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Recombination mapping of *Gli-5*, a new gliadin-coding locus on chromosomes 1A and 1B in common wheat

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Abstract. Inheritance studies of gliadin loci on chromosomes 1A and 1B were carried out in the progeny from crosses between cv "Salmone" and six other common wheat varieties. The map distance between the *Rg-1* locus for glume colour and the gliadin locus *Gli-B1* on the satellite of chromosome 1B was calculated as 2.0 ± 0.6 cM. An additional gliadin locus, *Gli-B5*, was mapped between *Gli-B1* and *Rg-1*, 1.4 cM from the former. A genetic distance of 1.8 ± 0.4 cM was obtained between the *Hg-1* locus for hairy glumes and a gliadin locus that seems to be remote from *Gli-A1* and homoeologous to *Gli-B5*. Statistically significant differences in recombination values were found in the six crosses, indicating the influence of genotype on the frequency of recombination. The similarity in chromosomal location of seed storage protein genes in wheat, barley and rye is discussed.

Key words: Gliadin genes – Storage proteins – Morphological markers – Recombination mapping

Introduction

Several polypeptides belonging to the glutenin or gliadin fraction of storage proteins of the wheat kernel have been found to be encoded by genes on the short arms of chromosomes 1A and 1B. The *Gli-A1* locus on chromosome 1A and the *Gli-B1* locus on chromosome 1B each contains three to ten active genes coding for ω-, γ- and some β-gliadins (Payne 1987; Metakovsky 1991), whereas the *Glu-A3* and *Glu-B3* loci, which are tightly linked to *Gli-A3* and *Gli-B3*, respectively (Singh and Shepherd 1988; Pogna et al. 1990), control the synthesis of several low-molecular-weight (LMW) subunits of glutenin (Gupta and Shepherd 1990).

In addition, other loci coding for grain storage proteins have been mapped on the short arms of chromosomes 1A and 1B. Most of these proteins relate to the ω-gliadins on the basis of their solubility in alcohol-water solutions under non-reducing conditions and their location in the ω-region of the gliadin pattern after acidic, polyacrylamide gel electrophoresis (A-PAGE). For example, an additional *Gli-B3* locus has been mapped on the short arm of chromosome 1B between *Gli-B1* and the centromere, 22–28 cM from the former (Galili and Feldman 1984; Jackson et al. 1985; Metakovsky et al. 1986a, b; Dachkevitch et al. 1993). It was suggested that in different genotypes this locus codes either for ω-gliadins or for subunits of the D group of LMW glutenin (Payne et al. 1988). On the short arm of chromosome 1A, a gliadin locus was mapped at a position comparable to that of *Gli-B3* (Sobko 1984; Sobko et al. 1986; Metakovsky et al. 1986a; Payne and Metakovsky 1986, unpublished results), and therefore named *Gli-A3* (Payne et al. 1988). Moreover, the short arm of this chromosome in cv 'Bezenchukskaya 98' has been found to produce at least three ω-gliadins whose synthesis is controlled by genes located on both sides of the *Gli-A1* locus, 13%, 5% and about 1% recombination from it, respectively (Metakovsky et al. 1986a). The first of these three genes is likely to be an allele of the new locus, *Gli-A4*, which lies between *Gli-A1* and the centromere, 10 cM from the former (Redaelli et al. 1992).

The aim of the investigation presented here was to study the inheritance of gliadin genes on the short arms of chromosomes 1A and 1B using the *Hg-1* and *Rg-1* loci conditioning glume morphology as markers for recombination mapping.

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Materials and methods

Plant material

The F_2 progeny from four double-parent crosses between bread wheat cv 'Salmone' and cvs 'Asiago', 'Centauro', 'Claudia' and 'Pandas' were analysed. The BC-like progenies from the three-parent crosses ('Salmone' × 'Irnerio') × 'Orso' and ('Salmone' × 'Orso') × 'Irnerio' were also used for analysis.

Cultivar 'Salmone' has hairy, red glumes due to the presence of the dominant alleles *Hg-1* and *Rg-1*, respectively (McIntosh and Bennet 1978). All of the other parents possess the recessive alleles *hg-1* (hairless glume) and *rg-1* (white glume).

The F_2 plants from the double-parent crosses and the F_1 plants from the three-parent crosses were grown in the field and analysed for spike morphology.

Electrophoretic analyses

Gliadins were extracted from 50 mg of whole meal obtained from more than 20 seeds from each spike using 150 μl of a solution containing aqueous 35% (v/v) ethanol, 30% (w/v) glycerol and 0.03% (w/v) pyronine G, for 1 h at room temperature. After centrifugation for 5 min at 20,000 *g*, the clarified supernatant was fractionated by A-PAGE at pH 3.1 as previously described (Pogna et al. 1990). A-PAGE analyses of gliadins from single seeds were performed as described by Metakovsky and Novoselskaya (1991).

Gliadins were also fractionated by two-dimensional electrophoresis: in the first dimension by A-PAGE, and in the second dimension by sodium dodecyl sulfate, polyacrylamide gel electrophoresis (SDS-PAGE), as described by Payne et al. (1984b), except the separating gel in the second dimension was 15% acrylamide, pH 8.4.

Calculation of recombination frequency

The recombination frequency between the genes and its standard deviation were calculated using the method of maximum likelihood (Allard 1956). The genetic distances were calculated using the Kosambi function (Kosambi 1944).

Results

The fractionation of gliadins from cv 'Salmone' using two-dimensional A-PAGE/SDS-PAGE electrophoresis (Fig. 1A) showed about 28 major components including S3, S4, S5, S6, S7 and S8 whose inheritance patterns were investigated in this work using segregating progeny. In one-dimensional A-PAGE, gliadins S3, S6, S7 and S8 could be recognised for their distinctive mobilities, whereas S4 and S5 appeared as separate bands only in some gels.

Inheritance of genes located on the short arms of chromosomes 1A and 1B in six crosses

'Salmone × Pandas'

The segregation of gliadins S3, S6 S7 and S8 from 'Salmone' and P3, P4 and P5 from 'Pandas' could be followed in A-PAGE (Fig. 2a). The 205 progenies of this cross were also classified for glume colour and hairiness. Gliadins S7 and S8 and gliadins P3, P4 and P5 behaved as single Mendelian units. The ratio of the phenotypic classes for ω-gliadins S7+S8 and P3+P4+P5 agreed well with the expected 2:1:1 if two codominant alleles at a single locus controlled the synthesis of these proteins. Moreover, S7+S8 showed linkage with the red-glume allele *Rg-1* located on the short arm of chromosome 1B (Poperelya et al. 1980, Payne et al. 1984a; Pogna et al. 1985) and, therefore, were assigned to the *Gli-B1* locus. Gliadin S3 showed no linkage with P3+P4+P5 or S7+S8. In contrast, its linkage with the hairy glume allele *Hg-1* on the short arm of chromosome 1A (McIntosh and Bennet 1978, Sobko and Poperelya 1982) was highly significant, therefore, protein S3 was assigned to this chromosome.

The analysis of two-dimensional A-PAGE × SDS-PAGE electrophoregrams of several F_2 genotypes suggested that gliadins S3 and S5 did not segregate independently; linkage was also observed between gliadins S7+S8 and S4+S6. Unfortunately, the segregation of gliadins S4 and S5 was difficult to follow by A-PAGE because of their similar electrophoretic mobilities. Therefore, it was decided to follow the segregation of proteins S4 and S5 in progeny lacking gliadins S3 or S7+S8, respectively. The results of this analysis confirmed a complete linkage between S4+S6 and S7+S8, and between S3 and S5. Co-segregation of S3 and S5 was observed in all of the crosses analysed in the present study.

'Salmone' × 'Centauro'

Figure 2b shows typical A-PAGE patterns of seeds from single F_2 plants. In total, 186 plants were studied in this cross. Gliadin C3 from cv 'Centauro' was always inherited with C4, the segregation data for this pair of bands and gliadin S7 being close to the 2:1:1 ratio for two codominant alleles. As expected, the linkage between band S7 and *Rg-1* and between band S3 and *Hg-1* was highly significant. In the progeny lacking S3, a complete linkage was found between S7 and S4+S6.

'Salmone' × 'Claudia'

Electrophoretic patterns of gliadins of some of the 265 plants obtained from this cross are shown in Fig. 2c. As in the previous cross, gliadin S7 and S3 showed significant linkage with *Rg-1* and *Hg-1*, respectively. Gliadin C4 from 'Claudia was found to be allelic to S7.

In the progeny lacking S3, four phenotypic classes for the presence/absence of S7 and S4+S6 were observed: two classes corresponded to the parental phenotypes, whereas the third and fourth class were represented by 1 white glume plant containing gliadin S7 in the absence of gliadins S4+S6 (Fig. 2c, line 4) and 1 red glume plant with S4+S6 but without S7 (Fig. 2c, lane 6) respectively. These genotypes originated from infrequent recombination between *Gli-B1* (band S7) and a new locus, provi-

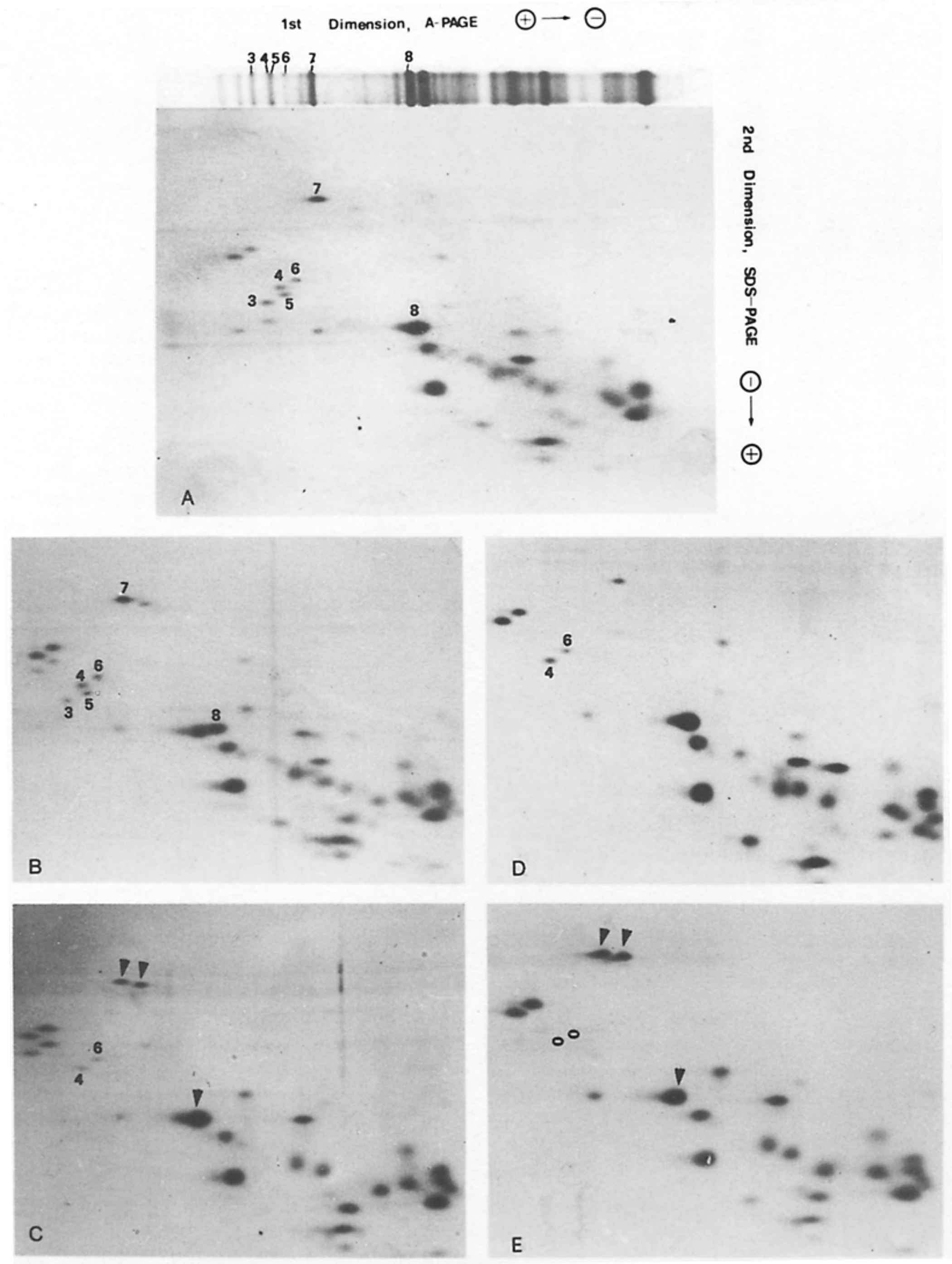

Fig. 1 A–E. Two-dimensional A-PAGE × SDS-PAGE fractionation of gliadins from **A** 'Salmone', **B** 1:1 mixture of 'Salmone' and 'Costantino', **C** 'Costantino', **D** 'Siete Cerros' and **E** 'Pandas'. One-dimensional A-PAGE (*top*) of gliadins from 'Salmone' is also shown. *Arrowheads* indicate ω- and γ-gliadins coded by the *Gli-B1m* allele in 'Costantino' and 'Pandas'. The *open circles* in E show the map positions of ω-gliadins 4 and 6 coded at the *Gli-B5* locus

sionally named as *Gli-B5*, which controls the synthesis of gliadins S4 + S6. As in the previous crosses, no recombination occurred between bands S4 + S6 and *Rg-1*, suggesting that the gene order is either *Gli-B1* – *Gli-B5* – *Rg-1* or *Gli-B1* – *Rg-1* – *Gli-B5*.

'Salmone' x 'Asiago'

In the 270 progenies from this cross, gliadin A3 from 'Asiago' was found to be allelic to gliadin S7 from 'Salmone' (Fig. 2d). In the progeny lacking S3 one white

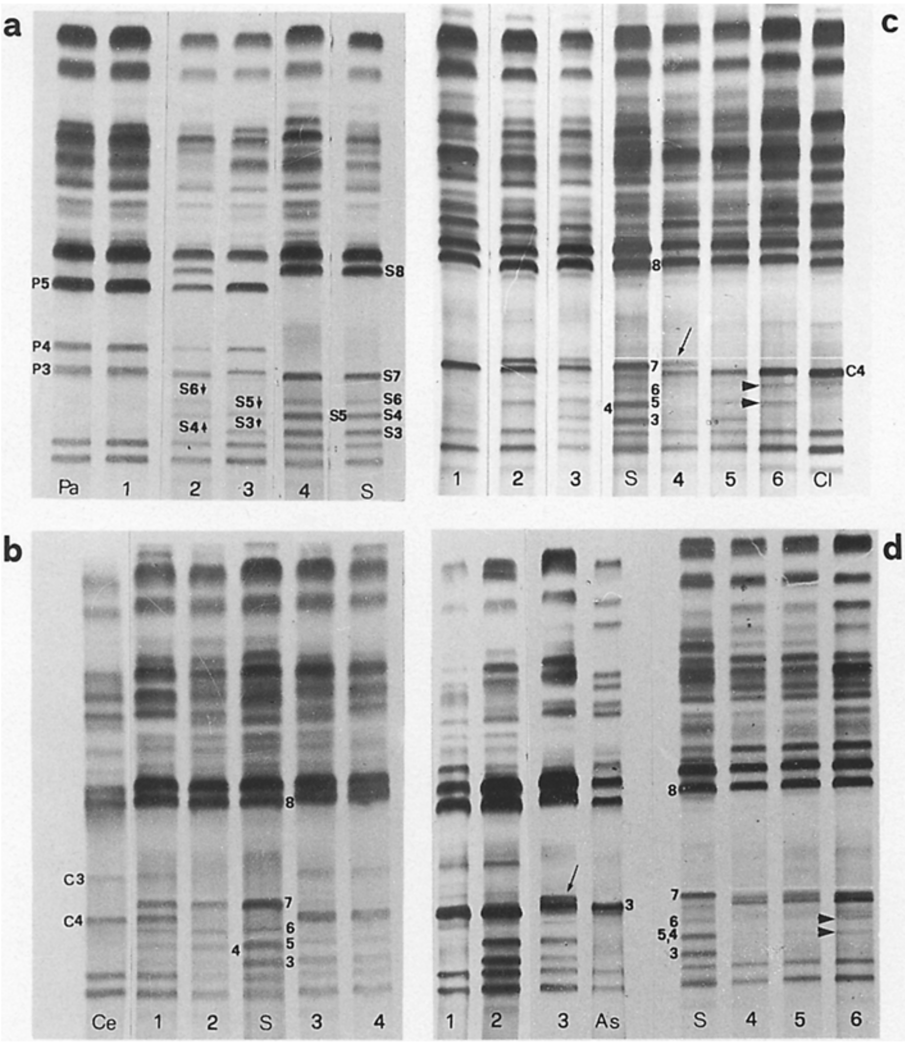

Fig. 2a–d. A-PAGE fractionation of gliadins of the progeny from crosses. Gliadins analysed by recombination mapping are *numbered*. **a** 'Salmone' (*S*) × 'Pandas' (*Pa*); *lane 1* white, hairless glumes, *2* red, hairless glumes, *3* white, hairy glumes, *4* red, hairy glumes. **b** 'Salmone' (*S*) × 'Centauro' (*Ce*); *Lanes 1–2* red, hairy glumes; *3–4* white, hairy glumes. **c** 'Salmone' (*S*) × 'Claudia' (*Cl*); *Lane 1* white, hairless glumes, *2* red, hairless glumes, *3* red, hairless glumes (recombinant genotype), *4* white, hairy glumes, *5* red, hairy glumes (recombinant), *6* red, hairless glumes (recombinant). *Arrow* indicates gliadin S7 in one genotype lacking bands S4+S6. *Arrowheads* show bands S4+S6 in one genotype lacking gliadin S7. **d** 'Salmone' (*S*) × 'Asiago' (*As*); *lane 1* white, hairless glumes, *2* white, hairy glumes, *3* red, hairy glumes, *4–6* red, hairless glumes (recombinant). *Arrow* indicates gliadin S7. *Arrowheads* show bands S4+S6 in one genotype lacking gliadin S7

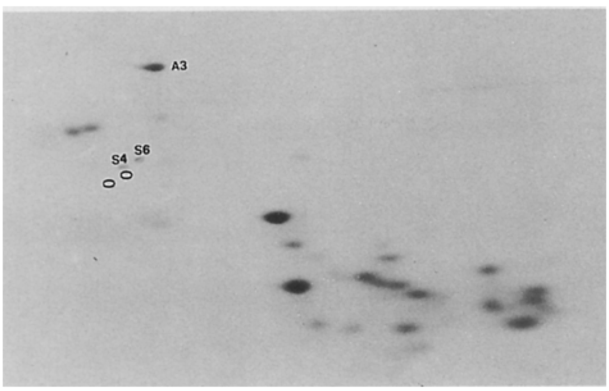

Fig. 3. Two-dimensional A-PAGE × SDS-PAGE fractionation of gliadins from the recombinant genotype shown in lane 6 of Fig. 2d. *A3* ω-gliadin encoded by the *Gli-B1* allele from 'Asiago', *S4* and *S6* ω-gliadins encoded by the *Gli-B5* allele from 'Salmone'. The *open circles* indicate the map positions of gliadins S3 and S5 from 'Salmone'

glume genotype had band S7 without bands S4+S6, whereas four red glume genotypes had bands S4+S6 without band S7 (Fig. 2d, lane 6). The presence of S4+S6 in one of these four recombinants is shown in the two-dimensional map of Fig. 3.

Moreover, one recombinant lacking both S4+S6 and S7 showed red glumes (Fig. 2d, lane 4) as a result of a rare recombination event between *Gli-B5* and *Rg-1*. The absence of gliadins S4+S6 and S7 in this genotype indicates that the most probable gene order is *Gli-B1* –*Gli-B5* – *Rg-1*.

('Salmone' × 'Orso') × 'Irnerio' and ('Salmone' × 'Irnerio') × 'Orso'

The A-PAGE patterns of some progeny from these crosses are shown in Fig. 4. No linkage between S3 and S7 and significant linkage between S7 and *Rg-1*, as well as between S3 and *Hg-1*, were observed in these crosses.

In progeny lacking S3, 2 recombinant plants were found for gliadins S4+S6 and *Rg-1* in the cross ('Salmone' × 'Irnerio') × 'Orso'. One of these had white glumes plus gliadins S4+S6 and S7, the other lacked all of these proteins and showed red glumes.

Recombination values between gliadin loci Rg-1 and Hg-1

The recombination values between *Gli-B5* and *Rg-1* in the six crosses varied from 0.0% to 3.0% (Table 1). The combined recombination percentage was calculated as $0.6 \pm 0.5\%$, and the χ^2 value of the homogeneity test was not significant.

The recombination values between *Gli-B1* and *Gli-B5* varied from 0.0% to 5.9%, and the χ^2 value of the homogeneity test for the combined recombination value of $1.4 \pm 0.4\%$ was highly significant, indicating genotypic influence on the frequency of recombination.

Recombination data from individual crosses suggest that *Gli-B5* lies between *Gli-B1* and *Rg-1*. This conclusion is supported by the segregation data reported in Table 1, thus making the alternative order *Gli-B1* – *Rg-1* – Gli-B5 quite unlikely. The appropriate genetic distance between *Gli-B1* and *Rg-1* (2.0 ± 0.6 cM) was assumed to be the sum of the distance between *Gli-B1* and *Gli-B5* (1.4 cM) plus the distance between *Gli-B5* and *Rg-1* (0.6 cM).

The frequencies of recombination between S3+S5 and *Hg-1* in the six crosses varied from 0.0% to 5.5%. The combined value of recombination was calculated to be $1.8 \pm 0.4\%$ (Table 1), the χ^2 value of the homogeneity test being highly significant. However, the map distance of 1.8 cM was assumed as the most appropriate estimation of the genetic distance between these loci.

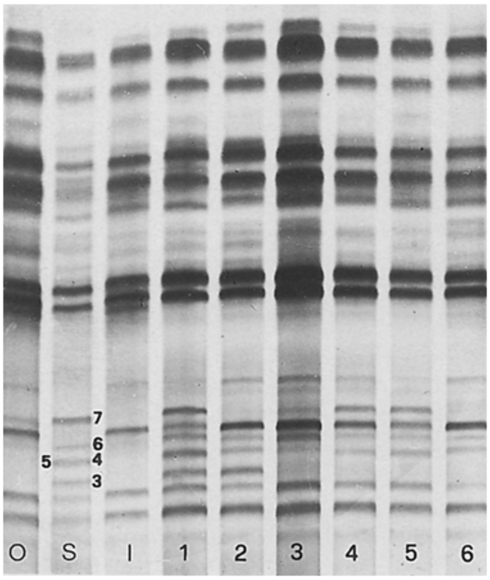

Fig. 4. A-PAGE fractionation of gliadins of the progeny from the cross ('Salmone' × 'Irnerio') × 'Orso'. Gliadins analysed by recombination mapping are *numbered. Lane 0* 'Orso', *S* 'Salmone', *I* 'Irnerio', *1* red, hairy glumes, *2* white, hairy glumes, *3* white, hairless glumes, *4* red, hairless glumes, *5* red, hairy glumes (recombinant genotype), *6* red, hairless glumes (recombinant)

Occurrence of gliadins S4+S6 in common wheat cultivars of different origin

Analysis of the A-PAGE gliadin patterns obtained by two different A-PAGE procedures (Pogna et al. 1990; Metakovsky and Novoselskaya 1991) showed that two bands with the same electrophoretic mobilities and staining intensities as gliadins S4 and S6 are present in apparently unrelated common wheat cultivars (Fig. 5). This result was confirmed by two-dimensional separations A-PAGE × SDS-PAGE (Fig. 1 C–E). Moreover, fractionation of the 1:1 mixture of gliadin extracts from the unrelated cultivars 'Salmone' and 'Costantino' showed coincidence of these gliadins in the two-dimensional map

Table 1. Percentage of recombination between pairs of segregating loci in the F_2 and BC-like progenies from six crosses

Cross	Type of cross	Number of plants analysed	Pair of loci[a]			
			Gli-A5-Hg-1	*Gli-B1-Gli-B5*	*Gli-B5-Rg-1*	*Gli-B1-Rg-1*
Salmone × Pandas	F_2	205	1.8 ± 1.0	0.0	0.0	0.0
Salmone × Centauro	F_2	186	0.5 ± 0.7	0.0	0.0	0.0
Salmone × Claudia	F_2	265	3.3 ± 1.1	2.7 ± 2.0	0.0	2.7 ± 1.1
Salmone × Asiago	F_2	270	0.0	5.9 ± 2.8	1.2 ± 1.1	4.76 ± 1.4
(Salmone × Orso) × Irnerio	BC-like	313	1.9 ± 0.8	0.0	0.0	0.0
(Salmone × Irnerio) × Orso	BC-like	116	5.5 ± 2.0	0.0	3.0 ± 2.1	2.4 ± 1.4
Average value			1.8 ± 0.4	1.4 ± 0.4	0.6 ± 0.5	1.7 ± 0.4
Homogeneity test (χ^2)			16.7**	19.2**	5.5 ns	30.0**
Map distance (cM)			1.8 ± 0.4	1.4 ± 0.4	0.6 ± 0.5	1.7 ± 0.4

** $P < 0.01$; ns, not significant

[a] The gliadins coded by each locus are: S3+S5 (*Gli-A5*), S7+S8 (*Gli-B1*) and S4+S6 (*Gli-B5*)

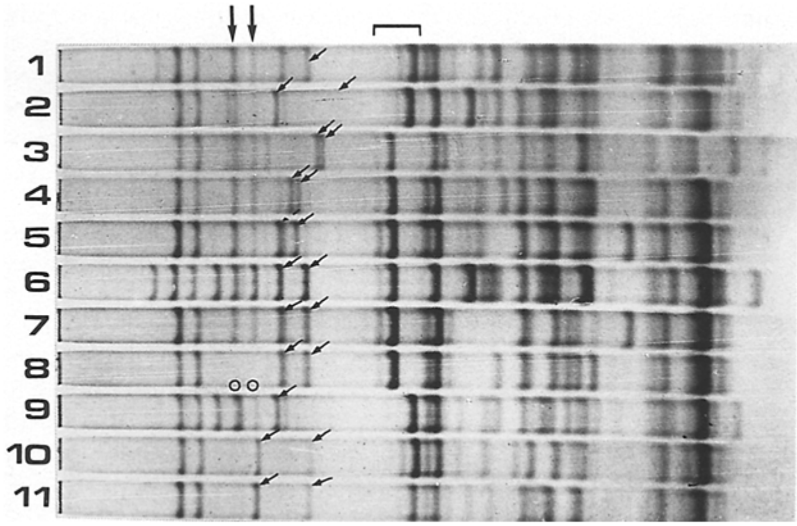

Fig. 5. Gliadin fractionation (A-PAGE) according to Metakovsky and Novoselskaya (1991). *Lane 1* 'Siete Cerros', *2* 'Kzul-Bas', *3* 'Insignia', *4* 'Levent' (biotype), *5* 'Kremena', *6* 'Pyrotrix 28', *7* 'Constantino', *8* 'Pandas', *9* 'Salmone', *10* 'Centauro', *11* 'Orso'. γ-Gliadins (*brackets*) and ω-gliadins (*small arrows*) controlled by *Gli-B1* are shown. ω-Gliadins controlled by *Gli-B5* (*big arrows*) are absent in cv 'Pandas' (*open circles*). Cultivars 'Orso', 'Centauro' and 'Pandas' have white glumes; all other cultivars have red glumes

(Fig. 1 B). These bands have been previously found to be controlled by chromosome 1B and assigned to different *Gli-B1* blocks (Metakovsky 1991).

There are several Italian cultivars whose gliadin patterns show evidence of recombination between *Gli-B1* and *Gli-B5*. For example, cvs 'Pandas' and 'Costantino' both possess three gliadins coded by the *Gli-B1m* allele (Figs. 1 C, E and 5); in addition, 'Costantino' contains the *Gli-B5*-controlled ω-gliadins S4 + S6 that are absent in 'Pandas'.

Discussion

There are several storage protein-coding loci on each of the chromosomes of the first homoeologous group of common wheat, including loci coding for HMW and LMW glutenin subunits (*Glu-1* and *Glu-3*, respectively), gliadins (*Gli-1*), triplet-band proteins (*Tri-1*) and some minor ω-gliadins (see Payne 1987; Shepherd 1988, for recent reviews). Most of these loci are complex and include several active genes coding for a group of jointly inherited polypeptides – intralocus recombination occurring very rarely if at all (Sozinov and Poperelya 1980; Payne and Lawrence 1983; Gupta and Shepherd 1990).

The complex locus *Gli-B1* and the gene *Rg-1* which controls the colour of the glumes (red or white) are both located on the satellite of chromosome 1B (Pogna et al. 1985; Payne et al. 1986). These loci are tightly linked and recombine at frequencies as low as $1.06 \pm 0.45\%$ (Poperelya et al. 1980) or $1.8 \pm 0.8\%$ (Payne et al. 1986). *Gli-B1* has at least 16 allele variants, each of which code for a group ("block") of jointly inherited electrophoretic bands located in ω-, γ- and β-regions of the gliadin pattern (Metakovsky 1991).

Previous investigators noticed that the *Gli-B1*-encoded band γ-40 (according to the nomenclature of Bushuk and Zillmann 1978) preferably occurs in common wheat cultivars containing the red glume allele *Rg-1* (Wrigley et al. 1982; Pogna et al. 1985). However, some *Gli-B1* alleles, such as *Gli-B1c* and *Gli-B1n*, do not code for gliadin γ-40 (Metakovsky 1991) but occur in red glume cultivars only (Koval et al. 1986).

A careful examination of the band composition of different *Gli-B1* blocks showed that all "red glume" blocks share two ω-gliadin components whose mobilities in A-PAGE correspond to those of gliadins S4 and S6 from cv 'Salmone'. The results reported here show that the locus coding for these gliadins, although tightly linked to *Gli-B1*, recombines with the latter at a mean frequency of 1.4% (Table 1) and lies between *Gli-B1* and *Rg-1*. As the *Rg-1* locus has been mapped distal to *Gli-B1* (Payne et al. 1986), this new gliadin locus, *Gli-B5* must also be distal to *Gli-B1*.

The frequency of recombination between *Gli-B1* and *Gli-B5* in the six crosses varied from 0.0% to 5.9%; this was not unexpected because polymorphism in nucleotide sequences between homologous chromosomes in hybrids of wheat cultivars has been found to reduce the likelihood of crossing-over (Dvorak and McGuire 1981). Moreover, evidence has been obtained that single genes can affect the frequency of recombination (Tulsieram et al. 1992).

The frequency of recombination between the *Hg-1* locus and the genes controlling S3 + S5 varied significantly in the six crosses (Table 1). The mean value of recombination obtained here, 1.8%, is less than the values of $3.88 \pm 1.0\%$ and $3.95 \pm 1.38\%$ between *Hg-1* and *Gli-A1* (scored as a group of jointly inherited bands including γ-gliadins) reported by Sobko and Poperelya (1982) and Howes (1986), respectively. This discrepancy can be clarified by the difference in parental genotypes used in these crosses. However, there are reasons for believing that polypeptides S3 and S5 are in fact controlled by a new locus distal to *Gli-A1* on chromosome 1A and, therefore, possibly homoeologous to *Gli-B5* on chromosome 1B.

First, the major γ-gliadin band, A6, in cultivar 'Asiago' (Fig. 6, arrows) was found to segregate at a 1:2:1 ratio with ω-gliadin S3 of 'Salmone' in most of the progeny of the cross 'Salmone' × 'Asiago'. This γ-gliadin is likely to be coded at the *Gli-A1* locus because all *Gli-A1*-controlled blocks include at least one γ-gliadin band (Metakovsky 1991). However, evidence of recombination between A6 and S3 has been obtained in a few genotypes. For example, lane 5 in Fig. 6 shows one genotype in which S3 is absent, whereas A6 appears as a faint band. This pattern can be accounted for by homozygosity for the absence of the gene coding for S3 and heterozygosity at the locus coding for A6.

Second, at least three ω-gliadin genes have been found to recombine with *Gli-A1* at frequencies of $13 \pm 3\%$, $5 \pm 1\%$, and about 1% in common wheat cv 'Bezenchukskaya 98'. Although these genes have not been mapped in relation to the centromere, it was reliably shown that *Gli-A1* lies between the first gene and the two others (Metakovsky et al. 1986a). We assume that the first gene is an allele of the *Gli-A4* locus recently mapped at 10 cM proximally to *Gli-A1* (Redaelli et al. 1992), whereas one of the last two genes is allelic to the genes coding for S3 + S5 at a new locus, *Gli-A5*, homoeologous to *Gli-B5*.

Third, all of the 18 *Gli-A1* alleles previously described (Metakovsky 1991) code for at least one γ-gliadin, whereas only 8 of them control the synthesis of one or more ω-gliadins. Moreover, some pairs of *Gli-A1* gliadin blocks differ only in the presence or absence of ω-gliadins. As previously suggested (Metakovsky 1991), these pairs can arise as a result of recombination between γ-gliadin and ω-gliadin genes, i.e. between *Gli-A1* and *Gli-A5*, respectively.

A recombination percentage of about 1% has been recently obtained between two gliadin loci on chromosome 1D (Metakovsky and Sozinov 1987; Metakovsky 1990), suggesting that a locus homoeologous to *Gli-B5* may also exist on chromosome 1D.

In barley, the main hordein locus *Hor2* (= *HrdB*) on the short arm of chromosome 5 (= 1H) controls the synthesis of polypeptides similar in their primary structure to the γ-gliadins of wheat (see Kreis et al. 1985; Shewry and Tatham 1990, for review). Several minor loci (*HrdC*, *HrdD* and *HrdE*) coding for ω-gliadin-like hordeins were mapped distal to the main locus, at 2.5–3 cM from it (Sozinov et al. 1978; Jensen 1987).

The short arm of chromosome 1R of rye contains one ω-secalin gene that has been included in the main *Gli-R1* locus (obviously homoeologous to *Gli-1* of wheat), but which nevertheless recombines with it at a low frequency. This locus is distal to the 40K γ-secalin genes at *Gli-R1*

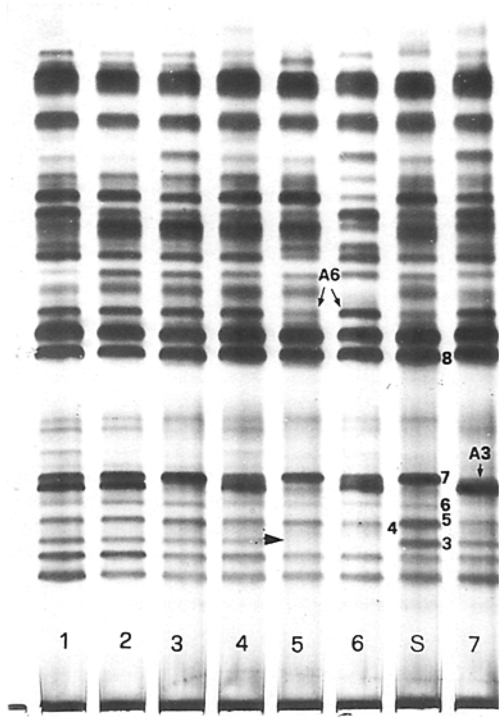

Fig. 6. A-PAGE fractionation of gliadins from the progeny of the cross 'Salmone' × 'Asiago'. Gliadins from 'Salmone' are *numbered. Lane S* 'Salmone'. *A3* and *A6* ω- and γ-gliadin from 'Asiago', respectively. *Arrowhead* indicates the position of ω-gliadin S3

(Carillo et al. 1992) and probably homoeologous to *Gli-5* in wheat.

In addition, both barley and rye possess an additional locus coding for ω-gliadin-like proteins that is proximal to the main locus and shows 7–17% recombination in barley (locus *Hor 1*) (Shewry et al. 1978; Doll and Brown 1979; Jensen et al. 1980; Ladogina et al. 1989) and $12.04 \pm 2.21\%$ in rye (locus *Sec 4*) (Carillo et al. 1992). These loci and the *Gli-A4* locus in wheat (Redaelli et al. 1992) apparently represent a homoeologous series.

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