Theor Appl Genet (1997) 94:68–74

M. Ciaffi · L. Dominici · D. Lafiandra

Gliadin polymorphism in wild and cultivated einkorn wheats

Received: 8 July 1996 / Accepted: 12 July 1996

Abstract To study the relationships between different species of the Einkorn group, 408 accessions of *Triticum monococcum*, *T. boeoticum*, *T. boeoticum* ssp. *thauodar* and *T. urartu* were analyzed electrophoretically for their protein composition at the *Gli-1* and *Gli-2* loci. In all the species the range of allelic variation at the loci examined is remarkable. The gliadin patterns of *T. monococcum* and *T. boeoticum* were very similar to one another but differed substantially from those of *T. urartu*. Several accessions of *T. boeoticum* and *T. monococcum* were shown to share the same alleles at the *Gli-1* and *Gli-2* loci, confirming the recent nomenclature that considers these wheats as different subspecies of the same species, *T. monococcum*. The gliadin composition of *T. urartu* resembled that of the A genome of polyploid wheats more than did *T. boeoticum* or *T. monococcum*, supporting the hypothesis that *T. urartu*, rather than *T. boeoticum*, is the donor of the A genome in cultivated wheats. Because of their high degree of polymorphism the gliadin markers may help in selecting breeding parents from diploid wheat germ plasm collections and can be used both to search for valuable genes linked to the gliadin-coding loci and to monitor the transfer of alien genes into cultivated polyploid wheats.

Key words Diploid wheats · *Triticum* · Wheat phylogeny · Gliadin · Electrophoresis

Introduction

The wheat taxon (*Triticum*) is a polyploid complex comprising both domesticated and wild species. Tetraploid macaroni wheat, *T. turgidum* L. var. *durum* (2n = 4x = 28; genome formula AABB), and hexaploid bread wheat, *T. aestivum* L. var. *aestivum* (2n = 6x = 42; AABBDD), are widely cultivated in temperate and subtropical regions of the world and are two of the most important cereals in world agriculture. The phylogeny of these polyploid wheats has been the subject of intense research and speculation during the past 70 years (see Kerby and Kuspira 1987; Kimber and Sears 1987, for reviews). On the basis of cytogenetical studies it is generally accepted that the wild and domesticated diploid species *T. boeoticum* and *T. monococcum* are the sources of the A genome in both *T. turgidum* and *T. aestivum* (Morris and Sears 1967; Kimber and Feldman 1987; Kimber and Sears 1987). Two morphological types of *T. boeoticum* are recognised: ssp. *aegilopoides* with a single fertile floret and usually a single awn to each spikelet, and ssp. *thaoudar* with two fertile florets and usually two awns per spikelet (Johnson and Dhaliwal 1976). The cultivated, less fragile, *T. monococcum* probably resulted from artificial selection of a more suitable form for cultivation. As it has only a single fertile floret to each spikelet, its progenitor was almost certainly the single-seeded *T. boeoticum* ssp. *aegilopoides* (Miller 1987).

Recent investigations suggest that *T. urartu*, another member of the Einkorn group, may be an alternative donor of the A genome (Dvorak et al. 1988; Galili et al. 1991; Takuni et al. 1993). Some wheat researchers fail to recognise *T. urartu* as a legitimate species (Kerby and Kuspira 1987; Kimber and Feldman 1987; Kimber and Sears 1987), although it meets the criteria of a species by reason of its reproductive isolation from the other Einkorn wheats *T. boeoticum* and *T. monococcum* (Johnson and Dhaliwal 1976; Sharma and Waines 1981). In spite of this evidence, *T. urartu* is often passed over for *T. boeoticum* and *T. monococcum* in phylogenetic and evolutionary studies because researchers are either unaware, or refuse to acknowledge, that *T. urartu* is a legitimate species (Waines and Barnhart 1992; Morrison 1993). Thus, *T. boeoticum* and *T. monococcum*, which appear as the only *Triticum* diploids in many classifications, still maintain their standing as the only A-genome donors for some researchers.

Because of their high degree of polymorphism and structural diversity, the prolamin storage proteins (gliadins and glutenins) of grasses (*Poaceae*) have proved to be valuable markers in taxonomic studies (Metakovsky et al. 1989; Fernandez-Calvin and Orellana

Communicated by H. F. Linskens

M. Ciaffi (✉) · L. Dominici · D. Lafiandra
Dipartimento di Agrobiologia ed Agrochimica, Università della Tuscia, 01100 Viterbo, Italy

1990; Shewry et al. 1991; Masci et al. 1992; Lafiandra et al. 1993). We have used this approach to provide additional information about the genome differentiation of diploid wheats belonging to the genus *Triticum* and for identification of the parental species of the A genomes in polyploid wheats. Comparative analyses of high-molecular-weight glutenin subunits in several accessions of *T. boeoticum*, *T. monococcum* and *T. urartu* have been reported in a previous paper (Ciaffi et al. submitted). The aim of the present work is to analyse and to compare the variability of the gliadins in the same material by using different one- and two-dimensional electrophoretic procedures.

Materials and methods

The material used in this study was obtained from different diploid wheat collections preserved at the Germplasm Institute of Bari (Italy), at the International Center for Agricultural Research in Dry Areas (ICARDA, Syria) and at the Plant Germplasm Institute of Kyoto (Japan). It included 160 accessions of *T. boeoticum* from Armenia, Iraq, Iran, Turkey and Lebanon; 24 accessions of *T. boeoticum* ssp. *thaoudar* from Turkey, Iran and Iraq; 150 accessions of *T. urartu* from Lebanon, Syria, Turkey, Iran and Iraq; and 74 accessions of *T. monococcum* from Italy, Greece, Turkey and Russia.

The nomenclature supplied for seeds of the 160 accessions of the *T. boeoticum* from different sources of germ plasm collections did not indicate the subspecies. However, these can be considered to belong to the ssp. *aegilopoides* because all contained a single seed to each spikelet.

The bread and durum wheat cultivars Torim, Lambro, Duramba and Creso were also included in the electrophoretic ayalyses for comparison.

Gliadins were extracted with 1.5 M dimethylformamide and fractionated using the one- and two-dimensional electrophoretic separations described by Lafiandra and Kasarda (1985).

Results

T. urartu

In polyploid wheats the synthesis of gliadins is controlled by clusters of tightly linked co-dominant genes located on the short arms of homoeologous group-1 and -6 chromosomes (Lafiandra et al. 1984). Each cluster codes for a number of proteins (a block) which is inherited as a Mendelian character, and multiple allelism of their coding loci in the two homoeologous groups of wheat has been established (Metakovsky et al. 1984). For this reason gliadin from *T. urartu*, as well as from the other diploid species used in this study, have been grouped into two blocks. The genetic basis for this classification is supported by recent inheritance studies of these proteins in cultivated and the wild diploid wheats *T. monococcum*, *T. boeoticum* and *Aegilops squarrosa* (Metakovsky and Baboev 1992a, b; Lagudah and Halloran 1988).

Electrophoretic migration patterns of gliadins from some accessions of *T. urartu*, together with those from durum wheats Duramba and Creso, are shown in Fig. 1. Components of gliadin in each accession of *T. urartu*

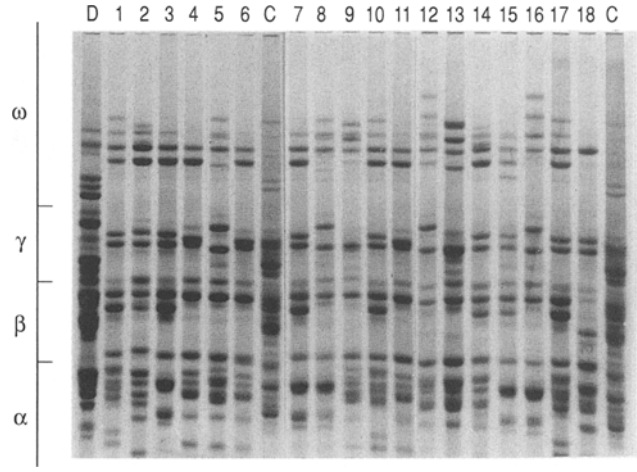


Fig. 1 One-dimensional electrophoretic separation of gliadins from 18 accessions of *T. urartu* compared with those of the durum wheat cultivars Duramba (*D*) and Creso (*C*)

analysed were located in all of the gliadin pattern region but are not scattered over the entire range of mobility from the alpha- to the omega-region as in tetraploid wheats. The distribution of gliadins in *T. urartu* resembles that of 1A- and 6A-controlled components of polyploid wheat, although the blocks of the diploid species include more bands than do the equivalent blocks of polyploid wheats. The *Gli-A1* locus, located on the short arm of chromosome 1A, usually controls the synthesis of omega-, gamma- and some slow-moving beta-gliadins, whereas the *Gli-A2* locus, on the short arm of chromosome 6A, codes mainly for components present in the alpha region and in some cases also for one fast-moving beta-gliadin (Lafiandra et al. 1984; Metakovsky et al. 1984).

In total 72 different gliadin electrophoretic patterns in the 150 accessions studied were identified. Some gliadin patterns were encountered in different accessions from the same location (lanes 1 and 10 in Fig. 1) or in populations from close locations in Turkey and Syria, respectively (e.g. lanes 3 and 7 and lanes 4 and 11 in Fig. 1). Polymorphism at the *Gli-A1* locus (42 variants) was significantly greater than that observed at the *Gli-A2* locus (16 variants).

Unlike most of the HMW-glutenin subunit patterns (Ciaffi et al. submitted), variation for most of the gliadin proteins appeared to be accession- or at least population-specific, rather than regionally (geographic) distributed. Out of 58 alleles detected at the *Gli-A1* and *Gli-A2* loci, 19 occurred in Turkish material (14 for *Gli-A1* and five for *Gli-A2*), 14 in Syrian material (11 for *Gli-A1* and three for *Gli-A2*), and ten in the Lebanese material (seven for *Gli-A1* and three for *Gli-A2*), whereas only eight and seven alleles were present in Iranian (six for *Gli-A1*) and Iraqi (four for *Gli-A1*) material, respectively. No allelic variants had a common origin between the different countries. However, some alleles, in particular for the

Gli-A2 locus, were widespread across different locations of each country (e.g. lower block in lanes 7, 8 and 16 from different Turkish accessions, or in lanes 12 and 13 from two Syrian accessions).

T. boeoticum

The gliadin pattern of all the *T. boeoticum* accessions analysed was quite distinctive from that of *T. urartu*. Although the two diploid species were characterised by large intraspecific variation, *T. boeoticum* had a complex gliadin pattern, with components continuously present from the alpha- to the omega-region (Fig. 2), whereas, as previously discussed, *T. urartu* showed a relatively simpler pattern, with components separated into more discrete areas. It is interesting to note also that in many accessions of *T. boeoticum* some components with unusual slow mobility were observed in the omega-region (lanes 3, 8 and 15 in Fig. 2) but were not detected in any of the *T. urartu* accessions analysed. In contrast to *T. urartu*, the lower block of all the *T. boeoticum* accessions used in this study was, other than by some alpha-gliadins, constituted by different components located in the middle and fast-moving beta region.

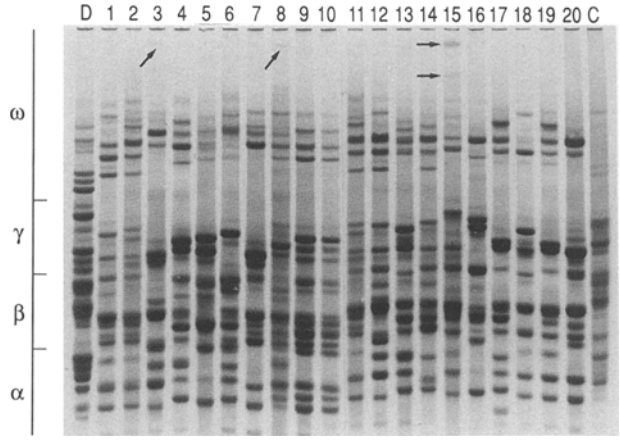


Fig. 2 One-dimensional electrophoretic separation of gliadins from 20 accessions of *T. boeoticum* and the durum wheat cultivars Duramba (*D*) and Creso (*C*). *Arrows* indicated the presence of components with unusual slow mobility in some *T. boeoticum* accessions

Two-dimensional analyses of gliadins (Fig. 3) revealed that *T. boeoticum*, in comparison with *T. urartu*, had a very low number of alpha-gliadin components (ranging from two to four), whereas the number of the bands located in the middle and fast-moving beta re-

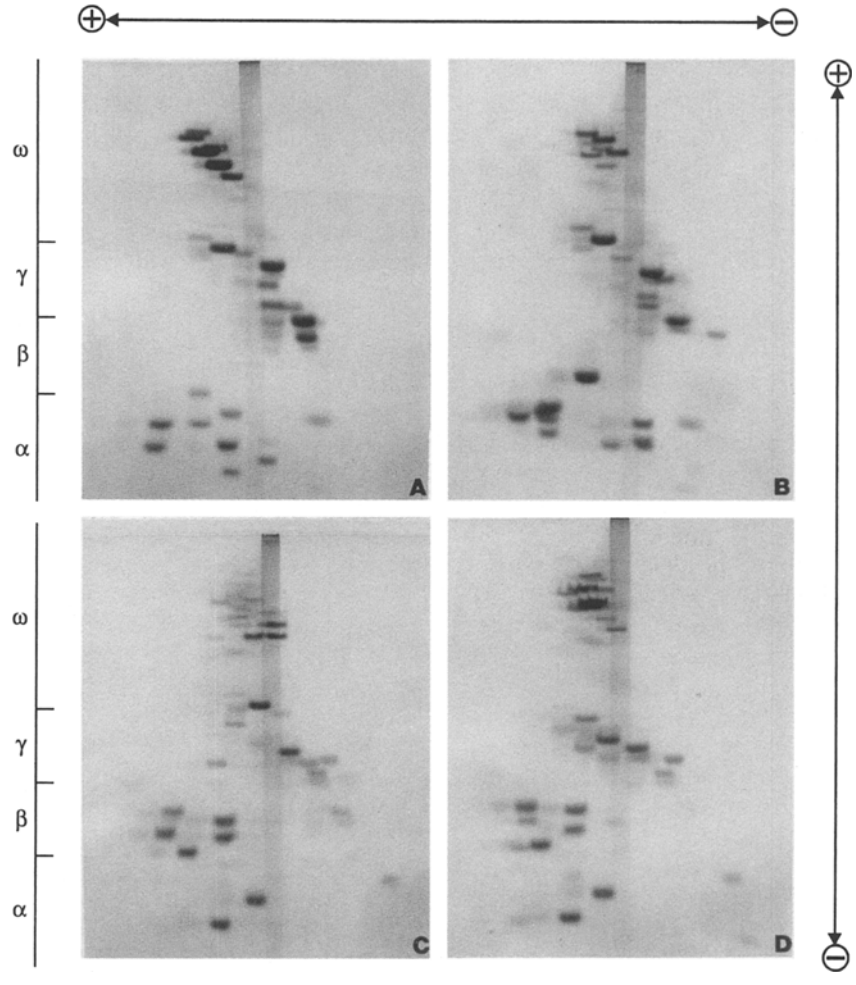


Fig. 3 Two-dimensional electrophoretic separation of gliadins from two *T. urartu* (**A** and **B**) and two *T. boeoticum* (**C** and **D**) accessions

gion, where usually *T. urartu* only one component was present, was much higher.

In *T. boeoticum*, more than in *T. urartu*, A-PAGE analysis of gliadins offered the possibility of the unambiguous differentiation and identification of genotypes. More than 100 different electrophoretic patterns were found in the 160 accessions analysed (some of them are shown in Fig. 2), the most common (lanes 3 and 4) occurring in ten and seven different accessions collected at the same locations from Turkey and Iraq, respectively. In the other cases we found a similar pattern only in two different accessions from the same locations (e.g. compare lanes 2 and 11 from two Turkish accessions, or lanes 9 and 10 from two Iranian accessions). A total of 79 and 58 variants were identified for the upper and the lower blocks, respectively. Some blocks found in these analyses were present in different genotypes. For example, two accessions from closely related locations in Turkey had the same variants for the lower blocks but differed for protein composition in the upper block (lanes 1 and 2). Conversely, other genotypes from the same location in Iran possessed the same components in the omega- and gamma-regions but differed for those present in beta- and alpha-moving zone (lanes 17 and 19).

As revealed also in *T. urartu*, some variants of the two blocks were very similar. For example, out of the eight components detected in the upper blocks of two accessions from close locations in Turkey (lanes 12 and 14 in Fig. 2) seven were identical, whereas there was only a small difference in the mobility of the slowest omega-gliadins between the two patterns. Other genotypes from the same locations in Iraq (lanes 18 and 19) differed in the composition of the lower blocks only by the absence of one component. These and other examples (data not shown) indicate that different blocks might have originated from a common ancestral block by mutation of a single gliadin-coding gene.

Electrophoretic migration patterns of gliadins from 16 of the 24 accessions of *T. thaoudar* used in this study are shown in Fig. 4. The banding patterns were similar to those of *T. boeoticum* with most of the components of the lower blocks located in the middle and fast-moving beta region. The only difference was that none of the 24 accessions analysed showed components in the omega-region with the unusual slow mobility characteristic of some *T. boeoticum* genotype. Contrary to the HMW-glutenin patterns (Ciaffi et al. submitted), each accession could be clearly identified on the basis of gliadin composition. The number of different gliadin patterns was equal to the number of accessions studied with 24 different variants for both the upper and lower blocks. A careful comparison of gliadin patterns indicated that none of these variants coincided with those found in *T. boeoticum*.

T. monococcum

As revealed also for the HMW-glutenin subunits (Waines and Payne 1987; Ciaffi et al. submitted), ana-

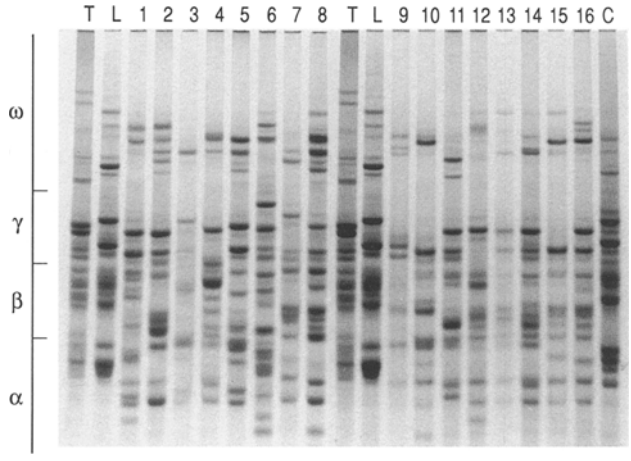
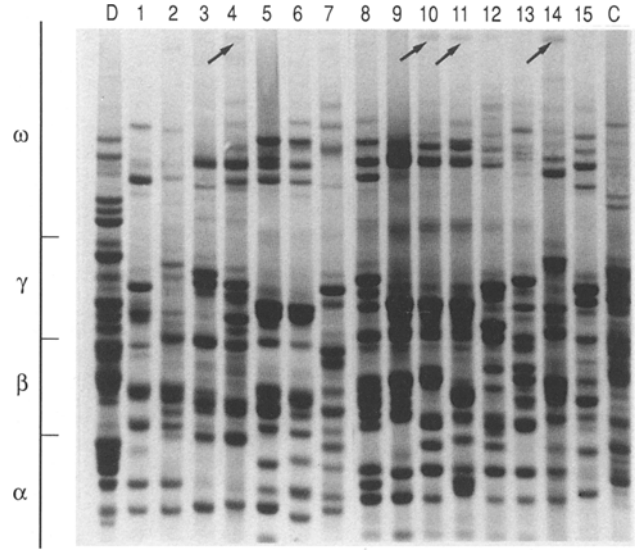


Fig. 4 One-dimensional electrophoretic separation of gliadins from 16 accessions of *T. boeoticum* ssp. *thaoudar* compared with those of the bread and durum varieties Torim (*T*), Lambro (*L*) and Creso (*C*)

lyses of the gliadin fraction of *T. monococcum* indicated an equivalence between the domesticated diploid species and *T. boeoticum*, and differences between the gliadin composition of these wheats and those of *T. urartu*. The gliadin patterns of *T. monococcum* (Fig. 5) were characterised by the presence of components scattered over the entire range of mobility from the alpha- to the omega-region with most of bands of the lower blocks located in the middle and fast-moving beta-region. However, in contrast to *T. boeoticum* ssp. *thaoudar*, some *T. monococcum* accessions had omega-components with an unusual molecular mass that were also

Fig. 5 One-dimensional electrophoretic separation of gliadins from 15 accessions of *T. monococcum* and the durum wheat cultivars Duramba (*D*) and Creso (*C*). *Arrows* indicated the presence of components with unusual slow mobility in some *T. monococcum* accessions



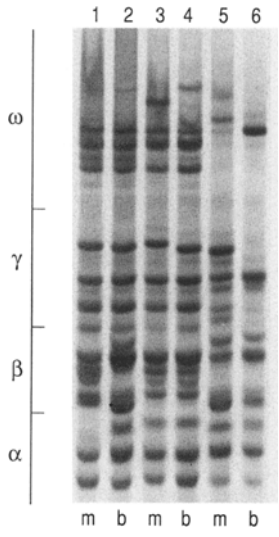


Fig. 6 One-dimensional electrophoretic separation of gliadins from some *T. monococcum* (*m*) and *T. boeoticum* (*b*) accessions with similar allelic variants at the *Gli-1* and *Gli-2* loci

characteristic of many *T. boeoticum* ssp. *aegilopoides* genotypes (lanes 4, 10, 11 and 14 in Fig. 5).

The close relationship between *T. boeoticum* ssp. *aegilopoides* and *T. monococcum* was confirmed by the finding that some variants of the upper and lower blocks detected in wild and cultivated diploid wheats were identical, whereas no allelic variants in common were found among the *T. monococcum* and *T. boeoticum* ssp. *thaoudar* accessions analysed. Electrophoretic separation of gliadins from some *T. monococcum* and *T. boeoticum* accessions with similar allelic variants at the *Gli-1* and *Gli-2* loci are shown in Fig. 6. The first two accessions of *T. monococcum* (lane 1) and *T. boeoticum* (lane 2) showed the same components in the omega-, gamma- and slow-moving beta-regions, whereas they differed in the allelic variants of the lower block. On the other hand, the accessions reported in lanes 3 and 4, and 5 and 6 had identical patterns for the alpha- and the faster beta-gliadin components but differed in the gliadin composition of the upper block.

A total of 52 gliadin patterns were identified in the 74 accessions analysed, derived from the combination of 38 variants at the *Gli-A1* locus and 22 at the *Gli-A2* locus. The highest variability was observed in the material from Turkey and Greece, with 22 and 15 different patterns, respectively, whereas nine and six gliadin patterns were present in the Russian and Italian accessions.

Discussion

Wild diploid wheat species have been investigated to elucidate their contribution to the phylogeny of tetraploid and hexaploid wheats. On the basis of cytogenetical studies, *T. urartu*, *T. boeoticum* and *T. monococcum* have been considered as the same species and it was generally accepted that their genomes were the A-genome donors of polyploid wheats (Kimber and Feldman 1987; Kimber and Sears 1987). However, *T. urartu* and *T. boeoticum* were found to differ with regard to some isozymes (Smith-Huerta et al. 1989; Jaaska 1993) and in respect of the non-prolamin fraction of their seed storage proteins (Johnson 1975; Dvorak 1976; Konarev et al. 1979). More recently, restriction fragment length polymorphism (RFLP) analysis using single-copy or repetitive DNA sequences indicated that *T. monococcum* is closely related to *T. boeoticum* and that the genomes of both of these diploid wheats are differentiated from that of *T. urartu* (Dvorak et al. 1988; Galili et al. 1991; Takuni et al. 1993). These studies also showed that the A-genome donor of the *T. turgidum* and *aestivum* groups is *T. urartu*, not *T. boeoticum*. In view of these differences, as well as the reproductive isolation by hybrid sterility between *T. urartu* and *T. boeoticum* (Johnson and Dahlivall 1976; Sharma and Waines 1981), it is justifiable to consider their genomes modified relative to each other as proposed by different authors (Waines and Barnhart 1992; Dvorak et al. 1993; Morrison 1993, 1994). As discussed by these same authors the failure of some classifications to recognise the specific status of *T. urartu* (Kimber and Feldman 1987; Kimber and Sears 1987) may cause researchers unfamiliar with the taxonomy to select *T. boeoticum* for studies of wheat evolution when *T. urartu* may be the more appropriate choice.

Although the genetic control of seed storage proteins involves a limited number of loci, which consequently cover only a small part of genome, a comparative analysis of glutenins and gliadins could provide additional information about the phylogenetic relationships among the three *Triticum* diploid species and between them and the polyploid wheats. Waines and Payne (1987), while analysing HMW-glutenin subunits, found that *T. monococcum* and *T. boeoticum* had similar banding patterns, whereas the banding patterns of equivalent proteins from *T. urartu* were quite distinct. More recent results (Ciaffi et al. submitted), based on one- (SDS-PAGE and Urea/SDS-PAGE) and two-dimensional (IEF × SDS-PAGE) analyses of the same proteins, confirmed the equivalence between *T. monococcum* and *T. boeoticum*, and the differences between genomes of these wheats and that of *T. urartu*. The similarity in the one- (SDS-PAGE and Urea/SDS-PAGE) and two-dimensional (IEF × SDS-PAGE) migration patterns of the HMW-glutenin subunits of *T. urartu* and those of the A genome in *T. dicoccoides* with both x- and y-subunits (Ciaffi et al. 1993, submitted) supports the hypothesis that *T. urartu*, rather than *T. boeoticum*, is the donor of the A genome to the cultivated polyploid wheats. This hypothesis was confirmed by a comparison of the gliadin patterns of the diploid species with those of polyploid wheats. The present results demonstrate that analyses of the gliadin fraction of *T. monococcum*, *T. boeoticum* and *T. urartu* allowed us to distinguish *T. monococcum* and *T. boeoticum* from *T. urartu*, and that the gliadin pattern of *T. urartu* resembled that of the A genome of polyploid wheats better than did *T. boeoticum*

or *T. monococcum*, in particular for the gliadins components controlled by chromosome 6A. In contrast to *T. urartu*, the lower block of all the *T. boeoticum* and *T. monococcum* accessions used in this study was, other than by some alpha-gliadins, constituted by different components located in the middle and fast-moving beta region, which are usually not detected in polyploid wheats (compare the gliadin patterns of the two tetraploid cultivars Duramba, D, and Creso, C, with those from different accessions of *T. boeoticum*, 1–20, in Fig. 2). Two-dimensional analyses also showed that *T. boeoticum*, in comparison with *T. urartu*, had a very low number of alpha-gliadin components (ranging from two to four), whereas the number of bands located in the middle and fast-moving beta region, where usually only one component was present in *T. urartu*, was much higher. This confirmed that the lower block revealed in the spectra of *T. boeoticum* showed much less resemblance in component composition and distribution to the 6A-controlled blocks of polyploid wheats. In tetraploid and hexaploid wheats almost all of the *Gli-A2*-coded bands (ranging from five to eight) detected in two-dimensional analyses were located in the alpha region (Lafiandra et al. 1984, 1987).

The presence of identical gliadin blocks in *T. boeoticum* ssp. *aegilopoides* and *T. monococcum*, but not between this last species and *T. boeoticum* ssp. *thaoudar*, confirmed that the progenitor of the primitive domesticated diploid wheat was almost certainly *T. boeoticum* ssp. *aegilopoides* which, like *T. monococcum*, has only a single fertile floret to each spikelt.

In addition to phylogenetic studies, gliadins could represent useful markers for the evaluation of the genetic variability present in different wild diploid wheat collections. In particular, as discussed by Metakovsky and Baboev (1992 a, b), the multiple allelism for the gliadin loci found in diploid wheats will provide a system for the unambiguous differentiation and identification of genotypes in these species. The genetic diversity in enzyme loci of the *Triticum* diploid species was very low compared to the large variation detected for gliadin proteins in these species. For example, in *T. boeoticum* all 26 accessions examined by Jaaska (1978) and all 134 examined by Nakay (1979) were uniform in the electrophoretic patterns of alcohol dehydrogenase and esterase isoenzymes, respectively. Smith-Huerta et al. (1989), using 16 enzyme systems in 13 and four populations of *T. boeoticum* and *T. urartu*, respectively, showed that genetic diversity was uniformly low in both species, with a mean number of alleles per locus (A) of 1.22 for *T. boeoticum* and 1.19 for *T. urartu*. The problem of genotype identification is especially complex for *T. monococcum* which has been considered to be a very uniform species (Kuspira et al. 1989). In this species, only 2 out of the 16 enzyme loci studied were found to be polymorphic and the average number of alleles per locus was about 1.1 (Kuspira et al. 1989). A comparatively lower level of polymorphism was also found for HMW-glutenin loci than for gliadin loci in diploid wheats, although their genetic diversity was much higher than that detected for isoenzyme loci (Waines and Payne 1987; Metakovsky and Baboev 1992 a; Ciaffi et al. submitted). For example, only two different HMW-glutenin patterns were found in the 24 accessions of *T. thaoudar* used in this study (Ciaffi et al. submitted), whereas present results showed that each accession could be clearly identified on the basis of gliadin composition. Because of their high degree of polymorphism, the gliadin markers may help in selecting breeding parents from diploid wheat germ plasm collections and can be used both to search for valuable genes linked to the gliadin-coding loci and to monitor the transfer of alien genes into cultivated polyploid wheats.

References

Ciaffi M, Lafiandra D, Porceddu E, Benedettelli S (1993) Storage protein variation in wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides*) from Jordan and Turkey. I. Electrophoretic characterisation of genotypes. Theor Appl Genet 86:474–480

Ciaffi M, Dominici L, Lafiandra D (1996) High-molecular-weight glutenin subunit variation in wild and cultivated einkorn wheats. P1 Syst Evol (submitted)

Dvorak J (1976) The relationship between the genome of *Triticum urartu* and the A and B genomes of *Triticum aestivum*. Can J Genet Cytol 18:371–377

Dvorak J, McGuire PE, Cassidy B (1988) Apparent sources of the A genomes of wheats inferred from polymorphism in abundance and restriction fragment length of repeated nucleotide sequences. Genome 30:680–689

Dvorak J, Di Terlizzi P, Zhang HB, Resta P (1993) The evolution of polyploid wheats: identification of the A-genome donor species. Genome 36:21–31

Fernandez-Calvin B, Orellana J (1990) High-molecular-weight glutenin subunit variation in the *Sitopsis* section of *Aegilops*. Implication of the B genome of wheat. Heredity 65:455–463

Galili S, Galili G, Feldman M (1991) Chromosomal location of genes for Rubisco small subunit and Rubisco-binding protein in common wheat. Theor Appl Genet 81:98–104

Jaaska V (1978) NADP-dependent aromatic alcohol dehydrogenase in polyploid wheats and their diploid relatives. Theor Appl Genet 53:209–217

Jaaska V (1993) Isoenzymes in the evaluation of germplasm diversity in wild diploid relatives of cultivated wheat. In: Damania AB (ed) Biodiversity and wheat improvement. John Wiley and Sons, New York, pp 247–257

Johnson BL (1975) Identification of the apparent B-genome donor of wheat. Can J Genet Cytol 17:21–39

Johnson BL, Dhaliwal HS (1976) Reproductive isolation of *T. boeoticum* and *T. urartu* and the origin of tetraploid wheats. Am J Bot 63:1088–1094

Kerby K, Kuspira J (1987) The phylogeny of polyploid wheats *Triticum aestivum* (bread wheat) and *T. turgidum* (macaroni wheat). Genome 29:722–737

Kimber G, Feldman M (1987) Wild wheat: an introduction. Special report no. 353, University of Missouri, Columbia, USA

Kimber G, Sears ER (1987) Evolution in the genus *Triticum* and the origin of cultivated wheat. In: Heyne EG (ed) Wheat and wheat improvement. American Society of Agronomy, Madison, Wisconsin, USA, pp 154–164

Konarev VG, Gavriulyuk IP, Gubareva NK, Peneva TI (1979) Seed proteins in genome analysis, cultivar identification and documentation of cereal genetic resources: a review. Cereal Chem 56:272–278

Kuspira J, Maclagan J, Bhambhani RN, Sadasivaiah RS, Kim NS (1989) Genetic and cytogenetic analyses of the A genome of *T.*

monococcum L. V. Inheritance and linkage relationships of genes determining the expression of 12 qualitative characters. Genome 32:869–881

Lafiandra K, Kasarda DD (1985) One- and two-dimensional (two-pH) polycrylamide gel electrophoresis in a single gel: separation of wheat proteins. Cereal Chem 62:314–319

Lafiandra D, Kasarda DD, Morris R (1984) Chromosomal assignment of genes coding for the wheat gliadin protein components of the cultivars "Cheyenne" and "Chinese Spring" by two-dimensional (two-pH) electrophoresis. Theor Appl Genet 68: 531–539

Lafiandra D, Colaprico G, Kasarda DD, Porceddu E (1987) Null alleles for gliadin blocks in common and durum wheat cultivars. Theor Appl Genet 74:610–616

Lafiandra D, Ciaffi M, Benedettelli S (1993) Seed storage proteins of wild wheat progenitors. In: Damania AB (ed) Biodiversity and wheat improvement, ICARDA, John Wiley and Sons, New York, pp 329–340

Lagudah ES, Halloran GM (1988) Phylogenetic relationships of *Triticum tauschii* the D-genome donor to hexaploid wheat. 2. Inheritance and chromosomal mapping of the HMW subunit of glutenin and gliadin gene loci of *T. tauschii*. Theor Appl Genet 75:599–605

Masci S, D'Ovidio R, Lafiandra D, Tanzarella OA, Porceddu E (1992) Electrophoretic and molecular analyses of alpha-gliadins in *Aegilops* species (*Poaceae*) belonging to the D-genome cluster and their putative progenitors. P1 Syst Evol 179:115–128

Metakovsky EV, Baboev SK (1992 a) Polymorphism and inheritance of gliadin polypeptides in *T. monococcum* L. Theor Appl Genet 84:971–978

Metakovsky EV, Baboev SK (1992b) Polymorphism of gliadin and unusual gliadin alleles in *Triticum boeoticum*. Genome 35:1007–1012

Metakovsky EV, Novoselskaya AY, Kopus MM, Sobko TA, Sozinov AA (1984) Blocks of gliadin components in winter wheat detected by one-dimensional polyacrylamide gel electrophoresis. Theor Appl Genet 67:559–568

Metakovsky EV, Kudryavtsev AM, Iakobashvili ZA, Novoselskaya AY (1989) Analysis of phylogenetic relations of *durum, carthlicum* and common wheats by means of comparison alleles of gliadin-coding loci. Theor Appl Genet 77:881–887

Miller TE (1987) Systematic and evolution. In: Lupton FGH (ed) Wheat breeding: its scientific basis. Chapman and Hall, London, UK, pp 1–30

Morris R, Sears ER (1987) The cytogenesis of wheat and its relatives. In: Quisenberry KS, Reitz LP (eds) Wheat and wheat improvement. American Society of Agronomy, Madison, Wisconsin, USA, pp 19–87

Morrison LA (1993) *Triticum-Aegilops* systematics: Taking an integrative approach. In: Damania AB (ed) Biodiversity and wheat improvement, John Wiley and Sons, New York, pp 59–66

Morrison LA (1994) Taxonomy of the wheats: a commentary. In: Proc VIIIth Int Wheat Genet Symp, Beijing, China, pp 65–71

Nakay Y (1979) Isozyme variation in *Aegilops* and *Triticum*. IV. The origin of common wheats revealed from the study of esterase isoenzymes in synthesized hexaploid wheats. Jpn J Genet 54:175–189

Sharma HC, Waines JC (1981) The relationship between male and female fertility and among taxa in diploid wheats. Am J Bot 68:449–451

Shewry PR, Sabelli PA, Parmar S, Lafiandra D (1991) Alpha-type prolamins are encoded by genes on chromosomes 4Ha and 6Ha of *Haynaldia villosa* Schur (syn. *Dasypyrum villosum* L.). Biochem Genet 29:207–211

Smith-Huerta NL, Huerta AJ, Barnhart D, Waines JG (1989) Genetic diversity in wild diploid wheat *Triticum monococcum* var. *boeoticum* and *T. urartu* (*Poaceae*). Theor Appl Genet 78:260–264

Takuni S, Nasuda S, Liu YG, Tsunewaky K (1993) Wheat phylogeny determined by RFLP analysis of nuclear DNA. 1. Einkorn wheat. Jpn J Genet 68:73–79

Waines JG, Barnhart D (1992) Biosystematics research iin *Aegilops* and *Triticum*, Hereditas 116:207–212

Waines JG, Payne PI (1987) Electrophoretic analysis of the high-molecular-weight glutenin subunits of *T. monococcum*, *T. urartu* and the A genome of bread wheat (*T. aestivum*). Theor Appl Genet 74:71–76