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Nutritional Aspects of Cereal Proteins and Approaches to Overcome Their Deficiencies [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1984 **304**, 373-380
doi: 10.1098/rstb.1984.0032

Phil. Trans. R. Soc. Lond. B **304**, 373–380 (1984)
Printed in Great Britain

Nutritional aspects of cereal proteins and approaches to overcome their deficiencies

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The inferior nutritional value of cereal protein is primarily because of the high content of the storage protein prolamin. These proteins are in general characterized by a very high content of proline and glutamine and a low content of lysine and other nutritionally essential amino acids. The cereals vary with respect to prolamin and lysine content. Rice and oats have a relatively low prolamin content, around 10%, and an acceptable lysine content. Wheat and barley contain 40–45% prolamin and about 3.5% lysine, while maize and sorghum contain more than 50% prolamin in their seed protein, that results in a lysine content below 2.5%.

Intensive screenings for changes in endosperm morphology, protein composition, or lysine content have led to the detection of a number of mutants with reduced prolamin content and increased content of lysine and other essential amino acids. These high-lysine and low-prolamin mutants have a considerably improved nutritional value of the seed protein. However, all the mutants found so far are also characterized by a reduced starch content and grain yield, and high-lysine varieties have only been grown to a very limited extent.

The present main approaches studied to improve the nutritional value of cereal proteins are (i) the replacement of some of the prolamin with lysine-rich storage proteins present in low amounts in the seed, and (ii) the improvement of the nutritional value of prolamin by genetic engineering.

Introduction

Cereals are not only the main crops for producing energy in food and feed, but they also supply most of the protein consumed by humans or used for animal production. The importance of cereal proteins for human and animal nutrition has been debated intensively, and opinions still differ as to whether or not it is worth while and necessary to improve the nutritional value of cereal seed protein. Nevertheless, about half of the seed protein in two of the most important crops in the world, wheat and maize, consists of storage protein with a very low nutritional value. Large amounts of this protein are probably used as energy rather than as protein in nutrition. If the nutritionally inferior storage protein could be converted into proteins with a better nutritional value by plant breeding, it would certainly have great impact on human nutrition in many areas as well as on animal production.

This paper gives an introduction to the composition of cereal proteins from a nutritional point of view, and a brief summary of the results obtained so far of the considerable efforts made to improve the nutritional value of cereal protein.

Protein composition of cereals

All cereals contain an alcohol-soluble protein fraction, that was termed prolamin by Osborne (1895). The proteins in this fraction are normally deposited in special organelles, protein bodies, and they are therefore considered as storage proteins; for a survey see Thomson & Doll (1979). The cereals differ with respect to their prolamin content. Rice and oats contain only about 10% prolamin in the seed protein, while half or even more of the seed protein in maize and sorghum is prolamin (table 1). The actual prolamin content depends on the N-nutrition of the plants during seed development, and also on the method used for protein extraction (Shewry *et al.* 1980). Therefore, the values presented in table 1 may vary with growing conditions and analytical methods.

Table 1. Prolamin and lysine content of seed protein, and content of three amino acids in the prolamin of different cereals

cereal	prolamin (% of seed N[1])	amino acids in prolamin, %[2]			lysine (% of protein)
		Glx	Pro	Lys	
rice	8	32	6	0.3	3.5[3]
oats	12	36	10	0.7	4.2[4]
barley	40	37	19	1.0	3.5[5]
wheat	45	38	15	0.6	3.1[6]
maize	50	23	11	0.1	1.6[7]
sorghum	60	24	10	0.1	2.1[8]

(1) Mossé 1966; (2) rice: Mandac & Juliano 1978, sorghum: Paulis & Wall 1979, other cereals: Waldschmidt-Leitz & Metzner 1962; (3) Mandac & Juliano 1978; (4) Robbins *et al.* 1971; (5) Køie & Doll 1979; (6) Mattern *et al.* 1970; (7) Nelson *et al.* 1965; (8) Singh & Axtell 1973.

The name prolamin refers to the exceptionally high content of glutamine and proline. These two amino acids constitute about 50% of prolamin in oats, barley, and wheat, and about 35% in maize, sorghum, and rice (table 1). Another difference between the prolamin of the cereals is that the prolamin of rice and oats contain less proline that that of barley and wheat. Prolamin is further characterized by a low content of the amino acids that are essential for humans and animals. Particularly, the lysine content of prolamin is very low (table 1), but there is also some variation among the cereals in this respect.

The lysine content of the total seed protein in the cereals is also shown in table 1. Lysine has been reported to be the first limiting amino acid in all the cereals (Eggum & Beames 1983). The second limiting amino acid is tryptophan in maize and threonine in the other cereals. The content of these and a few other amino acids is in general too low in cereal protein to meet the nutritive requirement of humans and animals, although the exact requirements are not known in detail.

The low content of essential amino acids in cereal protein is a direct consequence of the high content of prolamin. Not only is the lysine content of prolamin low; the content of the essential amino acids threonine, valine, and isoleucine is also rather low (Waldschmidt-Leitz & Metzner 1962). The nutritionally inferior amino acid composition is an important characteristic of the cereal storage proteins found in the prolamin fraction. The other Osborne protein fractions have in general an amino acid composition that fits the requirements of humans and animals. The only exception is the glutelin fraction in which an intermediate lysine content has been reported.

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However, this may be caused by contamination with proteins from the prolamin fraction, because prolamin is often extracted incompletely. These considerations show that the low nutritional value of the seed protein of all cereals except rice and oats is because of the storage protein prolamin. Hence, attempts to improve the nutritive value of cereal protein should concentrate on altering the content or composition of prolamin.

High-lysine mutants

The nutritionally inferior amino acid composition of cereal seed protein has led to extensive searches for mutants with an improved nutritional value of the protein. Somewhat different approaches have been followed in different cereals to find such mutants. The first successful

Table 2. Prolamin and lysine content of representative mutants in maize, sorghum and barley

cereal	line	gene	prolamin (% of N)	lysine (% of protein)	reference
maize	normal	—	55	1.6	Sodek & Wilson 1971; Nelson *et al.* 1965
	opaque-2	o_2	17	3.7	
	floury-2	fl_2	52	3.3	
sorghum	normal	—	54	2.1	Paulis & Wall 1979; Singh & Axtell 1973
	IS11758	*hl*	33	3.1	
barley	normal	—	54	2.8	Miflin & Shewry 1979
	Hiproly	*lys*	43	3.5	
	normal	—	41	3.5	Køie & Doll 1979
	Risø 56	*Hor2ca*	31	4.6	
	Risø 1508	*lys3a*	15	5.1	

attempt was made in maize, in which Mertz *et al.* (1964) and Nelson *et al.* (1965) analysed mutants with changed seed morphology and assumed that drastic changes in protein composition would affect seed structure. This led to the detection of two mutants, opaque-2 and floury-2 (table 2), both of which have a much higher content of essential amino acids, especially lysine, than ordinary maize. Several other maize mutants with increased lysine content in the seed protein have been reported; see Denić (1983). In sorghum, screening of about 9000 lines from the world collection for mutants with floury seeds (Singh & Axtell 1973) led to the detection of a high-lysine line, IS11758 (table 2). Another high-lysine sorghum mutant has been found by screening the offspring of mutagenically treated seeds for opaque mutants (Axtell 1976).

In barley screening for high-lysine mutants has been done by combined analyses for dye-binding capacity (d.b.c.) and Kjeldahl nitrogen content as suggested by Mossberg (1969), who showed that the d.b.c. is highly correlated with the content of basic amino acids of the sample. Hence, a sample with a higher content of one of the basic amino acids, e.g. lysine, will have an increased d.b.c. while the nitrogen content will be unchanged. The combined use of N% and d.b.c. to detect high-lysine mutants has proved very useful and highly reliable, and relatively small changes in lysine content have been detected by this method.

The first high-lysine barley detected by the N%–d.b.c. method was the variety Hiproly (table 2), that was found among 2500 entries of the world barley collection (Munck *et al.* 1970). A number of barley high-lysine mutants, of which a few are presented in table 2, have been

detected by combined d.b.c. and N% analyses of mutagenically treated materials. A survey of these screenings that gave a total of 17 mutants has been made recently (Doll 1983). Attempts have also been made to find high-lysine wheat (Johnson *et al.* 1970; Siddiqui & Doll 1973), but no varieties or mutants with a drastically increased lysine content in the seed protein have been found. However, this may be because of the hexaploidy of bread wheat, that makes the detection of recessive mutants much more difficult.

Studies of the protein composition of high-lysine cereals have shown that the increase in lysine content is always followed by a prolamin content reduced by a greater or lesser amount (table 2). Further it has been shown that the changes are normally due to the effect of single genes. None of these genes have been shown to have a direct effect on the synthesis of lysine or other

TABLE 3. NUTRITIONAL VALUE OF THE SEED PROTEIN OF THE HIGH-LYSINE MUTANT Risø 1508 AND THE PARENT VARIETY BOMI

line	true digestibility, %	biological value, %
Risø 1508	78	90
Bomi	83	76

From Doll *et al.* (1974).

amino acids, but at least some of them are directly related to prolamin synthesis. This is for instance the case for *Hor2ca* of Risø 56 that appears to be a non-functional allele of one of the loci containing the structural genes for barley prolamin (Doll 1980). Therefore, the mutants described here should probably be considered as low-prolamin rather than high-lysine mutants.

A completely different approach to improving the nutritional value of seed protein has been used by Bright *et al.* (1982), who selected for barley mutants in which feedback controls on the synthesis of the required amino acids are relaxed; this led to enhanced production of free amino acids. Embryos from mutagenically treated materials were screened for growth on a medium containing lysine and threonine. One mutant that accumulates threonine and, to a lesser extent, methionine in the seed was selected. The total content of both threonine and methionine in the seeds was increased by 6% compared with normal seeds with the same protein content.

The nutritional value of the protein of Risø 1508 and the parent variety Bomi is shown in table 3. The two lines were fed to rats for 5 d in an experiment in which the protein content of the diet was adjusted to the same level. True digestibility (t.d.) was estimated as the percentage of feed-N not found in the faeces after correction for losses in metabolic N. Likewise, the biological value (b.v.) is the percentage of the digested protein retained in the body, i.e. that part not found in the urine. It is seen from table 3 that the high-lysine mutant 1508 had a much higher b.v. than Bomi. However, the t.d. of the mutant protein was a little reduced. This is probably because prolamin has a higher t.d. than other seed proteins because it is more accessible to the digestion enzymes (Büchmann 1979). Many other feeding trials have been performed with different high-lysine types of maize, sorghum and barley. These studies have in general revealed a higher b.v. of the protein and/or a faster growth rate of animals fed with the high-lysine mutants. Hence, there is no doubt that the nutritional value of the seed protein of these cereals can be considerably improved by decreasing the prolamin content and thereby increasing the content of lysine and other amino acids.

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The main problem encountered with the high-lysine cereals has been that the high-lysine genes not only affect protein composition and lysine content, but also reduce grain production. This is illustrated for two barley high-lysine genes in tables 4 and 5. The effect of each gene on productivity was studied by comparison of segregated high-lysine and normal lines derived from chromosome-doubled haploids produced on F_1 (Doll & Køie 1978). This procedure ensures that the influence of unknown genes on the estimated effect of the high-lysine gene is minimized.

The *lys3a* gene of mutant Risø 1508 reduced grain yield 20%. It is seen from table 4 that the reduction in grain production was almost completely due to a reduction in non-structural

TABLE 4. EFFECT OF THE BARLEY HIGH-LYSINE GENE *lys3a* (RISØ 1508) ON THE PRODUCTION OF GRAIN, NON-STRUCTURAL CARBOHYDRATES, PROLAMIN AND LYSINE. AVERAGES OF 30 NORMAL AND 20 HIGH-LYSINE LINES

	grain production	carbohydrate production	prolamin production	lysine production
genotype	g m^{-2}	g m^{-2}	g m^{-2}	g m^{-2}
lys3a/lys3a	287	132	5.3	2.09
+/+	357	197	20.6	1.66
difference	−70	−65	−15.3	+0.43
difference, %	20	33	74	26

From Doll & Køie (1978).

TABLE 5. INFLUENCE ON THE PRODUCTION OF GRAIN AND DIFFERENT PROTEINS OF THE BARLEY HIGH-LYSINE GENE *lys* FROM HIPROLY

	grain production	prolamin production	protein Z production	β-amylase production
genotype	g m^{-2}	g m^{-2}	g m^{-2}	g m^{-2}
lys/lys	387	18.4	2.70	1.22
+/+	461	22.4	1.44	0.40
difference	−74	−4.0	1.26	0.82
difference, %	16	18	88	205

From Balasaraswathi *et al.* 1983.

carbohydrates, i.e. starch plus sugar, in the seeds. The largest relative reduction was found in the production of prolamin. Therefore, although the absolute hordein reduction was much less than the reduction in carbohydrates, Risø 1508 should probably be considered a prolamin rather than a carbohydrate mutant. There was a highly significant increase in the production of lysine per unit area in the lines having the *lys3a* gene. However, the increase in lysine production is obviously far too small to pay for the large decrease in carbohydrate production.

Grain yield was also substantially reduced in the presence of the high-lysine gene *lys* of Hiproly (table 5). The *lys* gene also reduced prolamin production significantly, but not to the same extent as the *lys3a* gene of Risø 1508. Hiproly and high-lysine lines derived from this variety have been reported to have a higher content of four lysine-rich, salt-soluble proteins that contribute very much to be increased lysine content of the seeds (Hejgaard & Boisen 1980). These are protein Z (Hejgaard 1982), β-amylase, and two chymotrypsin inhibitors, CI-1 and CI-2 (Boisen *et al.* 1981), with lysine content of 5, 7, 9, and 11%, respectively. The study presented in table 5 showed large increases in protein Z and β-amylase in the lines with the

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lys gene, but the increase in the total production of these two proteins was only about half as large as the decrease in prolamin production.

The results presented here of the attempts to improve the nutritional value of cereal seed protein can be summarized as follows. Drastic increases in lysine content and nutritional value of the seed protein have been obtained in maize, sorghum, and barley. The improvement is normally because of a reduced content of the main cereal storage protein, prolamin, that has a very low content of lysine and several other essential amino acids. Most of the selected mutant genes should probably be considered as low-prolamin, rather than low-lysine, genes, i.e. gene mutations causing a more or less complete block in storage protein synthesis. These results are in agreement with the views forwarded by Nelson (1969), that is, drastic changes of protein quality are only feasible by changing the storage proteins, and that such changes probably would not be lethal. However, in spite of great efforts of plant breeders, it has not been possible to combine the low-prolamin/high-lysine character with an acceptable grain production. This indicates strongly that storage protein synthesis is essential for an efficient starch accumulation in the cereal grain. Although this hypothesis needs further testing it indicates that the desired protein improvement should be obtained without reducing the total amount of storage protein. If this is true the lysine-poor prolamin should not just be decreased or removed, but should be replaced by improved prolamin and/or other storage proteins.

Future breeding possibilities

The following short survey of the possibilities for the improvement of the nutritional value of cereal protein is mainly based on present work in barley that has been reviewed in more detail elsewhere (Doll 1981, 1983). The breeding strategy suggested is based on the assumption that improvements in protein quality that do not affect grain production can only be obtained by changing the amino acid composition of prolamin or by increasing the content of storage proteins with a better nutritional value. It should be realized that such genetic changes are undoubtly much more difficult to achieve than the reductions in prolamin content obtained so far by mutations.

Drastic changes in the amino acid composition of storage proteins can be envisaged by means of genetic engineering (Miflin *et al.* 1981). However, while such techniques are now used intensively in studies of the organization and function of storage protein genes, there are many constraints to be solved before plant genes can be improved by genetic manipulations.

An easier way to improve the composition of prolamin was suggested for barley by Blake (1981) who pointed out that the large genetic variation in the composition of barley prolamin (Shewry *et al.* 1979; Linde-Laursen *et al.* 1982) also may represent some variation in the lysine content of the polypeptides. A difficulty of this approach is that the structural storage protein genes consist of multigene families coding for several different polypeptides. This makes the combination of genes coding for better polypeptides very difficult.

While the prospects for the improvement of the amino acid composition of prolamin at present seem rather limited, attempts to replace prolamin by more lysine-rich proteins already present in the barley seed may be more promising. Changes in that direction are already present in Hiproly (see above) and in mutant Risø 56 (Giese & Andersen 1983), in which the content of protein Z, β-amylase, and the chymotrypsin inhibitors CI-1 and CI-2 are strongly increased. These increases are probably a secondary effect caused by the reduction in prolamin that makes more amino acids available for the synthesis of other proteins.

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The four lysine-rich proteins that are present in larger amount in Hiproly and Risø 56 are probably not storage proteins in the sense that they are only synthesized to store nitrogen. However, their quantity is increased by enhanced N-nutrition (Hejgaard & Boisen 1980) cf. the behaviour of storage proteins, and they are further synthesized at the same time as prolamin during seed development (Giese & Andersen 1983). Hence they appear to have some of the properties required for proteins that can be used to replace prolamin as storage protein. However, further studies are needed to evaluate how efficiently the lysine-rich proteins can store nitrogen in the endosperm, and also to see whether there are physiological limits on the amount of salt-soluble protein that can be accumulated in the seed.

So far the progress in breeding for improved nutritional value of the seed protein of cereals has been very limited in terms of released varieties. Nevertheless, the attempts to improve the protein quality have improved knowledge of the seed proteins, and the more fundamental aspects of the genetics and synthesis of storage proteins are now studied intensively in many laboratories. These studies will undoubtly disclose new and more efficient ways of improving protein quality without affecting grain production. Therefore, I feel we still have reason to believe that plant breeding will eventually provide high yielding cereal varieties with protein of better nutritional value, and that the support to this important breeding aspect should be continued.

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Discussion

R. W. Welch (*Welsh Plant Breeding Station, Aberystwyth, U.K.*). In the U.K. over half the barley crop is fed to ruminants in which protein quality is of little importance. Furthermore the protein content of barley is generally inadequate for non-ruminant feeding. In view of this does Dr Doll think that increasing grain protein content may be more important than improving protein quality?

H. Doll. It is important to obtain the maximum grain protein production from barley and this is being achieved by current high yielding varieties.

R. W. Welch. Would is not be beneficial to try to increase the protein content and protein production of feed barley to the levels found in wheat?

H. Doll. The higher protein production in wheat is the result of the higher levels of nitrogen fertilizer used on this crop.

R. W. Welch. It is not easy to make interspecific comparisons, however, we have evidence that the differences in protein production between wheat and barley are not only environmental. Wheat has a higher nitrogen harvest index than barley.

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