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Genetic Analysis of Plant Height in Wheat

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Summary. Genetic studies of plant height were made of 8 wheats and the 28 crosses between them using the diallel method of analysis. The inheritance of plant height in a glasshouse-grown F_1 diallel set in which vernalization and photoperiodic responses had been removed, indicated close to complete dominance in its expression. A similar F_1 set of crosses in the field environment indicated non-allelic interaction in its expression, attributable mainly to the cultivar Chile IB generally in its crosses with the other 7 wheats. Its removal gave close to complete average dominance in the inheritance of plant height.

In the F_2 generation in the field its inheritance was again subject to non-allelic interaction, attributed mainly to Chile IB which, on removal, gave a situation of average partial dominance in height expression.

Standardized deviations of Yr and $(Wr + Vr)$ for plant height for the diallels indicated a resonably close association of tallness with dominance and shortness with recessiveness.

Frequency distributions of plant height in the F_1 and F_2 of two crosses from the diallel confirmed certain findings of the diallel analysis.

At least two groups of dominant genes were found to influence plant height expression in the crosses of the diallel; this number must be regarded as a minimal estimate of the number of genes influencing plant height in wheat.

Introduction

A most significant achievement of present day wheat breeding has been the successful incorporation of dwarf habit of growth in commercial wheat cultivars. However, the subject of the inheritance of plant height in wheat still remains rather obscure and so too details of breeding and selection techniques for height alteration in wheat. The genetic control of height in wheat has been the subject of numerous studies. Early studies indicated it to be of a complex nature (Freeman, 1919; Clark, 1924; Torrie, 1936) in which it was also observed that tallness was pratically dominant.

A number of cytogenetic studies of wheat have been concerned with plant height. Observations on the nullisomics of Chinese Spring indicated that each of the chromosomes of homeologous groups 1, 2, 3 and 4, and chromosome 6A, had a strong influence on the expression of this character (Sears, 1954). Chromosome substitution lines of the individual chromosomes of the cultivars, Hope, Thatcher and Timstein in Chinese Spring enabled location to be made of three, six and one chromosome respectively in these cultivars which influenced plant height of Chinese Spring (Kuspira and Unrau, 1957). A genetic analysis of plant height in wheat using the Chinese Spring/Hope set of intervarietal substitution lines, in the absence of vernalization and photoperiodic responses, revealed comparatively simple genetic control (Halloran, 1974).

Monosomic analyses of the wheat variety Norin-10 × Brevor-14 crossed with the monosomics of Chinese Spring revealed 11 chromosomes of the former wheat which influenced plant height expression (Allan and Vogel, 1963). However, this analysis failed to reveal the exact location of two major semi-dwarfing genes thought to have been present in Norin-10 × Brevor-14.

Material and Methods

This study of the genetic of plant height was based on a diallel set of 28 crosses, representing all the possible combinations, excluding reciprocals, of the 8 wheats Chile IB, Falcon, Gamenya, Mexico 120, Olympic A103, Pinnacle, Robin and Wren.

The F_1 of the crosses and parental lines were grown as a randomized block trial of 6 replicates over summer. The seed was vernalized at 4 °C for a period of 6 weeks prior to sowing. The trial was grown as single plants in 15 cm diameter plastic flower-pots, and for its duration an 18-hour photoperiod was given. This was provided by means of overhead incandescent lights in an outdoor area, operated through a time-clock to extend natural daylength to this duration.

Prior vernalization and the 18-hour photoperiod would, it was hoped, minimize differential vernalization and photoperiodic responses of the lines to the natural environment. Plant height expression in wheat is known to be influenced by differences in the relative duration of the phases of development. It was hoped that closer to genetic differences might be reflected by studies of plant height under these conditions.

The F_1 and F_2 generations of the diallel were also grown as field trials in the normal growing season. These trials, which were also for the purpose of studying the genetics of yield and its components, were sown in separate, but adjacent, randomized block layouts, each of six replicates. The F_1 trial consisted of the 8 parents and their 28 crosses grown as single hand-sown rows. The rows were 36 cm apart and the seed of each row was placed at exactly a 5 cm. spacing. At each end of a row was sown a 46 cm. length of Chile IB which served to minimize the outside-row effect on yield expression.

The F_2 trial consisted of rows which were 4.5 m. long and 36 cm. apart with the seed in the row hand-sown at exactly a 5 cm. spacing.

Both trials were harvested by removing all plants from the soil, care being taken not to damage them on removal. Plant height was assessed as the distance from the base of the stem to the tip of the uppermost spikelet of the head, not including the length of awn.

Plant height assessment of the two F_1 trials was made by scoring the mean height of three of the main tillers per plant of every plant in the respective trials. In the F_2, a random selection of 20 plants per replicate was made of each line, and plant height scored similarly as with the F_1 trials.

Of the two crosses (Mexico 120 × Falcon) and (Mexico 120 × Robin) and each of the parents, random selections of 20 and 100 plants, respectively, were taken from the bulks of the replicates of the F_1 and F_2 field trials. They were scored, as above, for plant height.

Results

Plant height data of the two F_1 trials and the F_2 trial are shown in Tables 1 and 2 respectively. Analyses of variance for plant height were conducted for the three trials and the presence of significant differences for height in each trial enabled the diallel analysis to be performed upon them.

Frequency distributions were drawn of the expression of plant height in the F_1 and F_2, and the respective parents, of the two crosses (Mexico 120 × Falcon) and (Mexico 120 × Robin). Mean values and variance estimates for plant height were also calculated (Figs. 1–4).

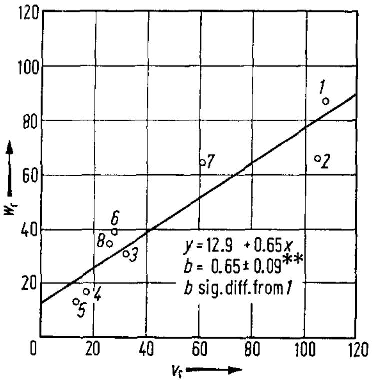
Correlation and regression analyses were carried out on height expression of the 8 parents of the diallel

Table 1. *Plant Height of the 8 Parents and their 28 Crosses in the F_1 in lasshouse and Field Sowings*

Parent or Cross No.	Parent or Cross	Plant F_1 G'House cm	Height F_1 Field cm	Cross No.	Cross	Plant F_1 G'House cm	Height F_1 Field cm
1	Chile lB	42.70	78.28	19	Gamenya × Mexico 120	43.65	84.00
2	Mexico 120	34.02	65.25	20	Wren × Mexico 120	42.00	77.40
3	Olympic A103	53.45	91.85	21	Falcon × Mexico 120	44.89	87.00
4	Pinnacle	57.94	83.33	22	Pinnacle × Olympic A103	60.22	89.58
5	Robin	42.77	82.43	23	Robin × Olympic A103	49.18	85.45
6	Gamenya	52.23	96.27	24	Gamenya × Olympic A103	54.42	89.75
7	Wren	46.54	86.87	25	Wren × Olympic A103	54.93	100.13
8	Falcon	49.87	97.82	26	Falcon × Olympic A103	55.29	99.72
9	Mexico 120 × Chile lB	39.19	64.42	27	Robin × Pinnacle	52.48	91.87
10	Olympic A103 × Chile lB	54.15	88.00	28	Gamenya × Pinnacle	56.54	93.23
11	Pinnacle × Chile lB	56.26	85.30	29	Wren × Pinnacle	60.13	91.08
12	Robin × Chile lB	52.13	90.97	30	Falcon × Pinnacle	60.19	95.83
13	Gamenya × Chile lB	56.68	91.95	31	Gamenya × Robin	51.59	91.57
14	Wren × Chile lB	51.35	92.65	32	Wren × Robin	50.20	90.63
15	Falcon × Chile lB	52.13	98.57	33	Falcon × Robin	45.44	90.10
16	Olympic A103 × Mexico 120	49.40	86.32	34	Wren × Gamenya	52.03	98.95
17	Pinnacle × Mexico 120	47.65	91.75	35	Falcon × Gamenya	56.12	100.48
18	Robin × Mexico 120	40.92	84.72	36	Falcon × Wren	53.02	100.53

Table 2. *Plant Height of the 8 Parents and their 28 Crosses in the F_2 Field Sowing*

Parent or Cross No.	Parent or Cross	Plant Height F_2 cm.	Cross No.	Cross	Plant Height F_2 cm.
1	Chile lB	78.64	19	Gamenya × Mexico 120	80.96
2	Mexico 120	62.12	20	Wren × Mexico 120	76.80
3	Olympic A103	90.19	21	Falcon × Mexico 120	86.51
4	Pinnacle	85.14	22	Pinnacle × Olympic A103	91.51
5	Robin	78.92	23	Robin × Olympic A103	88.89
6	Gamenya	92.37	24	Gamenya × Olympic A103	94.65
7	Wren	86.22	25	Wren × Olympic A103	91.74
8	Falcon	98.75	26	Falcon × Olympic A103	95.64
9	Mexico 120 × Chile lB	73.77	27	Robin × Pinnacle	86.74
10	Olympic A103 × Chile lB	87.56	28	Gamenya × Pinnacle	95.42
11	Pinnacle × Chile lB	88.12	29	Wren × Pinnacle	86.41
12	Robin × Chile lB	83.78	30	Falcon × Pinnacle	93.66
13	Gamenya × Chile lB	87.43	31	Gamenya × Robin	87.52
14	Wren × Chile lB	87.17	32	Wren × Robin	89.03
15	Falcon × Chile lB	97.06	33	Falcon × Robin	90.09
16	Olympic A103 × Mexico 120	83.06	34	Wren × Gamenya	92.83
17	Pinnacle × Mexico 120	80.51	35	Falcon × Gamenya	94.61
18	Robin × Mexico 120	77.57	36	Falcon × Wren	95.34



**Significant at the 1 per cent level

Fig. 1. Frequency distribution of plant height in the wheats Mexico 120 and Falcon and the F_1 of their cross

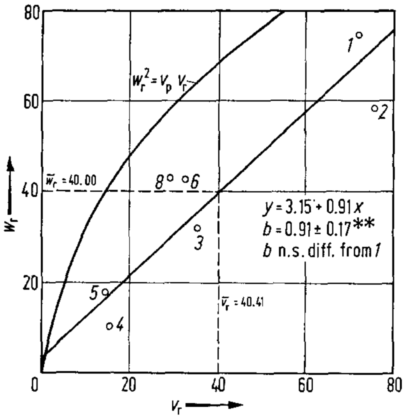


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Fig. 2. Frequency distribution of plant height in the wheats Mexico 120 and Falcon and the F_2 of their cross

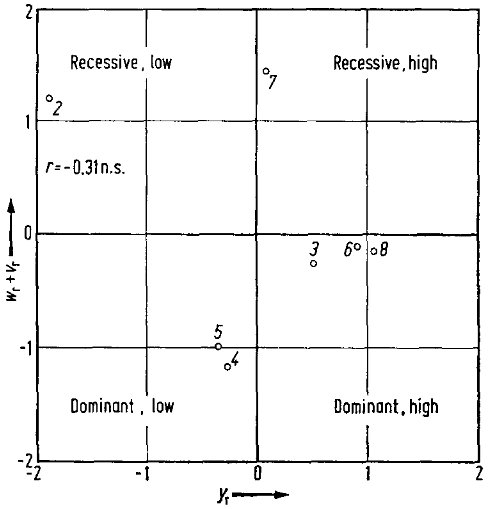
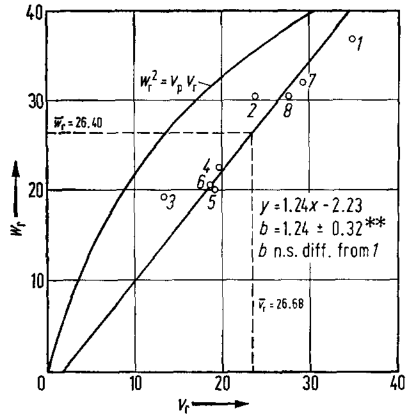


Fig. 3. Frequency distribution of plant height in the wheats Mexico 120 and K. F. Heron and the F_1 of their cross



**Significant at the 1 per cent level

Fig. 4. Frequency distribution of plant height in the wheats Mexico 120 and K. F. Heron and the F_2 of their cross

in both the glasshouse and field environments. Statistical analysis of the data was done separately for each of the three diallel trials — F_1 (glasshouse) and F_1 and F_2 (field), using the techniques of Hayman (1954a, 1954b) to estimate the genetic parameters D, H_1, H_2 and F, as defined by Jinks (1954), and outlined by Mather (1949). The components of variation for plant height in the F_1 and F_2 trials are shown in Tables 3 and 4 respectively.

F_1 *Plant Height — Glasshouse*

The Wr/Vr relationship for plant height of the diallel grown in the glasshouse is shown in Fig. 5. A regression of slope $b = 1.24 \pm 0.32$ was obtained which was significantly different from 0 and not significantly different from 1. The regression line cuts the Vr axis to the right of the origin which indicates the presence of overdominance amongst the crosses for plant height expression. The array points lie close to the regression line which indicates a low degree of interaction amongst the crosses for height expression. Parents corresponding to arrays 2, 8, 7, and 1, in increasing order, possess an excess of recessive over dominant genes for height expression. Parents corresponding to arrays 4, 5, 6 and 3, in increasing order, possess an excess of dominant over recessive genes for this character. Parents of the recessive arrays are generally of low plant height while those of the dominant arrays are generally of greater plant height. However, the presence of array 5, whose parent, Robin, was not tall, in the dominant group, and array 8 (Falcon), which was moderately tall, in the recessive group indicates that in some instances plant height may be under different genetic control from that generally indicated in this study. That is, increased plant height may show recessiveness and reduced plant height dominance.

The relationship of tallness with dominant genes was further studied in the correlation of the standardized deviations of the two values Yr and $(Wr + Vr)$. Standardized deviations were calculated from plant height data using the formula $(X_1 - \bar{X})/S$ where X_1 is the value of the individual parent, $\bar{X}$ the

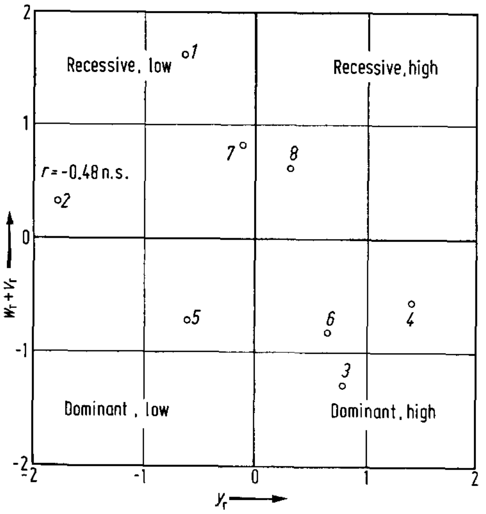
Table 3. *The Components of Variation of Plant Height in the Glasshouse and Field-Sown F_1 Diallel Analyses*

Components (estimated)	F_1 (Glasshouse) all arrays	F_1 (Field) all arrays	F_1 (Field) array 1 excluded
D	57.20**	112.28**	121.69**
H_1	43.88**	129.64**	123.32**
H_2	24.40**	72.04**	84.92**
F	7.96**	72.48**	83.36**
h_1	50.69**	82.45**	78.50**
$(H_1/D)^{1/2}$	0.88	1.07	1.01
$H_2/4H_1$	0.14	0.14	0.17
$(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$	1.28	1.86	2.03
h_1/H_2	2.08	1.14	0.92
H_2/H_1	0.56	0.56	0.69

** Significant at the 1 per cent level.

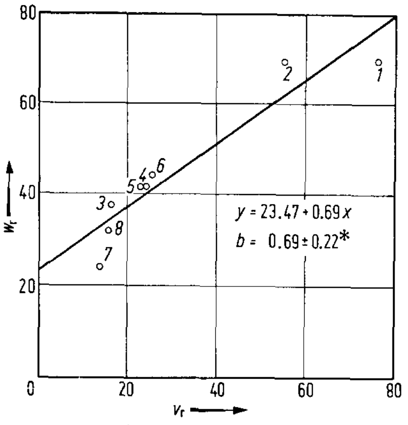
Table 4. *Order of Dominance of the Arrays of the Three Diallels Determined by* ($Wr + Vr$)*, in Relation to Order of Plant Height of the 8 Parents*

F_1 (Glasshouse)		F_1 (Field)		F_2 (Field)	
Order of Dominance ($Wr + Vr$) (Highest to Lowest)	Order of Plant Height (Parental) (Lowest to Highest)	Order of Dominance ($Wr + Vr$) (Highest to Lowest)	Order of Plant Height (Parental) (Lowest to Highest)	Order of Dominance ($Wr + Vr$) (Highest to Lowest)	Order of Plant Height (Parental) (Lowest to Highest)
1	2	1	2	1	2
7	1	2	1	2	1
8	5	7	5	6	5
2	7	3	4	4	4
4	8	6	7	5	7
5	6	8	3	3	6
6	3	5	6	8	3
3	4	4	8	7	8



◀ Fig. 5. Wr/Vr regression of plant height in the F_1 (glasshouse) (all arrays). Array Numbers — 1. Chile 1B, 2. Mexico 120, 3. Olympic A103, 4. Pinnacle, 5. Robin, 6. Gamenya, 7. Wren, 8. Falcon

Fig. 6. Correlation of the standardized deviations, Yr and ($Wr + Vr$) for plant height in the F_1 (glasshouse) (all arrays) ▶



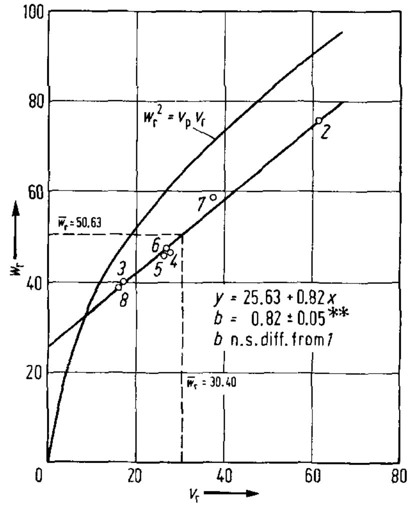
*Significant at the 1 per cent level

mean of the parents and S the standard deviation. Positive values of ($Wr + Vr$) denote recessive genes and minus dominant. Positive values of Yr denote high expression of height and negative values, low expression. The Yr, ($Wr + Vr$) relationship was, however, not close $r = -0.48$ and was not significant (Fig. 6). This result indicates only a tendency for tallness to be associated with dominant genes and short stature with recessiveness. Calculations were also made of ($Wr + Vr$) for each array of each diallel and the order of its value compared with the order of plant height of the respective parents (Table 4).

In the F_1 glasshouse diallel analysis the average degree of dominance over all loci, $(H_1/D)^{1/2}$, was near to unity-0.88, indicating close to complete dominance for height expression. The proportion of genes with positive and negative effects, $H_1/4H_1$, has a value of 0.14 which indicates asymmetry at loci showing dominance. The proportion of dominant and recessive genes in parents, given by the ratio, $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$, has a value of 1.28 indicating that dominant genes are in excess. The fraction, h/H_2 indicates the number of groups of genes in parents showing dominance for plant height. The present value, 2.08, suggests that there are at least two groups of dominant genes involved in influencing height expression.

F_1 Plant Height — Field

The Wr/Vr regression for the F_1 of the diallel sown in the field, for all the arrays is shown in Fig. 7. The slope of the regression line $b = +0.65 \pm 0.09$, was significantly different from 0 but was also significantly ($p < .01$) different from a slope of 1. This behaviour indicates non-allelic interaction amongst the crosses of the diallel for plant height expression. Removal of array 1, with the highest variance, gave a Wr/Vr regression of slope $b = +0.91 \pm 0.17$ which was significantly different from 0 and not significantly different from a slope of 1 (Fig. 8). Arrays 2 and 7, in increasing order, possess an excess of recessive over dominant genes for height determination, while arrays 6 and 8 possess recessive and dominant genes in about equal proportions. Arrays 3, 5 and 4, in increasing order, possess an excess of dominant genes for height expression. The regression line cuts the Wr axis a little above the origin indicating almost complete dominance averaged over the arrays in the inheritance of height in the F_1. There appears to be no clear association of tallness with dominance or recessiveness in a comparison of parental values with the distribution of the corresponding arrays on the regression line. The relationship of Yr with $(Wr + Vr)$ of $r = -0.31$ which was not significant, indicates only a slight tendency for tallness to be associated with dominance and short stature with recessiveness (Fig. 9).



**Significant at the 1 per cent level

Fig. 7. Wr/Vr regression of plant height in the F_1 (field) (all arrays)

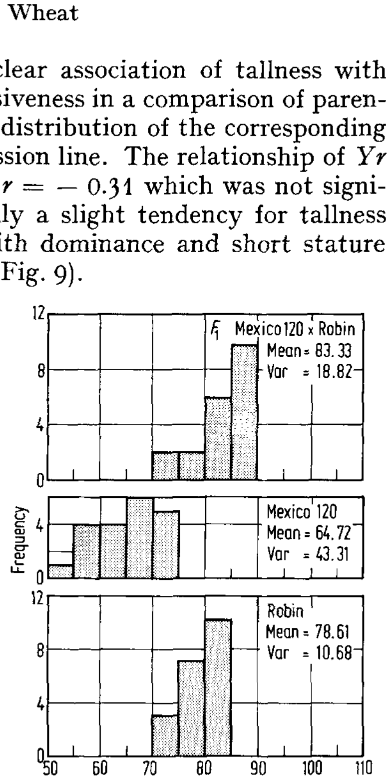


Fig. 8. Wr/Vr regression of plant height in the F_1 (field) (array 1 omitted)

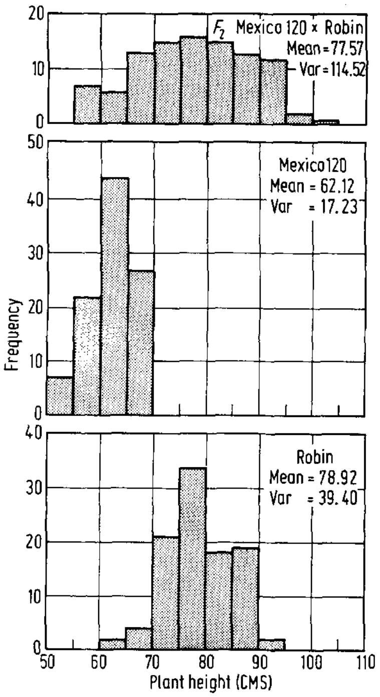


Fig. 9. Correlation of the standardized deviations, Yr and $(Wr + Vr)$ for plant height in the F_1 (field) (array 1 omittted)

The components of genetic variation for plant height in the F_1 field-sown diallel are shown in Table 3. The components have been calculated for both the complete set of arrays and with array 1 excluded. The value $(H_1/D)^{1/2}$ for the complete set was 1.07 and for the set in the absence of array 1 was 1.01 indicating that in both cases there was close to complete dominance of height expression. The very slight decrease in this value in the absence of array 1, which was contributing towards the non-allelic interaction of the complete set of crosses, may have been due to the non-allelic interaction of the complete set. The fraction, $H_2/4H_1$, which estimates the proportion of genes with positive and negative effects of parents is similar in the F_1 (complete) and F_1 (minus array 1) analyses with values of 0.14 and 0.17 respectively. These values suggest asymmetry at loci showing dominance. The ratio, $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$ for the complete analyses was 1.86, and that for the analysis lacking array 1 was 2.03, which measures the proportion of dominant to recessive genes in parents, indicates that dominant genes are in excess. The ratio, h_1/H_2, of 1.14 for the complete set and 0.92 for the set lacking array 1, indicates that there was only 1, or possibly 2, groups of genes in parents showing dominance for plant height. Usually, however, this ratio underestimates the number of dominant genes, and it provides no information about groups exhibiting little or no dominance.

F_2 *Plant Height — Field*

The Wr/Vr regression relationship for the F_2 of the complete diallel is shown in Fig. 10. The slope of the regression line $b = +0.69 \pm 0.22$ was significantly different from 0 and also significantly different ($p < .01$) from slope of 1. The slope was not significantly different from 1, at the 5 per cent level, but it was decided to repeat the diallel analysis in the absence of array 1, the array with the highest variance. The failure of the regression to approach a slope of 1 can be considered to be due to non-allelic interaction in crosses of the diallel. With the removal of array 1 the Wr/Vr regression of slope, $b = +0.82 \pm 0.05$, was significantly different from 0 and not significantly different from a slope of 1 (Fig. 11). The regression line cuts the Wr axis well above the origin indicating partial dominance in the inheritance of plant height averaged over the crosses of the diallel. Arrays, 3 and 8 possess an excess of dominant over recessive genes for height expression while arrays 5, 6 and 4, near the Wr, Vr point, possess recessive and dominant genes in about equal proportions. Arrays 7 and 2, in increasing order, possess an excess of recessive over dominant genes for plant height expression. The order of distribution of array points along the regression line in relation to the parental values for plant height suggests an association of dominance with high expression and recessiveness with low expression. The relationship of the standardized deviations Yr and $(Wr + Vr)$ of $r = -0.91$ which is significant ($p < .05$) confirms this observation.

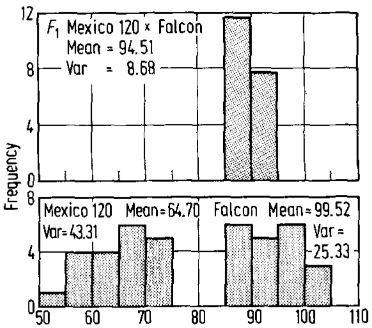


Fig. 10. Wr/Vr regression for plant height in the F_2 (field) (all arrays)

The average degree of dominance for plant height in the F_2 for the complete set of arrays, given by the ratio, $(H_1/D)^{1/2}$, was 0.74 (Table 5).

In the absence of interacting array 1 the value of this ratio was 0.65. The slight reduction in this value

Table 5. *The Components of Variation of Plant Height in the Field-Sown F_2 of the Diallel*

Components (estimated)	F_2 all arrays	F_2 array 1 excluded
D	123.63**	138.68**
H_1	68.12**	57.76**
H_2	38.76**	19.64**
F_2	57.00**	75.44**
h_1	48.44**	41.22**
$(H_1/D)^{1/2}$	0.74	0.65
$H_2/4H_1$	0.14	0.09
$(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$	1.90	2.46
h_1^2/H_2	1.25	2.10
H_2/H_1	0.57	0.34

** Significant at the 1 per cent level.

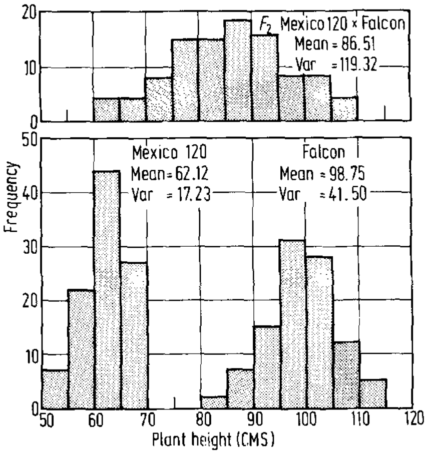


Fig. 11. Wr/Vr regression for plant height in the F_2 (field) (array 1 omitted)

may have been due to the removal of the interaction caused by array 1. These values for average dominance would mean F_1 values of 1.48 and 1.30 respectively because the H_1 value is reduced by $^1/_4$ in each succeeding generation after the F_1.

The $H_2/4H_1$ ratio, which indicates the proportion of positive to negative alleles at loci exhibiting dominance, was 0.14 for the complete diallel and 0.09 for the analysis lacking array 1. These values indicate an asymmetry in positive and negative genes at loci exhibiting dominance. An excess of dominant genes for plant height in the parents of the diallel is indicated by the ratio $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$ which had the value of 1.90 for the complete diallel and 2.46 for the analysis lacking array 1. Contrary to the values for $H_2/4H_1$, this value is affected by complementary gene interaction. Thus, the difference in this value between the two F_2 diallels may indicate an influence of complementary gene interaction on this ratio caused by the Chile 1B array.

The ratio h_1^2/H_2 which has a value of 1.25 for the complete diallel and 2.10 for the analysis lacking array 1 indicates that at least two genes controlling plant height exhibit some degree of dominance.

Discussion

The genetics of plant height in wheat have as yet not been resolved. One of the possible reasons for this situation is that plant height, as with many other 'agronomic' characters of wheat, as for instance yield and its components, is strongly influenced in its expression by differences in developmental behaviour of lines under study. In consequence of this, many studies of the genetics of plant height may not afford precise information of the genetic basis of this character, it being somewhat confounded by genetic differences in developmental responses.

The diallel analysis of plant height in the F_1 generation, both in the glasshouse and field environments, indicated generally additive genetic variance in its inheritance and close to complete dominance of tallness. In the field environment the general presence of non-allelic interaction between Chile 1B and the other wheats in its crosses was detected. This behaviour is due most likely to complementary gene action for height expression between parents of dissimilar genotypes.

Frequency distributions of plant height in the F_1 and parents of the crosses (Mexico 120 × Robin) and (Mexico 120 × Falcon) confirmed the presence of dominance of tallness. The F_1 distribution of (Mexico 120 × Robin) indicated the possible presence of a significant amount of overdominance for height expression in this particular cross.

The glasshouse-grown F_1 diallel analysis was hoped to provide a situation wherein differential developmental responses influencing plant height expression would be made minimal. The growing of the lines in the vernalized condition and under 18-hour photoperiod was to eliminate the influence of these two responses on development and hence on height expression. The correlation between plant height of the 8 parents of the diallel in these two environments was reasonably high $r = +0.74$ ($p < .05$). The mean height of the 8 parents in the glasshouse environment was 47.44 cm and that of the field set, 85.26 cm, indicating the marked influence environment can exert on the phenotypic expression of height in wheat. However, the correlation indicates the presence, most likely, of a reasonably strong genetic component in the control of plant height. That is, although developmental response genes do exert a secondary influence on height expression the heritable component would most likely generally determine, to a great extent, the relative order of height in a set of different genotypes.

In the F_2 generation in the field plant height of the complete diallel set exhibited non-allelic interaction in its expression. Removal again of array 1 gave a situation for the remaining crosses of partial dominance for height expression. Chile 1B therefore appears to possess a gene control of plant height which is peculiar to that of the other wheats. The interaction of Chile 1B appears to be in the direction of increased height and thus it may be expected that transgressiveness for increased plant height would be expressed in some of its crosses.

The estimates of dominance in the F_2 generation with and without array 1 suggest the presence of overdominance with respective values for $(H/D)^{1/2}$ of 0.74 and 0.65. These values indicate and F_1 value of 1.48 and 1.30 respectively. This inflation of the estimated F_1 value compared with the actual values of 1.07 and 1.01 respectively, is most likely due to the influence of non-allelic gene interaction.

The order of dominance of the parents, determined by $(Wr + Vr)$, in relation to the order of their respective heights, suggests an association of dominant genes with tallness and recessive genes with short stature. However, in the F_2 diallel, in the absence of array 1, the correlation between Yr and $(Wr + Vr)$ is -0.80 corroborating the results of the Wr/Vr regression, that tallness is partially dominant.

The estimate of the ratio $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$ is, in all instances, greater than unity which implies that dominant genes for height expression in the 8 wheats studied are in excess of recessives. As different from the values for $H_2/4H_1$, the values for the ratio $(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F$ are effected by complementary gene interactions, since they are all higher (e. g., 1.86 for F_1 (field) analysis of all arrays) than would be expected in a diallel showing no interaction. The fraction $H_2/4H_1$, which estimates the proportion of genes with positive and negative effects of parents is consistently positive and of a low order indicating considerable asymmetry at loci showing dominance. This ratio is not affected by increasing generation while the population retains some heterozygosity, at least so long as it is possible to detect dominance in a segregating population.

The removal of significantly interacting array 1 in both the F_1 and F_2 field diallel trials caused a decrease in this ratio, due most likely to a reduction in the inflationary effect of complementary gene action on height expression.

The fraction h^2/H_2-ranged in value for the different analyses from 0.92—2.10 which indicates that at least two groups of dominant genes were involved in determining plant height amongst the crosses of the diallel. However, this ratio underestimates the actual number of genes because it does not account for groups of genes which exhibit little or no dominance.

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