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The Relationship between HMW Glutenin Subunit Composition and the Bread-making Quality of British-grown Wheat Varieties

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ABSTRACT

Based on previous work, which related individual HMW glutenin subunits to bread-making quality by genetical analysis, quality scores were assigned to each of the commonly occurring subunits. The grain proteins of 84 home-grown wheat varieties were fractionated by SDS—PAGE to determine their HMW glutenin subunit composition. The quality scores of each of the subunits were summed to create a Glu-1 *quality score for each variety. The results indicated that 47–60% of the variation in the independently established bread-making qualities of this set of varieties could be accounted for by variation in HMW subunits of glutenin. The presence or absence in the varieties of a translocated chromosome, which consisted of the long arm of 1B and the short arm of 1R from rye, was also established because of its known association with poor bread-making quality. A correction factor was applied to the* Glu-1 *quality score of those varieties that contained the 1BL/1RS chromosome. The variations in the rye-adjusted* Glu-1 *quality scores were compared with those of the bread-making qualities of the varieties, and the proportion of variation in quality accounted for was raised to 55–67%. The* Glu-1 *quality score and the biscuit-making qualities of the same set of varieties were negatively related. The results are discussed in relation to future strategies recommended to wheat breeders for developing new varieties with improved bread-making quality.*

Key words: Wheat, protein, glutenin, electrophoresis, bread-making quality.

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1 INTRODUCTION

The high-molecular-weight (HMW) subunits of glutenin are coded by genes at three genetically unlinked loci, *Glu-A1*, *Glu-B1* and *Glu-D1*, which occur on chromosomes 1A, 1B and 1D, respectively.[1] Each locus exhibits extensive allelic variation,[2] and the allelic protein subunits can be easily distinguished by sodium dodecyl sulphate–polyacrylamide gel electrophoresis (SDS–PAGE). In previous studies, crosses were made between varieties with contrasting HMW subunits of glutenin, and the segregating progenies at later generations were tested for bread-making quality by the SDS-sedimentation test and for glutenin subunit composition by SDS–PAGE.[3,4] The presence of certain HMW subunits of glutenin in progeny was shown to be significantly associated with the volume of sediment in the quality test. After more extensive analyses the more commonly occurring subunits in Western European wheat varieties were ranked for quality in their three allelic groups.[1]

This genetic approach of relating individual proteins to the functional properties of doughs gives clear and unambiguous results, and some of this work has been independently confirmed.[5] However, as pointed out by Branlard and Dardevet,[6] the segregating-progeny approach cannot easily assess the contribution of allelic variation in one group of proteins to bread-making quality, relative to the variation in other components, whether protein or non-protein. For this reason our previous work on HMW subunits of glutenin and bread-making quality was used to create a *Glu-1* quality score for a given variety. The *Glu-1* quality scores of a large collection of wheat varieties grown in Great Britain during the last five years were determined and compared with the bread-making qualities of these varieties which had been established independently.[7–12]

2 MATERIALS AND METHODS

2.1 Varieties of wheat

The 84 varieties analysed in this study represent the complete list of varieties included in the pocket-guide series, *Milling and Baking Quality of Home-grown Wheat Varieties*, published in each of the years 1980 to 1985.[7–12] Samples of definitive stocks of these varieties, held at the National Institute of Agricultural Botany, Cambridge, were kindly provided by Dr A. Eade of that Institute. The stocks were either the original wheat samples submitted by wheat breeders for National List Trials, or were the first-generation progeny from these stocks.

2.2 SDS–PAGE

Total protein was extracted from segments of three grains of each variety and fractionated by SDS–PAGE using 10% gels.[13,14] All varieties were extracted and analysed at least twice on separate gels. Some varieties were additionally analysed using 5% gels.[2] The numbering system for the HMW glutenin subunits was that used previously.[15]

2.3 Two-dimensional electrophoresis

Selected varieties were analysed by two-dimensional electrophoresis to determine the presence or absence of rye γ-secalins, coded by genes on chromosome arm 1RS. The method[16] involves the extraction of aqueous ethanol-soluble proteins and their fractionation, in the first dimension by aluminium lactate-PAGE (APAGE) and in the second by SDS–PAGE.

3 RESULTS AND DISCUSSION

3.1 Elucidation of the *Glu-1* quality score

Prior to the analysis of the home-grown wheat varieties, a score for *Glu-1* quality was calculated, based on the relationship between individual HMW subunits of glutenin and quality, as determined by the SDS-sedimentation test. These results are summarised in Figure 4 of reference 1, and the scores currently assigned to each of these subunits are given in Table 1. The chromosome 1A-encoded subunits 1 and 2* were shown to be associated with large SDS-sedimentation volumes compared with the null allele which is not translated into a subunit. The former two are each given scores of 3 and the latter a score of 1. The difference between the SDS volumes associated with subunits 5+10 and 2+12, coded by chromosome 1D, is at least as great as that between subunit 1 and the null allele. However, there is another chromosome 1D-encoded subunit pair, 4+12, whose quality association is inferior to 2+12. Subunits 5+10 are therefore given a score of 4, 2+12 a score of 2 and 4+12 a score of 1. By similar reasoning, scores have been given also to 3+12 and all the chromosome 1B-encoded subunits shown in Table 1. The *Glu-1* quality score of a variety is simply calculated by summing the scores of the individual subunits it contains. In the collection of wheats studied here, the maximum score is 10 and the minimum is 3.

Some British-grown varieties contain the short arm of chromosome 1R from rye combined with the long arm of chromosome 1B (1BL/1RS). This translocated chromosome causes a decrease in bread-making quality, mainly by increasing dough stickiness.[17] To make allowances for this, a rye adjusted *Glu-1* quality score

TABLE 1
Quality Scores Assigned to Individual or Pairs of HMW Glutenin Subunits

Score	*Chromosome*		
	1A	*1B*	*1D*
4	—	—	5+10
3	1	17+18	—
3	2*	7+8	—
2	—	7+9	2+12
2	—	—	3+12
1	null	7	4+12
1	—	6+8	—

was calculated, based on the hypothesis that the decrease in quality caused by the presence of 1BL/1RS will be proportionately greater in genotypes which have better intrinsic quality. Varieties with a *Glu-1* quality score of between 8 and 10 had three points subtracted, those between 5 and 7 had two points subtracted, and those between 3 and 4 had one point removed. This system of allowing for the presence of the 1BL/1RS chromosome was arrived at from a complementary study with German-grown wheats (in preparation), many more of which contain this chromosome.

3.2 Effect of *Glu-1* quality score and rye-adjusted score on bread-making quality

The grain protein patterns of a selection of varieties, fractionated by SDS–PAGE using 10% gels, are shown in Fig. 1A. Individual HMW subunits of glutenin are numbered in Table 2 according to the method of Payne and Lawrence.[15] All the HMW subunits are clearly resolved by this technique, except, in some varieties, for subunit 2*, coded by chromosome 1A. Subunit 2* fractionates as a thin, fairly faint band with a marginally greater mobility than subunit 2 and virtually the same mobility as subunit 3. The latter two subunits occur as strong, broad bands (Fig. 1A) and when either is present they effectively obscure subunit 2*. Subunit 1 is chromosome 1A-encoded and allelic to subunit 2*. Therefore, varieties which contain subunit 1 plus either subunits 2 or 3 were assumed to lack subunit 2*. The

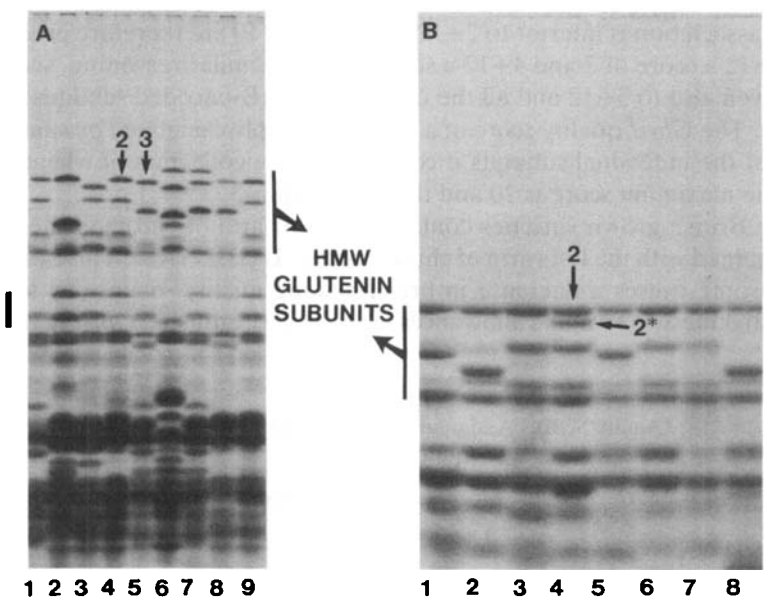

Fig. 1. Fractionation of protein extracts from varieties using (A) 10% and (B) 5% gels. The region of each gel which contains the HMW glutenin subunits is marked by a thin, vertical line, whereas the thick line marks the position of chromosome 1B-encoded ω-gliadins. The varieties analysed are (A) slots 1 to 9: Slejpner, Moulin, Mercia, Gawain, an unnamed breeding line, Axona, Sentry, Guardian and Fenman; (B) slots 1 to 8: Slejpner, Moulin, Waggoner, Timmo, Pageant, Mission, Marksman and Highbury.

presence or absence of subunit 2* in varieties containing subunits 2 or 3 but lacking subunit 1 could usually be inferred from the relative intensities of the HMW glutenin subunit bands, but for unambiguous classification they were additionally analysed by SDS–PAGE using 5% gels. In this procedure subunit 2* has a greater mobility than either subunit 2 or subunit 3 (Fig. 1B). In general, however, the fractionation of HMW subunits is inferior in 5% gels compared with 10% gels because subunit 1 has the same mobility as subunit 5, and subunits 2 and 3 and several of the chromosome 1B-encoded subunits are poorly resolved. The reason why chromosome 1A-encoded subunits have increasingly greater mobilities in gels with decreasing concentrations of polyacrylamide, compared with subunits coded by chromosome 1D, is not known.

The compositions of the HMW glutenin subunits deduced for the 84 varieties analysed are listed in Table 2. All but five of the varieties could be given a *Glu-1* quality score. The exceptional varieties contained subunits that had not been tested for associations with SDS-sedimentation volume. These were subunits 14+15, present in Axona, Maris Dove and Sappo, and subunits 2+11 in Ardec and Flinor.

To determine which of the varieties listed in Table 2 contain the 1BL/1RS translocated chromosome, SDS–PAGE separations were first examined for the presence of chromosome 1B-encoded ω-gliadins. Those varieties that clearly contained them (Fig. 1A, slots 2, 3, 4, 6, 7 and 9) were assumed not to contain chromosome 1BL/1RS. When 1B-encoded ω-gliadins appeared to be absent, or their presence was uncertain (Fig. 1A, slots 1, 5 and 8), protein extracts were fractionated by two-dimensional electrophoresis. The rye γ-secalins, coded by genes on chromosome arm 1RS, gave a unique pattern of spots (Fig. 2, arrows). The varieties that contain 1BL/1RS are listed in Table 2, together with their rye-adjusted *Glu-1* quality scores.

Also listed in Table 2 are the bread-making qualities of the varieties, determined by Stevens and Stewart,[8,9] and Stevens *et al.*[10–12] They used a ranking system from A to D: A-ranked varieties are likely to give large, soft-textured loaves; varieties ranked B are likely to give loaves poorer either in volume or texture; C varieties are poor in both characters; and D varieties give small, coarse-textured loaves.

The mean *Glu-1* quality scores of varieties belonging to the bread-quality ranks A, B, C and D were 6·6, 6·9, 4·6 and 4·4, respectively. When the standard errors of the differences between the two sets of means in all combinations were calculated (results not shown), significant differences were only found between the means of ranks A and C, A and D, B and C, and B and D. Therefore, as well as relating *Glu-1* quality score to the four bread-quality ranks, it was also related to two groups of pooled ranks, namely A+B and C+D.

In Table 3 (column 3), the relationship between the *Glu-1* quality scores of the set of 79 British-grown varieties and their published bread-quality ranks have been assessed by an analysis of variance. Comparison of lines 1 and 4, column 3, shows that the variation in *Glu-1* quality score between ranks A, B, C and D is much greater than that within the ranks. In Table 4 (column 2), expected mean squares, E(MS), were calculated from the data in Table 3 to determine the

TABLE 2
The Protein Composition and Technological Properties of Home-grown Wheats

Variety	*W/S*[a]	*Bread quality*	*Biscuit quality*	*HMW subunits*			Glu-1 *quality score*	*1BL/1RS*	*Rye-adjusted* Glu-1 *quality score*
				1A	*1B*	*1D*			
1. Abele	W	D	B	1	6+8	2+12	6	+	4
2. Alexandria	S	B	D	1	7+9	5+10	9	–	9
3. Ambassador	W	C	A	N	6+8	3+12	4	+	3
4. Anvil	W	C	B	N	6+8	2+12	4	–	4
5. Aquila	W	D	C	N	7	2+12	4	–	4
6. Ardec	S	C	C	N	7+8	2+11	?	–	?
7. Armada	W	C	D	N	6+8	2+12	4	–	4
8. Atou	W	C	D	N	7	3+12	4	–	4
9. Avalon	W	B	D	1	6+8	2+12	6	–	6
10. Avocet	W	D	B	N	6+8	2+12	4	–	4
11. Axona	S	B	C	1	14+15	5+10	?	–	?
12. Baron	W	D	A	1	6+8	2+12	6	+	4
13. Bounty	W	B	D	1	7	2+12	6	–	6
14. Bouquet	W	C	D	N	7	5+10	6	–	6
15. Boxer	W	B	C	N	6+8	2+12	4	–	4
16. Brigand	W	D	B	N	6+8	2+12	4	–	4
17. Brimstone	W	B	C	N	6+8	2+12	4	–	4
18. Brock	W	D	A	N	7	4+12	3	–	3
19. Broom	S	B	D	N	7+9	5+10	7	–	7
20. Cappelle-Desprez	W	C	C	N	7	2+12	4	–	4
21. Chalk	W	D	C	N	7	2+12	4	–	4
22. Champlein	W	C	C	N	7+8	4+12	5	–	5
23. Chieftain	W	C	C	N	7+8	5+10	8	+	5
24. Copain	W	B	D	1	7	2+12	6	–	6
25. Corinthian	W	C	A	N	6+8	3+12	4	+	3
26. Crossbow	W	C	B	N	6+8	2+12	4	–	4
27. Durin	W	D	B	N	6+8	2+12	4	–	4
28. Fenman	W	D	B	N	6+8	2+12	4	–	4
29. Flanders	W	B	C	N	6+8	5+10	6	–	6
30. Flinor	W	B	D	1	7	2+11	?	–	?
31. Galahad	W	D	C	N	7	2+12	4	–	4
32. Gamin	W	D	C	1	7+8	4+12	7	–	7
33. Gawain	W	D	C	N	6+8	2+12	4	–	4
34. Granta	W	D	D	N	6+8	2+12	4	–	4
35. Guardian	W	D	A	N	7	2+12	4	–	4
36. Hammer	W	C	C	N	6+8	2+12	4	+	3
37. Highbury	S	A	D	N	17+18	2+12	6	–	6
38. Hobbit	W	C	C	N	7	3+12	4	–	4
39. Hotspur	S	A	D	N	6+8	5+10	6	–	6
40. Hustler	W	D	D	N	6+8	2+12	4	–	4
41. Jerico	S	A	C	1	7+9	5+10	9	–	9
42. Kador	W	C	D	N	7+8	4+12	5	–	5
43. Kinsman	W	D	B	N	7	2+12	4	–	4
44. Longbow	W	D	B	N	7	2+12	4	–	4
45. Maestro	W	D	C	N	7	2+12	4	–	4
46. Mardler	W	D	C	N	6+8	2+12	4	–	4
47. Maris Dove	S	B	D	N	14+15	5+10	?	–	?
48. Maris Freeman	W	B	D	1	7	2+12	6	–	6
49. Maris Huntsman	W	D	C	N	6+8	2+12	4	–	4
50. Maris Nimrod	W	D	B	N	6+8	2+12	4	–	4
51. Maris Templar	W	D	C	N	7	2+12	4	–	4
52. Maris Widgeon	W	A	D	1	7	2+12	6	–	6
53. Marksman	W	C	D	N	6+8	2+12	4	–	4
54. Mega	W	C	D	N	6+8	2+12	4	–	4

TABLE 2 —*contd.*

Variety	*W/S*[a]	*Bread quality*	*Biscuit quality*	*HMW subunits*			Glu-1 *quality score*	*1BL/1RS*	*Rye-adjusted* Glu-1 *quality score*
				1A	*1B*	*1D*			
55. Mercia	W	B	D	N	6+8	5+10	6	–	6
56. Minaret	S	B	C	1	7+9	5+10	9	–	9
57. Mithras	W	D	B	N	6+8	2+12	4	–	4
58. Mission	W	B	C	N	6+8	2+12	4	–	4
59. Moulin	W	B	D	N	17+18	2+12	6	–	6
60. Musket	S	B	D	1	7+8	5+10	10	–	10
61. Norman	W	C	B	N	6+8	3+12	4	–	4
62. Pacer	W	D	A	N	7+9	2+12	5	–	5
63. Pageant	W	C	A	N	7+8	2+12	6	–	6
64. Prince	W	C	B	N	6+8	2+12	4	–	4
65. Rapier	W	D	B	N	6+8	2+12	4	–	4
66. Renard	W	D	B	N	7	4+12	3	–	3
67. Sabre	W	D	A	N	7+8	2+12	6	–	6
68. Sandown	S	C	C	2*	17+18	3+12	8	–	8
69. Sappo	S	A	D	2*	14+15	2+12	?	–	?
70. Score	W	D	D	N	7	5+10	6	–	6
71. Sentry	W	B	D	1	7	3+12	6	–	6
72. Shire	W	C	D	N	7	3+12	4	–	4
73. Sicco	S	B	D	1	7+9	5+10	9	–	9
74. Slejpner	W	C	C	N	6+8	2+12	4	+	3
75. Solitaire	S	B	D	2*	17+18	5+10	10	–	10
76. Sportsman	W	C	C	N	7	2+12	4	–	4
77. Stetson	W	D	C	1	6+8	2+12	6	+	4
78. Stuart	W	D	A	N	6+8	2+12	4	+	3
79. Timmo	S	A	D	2*	6+8	2+12	6	–	6
80. Tonic	S	B	D	N	7+8	5+10	8	–	8
81. Ventura	S	B	D	2*	7+8	2+12	8	–	8
82. Virtue	W	D	D	N	6+8	2+12	4	–	4
83. Waggoner	W	C	D	N	6+8	2+12	4	–	4
84. Wembley	S	B	C	2*	7+9	2+12	7	–	7

[a] S, spring sown; W, winter sown.

proportion of variation occurring between ranks and within ranks. The results (column 3) show that 47% of the variation in bread-making quality of varieties, when ranked into A, B, C and D, is due to variation in *Glu-1* quality score.

The mean squares of between-group (i.e. A+B versus C+D) and within-group variation is also shown in Table 3 (column 3, lines 2 and 3). As the former is highly significant and the latter non-significant, the grouping is effective with little residual variation not accounted for. Calculation of E(MS) shows that 60% of the variation in the bread-making quality of A+B and C+D varieties is due to the variation in *Glu-1* quality score (Table 4, column 3, line 3). The clear relationship between the *Glu-1* quality scores of the varieties and their subdivision into quality groups A+B and C+D is shown graphically in Fig. 3. Varieties with *Glu-1* quality scores of 3, 4 and 5 belong predominantly to the C+D quality group whereas those with scores of 6 to 10 are mainly in group A+B.

The *Glu-1* quality score of a variety, as shown in Table 2, is obtained by summing the individual scores of HMW glutenin subunits coded by chromosome

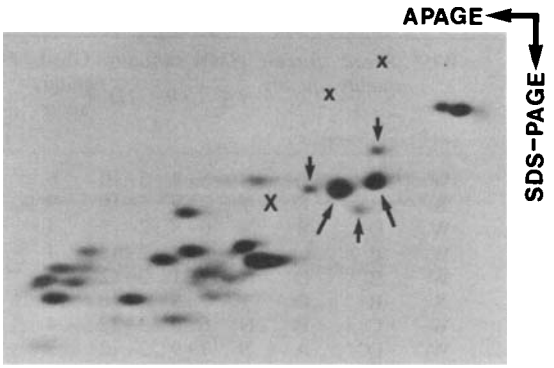

Fig. 2. Two-dimensional fractionation of the ethanol-soluble proteins of variety Abele. The γ-secalins, coded by genes on chromosome 1BL/1RS, are identified by arrows. Approximate positions of chromosome 1B-encoded ω- and γ-gliadins are marked by small and large crosses, respectively.

1A, 1B and 1D. The relationship between each of these scores and the bread-making qualities of the British-grown varieties was also determined by an analysis of variance. Variation in HMW glutenin subunits coded by chromosome 1A and 1D made a significant contribution to bread-making quality, in terms of variation between ranks A, B, C and D and especially between groups A+B and C+D (Table 4, columns 6, 7, 10 and 11). By contrast, variation in chromosome 1B-encoded subunits appeared to contribute much less to bread-making quality.

The remaining component that was examined for its effect on bread-making quality was the presence or absence of the 1BL/1RS translocated chromosome in varieties. It was assessed in combination with *Glu-1* quality score in the form of a rye-adjusted score. Variation in this score related best to variation in bread-making quality (Table 3), and accounted for 55% of the variation for placement of varieties into quality ranks A, B, C and D, and 67% for placement into quality groups A+B and C+D (Table 4, columns 4 and 5; Fig. 3).

TABLE 3
Analysis of Variance of HMW Glutenin Subunit Scores for Varieties in Different Bread-quality Ranks[a]

Source of variation	*df*	Glu-1 *quality score*	*Rye-adjusted score*	*1A subunit score*	*1B subunit score*	*1D subunit score*
1. Between ranks[b]	3	30·92***	38·02***	6·00***	1·47	4·30**
2. Between groups[c]	1	91·86***	113.55***	17·60***	3·34*	12·68***
3. Between ranks within groups	2	0·45	0·52	0·39	0·54	0·23
4. Within ranks	75	1·79	1·64	0·56	0·54	0·55

[a] Values given are mean squares.
[b] Between quality ranks A, B, C and D.
[c] Between groups of ranks A+B and C+D.
df, Degrees of freedom.
Significance levels: *P=0·05–0·01; ** P=0·01–0·001; ***P<0·001.

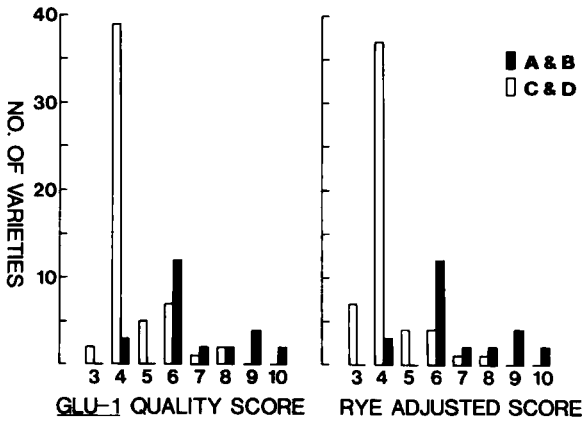

Fig. 3. Frequencies of A+B and C+D bread-quality varieties among different values of (left) *Glu-1* quality score, and (right) rye-adjusted score.

3.3 Effect of *Glu-1* quality score and rye-adjusted score on biscuit-making quality

The biscuit-making qualities of the 84 home-grown wheat varieties are listed in Table 2. As for bread quality, a ranking system from A to D was used. The classification is based on the extensibility of unyeasted doughs and on endosperm texture.[8–12] For any one variety an A ranking is given if more than 75% of samples tested give acceptable results, B if more than 50% do, C if over 25% do, and D if no samples are acceptable.

The mean *Glu-1* quality scores of varieties in biscuit-quality ranks A, B, C and D are 4·7, 4·1, 5·2 and 6·0, respectively. Thus, with the exception of rank A, which only contains nine varieties, there is a negative relationship between *Glu-1* quality score and the biscuit-making quality of British-grown varieties. This is in contrast to the positive correlation between *Glu-1* quality score and bread-making quality described above.

Table 5 shows, by analysis of variance, that the variation in *Glu-1* quality score between biscuit-quality ranks is much greater than that within ranks. The significance of the difference in mean squares is not, however, as great as the complementary comparison with bread-making quality (Table 3). This is reflected by the finding (Table 6) that only 20% of the variation in biscuit quality can be accounted for by variation in *Glu-1* quality score, compared with 47% for bread-making quality (Table 4). The negative contribution of HMW glutenin subunits to biscuit-making was primarily determined by chromosome 1D-encoded subunits (Table 6, column 11).

When the above comparisons with biscuit-making quality are made with the rye-adjusted score instead of *Glu-1* quality score, the mean squares between ranks are significantly increased (Table 5) and the contribution to variation in biscuit-making quality is raised from 20 to 25% (Table 6). This still compares unfavourably with the 55% contribution by rye-adjusted score to bread-making quality (Table 4).

TABLE 4
Estimation of the Components of Variance for Bread Making

Components of variance	Glu-1 *score*		*Rye-adjusted score*		*1A subunit score*		*1B subunit score*		*1D subunit score*	
	E(MS)	*%*	*E(MS)*	*%*	*E(MS)*	*%*	*E(MS)*	*%*	*E(MS)*	*%*
1a. Between ranks (σ^2b)	1·60	47·2	1·99	54·8	0·23	29·1	0·05	8·5	0·21	27·6
b. Within ranks (σ^2w)	1·79	52·8	1·64	45·2	0·56	70·9	0·54	91·5	0·55	72·4
2a. Between groups (σ^2b)	2·62	59·8	3·25	67·0	0·50	47·6	0·08	12·9	0·35	39·3
b. Within groups (σ^2w)	1·76	40·2	1·60	33·0	0·55	52·4	0·54	87·1	0·54	60·7

The ranks are A, B, C and D, and the groups are A+B and C+D. Components of variance were estimated from the analysis of variance using the method for unequal group sizes described by Snedecor and Cochran.[18]
E(MS), expected mean squares.

TABLE 5
Analysis of Variance of *Glu-1* Quality Score and Rye-adjusted Score for Varieties in Different Biscuit-making Ranks[a]

Source of variation	*df*	Glu-1 *score*	*Rye-adjusted score*	*1A subunit score*	*1B subunit score*	*1D subunit score*
1. Between ranks	3	13.68 **	18·41 ***	2·23	1·16	2·32 *
2. Within ranks	75	2·48	2·43	0·85	0·56	0·63

[a] Values given are mean squares.
Significance levels: *P=0·05–0·01; **P=0·01–0·001; ***P<0·001.

TABLE 6
Estimation of the Components of Variance for Biscuit Making

Components of variance	Glu-1 *score*		*Rye-adjusted score*		*1A subunit score*		*1B subunit score*		*1D subunit score*	
	E(MS)	*%*	*E(MS)*	*%*	*E(MS)*	*%*	*E(MS)*	*%*	*E(MS)*	*%*
1. Between ranks (σ^2b)	0·60	19·5	0·84	25·7	0·07	7·6	0·03	5·1	0·09	12·5
2. Within ranks (σ^2w)	2·48	80·5	2·43	74·3	0·85	92·4	0·56	94·9	0·63	87·5

TABLE 7
Frequencies in British-grown Wheat Varieties of HMW Subunits Commonly Found in Commercial Wheats

Chromosome 1A			*Chromosome 1B*			*Chromosome 1D*		
Subunit	*Variety (No.)*	*%*	*Subunits*	*Variety (No.)*	*%*	*Subunits*	*Variety (No.)*	*%*
Null	61	73	6+8	37	44	2+12	53	63
1	17	20	7	23	27	5+10	16	19
2*	6	7	7+8	10	12	3+12	8	10
			7+9	7	8	4+12	5	6
			17+18	4	5	2+11	2	2
			14+15	3	4			
			20	0	0			
			13+16	0	0			

3.4 Genotypic variation in HMW glutenin subunit composition

The frequencies of the HMW glutenin subunits in the 84 British-grown varieties analysed are shown in Table 7. The most commonly occurring subunits coded by all three chromosome groups are those which are associated with poor bread-making quality, namely the null allele of chromosome 1A, subunits 6+8 and 7 of 1B, and subunits 2+12 of 1D. Other subunits, such as 20 and 13+16, which occur moderately frequently in commercial varieties grown throughout the world, are not present in any variety.

The very common occurrence of a limited number of HMW subunits in this set of wheats has caused a restricted range of HMW glutenin-subunit compositions. Out of 84 varieties there are only 29 different compositions and only 15 varieties have HMW glutenin subunit compositions that are unique. Two compositions (null, 6+8, 2+12, and null, 7, 2+12) are present in 36 varieties. Both types have the low *Glu-1* quality score of 4, and this is the reason for the dominance of this group in Fig. 3.

4 GENERAL DISCUSSION

The HMW subunits of glutenin probably account for only about 1% of the dry weight of the mature endosperm. Nevertheless the results presented in this paper have shown that the variation in composition of these subunits among 79 varieties grown in the UK in the last 5 years makes a large contribution to the bread-making qualities of these varieties. These findings are entirely consistent with recent advances in the molecular biology and biophysics of wheat gluten, which indicate that they are the principal subunits that impart elasticity to native glutenin.[19] Insufficient elasticity, which causes poor dough strength, has long been recognised as the main deficiency in British-grown wheats for bread-making.

In contrast to the positive relationship between *Glu-1* quality score and bread-making quality, there is a negative relationship between this score and biscuit quality. These results support the hypothesis that *Glu-1* quality score is a guide to

potential elastic development (dough strength), desirable for bread but deleterious for biscuits. By the analysis of variance, *Glu-1* quality score related better to bread-quality groups A+B and C+D than it did to quality ranks A, B, C and D. This is consistent with the major, between-rank differences in bread-making quality being between B and C varieties (B. A. Stewart, personal communication). In the standardised bread-testing procedure used to assess the quality of varieties submitted for growing in the UK, loaves are baked after the dough is mixed for a set work input.[7-12] It is therefore possible that some varieties in rank B produce strong doughs that do not reach their potential in the set mixing procedure and so underperform on baking. Such varieties would be expected to have high *Glu-1* quality scores, and this may be the reason why the means of A- and B-ranked varieties are so similar.

British-grown wheats have rather low *Glu-1* quality scores. The mean score for A+B wheats for instance is only 6·8. Currently the most popular home-grown bread-quality wheat is Avalon, which superseded Bounty 4 years ago. In the near future, Avalon is likely to be joined or outclassed by Mercia. All these three varieties have *Glu-1* quality scores of 6 out of a possible maximum of 10. This contrasts with varieties Monopol, Severin and Rektor which currently represent the highest bread-quality class (A9) in West Germany.[20] They have *Glu-1* quality scores of 9, 9 and 7 respectively. A guide for wheat breeders who wish to develop varieties with improved bread-making quality is therefore to cross genotypes that have complementary good-quality subunits coded by different loci,[21] and to select progeny with high *Glu-1* quality scores.

The finding in Tables 3 and 4 that the presence of the 1BL/1RS chromosome is deleterious to bread-making is consistent with the results of others. However, a new finding is that this chromosome is actually beneficial for biscuit-making quality. There may be two reasons for this. First, the loss of the short arm of 1B reduces by one-third the numbers of genes coding for LMW glutenin subunits, thereby decreasing the total amount of elastic glutenin produced, and secondly the γ-secalins coded on 1RS are more soluble in water than 1BS-encoded ω- and γ-gliadins.[22] This may increase viscous flow and extensibility of doughs.

The relative contributions of variation in HMW subunits of glutenin, and of the presence or absence of the 1BL/1RS chromosome, in the classification of 79 British-grown wheat varieties into bread-quality groups A+B and C+D are summarised in Fig. 4. This pie diagram indicates that about one-third of the variation in quality is not accounted for. Since many of the varieties were assessed over several years, the majority of this variation is controlled genetically rather than by the environment. One character which must contribute to quality variation is the protein content of white flour, which is known to be positively related to bread volume.[23] The protein contents of white flours from incoming winter wheats for official assessment usually vary from 7 to 10% of the flour on a 14% moisture basis (B. A. Stewart, personal communication). This variation in protein content is likely to be caused at least partly by the different grain-yielding capabilities of the different varieties, for there is a negative relationship between the two characters.[24]

Another property of flour which will contribute to bread-making quality and

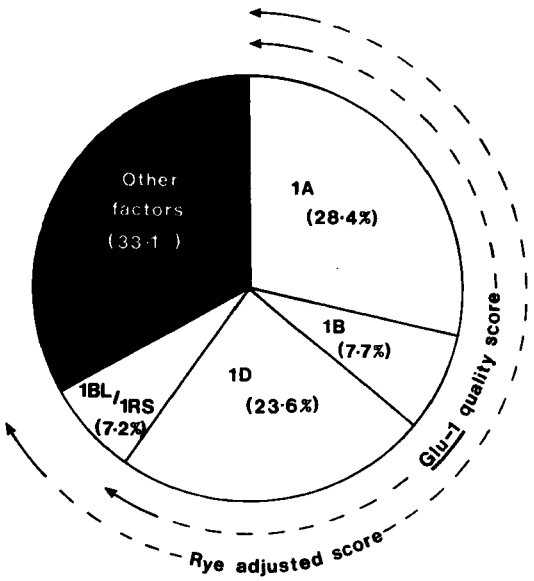

Fig. 4. Pie diagram of the relative contribution of factors which affect variation in the bread-making qualities of varieties when placed in groups A+B and C+D. The contributions of *Glu-1* quality score and rye-adjusted score are 59·8% and 67·0% of the total variation, respectively (Table 4). The relative contribution of 1A, 1B and 1D-encoded HMW glutenin subunits to *Glu-1* quality score is based on the values of % E(MS) for between-group variance (Table 4, line 2a). For instance the value of 28·4% in this figure for the contribution of 1A-encoded HMW subunits to variation in quality was calculated by [47·6/(47·6+12·9+39·3)]×59·8.

which varies between genotypes is water absorption. Varieties with hard-textured endosperms will suffer much more starch damage during milling than soft-textured wheats, and their flours will consequently absorb more water. Since the water content of doughs is optimised for each sample, this is likely to increase loaf volume since a fixed weight of dry flour is used in official bread-quality testing for placement on the National List.

The α-amylase activity of flours is strongly influenced by growing conditions but there is nevertheless an underlying genetic variation in the level of this enzyme in the mature grain. The α-amylase becomes active during dough handling and the early stages of baking and, if excessive, causes stickiness. The resulting loaves would receive a low loaf quality rating in official tests. High α-amylase activity causes more water to be released from the surface of starch granules than normal, due to excessive breakdown of starch to maltose, and this affects loaf volume.

All the varieties listed in Table 2 show extensive allelic variation for LMW subunits of glutenin and for gliadins, as well as HMW subunits. Six gene loci are involved:[1] LMW glutenin subunits, ω-gliadins and γ-gliadins are coded by genes on the short arms of chromosomes 1A, 1B and 1D, and the α- and β-gliadins on the short arms of the homologous group 6 chromosomes. Various research groups have shown that allelic variation at these loci strongly affects bread-making quality.[6,25–27]

The relative contributions of these four characters in accounting for the remaining third of the variation in the bread-making quality of home-grown wheats cannot yet be assessed. Three of them, protein content, α-amylase activity and gliadin/LMW glutenin-subunit polymorphisms, could be exploited by wheat breeders in developing new varieties with improved bread-making properties. Unfortunately, grain protein content is inversely correlated with grain yield[24] and is affected much more by growing conditions than by genotype, making it a very difficult character to breed for. There is scope for reducing the endogenous activity of α-amylase in grains and, to some extent, for reducing α-amylase in grains exposed to moist conditions., However, a drastic reduction is impracticable because stimulation of this enzyme is a physiological response to seed hydration and subsequent germination. In contrast to these approaches, selecting for optimal composition of LMW glutenin subunits and gliadins is likely to be the most promising. For this reason, these proteins are currently being characterised in this set of wheats by two-dimensional electrophoresis.

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