Theor Appl Genet (1993) 86:474–480

THEORETICAL AND APPLIED GENETICS

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Storage-protein variation in wild emmer wheat (*Triticum turgidum* ssp. *dicoccoides*) from Jordan and Turkey. I. Electrophoretic characterization of genotypes

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Received: 13 August 1992 / Accepted: 9 December 1992

Abstract. Seed storage-protein variation at the *Glu-A1*, *Glu-B1* and *Gli-B1*/*Glu-B3* loci in the tetraploid wild progenitor of wheat, *T. dicoccoides*, was studied electrophoretically in 315 individuals representing nine populations from Jordan and three from Turkey. A total of 44 different HMW-glutenin patterns were identified, resulting from the combination of 15 alleles in the A genome and 19 in the B genome. Twenty-seven new allelic variants, 12 at the *Glu-A1* locus and 15 at the *Glu-B1* locus, were identified by comparing the mobilities of their subunits to those previously found in bread and durum wheats. The novel variants include six alleles at the *Glu-A1* locus showing both x and y subunits. The genes coding for the 1Bx and 1By subunits showed no or very little (3%) inactivity, the 1Ax gene showed a moderate degree (6.3%) of inactivity whereas the gene coding for 1Ay showed the highest degree of inactivity (84.8%). A high level of polymorphism was also present for the omega- and gamma-gliadins and LMW-glutenin subunits encoded by genes at the linked *Gli-B1* and *Glu-B3* loci (19 alleles). Some Jordanian accessions were found to contain omega-gliadin 35, gamma-gliadin 45, and LMW-2 also present in cultivated durum wheats and related to good gluten viscoelasticity. The newly-discovered alleles enhance the genetic variability available for improving the technological quality of wheats. Additionally some of them may facilitate basic research on the relationship between industrial properties and the number and functionality of HMW- and LMW-glutenin subunits.

Key words: *Triticum turgidum* ssp. *dicoccoides* – Electrophoresis – Seed storage-proteins – Genetic resources – Wheat quality

Communicated by H. F. Linskens

Introduction

Endosperm proteins of wheat consist predominantly of two classes of storage proteins termed gliadin and glutenin, so classified on the basis of their solubility in different solvents. Biochemical and genetical aspects of these proteins have received a good deal of attention in recent years due to their importance in determining the nutritional and technological properties of cultivated wheats.

Gliadins are encoded by genes located on the distal part of the short arm of chromosomes belonging to homoeologous groups 1 and 6 of both durum (Lafiandra et al. 1983) and bread wheat (Lafiandra et al. 1984); their loci are designated *Gli-1* (group 1 chromosomes) and *Gli-2* (group 6 chromosomes). Glutenins are represented by high-molecular-weight (HMW) or A subunits, coded by *Glu-1* loci, located on the long arm group 1 chromosomes, and low-molecular-weight (LMW) subunits, subdivided into B, C and D according to their mobility in sodium dodecyl sulphate (SDS)-PAGE and their relative isoelectric point (Jackson et al. 1983). B and C subunits of LMW-glutenin are coded by *Glu-3* (Singh and Shepherd 1988), located on the short arm of group 1 chromosomes and linked tothe *Gli-1* complex loci.

Each of these nine loci displays allelic variation which is partly responsible for the differences observed in wheat technological properties. More specifically, allelic variation in HMW-glutenin subunits is largely responsible for quality differences in bread wheat (Payne et al. 1984a), whereas the variation in LMW-glutenin subunit alleles at the *Glu-B3* locus is mainly involved in determining the characteristics of cooked pasta (Pogna et al. 1990).

Promising sources of genes coding for novel proteins are represented by diploid and tetraploid wild relatives of wheat (Law and Payne 1983). Wild emmer wheat,

Triticum turgidum ssp. *dicoccoides*, genome AABB, is the progenitor of tetraploid and hexaploid cultivated wheats (Zohary 1970) and is distributed over the Near East Fertile Crescent, in Israel, Jordan, Lebanon, Syria, East Turkey, North Iraq and West Iran (Kimber and Feldman 1987). The diversity of HMW-glutenin subunits in *T. dicoccoides* has been extensively studied in material from Israel (Nevo and Payne 1987; Levy and Feldman 1988; Levy et al. 1988). These studies revealed the presence of wide allelic variation at both the *Glu-A1* and the *Glu-B1* loci and indicate that glutenin polymorphism could be at least partly accounted for by ecogeographical factors. No information was available on the variability of storage proteins present in wild emmer from other areas. The objective of this paper is to describe the polymorphism of seed storage-proteins at the four loci, *Glu-A1, Glu-B1, Gli-B1* and *Glu-B3,* present in different. *T. dicoccoides* accessions originating from plant explorations conducted in Jordan and Turkey.

Materials and methods

Plant material

The wild emmer wheat, *T. dicoccoides,* used in this study consisted of a collection of 315 genotypes from nine sites in Jordan and three in Turkey, maintained at the International Center for Agricultural Research in Dry Areas (ICARDA). The Jordanian material is part of an original collection from 30 locations in the mesic and xeric regions of Jordan (Jaradat and Jana 1987; Jaradat et al. 1988). Different bread and durum wheat cultivars were also included in the electrophoretic analyses for comparison (Table 1).

Table 1. Allelic composition at the *Glu-A1*, *Glu-B1* and *Gli-B1/Glu-B3* loci for bread and durum wheat cultivars included in the analyses

Locus	Allele	Subunits[a]	Variety standard	
			Bread	Durum
Glu-A1	*a*	None		Creso
	b	1	Torim	
	c	2*	Cheyenne	Duramba
	III	1′		Lambro
Glu-B1	*b*	7+8	Chinese Spring	Valnova
	c	7+9	Cheyenne	
	d	6+8		Creso
	e	20		Trinakria
	f	13+16		Duramba
	i	17+18	Manital	

Locus	Omega- and gamma-gliadins[b]		LMWG subunits[c]	Durum wheat cultivar standard
Gli-B1/	35	45	LMW-2	Creso
Glu-B3	33-35-38	42	LMW-1	Duramba

[a] Nomenclature proposed by Payne and Lawrence (1983) and Vallega and Waines (1987)
[b] According to the nomenclature of Bushuk and Zillman (1978)
[c] Nomenclature proposed by Payne et al. (1984b)

Electrophoretic analyses

Gliadin proteins were extracted from single seeds with 1.5 M dimethylformamide (DMF) and fractionated by polyacrylamide-gel electrophoresis in aluminium lactate buffer at pH 3.1 (A-PAGE) according to the procedure of Khan et al. (1985). To obtain good separation of LMW-glutenin subunits in a background free from gliadins and albumins/globulins a simple and rapid one-step 1-D SDS-PAGE procedure was used. The residue from samples used for gliadin extraction was resuspended in 1 ml of Tris HCl 0.125 M pH 6.8 buffer containing 1% sodium dodecil sulphate (SDS) to remove monomeric proteins overlapping in SDS-PAGE with LMW-glutenin subunits. After centrifugation, the residue was resuspended (1/10 w/v) in extraction buffer Tris-HCl 0.125 M pH 6.8 containing 2.75% SDS, 10% glycerol, 10% DMF and 0.2% dithiotreitol (DTT) and incubated for 1 h, at 70°C. Samples were then centrifuged and the supernatant was analyzed in a 1-D gradient SDS-PAGE (T= 8–15%, C=2.67%). Only the variation present in the B LMW-glutenin group was recorded.

Allelic variation at the *Glu-A1* and *Glu-B1* loci was determined by electrophoresis on 10% SDS-PAGE gels according to Payne et al. (1981). Samples were loaded several times, in different order, on gels to establish the relative mobilities of all principal glutenin subunits and gliadin components.

Nomenclature

Payne et al. (1982) designated HMW-glutenin subunit loci in hexaploid wheat as *Glu-A1, Glu-B1* and *Glu-D1* where alleles at each locus, i.e., the different subunit patterns, are named by the gene cluster designation followed by latin letters (Payne and Lawrence 1983), e.g., *Glu-A1a, Glu-A1b* etc. This nomenclature was adopted for bread and durum wheats whereas *T. dicoccoides* allelic variants are indicated using Payne's nomenclature for the gene cluster followed by Arabic numbering, i.e., *Glu-A1-1, Glu-A1-2* etc. Allelic variants for omega- and gamma-gliadins and the LMW-glutenin subunits, encoded at the linked *Gli-B1/Glu-B3* loci, are designated by the gene cluster nomenclature for the gliadin component, followed by arabic numbering, i.e., *Gli-B1-1, Gli-B1-2* etc.

Results

Variation in HMW-glutenin subunits

On the basis of extensive studies of this group of proteins in bread and durum wheats (Payne et al. 1981; Branlard et al. 1989) the HMW-glutenin subunits of *T. dicoccoides* were subdivided into those likely to be coded for by genes on chromosome 1A at the *Glu-A1* locus and those on chromosome 1B at *Glu-B1*. These assignments have been confirmed by Levy et al. (1988) and Ciaffi et al. (1991) by direct genetical analyses of wild emmer. In accordance with the nomenclature of Payne et al. (1981), subunits coded for by the same chromosome are separated into two types, x and y, according to their mobilities in SDS-PAGE, which also correspond to two different genes (Harberd et al. 1986). More specifically, HMW-glutenin

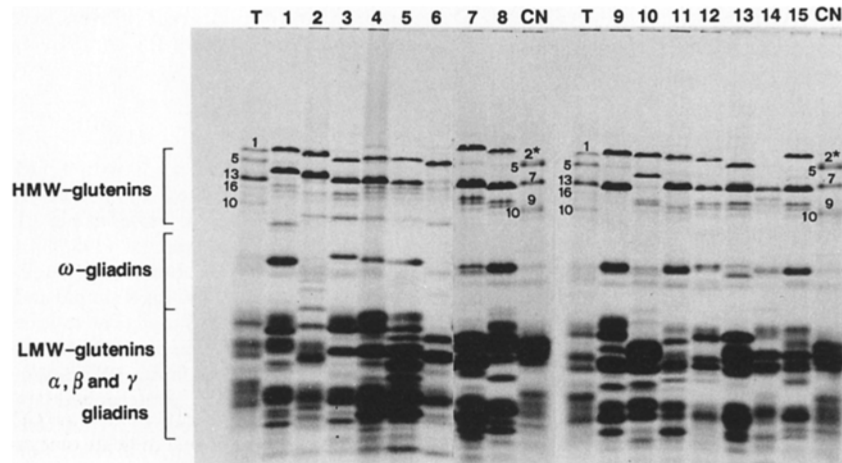

Fig. 1. SDS-PAGE (10% uniform gel) of total endosperm proteins from 15 *T. dicoccoides* accessions representative of the different allelic variants oberved at the *Glu-A1* locus. The HMW-glutenin subunits of the bread wheat cultivars, Torim (*T*) and Cheyenne (*CN*), have been numbered according to Payne and Lawrence (1983)

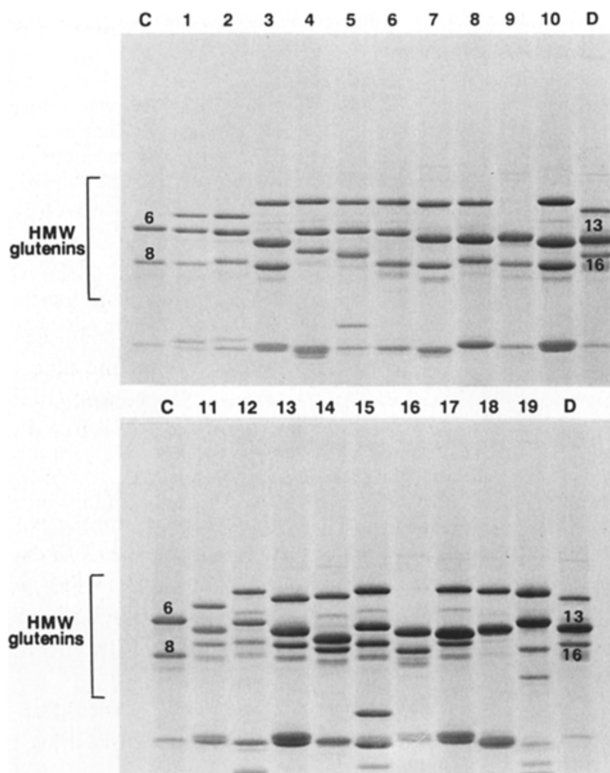

Fig. 2. SDS-PAGE (10% uniform gel) migration patterns of HMW-glutenin subunits from 19 accessions of *T. dicoccoides* representative of the different allelic variants detected at the *Glu-B1* locus. The *Glu-B1-* encoded glutenin subunits of the durum wheat cultivars, Creso (*C*) and Duramba (*D*), have been numbered according to Payne and Lawrence (1983)

subunits (1Ax and 1Ay) controlled by chromosome arm 1AL (1Bx and 1By) are those of the highest and lowest MW, whereas the intermediate MW subunits are controlled by chromosome arm 1BL.

Allelic variants at the *Glu-A1* locus are shown in Fig. 1, together with those from bread wheat cultivars Torim and Cheyenne which possess the 1 (*Glu-A1a* allele) and 2* (*Glu-A1c* allele) subunits, respectively. A total of 15 different allelic variants at the *Glu-A1* locus were detected in the 315 accessions of *T. dicoccoides* studied. Six of these variants showed both 1Ax and 1Ay subunits, with the latter always faintly stained (lanes 1–6 in Fig. 1). Most of the *T. dicoccoides* x subunits showed mobility ranges equal to or narrower than those of bread and durum wheat (subunits 1 and 2*). The x subunits, encoded by the *Glu-A1-1* and *Glu-A1-9* alleles (lanes 1 and 9 in Fig. 1), have the same electrophoretic mobility as subunit 1, whereas *Glu-A1-5,* which codes for two subunits (lane 5 in Fig. 1), codes for the x subunit migrating like that encoded by *Glu-A1c* (subunit 2*). Alleles *Glu-A1-2*, *Glu-A1-4*, *Glu-A1-10*, *Glu-A1-11*, and *Glu-A1-12* (lanes 2, 4, 10, 11 and 12 in Fig. 1) code for x subunits that have mobilities intermediate to those of subunits 1 and 2*. Allele *Glu-A1-12* (lane 12 in Fig. 1) appears similar to subunits named 1′ (*Glu-A1 III* allele) by Vallega and Waines (1987) in *T. dicoccum* and by Branlard et al. (1989) in durum wheat. Three alleles (*Glu-A1-7*, *Glu-A1-8* and *Glu-A1-15*), encoding x subunits which possess a lower mobility in SDS-PAGE than subunit 1, have been found (lanes 7, 8 and 15 in Fig. 1), whereas only two *Glu-A1* alleles, encoding an x-type subunit having a relatively higher molecular mass in SDS-PAGE than subunit 1, have been previously detected in *T. dicoccum* (Vallega and Waines 1987) and in *T. dicoccoides* (Levy et al. 1988). The x subunits encoded by *Glu-A1-3*, *Glu-A1-6* and *Glu-A1-13* (lanes 3, 6 and 13 in Fig. 1) showed electrophoretic mobilities greater than subunit 2* from the cultivar Cheyenne.

The 1Ay subunits of *T. dicoccoides* have electrophoretic mobilities greater than the 1Dy subunits of bread wheats. Four different 1Ay subunits were detected in the collection (lanes 1, 2, 3 and 6 in Fig. 2). The range of mobility of the y subunits was very similar to that deteced in *T. urartu,* whereas not a single *T. dicoccoides*

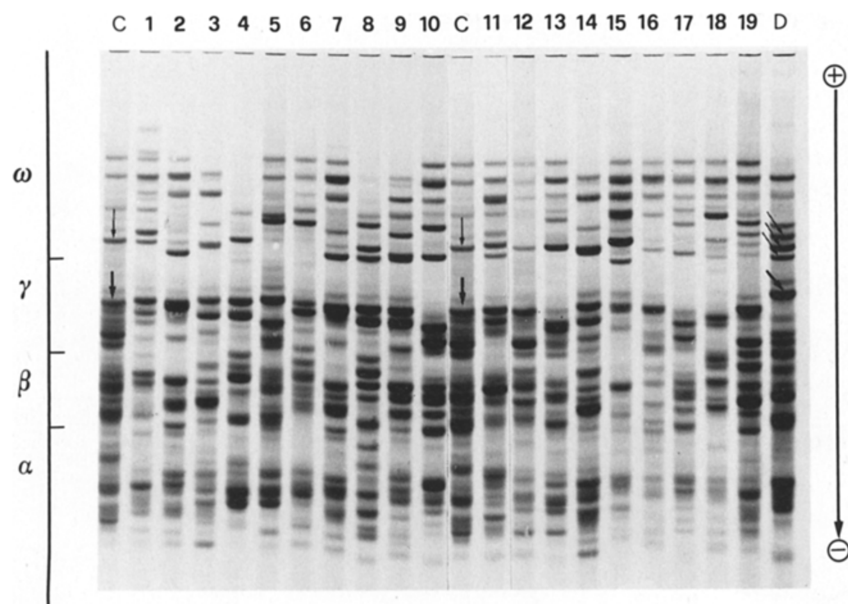

Fig. 3. One-dimensional electrophoretic separation of gliadins from 19 accessions of *T. dicoccoides* representative of the different allelic variants observed at the *Gli-B1* locus. *Vertical arrows* indicate omega-gliadin 35 and gamma 45 in cultivar Creso (*C*). The omega-gliadins 33-35-38 and the gamma-component 42 are also indicated by *diagonal arrows* in cultivar Duramba (*D*)

accession showed the multitude of minor 1Ay subunits which is characteristic of *T. boeoticum* and *T. monococcum* (Waines and Payne 1987; Ciaffi et al. 1992).

A total of 19 different *Glu-B1*-encoded allelic variants were identified amongst the 315 genotypes of *T. dicoccoides*, resulting from the combination of 11 Bx and 13 By subunits (Fig. 2). Two major HMW-glutenin subunits are encoded by the *Glu-B1* locus, as is usual in bread and durum wheats, but in some genotypes only one of them was detected (lane 18 in Fig. 2). Other genotypes possess similar 1Bx subunits (e.g., lanes 4 and 5 or lanes 7 and 8 in Fig. 2) but different 1By subunits. Conversely, genotypes with the same 1By subunits (e.g. lanes 6 and 10 in Fig. 2) showed alternative 1Bx subunits. Out of the six *Glu-B1* alleles generally found in durum and bread wheat cultivars, four were present in *T. dicoccoides*. More specifically *Glu-B1-1* (lane 1 in Fig. 2) coincides with subunits 6+8 of the cultivar Creso, *Glu-B1-11* (lane 11 in Fig. 2) with subunits 13+16 of the cultivar Duramba, *Glu-B1-9* (lane 9 in Fig. 2) with subunits 7+8 of the cultivar Valnova, whereas *Glu-B1-18* (lane 18 in Fig. 2) encodes for a subunit with electrophoretic mobility similar to subunit 20 of the cultivar Trinakria. No genotypes possess subunits 17+18 (*Glu-B1i* allele) and 7+9 (*Glu-B1c* allele).

Variation in gliadin components and LMW-glutenin subunits coded by genes at the linked Gli-B1/Glu-B3 loci

Electrophoretic migration patterns of gliadins from some genotypes of *T. dicoccoides*, representative of the different allelic variants detected at the *Gli-B1* locus, are shown in Fig. 3. Tremendous variation occurs, but only that due to the fast-moving omega and slow-moving gamma regions, where gliadin components controlled by chromosome 1B are usually located, was considered in the analyses. The chromosomal location of genes controlling these gliadin components has been established at the tetraploid level in durum wheat (Lafiandra et al. 1983) as well as in several *T. dicoccoides* lines (Ciaffi et al. 1992). 1-D gradient SDS-PAGE of proteins obtained after monomer removal was carried out on the same accessions as in Fig. 3, in order to determine the composition of the B group of LMW-glutenin subunits (Fig. 4). Gliadins and glutenins from the durum wheat cultivars Creso and Duramba were included in the analyses since they possess the two major allelic variants detected in the durum wheat world collection at the linked *Gli-B1/Glu-B3* loci, and known as alleles '45' and '42' according to the relative mobility of two gamma-gliadin components in polyacrylamide gels with aluminium lactate buffer at pH 3.1

Since *Gli-B1* and *Glu-B3* are closely linked, the different allelic variants were identified on the basis of the variation observed simultaneously in the omega- and gamma-gliadin regions and for the B group of LMW-glutenin subunits of each genotype. Some genotypes possess the main *Gli-B1* gamma-gliadins with the same electrophoretic mobility but contain different gliadin components in the omega region (lanes 3 and 4 or lanes 8 and 9 in Fig. 3) and different LMW-glutenin B subunits (lanes 3 and 4 or lanes 8 and 9 in Fig. 4). Conversely, other genotypes possess the same *Gli-B1* omega- and gamma-gliadins but different LMW-glutenin B subunits (lanes 2 and 7 in Figs. 3 and 4), while a third group of genotypes have different *Gli-B1* omega- and gamma-gliadins but very similar LMW-glutenin composition (lanes 7 and 13 in Figs. 3 and 4).

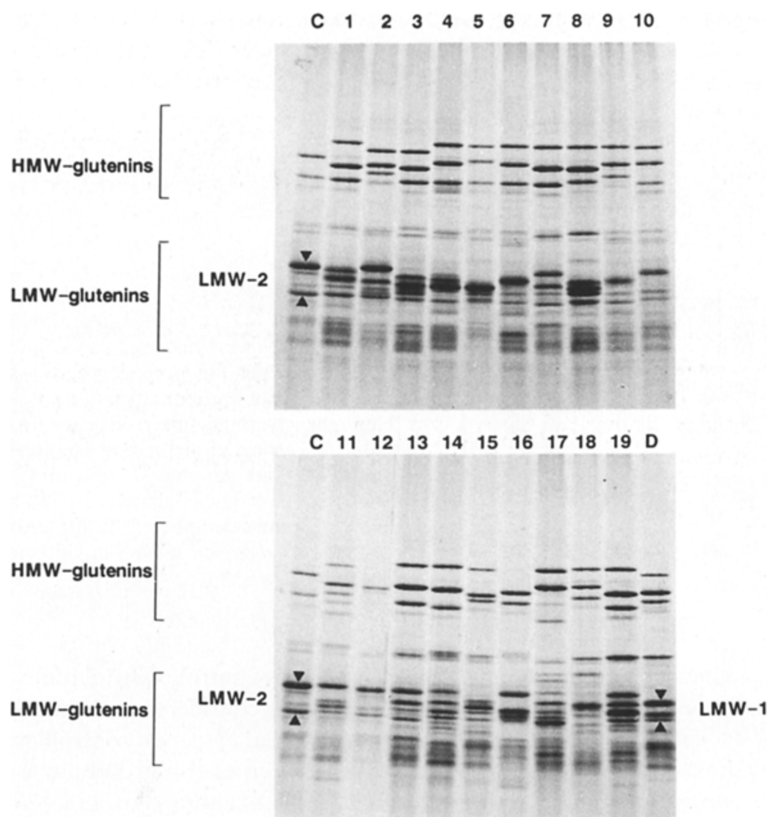

Fig. 4. One-dimensional SDS-PAGE (8–15% gradient gel) of the proteins, obtained after removal of the monomers, from 19 accessions of *T. dicoccoides* representative of the different allelic variants observed at the *Glu-B3* locus. LMW-2 and LMW-1 are indicated in the durum wheat cultivars Creso (*C*) and Duramba (*D*), respectively

Altogether 19 allele combinations were found for the *Gli-B1*/*Glu-B3* loci in the 12 populations. *Gli-B1-11* had been previously detected in a *T. dicoccoides* accession collected in Israel (Ciaffi et al. 1991). The main *Gli-B1* gamma-gliadin component of most *T. dicoccoides* genotypes was similar to that identified as '45', whereas the '42' band was not detected. Comparison of *T. dicoccoides* gliadin patterns and LMW-glutenin subunits with those of durum wheat in indicated that only some Jordanian accessions, those possessing the *Gli-B1-12* allele (lanes 12 in Fig. 3 and 4), contained the omega-, gamma-gliadin components and the LMW-glutenin B subunits present in the cultivar Creso.

Discussion

In agreement with the findings of Nevo and Payne (1987) and Levy et al. (1988), polymorphism for HMW-glutenin genes in *T. dicoccoides* was much higher than that of cultivated wheats. A total of 44 different HMW-glutenin patterns was observed in the present analysis, resulting from the combination of 15 alleles in the A genome (vs 3 described in cultivated wheats) and 19 subunits patterns of the B genome (vs 11 described in cultivated wheats). Two major HMW-glutenin subunits produced by *Glu-B1* were most commonly present, as in bread and durum wheats, although occasionally only one was detected. The usual situation for *Glu-A1* was the presence of only one subunit although, unlike bread and durum wheats, two subunits were also produced at times. The genes coding for the 1Bx and 1By subunits appeared to have no or very little (3%) inactivity while the 1Ax gene a moderate degree (6.3%) of inactivity. The gene coding for the 1Ay subunit, however, showed a very high degree (84.8%) of inactivity, in contrast to the low frequency exhibited by the diploid putative donor of the A genome (Waine and Payne 1987; Galili et al. 1988; Ciaffi et al. 1992). The genetic processes of diploidization, which may cause gene inactivation, and gene-dosage compensation due to differential gene expression, both of which have been involved in the evolutionary process of allopolyploid wheats in the wild and under cultivation, may be responsible for the reduction in the number or activity of duplicated genes. According to Galili et al. (1988) HMW-glutenin gene inactivation, following diploidization, affected mainly the A genome. Non-randomness was also evident in the order of diploidization: first to be affected was the gene that codes for the rapidly-migrating subunit (1Ay) and later the gene that encodes for the slowly-migrating one (1Ax). The fact that in F_1 hybrids between diploid, tetraploid and hexaploid

types, the two HMW-glutenin genes of chromosome 1A are active (Ciaffi et al. 1991) indicates that gene suppression is not brought about by diploidization per se. Evidence that chromosome 1A of the hexaploid Chinese Spring carries the DNA sequences for HMW-glutenin subunits but does not produce HMW-glutenin subunits (Thompson et al. 1983), supports the hypothesis of inactivation through mutation. Recent data indicated that the gene encoding the 1Ay subunit could be transcriptionally inactive due to single base-pair substitions within the 280-bp sequence immediately upstream of the transcription start site (Halford et al. 1989). However, it is not clear why such a change has occurred specifically in chromosome 1A.

In spite of the high degree of polymorphism for the *Glu-B1* HMW-glutenin subunits, alleles such as *Glu-B1-c* (subunits 7–9) and *Glu-B1-i* (subunits 17–18), which are very common in bread wheat, were absent in *T. dicoccoides* from Jordan and Turkey. Since these alleles were also absent in the cultivated tetraploids *T. dicoccum* (Vallega and Waines 1987) and *T. durum* (Branlard et al. 1989) the present results support the Branlard et al. (1989) hypothesis that these glutenin subunits may derive from mutations which occurred only in hexaploid wheats. Thanks to their positive influences on bread making quality (Payne 1987) breeding for technological properties could have increased the frequency of these alleles in common wheat.

Most of *T. dicoccoides* accessions showed the main *Gli-B1*-encoded gamma-gliadin component with an electrophoretic mobility similar to that of the band identified as 45 in durum wheat cultivars, whereas none of the *T. dicoccoides* lines analyzed showed band 42. However, a more accurate inspection of gliadin- and glutenin-patterns of *T. dicoccoides* lines, showed that only some Jordanian accessions contained omega-gliadin 35, gamma-gliadin 45 and the LMW-glutenin subunits referred as LMW-2 (*Gli-B1-12* allele), which are present in the durum cultivar Creso. This allele occurred in only two Jordan populations and then at only a low relative frequency. Moreover, most of the lines carrying it showed complete diploidization of the 1AL genes of the HMW-glutenin subunits and morphological characters, such as trough rachis, typical of cultivated wheats. The *Gli-B1-12* allele may then derive from introgressive hybridization with cultivated forms which were growing not far from the *T. dicoccoides* stands. Sympatrically distributed accessions of *T. dicoccoides* and *T. durum* were in fact present in different Jordanian collection sites (Jaradat and Humeid 1990).

Variation in protein type and amount is the main factor responsible for grain technological and nutritional properties. The wide polymorphism detected should be evaluated for its effects on technological properties through the transfer of new allelic variants and/or increasing the number of HMW-glutenin subunits by using those lines in which both x and y *Glu-A1* subunits are actively expressed. Evidence that an increase in the number of HMW-glutenin subunit might produce an improvement in gluten strength is largely indirect, due mainly to a reduction in quality when certain subunits are removed (Lawrence et al. 1988). Quantitative analyses carried out on total-protein extracts from 22 cultivars of bread wheat showed that the presence of either subunit 1Ax1 or 1Ax2* increases the proportion of HMW-glutenin proteins by about 8% to 10%, when compared with a null allele (Halford et al. 1992). This would indicate that individual subunits may account for about 2% of the total grain proteins and that the increase in bread making quality associated with the presence of the of 1Ax subunit may derive from an increase in high-molecular-weight gluten polymers, due to the greater amount of HMW-glutenin subunits.

The introduction in cultivated wheats of genes encoding the 1Ay subunit may also have important implications for gluten structure and functionality. The recently published (Shewry et al. 1989) HMW-glutenin subunit DNA sequences indicate that each subunit consists of three distinct structural domains: an N-terminal domain, a C-terminal domain and a central domain. Both the C- and the N-terminal domains are non-repetitive and contain most of the cysteine residues, whereas the central domain is made up of repeat motifs. Usually x-type subunits possess four cysteines, whereas y-types, including the 1Ay, have seven cysteine residues. The precise number and distribution of the cross-links can be expected to influence the elastic modulus of gluten, as in classical rubber theory. The additional cysteine residues present in the y-type subunits may be important, as they could lead to more highly cross-linked polymers.

Acknowledgements. We acknowledge the contribution of Mr. A. B. Damania in providing seeds of the *T. dicoccoides* accessions form Jordan and Turkey. We are also grateful to Mr. E. Cannarella for technical assistance in the electrophoretic analyses. This research was supported by C. N. R., Italy; Special Grant R.A.I.S.A., sub-project 2, paper no. 760.

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