Recent perspectives on the genetics, biochemistry and functionality of wheat proteins

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Wheat protein is unique among cereal and other plant proteins in its ability to form a dough with viscoelastic properties ideally suited to make bread, biscuit or pasta products. Despite many years of study, we do not have a detailed understanding at the molecular level of the basis for the unique properties of doughs or the ways in which the various constituents contribute to the functional properties of different wheat flours. This paper reviews some recent aspects of the genetics, biochemistry and functionality of wheat proteins, based on new concepts or analytical approaches, that are relevant to the processing qualities of wheat and that provide the potential to make a significant step forward in both our understanding of protein properties and the development of better wheat varieties for the future.

Wheat ranks first among our cultivated plants. Production in 1992 approached 6×10^8 t. Despite increasing industrial end uses, most wheat is used for food. In addition to providing a range of nutrients, wheat also possesses remarkable technological properties that allow the production of a variety of different processed foodstuffs such as breads, biscuits and pastas. In addition, upon removal of the water-soluble components of a flour, wheat proteins (Box 1) have the unique ability to form an insoluble and viscoelastic proteinaceous mass termed gluten, which forms the basis of the rheological properties of dough. Dry gluten, also, is increasingly used as an improver or additive in flours and in various foods.

Wheat proteins: what they are; what they do

The great nutritional and functional importance of wheat proteins has stimulated investigation of the genetics and biosynthesis of wheat storage proteins, while the traditional interests of physical chemists in understanding the contributions of wheat protein components to the milling, dough-forming and baking properties of wheat have continued undiminished. The protein content of wheat grain is one of the basic measurements of its quality in marketing, while protein composition is primarily responsible for quality differences among different varieties. For instance, the presence or ratio of certain allelic variants of gliadin or glutenin fractions are used as valuable indicators of bread-making potential in wheat breeding programs.

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Box 1. Roles of the major functional wheat proteins

Traditionally, proteins have been classified into four types according to their solubility. This classification is based on the classical work of T.B. Osborne at about the turn of the last century.

- **Albumins** are proteins that are soluble in water. Their solubility is not affected by reasonable salt concentrations. These proteins are coagulated by heat, such as those of egg white.
- **Globulins** are proteins that are insoluble in pure water, but soluble in dilute salt concentrations and insoluble at high salt concentrations.
- **Gliadins** are proteins that are soluble in 70% ethanol.
- **Glutenins** are proteins that are soluble in dilute acid or bases, in detergents, or in dissociating (urea) or reducing (mercaptoethanol) agents.

This classification, based on solubility, is used because it works and has stood the test of time. It gives reproducible results that tell something about the protein, although the fractions obtained are not clear cut. For examples, gliadins have limited solubility in water, while some low molecular weight glutenins can be extracted by ethanol.

Most of the physiologically active proteins (enzymes) are found in the albumin or globulin groups. Nutritionally, the albumins and globulins have a very good amino acid balance. They are relatively high in lysine, tryptophan and methionine. The gliadins and glutenins are the storage proteins of wheat endosperm. They are very low in the nutritionally important amino acids lysine, tryptophan and methionine.

The **storage proteins** of wheat are unique because they are also functional proteins. They do not have enzyme activity, but they are the only cereal proteins to form a strong, cohesive dough that will retain gas and produce light baked products. They are also called **'gluten proteins'** because they can be easily isolated by removing starch and albumins/globulins by gently working a dough under a small stream of water. After washing, a rubbery ball is left, which is called 'gluten'.

The gliadins have molecular weights in the range of 30 000–70 000, are single-chained and are extremely sticky when hydrated. They have little or no resistance to extension, and appear to be responsible for the extensibility of the dough. In contrast, glutenins are multichained and vary in molecular weight from 40 000 to several million. They apparently give dough its properties of strength and elasticity. In fact, glutenins are highly heterogeneous. Upon reduction of the intramolecular disulfide bonds, they yield two types of subunits: high molecular weight (HMW) subunits with molecular weights of 70 000–88 000 and low molecular weight (LMW) subunits with molecular weights of 40 000–45 000. Whereas the former (which make up the backbone of the largest polymers) clearly determine dough strength, the latter (which contribute to smaller polymers) may be associated with dough extensibility.

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There is some evidence that the proper combination of the two major wheat protein classes – gliadin, which is viscous, and glutenin, which is elastic – as well as the conformations adopted by some specific protein components (e.g. the spiral structure of the central domain of the high molecular weight (HMW) subunits of glutenin and the occurrence of cysteine residues only near the ends of the polypeptide chain) play an important role in dictating the functional properties of wheat gluten. Unfortunately, these proteins are highly heterogeneous and largely insoluble: their functionality appears in a weakly hydrated dough medium in which hundreds of constituents interact to determine cohesive, extensible and elastic characteristics. Detailed investigations of their basic components cannot be carried out while respecting the integrity of their native structure. Despite many years of study, therefore, we do not have a detailed understanding at the molecular level of the basis for the unique properties of doughs and the ways in which gliadins, glutenins and other constituents contribute to the functional properties of different wheat flours[1].

However, several advances provide the potential to make a significant step forward in both a more complete understanding of the fundamental bases of quality and in the development of improved wheat varieties and wheat products or dietary foods that come within legal requirements. In this paper we will review some recent aspects of the genetics, biochemistry and functionality of wheat proteins that are relevant to the processing quality of wheat.

Genetics and protein quality in breadmaking and biscuit-making

The concept of 'protein quality' was born several decades ago, when it was realized that different wheat varieties gave different baking scores (see Glossary). In the early 1970s it was demonstrated that the electrophoretic pattern of gliadins was a 'fingerprint' of the wheat variety. At about the same time, wheat breeders in several countries began to develop varieties that had extremely high yield potential; however, many of these varieties had unacceptable baking quality. Electrophoretic analysis of gliadins was quickly adopted for detecting the presence of admixtures in official grades of wheats or of undesirable varieties in deliveries to the flour mill.

While widespread use is being made of the polymorphism of the gliadin proteins in wheat variety identification, it is the research on glutenin proteins that has contributed most significantly to the understanding of protein quality. During the last decade, researchers at the Plant Breeding Institute, Cambridge, UK have shown that certain subunits of glutenin (e.g. '1', '2*', '5+10' or '7+9') were correlated with high breadmaking quality[2]. Several countries took immediate advantage of this relation between genetics and the quality of wheat proteins to develop new varieties that are better adapted to the modern baking technologies that require a higher baking strength (e.g. the Chorleywood Bread Process, fast-food breads, rolls, buns, frozen doughs).

Glossary

Aneuploid lines: Viable genetic stocks that either lack or have additional whole chromosomes or chromosome arms, compared with normal (euploid) stocks. For instance, a monosomic is a stock that lacks one chromosome out of the 21 pairs that comprise the three genomes of wheat, and a nullisomic lacks one pair out of the 21 pairs of chromosomes. Because common wheat plants are hexaploid (having three genomes, each consisting of seven pairs of chromosomes), and therefore genetically redundant, the loss or increase of a fraction of the genetic information, which would normally be lethal to diploid species, is only more or less deleterious. A substitution line is a line in which individual chromosome pairs have been replaced by their homologues from donor varieties, while in an isogenic line, genes of interest are transferred into the genome of a donor variety by repetitive backcrossing.

Baking score: In plant breeding programmes as well as in the baking industry, flours are tested for their breadmaking potential. Loaves varying from 40 g to 1 lb are produced and a number of baking tests factors are scored. The baking score integrates loaf volume, crust and crumb characteristics, handling properties and mixing characteristics of dough.

Damaged starch: During milling, a small but significant number of the starch granules in the flour are damaged – they are either broken or cracked, or lose their birefringence. Such granules are susceptible to α-amylase, while undamaged starch is not. The level of damage varies with the severity of grinding and the hardness of the wheat. Damaged starch usually increases the water absorption of dough and produces weak side walls and a sticky crumb. It is a strong negative factor in soft wheat flour used as cookie flour.

Dough testing: Physical dough-testing devices are used to evaluate breadmaking potentialities (strength) and performance characteristics of flours under mechanized conditions. The main parameters measured from a dough are its tenacity (resistance to deformation) and its extensibility (ability to undergo deformation under low strain, without rupture).

Dough rheology: If a piece of dough is deformed to a certain extent, after which the deformation is maintained at a constant level, the stress built up during deformation gradually relaxes. Relaxation time is an important rheological parameter. For instance, a slow stress relaxation has been associated with good baking quality. Another rheological approach is based on the application of oscillatory or dynamic measurements to dough. To describe the behaviour of the dough, the stress can be resolved into a component that is in phase with the strain, and one that is a quarter of a cycle ahead of it. The amplitudes of these two components, divided by the amplitude of strain, are called the storage modulus (G') and the loss modulus (G''), respectively. A complex modulus (G^*) can be also defined as $(G'^2+G''^2)^{1/2}$.

NADPH: The reduced form of NADP (nicotinamide adenine dinucleotide phosphate), NADPH is a coenzyme for a large number of oxidoreductases. Transporting electrons, and rich in energy, NADP acts as electron acceptor during the enzymatic removal of hydrogen atoms from specific substrates. One hydrogen atom from the substrate is transferred to the nicotinamide portion of the oxidized form of the coenzyme (NADP) to yield the reduced coenzyme (NADPH); the other hydrogen atom from the substrate becomes a hydrogen ion.

Not all baking technologies, however, could benefit from the development of this relationship. For instance, for wholemeal bread, protein quantity is generally more important than protein quality[3]. On the other hand, in Southwestern Europe, breadmaking technologies are quite different from those commonly used in North America or in Northern Europe. For instance, in France, breads are typically made of essentially four ingredients – flour, water, yeast and salt – with few or no additives, and they are normally baked on the oven hearth rather than in a pan. In these cases, doughs with very high strength and tenacity are detrimental to the overall baking score or loaf volume, and a highly extensible dough

is required[4]. To better understand the physicochemical bases of dough extensibility and to allow the breeding of new types of wheats with a satisfactory balance between dough strength and extensibility, it has been necessary to study protein fractions other than HMW subunits of glutenin. The most recent reports have emphasized the possible role of low molecular weight (LMW) subunits of glutenins[5] (which are genetically linked to some of the gliadins on the short arms of chromosomes 1A and 1B) and have proposed new protein markers for use in wheat breeding. For instance, the ability to select for both the *Glu-D1* alleles that impart a high dough tenacity (e.g. subunits '5+10') and the *Glu-A3* alleles *o* and *n*, which impart a high extensibility, should result in the development of new wheats adapted to the modern baking technologies of Southwestern Europe[6]. When aiming at breeding of biscuit-type wheats, it can be recommended to screen lines containing both the *Glu-D1* allele '2+12' and the *Glu-B3* allele III (Fig. 1). Moreover, because many of the food products made from soft-milling wheats require doughs or batters with little or no elasticity, a new type of wheat has been produced by transferring the null alleles of *Glu-D1* and *Glu-A1* into the soft wheat 'Galahad'. The final line, called 'Galahad-7' because it only contains one HMW subunit, subunit 7, produces extremely extensible doughs[7].

Functional properties of glutenin polymers

To evaluate the functionality of wheat proteins and to manipulate it intelligently in breeding and during food processing, studies based on electrophoresis (which can separate only monomers or subunits) may not be adequate, because functionality is primarily determined by the occurrence of large protein aggregates. Pioneering studies relating the molecular weight distribution of glutenins to breadmaking quality were based on solubility methods or on conventional chromatography, and hence suffered from many disadvantages: they were tedious, lengthy and difficult to reproduce or to quantify. The advent of high-performance liquid chromatography (HPLC) techniques for wheat protein analyses, which have the capabilities of automation, reproducibility and quantification, have raised both breeders' and food processors' hopes that it will soon be possible to screen large series of samples routinely. In contrast with studies based on reversed-phase type HPLC (RP-HPLC), which are generally aimed at fingerprinting varieties from gliadins or reduced glutenin subunits, size-exclusion type HPLC (SE-HPLC) has the potential to keep relatively large aggregates in a quasi-native state, to retain information on the level of aggregation. For instance, following studies by Huebner and Bietz[8], Dachkevitch and Autran[9] demonstrated that SE-HPLC of unreduced phosphate–SDS (sodium dodecyl sulfate) extracts is a powerful tool for studying the physicochemical and structural basis of wheat quality and is applicable to rapid assessment of the baking potential of wheat genotypes, wheat flours and industrial glutens (Fig. 2).

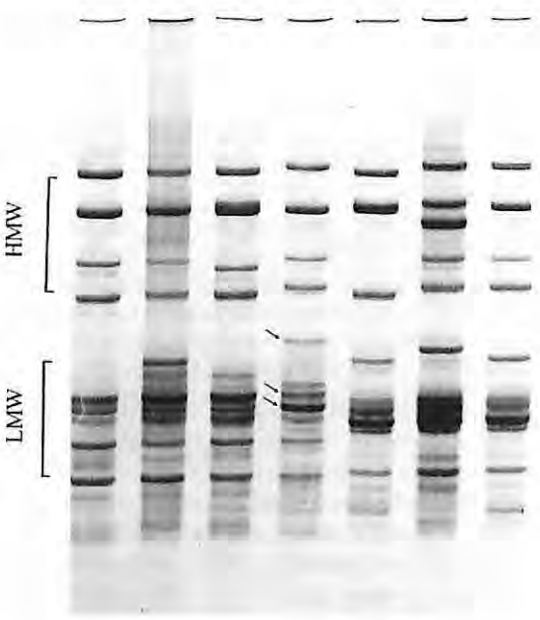

Fig. 1

Acid polyacrylamide gel electrophoresis of alkylated glutenin subunits of seven wheat varieties. Low molecular weight (LMW) and high molecular weight (HMW) subunits of glutenin are labelled. Arrows indicate LMW glutenin subunit alleles (*Glu-A3* and *Glu-B3*) with effects on biscuit quality. (Courtesy of M.H. Morel.)

Recently, large-size protein aggregates (or 'polymeric glutenin') have been investigated in a more dynamic way by Weegels *et al.*[10] For instance, the amount of polymeric glutenin estimated by the amount of SDS-insoluble fraction or the amount of 'gel protein' (although the latter contains constituents other than proteins) decreased during dough mixing; the amount increased again during dough resting. On the other hand, there are differences in the reactivities of the various HMW glutenin subunits. In particular, the subunits '9', '10' and '12' incorporated into polymeric glutenin more rapidly and to a greater extent than the subunits '2', '5', '7' and '1/2*', which can be of importance when blending flours of different subunit composition[10]. Using a sequential gluten extraction and fractionation procedure that preserves functionality, as well as dynamic measurements in shear, Popineau *et al.*[11] investigated large glutenin polymers of various isogenic lines of the variety 'Sicco', and found a very high correlation between the amount of large glutenin polymers and the viscoelasticity of gluten subfractions. They concluded that both the quantity of HMW subunits and subunit composition influence gluten viscoelasticity by modifying the polymerization state of gluten proteins.

Complementary to biochemical techniques, the potential of immunochemical methods, especially those based on monoclonal antibodies, has been exploited for the recognition of protein conformation, to yield information on the functionally important sites, and to quantify specific flour polypeptides. For instance, Skerritt and MacRitchie[12] reported positive correlations between

antibody binding to D-genome HMW glutenin subunits (i.e. allelic types '5+10' and/or '2+12') and dough strength. Similarly, Chan *et al.*[13] developed monoclonal antibodies to detect HMW glutenin sequences that were assumed to indicate desired wheat characteristics (e.g. the amino acid sequence Thr–Cys–Pro, a characteristic of the HMW subunit '5').

Effects of protein composition and content on pasta quality

Durum wheat is widely considered to be the best type of wheat for pasta products due to its excellent amber color and superior cooking quality. Differences in cooking quality (i.e. high firmness and good surface condition of the cooked pasta) are attributed to the protein content and composition of the grain endosperm[14].

A major breakthrough in understanding of the biochemical and genetic basis of pasta quality was realized by Damidaux *et al.*[15], with the discovery of a clear-cut relationship between the electrophoretic pattern of γ-gliadins and gluten strength, an indicator of pasta firmness. The allelic type γ-45 was associated with a strong gluten, whereas the allelic type γ-42 was associated with a weak gluten. In fact, the positive effect of the γ-gliadin 45 (*Gli-B1*) locus originates from its genetic linkage with LMW subunits of glutenin of the *Glu-B3* locus[16] and results from differences in the levels of these LMW subunits.

New wheat specifications for durum wheat proteins have recently become necessary as a result of the use of increased drying temperatures in the pasta industry. While protein content and protein composition are almost equally important in determining pasta quality when the pasta is dried at a low temperature (55°C), at 70–90°C the importance of protein content becomes prevalent[17]. Present investigations are therefore aimed at understanding the role of proteins as markers of mechanical denaturation during extrusion, and improving control of the second main parameter of cooking quality – the surface condition of cooked pasta.

Low molecular weight proteins and wheat technology

In addition to gluten proteins, flour contains 15–25% of water-extractable LMW proteins. LMW wheat proteins differ from gluten proteins in extractability, lipid affinity and amino acid composition. A variety of terms have been used to describe various LMW protein fractions, such as 'CM-proteins' (extractable with chloroform–methanol mixtures), 'S-fraction', 'ligolin', 'friabilin', 'purothionin' or 'puroindolin'. Most of these are sulfur-rich proteins. Some have well-characterized biological functions (e.g. membrane protein, thioredoxin activity, exogenous α-amylase or trypsin inhibitors).

Although homologies have been demonstrated between some of these protein fractions, very few comparisons are available and, in many cases, conflicting information exists on their functional properties in dough and bread[18]. We will therefore review the few that have recently been investigated from a food science perspective.

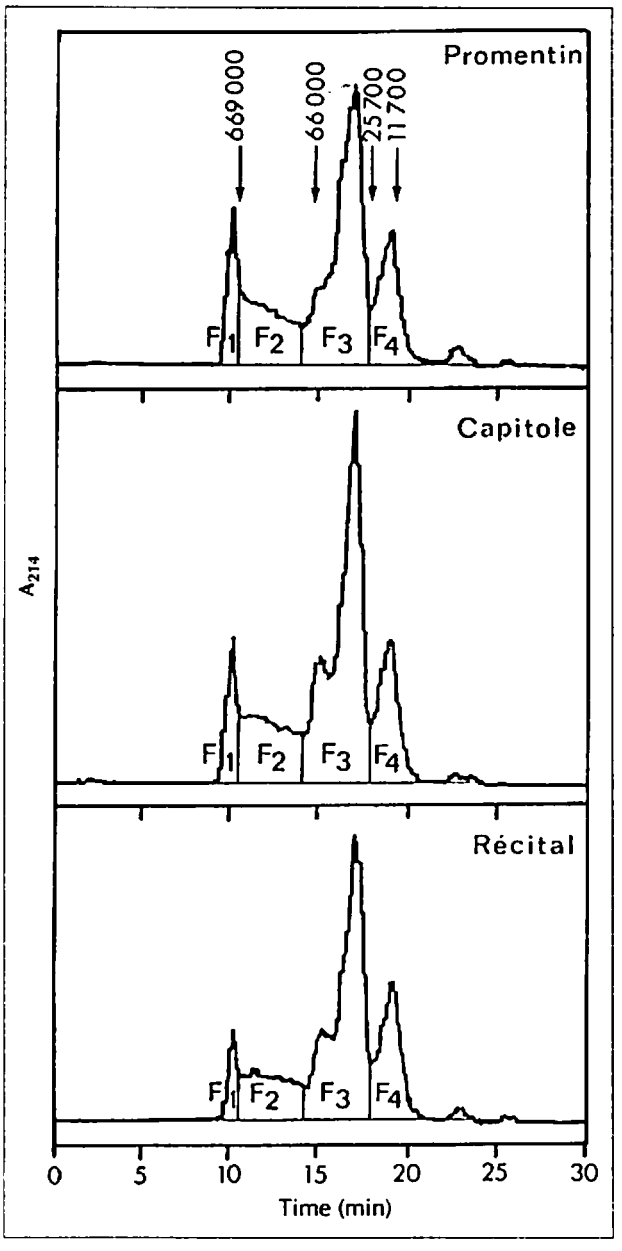

Fig. 2
Elution profiles obtained by size-exclusion high-performance liquid chromatography (SE-HPLC) on a TSK-4000SW column of non-reduced flour proteins extracted with phosphate–SDS from three bread cultivars with different baking strength potentials. Arrows indicate the positions of standard molecular weight markers: 669 000, thyroglobulin; 66 000, bovine serum albumin; 25 700, chymotrypsinogen A; 11 700, cytochrome c. Low percentages of fraction F_1, or high $F_1 : F_2$ ratios indicate high baking strength values. A_{214}, light absorbance at 214 nm. (Courtesy of T. Dachkevitch.)

Starch granule proteins and endosperm texture

Endosperm texture is an important inherited criterion of quality in wheat because it influences not only the milling performance of the grain but also some aspects of the quality of the resultant flour (e.g. protein–starch surface interaction may influence starch–gluten separation efficiency, as well as dough properties, through the degree of damaged starch). It is essential, therefore, to discover the underlying molecular causes of endosperm

texture, in order to screen for milling quality at the breeder level. The physical difference between hard and soft endosperm lies in the strength of adhesion between the starch granules and the surrounding matrix of endosperm protein. In soft endosperm the adhesion is weaker and fracture during milling tends to occur at the starch granule – protein matrix interface. This does not occur with hard endosperm, with the overall result that flour particles from hard wheat are larger, smoother and experience more starch damage.

In 1986, Greenwell and Schofield[19] identified ten polypeptides that are extractable with SDS from the surface of water-washed wheat starch granules, including a major 15 kDa protein fraction (encoded on the short arm of chromosome 5D) that is consistently present in soft wheats and absent from hard wheats or durum wheats. This 'softness' protein, called friabilin, was assumed to function by reducing adhesion between starch granule and endosperm protein matrix.

The major friabilin component was purified and was used to raise a monoclonal antibody[20]. Determination of the N-terminal amino acid sequences of various friabilin components suggested strong homologies with lipid-binding proteins, including a major protein called puroindoline, because of its tryptophan-rich and basic domain[21].

However, these studies have not produced the desired assay for endosperm texture. Whereas purified starches obtained from hard or soft wheats were characterized as having low or high levels of friabilin, such a difference was not confirmed when wholemeal flour was tested instead of purified starch, suggesting that the presence of friabilin on the starch granule might occur during the purification of starch. Thus, the anti-friabilin antibody cannot provide a predictive small-scale test of endosperm texture in bread wheat, although a useful application for it has been found in the development of a rapid diagnostic assay for the adulteration of pasta materials[20]. The unexpected similarity of friabilin to lipoproteins has now led to studies of starch surface lipids to clarify whether granule-surface friabilin or surface lipids are likely to be the main determinant of endosperm texture[22].

Lipid-binding proteins

Lipids are minor components of wheat seeds (2–3% of the dry weight) that exert important effects in wheat technology in relation to the main macromolecular wheat components: starch and proteins. In the past ten years, many efforts have been made to study starch–lipid or protein–lipid interactions and their effects on albumen texture or dough properties. However, according to Marion[23], the classical methods of biochemistry do not apply to wheat lipids because the study of lipids has to take into account their physiological role, organelle location and interactions with starch and proteins. Obviously, membrane proteins are the first candidates to bind polar lipids. If we consider that membranes are composed of equal quantities of polar lipids and proteins, wheat flour, whose content of polar lipids is about 1%, would also be expected to contain ~1% membrane proteins – approximately 10% of total wheat flour proteins[23]. Because the extraction of lipid-binding proteins does not induce a loss in the rheological properties of gluten, the technological effects of lipid-binding proteins or polar lipid-transfer proteins are more likely to be expressed through the formation and stability of a monomolecular layer at the gas–water interfaces of dough rather than in the viscoelastic properties of wheat gluten. Before the formation of these monolayers, the dispersion of polar lipids in doughs as small vesicles is an important phenomenon, in which lipid-binding protein might play a role by continuously supplying interfaces with amphiphilic molecules during gas expansion in the proof stage and at the beginning of baking[23].

Because lipid-binding proteins have an amphiphilic character, with secondary amphiphilic structure spanning the hydrophobic core of membrane bilayers and a globular polypeptide region exposed to water, they can be concentrated at the interface between a detergent and an aqueous solvent. Recently, this method of 'phase partitioning' was applied to wheat protein extracts by the detergent Triton X114. Among the various LMW cysteine-rich and basic proteins thus isolated, two novel entities exhibiting homologous N-terminal sequences have been discovered, including friabilin and puroindolin[21].

Cysteine-rich low molecular weight proteins

In 1989, Kobrehel and Alary[24] isolated a LMW sulfur-rich protein fraction whose content of sulfhydryl and disulfide groups was positively correlated with the surface condition of cooked pasta. In fact, the main components of this fraction belonged to the CM-proteins, which are subunits of a tetrameric α-amylase inhibitor. Subsequently, the cDNA clones of all the CM-proteins found in bread wheats and in durum wheats have been isolated and sequenced[25].

On the other hand, several LMW protein components have been isolated from the soluble fraction after gluten extraction from flour. These LMW proteins have a large effect on biochemical and rheological dough properties. Recently they have been more specifically shown to decrease the rate of polymeric glutenin reassembly (Fig. 3). They also have a marked influence on the rheological properties, resulting in a less elastic dough with a less stiff character[10]. In fact, the LMW protein fraction consists of a variety of proteins. Some fractions increase the complex modulus of dough and some decrease the relaxation time. Accordingly, these various proteins are currently undergoing thorough characterization and comparison with other members of the CM-protein family, using biochemical and immunological methods, as well as sequencing of cDNA clones and expression in bacteria cells (Lullien-Pellerin, V. *et al.*, submitted).

Redox reactions during dough mixing

Because disulfide bonds play a significant role in the formation of the protein network of the dough, disulfide reducing agents such as cysteine, glutathione and sulfite change the physical properties of a dough considerably. On the other hand, when dough is resting, re-formation

(polymerization) takes place via the formation of disulfide bonds. A mechanism for the depolymerization and polymerization of glutenins in the presence of oxygen, a reducing agent and a metal–protein complex was described by Graveland *et al.*[26] Recently, the various mechanisms of reduction of protein disulfide groups in wheat seeds have been investigated[27,28]. Among these, the NADP–thioredoxin system (NTS; consisting of NADPH, the enzyme thioredoxin reductase, and the redox carrier protein thioredoxin *h*) specifically reduced the major seed proteins: albumins, globulins, gliadins and glutenins. In addition to giving new insights into the mechanism of germination, these findings suggest that the NTS may play a role in the formation of the protein network during dough mixing and that thioredoxin has the potential as a technological tool both to improve breadmaking from wheats and – for those with intolerance to wheat gluten ('celiac disease') – perhaps to produce bread from non-gluten cereals[28].

Conclusions

One of the questions that has challenged wheat chemists and technologists for a long time is why wheat protein is unique among cereal and other plant proteins in its ability to form a dough with viscoelastic properties ideally suited to make bread, biscuit or pasta products. Despite many years of studies, protein quality still defies all attempts to explain it on the basis of the molecular properties of the many protein components. Recent studies, however, provide the potential to make a significant step forward in both more effective utilization of current wheat varieties and the development of better wheat varieties for the future. In summary, the important recent developments are:

- the availability of isogenic, aneuploid and substitution stocks that enable pinpointing of the gene products that are important in functional performance;
- the introduction of original approaches based on new concepts (e.g. intrinsic quality of wheat genotypes) or of new protein fractions (e.g. friabilin, lipid-transfer proteins, CM-proteins, etc.) that stand out clearly against the classical Osborne's solubility scheme;
- the acknowledgement that quality is not determined (and cannot be predicted) solely by allelic variation or subunit composition, but depends on a complex combination of many independent and interrelated structural features and also on interactions of the proteins with various other flour components such as starch, pentosans and lipids;
- the development of modern physical (rheological and spectroscopic) and physicochemical methods that can observe the behaviour of individual components (e.g. proteins and lipids) in a complex mixture and that can determine interfacial and aggregation behaviour;
- the demonstration of the potential of monoclonal antibodies to quantify specific components in a mixture and to probe their dynamics and distribution during processing.

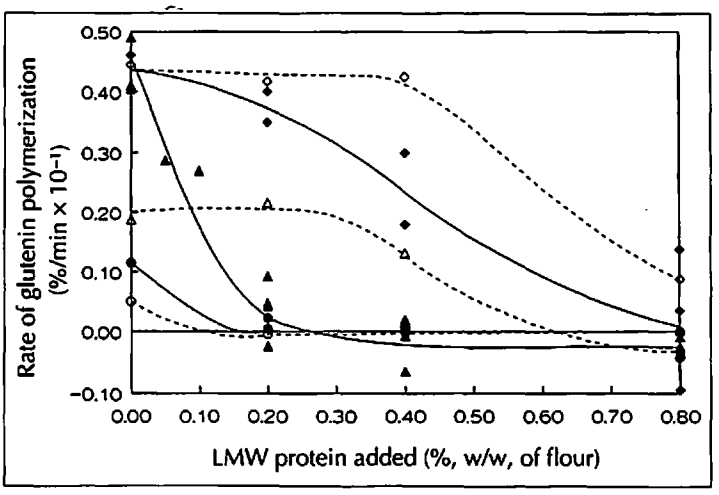

Fig. 3
Effect of concentration of LMW proteins on rates of glutenin polymerization in doughs from varieties: 'Obelisk' (circles), 'Camp Rémy' (triangles) and 'Rektor' (diamonds), directly after mixing for 5 min at 23°C (------) or at 27–29°C (———) (Reprinted, with permission, from Ref. 10.)

Work is now in progress in many laboratories on determining the polymeric structure of glutenins and how this structure is genetically controlled through the type and amount of subunits produced by gene activation. Studies are aimed at understanding whether different contributions to functionality result from differences in the type and structure of subunits or simply in the amount of the relevant proteins. This could be the next milestone on the road to our full understanding of wheat protein functionality and its inheritance. Research on most of the protein markers reviewed above is currently being carried out using molecular biology techniques to determine more easily their complete protein sequences and to better control their *in vivo* or *in vitro* (in a microorganism) synthesis, with a view to preparing bioengineered wheats by manipulating the structure of genes involved in processing quality or of regulatory genes that control protein synthesis and expression.

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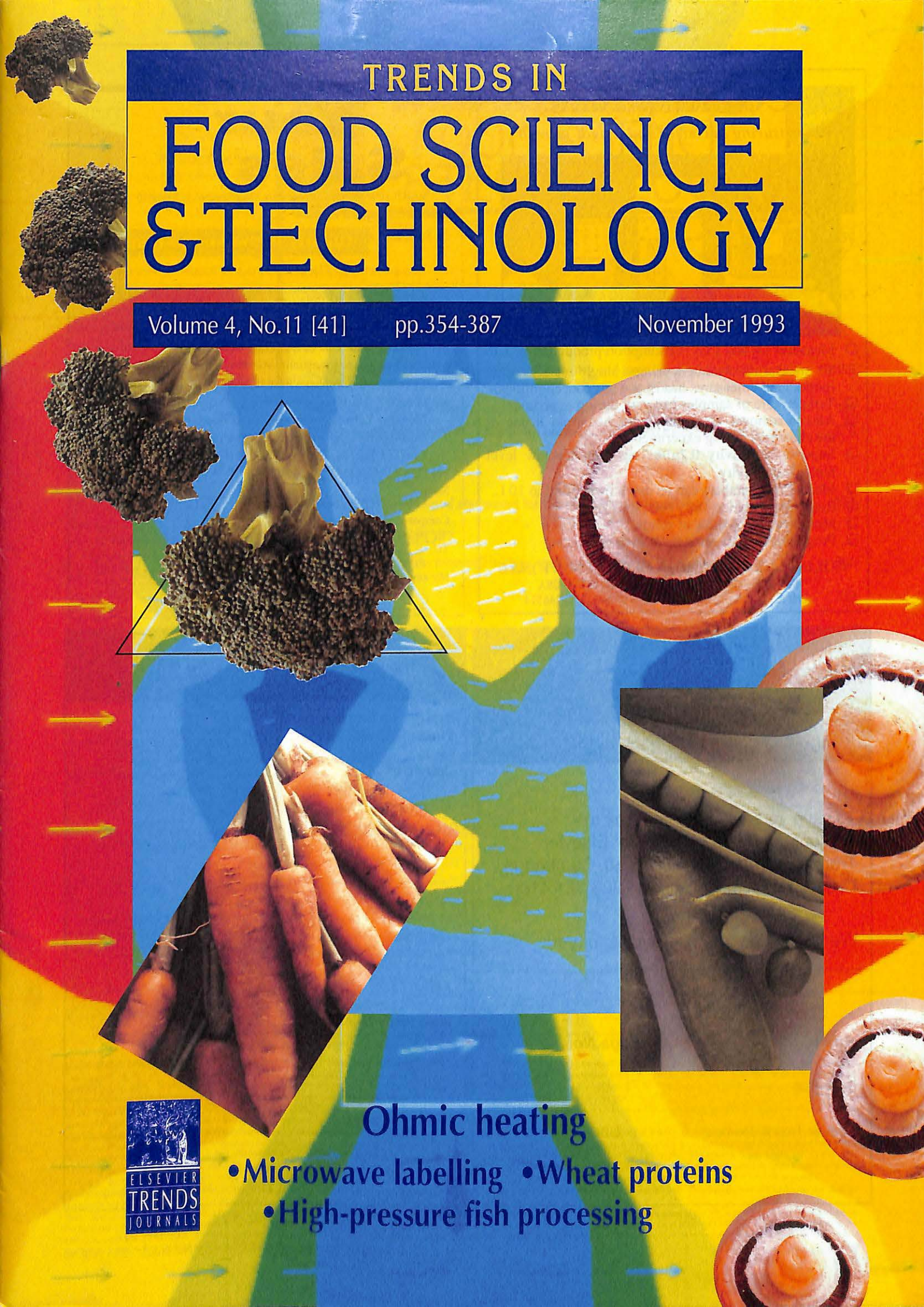

Ohmic heating

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