contributing towards shortness are mostly dominant. With respect to parental order of dominance (Fig. 3d & 4d), Marquis rates as the highly recessive parent for tallness at Ellerslie and Khush-hal likewise at Parkland. Ciano ranks as the most dominant for shortness at Ellerslie and similarly Inia at Parkland. Examination of figure 4d reveals that though Marquis and Khush-hal rank as the highly recessive parents, Khush-hal nevertheless contributes towards reduced expression of the character (+, -) as compared to Marquis (+, + quadrant). Ciano and Inia rank as the most dominant parents for shortness because of their position in the (-, -) quadrant. Chinook, contributing towards tallness; has recessive and dominant genes in equal proportion.

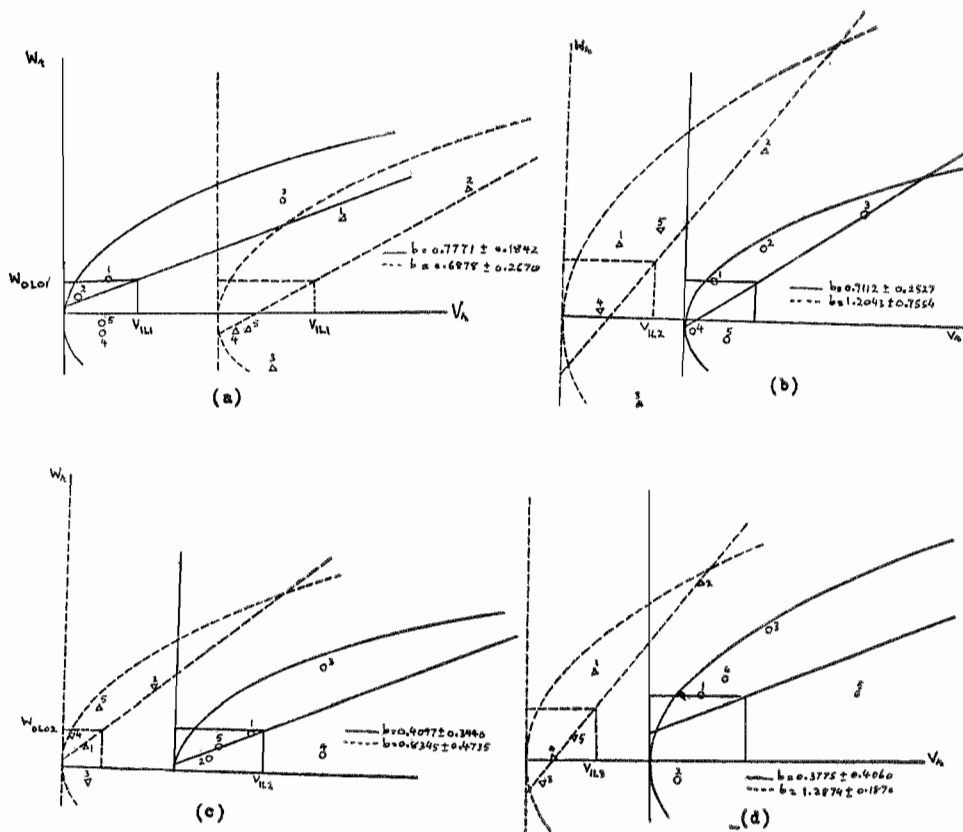


Fig. 5. W_r , V_r graph for heading-span from (a) F1 (b) F2 (c) backcross and (d) selfed backcross diallel sets.

—○— = W_r , V_r intercepts at Ellerslie.
 - - - - -△- - - - - = W_r , V_r intercepts at Parkland.

Backcross diallel set

The mean degree of dominance (Table 6) and the regression of W_r upon V_r (Fig. 5a) at both locations show that onset-of-heading is partially dominant in inheritance. Table 3 showed W_r - V_r heterogeneity which can be ascribed to either non-allelic interaction, multiple allelism or correlated gene distribution. It could be ascertained from figure 5a that the regression line does not deviate significantly from the expected unit slope and the W_r , V_r graph does not appear to be distorted. Therefore the question of non-validity of any of the above-mentioned assumptions has been

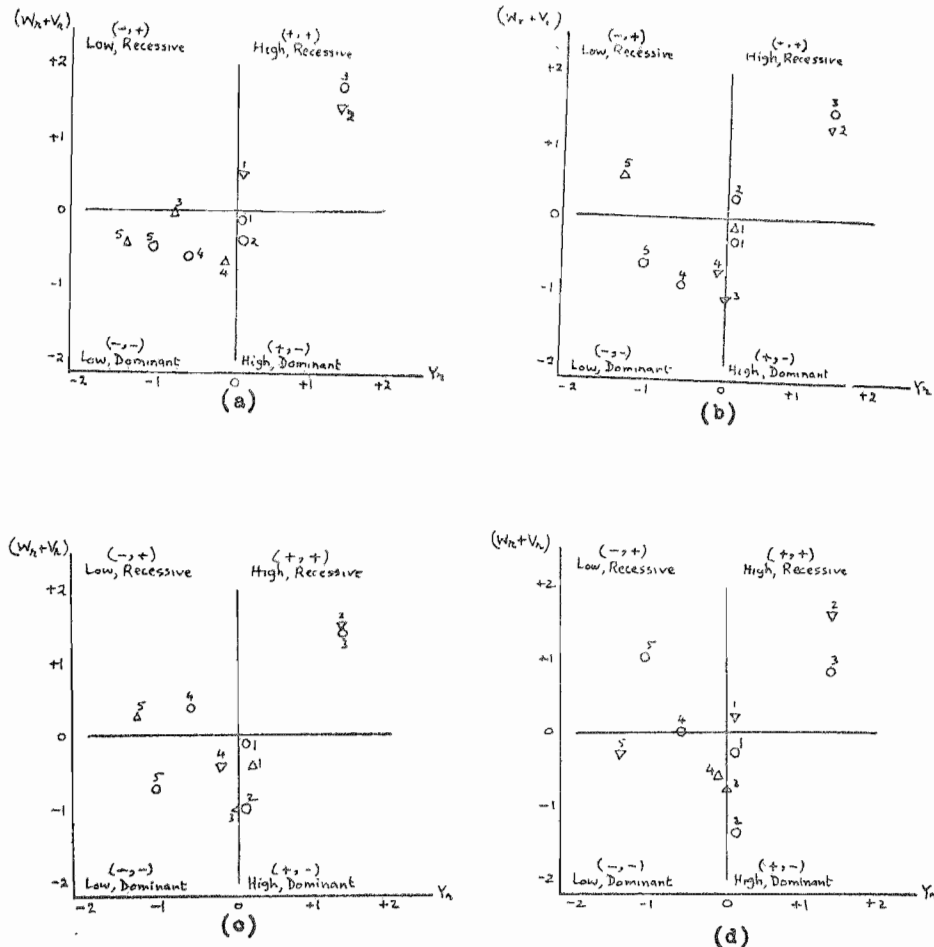


Fig. 6. Standardized deviation graph of parental order of dominance ($W_r + V_r$) and parental measurements (Y_r) for heading-span from (a) F1 (b) F2 (c) backcross and selfed backcross diallel sets.

- Y_r , $W_r + V_r$ intercepts at Ellerslie.
 . . △ Y_r , $W_r + V_r$ intercepts at Parkland.

ignored. The general quantitative genetic interpretation with respect to inheritance pattern of onset-of-heading (Figures 5a, 6a), final heading (Figures 5b, 6b) and heading-span (Figures 5c, 6c) may accordingly be followed keeping in view the estimates of the genetic parameters, position of the parents on the regression line with respect to limiting parabola and the occupancy of the quadrants of standardized deviation graphs.

For plant height, all the components of genetic variation except D were non-significant at both locations. The W_r - V_r heterogeneity at Parkland (Table 3) has been ignored, since the regression of W_r upon V_r is not significantly different from unity (Fig. 5d) and the W_r , V_r array-intercepts do not show distortion. Because of the non-significance of components of variation, interpretation of proportional estimates and genetic parameters will be meaningless (Hayman, 1954b; Mahter & Jinks 1971). However, the mean degree of dominance may be given as $(H_1/D)^{1/2} < 1$ indicating partial dominance (see also fig. 5d). The correlation between the parental order of dominance and parental measurements is 0.32 at Ellerslie and -0.607 at Parkland. The positive correlation at Ellerslie indicates that genes for shortness are mostly dominant; the negative correlation at Parkland that genes for tallness are mostly dominant (see also Fig. 6d).

Selfed backcross diallel

The ratio $(H_1/D)^{1/2} < 1$ for onset-of-heading at both locations shows that the dominance is partial (see also Fig. 7a). The estimate of $(H_2/4H_1) = 0.21$ at Ellerslie and 0.24 at Parkland implies some asymmetry and equal proportions of positive and negative allele effects at Ellerslie and Parkland, respectively. The proportion of dominants to recessives in the parents is > 1 at both locations indicating thus a preponderance of dominant genes. $(h^2/H_2) > 1$ at both locations suggests that at least two groups of genes exhibiting dominance contribute to the control of onset-of-heading. The coefficients of correlation between parental order of dominance and parental measurements (0.916 at Ellerslie and 0.687 at Parkland) indicate that earliness is dominant over lateness. Fig. 7a shows that Marquis at Ellerslie and Chinook at Parkland are the most recessive parents while Khush-hal at both locations is the most dominant one. Fig. 8a places Marquis and Chinook in the (+, +) quadrant indicating that the lateness of these parents is associated with recessive genes. Khush-hal, Ciano and Inia occupy the (-, -) quadrant at both locations, suggesting that these parents are early maturing dominants.

The interpretations from Tables 5 and 6 for final heading (Figures 7b, 8b) and for heading-span (Figures 7c, 8c) may be made in the similar fashion. The changes in the relative position of the parents with respect to their order of dominance at the two locations could be attributed to environmental effects of interlocation type.

In case of plant height, the ratio of $(H_1/D)^{1/2} < 1$ at both locations indicates that the character is inherited as a partially dominant trait. Since all other components of variation except D and E are non-significant at both locations (Table 5), the interpretation of the proportional values of genetic parameters is meaningless. Fig. 7d classifies Ciano at Ellerslie and Khush-hal at Parkland as the most recessive parents and Chinook as the most dominant at both locations. Fig. 8d indicates that the most dominant parent (Chinook) at both locations, contributes to tallness, while the most recessives (Ciano and Khush-hal) contribute to shortness; i.e., the order

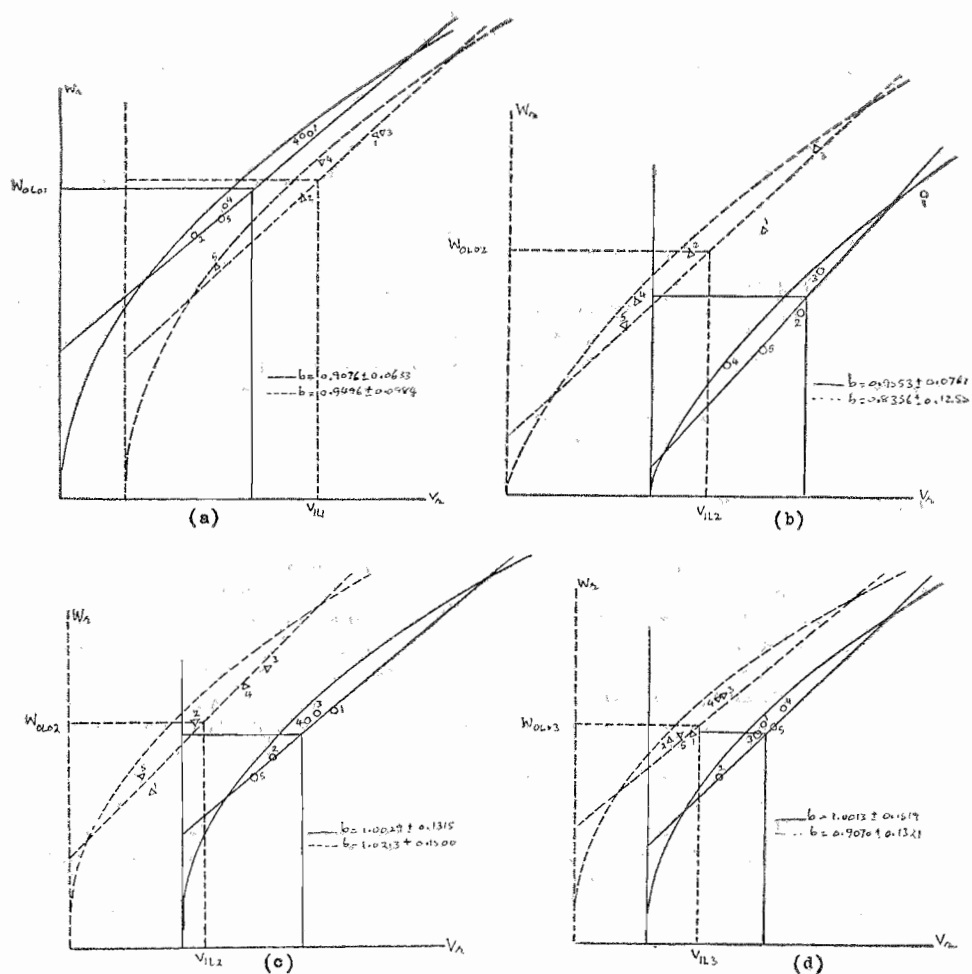


Fig. 7. W_r, V_r graph for plant height from (a) F1 (b) F2 (c) backcross and (d) selfed backcross diallel sets.

—○ = W_r, V_r intercepts at Ellerslie.
△ = W_r, V_r intercepts at Parkland.

of dominance of the parents is negatively correlated with their measurements. The most recessive parent at Parkland (Fig. 8d) possesses an excess of dominant genes (—,— quadrant) at Ellerslie. Inia with an excess of recessive genes at Ellerslie (—,+ quadrant) appears to have a preponderance of dominants at Parkland (—,— quadrant). Marquis, recessive at Ellerslie becomes dominant at Parkland. The ranking order of Ciano and Chinook remained unchanged.

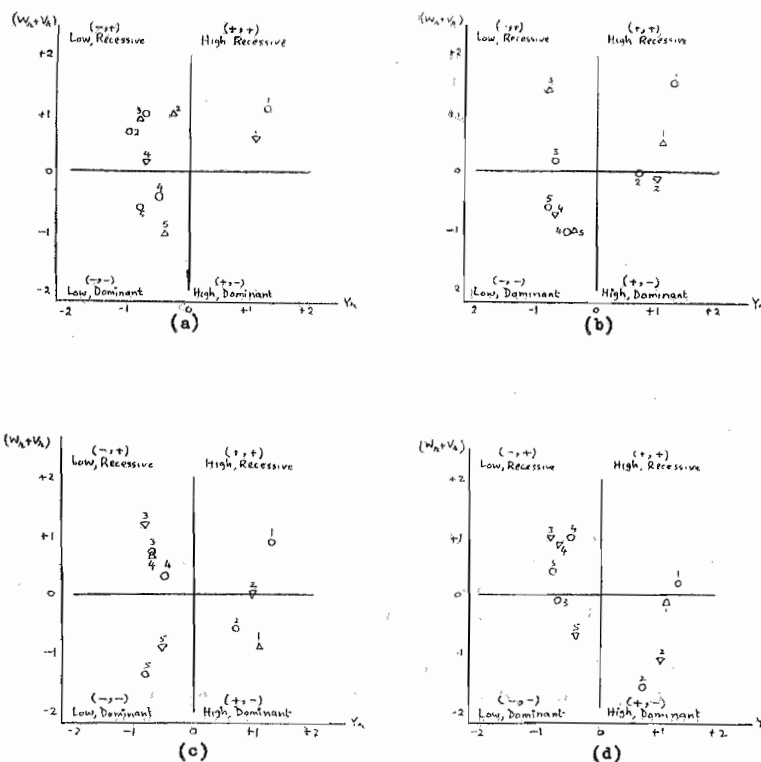


Fig. 8. Standardized deviation graph of parental order of dominance ($W_r + V_r$) and parental measurements (Y_r) for plant height from (a) F1 (b) F2 (c) backcross and (d) selfed backcross diallel sets.

—○ = Y_r , $W_r + V_r$ intercepts at Ellerslie.
Δ = Y_r , $W_r + V_r$ intercepts at Parkland.

Genotype-environment interaction

This section of the experimental results deals with the comparison of the estimates of genetic components of variation obtained from the analysis of four diallel sets over two locations. The genetic components of variation, i.e., 'D', 'F' and 'H1' were considered themselves as variables and factorially analysed over generations and locations in order to study their consistency over the two environments. Before performing the 'factorial ANOVA', the values of genetic components for each character were standardized at each location. Thus each D value was divided by the VOL0 for the same character, generation and location. Similarly F's were divided by their corresponding mean covariances (WOL01 in F1 diallel, WOL02 in F2 and backcross diallels and WOL03 in the selfed backcross diallel) and H1's by their respective mean variances (VIL1 in F1 diallel, VIL2 in F2 and backcross diallels and VIL3 in the selfed backcross diallel). Thus, for example, the F for plant height

at Ellerslie in the selfed backcross diallel set of Table 5 was divided by the corresponding WOL03 from Table 4 (at Ellerslie) as follows: $-4.1831 \div 243.1029 = -0.0172$. The aim of such standardization preceding 'factorial ANOVA' was to normalize the scale differences for different characters. For example, heading data were taken in number of days and plant height was measured in centimeters. The use of these different multipliers in normalizing the scale-effects not only preserved the order of magnitude of respective parameters but also homogenized the inter-location scale differences into a common proportional variable.

The process of standardizing the scale is analogous to Allard's technique, where prior to factorial ANOVA, each variance and covariance was divided by VOL0 of the respective block for that character (Allard, 1956; Crumpacker & Allard, 1962). In the present study the additive (D), dominance (H1) and additive x dominance (F) components are subsequently considered separately and analysed independently for their stability over generations and locations. The reciprocals of the variances of the parents, of the array mean variances and of the array mean covariances were therefore used as weights in standardizing the values of D's, H1's and F's respectively.

The factorial ANOVA of weighted values of D's, H's and F's is given in Table 7. The results show that additive effects of the genes (component D) are the same for two locations. Dominance gene effects (component H1) and additive x dominance effects (component F) differ significantly at the two locations. On the whole, generations do not seem to affect the values of genetic components of variation. Significant mean squares for location with respect to H1 and F raises the question of heterogeneity of location effects on the parameters in different generations. To answer this, the unweighted values of D's, H1's and F's at Parkland were respectively regressed for each generation upon those of Ellerslie, and the sum of squares of deviations were partitioned into variation due to regression and remainder (error). It may be pointed out that unweighted values of genetic components of variation were

TABLE 7. Factorial analysis of variance of genetic components of variation over generations and locations. The sum of squares are respectively partitioned for D, H1 and F.

Component	Source of variation	D.F.	Sum of squares	Mean squares	F ratio
D	Locations	1	0.14331	0.14331	1.10820
	Generations	3	0.03176	0.01055	0.08164
	Locations x Generations	3	0.07301	0.02433	0.18820
	Error	72	9.31106	0.12932	
H1	Locations	1	10.38381	10.38381	7.77135***
	Generations	3	2.16681	0.72227	0.54056
	Locations x Generations	3	1.10066	0.36688	0.27548
	Error	72	96.20391	1.33616	
F	Locations	1	15.78510	15.78510	7.34709***
	Generations	3	7.28304	2.42768	1.13021
	Locations x Generations	3	0.43955	0.14651	0.06821
	Error	72	154.65565	2.14799	

***Significant at 0.1% level of probability.

TABLE 8. Analysis of variance of regression of genetic components of variation of Parkland upon those of Ellerslie for each generation.

Component	Generation	Source of variation	D.F.	Mean squares	F. value	
Additive component (D)	F1 diallel	Due to regression	1	228 57.5229	45 8.6540***	r = 0.9990
		Due to error	8	49.9399		b = 1.0658
	F2 diallel	Due to regression	1	227792.7663	3549.9323***	r = 0.9998
		Due to error	8	64.1682		b = 1.0603
	Backcross diallel	Due to regression	1	228207.7135	4597.8009***	r = 0.9990
		Due to error	8	49.6341		b = 1.0630
	Selfed back-cross diallel	Due to regression	1	229349.4236	4251.7073***	r = 0.9990
		Due to error	8	53.9429		b = 1.0642
Dominance component (H1)	F1 diallel	Due to regression	1	1532.9815	81.7304***	r = 0.9534
		Due to error	8	18.7562		b = 0.8233
	F2 diallel	Due to regression	1	2001.8299	391.1351***	r = 0.9898
		Due to error	8	5.1180		b = 1.3637
	Backcross diallel	Due to regression	1	2619.8806	74.1992***	r = 0.9500
		Due to error	8	35.3087		b = 2.4385
	Selfed back-cross diallel	Due to regression	1	412.1566	39.0566***	r = 0.9109
		Due to error	8	10.5528		b = 1.0823
Additive x dominance component (F)	F1 diallel	Due to regression	1	812.9743	80.8326***	r = 0.9538
		Due to error	8	10.0575		b = 0.4664
	F2 diallel	Due to regression	1	1190.1414	31.2178***	r = -0.8921
		Due to error	8	38.1237		b = -1.4409
	Backcross diallel	Due to regression	1	40.3149	2.8143	r = 0.5100
		Due to error	8	14.3248		b = 0.3220
	Selfed back-cross	Due to regression	1	8.6977	0.8605	r = 0.3098
		Due to error	8	10.1077		b = 0.3603

***Significant at 0.01 level.

used in regression analysis since the effect of change in the degree of expression of one character relative to the other can be studied regardless of the unit of scale used. Extremely high variance ratios (Table 8) for the parameters D and H1, and close agreement between the coefficients of correlation and regression, both in sign and magnitude, indicate stability of these parameters over the two locations. The case of parameter F is rather confusing. The diallels based on backcross and selfed backcross generations show a lack of correspondence between F values at two locations (variance ratio for regression non-significant). This may be ascribed to a change of relationship between additive and dominance gene effects ($F = \sum dh$) caused by altered environmental conditions. A more drastic relational change is between F1 and F2 generations of the diallel sets ($r=0.95$, $b=0.47$; and $r = -0.89$, $b = -1.44$, respectively). It is rather difficult to think of a logical explanation for this reversed relationship.

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