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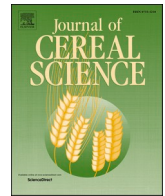
Can we increase the use of wheat and other cereals as sources of protein?

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ABSTRACT

Wheat and other cereals are important sources of dietary protein and have the potential for exploitation to replace products based on animal proteins. However, grain protein contents are low, about 10–15%, compared to more protein-rich legumes and oilseeds. Grain protein content is determined by genetic and environmental factors, particularly nitrogen fertilisation, and is also inversely correlated with grain yield. Strategies to increase grain protein content are reviewed including exploiting genetic variation in the relationship between yield and protein content (grain protein deviation). The functional properties of cereal grains for processing are determined by the properties of the prolamin storage proteins, which include the gluten proteins of wheat. Understanding the structures and functional properties of these proteins will therefore facilitate their modification to generate a wider range of properties to extend the use of cereal proteins to replace animal proteins in food systems.

1. Introduction

There is a vast scientific literature on cereal grain proteins and in particular on the proteins of wheat grain. The major stimulus for these studies has been the impact of proteins on grain utilisation, including their contribution to the nutritional requirements of humans and livestock and their functional properties which underpin the production of processed foods. Seed proteins have also been of more academic interest, providing attractive systems for the developing technologies of molecular genetics in the late 20th century, and for exploring the organisation and regulation of expression of multigene families.

The application of high throughput automated DNA sequencing has led to the availability of massive databases of seed protein sequences which have underpinned detailed proteomic analyses using high resolution mass spectroscopy. However, our knowledge is still far from complete, particularly in understanding the relationships between the amino acid sequences of grain proteins, their structures and interactions and how these determine their functional properties.

Although seed proteins have formed part of the human diet for millenia, the demand for foods from non-animal sources is leading to their increased consumption, both in traditional forms and after processing to mimic foods based on animal proteins.

This article therefore discusses two factors which may limit the wider use of cereal grains to replace animal proteins in food processing and human diets: increasing grain protein content and manipulating functional properties. The importance of gluten proteins in underpinning the use of wheat for breadmaking and other processes has resulted in a vast volume of literature, probably greater than on all other cereal proteins combined. The discussion will therefore focus on wheat grain with information on other cereals where relevant. In addition, the current importance of cereal grains as sources of protein for human nutrition will be discussed.

2. Importance of cereals as protein sources

Cereals are the single most important group of crops in terms of total production and contribution to the human diet. FAO data show that the total annual production of all cereals averaged over 3000 million tonnes over the period 2019–2021, with three crops accounting for almost 90% of this. These were maize (average 1,170 million tonnes), rice (average 770 million tonnes) and wheat (average 764 million tonnes) (Table 1). However, wheat is produced over a wider geographical range than any other crop.

In terms of global food supply, rice and wheat are the two major crops, providing approximately equal amounts of calories (531 and 539 kcal/capita/day, respectively). However, wheat provides almost twice the amount of protein than rice, 16.25 compared with 9.95 g/capita/day. In fact, wheat provides about 15–20% of total protein in the global

Table 1

Production and contributions of cereals to global food supply (means for 2019, 2020 and 2021) and range of grain protein content.

Cereal	Production (million tonnes)[a]	Food supply (kcal/capita/day)	Protein supply (g/capita/day)	Grain protein content (%)[c]
maize	1169	159.02	3.87	8–13
rice	770	531.39	9.95	8–10
wheat	764	539.62	16.25	8–17
barley	154	7.91	0.22	8–15
sorghum	59	29.6	0.88	7–15
millets	31[b]	23.7	0.63	5–19
Oats	24	4.08	0.16	12–24
Rye	14	4.39	0.12	12–15

[a] rounded to nearest million tonnes.

[b] Includes separate dataset for fonio.

[c] Data from FAOStat except based on compilation presented by Serna-Saldivar (2016).

human diet but much greater proportions in regions (such as parts of North Africa, the Middle East and Central Asia) where wheat provides over 50% of the total calories.

Even in Western Europe, where diets are generally varied, cereals are still important sources of protein, with total cereals and breads providing 24% and 9%, respectively, of total protein intake in UK adults (Bates et al., 2020). Less important sources of protein in temperate zones are oats, rye, barley and triticale.

Sorghum and millets are minor crops in global terms but make significant contributions in some countries, notably in Africa. For example, sorghum and millets together provide 186 kcal/capita/day and 5.25 g protein/capita/day in Africa, but 250 kcal/day and 6.72 g protein per day in Senegal which is located in the Sahel region of Sub-Saharan Africa. Maize (corn) is consumed widely in Central and South America and parts of Africa but much of the global production is used for livestock feed and industrial raw material, including the production of glucose syrups for processed foods and drinks and ethanol for biofuel.

3. Protein content

3.1. Variation in protein content

Cereal grains have low total protein contents compared with many other seed crops (notably protein-rich legumes/pulses and oilseeds). The data compiled in Table 1 show that the protein contents of samples of individual cereal species vary by about two-fold, with many species falling within the range 8%–15% of the dry weight. However, there are differences between the protein contents of commercial samples of different species, with rice having a lower protein content than wheat (accounting for its lower contribution to global protein intake) and oats a higher protein content.

Grain protein content has been most widely studied in wheat where it has a major impact on grain processing quality. Most of the wheat grown globally is consumed by humans, after processing into bread, other baked goods, noodles and (for durum wheat) pasta. Most of these uses require a high protein content and hence wheat breeders select for this. However, in some countries a significant proportion of the wheat grown (for example, over half of the production in the UK) is used for livestock feed and for the production of ethanol, either for human consumption (in beer and spirits) or for biofuel. In these applications the grain is used mainly as a source of starch and breeders select for high yield (which is determined by starch accumulation) and low protein content. Consequently, two types of wheat cultivar have been developed, for breadmaking and for feed/alcohol production, which may differ in protein content by about 2% dry weight when grown under the same conditions. This is illustrated in Fig. 1a.

The protein content of grain of wheat (and other cereals) is determined by genetics (as illustrated in Fig. 1a) and environment, particularly the availability of nitrogen but also of sulphur which is required for the synthesis of the sulphur-containing amino acids (cysteine and methionine) present in proteins.

3.2. Effect of nitrogen nutrition on protein content

The effect of nitrogen fertilisation on grain yield and protein content of wheat is illustrated in Fig. 1b, which shows data from the Broadbalk long term wheat nutrition experiment at Rothamsted. In this example the increasing application of nitrogen (from 48 to 288 kgN/Ha) resulted
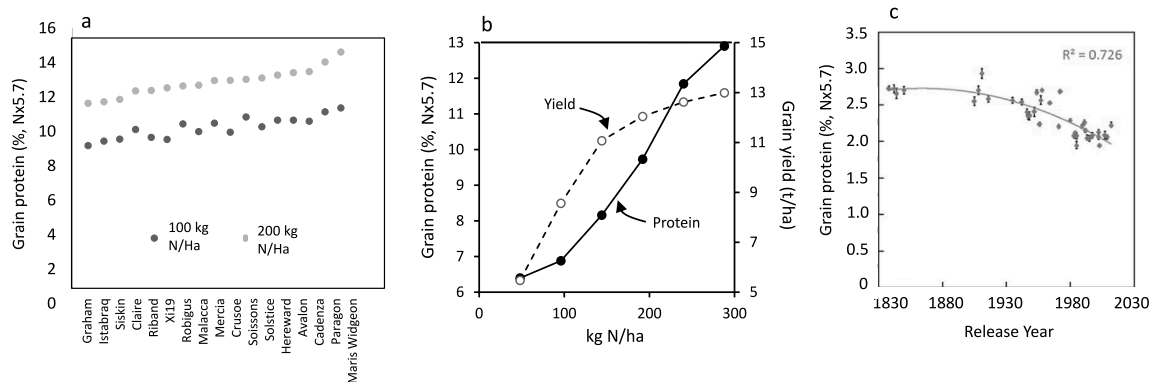

Fig. 1. Variation in grain protein content of wheat

a. Variation in the protein content of wheat cultivars grown with low (100 kg N/Ha) and high (200 kg N/Ha) nitrogen fertilisation. Data are means for three replicate plots grown for 4 four years and form part of the Wheat Genetic Improvement Network nitrogen end use efficiency trials at Rothamsted Research and are kindly provided by Andrew Riche and Malcolm Hawkesford (Rothamsted Research).

b. Relationship between application of nitrogen fertiliser, grain yield and grain protein content for the breadmaking cultivar Crusoe grown as first wheat in the Broadbalk experiment at Rothamsted Research in 2014. Yield is expressed on an 85% dry matter basis and protein content on a dry weight basis. We thank the Lawes Agricultural Trust and Rothamsted Research for data from the e-RA database. The Rothamsted Long-term Experiments National Capability (LTE-NCG) is supported by the UK Biotechnology and Biological Sciences Research Council and the Lawes Agricultural Trust. Taken from Gooding and Shewry (2022) with permission.

c. Contents of protein in grains of wheat cultivars grown commercially in the UK between 1838 and 2012, based on analyses of replicate field trials grown at Rothamsted in 2014 and 2015. Taken Shewry et al. (2016), with permission.

in progressive increases in grain protein content, from 6.4 to 12.9 % dry weight.

However, it should be noted that the most important effect of nitrogen application is to increase yield, from 5.5 to 13 tonnes per hectare in Fig. 1b, by enabling the formation of a crop canopy to fix carbon. The development of crops which are able to produce such high yields with nitrogen fertilisation underpins global food supply.

The application of high levels of nitrogen fertiliser in intensive wheat production systems, combined with the demonstrated effects of nitrogen application on grain protein content in crop trials (as shown in Fig. 1b), has led to the suggestion that modern types of wheat have higher grain protein contents than older types which were grown with lower levels of nitrogen fertilisation. However, this suggestion is not supported by historical datasets for the protein content of grain samples harvested and marketed in North America (Kasarda, 2013) or by comparisons of older and modern types of wheat grown together in field trials (Fig. 1c).

3.3. Genetic control of protein content

The ability of breeders to select for high and low protein content in wheat indicates strong genetic control and this can be quantified by estimating the variance components for protein content in multisite field trials. Table 2 is based on nine field trials of 40 (mainly winter) wheat cultivars, which were carried out on sites in south-east England over two seasons. It shows that 48% of the variance in grain nitrogen content was determined by genotype which increased to 69% when the interactions of genotypes with nitrogen, year/site and nitrogen + year/site were considered (see Table 2).

Classical genetic studies show that grain protein content is a quantitative trait with multiple genes each having relatively small effects. For example, Saini et al. (2022) predicted 57 meta-QTLs for wheat grain protein content from 48 linkage studies. Consequently, wheat breeders select directly for protein content (usually using near-infra-red spectroscopy, NIRS) rather than using marker-assisted selection. However, the increasing use of genome-wide association studies (GWAS) and genomic selection (GS) in commercial wheat breeding should facilitate the selection of grain protein content in the future (Sandhu et al., 2021).

3.4. Increasing protein content: "high protein genes"

Several single genes have been shown to have significant effects on grain protein content.

Early studies identified the American cultivars Atlas 50 and Atlas 66 (derived from the South American cultivar Frondoso), the Indian cultivar Nap Hal and the Canadian wheat Plainsman V (which contains a gene from *Aegilops*) as sources of high grain protein (reviewed by Shewry, 2007). However, recent studies have focused on exploiting high protein genotypes of wild emmer (*Tririum turgidum* var. *dicoccoides*) and in particular the *Gpc-B1* gene. *Gpc-B1* is located on chromosome 6B and encodes a NAC transcription factor (called NAM-B1) which accelerates the senescence of the vegetative tissues, increasing the mobilisation of nitrogen and minerals (iron and zinc) and their accumulation in the

grain (Uauy et al., 2006). Homoeologous genes also occur on chromosomes 6A (*Gpc-A1*) and chromosome 6D (*Gpc-D1*) and paralogous (related) genes on the group 2 chromosomes (reviewed by Tabbita et al., 2017). Most modern bread wheat cultivars have non-functional forms of *Gpc-B1* and hence it can be widely deployed in bread whear breeding programmes.

The role of *Gpc-B1* in promoting senescence has led to the suggestion that the higher protein content is associated with reduced yield and this is indeed observed in some studies. However, Tabbita et al. (2017) reviewed progress in using breeding using *Gpc-B1* over the first 10 years and concluded that effects on yield can be minised. Nevertheless *Gpc-B1* has failed to have a significant impact on wheat breeding globally.

3.5. Increasing grain protein content: increasing source and sink activity

The relative importance of source and sink activity in determining grain yield and protein content have been the subject of a long running debate. The *Gpc-B1* gene clearly operates by increasing source activity, by increasing the amounts of amino acids translocated into the developing grain. The mechanism is therefore similar to the effects of increased fertilisation with nitrogen or sulphur. Increased grain protein content can also result from other genes which affect the translocation of amino acids into the grain, such as the *HOMEOBOX DOMAIN-2* (*HB-2*) gene which encodes a transcription factor. Higher expression of *HB-2* results in modified development of the leaves and vascular tissue leading to increased supply of amino acids to the inflorescence and developing grain (Dixon et al., 2022). However, grain protein content can also be increased by increasing the rate of protein synthesis in the grain (ie. increased sink activity). For example, increasing the amount of HMW glutenin subunit protein by expression of a 1Ay subunit (compared to the null allele) (Lee et al., 2023) or the overexpressed form of subunit 1Bx7 (compared to the normal form) (Roy et al., 2020).

Increased protein content in maize grain also results from transgenic expression of the *TEOSINTE HIGH PROTEIN 9* (*THP9*) locus from teosinte (a wild subspecies of maize) in cultivated maize (Huang et al., 2022). The locus contains an *asparagine synthetase 4* (*ASN4*) gene that plays a central role in the accumulation of amino acids within the plant. The transgenic plants had higher contents of protein in the grain which was associated with higher nitrogen use efficiency in the plant. However, the increase in free asparagine associated with *THP9* would not be acceptable in wheat due to the relationship between free asparagine and the formation of acrylamide during processing. In addition, a non-transgenic route would clearly be preferable in relation to the acceptability of transgenic crops in many countries. Nevertheless, the study demonstrates that increasing grain sink activity is a valid strategy for increasing grain protein content in cereals.

3.6. Increasing grain protein: grain protein deviation (GPD)

The most important target for cereal breeders is yield, which is essentially determined by the accumulation of starch (which accounts for 70–80% of the mature grain). Increased starch results in dilution of other grain components, resulting in a well-established inverse correlation between yield and grain protein content. This is illustrated in Fig. 2, which shows that a simple regression line can be fitted. However, some genotypes consistently deviate from this line, having higher or lower protein contents than expected based on yield. This is termed positive and negative grain protein deviation (GPD), respectively (Monaghan et al., 2001). GPD is a particularly attractive trait for wheat breeders as it reflects higher nitrogen use efficiency by the crop.

GPD is under genetic control (Oury and Godin, 2007) and Mosleth et al. (2020) calculated that genotype (G), G x nitrogen fertilisation (G x N) and G x environment (year/site) accounted for 0.3, 0.03 and 0.11 of the variance, showing moderate heritability. This is illustrated in Fig. 3 which compares GPD for genotypes grown on multiple sites for three years. In addition to showing consistent differences in GPD between
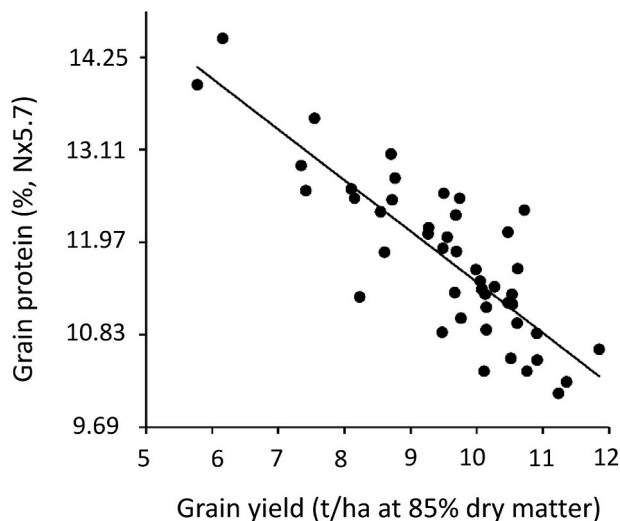
Table 2
Estimated variance components for genotype (G), the interaction between G and N fertilizer level (N), the interaction between G and year_site (YS), and the three-way interaction as fraction of total phenotypic variance for 40 cultivars grown in nine environments (sites or years) in the UK. Fixed effects of YS, N and the interaction term YS x N were fitted. Taken from Mosleth et al. (2021) with permission.

Trait	G	G x N	G x YS	Gx YSx N	Sum
Yield_corr	0.42***	0.002[NS]	0.21***	0.06***	0.69
grainN_corr	0.48***	0.025***	0.17***	0.01[NS]	0.69
GPD	0.30***	0.030**	0.11***	0.00[NS]	0.44

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, [NS] $p > 0.05$.

Fig. 2. Mean grain N contents and yields for 47 wheat cultivars grown at Rothamsted Research between 2004 and 2012.
Data are from the Wheat Genetic Improvement Network nitrogen use efficiency trials and are kindly provided by Andrew Riche and Malcolm Hawkesford (Rothamsted Research). Taken from Gooding and Shewry (2022) with permission.

genotypes, some cultivars (such as Cadenza which is indicated by the red circles) also appear to show greater stability of GPD compared with others.

Paina and Gregersen (2023) recently reported a meta-analysis of QTLs for GPC and GPD in wheat. They identified 41 QTL for GPD but focused particularly on genomic regions on chromosomes 3A and 5A. QTLs for GPD have also been reported on chromosome 5B in bread wheat (Geyer et al., 2022; Paina and Gregersen, 2023) and durum wheat (Rapp et al., 2018; Nigro et al., 2019) and on chromosome 3B of durum wheat (Rapp et al., 2018; Nigro et al., 2019) but not bread wheat. More recently, Nigro et al. (2024) have reported six robust QTLs for GPD in durum wheat, located on chromosomes 1B, 2B (two loci), 4B, 5A, and 6A.

It therefore appears that GPD is controlled by a small number of genes, some of which are independent of grain protein content. The availability of high-density marker systems and extensive genomic sequences will facilitate the introgression of these QTLs into commercial cultivars as well as the identification and characterisation of candidate genes to explore mechanisms.

4. Nutritional quality: essential amino acid composition

The nutritional quality of grain proteins is important when formulating feed for monogastric livestock and poultry and will become increasingly important as plant proteins are used to substitute for animal proteins in processed foods.

The nutritional quality of proteins is determined by their contents of essential amino acids (EAA). These cannot be readily synthesized by animals and therefore must be provided in the diet. Furthermore, if the amount of only one EAA is limiting the others will be broken down and excreted. Ten amino acids are strictly essential for humans: lysine, isoleucine, leucine, phenylalanine, tyrosine, threonine, tryptophan, valine, histidine, and methionine. However, cysteine is often included as it is synthesized from methionine and a combined value for tyrosine and phenylalanine as tyrosine can be derived from phenylalanine. The requirements for EAA also differ with age, with higher levels being required by children than by adults as they require amino acids for growth as well as maintenance. Furthermore, the requirements of children differ with age and development.

Protein nutritional quality is discussed in detail in an accompanying paper in this special issue and has been reviewed for cereals previously (Shewry, 2007). The most important point to note is that lysine is the first limiting amino acid in all cereals, although the concentration varies between species being highest in oats and rice and lowest in wheat and maize. This is illustrated in Table S1.

The deficiencies in lysine and other essential amino acids result from the unusual amino acid compositions of the prolamin storage proteins (discussed below). These proteins are only present in the starchy endosperm of the grain and therefore the deficiencies are more severe in white flour than in whole grain samples (due to the removal of the aleurone layer and embryo which contain higher quality proteins). Furthermore, the relative contents of lysine and other limiting amino acids are lower in grain of higher protein content. This is because high nitrogen availability results in increased accumulation of prolamins relative to other proteins. The precise impacts of nitrogen fertilization differ between cereals but in wheat the difference in lysine content between high and low protein grain can be over 1% (from about 3.5g/100g protein to less than 2.5 g/100g protein) (Mossé and Huet., 1990).

5. Types of grain proteins

Cereal grains contain many thousands of proteins and proteomic studies of white flour and whole grain of wheat have resolved about 500 and 1000 individual proteins, respectively. Many of these proteins are present at low concentrations and have little impact on the properties of the whole grain or flour fractions, either for human nutrition or processing. These properties are predominantly determined by the grain storage proteins.

Cereal protein chemistry has a long history, extending back over 250 years. However, "modern" studies are underpinned by work carried out at the end of the 19th and start of the 20th centuries by the great American protein chemist T.B.Osborne.

Osborne classified proteins into groups (called Osborne groups or fractions) based on their extraction and solubility in a series of solvents. Most metabolic proteins are soluble in water (albumins) or dilute saline (usually 0.5M or 1M NaCl) (globulins). However, these fractions may also include albumin and globulin storage proteins.

Globulins with sedimentation coefficients ($S_{20,w}$) of 7–8 and 11–12 are major storage proteins in most crops plants, including legumes, while lower proportions of 2S albumin storage proteins also occur widely in seeds of dicotyledonous plants including brassicas. Although types of 7-8S and 11-12S globulin storage proteins are also present in the aleurone/scutellum and starchy endosperm, respectively, of cereal grains they are minor components in all commercial cereals except oats and rice. In both rice and oats the major endosperm storage proteins are "11S-type" globulins but they differ in their properties from the typical 11S globulins present in legume seeds. Notably, the oat globulin has an $S_{20,w}$ value of 12.1 and requires a high salt concentration (approximately 1M) for extraction while the rice globulin is insoluble in salt solutions (and hence often described as a glutelin, see below).

Osborne showed that the major storage proteins in the starchy endosperms of most cereals are only extracted in aqueous alcohols: classically 60–70% (v/v) ethanol but 50% (v/v) propan-1-ol is now more widely used. He defined these proteins as "prolamins" based on their high contents of the amino acid proline and amide nitrogen (now known to be present in the amino acid glutamine). He also suggested that these proteins are present only in the seeds of cereals and other grass species. The prolamins were given names based on their species of origin: gliadin (wheat), hordein (barley), secalin (rye), avenin (oats), zein (maize), kafirin (sorghum) and oryzin (rice).

Although prolamins are still accepted as a class of protein they are now known to be related to many other plant proteins, including the 2S albumin storage proteins and other small sulphur-rich seed proteins including puroindolines, non-specific lipid-transfer proteins (nsLTPs) and avenin-like proteins (farinins) of wheat, forming part of the "prolamin superfamily" of plant proteins (Shewry, 2019). The definition of
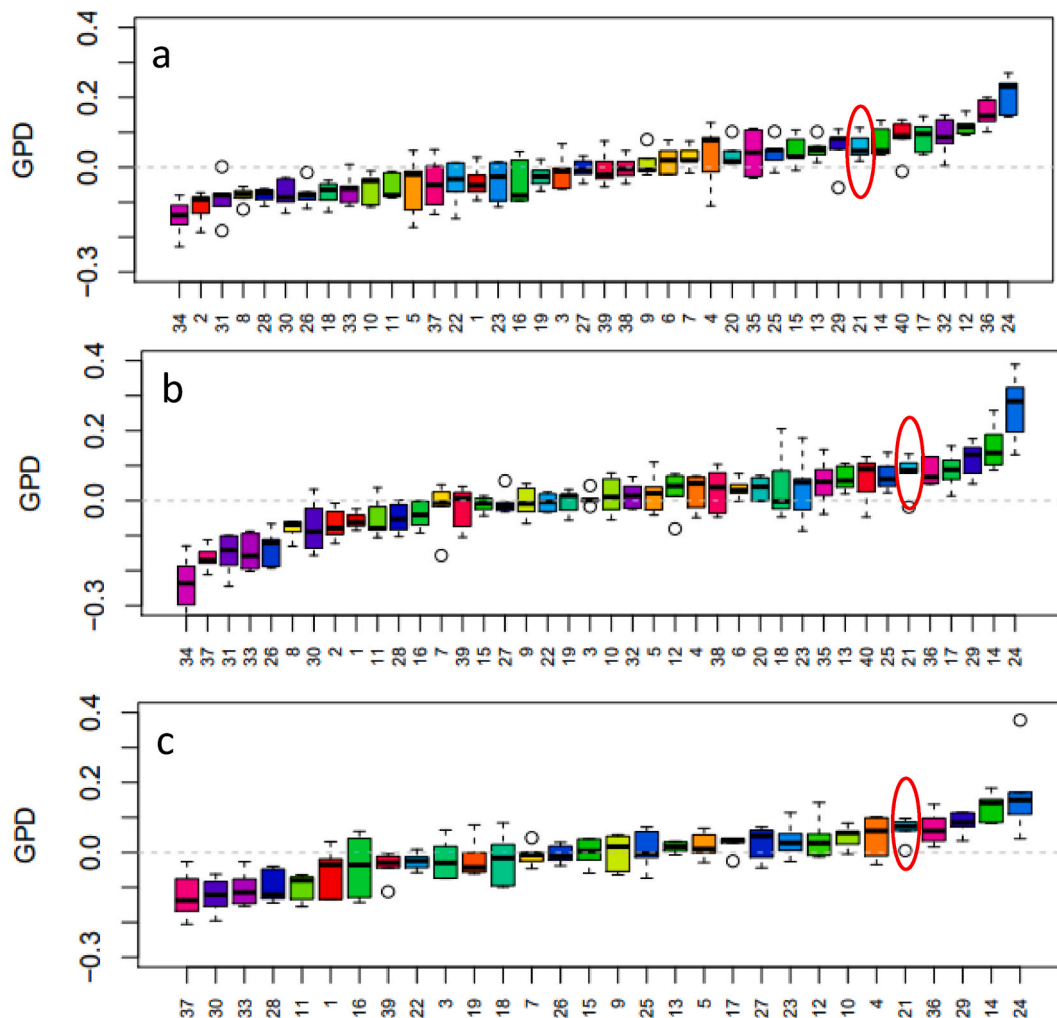
Fig. 3. Boxplot of the mean values for GPD for a set of 40 genotypes grown on five sites in 2016 (A) and six sites in 2017 (B) and 30 genotypes grown on six sites in 2018 (C). The same colours are used for the genotypes in all years. The red circles indicate the cultivar Cadenza which appears to show greater stability of GPD. Names of cultivars are given in Mosleth et al. (2020) from which the figure is reproduced with permission.

prolamins has also been revised to include closely-related proteins which are not soluble in aqueous alcohols in their native state due to the formation of large insolubly polymers stabilised by inter-chain disulphide bonds. These proteins were therefore considered by Osborne to form part of a fourth protein fraction which was only extracted using acidic or alkaline solvents. This fraction, which also includes insoluble structural and metabolic proteins, was given the name "glutelins" with the prolamin-related glutelin components in wheat being called "glutenin". Once the disulphide bonds that stabilise the glutenin polymers are reduced the protein monomers are readily soluble in aqueous alcohols and are closely related in their amino acid sequences and properties to classical prolamins. The prolamins and glutenins are present in about equal amounts in wheat grain and account for 70% or more of the total grain proteins.

The gliadin and glutenin proteins together form the gluten fraction which is responsible for the unique functional properties of wheat flour and dough, providing the cohesiveness and visco-elasticity which allow doughs made from wheat flour to be expanded by fermentation to give leavened foods. Although the prolamins of barley and rye are closely related to those of wheat they do not form a similar visco-elastic network and wheat is regarded as unique in this respect.

Prolamins, and in particular wheat gluten proteins, have been reviewed recently (Shewry, 2023; Scherf, 2023; Shewry and Belton, 2024) and will therefore not be discussed in detail here. However, it is important to note two structural features.

The first is the presence of domains comprising repeated amino acid sequences based on one or more short peptide motifs. These domains vary in extent, from less than half to almost all of the whole proteins, and are rich in the amino acids glutamine and proline. They contain few if any charged (acidic and basic) amino acids and rarely contain cysteine residues. These repeated sequences are therefore responsible for the high contents of glutamine and proline in the whole proteins and also contribute to non-covalent interactions (electrostatic, hydrophobic and hydrogen bonds) between gluten proteins (gliadins monomers and glutenin polymers) (discussed by Shewry and Belton, 2024). In particular, the regularly-spaced glutamine residues in some proteins may form arrays of hydrogen bonds between adjacent proteins which contribute to the elasticity of gluten.

Secondly, most gluten proteins contain cysteine residues most of which are located in the non-repetitive domains of the proteins. These cysteine residues form intra-chain disulphide bonds which stabilise the folded structures of the monomeric gliadins and inter-chain disulphide bonds which stabilise the glutenin polymers.

5.1. Modifying gluten protein structure and properties

Understanding the structures of grain storage proteins should facilitate their further exploitation in foods systems.

Although the "globulin" storage proteins of oats and rice differ in their properties from the typical 11S globulins of legumes it should

nevertheless be possible to exploit knowledge from processing legume grains, and in particular the detailed understanding of the functional properties of soybean proteins (Jideani, 2011).

The unusual structures and properties of the prolamins pose more of a challenge but also significant opportunities for modification. In particular, three properties can be targeted.

1. Solubility can be increased by partial deamidation to convert some of the glutamine residues (which form inter-chain hydrogen bonds) to glutamate. Solubility may also be increased by partial proteolysis as individual protein domains, including repetitive sequences, may be water-soluble.
2. Proteolysis may be used to reduce protein size, prepare separate protein domains and increase solubility. However, this will require specific enzymes which differ from those widely used in the food industry. This is because the repetitive domains of gluten protein lack the cleavage sites recognised by widely used enzymes while their high contents of proline residues also hinder proteolytic digestion. Digestion-resistant gluten peptides are responsible for triggering coeliac disease and possibly other adverse reactions. Consequently, a range of enzymes have been developed which are able to digest these peptides when added to food or expressed in transgenic plants (discussed by Rey et al., 2016; Rustgi et al., 2019)
3. Cross-linking. Glutenin polymers are stabilised by disulphide bonds which can be disrupted during processing. However, the high glutamine contents of gluten proteins also allow the introduction of additional cross-links, by treatment with the enzyme trans-glutaminase which is widely used in the food industry (Motoki and Seguro, 1998).

6. Conclusions

Cereals have been the most important staple crops globally for millenia and are important sources of protein for human nutrition and feed for livestock. Cereal grain proteins, and particularly wheat proteins, are also important for processing as their properties underpin the ability to make staple foods which are healthy, affordable and have high cultural acceptability. Cereal grains also have good storage properties with highly efficient and well-established systems for production, storage, distribution and processing. Cereal grain proteins therefore provide an attractive alternative to animal proteins in food systems.

The prolamin storage proteins of cereal grains have unusual properties compared to other proteins used in the food industry which may initially be seen as a disadvantage in extending their use. However, it also provides opportunities to develop new products, exploiting our detailed understanding of prolamin structures and properties.

Declaration of competing interest

I declare no conflicts of interest.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcs.2024.103899.

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