Genetic Improvement of Plant Protein

The status of genetic improvement of nutritional quality of the major food cereals, food legumes, and potatoes is reviewed. There is good evidence that all are amenable to breeding improvement either by increasing protein content or improving amino acid balance of the protein. Usable genetic variability for protein content appears to exist in most food crops. Large genetic variation in lysine has been uncovered in maize and barley.

The importance of the cereal grains to world nutrition is well recognized. Wheat and rice alone are dietary mainstays for two-thirds of the world's three billion people. Maize occupies a similar role in tropical and sub-tropical parts of Central and South America as does sorghum in parts of Africa and Asia. Although commonly classified as calorie sources, the cereals also are the world's most important protein source. Food legumes are particularly important plant sources of protein, vitamins, and minerals. They are widely grown in a range of environments from humid, low-elevation tropics to arid, high-elevation environments. They are usually eaten in small amounts as part of a mixed diet.

Protein deficiency is generally regarded as the world's most serious nutritional problem, probably because of its serious implications for the very young. Many food-deficient countries have a serious calorie problem as well. The two problems cannot be dealt with separately because protein deficiency is difficult or impossible to correct if a serious calorie deficiency also exists. Thus, plant protein cannot be improved effectively at the sacrifice of productivity.

The challenge to plant breeders is to develop crop varieties that are both more productive and more nutritious than the ones we now have. The task is not easy because high grain yield tends to be associated with depressed grain protein content in many crop species. Further, high grain protein content may be associated with undesirable shifts in amino acid balance, particularly in the cereals.

Plant proteins are less balanced than animal protein. This imbalance has led some to suggest more reliance on the animal protein. In some developed countries of the western world, this is an acceptable approach to improved nutrition. In overpopulated, food-deficient, developing countries it is unrealistic because animals produce protein and calories less efficiently than plants.

STATUS OF FOOD CROPS AS PROTEIN SOURCES

Protein Production. Cereals and legumes are the two most important sources of protein among plant species. Tubers and root crops, with the possible exception of white potato, are a poor source of protein (FEDS Staff Paper 2, 1970). Interestingly, white potato is second only to soybeans in the United States in protein production per acre (Table I). Its protein content is very low, but tremendous per acre yield results in higher protein production than that of other lower yielding crops. Maize, sorghum, peas, and beans are the next highest producers of protein per acre. Maize, because of its high yield, is the best producer of both calories and protein per acre among the cereals. Rice and sorghum rank next highest as combined calorie-protein sources. Soybean is best among the legumes.

Direct comparisons of per acre protein production of crops may have limited validity. Crop species are frequently noncompetitive for available acres because each has its own peculiar environmental requirement and areas of adaptation. Rice and wheat are noncompetitive because of their widely different environmental requirements. Maize and wheat in the United States generally do not compete directly with one another for available acres. Maize, which is admirably suited to the moderate to high rainfall areas of the east and midwest, gives way to wheat in the high plains where rainfall is low and unpredictable. Caution must be exercised, therefore, in making direct comparisons of per acre protein and calorie production between these two noncompeting cereals.

Among the cereals, wheat has the highest and rice the lowest protein content per pound (Table II). Maize and barley produce the most calories per pound. The legumes provide more than twice as much protein per pound as the cereals and are comparable with or superior to the cereals in calories produced per pound. However, they produce substantially fewer pounds per acre in the United States than do such cereals as maize, rice, and sorghum (Table I).

Per acre protein comparisons do not take into account existing differences among crop species in the quality of protein produced. None of the plant proteins has biological value equal to that of meat and animal products. The shortcoming of each species may be different. Cereals as a group, although not identical in amino acid composition of their protein, are seriously deficient in lysine. In contrast, food legumes are likely to be most deficient in methionine. Total protein production, therefore, may not reflect the true nutritional contribution of the various food crops.

Protein Fractions. Four protein fractions based on solubility comprise the total grain protein of the cereals (Neurath and Bailey, 1954). The amino acid composition of a fraction may not be identical in different species but it tends to be similar. The proportion of each fraction varies according to the cereal species (Table III). Wheat, rye, and barley are similar to each other in the quantity of each protein fraction they possess. Rice is unique in that its protein is largely glutelin. Maize and sorghum proteins are mainly prolamin and glutelin, whereas oats protein is mainly globulin. Because each fraction tends to have different characteristic amino acid composition, the relative proportion of each strongly affects the level of an amino acid in the total grain protein. Prolamin is notably low in lysine. Glutelin is higher in lysine than is prolamin. Albumin and globulin, concentrated in the embryo and aleurone, are highest in lysine.

The proportion of protein fractions largely accounts for differences in amino acid content of different cereals. Values shown in Table IV, which were compiled in 1966 (U. S. Dep. Agr. Home Econ. Res. Rep.), differ in several

U. S. Department of Agriculture, Agricultural Research Service, North Central Region, University of Nebraska, Lincoln, Nebraska 68503.

¹Research Agronomist, U. S. Department of Agriculture, Agricultural Research Service, North Central Region, Lincoln, Neb. 68503, and Research Associate, Campbell Institute for Agricultural Research, Cinnaminson, N. J. 08077.

| Table I. Rank of Selected Crops in the United States |
|--|
| According to Production of Calories and |
| Protein per Acre ^a |

| | Calo | ries | Protein | | |
|----------------|--------|------|---------|------|--|
| Crop | 1000 g | Rank | 1000 g | Rank | |
| Sugar cane | 34,940 | 1 | | | |
| White potatoes | 10,518 | 2 | 290 | 2 | |
| Sugar beets | 9,311 | 3 | | | |
| Maize | 8,462 | 4 | 216 | 3 | |
| Rice | 7,019 | 5 | 146 | 8 | |
| Sorghum | 5,355 | 6 | 177 | 4 | |
| Barley | 4,020 | 8 | 111 | 9 | |
| Winter wheat | 3,739 | 10 | 105 | 10 | |
| Soybeans | 3,510 | 11 | 297 | 1 | |
| Beans | 2,617 | 15 | 172 | 7 | |
| Peas | 2,487 | 16 | 176 | 6 | |
| Rye | 2,477 | 17 | 90 | 15 | |
| Oats | 1,861 | 19 | 68 | 17 | |

^a Source: FEDS Staff Paper 2, 1970.

Table II. Calorie and Protein Production of Selected Cereals and Food Legumes in the United States^a

| Crop | High state av yield, lb | Calorie content per lb | Protein content per lb |
|--------------|-------------------------------|------------------------------|------------------------------|
| Cereals | | | · · · · |
| Maize | 5359 | 1579 | 40.4 |
| Spring wheat | 1518 | 1497 | 63.5 |
| Winter wheat | 1800 | 1497 | 55.8 |
| Rice | 5242 | 1339 | 27.9 |
| Sorghum | 3556 | 1506 | 49.9 |
| Barley | 2545 | 1579 | 43.5 |
| Oats | 1818 | 1024 | 37.3 |
| Rye | 1635 | 1515 | 54.9 |
| Legumes | | | |
| Soybeans | 1920 | 1828 | 154.7 |
| Beans | 1697 | 1542 | 101.2 |
| Peas | 1613 | 1542 | 109.3 |

^a Source: FEDS Staff Paper 2, 1970.

cases from currently accepted values. According to recent analysis of 12,500 wheats in the World Wheat Collection, the average lysine content of wheat is nearer to 3.1 than to 2.8% (Summary Report of Research Findings, 1972). The lysine content of sorghum is nearer to 2.1 than to 2.7% (Axtell, 1972). Sorghum and maize proteins with high prolamin and relatively low globulin and only a trace of albumin tend to be low in lysine. Rice with 85% glutelin has a much higher level of lysine in its total grain protein.

RESEARCH PROGRESS

Research to improve nutritional quality is under way in many crop species. Substantial progress has been made in barley in which a high lysine mutant, "Hiproly," was identified (Munck, 1972). Additional genes for high lysine may also have been identified in barley. A high protein exotic oat species Avena sterilis is being investigated for its usefulness as germplasm for the nutritional improvement of Avena sativa.

A new man-made cereal species, triticale, derived from combining rye with durum wheat has nutritional promise (Report on Maize and Wheat Improvement, 1972). Protein and lysine levels substantially higher than in wheat were reported for unimproved initial selections. Whether this superiority in level of protein and lysine can be maintained in improved lines of triticale has not been fully established.

The discussion that follows will be limited to selected cereal and noncereal species. It includes: the four principal food cereals, wheat, rice, maize, and sorghum; the leguminous species, soybeans, dry beans, mung beans, and peas; and the tuber crop, white potato.

CEREALS

Wheat. Protein Content. Genes with a major effect on the level of grain protein were identified in 1951 in the "Atlas 50" and "Atlas 66" varieties (Middleton *et al.*, 1954). These varieties have been widely used in breeding programs to increase the protein content of wheat. Data from cooperative Agricultural Research Service-Nebraska Agricultural Experiment Station (ARS-NAES) research to improve the nutritional value of wheat suggest the operation of two major genes for high protein from the Atlas 66 variety. One gene is linked to a gene for leaf rust resistance (Johnson *et al.*, 1963). Heritability estimates for protein content as high as 0.83 were computed (Stuber *et al.*, 1962).

The Atlas genes can increase grain protein content by as much as 2-3 percentage points (Johnson *et al.*, 1963). The increase has been demonstrated in lines equally as productive as normal protein lines. The protein genes are effective in an array of production environments. There was excellent expression of the high protein trait at a large number of International Winter Wheat Performance Nursery sites (Stroike *et al.*, 1971) (Table V). A high protein experimental line (C.I. 14016) derived from Atlas 66 maintained an advantage of two percentage points over "Lancer" at several levels of soil fertility at test sites in Nebraska during a 3-year period (Johnson *et al.*, 1973). Data are summarized in Table VI.

The Atlas protein genes appear to alter nitrogen metabolism in the wheat plant. Nebraska data indicate that Atlas-derived high protein plants have a more efficient nitrogen transport system (Johnson *et al.*, 1967) than ordinary wheat. Illinois research established that Atlas high protein lines have a higher level of nitrate reductase activ-

Table III. Protein Content and Solubility Fractions of Cereal Grains^a

| | | | Protein fract | ions, % of total protein | n |
|--------------------|--------------------|--------------------------------|--------------------------------|-----------------------------------|----------------------------------|
| Cereal grain | Protein, % dwb⁵ | Albumins (water soluble) | Globulins (salt soluble) | Prolamins (alcohol soluble) | Glutelins (alkali soluble) |
| Wheat | 10-15 | 3–5 | 6-10 | 40 –50 (gliadin) | 30-40 (glutenin) |
| Rice | 8-10 | Trace | 2-(8)? | (1-5)? | 85-90 |
| Maize | 7–13 | Trace | 5-6 | 50-55 (zein) | 30-45 |
| $\mathbf{Sorghum}$ | 9-13 | Trace | Trace | >60 (kafirin) | Considerable |
| Rye | 9–14 | 5-10 | 5–10 | 30-50 (secalin) | 30-50 |
| Barley | 10–16 | 3–4 | 10-20 | 35–45 (hordein) | 35-45 |
| Oats | 8-14 | 1 | 80 | 10-15 (avenin) | 5 |

" Source: Neurath and Bailey, 1954. ^b Per cent, dry weight basis.

| Table IV. Protein | Content and Amin | o Acid Composition | of Selected Food I | Legumes and Cereals ^a |
|-------------------|------------------|--------------------|--------------------|----------------------------------|
| | | | | |

| Protein. | | | | \mathbf{Amin} | o acid com | position, | % of total p | protein | | |
|--------------------|----------|-----|-----|-----------------|------------|-----------|--------------|---------|-----|-----|
| \mathbf{F} ood | <i>%</i> | Lys | Met | Thr | Trp | Ile | Leu | Tyr | Phe | Val |
| Soybean | 34.9 | 6.9 | 1.5 | 4.3 | 1.5 | 5.9 | 8.4 | 3.5 | 5.4 | 5.7 |
| Peas | 23.8 | 7.3 | 1.2 | 3.9 | 1.1 | 5.6 | 8.3 | 4.0 | 5.0 | 5.6 |
| Beans | 21.4 | 7.4 | 1.0 | 4.3 | 0.9 | 5.7 | 8.6 | 3.9 | 5.5 | 6.1 |
| Oats | 14.2 | 3.7 | 1.5 | 3.3 | 1.3 | 5.2 | 7.5 | 3.7 | 5.3 | 6.0 |
| Barley | 12.8 | 3.4 | 1.4 | 3.4 | 1.3 | 4.3 | 6.9 | 3.6 | 5.2 | 5.0 |
| Wheat | 12.3 | 2.8 | 1.5 | 2.9 | 1.2 | 4.3 | 6.7 | 3.7 | 4.9 | 4.6 |
| Rye | 12.1 | 4.1 | 1.6 | 3.7 | 1.1 | 4.3 | 6.7 | 3.2 | 4.7 | 5.2 |
| Sorghum | 11.0 | 2.7 | 1.7 | 3.6 | 1.1 | 5.4 | 16.1 | 2.8 | 5.0 | 5.7 |
| Maize | 10.0 | 2.9 | 1.9 | 4.0 | 0.6 | 4.6 | 13.0 | 6.1 | 4.5 | 5.1 |
| Rice | 7.5 | 4.0 | 1.8 | 3.9 | 1.1 | 4.7 | 8.6 | 4.6 | 5.0 | 7.0 |
| Ref (whole egg) | 12.8 | 6.4 | 3.1 | 5.0 | 1.7 | 6.6 | 8.8 | 4.3 | 5.8 | 7.4 |

^a Source: U. S. Dep. Agr. Home Econ. Res. Rep., 1966.

Table V. Grain Yield and Protein Content of Comparably Yielding Varieties Grown in the International Winter Wheat Performance Nursery in 1969 and 1970

| | Mean | yield, | bu/acre | Mean p | rotein co | ntent, % |
|-----------------------|-----------------------|-----------------------|------------------------|-----------------------|-----------------------|--------------|
| Variety | 1969 (16 sites) | 1970 (32 sites) | 2-year ave- rage | 1969 (18 sites) | 1970 (25 sites) | 2-year av |
| Atlas 66 Atlas 66/ | 50 | 42 | 46 | 17.5 | 19.3 | 18.4 |
| Comanch | ne 52 | 44 | 48 | 16.4 | 17.2 | 16.8 |
| Triumph 64 | 4 50 | 47 | 49 | 14.7 | 15.6 | 15.2 |
| Winalta | 48 | 43 | 46 | 13.8 | 14.5 | 14.2 |
| Gaines | 46 | 40 | 43 | 13.0 | 13.7 | 13.4 |
| Yorkstar | 54 | 48 | 51 | 12.4 | 13. 1 | 12.8 |

ity than ordinary wheat, even in the early stages of plant development (Croy and Hageman, 1970). This high level suggests that reduction of nitrate to nitrite may be the rate-limiting step in nitrogen transport leading to high grain protein content. Measurement of nitrate reductase activity in wheat seedlings may offer an efficient, rapid method of identifying wheat plants with high grain protein potential. Whether genetic sources of high grain protein other than the Atlas varieties also affect the nitrate reductase enzyme system has not yet been established.

The search for additional genetic sources of high grain protein in wheat is being continued in cooperative Agricultural Research Service-Nebraska Agricultural Experiment Station research with financial support from the Agency for International Development, U. S. Department of State. Over 17,000 common and durum wheats from a World Collection maintained by the Agricultural Research Service have been analyzed for protein and lysine (Johnson *et al.*, 1972). Total protein variation ranged from approximately 7 to 22% in both the common and durum groups. A large part of this variation is believed to be nongenetic. The genetic component of the total protein variation probably does not exceed 5 percentage points. Several wheats have been identified that show promise as new genetic sources of high grain protein (Table VII).

Evidence shows that the high protein of one of the wheats is associated with genes other than those in Atlas 66. The Indian variety Nap Hal produces grain with a protein content approximately equal to that of Atlas 66. In a cross of Atlas $66 \times$ Nap Hal there was apparent transgressive segregation for both high and low protein in F_2 progeny bulk populations analyzed in F_3 and F_4 generations (Figure 1). This segregation is interpreted as evidence for different protein genes in the parent varieties that function additively. There appears to be opportunity to increase grain protein content in wheat beyond the level of Atlas 50 and Atlas 66.

The high protein content of Atlas 66 derived lines persists in milled flour. In normal wheat, milled flour has approximately 1 percentage point lower protein content than the whole grain. In high protein lines, the protein difference between flour and whole grain continues to be approximately 1 percentage point. The high protein phenomenon obviously affects the level of protein in the endosperm and aleurone as well as in other parts of the kernel.

Amino Acid Composition. Lysine is the nutritionally limiting amino acid in wheat. Common wheats totaling 12,651 from the World Collection averaged 3.14% lysine when lysine was expressed as percentage of total protein (Summary Report of Research Findings, 1972). A lysine level of 4% would bring it into reasonably good balance with other essential amino acids. The range in lysine among World Collection wheats was from 2.2 to 4.2% (Summary Report of Research Findings, 1972). The genetic component of total lysine variation identified to date is believed to be approximately 0.4–0.5%. This amount is less than one-half of that needed to bring lysine into balance with other amino acids.

Lysine is negatively correlated with protein in wheat (Summary Report of Research Findings, 1972). A signifi-

 Table VI. Average Grain Yield and Protein Content of the Lancer Wheat Variety and a High Protein Wheat Line

 (C.I. 14016) on Different Nitrogen Fertility Levels at Test Sites in Nebraska in 1969 and 1970^a

| Nitrogen applied, | G | rain yield, bu/acr | е | | Protein content, % | |
|----------------------|--------|--------------------|-----------------|--------|--------------------|-------|
| lb/acre | Lancer | C.I.14016 | Diff. | Lancer | C.I.14016 | Diff. |
| 0 | 38 | 38 | 0 | 10.8 | 12.5 | +1.7 |
| 20 | 44 | 41 | -3 | 11.2 | 13.3 | +2.1 |
| 40 | 47 | 44 | -3 | 11.8 | 14.0 | +2.2 |
| 60 | 46 | 45 | -1 | 12.6 | 14.9 | +2.3 |
| 80 | 46 | 45 | -1 | 13.2 | 15.4 | +2.2 |
| 100 | 46 | 45 | $-\overline{1}$ | 13.6 | 15.8 | +2.2 |
| 120 | 45 | 46 | +1 | 13.0 | 16.3 | +2.3 |

^a Source: Johnson et al., 1973.

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Table VII. Potentially Useful Sources of Genes in Wheat for High Protein and High Lysine

| Variety or line | Sel., P.I. , or C.I. no. | Source | Useful trait |
|--|------------------------------------|-----------|-------------------------|
| Aniversario | 12578 | Argentina | High protein |
| Frondoso | 12078 | Brazil | High protein |
| Aniversario-derived line | NB66565 | U. S. | High protein |
| Atlas 50 | 12534 | U. S. | High protein |
| Atlas 66 | 12561 | U. S. | High protein |
| Atlas-derived lines | a | U. S. | High protein |
| Frondoso-derived line | Purdue 28-2-1 | U. S. | High protein |
| ${ m Hume^2} 	imes { m Nb^4-Agrus-Tc^7}$ | SD69103 | U. S. | High protein |
| Male fertility restorer | NB542437 | U. S. | High protein |
| Pearl | 3285 | Sweden | High lysine (?) |
| m Fultz 	imes Hungarian | 11849 | U. S. | High lysine (?) |
| Fultz 	imes Hungarian-derived line | 12756 | U. S. | High lysine (?) |
| Norin 10 \times Brevor, Sel. 10 line | 13447 | U. S. | High lysine |
| Norin 10 \times Brevor, Sel. 10 line | 13449 | U. S. | High lysine |
| 22A | 5484 | USSR | High lysine (?) |
| April Bearded | 7337 | England | High protein and lysine |
| Hybrid English | 6225 | England | High protein and lysine |
| Nap Hal | 176217 | India | High protein and lysine |

^a Source: Johnson et al., 1971.

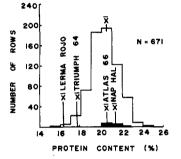


Figure 1. Protein frequency distribution of F₂ progeny bulk rows from a Nap Hal \times Atlas 66 wheat cross grown at Yuma, Ariz., in 1971.

cantly larger part of the protein is comprised of lysine at low levels of protein than at high levels. However, the depression of lysine with higher protein is not proportionate to the increase in protein. When lysine is expressed as percentage of dry grain weight, it is strongly positively correlated with protein content. Clearly, lysine per unit weight of grain can be effectively increased by increasing the protein content of the grain.

The relationship between protein content and lysine level in wheat grain is curvilinear (Summary Report of Research Findings, 1972). Between 8 and 15% of protein, the relationship is strongly negative. As protein increases above 15% its effect on lysine diminishes and finally disappears. In the ARS-NAES research, all lysine values are adjusted to a common protein level based on this relationship to permit valid lysine comparisons among wheats differing in protein content.

An explanation for the negative relationship between total protein and lysine in wheat can be found in examination of protein fractions at various levels of total protein. The albumin and globulin proteins are rich in lysine, whereas the gluten proteins, especially prolamin, are relatively poor in lysine (Johnson *et al.*, 1970). The ratio of water-soluble to gluten protein varies. Low protein wheats characteristically have a higher percentage of the watersoluble protein fraction than high protein wheats.

Protein Quality. The amino acid composition of high protein wheats derived from Atlas 66 has been analyzed in vitro. These laboratory analyses indicate that wheat with high grain protein content provides more of each essential amino acid than wheat with ordinary grain protein content. This assumes no undesirable shifts in digestibility or availability of the amino acids in the high protein wheats.

Table VIII. Mean Mouse Weight Gains and Feed Efficiency Ratios from Wheat Samples Differing in Protein Content Fed to Weanling Mice for a 28-Day Period (5 Mice per Sample)

| No. of sam- ples | Protein content, % | \overline{x} protein, % | \overline{x} weight gain, g | x feed efficiency ratio ^a |
|------------------------|-----------------------|------------------------------|-------------------------------------|--|
| 14 | 17.0-18.6 | 17.5 | 15.1 | 8.6 |
| 16 | 15. 1–16 .8 | 16 .1 | 12.9 | 9.4 |
| 14 | 13.5 - 14.8 | 14.3 | 13.5 | 9.3 |
| 5 | 13.8-12.9 | 11.7 | 10. 2 | 11. 1 |

^a Feed consumption/weight gain.

Preliminary results from mouse feeding trials at the University of Nebraska tend to support the *in vitro* amino acid analyses. Weight gains of mice fed wheat that averaged 17.5% protein were substantially higher than gains from lower protein wheats (Table VIII). The difference in mean weight gains was reflected in better feed efficiency ratios for the high protein wheats.

Breeding Progress. In 1970, 26 high protein winter wheat lines derived from Atlas 66 crosses were released for public use as high protein germplasm in breeding programs. All of the lines were from the first breeding cycle for high protein.

Advanced high protein lines from the second breeding cycle are being evaluated in Nebraska and regional trials as potential new varieties in which high grain protein content has been combined with excellent productivity. Some of these lines also are being evaluated in Turkey, Iran, and Afghanistan for possible use as commercial varieties.

Promising F_2 progeny bulks from crosses of Nap Hal (high protein and high lysine) with Atlas 66 (high protein) have been identified. Some appear to have not only grain protein content that is higher than that of either parent variety but also the lysine level of Nap Hal. These progeny bulks should be useful as parental materials in breeding for improved nutritional value in wheat.

Rice. Rice is the main source of protein and calories for Asians. It is nearly 80% of their total calories. Brown rice has approximately 8% protein. Together, starch and protein are 98.5% of the constituents of milled rice. At 12% moisture, milled rice will average 80% starch and 7% protein. Rice protein is nutritionally better than that of most other food cereals.

Protein Variation. Variation in protein content of milled rice ranges from 5 to 14%. Environment can cause as much as 6 percentage points of protein variation in the grain of a rice variety (Juliano, 1972).

Table IX. Average Yield and Protein Content of Two High Protein Lines and IR8 in Five Trials at the International Rice Research Institute in 1971^a

| | Mean yield of brown | Mean protei | n content, % |
|-----------------------------|------------------------|----------------|----------------|
| Line | rice, ton/ha | Brown rice | Milled rice |
| IR8 | 5.0 | 7.3 | 6.8 |
| IR160-27-3 | 4.8 | 8.6 | 8.1 |
| IR480-5-9 | 4.6 | 9.0 | 8.6 |
| ^a Source: Intern | ational Rice Re | search Institu | ıte, 1972. |

Changes in the protein content of a rice variety involve mainly changes in the percentage of glutelin and prolamin. The difference in grain protein content between brown rice and milled rice tends to decrease as protein content increases. The polished fraction of high protein rice has been found to contain more protein than bran from the same sample. The protein content of milled rice and that of its outer layer are positively correlated.

The rice collection maintained by the International Rice Research Institute was screened for protein content. Protein ranged from 5 to 17% among 7760 varieties. The mean was 10.6% (Beachell *et al.*, 1972).

Rice protein is unique among the cereals in that it is comprised mainly of glutelin. It averages over 80% glutelin and less than 5% prolamin, 5% albumin, and 10% globulin (Juliano, 1972).

Amino Acid Composition. The excellent nutritional value of rice protein is associated with its very high glutelin content (Table III). Protein increases tend to increase the proportion of prolamin in relation to glutelin. As in wheat, high protein in rice results in lower levels of some amino acids, particularly lysine, than are found in lower protein rice. The increase in the prolamin fraction, which is very low in lysine, accounts for this.

The decrease in lysine content with increased level of protein is less than proportional to the increase in protein. The result is that high protein rice will provide more lysine and other essential amino acids per unit weight of grain than lower protein rice will provide. The negative relationship between protein and lysine disappears above 10% (International Rice Research Institute, 1972).

The amino acid composition of rice is compared with that of other cereals and selected food legumes in Table IV. It clearly has better amino acid balance than the other major food cereals although its protein content is the lowest among the cereals.

The high lysine mutant in maize identified by Nelson, Mertz, and Bates in 1963 and in barley by Munck and associates in 1970 involves a decrease in prolamin and increases in albumin and nonprotein nitrogen. The endosperm protein of rice normally contains as much lysine (3.5-4.0%) as the endosperm of opaque-2 maize. Because rice protein is mainly glutelin instead of prolamin and glutelin, high lysine mutants similar to those in maize and barley will not likely be found in rice.

Protein Quality. Protein efficiency ratios (PER's) were determined for diets composed of 90% rice. Milled rice samples containing 5.7, 7.3, 9.7, and 14.3% protein were used in the diets. PER's were identical for the first three protein levels and only slightly lower for the 14.3% protein sample. Protein content rather than protein quality was the major influence on nutritional value of the milled rice (Juliano, 1972).

The major nutritional problem with rice is its low protein content, particularly in the milled grain. To date the effort to improve its nutritional quality has been mainly to increase protein content without adversely affecting protein quality. The International Rice Research Institute (IRRI) has set as a breeding goal an increase in protein content of 2 percentage points over the variety IR8 without a reduction in the high yield of IR8. Breeding Progress. Six varieties from 7760 in the IRRI collection were used for breeding on the basis of their high protein content through four crop seasons (Beachell *et al.*, 1972). None had commercial value in the Phillipines. Progenies from crosses with IR8 had been advanced through the F_8 generation by 1971. Lines were recovered in which higher than normal protein was combined with improved plant type and productivity (Table IX).

Six lines in the F_9 generation exceeded IR8 in protein content by 1.7 to 4.4 percentage points or by 22.7 to 58.7%. Their average yield was only 77% of IR8. However, four of the lines produced an average rough rice yield nearly equal to that of IR8 and they averaged 3.1 percentage points higher in grain protein content.

High and low protein lines from six crosses were analyzed for amino acid composition of their protein. Lysine and tryptophan decreased as protein content increased. Genetically induced protein differences produced the same shifts in amino acid composition as environmentally induced differences. Substantial variation in lysine content was detected among lines of comparable protein content. It was concluded that, from crosses involving parents of normal lysine content, high protein lines with normal levels of lysine could be found.

Cooked milled rice of high protein lines was subjected to taste-panel evaluation at the University of the Philippines. Color scores did not differ significantly among lines from the same cross in which the protein content differed by as much as 4 percentage points.

Beachell and others have suggested that an increase in protein content of 25% in rice without reduction in grain yield is possible. Studies in the United States in which heritability of protein content between F_2 plants and F_3 lines was low have shown that protein content in rice is not simply inherited (Beachell *et al.*, 1972).

An induced mutant in rice was reported by Tanaka and Tamura in 1968 to be higher than normal in protein content and level of lysine. The high protein potential of the mutant line was verified by IRRI in 1971 (International Rice Research Institute, 1972). Combination of this mutant with the high protein lines selected by IRRI could lead to a significant additional increase in the protein content of rice.

Maize. There has been more research on the nutritional improvement of maize than of the other cereals. The discovery in 1963 of the effect of the opaque-2 gene on amino acid composition of maize protein was the first clear-cut evidence in cereals of the genetic control of protein composition (Mertz *et al.*, 1964). Nutritional implications of the discovery became fully apparent at a high lysine corn conference held in 1966 (Proceedings of the High Lysine Corn Conference, 1966). The discovery provided immediate impetus for search in other cereals for genetically controlled amino acid variation that would enhance nutritional value.

Kernel Composition and Texture. Maize protein is comprised largely of zein, which is so low in the essential amino acids lysine and tryptophan that it will not support normal growth of young nonruminant animals. The opaque-2 gene significantly increases the proportion of the glutelin protein fraction that is rich in lysine and tryptophan. Feeding experiments with undernourished children in which opaque-2 maize was the source of protein indicated the biological value of opaque-2 protein to approach that of skim milk.

The initial opaque-2 and floury-2, high lysine-high tryptophan maize had soft textured low density kernel endosperm and below normal productivity. Most maize researchers attributed the low productivity in part to low test weight grain resulting from the low density endosperm. Because the same agronomic requirements—high yield, resistance to pests, and acceptable seed—apply to high lysine-high tryptophan maize as they do to ordinary maize, breeders immediately undertook to modify the texture of opaque-2 and improve productivity.

Genetic modifiers that significantly improve the texture of opaque-2 grain have been identified. In a few modified opaque-2 lines, high lysine and high tryptophan apparently have been combined with vitreous endosperm although there is evidence to suggest that texture modification usually results in decreases in lysine and tryptophan. A few of the lines approach normal corn in productivity.

Protein Content. Maize commonly produces grain that contains less than 10% protein. Increased protein content in combination with high lysine and high tryptophan would provide significant additional potential improvement in the biological value of maize. Opaque-2 tends to be equal to or higher than ordinary maize in the protein content of its whole grain (Report on Maize and Wheat Improvement, 1972). However, much less of its total protein appears to reside on the endosperm (Table X). The endosperm of opaque-2 maize contained substantially lower protein content than normal maize although, on a whole-grain basis, their protein contents were similar. Associated with the lower protein content of the endosperm of opaque-2 is a very high tryptophan level (more than double that of normal maize endosperm).

Modified opaque-2 kernels in which protein content was substantially higher than in their opaque-2 counterparts on the same ear were analyzed (Table XI). The higher protein was associated with a decrease in level of tryptophan. This suggests possible difficulties in combining high protein content with high tryptophan level in maize.

Recently, the high protein content of South American Coroico maize was determined to be associated in part with multiple layers of aleurone cells (Wolf *et al.*, 1972). Normal maize aleurone has only a single layer of aleurone cells. Aleurone tissue is substantially higher in protein than endosperm tissue (22 vs. 7%). Both the aleurone and endosperm tissues of the Coroico maize also were found to be substantially higher in protein content than the yellow dent maize. Lysine percentage of total protein was similar in the Coroico and yellow dent. The multiple aleurone of Coroico appears to be transmitted as a partially dominant genetic trait. It may be useful for additional genetic improvement of maize nutritional quality.

Protein Quality. The whole grain endosperm differences in protein level in opaque-2 maize probably do not have the serious nutritional implications that they would have in cereals like wheat or rice in which the endosperm is the main component of the milled grain used as food. In contrast, the whole grain of maize is commonly used as food or feed.

High lysine maize does not always have the same nutritive value when assayed by animal feeding tests (International Review of Action to Improve World Protein Nutrition, 1972). This difference in values is believed to be associated with differences in lysine availability that *in vitro* amino acid assays do not detect. Digestibility differences probably are involved.

Rapid *in vitro* tests are needed that will reflect more precisely the results of biological test methods. To be most useful, such tests should accommodate large numbers of breeding materials. Also, as breeders combine high lysine-high tryptophan traits with vitreous endosperm, they no longer will be able to rely upon visual identification of the high lysine kernels. Laboratory analyses of amino acid composition will be necessary.

A decade of research at several experiment stations in the United States, Mexico, and South America has amply established the nutritional superiority of high lysine-high tryptophan maize as food and feed. In these countries, this type of maize still occupied only a small part of the maize acreage in 1972. Until its performance in the field is equal to that of normal maize, high lysine maize cannot be expected to increase dramatically in acreage.

| Table X. Comparison of Protein and Tryptophan |
|---|
| Levels in the Whole Grain and Endosperm of Normal |
| and Opaque-2 Maize ^a |

| | Protein, % | | Trp in protein, % | |
|--------------------|----------------|----------------|-------------------|----------------|
| Group | Whole grain | Endo- sperm | Whole grain | Endo- sperm |
| Low protein maize | | | | |
| Normal | 8.9 | 7.7 | 0.67 | 0.47 |
| Opaque | 9.2 | 5.9 | 1.10 | 1.15 |
| High protein maize | | | | |
| Normal | 13.3 | 12.2 | 0.60 | 0.39 |
| Opaque | 12.8 | 10.4 | 0.99 | 0.86 |

^a Source: Report on Maize and Wheat Improvement, 1972.

Table XI. Comparison of Percentage of Protein and Percentage of Tryptophan in the Protein of High Lysine Opaque-2 and Modified Opaque-2 Kernels^a

| Ear | Protein, % | | Trp in protein, % | |
|------------|------------|----------|-------------------|----------|
| ident. no. | Opaque | Modified | Opaque | Modified |
| 69 | 9.0 | 9.8 | 0.84 | 0.66 |
| 147 | 8.3 | 9.0 | 1.09 | 0.91 |
| 159 | 6.4 | 7.3 | 0.98 | 0.87 |
| 250 | 9.1 | 12.9 | 0.72 | 0.53 |
| 292 | 11.3 | 11.5 | 0.63 | 0.60 |
| 63 | 9.9 | 9.8 | 0.89 | 0.86 |

 $^{\rm a}$ Source: Report on Maize and Wheat Improvement, 1972.

Sorghum. Many millions of people in Africa and parts of Asia depend upon grain sorghum as their principal energy source. For these people, grain sorghum also is a major source of protein. Sorghum ranks fourth in importance to wheat, rice, and maize as a food cereal. Improvement of productivity and nutritional quality of sorghum is urgently needed in those parts of the world in which it is the main food staple.

Serious research effort to improve the nutritional quality of sorghum dates to 1966 with the establishment of an AID-supported program at Purdue University. Major objectives were to develop sorghum germplasm with higher protein content, improved amino acid balance, and improved digestibility.

Sorghum quality is limited by the low lysine content of its protein. This low lysine content is related to the very high content of lysine-poor prolamin in the endosperm and to the small size of the embryo in relation to grain size. An equally serious nutritional problem is the limited, variable protein availability believed to be associated with unidentified polyphenolic compounds (tannins) in the grain (Axtell, 1972). Scientists have suggested that tannins alter the solubility of the protein, possibly by binding and forming complexes with the protein. Differences in protein availability in varieties ranging from only 30 to approximately 70% have been measured.

Protein Content. The average protein content of 522 lines from the World Sorghum Collection was 12.6% (Axtell, 1972). The standard deviation was 1.89. As with other cereals, high grain protein content in sorghum tends to be associated with low yield. Based upon comparisons with selected commercial hybrids, 20 lines with relatively stable high protein yield have been identified by the Purdue sorghum research team. These are being evaluated in protein yield trials at sites in several countries in which sorghum is an important crop. Sorghums with stable, improved levels of grain protein should be identified from this international network of trials.

Amino Acid Composition. The average lysine content of 522 sorghum lines analyzed at Purdue University was only 2.1%. This is considerably lower than the 2.7% content

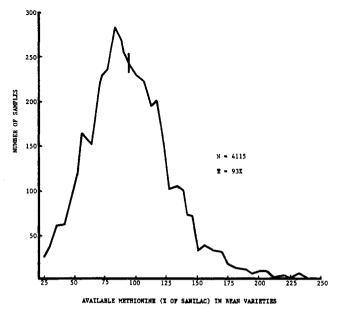


Figure 2. Frequency distribution for available methionine among 4115 common bean varieties (*Phaseolus vulgaris*) from the U. S. Department of Agriculture germplasm collection.

listed in Table IV and is less than one-half the amount required for balance with other essential amino acids based on rat tests. Methionine is the next most deficient amino acid. Leucine in contrast to lysine and methionine is present in large excess of rat requirement.

Highly significant positive correlations between oil content of sorghum seed and the lysine content of its protein have been found. Oil content also was significantly correlated with embryo lysine as well as endosperm lysine. These correlations suggest the possibility of using oil content as a selection indicator of higher lysine in sorghum.

Protein Quality. Wide differences in biological value between sorghum lines with comparable protein and lysine content have been demonstrated. In one group of samples, PER values ranged from 0.18 to 0.90. The basis for differences of such magnitude is not understood but protein nonavailability must be involved (Axtell, 1972).

The level of tannin varies widely among sorghum lines. Low and high tannin lines were compared in rat feeding trials. Results established that lysine is the first limiting amino acid in low tannin sorghum lines. Among the high tannin lines, factors other than level of lysine limited biological value. The regression of rat weight gain on lysine content for the high tannin lines was essentially zero in contrast to a regression coefficient of 0.65 for the low tannin group of lines.

Over 60% of 472 sorghums from the World Collection were classified as low tannin by Purdue researchers, but 80% of 288 sorghums from Cameroon, Africa, were classified as high tannin lines. A relatively simple rapid and apparently reliable chemical assay for tannin content in sorghum has been developed.

Grain sorghum is marginal in the lysine content of its protein. There exists the additional problem of substantial protein nonavailability in the high tannin sorghum lines. This knowledge should aid breeders in their efforts to improve the biological value of sorghum. The high prolamin content of sorghum endosperm parallels that of maize. Existing mutants may reduce prolamin level in sorghum as the opaque-2 gene reduces the level in maize. Normal sorghum seed has very small germ size, which largely accounts for the lower lysine content of sorghum than of normal maize. However, some existing sorghum lines have large germ size and significant improvement in nutritional value of whole sorghum grain should accrue from development of productive large germ lines.

Table XII. Estimates of Heritability for Seed Protein Content of Soybeans

| | • | | |
|-------------------------|---------------------------------------|--|------------------------------|
| Herit- ability, % | No. of environ- ments tested | Test populations | Reference |
| 71–90 | 3 | \mathbf{F}_2 and \mathbf{F}_5 derived lines in \mathbf{F}_6 and \mathbf{F}_7 genera- tions | Byth <i>et al.</i> , 1969 |
| 76–77 | 1 | \mathbf{F}_6 to \mathbf{F}_8 populations after 3 cycles of mass selec- tion for seed size and sp gravity ^a | Fehr and Weber, 1968 |
| 57 | 2 | \mathbf{F}_3 and \mathbf{F}_4 populations | Kwon and Torrie, 1964 |
| 71–92 | 2 | F_4 and F_6 derived lines in F_7 and F_8 genera- tions following 2 cycles of mass selection for sp gravity | Smith and Weber, 1968 |
| 83–96 | 1 | gravity 2-Way and 3-way crosses of adapted and non- adapted selections | Thorne and Fehr, 1970 |

^a High specific gravity in a glycerol-water solution is associated with high seed protein content.

LEGUMES

Legumes have not had the food prestige of staple cereals such as wheat and rice. Although consumed in smaller amounts than the cereals, the legumes' contribution to the total diet is considerable because of their high protein content. Most food legumes contain 20-25% protein, groundnuts contain 27%, and soybeans range from 35 to 40%. Low protein digestibility is a serious nutritional problem in most food legumes.

Contribution of legumes to diets in developing countries is limited by their scarcity. In India, diets comprised of 80% ragi, rice, and maize plus 20% legumes would meet the nutritional needs of growing children and expectant or nursing mothers (Swaminathin and Parpia, 1971). Available legumes in India can provide only 14% of the diet. The use of food legumes in the preparation of balanced protein diets is limited by their generally low levels of the sulfur-bearing amino acids methionine and cystine. Cystine is not an essential amino acid but it can partly replace dietary requirements for methionine.

Research to improve the nutritional quality of food legumes has been seriously neglected. The Protein Advisory Group of the United Nations has urged research on eight major species of food legumes and oilseed legumes for genetic improvement of nutritional factors. These include higher protein, higher methionine and cystine, and improved protein digestibility.

Soybean. Soybean contains the highest protein content of the food legumes. Germplasm in the U. S. Department of Agriculture soybean collection has been analyzed for protein content. When soybeans are grown under adequate nitrogen nutrition, the protein content of their germplasm varies from 36 to 50%, on a moisture-free basis. Commercial soybean varieties in the United States average 40.5% protein (Hartwig, 1969).

Estimates of heritability for seed protein in soybeans before 1962 ranged from 39 to 83%. More recent estimates are summarized in Table XII. Heritability in excess of 90% was reported by several investigators.

High protein soybean varieties tend to be lower yielding than average protein varieties (Hartwig, 1969). However, among crosses of high protein and high yielding varieties, recovery of lines in which high yield and above-normal protein were combined has been reported (Shannon *et al.*, 1972). The development of productive soybean varieties with 15-20% higher seed protein content than currently grown varieties is considered feasible.

| Table XIII. Avail | able Methionine | e Levels in Seed of |
|--------------------|-----------------|--------------------------|
| Phaseolus vulgaris | Selections and | Cultivars Grown |
| under Different E | nvironmental C | $\mathbf{onditions}^{a}$ |

| | Available methionine, % Sanilac | | | |
|-----------------------------|------------------------------------|----------|---------------|--|
| | Rancoca | s, N. J. | J. Green | |
| Variety name or P.I. no. | 1967 or 1968 | 1969 | house 1969 | |
| Bush Blue Lake 274 | 213 | 278 | 232 | |
| P.I. 169880 sel. 1 | 152 | 175 | 147 | |
| P.I. 180750 sel. 5 | 162 | 162 | 177 | |
| P.I. 207206 (U. S. #3) | 152 | 173 | 137 | |
| P.I. 207208 (780 Kentucky) | 158 | 180 | 220 | |
| P.I. 226934 sel. 3 | 196 | 164 | 253 | |
| P.I. 264788 sel. 6 | 221 | 152 | 228 | |
| P.I. 282693 sel. 7 | 162 | 129 | 177 | |
| P.I. 302542 sel. 5 | 198 | 208 | 212 | |
| P.I. 302542 sel. 6 | 236 | 188 | 185 | |
| P.I. 302542 sel. 8 | 187 | 223 | 176 | |
| P.I. 302542 sel. 9 | 187 | 180 | 171 | |

^a Source: Kelly, 1971.

The relationship of protein content of soybeans to methionine level has been studied (Krober and Cartler, 1966). Four experiments involving a wide range of protein content and environmental conditions provided no evidence of a significant decrease in methionine with increase in protein content. Development of higher protein soybean varieties with protein quality equal to that of lower protein varieties appears to be possible.

Common Bean. Common bean, *Phaseolus vulgaris*, is an important food legume. Based on a study of F_2 populations from crosses among five lines differing in seed protein content, the protein content of the seed is a heritable trait (Leleji *et al.*, 1972a). Although high protein segregates tended to be low yielding, F_2 and F_3 plants with high seed yield and above-average protein content were identified.

Bean varieties contained in the germplasm collection maintained by the U. S. Department of Agriculture have been assayed for available methionine (Kelly *et al.*, 1970). A microbiological assay involving *Streptococcus zymogenes* was used. The results from analysis of 4115 lines appear in Figure 2.

Data are expressed as percentage of the navy bean variety "Sanilac." Values ranged from 20 to 243% of Sanilac. The magnitude of environmental influence on methionine values is not known because not all of the seed samples were produced in the same environment.

Single plant selections were made from promising lines based on results from the initial assay. They were grown in different environments from 1967 to 1969 and reanalyzed for available methionine (Kelly, 1971). Methionine values for a few of the more promising lines appear in Table XIII. Some exhibited greater stability for high methionine than others. "Blue Bush Lake 274" was consistently high in available methionine. These data suggest genetic differences for methionine, which may be used for the nutritional improvement of this important food legume.

Only preliminary data are available on the inheritance of available methionine content in *Phaseolus vulgaris* (Leleji *et al.*, 1972b). Methionine determinations were made on greenhouse-grown F_1 , F_2 , and parental single seeds. The methionine content of F_1 hybrid seed was controlled by the maternal parent. Mean values of F_1 and F_2 seed indicated partial dominance of low available methionine.

Mung Bean. There has been only limited nutritional study of this legume. Protein, lysine, and methionine contents of 321 strains were measured from seed production at Columbia, Mo. in 1970 (Yohe and Poehlman, 1972). Wide variability was recorded for percentage of protein, percentage of lysine in total protein, and percentage of methionine in total protein. Three strains with combined high protein and high lysine and one strain with combined high protein and high methionine were identified. Two strains had a favorable combination of high lysine and high methionine. No strains were found in which high protein was combined with both high lysine and high methionine.

Peas. Some protein research has been conducted on this legume at Michigan State University (Salinder *et al.*, 1971). Bioassays involving weanling rats as the test animal were performed on 28 lines. Values ranging from only 18 to as much as 78% of casein were reported. The wide variation indicates possibility for nutritional improvement. Results of rat bioassays of peas were correlated with albumin content (Bajaj *et al.*, 1971). The level of albumin may be a useful nutritional quality indicator in pea breeding programs.

TUBER AND ROOT CROPS

White Potato. The white potato probably offers the best protein potential among species in tuber and root crops. It is a basic food in Central and Eastern Europe. Although considered a carbohydrate source, the white potato also ranks very high in protein production (Table I).

In its fresh state potato contains on the average 2% protein. On a dry weight basis, its protein content is similar to that of wheat. Potato protein has a biological value comparable with that of soybean. The white potato could make a significant contribution to world nutrition if its protein-carbohydrate ratio could be shifted toward more protein. There has been minimal research effort on potato protein to date.

Seventy-three seedling samples grown in Maine and ten selections grown in Idaho were analyzed for protein and nonprotein nitrogen. The total nitrogen ranged from 0.30 to 0.56%. The variety "Lenape" (B5141-6) was common to both locations. The nitrogen contents of Idaho and Maine grown seedlings were 0.56 and 0.43%, respectively. The data suggest possible genetic variation for total nitrogen content (Fitzpatrick *et al.*, 1969). Ploidy level and growing location have been shown to exert measurable influence on levels of total and soluble protein (Desborough and Weiser, 1972).

The progeny of ten potato crosses were analyzed for total tuber nitrogen content during a 2-year period at one location (Sanford *et al.*, 1971). Nitrogen heritability values ranged from 10 to 34% depending on the method of estimation. There was evidence of usable genetic variation for tuber nitrogen content suggesting the potential for breeding potato varieties with higher protein content.

Methionine is the first limiting amino acid in white potato protein. A bioassay for methionine using *Streptococcus zymogenes* has been developed (Luescher, 1971). Onehundred eighty clones were assayed. Evidence of genetic variation for methionine was obtained.

Potato tubers are able to provide adults their full nitrogen requirements. A man and a woman were maintained in good health for 167 days on a daily consumption of 1680 and 1120 g of potatoes, respectively, an amount sufficient for nitrogen equilibrium (Kon and Klein, 1928). With increased protein content the potato could provide significant protein intake at reduced consumption levels.

OUTLOOK

Genetic improvement in protein quantity or quality or both is possible in food crops. Substantial progress has already been made in the food cereals that tend to be low in protein content and in certain amino acids, particularly lysine. Genes with significant effect on lysine and tryptophan have been identified and are being used to improve the nutritional value of maize and barley.

A decade of research in the United States, Mexico, and South America has amply established the nutritional su-

periority of high lysine-high tryptophan maize as food or feed. In these countries, this type of maize still occupied only a small part of the maize acreage in 1972. Until its performance in the field is equal to that of normal maize, high lysine maize cannot be expected to increase dramatically in acreage.

Genes for high protein and modest increase in lysine are being used widely in wheat. Until they can be introduced by breeders into varieties that possess the host of agronomic and processing quality traits demanded in commercial varieties they will not make an impact on commercial wheat production in the United States. The Nebraska Experiment Station is currently increasing a high protein hard winter wheat variety for possible release to commercial wheat producers in 1974 or 1975. The high protein trait has been combined with acceptable productivity, and agronomic traits, good disease resistance, and acceptable processing quality in the variety.

Progress in increasing the protein content of rice already has been substantial. Genetic variation to increase the protein content of rice by as much as 20% apparently exists among rice cultivars.

Limited research has provided evidence that food legumes and the white potato also are amenable to nutritional improvement by genetic means. As a group, the food legumes are characterized by high protein content and deficiency in methionine. They are usually consumed with and complement the cereals in protein quantity and quality. Genetic variation in both protein content and methionine level has been detected. The need to improve the productivity of the legumes and the digestibility of their protein is as great as that for amino acid modification.

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