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Study of Genetic Determination of 20 Gliadin Bands

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Summary. Study of the genetic determination of the gliadins of two F_2 progenies from bread wheat has enabled (1) confirmation of the co-dominant heredity of the presence of these bands in the F_1, and (2) determination of the transmission of the presence/absence character for 20 bands. 10 bands are monogenically controlled; 10 others are coded by two pairs of alleles. Among the latter 2 bands split into two proteins in 2 dimensional electrophoresis. Analysis of the segregations, not taking into consideration the presence/absence character but only the concentrations of certain bands, led to the formulation of the hypothesis of regulator genes controlling the expression of structural genes.

Key words: Gliadin – Genetic control – Structural genes – Bread wheat – Wheat cultivars

Introduction

Study of the relations between gliadin polymorphism and several technological tests evaluating baking strength has enabled us to show the preponderant role of some bands in the expression of gluten quality (Branlard and Rousset 1980). Study of the genetic determinants of gliadins has thus become necessary in selection for the improvement in gluten protein quality. Research conducted by Wrigley and Shepherd (1973), Kasarda et al. (1976); Mitrofanova (1976) show that the genes controlling the synthesis of gliadins are localized on chromosomes 1 and 6 of genomes A, B and D. Studies of the genetic control of gliadins carried out by Doekes (1973), by Sozinov et al. (1974) and by Sozinov and Poperelya (1980) reveal that the bands seem to be transmitted in groups. Analyses made by Mecham et al. (1978) show that the characteristic presence/absence of a gliadin band is controlled by a single gene. The results obtained by Baker and Bushuk (1978), after observing a limited number of diagrams, suggest that several bands may be each coded by two genes. Thus, in order to improve knowledge of these storage proteins of the grain it appeared useful: (1) to specify if the character, presence or absence of a given band, is coded by one or several genes; (2) to try to analyse the genetic basis of the variation in concentration of the bands.

Cultivars and Methods

The gliadin diagrams of F_1 and reciprocal F_1 grains extracted from two crosses of bread wheat ("Courtot"×"Ciano 67" and "Mayo 54"×"Joss") were analysed. The electrophoresis of gliadins for F_2 grains was carried out on 206 grains for the first cross, and 312 for the second.

Gliadins of individual grains were extracted with a solution of chloro-2-ethanol at 25%. Electrophoresis of F_1 and F_2 grains extracts was made in starch gel according to the method of Autran and Bourdet (1975). Analysis of mobility and relative concentration of the bands was carried out according to the nomenclature given by these authors.

Densitometric analysis is carried out by Autran et al. 1975 and five classes of concentration 0, trace, +, ++, +++ are established corresponding to the following absorption of bands as a per cent of total obsorption 0, 0–1.5%, 1.5–4%, 4–6.5% and higher than 6.5% respectively. It is observed that for a given cultivar, the experimental fluctuations of relative concentrations of bands was always much less than the total interval of two classes. Autran et al. have deduced that for a given band two classes of relative concentration are sufficient in order to conclude that there is a significant difference between two diagrams from two cultivars.

In order to specify whether the bands of parental diagrams were each constituted by one or several proteins bidimensional electrophoresis was used. The first migration was made in acrylamide gel at pH 3.2 according to the Bushuk and Zillman method (1978). However, the quantity of proteins deposited was modified: the proportion solvent/weight of the grain was reduced from 0.015 to 0.00125 ml/mg. The second electrophoresis was carried out at pH 9.2 according to the conditions suggested by Mecham et al. (1978). The coloring of bidimensional diagrams was made with Coomassie R 250 according to Bushuk and Zillman (1978).

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Results

1 Polymorphism of the Parental Gliadins

Figure 1 displays the diagrams obtained on starch gel with the gliadins of the parents, "Courtot" and "Ciano 67", of the first cross, and "Mayo 54" and "Joss", for the second.

As F_1 and F_2 analyses had been carried out with starch as the electrophoresis support, it was necessary to know the correspondence between the mobilities of the band revealed for starch and acrylamide in order to make use of bidimensional diagrams. This point was partly solved by the research of Autran (1979) and with several trials comparing bidimensional electrophoresis in starch and acrylamide.

Results of this investigation show satisfactory correspondence between mobilities in these two gels for omega gliadins. Bands not detected in starch may appear in acrylamide gel mainly for the alpha, bêta and gamma gliadins. The order of mobilities seem to be the same for most of the bands found in starch gel, except for band 90 which splits in acrylamide and gives a band of greater mobility than that of the 93 band. This incomplete study is made difficult because there does not seem to be an unequivocal correspondence for all bands from one wheat genotye to another. From this data, it is possible nevertheless to specify which bands are composed of one or several proteins.

Thus, among the chosen bands differentiating the parents it can be noted:

– that no band belonging to "Courtot" or "Ciano" splits in bidimensional electrophoresis. Therefore, it is possible that each of the 8 bands which differentiates "Courtot" from "Ciano" is composed of a single protein.
– that 2 "Mayo" bands, 37 and 49, seem to split as well as band 44 in "Joss".

Autran and Bourdet's work (1975) has shown that there must be a difference of two classes of concentration to be able to conclude that a significant difference exists between two equally mobile bands. This test was used in order to determine the number of the differences between these diagrams.

Thus "Courtot" and "Ciano" can be distinguished by 8 bands: 22, 34, 37, 45, 56, 62, 68, 96. Mobility band 100 is absent in "Courtot" but is present in traces in "Ciano". It proved (according to whether it was present or absent) more easily distinguishable than mobility band 62. Thus, the analysis of the "Courtot" × "Ciano" cross dealt with bands 22, 34, 37, 45, 56, 68, 96 and 100. The "Mayo 54" and "Joss" diagrams are distinguished by 15 bands: 21, 22, 25, 26, 28, 30, 37, 39, 43, 44, 46, 49, 56, 62 and 79. Mobility band 34 in "Mayo 54" always had a relative concentration higher to that in "Joss" which sometimes did not appear on the diagrams. It was considered that such a difference, as visually important as that for band 46, justified taking into account the heredity of band 34. Therefore, the investigation was carried out on 16 bands for this second cross.

Before starting the genetic analysis of the progenies themselves it seemed essential to determine whether several proteins migrating on the same level of a given band could exist.

In order to answer this question bidimensional electrophoresis was carried out on the gliadins of 4 wheat genotypes. Migration was made in acrylamide gel at 6.3%; the first electrophoresis occurred at pH 3.2; the second at pH 9.2.

Figures 2 a, b and 3 a, b exhibit monodimensional (acrylamide gel) and bidimensional electrophoresis of respectively "Courtot", "Ciano 67", "Mayo 54" and "Joss".

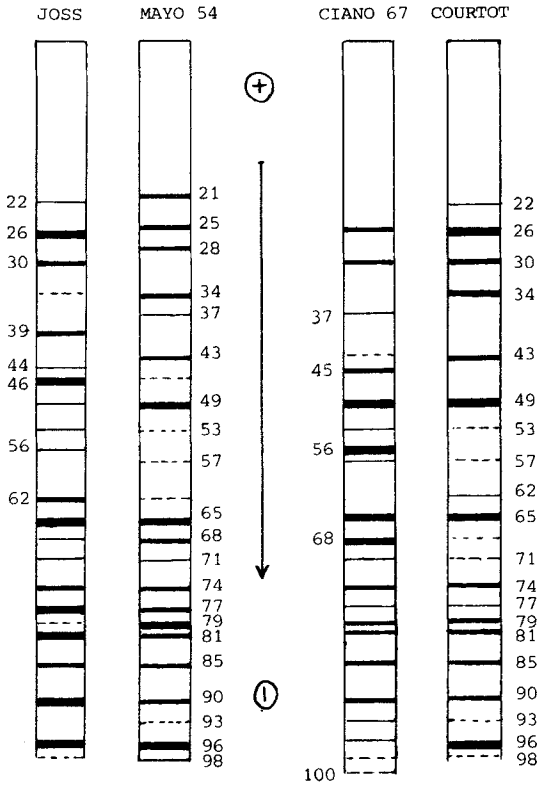

Fig. 1. Parental diagram of gliadin of the two crosses "Courtot" × "Ciano" and "Mayo" × "Joss". Concentrations scale: - - - - = trace; —: +; —: + +; ▬: + + +

2 Study of the F_1

The observation of F_1 and reciprocal F_1 diagrams of the two crosses enables the corroboration of the results of other workers, especially those of Mecham et al. (1978) and Damidaux et al. (1980).

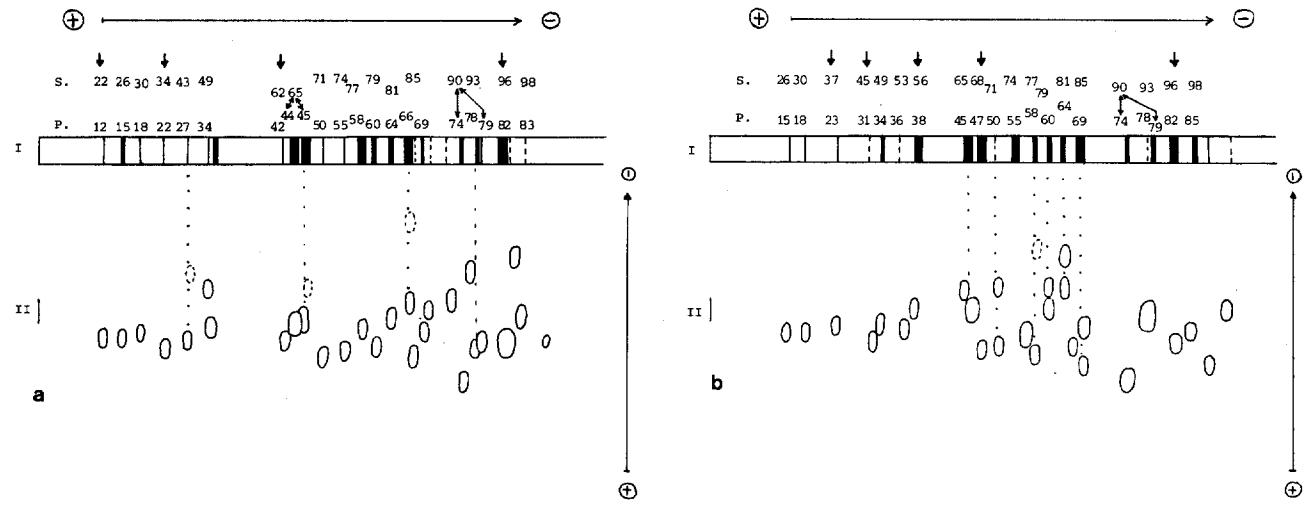

Fig. 2a and b. One dimensional electrophoresis (I) and 2 dimensional electrophoresis (II) of gliadins from (**a**): "Courtot" and (**b**) "Ciano 67". Mobility of gliadin bands is given for starch (*S.*) and polyacrylamide (*P.*) gel. The bands studied are indicated by arrows

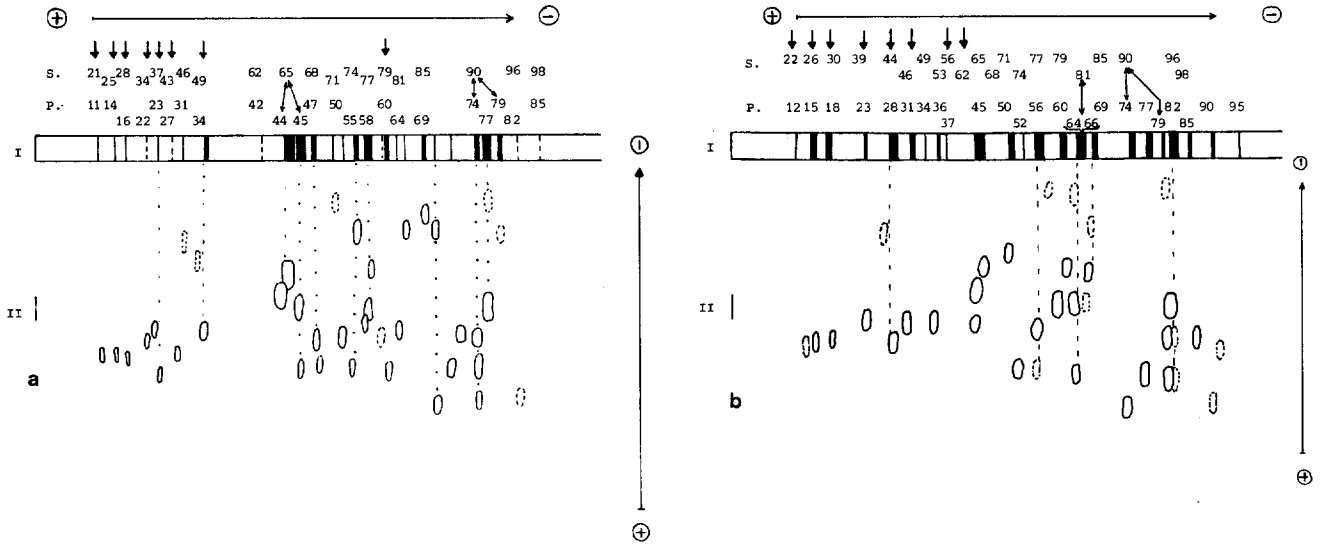

Fig. 3a and b. One dimensional electrophoresis (I) and 2 dimensional electrophoresis (II) of gliadins from (**a**): "Mayo 54" and (**b**) "Joss". Mobility of gliadin bands is given for starch (*S.*) and polyacrylamide (*P.*) gel. The bands studied are indicated by arrows

Band concentrations characteristic of the female parent prevailed. This well known phenomenon is related to the triploid character of endosperm.

Secondly all bands of the parents were present in the heterozygous F_1 genotypes, with no band of one parent excluding any other band of the second parent. This lack of dominance in the heterozygote state indicate that the genes controlling the gliadins are co-dominant.

3 Study of the F_2

The study of F_2 diagrams for each of the two crosses consisted in:

- regrouping all the diagrams not significantly different from one another.
- counting for each of the 8 or 16 bands, whose genes were submitted to genetic recombinations, the number of grains with 0, trace, +, + +, or + + + concentrations.
- establishing hypotheses (one pair, two pairs of alleles) indicating every time a theoretical distribution.
- and testing their validities.

3.1 The Types of Diagrams

To conclude in favour of a significant difference between two diagrams it is sufficient to have:

– either a band present in one diagram and absent in the other.
– or the same number of bands with a similar mobility but at least one must show a difference of concentration equal or superior to two classes between the two diagrams (Autran 1975). These electrophoregrams thus regrouped into types of diagrams give an idea of the importance of the genetic exchange which occurred during meiosis for the genes controlling the gliadins.

a) First Progeny. In the "Courtot" × "Ciano 67" cross, 206 F_2 grains have been analysed by electrophoresis in starch gel.

Among the 206 diagrams we counted:

– 45 types of diagrams
– 1 electrophoregram similar to "Courtot" and another to "Ciano 67".

This low percentage of grains phenotypically similar to the parents indicates that a large number of genes are involved in the genetic determination of the 8 bands which distinguish "Courtot" from "Ciano 67".

b) Second Progeny. 312 F_2 grains from "Mayo 54" × "Joss" were analysed with electrophoresis in starch gel. The count was made of:

– 144 types of diagrams significantly different from one another. In Fig. 4 some of these diagrams are assembled.

– no parental type.

In this progeny where 16 bands distinguish the two parents a large number of diagram types can be expected. If we assume that there is a single pair of alleles (*A/a*) controlling the presence or absence of each of the bands and that the 16 genes, thus structured, are independent, $2^{16} = 65{,}536$ types of diagrams should be obtained. Because of the low number of diagrams obtained after the analysis of the 206 and 312 F_2 grains, it is concluded, a priori that it is likely that not all the genes controlling the synthesis of these different protein bands are independent.

3.2 Number of Grains in the Different Concentration Classes

Table 1 displays the number of grains observed in a class of concentration for one band analysed. Thus, for the "Courtot" × "Ciano 67" cross, 78 diagrams which do not have band 22 were counted; it is present in 118 in concentration (+) but none seem to have it with concentrations (+ +) or (+ + +).

The numbers of grains in each class are of course related to the class of concentration of each parent for a given band. For example, band 34 is in concentration (+ +) in "Courtot", and absent in "Ciano 67". The whole group of F_2 grains is found between these two classes. However, all the distributions of these numbers are not as consistently localized between the concentration classes from parental diagrams; thus, band 34 of "Mayo 54" × "Joss" is absent on 69 diagrams and at concentration (+ + +) on 38 other diagrams. This exceeding of parental classes ("Mayo 54" has concentration (+ +) and "Joss" in trace) may be explained by the fluctuations of relative concentrations (these fluctuations are usually limited to within two classes) and by the inaccurate reading of the concentrations.

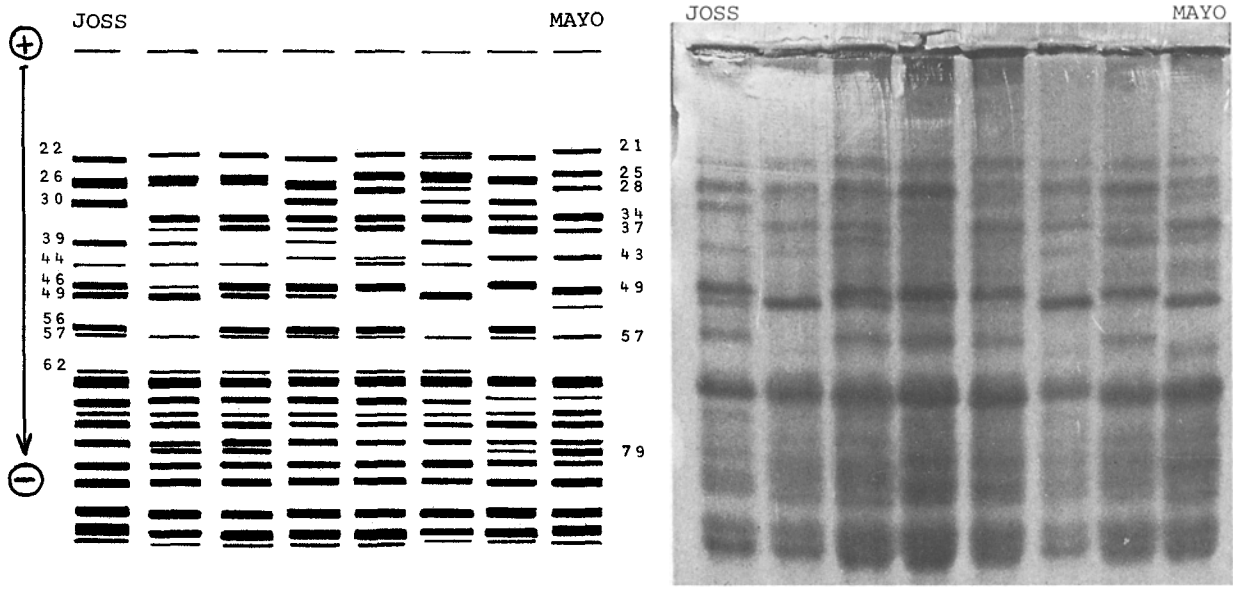

Fig. 4. Gliadin patterns on starch gel (pH 3.2) of F_2 seeds of the "Mayo 54" × "Joss" cross

Tabelle 1. Number of seeds with the protein band absent of present for given concentration class

Bands			Classes				
			0	Trace	+	++	+++
	Courtot	Ciano					
22	+		78	10	118	0	0
34	++		59	32	59	56	0
37		+	55	15	35	94	7
45		++	14	56	135	0	1
56		+++	42	13	12	63	76
68	trace	+++	57	2	7	27	113
96	+++	+	40	0	85	64	17
100		+	100	24	75	7	0
	Mayo	Joss					
21	++		146	0	22	141	3
22		+	165	2	64	82	0
25	++		163	2	19	104	24
26		+++	126	5	15	46	120
28	++		149	34	43	86	0
30		++	125	10	82	80	15
34	++	trace	69	11	74	120	38
37	+		89	24	91	104	4
39		++	86	57	124	43	2
43	++		77	98	131	6	0
44		+	44	99	165	2	2
46	trace	+++	67	0	54	99	92
49	+++	+	19	0	50	113	130
56		+	66	32	106	101	7
62	trace	++	69	25	208	10	0
79	+++	trace	65	20	61	103	63

Autran and Bourdet (1975) have shown that the standard deviation of low concentration classes (mainly in trace) was higher than in the other classes. Nevertheless this does not explain bands 96 of the first cross ("Courtot" (+++), "Ciano 67" (+)) are respectively absent on 40 and 19 diagrams when they should normally be present. Such disappearance of a band probably also happens for other less concentrated bands. The simplest explanation would be the formation of unequal crossing-overs during meiosis.

But the frequencies here are too high to be only a matter of unequal crossing-overs. The genetic analysis discussed below will suggest another explanation.

3.3 Hypothesis Chosen to Explain the Disjunctions

For each hypothesis it is easy to establish the frequencies per concentration class as well as those related to be presence/absence character of the band.

Hypothesis 1: a pair of alleles (A/a) codes for a protein band

$P_1 \times P_2$

$\frac{A}{A} \times \frac{a}{a}$

Genetic structure of F_2 endosperm

♀\♂	A	a
AA	*AAA*	*AAa*
aa	*Aaa*	*aaa*

Analysis when the classes are regrouped:

Presence (+++, ++, +, tr) + (*AAA, AAa, Aaa*) 3/4

Absence (0) = (*aaa*) 1/4

Hypothesis 2: two pairs of independent alleles (A/a, B/b) code for a protein band

$P_1 P_2$

$\frac{A}{A}\frac{B}{B} \times \frac{a}{a}\frac{b}{b}$

Several hypotheses may be considered:

Hypothesis 2-1: A produces the synthesis proportional to B

Analysis when classes are regrouped

Présence (+++, ++, +, tr) 9/16

Absence (0) 7/16

Hypothesis 2-2: The synthesis of the protein band occurs only with A and B as the concentration is related respectively to A and B in an equal proportion.

The analysis by class of concentration leads to the same frequencies as mentioned above. The same holds true when the classes are regrouped.

Hypothesis 2-3: There is a synthesis only if A and B are both absent.

Analysis when the classes are regrouped

Presence (+++, ++, +, tr) 7/16

Absence (0) 9/16

Hypothesis 2-4: A and B code independently for the same protein.

Analysis when the classes are regrouped

Presence (+++, ++, +, tr) 15/16

Absence (0) 1/16

3.4 The Tests of the Hypothesis on the Disjunctions

The different theoretical distributions have been compared by means of the Chi square test for the presence/absence character of a given band.

a) "Courtot" × "Ciano 67". In Table 2 the distributions observed as well as the values of adjustment tests to segregations 3-1 (Hypothesis 1), 9-7 (Hypothesis 2-1 or 2-2) and 15-1 (Hypothesis 2-4) are indicated.

It is ascertained that among the 8 bands investigated in this cross:

– 5 seem to be controlled by one pair of alleles: these are bands 34, 37, 56, 68 and 96.

– 3 may be controlled by 2 independent pairs of alleles: these are bands 22, 45 and 100. Band 45 may be independently coded by two genes.

b) "Mayo 54" × "Joss". In table 3 the distribution observed as well as the values of CHI-square tests corresponding to the five hypotheses discussed are indicated.

In this cross it appears that among the 16 bands studied:

Table 2. "Courtot" × "Ciano 67": F_2 segregation and CHI-square tests for their fit with 3/4 – 1/4 (1 gene) or 9/16 – 7/16 or 15/16 – 1/16 (2 genes) distributions

Bands	Number of seeds with protein		Ratio Present/ Absent	CHI-2		
	Present	Absent		3:1	9:7	15:1
22	128	78	1.64	18.18*	2.89**	–
34	147	59	2.49	1.45**	–	–
37	151	55	2.74	0.32**	–	–
45	192	14	13.71	36.40*	114.3*	0.10**
56	164	42	3.90	2.34**	–	–
68	149	57	2.61	0.78**	–	–
96	166	40	4.15	3.42**	–	–
100	106	100	1.06	60.90*	2.59**	–

* $p < 0.01$
** $p > 0.95$

Table 3. "Mayo 54" × "Joss": F_2 segregations and CHI-square tests for their fit with 3/4 – 1/4 (1 gene) or 9/16 – 7/16 or 15/16 – 1/16 (2 genes) distributions

Bands	Number of grain with protein		Ratio Present/ Absent	CHI-2		
	Present	Absent		3:1	9:7	15:1
21	166	146	1.13	79.04*	1.17**	–
22	147	165	0.89	129.38*	1.43**	–
25	149	163	0.91	123.50*	2.03**	–
26	186	126	1.48	39.38*	1.43**	–
28	163	149	1.09	86.17*	2.03**	–
30	187	125	1.49	37.76*	1.72**	–
34	243	69	3.52	1.38**	–	–
37	223	80	2.50	2.07**	–	–
39	226	86	2.63	1.09**	–	–
43	235	77	3.05	0.02**	–	–
44	268	44	6.09	19.76*	111.4*	32.8*
46	245	67	3.65	2.07*	–	–
49	293	19	15.42	59.50*	179.8*	0.01**
56	246	66	3.72	2.46**	–	–
62	243	69	3.52	1.38**	–	–
79	247	65	3.80	2.89**	–	–

* $p < 0.01$
** $p > 0.95$
*** For the bands 22 and 25 the distribution is 7:9

– 8 would be controlled by one pair of alleles: these are bands 34, 37, 39, 43, 46, 56, 62 and 79.
– 7 seem to be coded by two pairs of alleles: they are bands 21, 22, 25, 26, 28, 30 and 49.
– band 44 is controlled by two linked genes with a distance of 24.8 ± 0.02 recombination units.

Discussion

For the bands common to the two crosses (bands 22, 34, 37 and 56) there is a good concordance between the types of genetic determination which are obtained from two analyses. Thus, bands 34, 37 and 56 seem to be coded by a pair of alleles. However, for the latter, the same theoretical distribution is not verified in the two series of progenies. In the first cross, the frequencies 9/16–7/16 seem to be closer to the observed distribution whereas the reverse is true in the second cross. Calculation of the power of the test does not allow the choice of one theoretical distribution over the other.

The bidimensional electrophoresis of "Mayo 54" and "Joss" grains has revealed that in fact, bands 37, 44 and 49 are each composed of two proteins.

For band 49 the frequencies presence/absence (15/16–1/16) proved to be those given by two genes segregating independently from each other and each coding for one of the two proteins.

For band 44, no simple theoretical distribution fits the observed distribution. If it is assumed that the genes controlling the two proteins are localized on the same chromosome, the presence/absence character of this band appears to be coded by two genes (*A/a, B/b*) with 24.8 ± 0.02 recombination units between them. These two genes would each code one of the two proteins.

The frequencies of band 37 do not fit those given by two pairs of alleles. Only one gene for this band which seems composed of two distinct proteins in bidimensional electrophoresis was found.

This phenomenon could be explained by post-transcriptional modifications of a part of the messengers controlling the synthesis of one of these proteins; or by modifications of the protein itself (alkylation, glucosylation especially) which would not be systematic. Although these hypotheses are probable, they remain unconvincing for such a phenomenon for the other bands is not observed.

Another explanation may be considered: these results have been obtained without taking into account the level of concentration of the bands. Further data concerning the genetic determination of the bands appear when the respective levels of concentration of the bands are taken into account. Although it is a critical point because of the fluctuations which may occur in some bands, several bands and especially 37, are worth studying.

Band 37

Band 37, absent in "Joss" but at concentration (+) in "Mayo", is composed of at least two proteins. This band is present in almost 3/4 ths of the F_2 diagrams. The distribution of F_2 grains in the classes of concentration (table 1) has shifted towards classes (+ +) and (+ + +). The latter is significantly different from class (+) where "Mayo 54" is localized; and if we study the disjunction of character (+ + + / +) of this band 37, it

can be seen that it follows the distribution given by two independant pairs of alleles. There are several hypotheses which could explain these observations.

Hypothesis 1: the genetic composition of "Mayo 54" is (*S1 S1, S2 S2*) and that of "Joss" is (*s1, s1, s2 s2*) in which *S1* and *S2* are the alleles of structural genes of the 2 proteins in band 37 and *s1, s2* are null alleles. In this case, two proteins in "Mayo 54" are found, and none in "Joss" but this hypothesis cannot explain the exceeding of the class of concentration in "Mayo 54".

Hypothesis 2: the genetic composition of "Mayo 54" (*S1 S1, s2 s2*) and that of "Joss" is (*s1 s1, S2 S2*). In this hypothesis an excessive concentration is found compared with that of "Mayo 54" as concerns some recombined F2. However, in order to have two proteins in "Mayo 54" and none in "Joss", one would have to admit that null allele *s2* of *S2* codes for the second protein and that *S2* is not expressed.

Hypothesis 3: the genetic composition of "Mayo 54" and "Joss" includes two kinds of genes: a regulatory gene (R/r) which would interfere in the level of expression of structural genes (*S1/s1, S2/s2*). When r is present, the allele *S1* or *S2* is little expressed, which leads to a low concentration of the band. When R is present, the allele *S1* or *S2* is expressed to a greater extent. Then, for the two wheats, the following genetic composition would be present:

	"Mayo 54"			"Joss"		
	r	*S1*	*S2*	R	*s1*	*s2*
	r	*S1*	*S2*	R	*s1*	*s2*
Concentration		(+)			(0)	

This hypothesis enables the explanation of the observations made on band 37: two proteins in "Mayo 54" and none in "Joss".

Calculation of CHI-square with 3 degrees of freedom indicates that the numbers in the class concentration fit theoretical distribution given by 3 independent genes: $\chi^2 = 3{,}17$.

In Table 1 it can be seen that among the bands studied, 6 are present (at very varied concentrations) in both the parents. These bands which appeared to be composed of one protein are the following:

	"Courtot"	"Ciano"
68	tr	+ + +
96	+ + +	+
	"Mayo"	"Joss"
34	+ +	tr
46	tr	+ + +
62	tr	+ +
79	+ + +	tr.

The presence/absence character of each band is controlled by a pair of alleles.

If the disjunctions (+ + + /tr or + + + /+ or + + /tr as the case may be) are studied according to the date given on Table 1, no simple distribution is obtained for each of the 6 bands except for band 96 in which two pairs of independant alleles are found.

In order to explain the genetic composition of each parent for these 6 bands it is necessary:

– to suppose that there exists at least two linked or independent genes *A/a, B/b* coding the same protein.
– to determinate why these genes seem to be transmitted as one single gene, that give, overall, a ratio 3/4–1/4 for the frequencies presence/absence in the F_2.
– to suppose that, for example, allele *A* codes the synthesis of 3 to 5 or even ten times as much protein as allele *B* (difference between + + + and in trace).

If, for example, the genetic composition of the parents is *AAbb* (+ + +) and *aaBB* (trace) and if these two genes are independent, then the frequency of grains with the absent band in the F_2 will be, in theory, 1/16. In fact, it is observed that for these 6 bands (Table 2 and 3) the frequency is about 1/5 and always less than 1/4. This large proportion of grains with an absent band is probably due to this character giving trace amount in one of the parents. This parent where allele B is localized, has a *aaaBBB* endosperm for the band in trace. Therefore the F_2 grains with structures (*aaa Bbb* and *aaaBBb*) have probably not been detected and consequently, not added to the constitutive ones (*aaabbb*). When there are two independent genes the frequency can exceed 1/5 if it is taken into account how hard it is sometimes to distinguish a band in trace from the background of migration. Thus, considering the power of the CHI-square test, it is very easy to conclude that there exists a pair of alleles for the presence/absence character of a band which is very concentrated in one of the parents, and absent or in trace amounts in the other.

This probably leads to a simplification of the type of genetic determinism of these bands. It seems possible that the frequencies of a band can appear to fit a theoretical distribution of the type 3/4–1/4 for the presence/absence character whereas in fact, they correspond to another distribution.

A less simple structure such as that given for band 96 and including a regulatory gene and 2 genes with similar structures (Branlard 1980) explains both the frequencies of presence/absence and the distribution of the number of grains hoving a particular band concentration. It is likely that, as it was suggested especially by Mecham et al. (1978), the genes coding these proteins are, in fact, composed of series of the same nucleotidic

sequence. In so far as these series would be transmitted and transcribed, this would explain why the quantity of a given proteic band can be 3 or 4 times as great in one genotype as in another.

Conclusion

The study of the genetic determination of the gliadins of two F_2 progenies has suggested a solution for the presence/absence character of the 20 different bands investigated in the two progenies; 10 of them are monogenically controlled, 10 others are coded by 2 pairs of alleles. Among the latter, bands 44 and 49 proved to be composed of two proteins. These results are rather different from those put forward by Mecham et al. (1978) who, through the analysis of two F_2 progenies, observed that all the bands were monogenically controlled except for two which split in bidimensional electrophoresis. It is likely that if they had studied, as here, the slow omega gliadins, (21, 22, 25, 26, 28 and 30) they would have found a bigenic control for each band. The size of their F_2, 130 and 136 grains (compared with the 206 and 312 in this study), can also partly account for these different results. Only in part, for when Baker and Bushuk (1978) analyses 78 lines at the sixth generation of selfing they found a monogenic control for 9 bands and a bigenic one for the slow omega gliadins. The study of associations between bands enables the specification of the heredity of these six omega gliadins (Branlard 1982). In addition this analysis has confirmed that there exists genes regulating the expression of structural genes thus accounting for the distribution of classes of concentration of some bands.

Therefore, other progeny analyses are necessary to verify these hypotheses especially using densitometric measurements of relative concentrations. Systematic use of bidomensional electrophoresis whould also permit a better understanding of the genetic determination of alpha, bêta, and gamma gliadins.

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