

Polymorphism and inheritance of gliadin polypeptides in *T. monococcum* L.

E. V. Metakovsky and S. K. Baboev

N. I. Vavilov Institute of General Genetics, Gubkin St., 3, Moscow B-333, Russia

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Summary. More than 80 different gliadin electrophoretic patterns (spectra) have been found in 109 accessions of the diploid wheat *Triticum monococcum*. Each pattern consists of 15–20 gliadin bands. Some patterns are clearly related and might arise from one another through single mutations in the gliadin-coding loci. From the analysis of 15 grains of each, only 61 accessions were found to be uniform; others consisted of two or more grain variants differing in their gliadin spectrum. An analysis of F₂ grains from three crosses between different accessions showed that groups (blocks) of components are jointly and codominantly inherited. Two independent major *Gli* loci were established. The close resemblance of the composition of some blocks of *T. monococcum* to some of those in polyploid wheats indicates that one locus in each *T. monococcum* genotype is located on chromosome 1A (*Gli-A1*) and the other on 6A (*Gli-A2*). However, the blocks of *T. monococcum* include more bands than corresponding (equivalent) blocks of polyploid wheats. Two out of 275 F₂ grains of the cross k-14244 × k-20409 were found to have gliadin spectra which can be explained as a result of intralocus recombination. Also, a second gliadin-coding locus on chromosome 1A was found in the cross k-46140 × k-46753. This locus recombines with the main *Gli-A1* locus with a frequency of about 22% and was clearly analogous to the additional *Gli* locus found earlier on chromosome 1A of certain polyploid wheats.

Key words: Hybridological analysis – Blocks of gliadins – Recombination – *Triticum monococcum*

Introduction

Modern breeding practices have eroded the genetic diversity of cultivated polyploid wheats (Porceddu et al. 1988). One of the manifestations of this erosion is the uniformity of genotypes of wheat cultivars developed in a particular region or country, as indicated by storage protein composition (Metakovsky et al. 1987, 1990, 1991). This may lead to a decrease in the efficiency of breeding, making new cultivars more sensitive to pathogens. Alien species offer a rich source of novel genes by which this imbalance might be redressed. An introgression of alien genes would increase the genetic diversity of, and may provide valuable new characteristics for, common wheat (Sharma and Gill 1983; Fedak 1985, Levi and Feldman 1987). However, the transfer of desirable traits from alien species into common wheat is complicated by a lack of knowledge about the inheritance of these traits in alien species and about the genotype of prospective donors. Therefore, there is a need for more intense study of the genetics of alien species.

A diploid wheat *T. monococcum* L. *ssp monococcum* may serve as a source of high protein content and disease resistance for polyploid wheats (The 1973; Fedak 1985). Our aim is to provide an appropriate system of genetic markers for the identification of *T. monococcum* genotypes, as well as distinguishing methods for linkage and chromosome mapping (with respect to valuable traits and their encoding genes), and for the analysis of evolutionary relationships between *T. monococcum* and polyploid wheats. A family of genes controlling a highly polymorphic storage protein, gliadin, has proved to be very useful as a genetic marker (Metakovsky and Sozinov 1987).

Correspondence to: E. V. Metakovsky, on the present address: Istituto Sperimentale per la Cerealicoltura, via Mulino, 3, 20079 S. Angelo Lodigiano (Milano), Italy

Materials and methods

Gliadin composition was determined for 15 single grains from each of 109 accessions of *T. monococcum* L. ssp *monococcum* from the collection of the N.I. Vavilov All-Union Institute of Plant Breeding (Leningrad). Grains (F₂ generation) from three crosses between six different accessions were analysed: k-14379 (var. *macedonicum*, *vulgare*, from Turkey) × k-105 (var. *hornemarii*, from Checheno-Ingushetiya, USSR); k-20409 (var. *monococcum*, from Spain) × k-14244 (var. *atraristatum*, *vulgare*, from Bulgaria); and k-46140 (var. *soflanum*, from Balkani) × k-46753 (var. *vulgare*, from Sweden). Hybridization was "spike to spike" under field conditions, but F₁ plants were bagged.

Gliadin was extracted from crushed single seeds with 70% aqueous ethanol and fractionated in an 8.3% polyacrylamide gel in Al-lactate buffer (pH 3.1) as described (Metakovsky and Novoselskaya 1991). All comparisons of electrophoretic patterns were repeated 2–3 times (in different runs) in the neighbouring slots of a slab. The new nomenclature for gliadin alleles in common wheat was used (Metakovsky 1991).

Results

Gliadin genotypes and the homogeneity of accessions

Only 61 out of 109 *T. monococcum* accessions were homogeneous, i.e., had identical gliadin spectra for all of the 15 grains studied. Eleven out of 48 heterogeneous accessions had three or more genotypes differing in their gliadin pattern (Baboev et al. 1990). Some gliadin patterns were encountered in different accessions. Therefore, in total, only 82 variants of gliadin electrophoretic pattern in 109 accessions were identified (some of them are

shown in Fig. 1). Each pattern consisted of 15–20 gliadin components of differing intensities.

Sixteen out of 48 heterogeneous accessions had only one grain which differed in gliadin pattern from the other 14 grains studied. These 16 accessions fell into four groups. Firstly, in two accessions, the gliadin pattern of the deviating seed showed only a minor difference from the main spectrum for the accession. This difference was either a slight change in the mobility of one band of the spectrum (in one accession) or the disappearance of a band (in the other accession). The patterns of these non-uniform seeds were not found in any other accession studied. One may speculate that the slight differences from the main spectrum might arise as a result of spontaneous mutations in one of the gliadin-coding genes. Analogous minor differences were also noticed between some other variants of *T. monococcum* gliadin patterns (Fig. 1, lanes 14–16). Analogous spontaneous and inherited changes of gliadin pattern have in fact been described previously in polyploid wheats (Lafiandra et al. 1987; Metakovsky and Sozinov 1987; Metakovsky et al. 1990).

A second group consisted of five accessions in which single deviating grains had only a few bands in their electrophoretic patterns which were identical in mobility to those in the main spectrum of an accession. However, these non-uniform seeds had the same gliadin patterns as some other accessions. Presumably, these non-uniform seeds were admixtures resulting from errors during the handling of the wheat collection studied. Analogous off-types were found earlier in common wheat cultivars (Appleyard et al. 1979; Pogna et al. 1982; Metakovsky 1990).

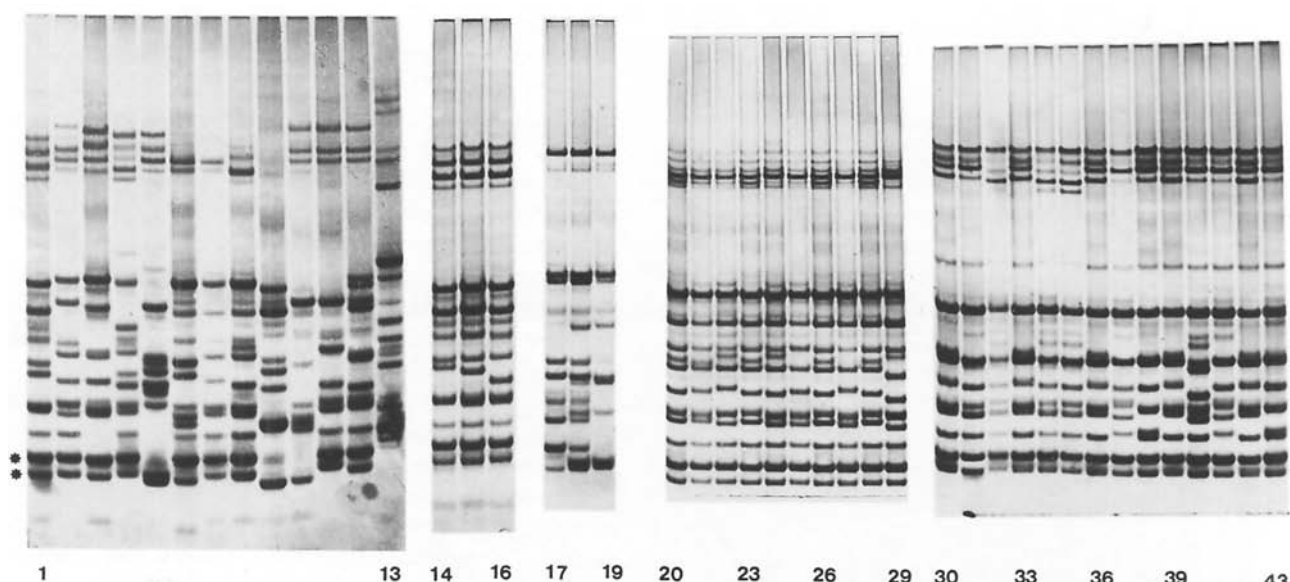


Fig. 1. Gliadin electrophoretic spectra of some accessions of *T. monococcum*. Lanes 1–12, typical gliadin spectra of *T. monococcum*; lanes 20, 23, 26 and 28, accession k-14379; lanes 30, 33, 36, 39, 42, accession k-105; lane 13, bread wheat line (a standard). A pair of the fast-moving gliadins which are common for many *T. monococcum* accessions are marked by an asterisk

Thirdly, in eight accessions there were single grains with gliadin patterns which also differed considerably from the main spectrum of the relevant accession, but which were not found in any other accession studied. These grains might either represent true (rare) variants of the accessions, or might be admixtures of some accession of *T. monococcum* not studied in our work, or they might be a result of segregation of a hybrid after natural outcrossing.

The fourth group included a deviating pattern in which (Fig. 1, lane 18) one could find all the bands belonging to two other variants of the gliadin pattern of *T. monococcum* (lanes 17, 19). We suggest that this seed is a product of natural cross-pollination between different accessions. Codominant inheritance of gliadin bands is well known in polyploid wheats (Sozinov and Popereya 1979; Kudryavtsev et al. 1988) and *T. tauschii* (Lagudah and Halloran 1988 b).

Analysis of the inheritance of gliadin bands

To study the inheritance of gliadin electrophoretic components, progeny from three crosses between different *T. monococcum* accessions (genotypes) was analysed. The first cross was k-14379 × k-105 in which 109 grains were studied. There were nine components in the spectrum of k-14379 which were absent in k-105, and k-105 had seven bands which were absent in k-14379 (Fig. 2, lanes 1,4). Gliadin patterns of F₂ seeds were classified in accordance with the presence or absence of these bands. Each genotype was found to have two groups (blocks) of jointly inherited components. The first block (in the upper region of the pattern) and the second block (in the lower region) consisted of five and four components, respectively, in k-14379. Analogous groups in k-105 included four and three bands (see Fig. 2). No seed was found in which any of these four blocks was represented by less than the full complement of bands. Each of the four blocks was clearly inherited in a 3:1 (presence/absence) ratio with a χ^2 of 0.00; 0.08; 0.03 and 2.23, respectively (see Table 1).

The gliadin pattern of each F₂ grain had either one or both of the first (upper) blocks. It was evident that these blocks are codominant and allelic: for a 1:2:1 ratio $\chi^2 = 0.03$, $P > 0.95$. The second (lower) blocks were also allelic: $\chi^2 = 2.28$, $P > 0.20$ (see Table 1). In total, nine main phenotypic classes of gliadin pattern were found in 109 grains studied in this cross. The distribution of grains in these classes was in accordance with the 1:2:1:2:4:2:1:2:1 segregation, which was expected for two independent pairs of codominant and allelic characters ($P > 0.20$, Table 1). Also, there were two groups of spectra in each phenotypic class of heterozygotes: components of blocks of either k-14379 (Fig. 2, lane 3) or k-105 (lane 2) were more intensely stained. The two main independent gliadin-coding loci in each genome of polyploid

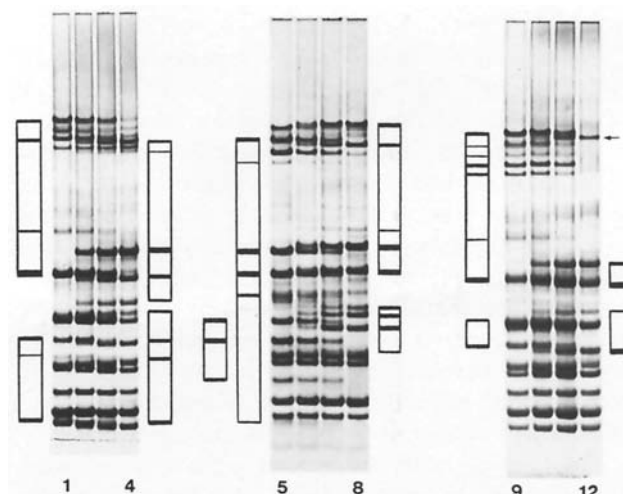


Fig. 2. Gliadin patterns of *T. monococcum* genotypes used for hybridization and some F₂ grains of their crosses. Lanes 1, k-105; 2, 3, F₂ from k-14379 × k-105 cross; 4, k-14379; 5, k-14244; 6, 7, F₂ from k-14244 × k-20409; 8, k-20409; 9, k-46753; 10, 11, F₂ from k-46140 × k-46753; 12, k-46140. Blocks of jointly inherited gliadin components are shown schematically near each parental spectrum. A band controlled by a gene which recombinates with the main gliadin-coding locus is marked by an arrow

Table 1. Number of F₂ grains from the cross k-14379 × k-105 in different phenotypic classes

Block	Accession	Presence of the block in the spectrum (+)								
First	k-14379									
First	k-105	+	+	+	+	+	+	+	+	+
Second	k-14379									
Second	k-105	+	+	+	+	+	+	+	+	+
Category	Number of grains in the phenotypic class									
Experimental	7	11	9	14	28	12	5	10	13	109
Expected	6.8	13.6	6.8	13.6	27.3	13.6	6.8	13.6	6.8	109
χ^2	0.01	0.51	0.70	0.01	0.02	0.19	0.48	0.97	5.62	8.50

wheats and in *T. tauschii*, the blocks of jointly inherited components controlled by each of these loci, as well as the dosage effects of gliadin-coding genes in triploid endosperm, have all been described earlier (Sozinov and Poperelya 1979; Lagudah and Halloran 1988b; Metakovsky and Iakobashvili 1990; Metakovsky et al. 1984; Kudryavtsev et al. 1988).

Two independent and jointly inherited groups of gliadin components (blocks) were also found in each of the two parents of the cross k-14244 × k-20409. The first (upper) and the second (lower) blocks in k-14244 consisted of six and three, and in k-20409 of five and four, components, respectively (Fig. 2, lanes 5, 8). A peculiarity of the first block of k-14244 is the presence of an unusually fast-moving component (Fig. 2). All components of each block were either present or absent in the patterns of 273 out of 275 grains studied in this cross. Two independent pairs of allelic blocks were identified: for a 1:2:1:2:4:2:1:2:1 ratio $P > 0.50$ (Table 2).

One of the blocks had fewer components in the patterns of two out of 275 grains of this cross. The first block of k-20409 lacked two ω -gliadins and a minor γ -gliadin in one of these two seeds (Fig. 3, lane 2), while the first block of 14244 had lost its two ω -gliadins in the other seed (lane 7). Possibly the absence of some components in a block might be caused by intralocus recombination in the gliadin-coding locus. The small number of these assumed recombinants (two out of 275) shows that the approximate largest distance between genes in a gliadin-coding locus may be about 1% or less. A similar estimate was obtained earlier for common wheat (Payne et al. 1984; Metakovsky and Sozinov 1987).

Two main gliadin-coding loci in each parent were identified in the cross k-46140 × k46753 (102 grains analysed). There were seven and two components in the upper and lower blocks of k-46753, and two and two bands in the corresponding blocks of k-46140, respectively (Fig. 2, lanes 9 and 12). The first two blocks and the second two blocks represented allelic pairs with 1:2:1 ratios ($\chi^2 = 1.18$, $P > 0.90$, and $\chi^2 = 3.47$, $P > 0.10$, respectively).

One of the bands in the ω -region of the spectrum of k-46140 was inherited in accordance with a 3:1 (presence or absence) ratio: $\chi^2 = 0.12$, $P > 0.50$. This band (see Fig. 4) was not a member of the first block but the gene controlling its synthesis was clearly linked to the first main gliadin-coding locus in this accession: for a 3:6:3:1:2:1 ratio, the χ^2 was 21.94, with $P < 0.01$ (Table 3). The frequency of recombination between these two gliadin-coding loci, calculated from the data of Table 3, was about 22.05 ± 2.8 .

Correspondence of *T. monococcum* blocks to those in polyploid wheats

Thus, each of the accessions (genotypes) studied has two main independent and codominantly inherited gliadin-coding loci. One of them (the upper) usually controls the synthesis of ω - and γ -gliadins, the other (the lower) of α - and β -gliadins (Fig. 2). Gliadin-coding loci located on

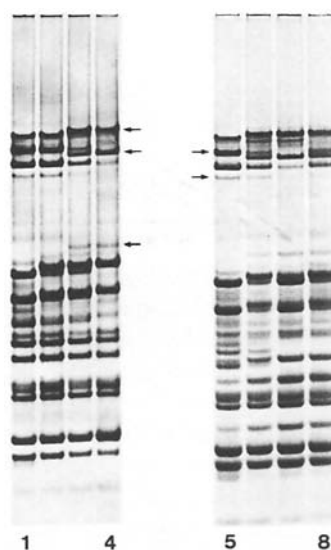


Fig. 3. Some F_2 grains from the cross k-14244 × k-20409. Grains with recombinant patterns (lanes 2 and 7) and components of a block missing in these grains are shown

Table 2. Number of F_2 grains from the cross k-14244 × k-20409 in different phenotypic classes

Block	Accession	Presence of the block in the spectrum (+)								
First	k-14244	+	+	+	+	+	+	+	+	+
First	k-20409	+	+	+	+	+	+	+	+	+
Second	k-14244	+	+	+	+	+	+	+	+	+
Second	k-20409	+	+	+	+	+	+	+	+	+
Category	Number of grains in the phenotypic classes									
Experimental	21	32	16	30	69	24	22	40	19	273
Expected	17.1	34.2	17.1	34.2	68.4	34.2	17.1	34.2	17.1	273
χ^2	0.91	0.31	0.07	0.50	0.01	3.01	1.43	1.01	0.22	7.25

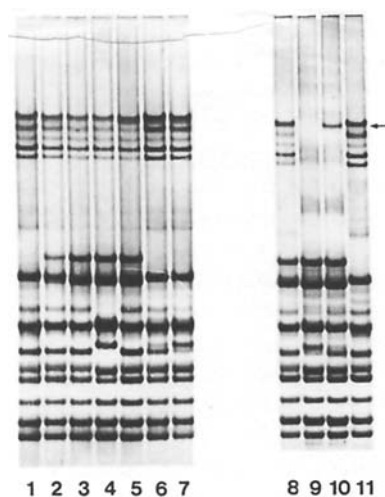


Fig. 4. Some F₂ grains from the cross k-46140 × k-46753. Lanes 3, 4, 6, 7, 8, 9, recombinants (see Table 3)

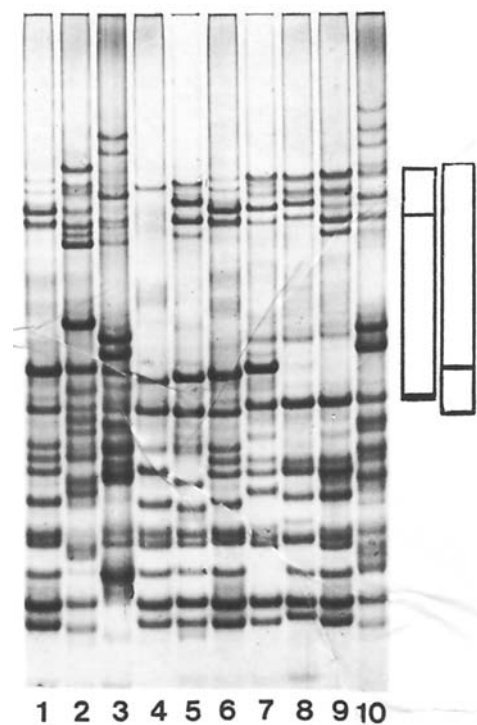


Fig. 5. Comparison of the electrophoretic patterns of the gliadin of different wheats. 1, *T. monococcum* (k-14379); 2, *T. durum* (cv Kubanka Karakalskaya); 3, *T. aestivum* (line from cv Dankowska); 4–9, *T. monococcum* (k-46140, k-14244, k-14379, k-20409, k-105, k-46753, respectively); 10, *T. aestivum* (cv Odesskaya 16). The *Gli-A1o* (left of the two) and *Gli-A1d* blocks are shown schematically to the right

Table 3. Number of F₂ grains from the cross k-46140 × k-46753 in different phenotypic classes

Gliadin bands	Accession	Presence of bands in spectrum (+)					
ω -gliadin	46140	+	+	+			
First block	46140	+	+		+	+	
First block	46753		+	+		+	+
Number of grains found		26	42	10	1	9	14
Lanes on Fig. 4		10	2,5	6,7	9	3,4	1,11
(examples of patterns)							

chromosomes 1A and 6A of polyploid wheats control the synthesis of blocks located in the same regions of the electrophoretic spectrum (Metakovsky et al. 1984; Metakovsky 1991). It is well-known from the results of analysis of chromosome pairing in interspecies hybrids that *T. monococcum* has an A genome (Kihara 1954, 1982). Moreover, there is a resemblance in component composition between the blocks of *T. monococcum* and the blocks controlled by the A genome in polyploid wheats.

For example, the *Gli-A1o* block of common wheat (chromosome 1A of cvs Odesskaya 16, Riband, Ducat and many others) consists of three major components located in the γ - and ω -regions of the spectrum. The same, or similar, three components are present in the upper block of k-46753, and the upper block of k-105 shares at least two components with *Gli-A1o* (Fig. 5). The same, or nearly the same, three components make up a block in *T. durum* (for example, cv Kubanka Karakalskaya) and in *T. monococcum* (k-14379). Two out of these three components are present in *Gli-A1d* of *T. aestivum* (line of cv Dankowska) (Fig. 5). Clearly related pairs of components resembling *Gli-A1d* are present and jointly inherited in the upper blocks of k-46140, k-14244 and k-14379 (see Fig. 5). On the basis of a resemblance in component composition of the first blocks of *T. monococcum* and the chromosome 1A-controlled blocks of polyploid wheats, we suggest that the first (upper) blocks in *T. monococcum* are also controlled by chromosome 1A.

The second blocks revealed in the spectra of *T. monococcum* bear less resemblance in component composition to the chromosome 6A-controlled blocks of polyploid wheats. However, a pair of very fast-moving components in the α -region of gliadin spectra is found in most of the *T. monococcum* accessions (Fig. 1). This pair resembles a pair of bands in a widespread type of α -gliadin from common wheat (Fig. 5) which has been called the "Chinese Spring type" (Kasarda 1980). This pair of bands was present, and had identical intensity, in all F₂ grains studied (see for example Fig. 2). Therefore, the bands are probably controlled by the same locus in different accessions. Moreover, in the cross k-14379 × k-105 the faster component of the pair proved to be a member of the lower block. Therefore, the lower blocks of *T. monococ-*

cum are very probably controlled by genes on chromosome 6A.

Frequency of some blocks in the collection of *T. monococcum* accessions

Some blocks found in this study clearly were present in several different genotypes of *T. monococcum*. For example, all components of the block presumed to be controlled by chromosome 1A of k-14379 were found in five other spectra (Fig. 1, lanes 20–29). Obviously, these spectra differed in allelic variants of the second block. The upper block of k-105 was present also in five other spectrum variants (Fig. 1, lanes 30–43) some of which were found in several different accessions. Therefore, this block was present in a total of 16 accessions. In contrast, there was no other pattern which included the first block of k-46753. In some cases the spectrum of an accession might include several, but not all, components of a block identified in the present study.

More rarely definite 6A-controlled blocks could sometimes be found in different genotypes (patterns).

Discussion

To our knowledge, this is the first report of studies on the inheritance of gliadin electrophoretic components in diploid wheat. The results complement those obtained earlier on the common wheats, *T. macha*, *T. durum* and *T. tauschii*.

Nearly all bands in the electrophoretic spectra of the collection of *T. monococcum* studied were inherited as two independent blocks. The resemblance of component composition indicated that one of these blocks can be attributed to the *Gli-A1* locus located on chromosome 1A and the other to the *Gli-A2* locus located on chromosome 6A (although some gliadin alleles present in cultivated wheats do not have any analogues in *T. monococcum*, while many blocks of *T. monococcum* are clearly specific to this species). All six parental forms used in crossing experiments had different blocks at each locus.

A careful comparison of gliadin patterns permits an evaluation of the allelic variants of blocks in *T. monococcum*. There are probably at least 50 different blocks controlled by *Gli-A1* and more than 70 blocks controlled by *Gli-A2* in the 109 accessions studied. Roughly the same number of variant blocks have been described in two other diploid cereals, barley (Pomortsev et al. 1985) and *T. tauschii* (Lagudah and Halloran 1988a).

A comparison of the component composition of blocks, revealed by the help of hybridological analysis, confirmed the suggestion that new alleles (block variants) arose as a result of mutations and indicated that recombinations were very rare in gliadin-coding loci (Metakovsky and Sozinov 1987). For example, chromosome 1A-controlled blocks in k-105 and k-20409 have three identical components (ω -gliadin and 2 γ -gliadins), but the block of k-20409 includes an additional major γ -gliadin. The two blocks differ also in the electrophoretic mobility of a ω -gliadin (see Fig. 5).

The genetic diversity in enzyme loci of alien wheat species is very low. For example, 12 enzyme systems were studied in 17 wild populations of *T. boeoticum* and *T. urartu* and the number of alleles per locus was found to

be not more than 1.22 (Smith-Huerta et al. 1989). The highest figure, of only 1.63 alleles per locus, was found in an analysis of 37 populations of wild emmer wheat studied for 42 enzyme loci (Nevo and Beiles 1989). The problem of genotype identification is especially complex for *T. monococcum* which has been considered to be a very uniform species (Riley 1965; Kuspira et al. 1989). In this species, only two out of 16 enzyme loci were found to be polymorphic and the average number of alleles per locus was about 1.1 (Kuspira et al. 1989).

By contrast, the electrophoretic spectra of gliadins have proved to be highly polymorphic in alien diploid wheats (Baboev et al. 1990). We believe that multiple allelism at the *Gli* loci will provide a system of effective genetic markers for genotype identification in these species. These markers can be used to search for valuable genes linked to the gliadin-coding loci and to monitor the transfer of alien genes into cultivated polyploid wheats. Storage protein loci of alien species can also be regarded as a source of novel polypeptides which may possibly influence the dough quality of cultivated polyploid wheats. For example, we have found a gene in *T. boeoticum* which is closely linked to the gliadin-coding locus, producing a polypeptide with a molecular mass similar to that of an average high-molecular-weight glutenin subunit (Metakovsky and Baboev 1992).

Gliadin markers may also prove useful for phylogenetic studies.

However, merely counting the number of bands having similar electrophoretic mobility in different wheats cannot give unambiguous data on phylogenetic relations: two bands with identical mobility may actually be different polypeptides with different genetical control. Furthermore, many accessions of the same species could be studied instead of the few "typical representatives" because closely related accessions may differ in the presence or absence of some bands or blocks of bands.

Our approach to the analysis of wheat phylogenetic relations is based on the assumption of the improbability of repeated and independent origins for the complex blocks of gliadin components in different genotypes.

Such an event would demand the occurrence of a highly unlikely series of mutations in the gliadin-coding loci. Much more probably, blocks have been transferred from one genotype or another only as a result of cross-pollination. According to the latter assumption, the presence of identical blocks in two genotypes unambiguously shows a close relationship between these genotypes (Kudryavtsev et al. 1988; Metakovsky et al. 1989).

It was found in this work, that three bands of the spectrum of k-46753 are inherited together and are identical to the corresponding components of the *Gli-A1a* block of common wheat. This block was also found earlier in *T. durum*, but not in *T. carthlicum* (Metakovsky et al. 1989). The presence of the same jointly inherited group of gliadin bands in these wheats of different ploidy indicates their close relationship and common origin. However, gliadin blocks in *T. monococcum* always included more components than the corresponding blocks of polyploid wheat. This result is in agreement with the finding that more genes are expressed at the *Gli-A1* locus in most accessions of *T. monococcum* as compared with polyploid wheats (Waines and Payne 1987; Galili et al. 1988).

The existence of two recombinable gliadin-coding loci on the same chromosome in common wheat (Sobko 1984), *T. macha* (Metakovsky and Iakobashvili 1990) and *T. monococcum* (this work), emphasizes the similarity of chromosomes 1A in these wheats. Groups of morphological traits linked in *T. monococcum* as well as in *T. aestivum* have been described before (Kuspira et al. 1989).

It is assumed that *T. urartu* is a probable donor of the A genome for common wheat (Chapman et al. 1976; Dvorak 1979; Konarev et al. 1979; Galili et al. 1991), although the contribution of other species is still not excluded (Kerby and Kuspira 1987). It has been shown that *T. aestivum* and *T. durum* and their A genomes could originate only as a result of several (not single) acts of inter-species cross-pollination (Kudryavtsev et al. 1988; Metakovsky et al. 1989). Our results do not exclude the possibility that *T. monococcum* might contribute to the origin of the A genome of cultivated polyploid wheats or that these wheats have a common progenitor(s).

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