Theor Appl Genet (1989) 78:353–358

High molecular weight glutenin subunit in durum wheat (*T. durum*)

G. Branlard [1], **J.C. Autran** [2] **and P. Monneveux** [3]

[1] INRA, Station d'Amélioration des Plantes, Domaine de Crouelle, F-63039 Clermont-Ferrand, France
[2] INRA, Laboratoire de Technologie des Céréales, 9, Place Viala, F-34060 Montpellier, France
[3] INRA, Station d'Amélioration des Plantes, 9, Place Viala, F-34060 Montpellier, France

Received February 8, 1989; Accepted February 15, 1989
Communicated by H.F. Linskens

Summary. The diversity of high molecular weight (HMW) glutenin subunits of 502 varieties of durum wheat (*Triticum durum*) from 23 countries was studied using sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE). Twenty-nine types of patterns were observed with 18 mobility bands. A total of 18 alleles were identified by comparing the mobilities of their subunits to those previously found in hexaploid wheat (*T. aestivum*) and in *Triticum turgidum* var. *dicoccum*. Five new alleles were detected: two on the *Glu A1* and three on the *Glu B1* locus. Comparison of the frequency of alleles in the three species *T. aestivum, T. dicoccum* and *T. durum* was investigated. Significant differences exist between each of these species on the basis of the frequency distributions of their three and four common alleles at the *Glu A1* and *Glu B1* locus, respectively. The *Glu B1c* allele occuring very frequently in hexaploid wheats was not found in the two tetraploid species. More than 83% of the *T. durum* analysed were found to have the *Glu A1c* (null) allele.

Key words: Durum wheat – *T. durum* – SDS-PAGE – Novel subunits – Glutenin-diversity

Introduction

As far as bread wheat is concerned, examination of high molecular weight glutenin subunits revealed three to five main bands using electrophoretic analysis in SDS medium (SDS-PAGE). These proteins correspond to structure genes located on long chromosome arms 1 A, 1 B and 1 D (Bietz et al. 1975; Lawrence and Shepherd 1981). Genetic determinism of these high molecular weight subunits was made clear. Two loci closely linked on each chromosome, 1 DL and 1 BL, code for two subunits (*Glu D1*) and for one or two subunits (*Glu B1*). Chromosome 1 AL also carries these two genes but only one of them gives a subunit (Lawrence and Shepherd 1980; Payne et al. 1981). For each of these genes, a very significant multiallelism is observed at locus *Glu B1*, sharply less important for *Glu D1* and weak for *Glu A1* (Payne and Lawrence 1983). Combinations of these alleles allow hundreds of possible genotypes to be obtained. But for the wheats of a given country, the number of diverse patterns is not generally very high, about fourty (Branlard and Le Blanc 1985).

Our present knowledge of HMW glutenin subunit variation in durum wheats is, however, limited: analysis of HMW glutenin subunits has only been reported on a relatively small number of Australian (Du Cros 1987), Italian (Pogna et al. 1985; Vallega 1986; Boggini et al. 1987; Margiotta et al. 1987) and French (Branlard and Le Blank 1985; Autran and Feillet 1987) varieties, and also on accessions of *T. dicoccoides* (Levy and Feldman 1988; Levy et al. 1988; Nevo and Payne 1987), of *T. dicoccum* (Vallega and Waines 1987; Vallega 1988) and of *T. turgidum* (Vallega and Mello-Sampayo 1987; Levy et al. 1988).

In this paper, in order to get a better understanding of the HMW glutenin subunit variation, we report the analysis of a very large set of durum wheat varieties with very different origins.

Other objectives of this study were to: (1) compare the distribution of HMW subunits between *T. durum, T. dicoccum* and *T. aestivum*; (2) identify the new alleles and propose a nomenclature for them.

Materials and methods

Material. A total of 502 varieties of durum wheat was analysed. The list of these varieties is given in Table 1. These wheats come

Table 1. *T. durum* varieties analysed by SDS-PAGE, grouped according to the 29 different types of HMW glutenin subunits

Type 20
Ak-Bugday 13; Alpidur; Amidur; Alforge; Ambral; Ana-Bugday; Antalya 1517; Appulo; Aric 551/1; Aric 561/1; Aric 571/1; Arnaut de Studina; Atogs; Belgrade 9; Beyaz Bugday; Biancuccia; Bidi 17; Biskrix Bouteille; Blondur; Bohoth 1; Bulgarischer 2; Candeal; Cannizzara; Capeiti; Cappeli; Cargivox; Cargitoro; Casoar; Castiglione Glabor; Cibre; Clairdoc; Damoiso; Derbent-Skaja; Diabola; Douru Boukowa; Durox; Durelle; Electra; Gabbiano; Gezira 17; Ilektra; Inbar; Karaklek; Kirkpinar 79; Kislik-Koncine; Leeds; Line 68; Line 305; Line 348; Line 1366; Line A 97; Line A 166; 20 French Lines; Mahmoudi 981; Malav Raj (HI-7747); Mandon; Maristella; Marques 9197; Marroquina Preto 7225; Mohamed Ben Bachir; Monrisco Preto da Grao Escuro; Neodur; Nursith; Oued Zenati; Oued Zenati 368; Oued Zenati 26972; Pasdur; Pavone; Polinicum; Preto Algarvio 10026; Psathas; Ramsey; Ranger; Roma; Romeo; Sadouo 17; Safari; Santa; Sebera; Tanganrog Buck Balcarce; Taganrog Selection Buck; Taganrog Vilela Fideos; Telez 3; Tito; Tomclair; Trinakria; Tunisima; Turkischer Weizen 14; Urfa 1366; Urria; Valaniere; Valdur 1; Valfiora; Valgiogio; Valitalico; Valsacco; Valselva; Valsforgio; Viprior; Vixosabra; Wells; Zeramek; Zeramek Cra

Type 7-8
Akmolinska 2; Akmolinska 5; Altai 80; Altai 410; Altai 426; Altajka; Altyn Bugdai; Anatolien 6511; Anatolien 6618; Arandany; Balcarceno Inta; Barnaul 80.1; Barnaul 82; Barnaul 83; Barnaul 431; Bezostaja 54; Bieloturka; Bonaerense Valverde; Bulgarischer C; Cargiflax; Celabinskaja; Cocorit 71; Donskaja 309; Durazio-Ripo 640; Durazio-Ripo 2312; Entrelargo de Montijo; Espagnol; Gigante Ingles 2632; Griechischer Von Atlant; Griechischer Von Mittojen; Harnovka; Hordeiforme 10; Hordeiforme 27; Hordeiforme 496; Inchusa; Jaguar, Khackovstaja 46; Korall; Ku 05781001; Line 304; 21 French Lines; Mina; Mindum; Minos; Narodnaja; Novopodolskaja; Otrada; Palermo; Parus; Phiribol; Raj 1555; Sadovo 5; Sansone; Steward; Stewart 63; Tiflis; Topaz; Tremez; Ripo 2098; Tripolitico; Valgerardo; Valnova

Type 6-8
Abyssinskaja; Agathe; Albanien; Amarelejo; Anafil Escuro 2337; Benor; Botno; Brumaire; Buck Candisur; Buck Mechongue; Caid Eleize 2; Calvinor; Cana Maciza 8194; Cando; Castiglione Glabra; Chandur; Cotrone; Cresco; Crosby; D 11; Edmore; Espanhol; Flodur; Gidia; Gloire de Montgolfier; Griechischer; Grodur; Jairaj (JNK-4W-183); Kidur; Lakota; Langdon; Lina; Line 303; Line A 105; Line A 177; 33 French Lines; Lobeiro 0342; Macoun; Menceki; Mida; Mondur; Monrisco Fino 4364; Montferrier; Montpellier; Pionerka; Poinville; Preto Amerelo; Primadur; Prolixe; Quilafen; Randur; Regal; Riente; Rolette; Rugby; Santa Maria; Semenzella, Scilla Lutri; Trigo Candeal; Tunisia; Valdur 2; Vermelho Joilo 2462; Wakooma; Ward; Wascana

Type 1'19
Belfugitto; Lambro

Type 1"6-8
Candeal 2314

Type 1"20
Escuro 6141; Candela da Grao Escuro

Type 23-18
Dritto; Durandal; Kyperounda 1; Kyperounda 2; Line FD 8601; Polesine; Purculu

Type 14-15
Anatolien 6523; Hebda

Type 6-16
BX Ipi; Geniteur N° 14; Novomicurinka; Sadovo 04; Turquie 1; Turquie 2

Type 13-16
Arcour; Biancuccia; Bonaerense 202; Candeal Seleccion La Prevision; Capdur; Corum 1583; Duramba (B, C, D); Farro Lungo; Isa 1; Indien; Line 28; Line 264; Line 5003; Line 15425; Ligne VR 8671; Polesine; Regina; Rikita; Rio Russelo; Russo; Semenzella; Scorsonera; Tripolinos Agatha; Vallelunga Pubescence; Xeres

Type 1 7-8
AK Bug; Akbugda; Azerbaidjan 18462; Krasnodarskaja 362; Micurinka; Mitschurinka; Szortadinskaja 71; URSS 3A; URSS 3D1; URSS 3D2; Lignées URSS 6; 414144

Type 1 6-8
Candeal 2314; Dagestan; Javardo 2530; Monrisco 063; Nita; Sadouo 07; Saridanis; Sivovska Besetchuk

Type 1 23-18
Apulicum 233; Pombinho 0317; Rainerio

Type 1 20
Anatolien 6615; Elazig 1495; Iran 1; Kabul 2; Line 073144; Line WA 6755; Lobeiro Da; Grao Escuro; Megadur; Midge 1375; Skopje; 073144

Type 1 6-16
Espanhol 8914

Type 1 14-15
Maroccos N° 14

Type 23-22
Greece 20

Type 7
Nursith 163

Type 7-15
Ardente; Kirmize; Line D 241; Line D 401; Line D 402; Roccia

Type 2 7*
Dalmatia; Dalmatia 5; Tuerdaja 931

Type 2 20*
Akbasak 2; Azerbaidjan 18471; Cirpan 22.70; Line CG 85.1; Ruscia; Zagorka

Type 2 13-16*
Durgam; Durtal

Type 2 23-18*
Akabasan 1; Bufala Nera Corta; Chrysowitza; Dalmatia 4; Fata-Bugday; Tunesischer-Weizen; Yerli-Yumuska

Type 2 6-8*
Barbala 11827; Tuerdaja 455/5

Type 2 7-8*
Barnaul 80.2; Silicio 0290

*Type 2** 7-8*
Anatolien 18477; Beloturka 69; Bezencukskaja 115; Bezostaja 116; Cernokotska; Enver Pascha; Hubice 47/3; Hubice 4714; Kubanka; Melianopus 69; Rostkovskaja 25

*Type 2** 6-8*
Griechenland Grosskornig

*Type 2** 20*
Aric 581/1; KU 0589/001; Meghdoot (HI 7483); Moskowskaja Tejskaya

*Type 2*** 7-8*
Bezencukskaja 139; Bezencukskaja 141; Melianopus 1528; Plastovskaja 2; URSS 1B

from 23 countries. Thirty-eight percent of the studied genotypes were of French origin. Most of these cultivars were grown at the INRA Plant Breeding Station (Durum Wheat Laboratory of Montpellier) in 1986 and 1987. Six or more kernels per cultivar were separately investigated.

Electrophoresis. Proteins were extracted from the brush half of the kernels in a TRIS-HCl buffer with SDS and then reduced to subunits by 2-mercaptoethanol, according to the method of Payne and Corfield (1979). The extract was separated by electrophoresis on acrylamide gel (11%) according to the method of Laemmli (1970). Staining of the proteins was carried out for 12 h in a 2-propanol, acetic acid, Commassie blue R 250 water solution of 25% (V/V), 10% (V/V), 0.2% (W/V), 65% (V/V), respectively.

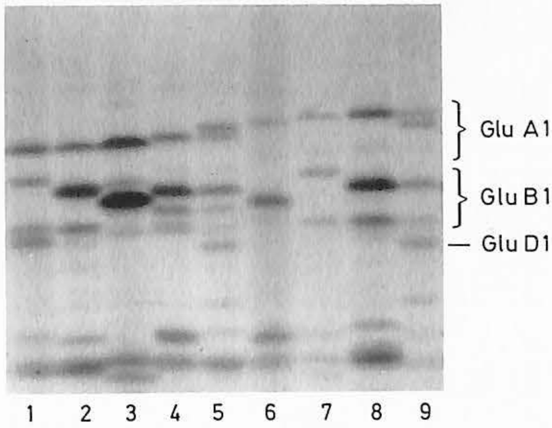

Fig. 1. SDS-PAGE patterns of HMW glutenin subunits of the following varieties: *T. aestivum* cv Goya (*Glu A1a*), cv Atlas 66 (*Glu A1c*) and cv Comtal (*Glu A1b*) (*lanes 1, 5 and 9*, respectively); *T. durum, lane 2;* cv Mélanopus 1528 (*Glu A1VI*); *lane 3;* cv Aric 581/1 (*Glu A1V*); *lane 4:* cv Durtal (*Glu A1c*); *lane 6;* cv Belfugitto (*Glu A1III*); *lane 7;* Candeal 2314 (*Glu A1IV*); *lane 8:* cv Mitchurinka (*Glu A1b*)

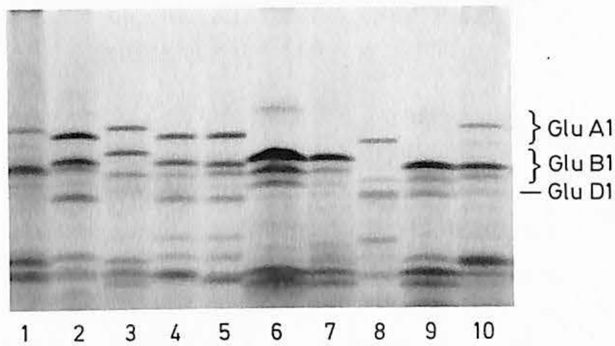

Fig. 2. SDS-PAGE patterns of HMW glutenin subunits of the following varieties: *T. aestivum, lane 2:* cv Frondoso (*Glu B1g*); *lane 4:* Atlas 66 (*Glu B1f*); *lane 5:* cv Sappo (*Glu B1h*); *lane 8:* cv Serbian (*Glu B1k*); *T. durum, lane 1:* cv Belfugitto (*Glu B1VI*); *lane 3:* cv Espanhol 8914 (*Glu B1* XIII); *lane 6:* cv Kirmize (*Glu B1XII*); *lane 7:* cv Roccia (*Glu B1XII*); *lane 9:* cv Greece 20 (*Glu B1XIV*); *lane 10:* cv Rainerio (*Glu B1IV*)

Results and discussion

Different HMW glutenin subunits observed on SDS-PAGE

Twenty-nine types of different diagrams were identified among the 502 HMW glutenin subunits of the analysed durum wheats (Table 1). Each diagram included from one to three bands of HMW glutenin subunits. The number of major bands having a different mobility was 18. Slightly stained bands were not considered in the diagram analysis. Mobility of these different subunits was compared with that of bread wheat. Figures 1 and 2 show the main bands observed on bread wheat and the ones having the same mobility on the 502 analysed durum wheats. Only subunits 17 and 21, corresponding to alleles on *Glu B1* and previously encoded (Payne and Lawrence 1983), were not found on analysed durum wheats.

On the other hand, three new bands were observed which were not, untill now, listed on bread wheat and *T. dicoccum.*

For the moment, these new bands are named 2**, 2*** and 23. Considering the mobilities of the other bands coded by the cultivars to which they belong, these bands are likely to be coded by alleles of *Glu A1* with regard to 2**, 2*** and by alleles of *Glu B1* with regard to 23.

Alleles of HMW glutenin subunits of durum wheat

For the 502 durum wheats, a total of 18 different alleles were identified, 7 corresponding to the *Glu A1* locus and 11 to the *Glu B1*. Five of these alleles were not identified previously by Payne and Lawrence (1983) on *T. aestivum* or by Vallega (1986) and Vallega and Waines (1987) on *T. durum* and *T. dicoccum.*

The nomenclature adopted by Vallega and Waines (1987) for the new alleles encountered in *T. dicoccum* was used for the new ones of *T. durum.*

Glu A1V, which codes for the band named 2**, was a new allele observed in durum wheat from Turquia, USSR, Yugoslavia, Ethiopia and India. Accessions carrying this new allele were not numerous: 2.9% of the *T. durum* analysed. Table 2 gives an example of these accessions gathered in three types of groups on Table 1. The subunit 2** has a mobility between 2* and 5 (lane 3, Fig. 1).

Allele *Glu A1VI* is very rare and has been found in five Russian durum wheats. The subunit 2*** corresponding to this novel allele has a mobility slightly higher than the 2** mobility (lane 2, Fig. 1).

Alleles *Glu A1III* and *Glu A1IV*, corresponding to the subunits named 1′ and 1″, previously observed by Vallega and Waines (1987) and Pogna et al. (1985), were both very rare in *T. durum* varieties. Subunit 1″ was found only in one Spanish and two Portuguese accessions (Table 1).

Table 2. Alleles of HMW subunits of glutenin found in the 502 *T. durum* wheat varieties

Locus	Alleles	Bands nomenclature attributed	Variety standard	
			Bread wheat (a)	Durum wheat
Glu A1	a (a)	None	Chinese Spring	–
	b (a)	1	Hope	–
	c (a)	2*	Besostaya-1	–
	III (b)	1′	–	Lambro
	IV (b)	1″	–	Candeal 2314
	V (c)	2**	–	Aric 581/1
	VI (c)	2***	–	Melanopus 1528
Glu B1	a (a)	7	Flinor	–
	b (a)	7-8	Chinese Spring	–
	d (a)	6-8	Hope	–
	e (a)	20	Federation	–
	f (a)	13-16	Lancota	–
	h (a)	14-15	Sappo	–
	IV (b)	23-18	–	Durandal
	VI (b)	19	–	Lambro
	XII (c)	7-15	–	Roccia
	XIII (c)	6-16	–	Espanhol 8914
	XIV (c)	23-22	–	Greece 20

(a) From Payne and Lawrence 1983
(b) From Vallega and Waines 1987
(c) Nomenclature proposed for the novel alleles
* Nomenclature proposed by Payne and Lawrence 1983
** and *** nomenclature attributed for the new bands of *Glu A1*

Three new *Glu B1* alleles, each coding for two subunits, were found on the 502. *T. durum* analysed.

Glu B1XII, which codes for subunits 7 and 15 (lanes 6 and 7, Fig. 2), was particularly found in French and Russian durum wheats. The name of these two subunits was assigned after comparing their mobility to those of alleles *Glu B1a* (subunit 7, contained in Chinese Spring) and *Glu B1h* (subunits 14–15, contained in Sappo).

Allele *Glu B1XIII* was present in one Spanish variety: Espanhol 8914, in one French: Géniteur No. 14, in one Bulgarian: Sadovo 04, in two Turkish: Turquie 1 and Turquie 2 and in one Russian variety: Novomicurinka. A durum wheat, BX Ipi, of unknown origin also had this novel allele.

The subunit referred to as 23 in this paper was associated with another subunit in 22 dicoccums by Vallega and Waines (1987). They named the corresponding allele *Glu B1IV*. This allele occurs in 3.4% of the durums analysed. The fast-moving band had the same mobility as subunit 18 contained in the *T. aestivum* Gabo (allele *Glu B1i*). Consequently, the attributed name of the subunits coded by this *Glu B1IV* allele is 23–18. The subunit 23 was found to be associated with the subunit 22 in only one cultivar: Greece 20. The two subunits 23–22, coded by the novel allele *Glu B1XIV*, could be named by comparing them to subunits contained in Serbian (subunit 22) and in Rainerio (subunits 23–18) in Fig. 2 (lanes 8 and 10, respectively).

The subunit corresponding to *Glu B1VI* detected by Vallega and Waines (1987) on dicoccum and durum seems to have the same mobility of the subunit 19 coded by the *Glu B1g* allele contained in Frondoso (Fig. 2, lanes 1 and 2). Consequently, the name proposed for this major subunit coded by *Glu B1VI* is 19.

Comparison of allele frequency

Table 1 indicates the distribution of the 502 varieties among the 29 types of HMW glutenin patterns. First of all, it is not possible to find a close relationship between a type of pattern and a given geographical origin of the varieties. Table 1 also indicates that some types of diagrams are very frequent: more particularly those having bands 20 (allele *Glu B1e*), 6–8 (allele *Glu B1d*) and 7–8 (allele *Glu B1b*). They represent, respectively, 33.5%, 26.3% and 25.9% of the analysed durum wheats (Table 3). But most of the durum wheats do not have HMW glutenin subunits coded by locus *Glu A1*. More than 83% of durum wheats carry the null allele (*Glu A1a*). This frequency is sharply different from the one observed on two collections of 195 cultivars of bread wheat, a world collection observed by Payne et al. (1981) and a French series (Branlard and Le Blanc 1985) (Table 3).

Durums were found different from bread wheats and dicoccums in the allelic frequencies at *Glu 1* loci. A comparison of the frequencies of alleles at *Glu A1* and *Glu B1* showed significant differencies between the three species. Only eight alleles (*Glu A1a, b, c* and *Glu B1a, b, d, e, h*) are common to the three species and 11 are common to *T. dicoccum* and *T. durum* (Table 3). A comparison of the frequencies of these alleles revealed significant differences (Chi-square test) between common wheat and durum or between dicoccum and durum. Vallega and Waines (1987) also noticed a difference between *T. dicoccum* and bread wheats. Nevertheless, some common features seem to characterize the tetraploïd species: both are lacking alleles *Glu B1c* and *Glu B1i* and the frequency of allele *Glu B1a* is very low in dicoccum and durum.

The absence of the very common allele of bread wheat *Glu B1c* (subunits 7–9) in the tetraploid species must be underlined. This feature and the strong differencies between the frequency of occurrence of the common alleles would have three explanations.

A first explanation could be related to the origin of the durum wheats presently grown. The patterns of the particular ancestors that have originally contributed to the A and B durum wheat genomes, or that have been predominantly used in the first breeding programs, may

Table 3. Comparison of allele frequencies for the loci *Glu A1* and *Glu B1* amongst 195 cultivars of bread *T. aestivum* from a world collection (b), from a French collection (c), amongst 167 *T. dicoccum* wheat (d), and amongst 502 *T. durum* wheats (e) with 195 of French original (f)

Locus	Alleles	Bands	Frequency (%)				
			Bread wheat cultivars		*T. dicoccum*	*T. durum*	
			(b)	(c)	(d)	(e)	(f)
Glu A1	a	1	28	16	56	7.0	1.0
	b	2*	28	5	16	4.6	1.6
	c	none	44	89	21	83.5	97.4
	I	(a)	–	–	rare	–	–
	II	(a)	–	–	rare	–	–
	III	1′	–	–	7	0.4	0
	IV	1″	–	–	–	0.6	0
	V	2**	–	–	–	2.9	0
	VI	2***	–	–	–	1.0	0
Glu B1	a	7	19	33.5	2	0.8	0
	b	7-8	20	32	11	25.9	15.8
	c	7-9	27	16	–	–	–
	d	6-8	19	13	18	26.3	37.9
	e	20	5	4	rare	33.5	32.8
	f	13-16	1.5	0	–	5.5	7.1
	g	13-19	0.5	0.5	rare	–	–
	h	14-15	1.5	0	11	0.6	0
	i	17-18	6.5	1	–	–	–
	j	21	rare	rare	1	–	–
	k	22	rare	rare	2	–	–
	I	(a)	–	–	4	–	–
	II	(a)	–	–	9	–	–
	III	(a)	–	–	11	–	–
	IV	23-18	–	–	13	3.4	0.9
	V	(a)	–	–	2	–	–
	VI	19	–	–	13	0.4	0
	XII	7-15	–	–	–	2.2	4.6
	XIII	6-16	–	–	–	1.2	0.9
	XIV	23-22	–	–	–	0.2	0

(a) Allele found in *T. dicoccum;* Vallega and Waines 1987
(b) 195 bread wheat varieties of a world collection from Payne et al. 1981
(c) 195 bread wheat varieties of French origin from Branlard and Le Blanc 1985
(d) 167 dicoccum wheat of 23 countries from Vallega and Waines 1987
(e) 502 durum wheat of 23 countries
(f) 195 durum wheat of French origin
*,**,*** see footnotes Table 2

explain the deviation observed from a random distribution of the alleles that are present today.

Secondly, the lack in tetraploïd species of some glutenin subunits, such as 7–9 or 17–18, that are present in common wheat, may also be the consequence of mutations which only occurred in *T. aestivum* (and conversely for HMW subunits, such as 1″, 2**, 2***, 7–15, 6–16, absent in *T. aestivum,* but present in *T. durum*).

A third explanation could derive from the strong difference in allelic frequencies of HMW glutenin subunits between very old populations (last century) of bread wheats and modern cultivars (G. Branlard, unpublished data): subunits 20 and 6–8, in particular, were found very frequently in old populations.

Because of the correlation between allelic diversity and bread wheat quality, breeding with conventional technological tests for more than 60 years could have increased the frequency of some "good" alleles like *Glu A1a,* or *b* and *Glu B1c.* Conversely, in durum wheats, since HMW glutenin subunits were not found to have a strong effect on pasta quality (Autran and Feillet 1987; Autran and Galterio 1989), breeding for pasta quality had probably very little influence on the frequencies of the different alleles.

Acknowledgements. M. Dardevet, R. Berrier and E. Berthon are gratefully acknowledged for their assistance in the electrophoresis of glutenin subunits.

References

Autran JC, Feillet P (1987) Genetic and technological basis of protein quality for durum wheat in pasta. In: Pattakou V (ed) Protein evolution in cereals and legumes. Seminar in the EEC Programm of Coordination of Agricultural Research on Plant Productivity, pp 59–71

Autran JC, Galterio G (1989) Association between electrophoretic composition of protein, quality characteristics and agronomic attributes of durum wheat. J Cereal Sci (in press)

Bietz JA, Shepherd KW, Wall JS (1975) Single-kernel analysis of glutenin: use in wheat genetics and breeding. Cereal Chem 52:513–532

Boggini G, Dal Belin Peruffo A, Mellini F, Pogna NE (1987) Storage protein composition, morphophysiological and quality characters of 24 old durum wheat varieties from Sicily. Rachis 6:30–35

Branlard G, Le Blanc A (1985) Les sous unités gluténines de haut poids moléculaire des blés tendres et des blés durs cultivés en France. Agronomie 5:467–477

Du Cros DL (1987) Glutenin proteins and gluten strength in durum wheat. J Cereal Sci. 5:3–12

Laemmli UK (1970) Cleavage of structural proteins during the assembly of the head of bacteriophage T4. Nature 227:680–685

Lawrence GJ, Shepherd KW (1980) Variation in glutenin protein subunits of wheat. Aust J Biol Sci 33:221–233

Lawrence GJ, Shepherd KW (1981) Chromosomal location of genes controlling seed proteins in species related to wheat. Theor Appl Genet 59:25–31

Levy AA, Feldman M (1988) Ecogeographical distribution of HMW glutenin alleles in populations of the wild tetraploid wheat *Triticum turgidum* var. *dicoccoides*. Theor Appl Genet 75:651–658

Levy AA, Galili G, Feldman M (1988) Polymorphism and genetic control of high molecular weight glutenin subunits in wild tetraploid wheat *Triticum turgidum* var. *dicoccoides*. Heredity 61:63–72

Margiotta B, Colaprico G, Lafiandra D (1987) Variation for protein components associated to quality in durum wheat lines and varieties. In: Lasztity R, Bekes F (eds) Proc 3rd Int Workshop on Gluten protein, 6–9 May, Budapest. World Scientific, Singapore, pp 314–330

Nevo E, Payne PI (1987) Wheat storage proteins: diversity of HMW glutenin subunits in wild emmer from Israel. 1. Geographical patterns and ecological predictability. Theor Appl Genet 74:827–836

Payne PI, Corfield KG (1979) Subunit composition of wheat glutenin proteins isolated by gel filtration in a dissociating medium. Planta 145:83–88

Payne PI, Lawrence GJ (1983) Catalogue of alleles for the complex gene loci, *GLU-A1*, *GLU-B1*, and *GLU-D1* which code for high-molecular-weight subunits of glutenin in hexaploid wheat. Cereal Res Commun 11:29–35

Payne PI, Holt LM, Law CN (1981) Structural and genetical studies on the high molecular weight subunits of wheat glutenin. 1. Allelic variation in subunits amongst varieties of wheat. Theor Appl Genet 60:229–236

Pogna N, Mellini F, Dal Belin Peruffo A (1985) The role of PAGE in varietal identification and in developing new varieties of durum wheat with good spaghetti-making quality. Int Symp Durum Wheat, May, Foggia. Monograf Genet Agric 7:199–212

Vallega V (1986) High-molecular-weight glutenin subunit composition of Italian *Triticum durum* cultivars and spaghetti cooking quality. Cereal Res Commun 14:251–257

Vallega V (1988) Comparative analysis of high-molecular-weight glutenin subunit composition in various *Triticum* species. Plant Breed 100:241–246

Vallega V, Mello-Sampayo T (1987) Variation of high-molecular-weight glutenin subunits amongst cultivars of *Triticum turgidum* L. from Portugal. Euphytica 36:755–762

Vallega V, Waines JG (1987) High-molecular-weight glutenin subunit variation in *Triticum turgidum* var. *dicoccum*. Theor Appl Genet 74:706–710