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Genetic Analysis of Grain Protein Percentage in Wheat

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Summary. Diallel analysis techniques were used to study the genetic basis of grain protein percentage expression in wheat using eight wheats ranging from high to low in grain protein percentage and assumedly genetically diverse for this character.

The F_2 set of crosses exhibited strong genetic interaction for protein percentage attributable greatly to the general behaviour of Argentine IX, of high grain protein percentage, in combination with the other seven wheats. Removal of its interaction revealed additive genetic variance and moderately strong overdominance averaged over the crosses of the remaining seven parents.

In the F_3 and F_4 generations grain protein content exhibited additive genetic variance with evidence of some non-allelic interaction in the F_3. The F_3 exhibited partial dominance in the inheritance of protein percentage while in the two F_4 trials in different environments one exhibited a strong degree of average dominance and the other exhibited only a small degree of average dominance over all arrays.

Close correspondence in the order of ranking of protein percentage of the lines (parents and hybrids) in the two F_4 trials in two different environments, indicated a significant influence of genotype on the expression of this character in wheat. However, sharp differences in the nature of inheritance of high grain protein percentage between the two environments, whether by dominant or recessive genes, indicates the magnitude of the influence of the environment on its genetic expression in populations segregating for this character.

Introduction

The amount of protein laid down in the developing wheat grain is influenced markedly by environment but the presence also of a genetic component of grain protein percentage as a distinct varietal or genotype character, has led to interest in the possibility of breeding for its genetic improvement.

The demonstration of its reasonably high heritability (Aamodt and Torrie 1935; Davis 1959; Haunold 1960; Davis et al. 1961 ; Kaul and Sosulski, 1965) coupled with the general occurrence of increases in the level of available soil nitrogen, either as chemically applied or that fixed by legumes in most wheat-growing areas of the world, offers scope for producing genetic improvement in levels of grain protein percentage.

To enable the breeder to formulate an efficient breeding and selection programme for this purpose a knowledge of the genetic control of this character is of considerable value. The earliest reported study of the inheritance of grain protein percentage in wheat (Biffen, 1909) indicated the likelihood of a complex genetic control. Most subsequent studies of its inheritance have indicated polygenic control (Clark and Hooker, 1926; Aamodt and Torrie, 1935; Swen, 1940; Worzella, 1942). However, studies made by Haunold (1960) indicated it likely that it was under the control of only a few major genes. Cytogenetic analyses of grain protein percentage have indicated the possibility of polygenic control of its expression. Kuspira and Unrau (1957), using the 21 chromosome substitution lines of Thatcher in Chinese Spring, located five Thatcher chromosomes which influenced protein percentage of Chinese Spring. No chromosome was of major effect, which indicated the likelihood of polygenic control. Similar analyses using the 21 chromosomes of Hope in Chinese Spring (Halloran, unpublished) detected only one chromosome of Hope, namely 5D, which significantly influenced protein percentages relative to that in Chinese Spring. Its influence was of only minor effect. The genetic control of protein content was postulated to be due to polygenes each of small effect and very difficult to detect individually. Chapman and McNeal (1970) found that grain protein percentage exhibited highly significant additive genetic effects and in only two of five crosses examined was dominance for this character significant.

Material and Methods

In this study data were used from a diallel crossing programme involving the following wheat lines: Argentine IX, Baldmin, Bencubbin, Gabo, Hilgendorf, Insignia, Kenya C and Olympic. The wheats were chosen on the basis, both of assumed genetic differences for grain protein percentage and genetic diversity of origin. The assessment of genetic differences for grain protein percentage were based on local observation of the wheats for these characters over a number of seasons in Vic-

Table 1. Assumed genetic status for protein content and origin of the 8 wheats of the diallel analysis

Cultivar	Assumed genetic status for protein percentage	Origin
Argentine IX	High	Argentina
Kenya C	High	Kenya
Gabo	Moderately High	Australia
Hilgendorf	Moderately High	New Zealand
Insignia	Moderately Low	Australia
Olympic	Moderately Low	Australia
Baldmin	Low	Australia
Bencubbin	Low	Australia

toria. The wheats were rated on grain protein level as shown in Table 1.

The complete diallel crossing programme using these 8 cultivars was carried out to give 28 crosses; reciprocal crosses were not made. The F_1 of the diallel together with the 8 parents was grown in 20 cm. diameter earthenware pots with four plants of each line per pot and was a randomized block layout of six replicates. The four plants of each pot were harvested, the seed bulked and protein determinations made on each bulk.

The F_2 of the diallel was sown as a field trial in the subsequent sowing season. The trial was hand-sown as rows 4.5 m. in length and the seed placed in the rows at exactly a 5 cm. spacing in order to minimize on possible variation in protein content and yield due to unevenness of growth.

In layout the trial was a randomized block of six replicates of the 8 parents and the 28 crosses. The trial was hand-harvested and protein determinations made on all samples.

In the F_3, the diallel was sown as two identical trials, in two different field locations in Victoria in the following sowing season, denoted as environments 1 and 2. The trials, which were a randomized block design of six replicates were of hand-sown rows of 4.5 m. in length at a 36 cm. spacing and a rate of sowing equivalent to 68 kg/ha. Seed harvests of the two trials were analysed for protein content by the Biuret Method (Halloran and Moss, 1956).

Results

Analyses of variance for protein content were calculated for each of the diallel trials and in each instance there were significant differences between lines, indicating that the diallel analysis could then be performed. The mean values for protein content of each trial, are shown in Tables 2 and 3. The reference to generation in the protein data applies to the seed generation, e.g. F_2 analysis implies protein values of the grain from the F_1 plant.

F_2 Protein

The Wr Vr regression for protein content in the F_2 of the diallel is shown in Fig. 1. The shape of the regression line for all arrays was b = + 0.43 ± 0.31 which was significantly different from 0 and significantly different from a slope of 1. This indicated a considerable amount of genetic interaction for protein content amongst the crosses of the diallel.

Removal of the arrays of higher variance produced regression of slopes significantly different from 1. However, removal of array 1 gave a regression of slope b = + 0.96 ± 0.37 which was significantly ($p < .05$) different from 0 and significantly different ($p < .05$) from 1 (Fig. 2). Parents corresponding to arrays 5, 3, 6 and and 7 in increasing order, process an excess of recessive over dominant genes for protein content while parent 8 possesses an excess of dominant over recessive genes for

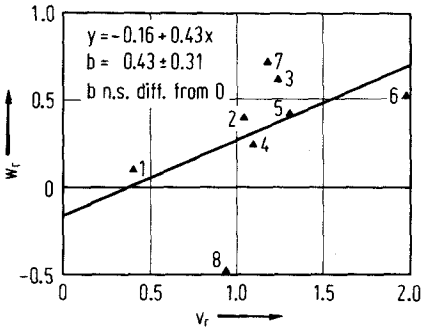

Fig. 1. Wr/Vr regression for grain protein percentage in the F_2 (all arrays)

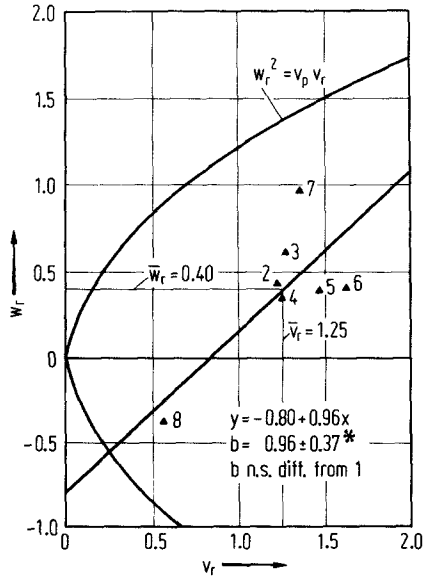

Fig. 2. Wr/Vr regression for grain protein percentage in the F_2 (array 1 omitted)

Table 2. Grain Protein percentage of 8 parents and the 28 crosses between them in the F_2 and F_3 generations

Array or Cross No.	Parent or Cross	Grain F_2	Protein % F_3	Cross No.	Cross	Grain F_2	Protein % F_3
1	Argentine lX	15.4	14.8	19	Baldmin × Gabo	13.0	11.5
2	Gabo	15.0	12.9	20	Olympic × Gabo	14.3	12.1
3	Insignia	13.2	11.9	21	Hilgendorf × Gabo	15.2	14.0
4	Bencubbin	14.5	12.0	22	Bencubbin × Insignia	13.8	11.8
5	Kenya C	14.3	13.8	23	Kenya C × Insignia	13.4	12.4
6	Baldmin	14.7	11.2	24	Baldmin × Insignia	13.7	11.2
7	Olympic	16.9	12.1	25	Olympic × Insignia	13.6	11.9
8	Hilgendorf	16.3	14.4	26	Hilgendorf × Insignia	16.4	13.8
9	Gabo × Argentine lX	14.6	12.8	27	Kenya C × Bencubbin	16.5	13.0
10	Insignia × " lX	15.0	12.5	28	Baldmin × Bencubbin	14.2	12.8
11	Bencubbin × " lX	14.6	13.1	29	Olympic × Bencubbin	15.1	11.8
12	Kenya C × " lX	15.5	13.7	30	Hilgendorf × Bencubbin	15.6	13.0
13	Baldmin × " lX	16.5	12.6	31	Baldmin × Kenya C	14.2	12.1
14	Olympic × " lX	15.1	13.3	32	Olympic × Kenya C	14.1	12.5
15	Hilgendorf × " lX	15.8	14.8	33	Hilgendorf × Kenya C	16.3	14.1
16	Insignia × Gabo	13.2	12.0	34	Olympic × Baldmin	13.5	11.4
17	Bencubbin × Gabo	13.2	12.5	35	Hilgendorf × Baldmin	16.9	13.6
18	Kenya C × Gabo	15.7	13.1	36	Hilgendorf × Olympic	14.8	13.1

Table 3. Grain Protein percentage of 8 parents and the 28 crosses between them in the F_4 generation sown in two different environments

Array or Cross	Parent or Cross	Grain Protein % Environment 1	Environment 2	Cross No.	Cross	Grain Protein % Environment 1	Environment 2
1	Argentine lX	16.4	12.1	19	Baldmin × Gabo	11.9	9.3
2	Gabo	13.2	9.4	20	Olympic × Gabo	12.3	9.6
3	Insignia	12.4	8.1	21	Hilgendorf × Gabo	14.2	10.3
4	Bencubbin	11.6	9.4	22	Bencubbin × Insignia	12.3	8.9
5	Kenya C	14.6	10.8	23	Kenya C × Insignia	13.6	10.1
6	Baldmin	10.9	8.9	24	Baldmin × Insinia	11.6	9.3
7	Olympic	11.8	10.0	25	Olympic × Insignia	11.8	8.9
8	Hilgendorf	15.1	11.2	26	Hilgendorf × Insignia	13.3	8.8
9	Gabo × Argentine lX	14.7	10.1	27	Kenya C × Bencubbin	13.3	9.9
10	Insignia × " lX	13.5	9.3	28	Baldmin × Bencubbin	11.2	9.4
11	Bencubbin × " lX	14.1	10.1	29	Olympic × Bencubbin	11.3	9.4
12	Kenya C × " lX	15.2	10.7	30	Hilgendorf × Bencubbin	14.0	9.4
13	Baldmin × " lX	13.7	9.9	31	Baldmin × Kenya C	12.8	9.4
14	Olympic × " lX	14.2	9.9	32	Olympic × Kenya C	13.6	9.9
15	Hilgendorf × " lX	15.3	11.1	33	Hilgendorf × Kenya C	14.3	10.6
16	Insignia × Gabo	12.4	9.4	34	Olympic × Baldmin	11.3	8.7
17	Bencubbin × Gabo	12.0	9.7	35	Hilgendorf × Baldmin	13.1	10.1
18	Kenya C × Gabo	14.0	10.0	36	Hilgendorf × Olympic	13.6	9.4

this character. Parents 2 and 4 possess dominant and recessive genes in about equal proportions. The Wr Vr regression line, with the removal of array 1, cuts the Vr axis well to the right of the origin, which indicates strong overdominance on the average over all arrays for expression of grain protein percentage. The distribution of array points on the regression line shows no close correspondence with parental protein content. Excepting array 7, the arrays indicated to be recessive are of comparatively low protein content and array 8 in the

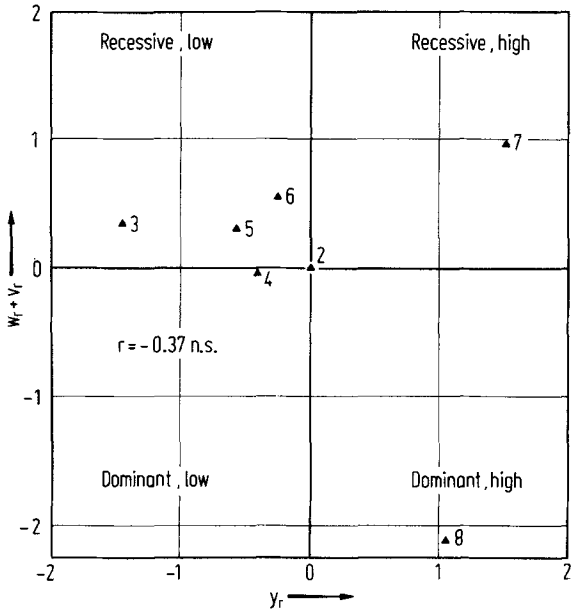

Fig.3. Correlation of the standardized deviations Yr and Wr + Vr for grain protein percentage (array 1 omitted)

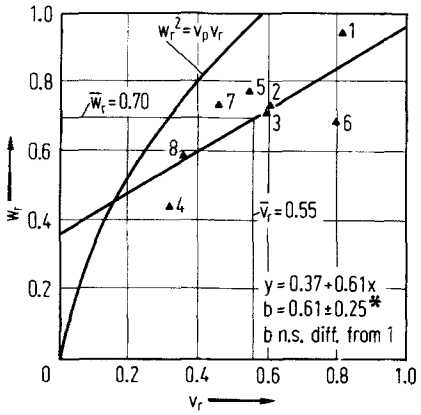

Fig.4. Wr/Vr regression for grain protein percentage in the F_3 (all arrays)

dominant end of the regression, has a high parental value for protein content. This suggests an association of recessiveness with low grain protein content. This suspected relationship was further examined in a correlation of the standardized deviation of Yr with Wr + Vr. The value Yr is a parental measurement calculated from the formula $(x_r + \bar{x})/S$ where x_r is the value of the individual parent, x the mean of the parents and S the standard deviation. The value of Wr + Vr is similarly calculated. The theory of diallel analyses (Hayman, 1954a, 1954b) states that the parental measurement, Yr is closely correlated with the number of dominant homozygotes and that the value Wr + Vr is closely correlated with the number of recessive homozygotes. In values

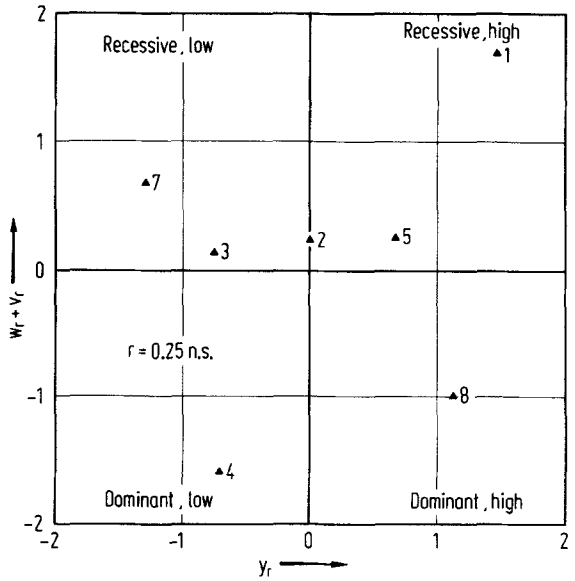

Fig.5. Correlation of the standardized deviations Yr and Wr + Vr for grain protein percentage in the F_3 (all arrays)

of (Wr + Vr), plus indicates recessive genes and minus dominant genes and for Yr, plus denotes high protein content and minus low protein content.

The standardized deviations of Yr and (Wr + Vr) for F_2 protein content are shown in Fig.3. The correlation coefficient between these two variables r = -0.31 was not significant and can be interpreted only as indicating a slight tendency for recessiveness to be associated with low grain protein content and dominance with high protein.

F_3 Protein

The Wr Vr analysis for the complete set of crosses in the F_3 gave a regression of slope b = + 0.61 ± 0.25 which was significantly different from 0 ($p < .05$) and not significantly different from a slope of 1 (Fig.4). Parents corresponding to arrays 5, 3, 2, 6 and 1, in increasing order, possess an excess of recessive over dominant genes for protein content while those corresponding to arrays 7, 8 and 4, in increasing order, possess an excess of dominant over recessive genes.

The intercept of the regression line quite high on the Wr axis indicates partial dominance in the expression of grain protein content.

There appears to be no close correspondence in the position of the array point along the regression line with protein content of the respective parents. This suggests

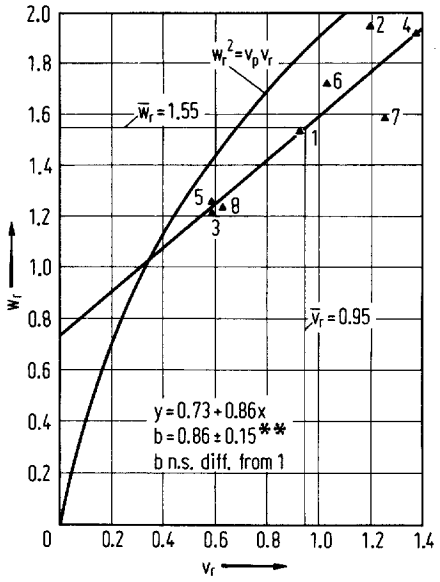

Fig.6. Wr/Vr regression for grain protein percentage in the F_4 - environment 1 (all arrays)

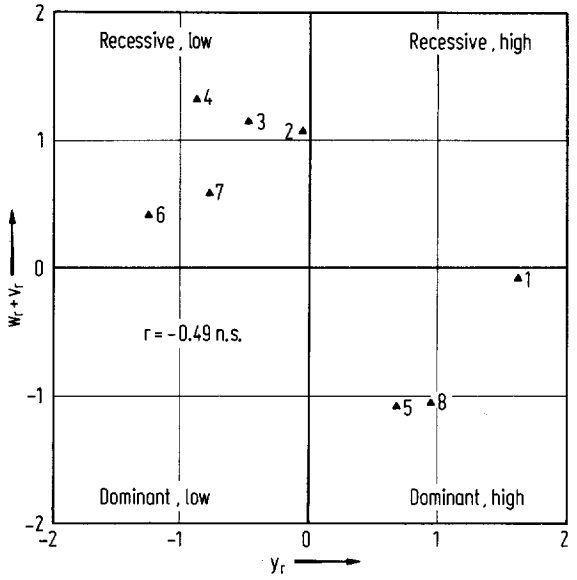

Fig.7. Correlation of the standardized deviations Yr and Wr + Vr for grain protein percentage in the F_4 - environment 1 (all arrays)

that high protein content in wheat may be determined by dominant genes in some instances and in others by recessive genes.

The standardized deviations of Yr and (Wr + Vr) are shown graphically in Fig.5. The correlation coefficient between these two variables r = + 0.25 was not significant and can be interpreted as indicating only a slight tendency for low protein content to be associated with dominance and high protein with recessiveness.

F_4 Protein - Environment 1

The Wr Vr analysis of F_4 protein content of all the arrays of the diallel is shown in Fig.6. The regression line was of slope b = + 0.86 ± 0.15 which was significantly different from 0 and not significantly different from 1.The array points were mostly situated close to the regression line indicating only a small amount of genetic interaction in the crosses of the diallel. The regression line cuts the Wr axis well above the origin and is fairly near the limiting parabola, indicating a moderate to small degree of dominance as an average over all arrays. Arrays 4, 2, 7 and 6 in decreasing magnitude, possess an excess of recessive to dominant genes for protein content expression while array 1 at the point Wr, Vr possesses recessive and dominant genes in about equal proportions. Arrays 8, 5 and 3 which are closely grouped at the lower end of the regression line possess an excess of dominant over recessive genes for grain protein content. There is a tendency for arrays of the low protein parents to show recessiveness and the higher protein parents to exhibit dominance in their arrays. This observation is supported by the relationship of the standardized deviations of Yr and Wr + Vr (Fig.7) with a correlation coefficient of r = - 0.49. The correlation however, is not significant which can only indicate therefore a tendency for low protein content to be recessive and high protein content dominant.

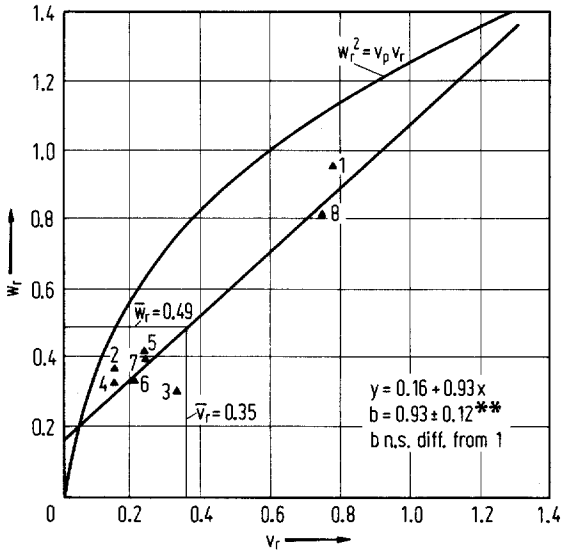

Fig.8. Wr/Vr regression for grain protein percentage in the F_4 - environment 2 (all arrays)

F_4 Protein - Environment 2

The graphical analysis of the 8 parent diallel for the F_4 grown in Environment 2 is shown in Fig.8. The Wr/Vr regression line b = 0.93 ± 0.12 was significantly different from 0 and not significantly different from a slope of 1. The regression line passes close to the origin which indicates a high degree of dominance averaged over all the arrays for the expression of grain protein content. The array points fall in two groups - 1 and 8 which, in decreasing order, possess an excess of recessive over dominant genes for grain protein content, and the remaining arrays which possess an excess of dominant genes. The position of all arrays are almost on the regression line which indicates very little genetic interaction. The positions of the array points on the regression line bear a close relationship to the order of protein content of the parents. The most recessive arrays have parents of high protein content and the most dominant parents of low protein content. Thus high protein content appears to be inherited as a recessive character in this instance.

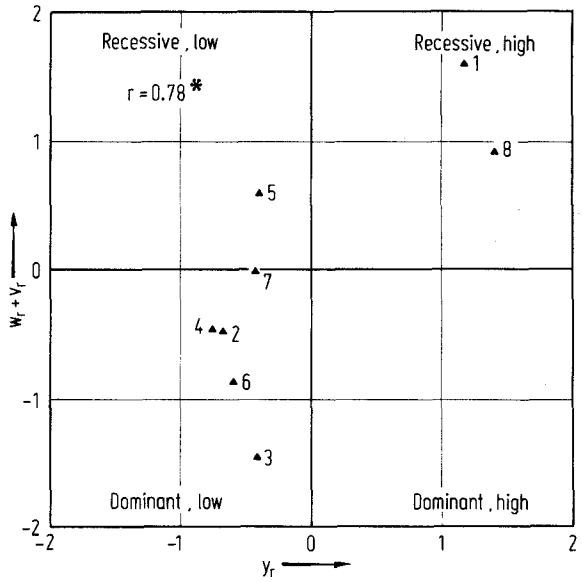

Fig.9. Correlation of the standardized deviations, Yr and Wr + Vr, for grain protein percentage in the F_4 - environment 2 (all arrays)

Confirmation of this observation was obtained from the correlation of the standardized deviations Yr and (Wr + Vr) which is plotted graphically in Fig.9. The correlation coefficient between these two variables of r = + 0.78 is significant ($p < .05$), indicating an association of high protein content with recessiveness and low protein content with dominance.

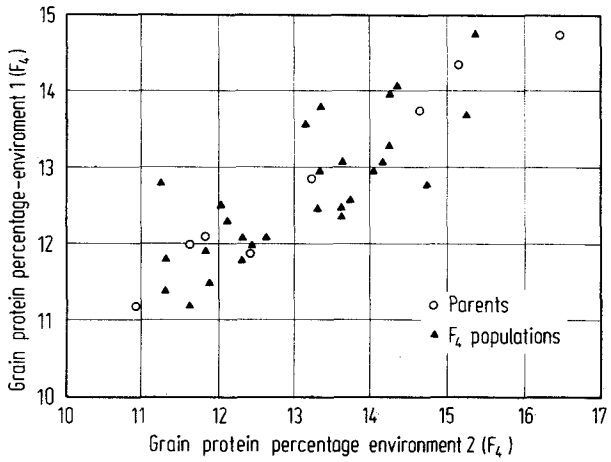

Fig.10. Relationship of grain protein percentage for all lines (parents and hybrids) between environments 1 and 2 for the F_4 trials

A plot was made of the parental and F_4 protein values between the two environments of the F_4 trials (Fig.10).

Discussion

Knowledge of the inheritance of grain protein content in wheat is of importance to wheat breeding, both for the purposes of formulating a breeding programme and of selecting objectively for its improvement. A great limitation to such improvement is the magnitude of the influence of environmental factors on the expression of protein content. Protein content of wheat has been shown to be strongly influenced by precipitation (Paull and Anderson, 1942; Fernandez and Laird, 1959), high temperature, either as a direct influence on metabolism (Mangels, 1927; Hopkins, 1935; Waldron et al., 1942) or indirectly through its influence on such factors as soil moisture and nitrification (Alsberg and Griffing, 1934; Shutt and Hamilton, 1934; and others).

Despite the generally strong influence of environment on its expression reports have often been made of the detection of significant genotypic, or varietal differences in this character (Whiteside 1936; Knjaginicev 1940; Akerman, 1949; Lee and Underwood, 1950; Butkevic, 1954; Halloran, 1956; Singh and Lamb, 1960; and others). Moreover heritability studies have confirmed a moderately strong genetic component in its expression (Aamodt and Torrie, 1935; Davis, 1959; Haunold, 1960; Davis et al., 1961; Haunold et al., 1962).

In the present study certain findings have been made of the genetics of grain protein content and of the influence of environment on its expression. The occurrence of rather pronounced overdominance in the ex-

pression of grain protein content in the F_2 generation could be of practical significance. If this was a general phenomenon it may be possible in the commercial production of hybrid wheat to obtain higher protein content through appropriate choice of high protein parents.

The F_3 diallel trial indicated only partial dominance in the inheritance of protein content. The lack of a close correspondence in parental protein content value with the order of the array positions in the Wr/Vr graph indicates that high protein content can be determined by dominant or recessive genes according to the genotypes being used. A similar observation on the inheritance of grain protein content has been made by Chapman and McNeal (1970).

The F_4 diallel trial in Environment 2 exhibited moderately strong overall dominance in the inheritance of protein content and, with most of the array points close to the regression line, very little genetic interaction. High protein content under these conditions was recessive and low protein content dominant. The most promising cross for selection of high protein content would appear to be (Hilgendorf × Argentina lX). In the F_4 diallel trial in Environment 1, protein content exhibited only partial dominance in its expression and only a small amount of genetic interaction, most of the array points being on or near the Wr/Vr regression line. In this instance however, high protein content appeared to behave as a dominant character, a reversal of its behaviour in the F_4 in Environment 2. The correlation of Yr with (Wr + Vr) in Environment 1 was $r = -0.49$ though not significant, indicated a tendency for an association of dominance with high protein.

A very close correspondence was observed between protein content values of the parents and hybrids of the F_4 diallels sown in the same season in Environments 1 and 2 with a correlation of $r = +0.78$ ($p < .01$). This relationship indicated a reasonably strong heritability of this character whose ranking is not greatly altered by sharp differences in environment. This marked difference in potential for producing a certain level of protein content in the two environments can be gauged by the mean difference of a 3.4 percent protein of the mean of parents and hybrids in these two environments. Despite the general correspondence in order of protein content value of the lines between the two environments it is of particular interest that the genetic control of protein content, whether by dominant or recessive genes, appeared to change with environment.

This behaviour points to the need to conduct protein inheritance and selection studies under environmental conditions closely appropriate to those for which higher protein genotypes are required and, advisedly, at a number of different sites within such environments. However, the comparatively close relationship between parents and hybrids in protein content for the F_4 diallels indicates that season to season selection within the one environment should be reasonably effective in retaining a genetically high protein component of the population. The greatest advance in protein content would be expected from selection within the highest protein crosses of the F_4 generations.

In the task of breeding for grain protein improvement in wheat the wheat breeder, in considering firstly its genetic control and, secondly, the influence of environment on its expression, can make a reasonably objective approach to the formulation of a breeding programme. Firstly, from the generally additive nature of its genetic control the highest protein segregates would be expected from those crosses involving the highest protein parents. It is important, therefore, in parental selection that as wide as possible a range of genotypes be screened for the high grain protein characteristic. In the choice of parents in a breeding programme, dissimilarity of pedigree of high protein genotypes would appear to be a worthy criterion in narrowing the selection because of the greater likelihood of obtaining genes of complementary function in producing high grain protein content. Secondly, because of the influence of maturity on grain protein content expression it is advisable, at least for selection of parents from large scale introduction programmes, that it be made within confines of maturity appropriate to the environment for which breeding is to be pursued. Because it has generally been shown that protein content is under either polygenic control (Clark and Hooker, 1926; Aamodt and Torrie, 1935; Worzella, 1942; Swen, 1940; Kuspira and Unrau, 1957; Halloran, unpublished) or that it may be less complex genetically, but not monogenic (Haunold, 1960) the most advisable breeding programme would appear to be a pedigree system. Such a programme would involve large numbers of protein determinations to be carried out on either F_2 or F_3 lines. The adaptation of the Biuret method of protein determination of wheat breeding (Halloran and Moss, 1956) enables large numbers of protein determinations to be rapidly and accurately carried out, thus making large scale selection in a pedigree protein breeding programme practically feasible.

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