

Use of genetic variation in the improvement of quality in durum wheat

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SUMMARY - Storage proteins, as currently defined by their chemical characteristics and genetic control, belong to three main families, that is, gliadins, HMW- and LMW-subunits of glutenins. Very large amounts of genetic variation with respect to both number of loci and number of alleles at these loci exist in durum wheat. A preliminary catalogue of gliadin alleles in durum wheat was compiled, it includes 8 gliadin allelic blocks encoded by the *Gli-A1* locus (chromosome 1A), 4 blocks encoded at *Gli-B1* (chromosome 1B) (namely γ -gliadins 42 and 45 whose presence was found to have contrasting effects on gluten quality), 17 blocks at *Gli-A2* (chromosome 6A) and 9 blocks at *Gli-B2* (chromosome 6B). Based on genetic and biochemical evidence, γ -gliadins 42 and 45 are thought to be only genetic markers of quality, their relationship with quality being due to their tight genetic linkage with the so-called respectively LMW-1 and LMW-2 subunits of glutenin encoded at the *Glu-B3* locus on chromosome 1B. Because of the good correspondence between the *Glu-3* and *Gli-1* allelic composition amongst the wheat cultivars, gliadin alleles can be used to indicate the LMW subunits contribution to gluten properties. Another important observation regards the occurrence of several additional "selfish" gliadin genes which are remote from *Gli-1* loci and homologous to *Gli-3*, *Gli-4*, and *Gli-5* loci from bread wheat. Genetic variability also exists in durum wheat for breadmaking characteristics. Although many durum wheat cultivars show large alveograph tenacity/extensibility (P/L) ratios typical of tenacious gluten character, that is probably due to the absence of the D genome, chromosome translocations can be utilised to introduce genes from alien species. For instance, the bread wheat cultivar Perzivan, biotype 2 (which possesses the spontaneous translocation 1AS/1DS where a small chromosome segment containing the *Gli-D1/Glu-D3* locus has been transferred to the short arm of chromosome 1A) offers the unique possibility to introduce the chromosome-1D genes coding for gliadins and LMW subunits of glutenin into durum wheat cultivar by conventional breeding. By crossing Perzivan biotype 2 with a number of durum cultivars, the resulting progenies (especially those containing the HMW subunit 1 coded by the *Glu-A1* locus on the long arm of chromosome 1) showed a positive effect of the introgressed genes on breadmaking quality.

Key words: Storage proteins, gliadins, low molecular weight, high molecular weight, subunits, alveograph tenacity/extensibility (P/L) ratio.

RESUME - "Utilisation de la variation génétique pour l'amélioration de la qualité chez le blé dur". Les protéines de réserve, telles qu'elles sont habituellement définies à partir de leurs caractéristiques chimiques et de leur contrôle génétique, appartiennent à trois familles principales : les gliadines, les sous-unités gluténines de haut (HMW) et de faible (LMW) poids moléculaire. Il existe chez le blé dur une importante variabilité génétique tant pour le nombre de loci que pour le nombre d'allèles. On a pu ainsi dénombrer 8 blocs alléliques codés par le locus *Gli-A1* (chromosome 1A), 4 blocs *Gli-B1* (chromosome 1B) (en particulier les γ -gliadines 42 et 45 dont on a démontré les effets opposés sur la qualité du gluten), 17 blocs *Gli-A2* (chromosome 6A) et 9 blocs *Gli-B2* (chromosome 6B). A partir de résultats génétiques et biochimiques, on a conclu que les γ -gliadines 42 et 45 ne sont que des marqueurs génétiques, leur relation avec la qualité provenant de leur étroite liaison génétique avec les sous-unités LMW-gluténines codées au locus *Glu-B3* sur le chromosome 1B et désignées respectivement LMW-1 and LMW-2. Du fait d'une bonne correspondance entre les compositions alléliques observées au niveau des loci *Glu-3* and *Gli-1*,

les allèles gliadines peuvent être utilisés comme indicateurs de la composition allélique des LMW et de leur contribution aux propriétés du gluten. Une autre importante observation est l'existence de plusieurs autres gènes gliadines ("selfish"), éloignés des loci *Gli-1*, et qui sont homologues aux loci *Gli-3*, *Gli-4*, et *Gli-5* du blé tendre. Une variabilité génétique existe également chez le blé dur du point de vue des aptitudes à la panification. Bien que de nombreuses variétés de blé dur aient des courbes alvéographiques présentant des rapports ténacité/extensibilité (P/L) typiques de glutens extrêmement tenaces - ce qui est vraisemblablement dû à l'absence de génome D - la translocation chromosomique peut être utilisée pour introduire des gènes d'espèces étrangères. Par exemple, le biotype 2 de la variété de blé tendre Perzivan (qui possède la translocation spontanée 1AS/1DS dans laquelle un court segment de chromosome renfermant le locus *Gli-D1/Glu-D3* a été transféré sur le bras court du chromosome 1A) offre la possibilité unique d'introduire les gènes du chromosome 1D codant pour les gliadines et les sous-unités LMW de gluténine dans un blé dur par sélection classique. Ainsi, en croisant Perzivan, biotype 2, avec de nombreuses variétés de blé dur, on a pu observer dans les descendances (particulièrement celles contenant la sous-unité HMW 1 codée par le bras long du chromosome 1A) un effet positif des gènes introgressés sur la qualité boulangère.

Mots-clés : Protéines de réserve, gliadines, faible poids moléculaire, haute poids moléculaire, sous-unités, alveograph ténacité/extensibilité (P/L) rapport.

Introduction

The objective of wheat breeding is to obtain improved varieties, adjusted to the requirements of farmers, processors and consumers. The most important aims are to increase yield, grain quality and disease resistance.

Wheat is not an easy crop to breed because of polyploidy. Moreover, the conditions under which wheat is grown have a marked effect on most characters. However, efforts aimed at defining the genetic structure of wheat have recently had a substantial impact on the improvement of wheat, mainly for quality related characteristics.

An important outcome of these studies is that very large amounts of genetic variation with respect to both number of loci and number of alleles at these loci exist in durum wheat.

The aim of this paper is to give the value of genetics in the improvement of wheat quality and to bring forward some salient points and highlight on future requirements of breeders.

Recent advances in genetics of storage protein in durum wheat

Storage protein composition is probably the most important single quality factor in wheat (Mifflin *et al.*, 1983). Storage proteins, as currently defined by their chemical characteristics and genetic control, belong to three main families, that is, gliadins, HMW- and LMW-subunits of glutenins. In bread wheat, the gliadin coding loci are located on the chromosomes of the first (*Gli-1*) and sixth (*Gli-2*) homoeologous groups (Payne, 1987). Each allele at any locus controls the synthesis of a group (block) of jointly inherited polypeptides. A vast multiple allelism was discovered at each gliadin locus (Sozinov and Poperelya, 1980; Metakovsky, 1991). As expected, a strong parallelism exists in the gliadin-gene architecture between bread and durum wheat. The genes coding for most γ - and ω -gliadins have been mapped on the short arms of chromosomes 1A and 1B, whereas the genes coding for most α - and β -gliadins have been located on chromosomes 6A and 6B (Payne *et al.*, 1982). However, the components encoded at each *Gli* allele have not been described yet.

From the analysis of intervarietal hybrids and of more than 100 durum wheat cultivars from several countries, and based on studies from Kudryavtsev *et al.* (1988), it has been possible to compile a preliminary catalogue of gliadin alleles in durum wheat. Fig. 1 shows the schemes of 8 gliadin allelic blocks encoded by the *Gli-A1* locus (chromosome 1A), 4 blocks encoded at *Gli-B1* (chromosome 1B), 14 blocks at *Gli-A2* (chromosome 6A) and 9 blocks at *Gli-B2* (chromosome 6B).

There are two important outcomes of this genetic analysis. The first one concerns γ -gliadins 42 and 45 whose presence was found to have contrasting effects on gluten quality (Damidaux *et al.*, 1978).

Based on genetic and biochemical evidence, these gliadins are thought to be only genetic markers of quality, their relationship with quality being due to their tight genetic linkage with LMW subunits of glutenin encoded at the *Glu-B3* locus on chromosome 1B.

However, there is a good correspondence between the *Glu-3* and *Gli-1* allelic composition amongst the wheat cultivars (Pogna *et al.*, 1988, 1990) and, therefore, gliadin alleles can be used to indicate the LMW subunits contribution to gluten properties (Autran and Berrier, 1984; Payne *et al.*, 1984).

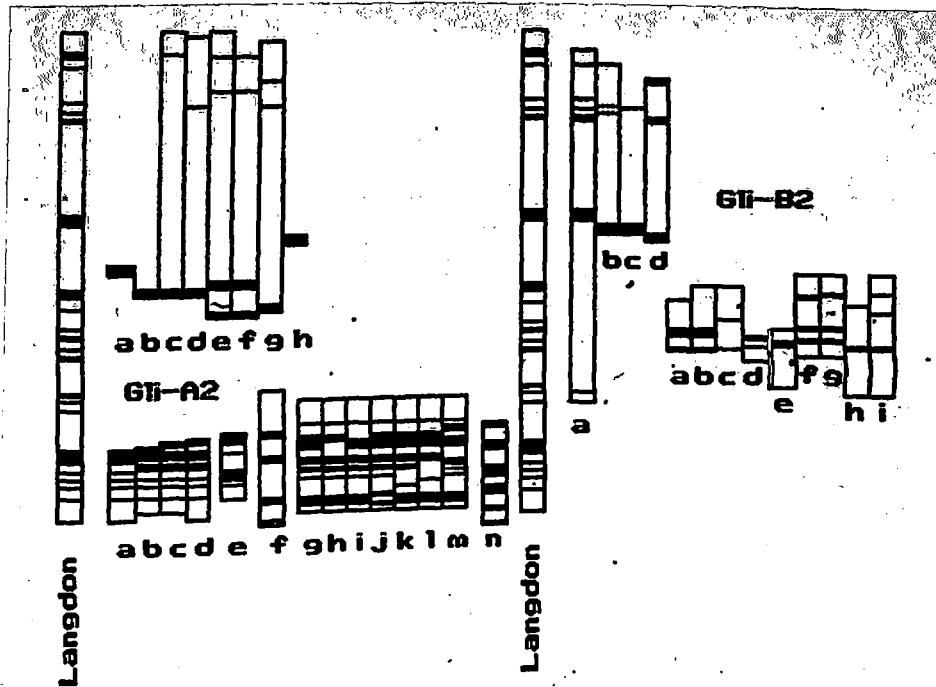


Fig. 1. Preliminary catalogue of durum wheat gliadin blocks.

The very common *Gli-B1a* and *Gli-B1c* alleles code for gliadins 42 and 45 respectively. They correspond to the so-called LMW-1 and LMW-2 glutenin subunits at the *Glu-B3* locus (Fig. 2). In addition, a γ -gliadin 45 is also encoded by the rare *Gli-B1b* allele which corresponds to a novel group of LMW subunits whose effects on gluten quality is currently being investigated.

The second important observation regards the occurrence of additional gliadin loci. It has been recently shown that the short arms of the group 1 chromosomes in bread wheat contain several minor gliadin genes which are remote from *Gli-1* loci (Metakovsky *et al.*, 1986; Redaelli *et al.*, 1992; Dachkevitch *et al.*, 1993; Pogna *et al.*, 1993). Fig. 3 shows the chromosome location of the *Gli-3*, *Gli-4*, and *Gli-5* loci with respects to *Gli-1*. There is now evidence that "selfish", remote gliadin genes also occur in durum wheat. The gliadin bands coded by these genes are indicated in Fig. 4.

A new development of breeding: breadmaking quality of durum wheat

Durum wheat is an important crop used for the production of various types of bread in some areas of the world. However, this use is rather limited because its breadmaking quality is inferior to that of bread wheat *Triticum aestivum*. However, genetic variability does exist in durum wheat and some genotypes approach the breadmaking characteristics of common wheat. In general, the durum wheat cultivars analyzed so far show high alveograph tenacity/extensibility (P/L) ratios typical of tenacious gluten character (Boggini and Pogna, 1989). Although the extreme hardness of durum wheat kernels results in a high percentage of damaged starch and then in an under-hydration of the protein network,

this lack of extensibility is likely to be mainly due to the absence of the D genome, particularly chromosome 1D, which carries genes that control some of the gluten proteins contributing to breadmaking quality, namely HMW and LMW subunits of glutenin. For example, it has been demonstrated that replacement of HMW subunits 5+10 by 2+12 increases extensibility in bread wheat (Khelifi and Branlard, 1992).

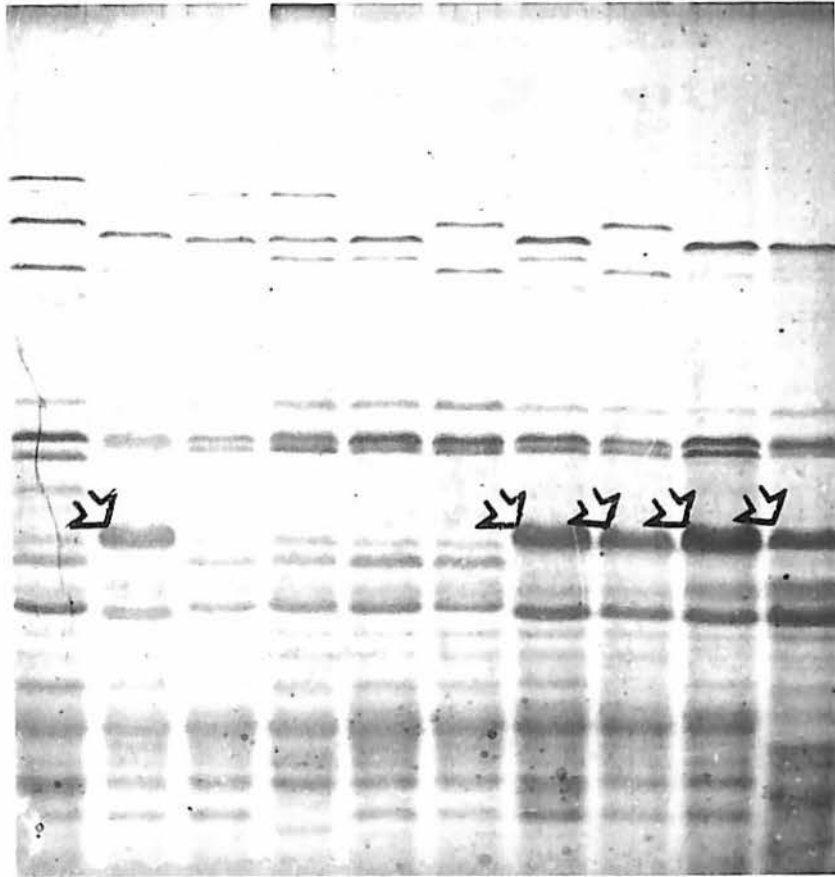


Fig. 2. SDS-PAGE patterns of several durum wheat cultivars with identification of LMW-2 glutenin subunits (arrowed) associated with γ -gliadin 45 (*Gli-B1c* allele) and indicating strong and elastic gluten characteristics.

Chromosome translocation has been utilised extensively in wheat breeding programmes in many countries to introduce genes from alien species.

The bread wheat cultivar Perzivan, biotype 2, offers the unique possibility to introduce the chromosome-1D genes coding for gliadins and LMW subunits of glutenin into durum wheat cultivar by conventional breeding. As a matter of fact, Perzivan, biotype 2 possesses the spontaneous translocation 1AS/1DS where a small chromosome segment containing the *Gli-D1/Glu-D3* locus has been transferred to the short arm of chromosome 1A (Fig. 5). Gliadins encoded by the translocated *Gli-D1* locus are numbered in Fig. 6 whereas LMW subunits encoded by the translocated *Glu-D3* locus are arrowed.

Perzivan biotype 2 was crossed as female parent with a number of durum cultivars and the resulting progenies backcrossed to the tetraploid parent for two generations. Fig. 7 shows the A-PAGE and SDS-PAGE patterns of some tetraploid progenies containing the *Gli-D1/Glu-D3* encoded proteins. The SDS sedimentation test carried out on some progenies indicates a positive effect of the introgressed genes on breadmaking quality, as previously shown in bread wheat cultivars (Benedettelli *et al.*, 1992). Obviously, their effects on dough extensibility should be estimated by rheological tests which, unfortunately, require large amounts of flour.

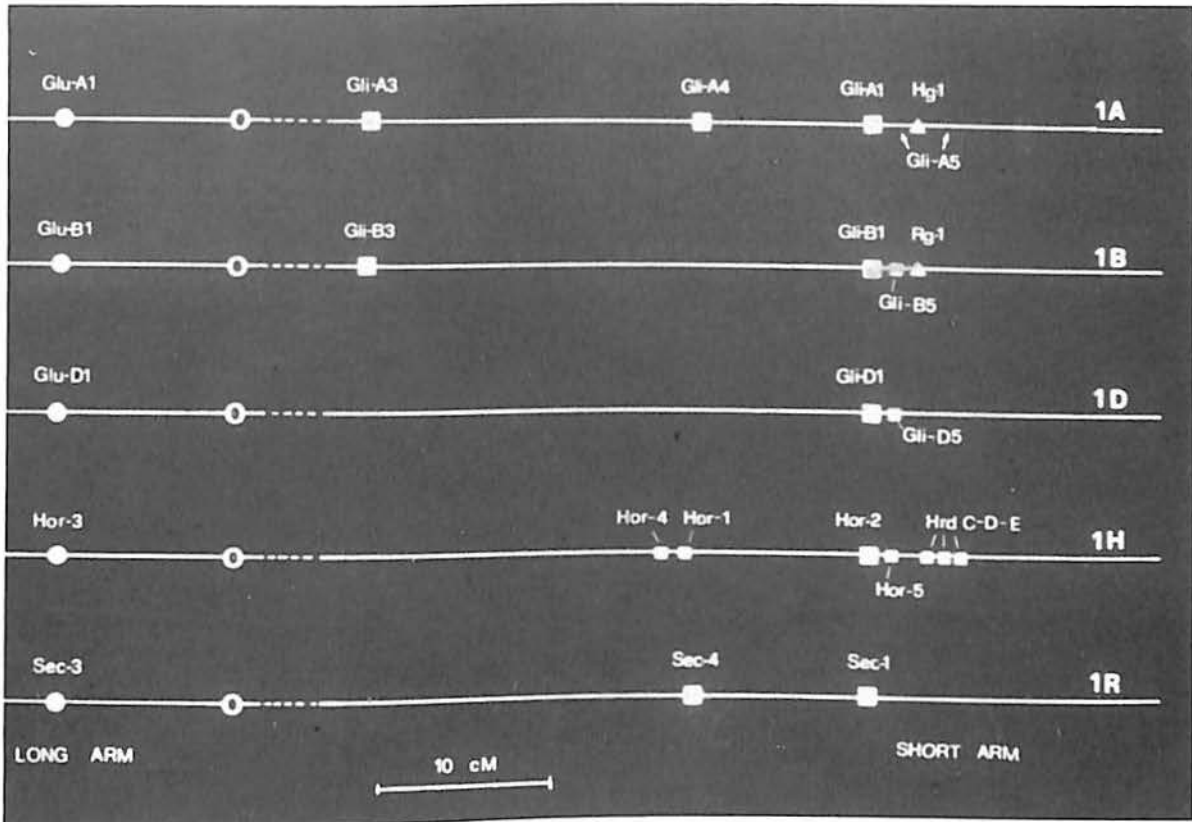


Fig. 3. Chromosomal location of the *Gli-3*, *Gli-4* and *Gli-5* loci, with respect to *Gli-1*.

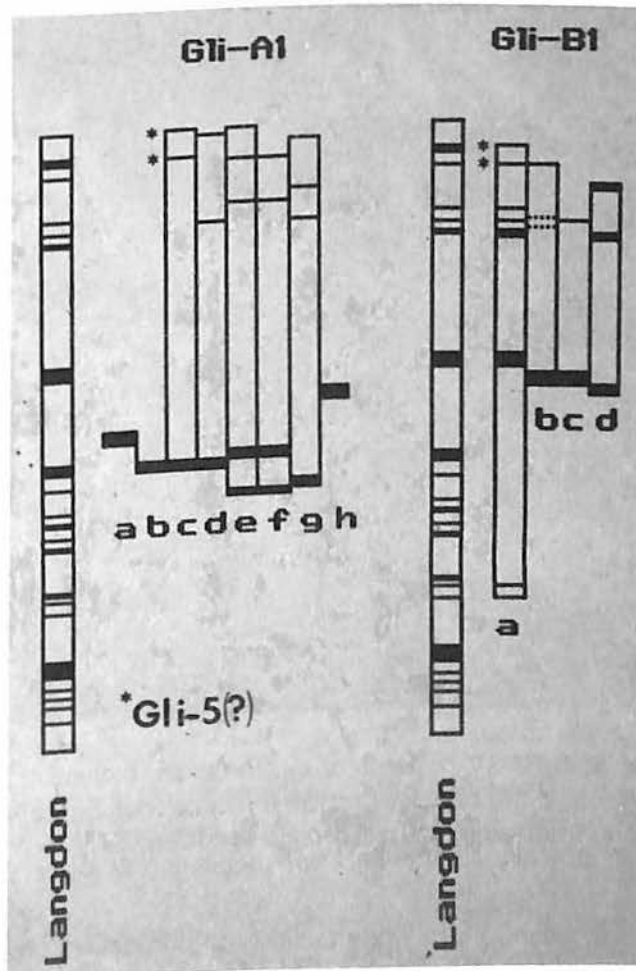


Fig. 4. Identification of "selfish" gliadin bands (*) in durum wheat patterns.

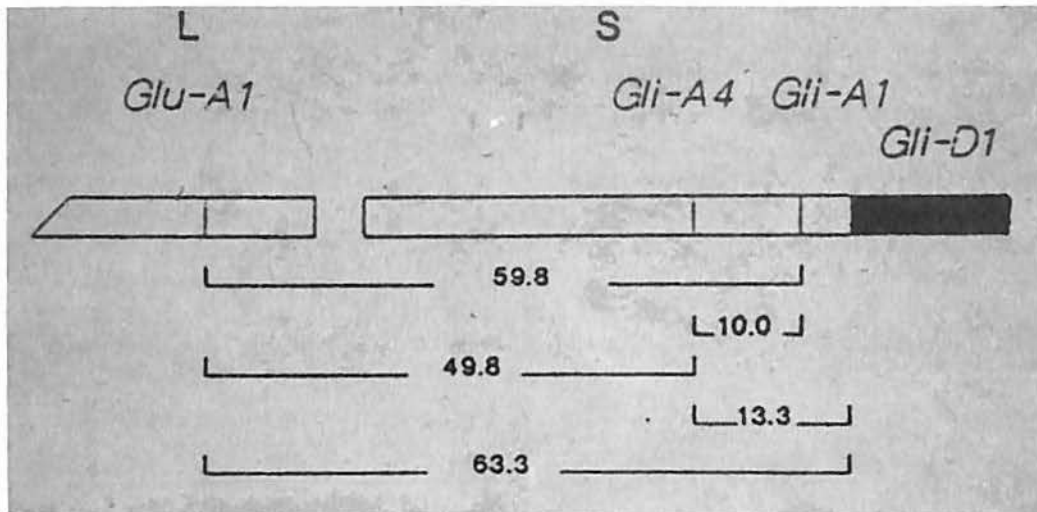


Fig. 5. Genetic map of chromosome 1A carrying the 1AS/1DS translocation. The distance between the storage protein loci *Glu-1* and *Gli-1* are in centi Morgan (cM). ■ = translocated segment from chromosome 1DS; S = short arm; L = long arm.

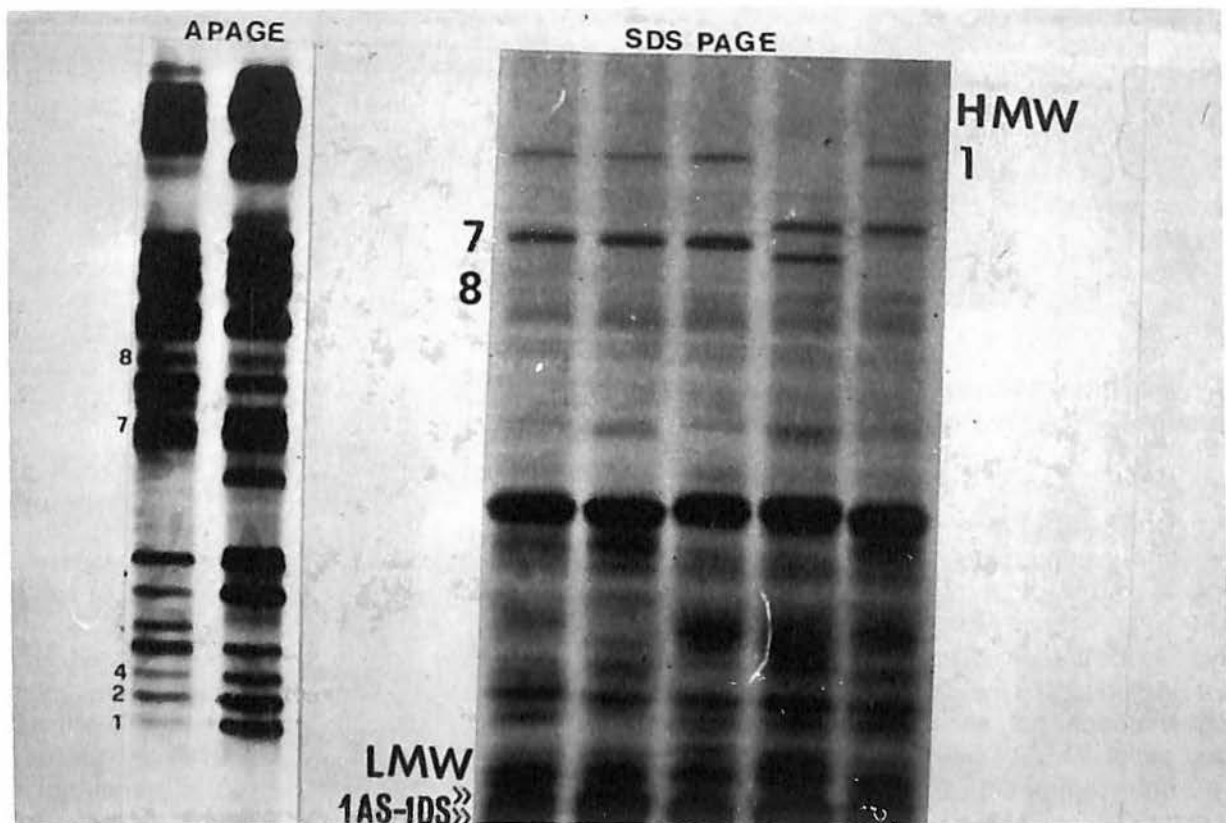


Fig. 6. A-PAGE and SDS-PAGE patterns of cv. Perzivan, biotype 2, with identification of the gliadins encoded by the translocated *Gli-D1* locus (numbered) and of the LMW subunits encoded by the translocated *Glu-D3* locus (arrowed).

In this context, it is worth noting that some translocated progenies contain HMW subunit 1 from Perzivan biotype 2. This subunit is coded by the *Glu-A1* locus on the long arm of chromosome 1A. Evidence has been recently obtained that the quantitative effects of glutenin on the differences in

breadmaking quality between durum and bread wheats reside importantly on differences at the *Glu-A1* locus, keeping in mind that durum wheats are lacking, in general, *Glu-A1* subunits (presence of the null allele).

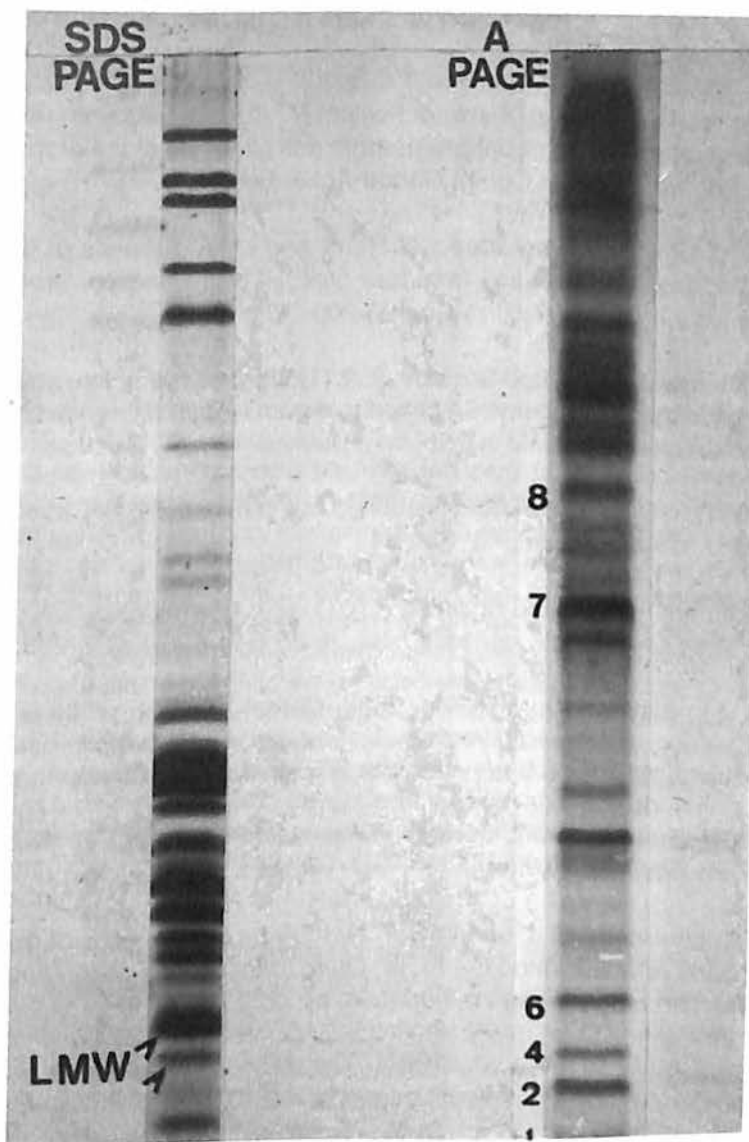


Fig. 7. A-PAGE and SDS-PAGE patterns of some tetraploid progenies containing the *Gli-D1/Glu-D3* encoded proteins.

In summary, it is quite evident that, in the future, plant breeders will rely more and more upon scientific information obtained by specialists in physiology, genetics and biochemistry.

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OPTIONS méditerranéennes

SERIE A: SEMINAIRES MEDITERRANEENS
Numéro 22

**Durum Wheat Quality
in the Mediterranean Region**

***La Qualité du Blé Dur
dans la Région Méditerranéenne***

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