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Genetic analysis of gliadin-encoding genes reveals gene clusters as well as single remote genes

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Summary. Analysis of F_2 grains from two different crosses has revealed a complex organization of the family of gliadin-coding genes located on chromosomes of the first homoeological group in hexaploid wheat. Chromosome 1A of variety 'Bezenchukskaya 98' was found to carry at least five gliadin-coding genes of which three genes form a cluster controlling the synthesis of the GLD1A1 block. Two additional genes are located on the both sides of this cluster and recombine with it at frequencies of $5 \pm 1.3\%$ and $13 \pm 2.9\%$. Gliadin-encoding genes recombining with the main clusters were also found on chromosomes 1B and 1A in the 'Bezenchukskaya 98' and 'Saratovskaya 210' varieties, respectively. In 'Chinese Spring', widely used in genetic studies, we discovered a recombination between genes located on chromosome 1A and controlling the synthesis of ω- and γ-gliadins. Varieties and biotypes of one variety may differ by the presence or absence of such "selfish" (not included in clusters) gliadin components. The similarity of organization of prolamine-coding genes on chromosomes in different cereals is considered.

Key words: Genetics – Gliadins – Gene clusters – Recombination

Introduction

It is now well known that a wheat storage protein, gliadin, consists of several tens of electrophoretically resolved components and is synthesized by genes located on chromosomes of homoeological groups 1 and 6 (see for reviews Payne et al. 1982, 1984a).

Genetic analyses of electrophoretic gliadin patterns carried out by different authors during the last 10 years have proved that gliadin is inherited, as a rule, in the form of definite groups or blocks of components (Baker and Bushuk 1978; Mecham et al. 1978; Sozinov and Poperelya 1980; Metakovsky et al. 1984a; Payne et al. 1984b). Practically no recombinations between components of allelic variants of blocks have been observed (Sozinov and Poperelya 1980; Metakovsky et al. 1984a; Payne et al. 1984a, b). This result suggests the existence of clusters of closely linked genes which have been mapped in the distal region of the short arms of corresponding chromosomes. On the basis of their study on the inheritance of several groups of storage proteins (low-molecular-weight glutenins, ω- and γ-gliadins), Payne et al. (1984) suggested the existence on wheat chromosomes of the first homoeological group of a complex locus at which closely linked genes controlling the synthesis of these proteins are located. At the same time, other authors reported the existence of a few gliadin-coding genes which were remote from the main cluster and which were able to recombine with it (Branlard 1983; Galili and Feldman 1984; Sobko 1984; Metakovsky et al. 1985a).

Our experience in the analysis of gliadin patterns in different hybrids (Metakovsky et al. 1984a and unpublished) prompted us to study the problem of the existence of such "removed" gliadin-coding genes (or additional gliadin loci) in hexaploid wheat. This paper presents the results of this study and indicates the existence of such genes in a number of varieties, including 'Chinese Spring'.

Materials and methods

The following spring bread wheat varieties were used: 'Bezenchukskaya 98', 'Saratovskaya 210' and 'Tselinogradka', as well as F_2 grains and F_2 plants of 'Bezostaya 1' × 'Chinese Spring' crosses and F_2 seeds of 'Bezenchukskaya 98' × 'Saratovskaya 210' crosses.

Gliadin was extracted from the flour of single grains (or half-grains) with 70% ethanol for 40 min at room temperature. Electrophoresis of extracted proteins was performed in vertical 8.3% polyacrylamide gel slabs in lactate aluminium buffer (1.5 g lactate aluminium per 1 l buffer, pH 3.1) at 550 V

(Novoselskaya et al. 1983; Metakovsky et al. 1984a). To improve the resolution in the ω-region, cathodic buffer with a lower pH value (to 2.9) was used. The gels were stained with Coomassie R-250.

Each one-seed sample was electrophoresed no less than 3 times (in questionable cases up to 7 times) in order to achieve a better resolution and confirm unambiguously the gliadin pattern of the sample. Recombination frequencies and standard errors were estimated according to Allard's (1956) formulae and tables.

Results

1 Intravarietal gliadin heterogeneity of spring bread wheat varieties

In the course of regular analysis of intravarietal gliadin heterogeneity of modern native spring wheat varieties we discovered a number of unrelated varieties whose biotypes differed only by the presence or absence of certain electrophoretic components in the ω-region. Three examples of such varieties are given in Fig. 1. Allelic variants of blocks for six main gliadin-coding loci in these varieties are recognizable (Metakovsky et al. 1984a) and genetic formulae of gliadins can be given. For example, the most frequent biotype of the variety 'Saratovskaya 210' has for chromosomes 1A, 1B, 1D, 6A, 6B, 6D allelic variants of blocks 3.4.3.16.14.2, respectively; in 'Bezenchukskaya 98' – 1.1.6.20.29.11 (Metakovsky et al. 1985a). At the same time, the bands indicated by arrows in Fig. 1 as well as some other components in the ω-region could not be attributed to any of the known blocks identified previously by genetic analysis. In variety 'Tselinogradka' all four biotypes differed only by the presence/absence of two such bands with different electrophoretic mobilities (Fig. 1c). These results suggest that genes controlling the synthesis of such "selfish" gliadin components are independent and are not included in gene clusters controlling the synthesis of any block.

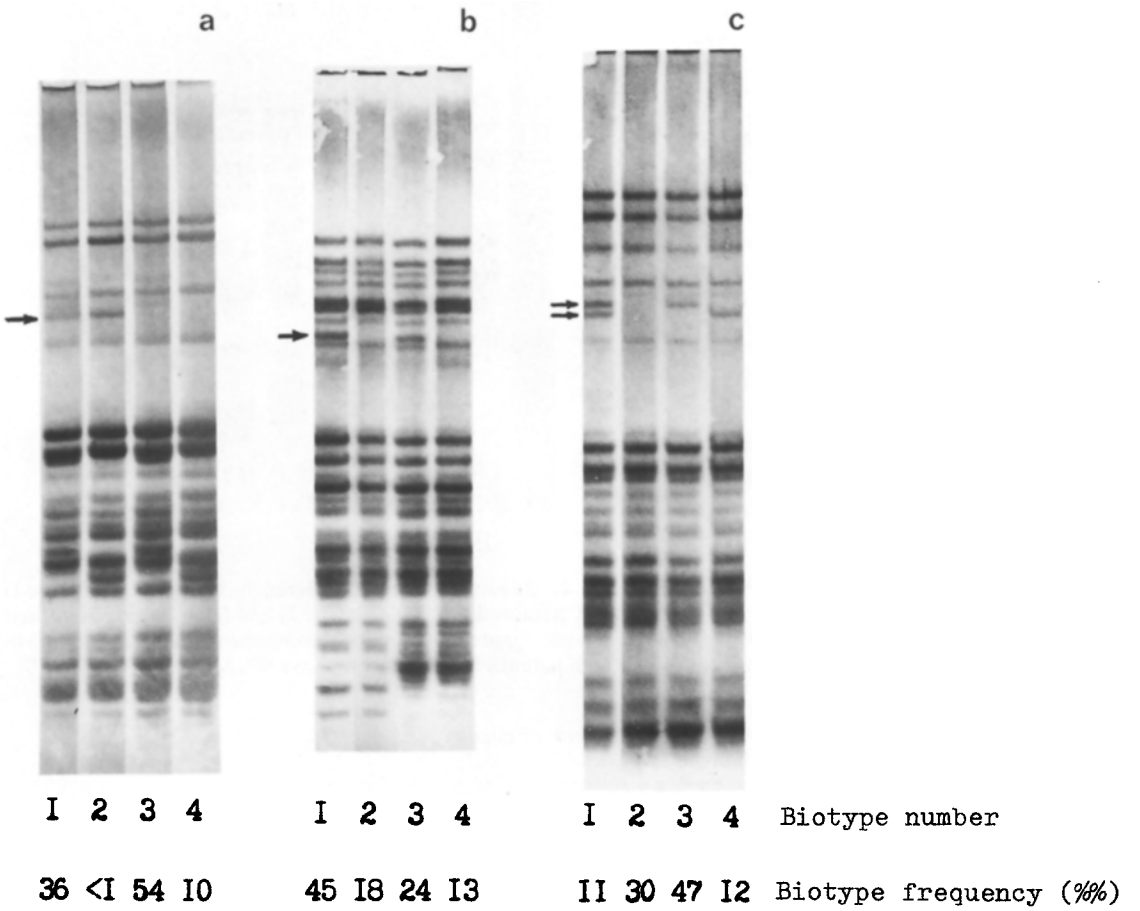

Fig. 1. Electrophoretic patterns of the biotypes of varieties 'Saratovskaya 210' (**a**), 'Bezenchukskaya 98' (**b**) and 'Tselinogradka' (**c**). *Arrows* indicate components that are not included in the blocks. A frequency for each biotype in the population of the variety is given

2 Analysis of F_2 grains from 'Saratovskaya 210'× 'Bezenchukskaya 98' crosses

2.1 'Saratovskaya 210' (biotype 1, Fig. 1a)× 'Bezenchukskaya 98' (biotype 1, Fig. 1b). We have established that "selfish" components of the varieties 'Bezenchukskaya 98' and 'Saratovskaya 210' are most likely identical: in all 30 F_2 grains studied this component had a similar staining intensity (Fig. 2).

2.2 'Saratovskaya 210' (biotype 3, Figs. 1a)× 'Bezenchukskaya 98' (biotype 1, Fig. 1b). Schemes of blocks of gliadin components in the parental biotypes are given in Fig. 3. For each pair of blocks the observed distribution of grains for three phenotypic classes (block from 'Saratovskaya' : both : block from Bezenchukskaya) is in good agreement with the theoretically expected ratio 1 : 2 : 1 (Table 1).

It should be noted that because of the overlapping of some components belonging to different blocks in any cross, an analysis of F_2 grains from a series of crosses of a given variety with others is required in order to determine the composition of all blocks in this variety by one-dimensional electrophoresis (Metakovsky et al. 1985 b). The varieties chosen for this work had blocks with well known component compositions. So, the presence of a certain block may be revealed through the presence of certain non-overlapping bands in the spectrum. Actually, the block *GLD1A1* was identified by the presence of band 14 (and also 6 and 7), *GLD1A3* – by the presence of band 13, *GLD1B1* – bands 10 and 12, *GLD1B4* – bands 9 and 11, *GLD1D6* – band 5 (under special electrophoretic conditions), *GLD1D3* – band 16 (Fig. 3). Unfortunately, under electrophoretic conditions leading to distinct separation of bands 5 and 6 (as in Fig. 1b) components 1 and 2 overlapped with band 10 in F_2 seeds. Therefore, we examined repeatedly the presence of bands 5 and 1/2 in each one-seed sample under slightly different electrophoretic conditions.

The analysis of F_2 grains for the presence-absence of gliadins 1, 2, 3, 4 (see Fig. 3) showed that the first three were inherited in accordance with a ratio of 3 : 1 and that each was therefore controlled by one gene (Table 2). The observed excess of F_2 grains lacking component 4 is apparently the result of a deficiency in the *Gld1A1* allele in the examined sample of F_2 seeds rather than the result of certain peculiarities in the control of its synthesis. It can also seen from Table 2 that component 1 is linked with *GLD1A1*, component 2 with *GLD1A3*, component 3 with *GLD1B1*, and component 4 again with *GLD1A1*. Each of these gliadins is inherited independently of the main gliadin-coding loci of chromosome 1D (Table 2) and chromosomes of the sixth homoeological group (not shown). Genes controlling the synthesis of proteins 1 and 2 are apparently allelic: the ratio of grains in three phenotypical classes is 32 : 75 : 46, which is close to the theoretically expected one for a pair of codominant characters – 1 : 2 : 1 ($\chi^2 = 2.62$, $0.25 < P < 0.50$). The frequency of recombination between genes controlling the synthesis of components 1, 2, 3 and 4 and the main gliadin loci is

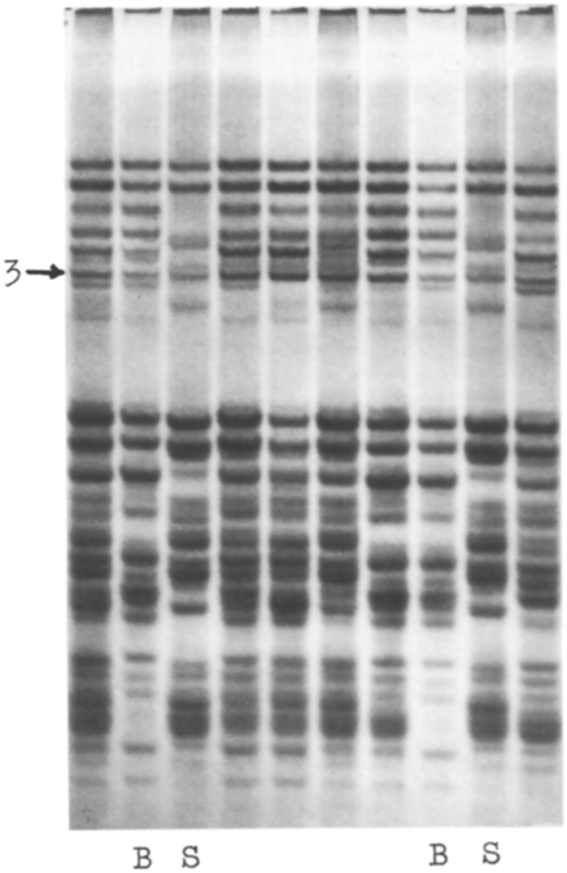

Fig. 2. Gliadin patterns for 'Bezenchukskaya 98' (biotype 1) and 'Saratovskaya 210' (biotype 1) and for F_2 grains from their crosses. Figure 3 designates a component which is identical in both parents. B = 'Bezenchukskaya 98', S = 'Saratovskaya 210'

Table 1. The number of F_2 grains with different allelic variants of block of gliadin components in 'Saratovskaya 210' (biotype 3)×'Bezenchukskaya 98' (biotype 1) crosses

Chromosome	1A	1B	1D	6A	6B	6D
Block from 'Saratovskaya 210'	44	30	35	44	33	40
Heterozygote	89	79	81	72	84	75
Block from 'Bezenchukskaya 98'	30	44	37	37	36	38
χ^2 for a ratio of 1:2:1	2.72	2.72	0.58	1.16	1.59	0.11
$P>$	0.25	0.25	0.75	0.50	0.25	0.90

Table 2. The presence of components 1, 2, 3, 4 on the background of different main gliadin-coding clusters (grain number)

Allelic variant of the main locus	Components							
	1		2		3		4	
	+	−	+	−	+	−	+	−
Gld1A3	3 (a)	41	44	0	29	15	7 (d)	37
Gld1A1 + 1A3	74	5 (e)	75	4 (f)	65	14	65	14 (h)
Gld1A1	30	0	2 (b)	28	23	7	30	0
χ^2 for 3:6:3:1:2:1		151.22		95.49		6.17		107.12
P		$\ll 0.01$		$\ll 0.01$		> 0.25		$\ll 0.01$
Recombination frequency			0.05 ± 0.013			unlinked		0.13 ± 0.03
Gld1B4	22	8	23	7	14 (c)	16	19	11
Gld1B4 + 1B1	52	27	61	18	61	18 (g)	52	27
Gld1B1	33	11	37	7	42	2	31	13
χ^2 for 3:6:3:1:2:1		6.43		5.21		24.31		8.66
P		> 0.25		> 0.25		< 0.01		> 0.10
Recombination frequency		unlinked		unlinked		0.29 ± 0.07		unlinked
Gld1D3	28	7	26	9	23	12	27	8
Gld1D3 + 1D6	56	25	67	14	65	16	50	31
Gld1D6	23	14	28	9	29	8	25	12
χ^2 for 3:6:3:1:2:1		5.71		3.32		3.53		9.77
P		> 0.25		> 0.50		> 0.50		> 0.05
Recombination frequency		unlinked		unlinked		unlinked		unlinked
Total		107:46		121:32		117:36		102:51
χ^2 for 3:1		2.09		1.35		0.26		5.67
P		> 0.25		> 0.25		> 0.75		> 0.025

a, b, c, d, e, f, g, h – types of recombinant spectrums (Fig. 4)
χ^2 for independent segregation of the given component and the main gliadin-coding locus of the given chromosome

given in Table 2. It is of interest that in the case of chromosome 1A recombinations occurred between genes controlling the synthesis of ω- and γ-gliadins, and in the case of chromosome 1B between genes of ω-gliadins since γ-gliadins of allelic blocks *GLD1B1* and *GLD1B4* are identical (Metakovsky et al. 1984a, and the present work). The frequency of recombination between genes controlling "selfish" ω-gliadins 1/2 and 4 calculated from the distribution of seeds in six classes (3 : 6 : 3 : 1 : 2 : 1) is $18 \pm 3.4\%$.

Figure 4 represents examples of most of the types of recombinant patterns. It is seen from Table 2 and Fig. 4 that components 1 and 4, both linked with *GLD1A1*, recombine with this block independently of each other. We found no seeds with simultaneous recombinations for bands 1 and 4. This unexpected result cannot be explained other than by the location of genes controlling the synthesis of proteins 1 and 4 on the opposite sides from the main gliadin-coding cluster (*Gld1A1* allele).

Of particular interest are two recombinants (Fig. 4, Nos. 4 and 11). It can be seen that in both cases recombinations between genes controlling component 1 and *GLD1A1* are accompanied by the loss (No. 11) or acquisition (No. 4) of band 7 which is an invariable member of the block *GLD1A1* (Metakovsky et al. 1984a). Under electrophoretic conditions at which components 5 and 6 differ in their electrophoretic mobility it was discovered that component 6 in recombinants Nos. 11 and 4 disappeared and appeared together with band 7 (not shown). No other cases of alteration in the composition of the *GLD1A1* block have been registered in the present work.

3 Analysis of 'Bezostaya 1' × 'Chinese Spring' crosses

3.1 Analysis of F_2 grains. The genetic control of all gliadin components identified under our conditions of one-dimensional electrophoresis in the varieties 'Bezostaya 1' (Metakovsky et al. 1985b) and 'Chinese Spring' (Metakovsky et al. 1984a) was established earlier (Fig. 5). The short arm of chromosome 1A in Chinese Spring is known to control the synthesis of at least 4 gliadin components: one in the ω-region, two in the γ-region and one in the β-region of the elctrophoretic spectrum (Metakovsky et al. 1984a; Payne et al. 1984a). In the present work we studied the recombination of

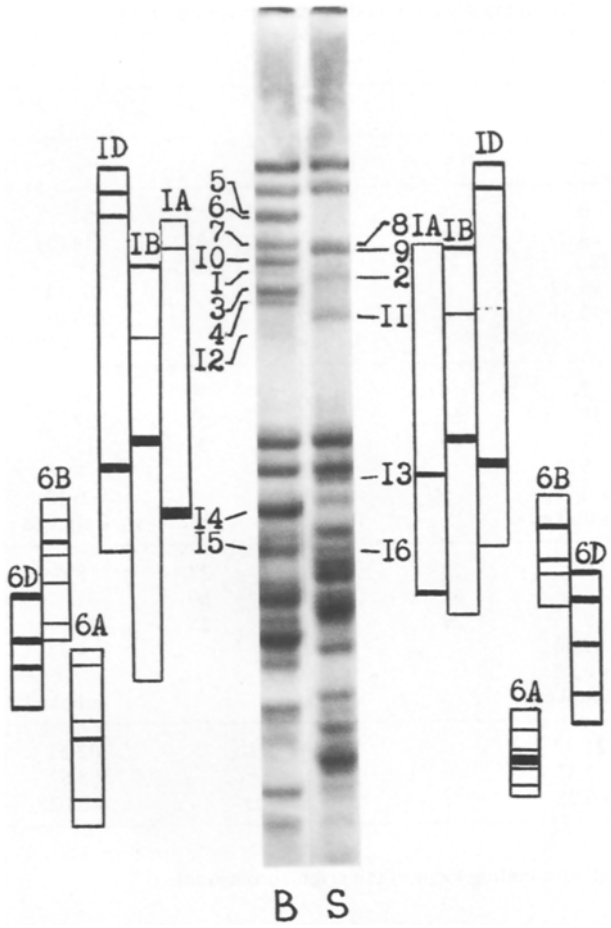

Fig. 3. Gliadin patterns for 'Bezenchukskaya 98' (biotype 1) and 'Saratovskaya 210' (biotype 3) and blocks of jointly inherited components. 1, 2, 3, 4, = "selfish" components that are not included in the blocks

genes coding for the synthesis of gliadins 1 and 2+3 (see Fig. 5) since the minor γ-gliadin controlled by chromosome 1A of 'Chinese Spring' and bands of 'Bezostaya 1' overlapped in F_2 grains.

Two hundred and sixty F_2 grains from 'Bezostaya 1' × 'Chinese Spring' crosses have been studied. The observed number of grains in 3 phenotypical classes for each of the 6 pairs of alleles of the main gliadin-coding loci (Fig. 5) is in good agreement with the theoretically expected ratio (1 : 2 : 1): for chromosomes 1A, 1B, 1D, 6A, 6B, 6D χ^2 is 2.03, 3.53, 1.68, 3.16, 0.74, 1.68, respectively. One hundred and eighty (out of 260) randomly selected samples were analysed for the presence or absence of components 1, 2+3, 4 and 5, controlled by chromosome 1A in the given varieties (Fig. 5). The presence/absence of component 1 and 4 was determined unambiguously in 170 and 155 grains (out of 180), respectively. The main difficulty was to distinguish the absence of the component from its presence when it was found in one dose in the triploid endosperm. Analogous difficulties in identifying the presence of some minor components have been encountered previously by other authors (Mecham et al. 1978).

Components 1 and 4 were shown to be inherited in accordance to a ratio of 3 : 1 and therefore to be controlled by one gene: $\chi^2 = 0.48$, $0.25 < P < 0.50$ for component 4; $\chi^2 = 0.38$, $0.50 < P < 0.75$ for component 1. The distribution of 146 out of 180 grains with the unambiguously determined presence/absence of both components 1 and 4 for three phenotypical classes shows that corresponding genes are allelic (Table 3). The data of Table 3 permitted us to estimate the

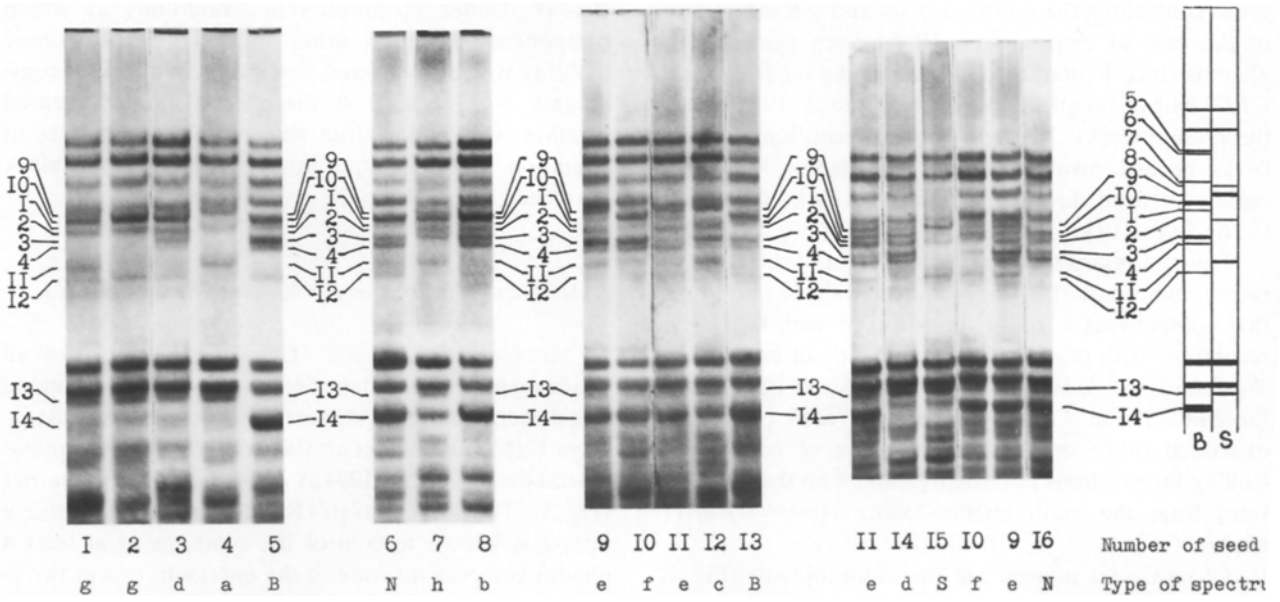

Fig. 4. Gliadin patterns for 16 different F_2 grains from crosses between 'Saratovskaya 210' (biotype 3) and 'Bezenchukskaya 98' (biotype 1). ω- and γ-regions of the electrophoretic spectrum are presented: a–h = types of recombinants (see Table 2). N = norm. On the right – a scheme of component distribution

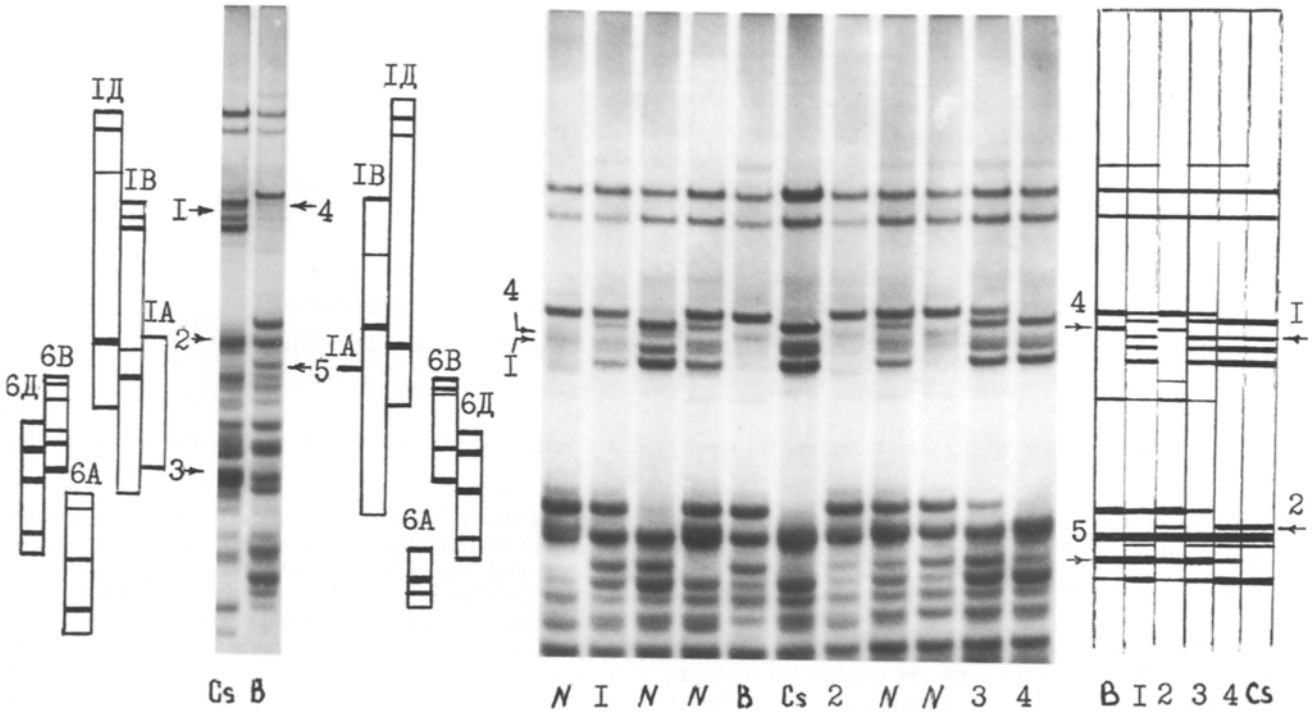

Fig. 5. Blocks of gliadin components in 'Bezostaya 1' and 'Chinese Spring' and several patterns patterns of gliadin of F_2 grains from their crosses: B = 'Bezostaya', CS = 'Chinese Spring'. N = norm, 1–4 = recombinant patterns

Table 3. The number of F_2 grains from 'Bezostaya 1' × 'Chinese Spring' crosses in different phenotypical classes

Components	2+3	(2+3)+5	5	Total
1	12	19	5	36
1+4	15	35	15	65
4	6	16	23	45
Total	43	70	33	
χ^2 (1:2:1) and P for components 2+3 and 5		$\chi^2 = 1.62$; $P > 0.25$		
χ^2 (1:2:1:2:4:2:1:2:1) for independent segregation of two pairs of components		$\chi^2 = 26.47$; $P < 0.01$		
χ^2 (1:2:1) and P for components 1 and 4		$\chi^2 = 2.92$; $P > 0.10$		

Table 4. The number of F_2 plants from 'Bezostaya 1' × 'Chinese Spring' crosses in different phenotypical classes

Components	4	4+5	5	Total
1	7	3	3	13
1+(2+3)	11	24	5	40
2+3	0	5	11	16
Total	18	32	19	
χ^2 (1:2:1) and P for components 2+3 and 5		$\chi^2 = 0.39$; $P > 0.75$		
χ^2 (1:2:1:2:4:2:1:2:1) for independent segregation of two pairs of components		$\chi^2 = 27.06$; $P < 0.01$		
χ^2 (1:2:1) and P for components 1 and 4		$\chi^2 = 1.89$; $P > 0.25$		

frequency of recombination between these genes and the main gliadin-coding locus of chromosome 1A which appeared to be $36 \pm 3.7\%$.

Several recombinant patterns are shown in Fig. 5. Of special interest are examples 1 and 3 which clearly have component 1 but lack a 1A-controlled block including components 2+3. Since there were no difficulties in identifying bands 2+3, patterns of such types may be interpreted only as recombinant.

3.2 Analysis of F_2 plants by F_3 grains. To prove the occurrence of a recombination between gliadin genes located on chromosome 1A in Chinese Spring, we determined genotypes for the character under study in 69 F_2 plants. In each plant 10 to 12 F_3 grains from the main spike were analysed. The plant was considered heterozygous if we observed segregation for the presence of components 1/4 and/or 2+3/5 among F_3 grains from this plant. The distribution of plants for

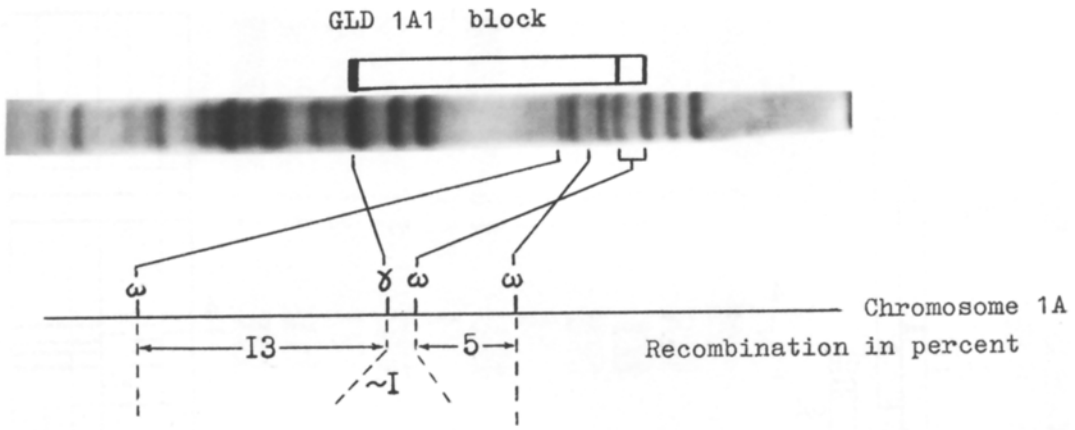

Fig. 6. The gliadin pattern in 'Bezenchukskaya 98' (biotype 1) and a scheme of distribution of some genes controlling the gliadin synthesis on chromosome 1A in this variety

phenotypical classes is presented in Table 4. It is seen that the analysis of F_2 plants through F_3 grains confirms the results of the analysis of F_2 grains.

Discussion

The results of the present work are interpreted by us as representing a complex organization of the family of gliadin-coding genes. On the one hand, the majority of gliadin electrophoretic bands are controlled by clusters of closely linked genes.

In bread wheats there are 6 gene groupings of such a kind due to which the electrophoretic spectrum of any variety or specimen is divided into 6 independently inherited groups (blocks) of components and may be described by a genetic formula (Sozinov and Poperelya 1980; Metakovsky et al. 1984a). One cluster may include up to 10 genes, and the recombination between genes of allelic clusters is undetectable in the analysis of hundreds of F_2 grains by one-dimensional electrophoresis (Sozinov and Poperelya 1980; Metakovsky et al. 1984a) or more than 100 grains by two-dimensional electrophoresis of high resolution (Metakovsky et al. 1984b).

On the other hand, the analysis of inheritance of some gliadin electrophoretic components shows that genes coding for them are not members of any of the six main clusters. The recombination between gliadin-coding genes located in one chromosome was described for the first time by Mecham et al. (1978). Judging by the patterns presented in this work, recombination was observed between ω- and γ-gliadins (ω_4 and γ_5) which are controlled by chromosome 1B in the 'Justin' variety and which are clearly a part of the *GLD1B1* block found widely spread in different varieties. When analysing F_2 grains from many intervarietal crosses involving varieties with the block *GLD1B1* we did not find recombinations between the mentioned components of this block (Metakovsky et al. 1984a and unpublished). They are apparently controlled by closely linked genes. Later the authors of this paper (Mecham et al. 1978) refused to interpret the observed patterns as recombinant (cited from Payne et al. 1984b). Branlard (1983) suggested that the differences noted by him between F_2 grains in the staining intensity of band 44 in the variety 'Joss' are due to the fact that this band consists of two proteins whose synthesis is controlled by genes located at a distance of 24.8 recombination units from each other. Judging by the spectra presented, component 44 is present in the same gel region where "selfish" components were detected by us. It cannot be excluded that in some electrophoresis systems two gliadins controlled by recombinating genes will have similar electrophoretic mobilities. Galili and Feldman (1984) discovered in the line CS ('Thatcher-1B') a band recombining with both the gliadin and glutenin loci of chromosome 1B. A similar frequency of recombination between the gene controlling the synthesis of the "selfish" component and the main gliadin cluster of chromosome 1B in the variety 'Bezenchukskaya 98' and in the line CS ('Thatcher-1B') as well as a similar molecular weight of corresponding components identified by SDS-electrophoresis (not shown) suggest a possible identity of these two proteins. Finally, monofactorially inherited components recombining with the main cluster of gliadin genes of chromosomes 1A and 1B were detected in varieties 'Bezostaya 1' (Sobko 1984) and 'Bogarnaya 56' (Seitova et al. 1986), respectively. The frequency of recombination between genes of chromosome 1A in 'Bezostaya 1' estimated in this work ($36 \pm 3.7\%$) is in good agreement with the data obtained by Sobko (1984) ($31 \pm 3.2\%$).

The results of the present work show clearly that a large number of members of the family of gliadin-coding genes are assembled into tightly linked clusters, some of them, however, being located at a distance from these clusters and able to recombine with them. There may be several "selfish" genes on one chromosome at once. According to our results, the family of gliadin genes of chromosome 1A in 'Bezenchukskaya 98' is organized as shown in Fig. 6. On this chromosome there are genes controlling the synthesis of at least 4 ω-gliadins and 1 γ-gliadin. Among these five genes there is a cluster which controls the synthesis of the *GLD1A1* block (2 ω-gliadins plus 1 γ-gliadin) widely spread in different varieties including the well-known variety 'Marquis' (Metakovsky et al. 1984a). On both sides of this cluster there are genes controlling the synthesis of two more ω-gliadins. The orientation of this family of gliadin genes with respect to the loci of LMW- and HMW-glutenins and with respect to the centromere remains unknown. It should be noted that we detected two recombinants in which both genes of ω-gliadins had separated from the gene of γ-gliadin, i.e. in which an intracluster recombination had occurred. Such a

recombination is a very rare phenomenon since an overwhelming majority of blocks which are found in the modern commercial varieties are also present in local and ancient wheats (Sozinov et al. 1986 and unpublished).

The organization of the family of gliadin genes in chromosomes of at least the 1st homoeological group (Fig. 6) is analogous to the situation with hordein-coding genes located on chromosome 5 in barley. Genetic analysis of electrophoretic hordein components in many varieties showed that three main hordein-coding clusters (*Hrd A, Hrd B, Hrd F*) control the synthesis of blocks and individual hordein components which constitute a major part of prolamines of grain.

There are multiple alleles for these loci differing in number, staining intensity and electrophoretic mobility of certain hordein bands (Pomortsev et al. 1986). The synthesis of some minor components is controlled by several genes (loci) recombining with each other and with the main clusters, all these additional loci being detected only by the presence or absence of certain hordein components in the spectrum (Sozinov et al. 1978). It should be noted in this connection that the application of the term "locus" with respect to such recombining prolamine-coding genes is hardly expedient. The inevitable future discovery of a recombination within the main cluster and estimation of genetic distances between genes composing it will compel us to regard this cluster also as a group of individual "loci". Considerable differences in the number of genes composing clusters in different varieties (Metakovsky et al. 1984a; Pomortsev et al. 1985) will complicate markedly the nomenclature used to describe this family of genes. In our opinion, the term "locus' is suitable only to designate genes and gene clusters for which alleles differing in the mobility of controlled prolamine components are known.

Several "selfish" gliadin-coding genes recombining with the main cluster were found in winter durum wheat (Panin et al. 1986). In maize zein-controlling genes are scattered over several chromosomes but three of them are linked in a tight cluster (Soave and Salamini 1984). The existence of clusters and removed single genes on the same chromosomes is probably a distinctive feature of the family of prolamine-coding genes in cereals.

Gliadin-coding genes removed from the main cluster and controlling the synthesis of minor components are apparently located on other gliadin-coding chromosomes also (probably on all). In most cases, however, only single gliadin components which do not overlap other components are accessible for analysis. The detection of such "selfish" genes removed from the main gene cluster will make it possible to use them as additional independent markers and therefore to control a significantly larger region of chromosomes of the 1st and 6th homoeological groups through analysis of the gliadin spectrum only.

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