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The effect of individual rye chromosomes on the amino acid content of wheat grains

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SUMMARY

At the present time attempts are being made to improve the nutritional value of wheat by increasing the content of certain essential amino acids, particularly lysine, in the proteins of the grain. Rye grain has a considerably higher lysine content than that of wheat. Consequently in the present work studies were made of the amino acid contents of the grains of the wheat variety Holdfast, the rye variety King II, the *Triticale* derived from these parental varieties and the seven lines in which, in turn, each pair of chromosomes of King II are separately added to Holdfast.

Rye chromosome I increased the lysine content of wheat by 8·7 % and associated changes in the proportions of other amino acids suggest that this increase is meaningful. Rye chromosome I is in homoeologous group 5 and other reports have indicated a relationship between changed lysine content and another character determined by chromosomes of this group. Consequently there is a suggestion that group 5 chromosomes may be of particular significance in the determination of lysine content in wheat grains. Confirmation of this would lead to a more rational approach to breeding for higher lysine content.

1. INTRODUCTION

The nutritional value of the grain of many cereal species, including the primary crops wheat, rice, barley and maize, is limited because of relative deficiencies of certain essential amino acids. Until recently it was thought that no opportunity existed for improvement because no variation has been observed in the amino acid composition of grain of different genotypes. The position changed dramatically with the recognition by Mertz, Bates & Nelson (1964) that the homozygous *opaque 2* mutant of maize had about twice the lysine content of normal maize. Subsequently a second mutant, *floury 2*, which had been described by Emerson, Beadle & Fraser (1935) at the same time as *opaque 2*, was shown to result in a similar increase in the production of lysine in protein of the grain (Nelson, Mertz & Bates, 1965). The significance of the changed protein composition of *opaque 2*

maize was revealed by feeding trials which showed a 3·5 fold increase in the weight gain of weanling rats fed on *opaque 2* compared with normal maize (Mertz, Veron, Bates & Nelson, 1965). Similar nutritional advantages of *opaque 2* maize have been shown in tests with children (Bressani, 1966) and with pigs (Pickett, 1966).

These results have stimulated the search in temperate cereal species for genetic variants in which the proportions of amino acids are changed and in particular for any with an increased lysine content. There are already reports of the recognition of a form of barley with an unusually high lysine content (Hagberg & Karlsson, 1969).

Naturally there has been considerable interest in the possibility of modifying the amino acid content of wheat grain. About 1000 million people, or nearly one-third of the population of the world, rely on wheat as their principal food, so improvement of its nutritional characteristics is of fundamental significance. The protein of the wheat grain is unbalanced for the purposes of human nutrition due to deficiencies of the three amino acids lysine, methionine and threonine, which are probably limiting in that order. Currently considerable effort is being given to the search for high-lysine variants. For example, in an examination of the grain of 4100 varieties, lysine ranged from 1·77 to 4·15 % of the total protein with a mean of 3·03 % but only five varieties exceeded 3·80 % (Johnson, Whited, Mattern & Schmidt, 1968). From these results it appears that there is some limited genetic variability in lysine content of wheat upon which selection could be practised for nutritional improvement.

However, in a survey of a range of species of wheat and rye, Villegas, McDonald & Gilles (1968) reported that in general the grain protein of rye showed higher levels of lysine than that of wheat. In this work, while bread wheat had from 2·15 to 3·55 % lysine, rye had from 2·42 to 4·26 %. Obviously, the possibility of improving the amino acid balance of wheat by the use of genetic variation from rye must be considered.

Lines have been developed in which each pair of rye chromosomes is separately added to the normal complement of wheat chromosomes (Riley & Chapman, 1958; Riley, 1960; Riley & Kimber, 1966). These rye chromosome addition lines make possible the allocation of genetic activities of rye to specific chromosome pairs, and clearly they are of some interest in the investigation of the genetics of the amino acid composition of the wheat-rye group. They may indicate the nature of the determination in rye of its distinctive amino acid composition and they may also show whether the nutritionally advantageous properties of rye grain protein can be readily transferred to wheat. This paper therefore describes the effects of individual rye chromosomes on the amino acid content of wheat grain, and the effects of rye chromosomes on the proteins present in the grain are also discussed.

2. MATERIALS

The construction of the wheat-rye chromosome addition lines studied in this work has been described by Riley & Chapman (1958), Riley (1960) and by Riley & Kimber (1966) and some of the genetic effects have been described by Riley & Macer (1966). The wheat parent used throughout was *Triticum aestivum* ssp. *vulgare* ($2n = 6x = 42$) variety Holdfast and the rye variety was *Secale cereale* ($2n = 14$) variety King II. The chromosome addition lines were constructed by simple backcross procedures using *Triticum aestivum* var. Holdfast as the recurrent parent. In the addition lines the genotype of Holdfast was reconstituted and to it was added, separately and in turn, each of the seven pairs of chromosomes of *Secale cereale* var. King II.

Roman numerals were originally assigned by Riley & Chapman (1958) to the rye chromosomes transferred to wheat in this way, and the same designations will be used in the present work. Thus the 44-chromosome addition lines I–VII will be discussed and these are represented by plants having 21 pairs of Holdfast chromosomes and the pair of rye chromosomes I–VII. These lines have been compared with the wheat and rye parental varieties and with the 56-chromosome amphiploid combining the full chromosome complements of the parents. The latter will here be referred to as *Triticale*.

3. METHODS

Cytological and cultural

All the plants used in this work were grown from seeds harvested, following self-pollination, from meiotically verified parents. They were also checked as seedlings, by root-tip squashes, to determine that they had the appropriate chromosome number and structure. As seedlings and juvenile plants they were planted out as adjacent spaced plants in nursery beds at Cambridge. The grains harvested and examined chemically came from heads that were bagged to ensure self-pollination.

Amino acid analysis

Whole grains (2g) were refluxed for 24–28 h with 500 ml of constant boiling hydrochloric acid. After cooling, the liquor was diluted to 1 l., centrifuged and a portion rotary-evaporated to dryness under reduced pressure with the aid of hot water ($< 50°$). The residue was taken up in the appropriate volume of 0·1 N-HCl, 0·1 mM in norleucine, and 1 ml portions applied to a Technicon amino acid analyser. Methionine values included methionine sulphoxide.

Starch-gel electrophoresis

This was carried out with 0·008 M aluminium lactate buffer at pH 3·3 as described previously (Ewart, 1966) except that water cooling was used. The 'Perspex' trough was modified so that tap water could be circulated below the gel platform and also through a 'Melinex'-insulated copper vessel lying on top of the gel. This was

merely an adaptation of the apparatus of Graham (1963) and enabled voltage gradients of 15–18 V cm^{-1} to be used for runs of 4 h (gliadins) or 2 h (albumins).

In the study of gladins, a tablet press and hammer were used to crush batches of 16 seeds, which were magnetically stirred for 1 h in 10 ml centrifuge tubes with 2 ml of 70% (w/w) ethanol. After centrifuging for 10 min the supernatant liquid was evaporated to dryness in a P_2O_5 desiccator overnight. This gave enough material to run in several channels of a starch gel when taken up in ~ 0·6 ml of aluminium lactate buffer.

In the study of albumins, crushed seeds (2 or 3) were magnetically stirred in ignition tubes with 0·2 ml albumin lactate buffer for 1 h and the liquor after brief settling used to load one gel channel.

4. RESULTS OF AMINO ACID DETERMINATIONS

Amino acid contents of the grains were calculated as the mean of two runs on the analyser. In the case of the wheat parent two hydrolyses were made to give four runs on the analyser.

The analyses are set out in Table 1. Figures beyond the first two are not significant and are added to avoid computational errors.

The proportions of amino acids are expressed in g per 100 g of recovered anhydro amino acids, which approximates to 100 g of protein except that tryptophan has not been determined. This method of expressing results seems more logical than using 16 g nitrogen as a basis, but the results can be converted to this basis by multiplying each column by the product of 0·00912 and the corresponding value of the recovery in the last line of Table 1.

No attempts were made to correct for destruction or for slow liberation of amino acids since it was only intended to look for differences, particularly in the lysine content.

In Fig. 1 amino acid contents for wheat and rye in this work are compared with determinations by other workers, the results being expressed in grams of amino acid obtained for 16 g of nitrogen in the sample before hydrolysis, in order to save recalculation of literature data. The scatter is wide partly because of differences in recovery. This demonstrates the need to eliminate this variable when making comparisons.

The errors in these analyses are such that it is unwise to consider that there is a real difference between genotypes in the proportion of an amino acid, unless it exceeds 7%. Some comments on procedure are necessary before the results contained in Table 1 are discussed.

Hydrolysis of whole seeds

The quantities of the grain available for the present work were too small to be milled mechanically without the danger of a preferential loss of endosperm or bran. Consequently the whole seeds were hydrolysed, although it is generally recognized that better results are obtained when the seeds are finely ground. In

Table 1. *Amino acid contents of the grains of wheat, rye,* Triticale *and the seven addition lines with single pairs of rye chromosomes added to wheat (g per 100 g of recovered anhydro amino acids)*

		Addition lines								
Amino acid	Wheat	I	II	III	IV	V	VI	VII	*Triticale*	Rye
Aspartic	6·06	6·13	5·74	5·54	6·18	5·83	6·47	6·11	5·81	7·45
Threonine	3·66	3·59	3·34	3·56	3·58	3·83	3·40	3·28	3·62	4·06
Serine	5·66	5·51	5·40	5·54	5·54	5·55	5·54	5·53	5·46	5·50
Glutamic	37·15	35·47	36·94	38·90	34·93	37·49	36·94	37·53	36·97	32·63
Proline	12·94	13·62	14·12	13·04	13·31	13·00	14·47	13·14	14·03	13·65
Glycine	4·89	4·86	4·60	4·58	5·11	5·19	4·70	4·90	4·71	4·97
Alanine	4·27	4·19	3·97	4·04	4·28	4·05	4·27	4·05	4·11	4·87
Valine	5·29	5·31	5·14	5·12	5·35	5·06	5·22	5·15	5·11	5·73
Cystine	1·78	1·97	1·80	1·84	1·81	1·94	1·89	1·80	1·80	1·83
Methionine	1·71	1·82	1·66	1·82	1·71	1·67	1·74	1·60	1·68	1·85
Isoleucine	4·43	4·44	4·50	4·32	4·43	4·30	4·30	4·39	4·32	4·44
Leucine	8.30	8·44	8·17	8·00	8·33	8·01	8·13	8·36	7·99	7·75
Tyrosine	2·55	2·67	2·98	2·70	3·00	2·58	2·56	2.72	2·49	2·06
Phenylalanine	6·09	5·97	6·44	5·85	6·19	5·79	5·82	6·11	6·12	6·27
Lysine	3·23	3·51	3·17	3·17	3·42	3·41	3·17	3·21	3·22	4·24
Histidine	2·83	3·03	2·80	2·83	3·05	2·71	2·66	2·83	2·88	2·70
Arginine	5·37	5·69	5·34	5·32	6·00	5·76	4·94	5·43	5·80	6·30
Total	116·21	116·22	116·11	116·17	116·22	116·17	116·22	116·14	116·12	116·30
Protein (%)	15·4	16·7	19·9	16·4	19·7	15·5	18·2	19·0	17·3	18·2
$N \times 5{\cdot}7$ Recovery (%)	87·1	84·1	82·9	91·4	82·3	89·2	84·8	81·5	83·6	86·3

order to ascertain the error resulting from the use of whole grains, separate samples of *Triticale* and wheat grains were ground before hydrolysis. This comparison showed that use of whole seeds caused significant losses in both wheat and *Triticale* of tyrosine, arginine, cystine and methionine. In Table 1 all the results are determined on hydrolysates of whole grains in order not to invalidate the comparison.

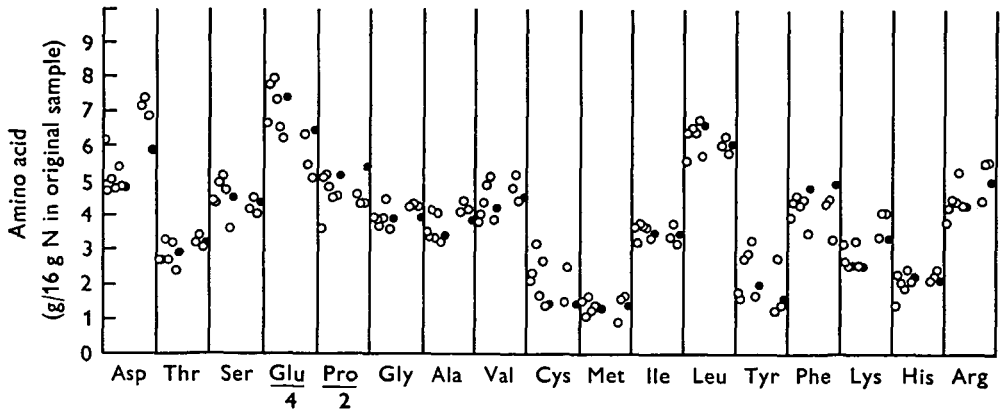

Fig. 1. Comparisons of present determinations of the amino acid contents in the grains of Hodfast wheat and King II rye with other determinations on the same species. Contents are expressed as g of amino acid per 16 g Nitrogen in the sample before analysis. For each amino acid the results are plotted in the following order from left to right: Wheats—(i) Bandemer & Evans (1963); (ii) Shoup, Pomeranz & Deyoe (1966); (iii) Bendicenti, Bogliolo, Montenero & Spadoni (1957); (iv) Hepburn & Bradley (1965); (v) Busson, Fauconneau, Pion & Montreuil (1966); (vi) Janicki & Kowalczyk (1964); (vii) Holdfast, present work. Ryes—(viii) Kihlberg & Ericson (1964); (ix) Busson *et al.* (1966); (x) Janicki & Kowalczyk (1964); (xi) King II, present work.

Humin

A large quantity of humin was found during hydrolysis, much of it in the form of black flakes resembling the seed coats. After the first wheat hydrolysis the humin was recovered and subjected to nitrogen determination and to further hydrolysis and amino acid analysis. This analysis showed that 3·2 % of the original nitrogen was in the humin but only ~ 5 % of this was recovered as amino acids. It was interesting that the humin, compared with whole wheat, was found to contain less glutamic acid and proline, and more cystine, methionine and basic amino acids. Bran proteins are known to have electrophoretic mobilities similar to those wheat albumins (Elton & Ewart, 1964) and it is known from unpublished work in these laboratories that the amino acid composition of a purified major component of wheat albumin compared with that of whole wheat also shows similar differences. This suggests either that some bran proteins are less accessible or are less easily hydrolysed than endosperm proteins, or that both these differences occur.

Recovery

Recovery was calculated as the percentage weight ratio of recovered anhydro amino acids to the protein ($N \times 5{\cdot}7$) taken for hydrolysis. Since amide and tryptophan contents were not determined the nitrogen recovery could not be calculated. The total weight of recovered anhydro amino acids is a good approximation to the quantity of protein. An error of less than 0·5 % is involved in a full analysis; this is because the amidation of glutamic and aspartic acids lowers their residue weight by under 1 %, and because of the neglect of one molecule of water for each polypeptide chain. As tryptophan was not determined the recoveries are underestimated.

5. INHERITANCE OF AMINO ACID CONTENT

In general the present observations on the amino acid content of *Triticale* seeds conform with the trend of previous work in that *Triticale* usually falls intermediate to wheat and rye (Fox & De Fontaine, 1956; Hall, 1959; Yong & Unrau, 1966; Villegas, McDonald & Gilles, 1968). Aspartic acid, threonine, serine, glutamic acid, proline, alanine, methionine and tyrosine, all fall outside the parental range, but in no case does the amino acid composition of *Triticale* differ from the nearer parent by more than 4·1 %. However, it may be noted that the addition of the entire rye genome to wheat raises the content of proline by 8·4 % and that of arginine by 8 % relative to wheat. Consequently, significant modifications of the amino acid composition of the seed proteins of wheat can be achieved by the incorporation of the rye genome.

The expression of rye is never epistatic to that of wheat in the amino acid content of the *Triticale*. By contrast wheat is epistatic to rye in its effect on the content of threonine, glutamic acid, proline, alanine, valine and lysine. However, marked activities of individual rye chromosomes may be reversed and concealed by additive or interactive effects of other members of the rye complement. Consequently it is worth considering the contribution of individual rye chromosomes.

Among the addition lines with single pairs of rye chromosomes added to wheat there are a few modifications of amino acid proportions, relative to wheat, that may be meaningful. For example, rye chromosome I increases cystine and lysine by 10·7 and 8·7 % respectively, while chromosome II increases proline by 9·1%. Chromosome II reduces aspartic acid by 8·6 %, while chromosome IV increases and VI reduces arginine by 11·7 and 8 %, respectively. Chromosome VI also increases proline by 11·8 % while chromosome VII reduces threonine by 10·4 %.

The nutritional value of wheat grain is limited by relative deficiencies of the essential amino acids lysine, methionine and threonine, so that only two of the modifications recognized are of practical significance. The addition of chromosome VII, which reduces the content of threonine, is counterproductive. By contrast the suggestion that chromosome I increases lysine content may indicate a change of potential significance. In spite of the destruction of cystine that occurs on hydrolysis, particularly in the presence of carbohydrates, it also seems likely that chro-

mosome I causes an increase in cystine content. Chromosome I may, in addition, increase arginine and reduce glutamic acid. Cereal seed proteins that are rich in lysine —the albumins and globulins— are usually rich in cystine (Matsumoto & Hlynka, 1959) and arginine and low in glutamic acid. In view of the associated modification of amino acid content in the chromosome I addition line it seems likely that this chromosome effects a genuine improvement in lysine content, possibly by changing the albumins and globulins. It may be noted that a similar pattern of changes accompanies higher lysine in *opaque 2* and *floury 2* maize.

Table 2. *The effects on the amino acid content of the grains of the addition to wheat of the entire chromosome complement of rye and the sum of the effects of each pair of rye chromosomes in turn*

Amino acid	Entire rye genome (*Triticale* – wheat)	Sum of effects of individual rye chromosomes (Addn. line – wheat)
Aspartic	– 0·25	– 0·42
Threonine	– 0·04	– 1·04
Serine	– 0·20	– 1·01
Glutamic	– 0·18	– 1·85
Proline	1·09	4·12
Glycine	– 0·18	– 0·81
Alanine	– 0·16	– 1·04
Valine	– 0·18	– 0·68
Cystine	0·02	0·59
Methionine	– 0·03	0·05
Isoleucine	– 0·11	– 0·33
Leucine	– 0·31	– 0·66
Tyrosine	– 0·06	1·36
Phenylalanine	0·03	– 0·56
Lysine	– 0 01	0·45
Histidine	0·05	0·10
Arginine	0·43	0·89

In the survey of 4100 wheat genotypes carried out by Johnson, Whited, Mattern & Schmidt (1968), eight of the ten varieties with the highest lysine content also had winter habit. Of course this might merely indicate close phylogenetic relationships, but it may also suggest a genetic association between the determination of high lysine in the grain and of winter habit. The latter possibility is suggested by the increse of lysine content apparently caused by the presence of rye chromosome I in the present work. Rye chromosome I is in homoeologous group 5 (Sears, 1968) and the winter/spring habit difference is also primarily determined in wheat by the chromosomes of group 5 (Tsunewaki, 1968). From this emerges a hint that homoeologous group 5 chromosomes may be of particular significance in the control of lysine content in the grain. Consequently wheat breeders concerned with the nutritional value of the grain should give especial attention to variants in which these chromosomes are changed, for example, in intervarietal chromosome substitution lines. It would also seem appropriate to examine the

group 5 tetrasomics. These proposals, which are the first to have been put forward concerning the inheritance of lysine content in wheat, may indicate the way to a more rational approach to breeding for the improvement of this character.

Using the present data it is also possible crudely to assess whether the effect of the rye genome on the amino acid content of *Triticale* simply derives from the additive effects of individual chromosome pairs, or whether interchromosomal interactions are involved. For any amino acid, the difference *Triticale*-minus-wheat should be approximately the same as the sum of the differences of all seven addition lines from wheat, if the effects of the individual chromosomes are merely additive. By contrast a deviation between these values will indicate chromosomal interaction in the *Triticale*.

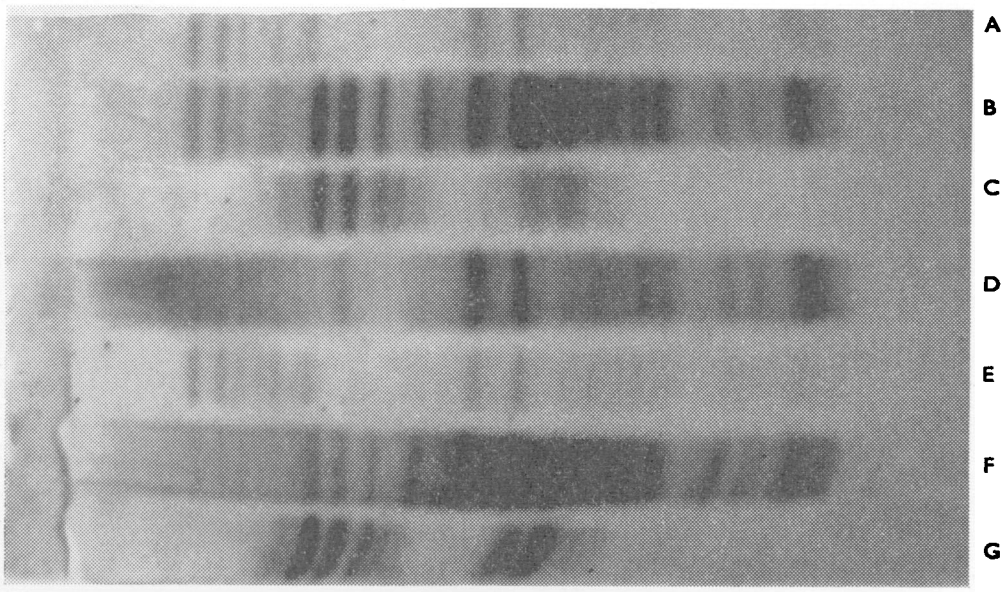

Fig. 2. Starch-gel electrophoresis of gliadin proteins A, Holdfast wheat, B, *Triticale*, C, King II rye; D, chromosome IV addition line, E, Holdfast wheat; F, chromosome V addition line, G, King II rye.

A comparison of the values has been made in Table 2, from which it appears that the contents in the *Triticale* of threonine, serine, glutamic acid, alanine, proline and tyrosine may be influenced by interchromosomal interaction. For the remaining amino acids there is no strong evidence that the contents of the *Triticale* grains cannot be accounted for by simple additivity.

6. STARCH-GEL ELECTROPHORESIS

The starch-gel electrophoretic patterns of cereal gliadins and albumins were complex. The gliadin pattern of King II (Fig. 2) can be divided into two groups of bands, of which the faster appears to coincide in mobility though not intensity

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with corresponding bands in Holdfast. The slower group of bands also appears in the *Triticale* and in the V addition, although its intensity distribution is somewhat altered. Chromosome IV seems to possess a definite strong band lying between the strongest pair of rye bands in the slower group. No change in gliadin pattern from that of Holdfast could be unequivocally ascribed to any other chromosomes. Yong & Unrau (1964) observed certain electrophoretic components in *Triticale* which were not present in either parent, *T. durum* or *Secale cereale*.

The albumin patterns were less easy to interpret, due to background tailing. There were one or two minor differences in mobility and intensity between the Holdfast, King II and *Triticale* albumins. There was some evidence that a stronger leading albumin band may be associated with chromosome IV, but otherwise no alterations in the albumin patterns could be attributed to the other chromosomes.

It was not possible to detect changes in the ratio of albumins to globulins from the electrophoretic experiments, nor have the poorly soluble glutenins been examined. The differing nitrogen contents of the seeds indicate that there have been differences in the amount of protein synthesis. Changes in quantitative distribution, even if no qualitative changes have occurred, could lead to differences in amino acid composition of the order observed.

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