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The HMW Glutenin Subunit Composition of Canadian Wheat Cultivars and their Association with Bread-Making Quality*

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ABSTRACT

The proteins of 70 Canadian-grown wheat cultivars were fractionated by SDS–PAGE to determine their HMW glutenin subunit composition. On the basis of previously established relationships between individual subunits and measures of bread-making quality, Glu-1 *scores were calculated for 67 cultivars. The three cultivars Chinook, Cypress and Supreza were found to contain novel HMW glutenin subunits previously uncatalogued. The* Glu-1 *scores accounted for 59–69% of the variation in bread-making quality of these cultivars whereas flour ash accounted for none. The implications of these results to wheat breeding programmes are discussed.*

Key words: HMW glutenin, Canadian wheat, bread-making quality.

1 INTRODUCTION

The bread-making quality of wheat is primarily influenced by its protein content and protein quality. Whereas protein content is an easily measured parameter, the determination of protein quality has remained more difficult. The unique

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rheological properties of bread doughs are largely conferred by the glutenin proteins (Wall 1979). The association of high-molecular-weight (HMW) glutenin subunits to SDS-sedimentation values, an indicator of bread-making quality, has been demonstrated (Payne *et al* 1979, 1981). The HMW glutenin subunits are coded by genes at the *Glu-A1*, *Glu-B1* and *Glu-D1* loci on chromosomes 1A, 1B and 1D, respectively (Payne *et al* 1982), and allelic variation at each locus (Lawrence and Shepherd 1980; Payne and Lawrence 1983) has produced extensive variability in wheat cultivars. The assigning of a score to each HMW subunit has permitted a statistical evaluation of the amount of variation in bread-making quality attributable to the HMW glutenin subunits (Payne 1987, Payne *et al* 1987). For British- and Spanish-grown wheat cultivars, 47% and 68% respectively of the variation in quality is directly related to the *Glu-1* score (Payne *et al* 1987, 1988).

The superior bread-making quality of Canadian-grown wheat is internationally recognised. Canadian wheat has been used extensively in UK bread grists to enrich the quality of home-grown wheat. The primary objective of the work reported in this paper was to determine if the positive and significant relationships previously found between *Glu-1* scores of Western European cultivars and their bread-making qualities also held true for Canadian-grown cultivars.

2 MATERIALS AND METHODS

2.1 Cultivars of wheat

Seventy cultivars of Canadian-grown wheat were included in the study. Stock samples of these cultivars are maintained at the Canadian Grain Commission, Winnipeg, Canada. All samples were derived from breeder's seed.

2.2 Electrophoresis

Total protein was extracted from segments of three kernels of each cultivar and fractionated by sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS–PAGE) using 10% w/v polyacrylamide gels as described previously (Payne *et al* 1980, 1982). To determine the presence or absence of glutenin subunit 2* in cultivars containing subunits 2+12, a further analysis by SDS–PAGE using 5% w/v gels was performed (Payne *et al* 1988). The numbering system for the HMW glutenin subunits was as used previously (Payne and Lawrence 1983).

Cultivars that did not clearly contain 1B ω-gliadins in their SDS–PAGE electrophoretograms were additionally examined for the presence or absence of rye ω-secalins by aluminium lactate–PAGE (APAGE) or by two-dimensional electrophoresis involving fractionation in the first dimension by APAGE and in the second dimension by SDS–PAGE (Payne *et al* 1984).

2.3 Quality analyses

Quality data for all cultivars was derived from the Minutes of the Canadian Expert Committee on Grain Quality. The baking strength index (BSI: Tipples and Kilborn 1974) was used as the indicator of bread-making quality. This protein quality parameter removes the effect of protein content on loaf volume. In this study, a

ranking system of 1 (poorest bread-making) to 4 (best bread-making) was used to classify cultivars as follows: 1-ranked cultivars with a BSI of 79 or less; 2-ranked cultivars with a BSI of 80–89; 3-ranked cultivars with a BSI of 90–99; and 4-ranked cultivars with a BSI over 100. Flour ash data were also derived from the Minutes of the Canadian Expert Committee on Grain Quality.

3 RESULTS AND DISCUSSION

The HMW glutenin subunit composition of Canadian-grown cultivars, determined by SDS–PAGE, permitted the calculation of *Glu-1* scores for all but three cultivars (Table 1). The cultivars Chinook, Cypress and Supreza contain unusual HMW glutenin subunits and were excluded from further analyses. One of the unusual subunits occurs in both Chinook and Cypress (see Fig 1, track B) and has a slower electrophoretic mobility than that of chromosome 1A encoded subunit 2*, but a much greater mobility than 1A-encoded subunit 1. The subunit, not previously described, is also very likely to be chromosome 1A-encoded because of its electrophoretic mobility and because the two varieties contain commonly occurring 1B- and 1D-encoded subunits (Table 2). The allele is now given the designation *Glu-A1l*. By similar reasoning, the unusual subunits of Supreza must be coded by genes on chromosome 1B. The main subunit (Fig 1, tracks H and K) is unusual in having a slightly slower mobility than that of subunit 7. The allele is described as *Glu-B1t*. The 1BL/1RS translocated chromosome, known to be associated with detrimental effects on dough mixing and on bread-making quality (Dhaliwal *et al* 1987), was absent in all Canadian-grown cultivars.

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	—
3	—	13+16[a]	—
2	—	7+9	2+12
2	—	—	3+12
1	null	7	4+12
1	—	6+8	—
1	—	20[a]	—

[a] The quality scores of these subunits were not assigned through genetical analysis, but were deduced from the relationships between the *Glu-1* quality scores of several collections of cultivars and their true bread-making qualities (unpublished results).

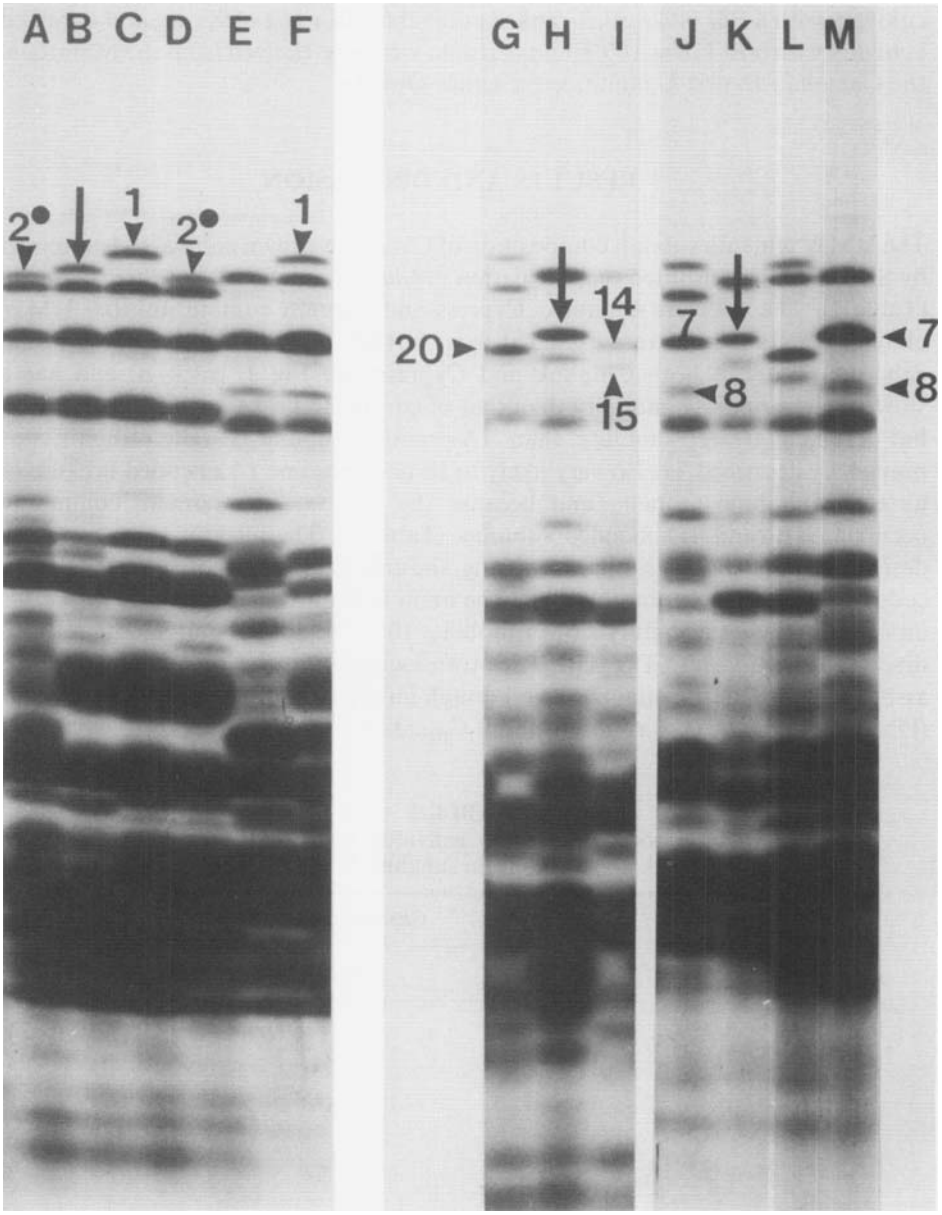

Fig 1. SDS–PAGE of unusual HMW glutenin subunits found in some Canadian cultivars. The subunit coded by allele *Glu-A1l* occurs in track B and the subunit coded by *Glu-B1t* occurs in H and K. These are indicated by the vertical arrows. Track A, Columbus; B, Chinook; C, Canuck; D, Benito; E, Chinese Spring; F, HY320; G, Federation; H, Supreza; I, Sappo; J, Fiorello-2; K, Supreza; L, Forlani; M, Chinese Spring.

TABLE 2
The HMW glutenin subunit composition and technological properties of Canadian-grown wheat cultivars

Cultivar	*Type*[a]	*Bread-making quality rank*	*HMW subunits*			Glu-1 *score*
			1A	*1B*	*1D*	
1. Absolvent	HRW	3	2*	7+9	5+10	9
2. Apex	HRS	3	1	7+9	5+10	9
3. Augusta	SWW	1	1	7+9	2+12	7
4. Benito	HRS	4	2*	7+9	5+10	9
5. Cadet	HRS	3	2*	7+8	5+10	10
6. Cajeme 71	HRS	3	1	17+18	5+10	10
7. Canthatch	HRS	3	2*	7+9	5+10	9
8. Canuck	HRS	3	1	7+9	5+10	9
9. Casavant	SRS	1	1	7	2+12	6
10. Chester	HRS	4	2*	7+8	5+10	10
11. Chinook	HRS	2	?	7+9	5+10	?
12. Columbus	HRS	4	2*	7+9	5+10	9
13. Concorde	HRS	3	2*	7+8	2+12	8
14. Conway	HRS	4	2*	7+9	5+10	9
15. Coronation	HRS	2	1	7+9	5+10	9
16. Cypress	HRS	4	?	7+9	5+10	?
17. Early Triumph	HRS	3	1	7+9	5+10	9
18. Favor	SWW	1	1	7+9	2+12	7
19. Frankenmuth	SWW	1	1	7+9	2+12	7
20. Fredrick	SWW	1	2*	7+9	2+12	7
21. Garnet	HRS	2	N	7+9	5+10	7
22. Glenlea	HRS	3	2*	7+8	5+10	10
23. Gordon	SWW	1	1	7+9	2+12	7
24. Harus	SWW	1	1	7+9	2+12	7
25. Houser	SWW	1	1	7+8	2+12	8
26. HY320	MRS	3	1	7+8	2+12	8
27. Inia	HRS	4	1	13+16	5+10	10
28. Katepwa	HRS	4	2*	7+9	5+10	9
29. Kenyon	HRS	4	2*	7+9	5+10	9
30. Kharkov	HRW	2	1	7+9	5+10	9
31. Kitchener	HRW	3	1	7+8	5+10	10
32. Lake	HRS	3	2*	6+8	5+10	8
33. Lancer	HRW	4	2*	7+8	5+10	10
34. Laura	HRS	4	1	7+8	5+10	10
35. Laval 19	HRS	2	1	7+9	5+10	9
36. Leader	HRS	4	2*	7+8	5+10	10
37. Lennox	SRW	1	1	7+9	5+10	9
38. Manitou	HRS	4	2*	7+9	5+10	9
39. Marquis	HRS	3	1	7+9	5+10	9
40. Max	HRS	4	1	7+9	5+10	9
41. McMurrachy	HRS	1	N	7+8	5+10	8
42. Monopol	HRW	4	1	7+9	5+10	9
43. Napayo	HRS	3	2*	7+9	5+10	9
44. Neepawa	HRS	4	2*	7+9	5+10	9
45. Norquay	HWS	4	1	13+16	5+10	10
46. Norstar	HRW	4	1	7+8	5+10	10

(*continued*)

TABLE 2—*contd*

Cultivar	*Type*[a]	*Bread-making quality rank*	*HMW subunits*			Glu-1 *score*
			1A	*1B*	*1D*	
47. Park	HRS	4	1	7+9	5+10	9
48. Pembina	HRS	3	2*	7+9	5+10	9
49. Pitic 62	SRS	1	1	7+8	2+12	8
50. Red Bobs 222	HRS	3	1	7+9	5+10	9
51. Red Fife	HRS	3	1	7+9	5+10	9
52. Red River	HRS	4	1	7+8	5+10	10
53. Regent	HRS	3	1	6+8	5+10	8
54. Renown	HRS	2	2*	6+8	5+10	8
55. Rescue	HRS	3	1	7+9	5+10	9
56. Reward	HRS	3	2*	7+8	5+10	10
57. Rideau	SWW	1	1	6+8	5+10	8
58. Roblin	HRS	4	2*	7+8	5+10	10
59. Saunders	HRS	3	2*	7+9	5+10	9
60. Selkirk	HRS	3	1	6+8	5+10	8
61. Sinton	HRS	4	2*	7+9	5+10	9
62. Sundance	HRW	3	1	7+9	5+10	9
63. Supreza	HRS	—	2*	?	2+12	?
64. Talbot	SWW	1	1	7+9	2+12	7
65. Thatcher	HRS	3	2*	7+9	5+10	9
66. Vernon	SRS	1	1	7+9	5+10	9
67. Vuka	HRW	3	N	7+9	5+10	7
68. Winalta	HRW	4	2*	7+9	5+10	9
69. Yecora Rojo	HRS	3	1	17+18	5+10	10
70. Yorkstar	SWW	1	1	7+9	2+12	7

[a] HRW, Hard red winter; HRS, hard red spring; HWS, hard white spring; MRS, medium red spring; SWW, soft white winter; SRS, soft red spring; SRW, soft red winter; SWS, soft white spring.
N, Null.

The *Glu-1* scores of the 67 Canadian-grown cultivars are listed in Table 2. In Table 3, the mean *Glu-1* scores of cultivars belonging to bread-making quality ranks 1 to 4 are presented. Standard errors of the differences between means were calculated (results not shown) which indicated that the means of ranks 2 and 3 were not significantly different. Therefore, as well as relating the *Glu-1* score to the four bread-making quality ranks, it was also related to ranks 1 and 4 and pooled ranks 2+3, hereafter referred to as groups.

Part of the association between HMW glutenin subunits and bread-making quality could be due to the similar predigree of many of the Canadian-grown wheat cultivars. To test this hypothesis, the relationship between flour ash, a quality parameter functionally unrelated to baking strength, and *Glu-1* score was determined. The means for flour ash were not significantly different for any of the four ranks or three groups of bread-making quality (Table 3).

The relationship between the *Glu-1* scores of the 67 Canadian-grown cultivars and their bread-making quality ranks was assessed by one-way analysis of variance

TABLE 3
Means of *Glu-1* scores and flour ash values for bread-making quality ranks and groups

Parameters	*Bread-making quality*						
	Ranks				*Groups*		
	1	*2*	*3*	*4*	*1*	*2+3*	*4*
Glu-1 score	7·5[c]	8·4[b]	9·0[b]	9·4[a]	7·5[c]	8·9[b]	9·4[a]
Flour ash	0·43[a]	0·40[a]	0·42[a]	0·41[a]	0·43[a]	0·42[a]	0·41[a]

Means followed by the same letter are not significantly different at $P=0{\cdot}05$.

TABLE 4
Analysis of variance of HMW glutenin subunit scores and flour ash values for cultivars in different bread quality ranks and groups[a]

Source of variation	*df*[b]	Glu-1 *score*	*Flour ash*
1. Between ranks[c]	3	12·04***	0·0017
2. Within ranks	63	0·52	0·0019
3. Between groups[d]	2	17·40***	0·0031
4. Between ranks within groups	1	1·32	0·0016
5. Within groups	63	0·54	0·0019

[a] Mean squares.
[b] Degrees of freedom.
[c] Between quality ranks 1, 2, 3 and 4.
[d] Between groups of ranks 1, 2+3 and 4.
Significance levels: ***$P<0{\cdot}001$.

for unequal sample size (Table 4). The between-ranks treatment effect was very highly significant (column 3, row 1) as was the between-groups treatment effect (column 3, row 3). There were no significant differences between ranks (column 4, row 1) or between groups (column 4, row 3) for flour ash (Table 4).

Calculation of expected mean squares, E(MS) (Table 5) showed that *Glu-1* score accounted for 58·5% of the variation between bread-making quality ranks (column 3, row 1) and 68·7% of the variation between bread-making quality groups (column 3, row 3). Therefore, there is a clear and significant relationship between the *Glu-1* scores of the Canadian-grown cultivars and their bread-making quality. In contrast, the proportion of variation in bread-making quality accounted for by flour ash treatment effects (Table 5) was zero both between bread-making quality ranks (column 5, row 1) and groups (column 5, row 3).

The frequencies of HMW glutenin subunits in the 70 Canadian-grown cultivars examined are shown in Table 6. The most frequent subunits of each chromosome are those associated with good bread-making quality, that is, subunits 1 and 2* of chromosome 1A, subunits 7+9 and 7+8 of 1B and subunits 5+10 of 1D. A limited range of different HMW glutenin subunits, particularly of chromosome 1D, is

TABLE 5
Estimation of the components of variance for bread-making quality

Components of variance	Glu-1 *score*		*Flour ash*	
	E(MS)[a]	%	*E(MS)*	%
1a. Between ranks (σ^2b)	0·74	58·5	0·0	0
b. Within ranks (σ^2w)	0·52	41·5	0·002	100
2a. Between groups (σ^2b)	1·18	68·7	0·0	0
b. Within groups (σ^2w)	0·54	31·3	0·002	100

The ranks are 1, 2, 3 and 4, and the groups are 1, 2+3 and 4. Components of variance were estimated from the analysis of variance using the method for unequal group sizes described by Snedecor (1956).
[a] Expected mean squares.

TABLE 6
Frequencies of HMW glutenin subunits in Canadian-grown wheat cultivars

Chromosome 1A			*Chromosome 1B*			*Chromosome 1D*		
Subunit	*Number of cultivars*	%	*Subunit*	*Number of cultivars*	%	*Subunit*	*Number of cultivars*	%
1	38	56	7+9	43	63	5+10	56	80
2*	27	40	7+8	16	23	2+12	14	20
NULL	3	4	6+8	5	7	3+12	0	0
			17+18	2	3	4+12	0	0
			13+16	2	3	2+11	0	0
			7	1	1			
			20	0	0			
			14+15	0	0			

clearly evident. Cultivars classified in quality rank 4 were composed of chromosome 1A subunits 1 or 2*, or chromosome 1B subunits 7+9, 7+8 or 13+16, but invariably contained chromosome 1D subunits 5+10. Therefore, the bread-making quality of Canadian wheat cultivars is determined by their 1D chromosome constitution and to a lesser degree by chromosome 1A since no rank 4 classified cultivars contained the null allele.

4 DISCUSSION

Whereas flour ash values had no association with bread-making quality, *Glu-1* scores had a highly significant association with bread-making quality. These results substantiate the authenticity of a relationship between HMW glutenin subunit composition and baking strength. However, as with other comparisons of this sort,

TABLE 7
Mean *Glu-1* quality scores of collections of cultivars from different countries

	Country	*No of cultivars*	*Mean* Glu-1 *score*
1	Argentina	23	9·5
2	Australia	110	8·0
3	Canada[a]	67	8·7
4	Denmark	22	5·6
5	Finland[b]	35	8·0
6	France	147	5·8
7	Hungary	37	7·8
8	New Zealand	21	6·9
9	Norway	18	8·8
10	Romania	17	8·2
11	Spain[c]	33	6·6
12	United Kingdom[d]	84	5·2
13	West Germany	57	5·8

[a] Results of this paper.
[b] Results from Sontag *et al* (1986).
[c] Results from Payne *et al* (1988).
[d] Results from Payne *et al* (1987).
All other data taken from Payne (1987).

there are a few exceptional cultivars with unexpected *Glu-1* scores. In the set of Canadian-grown cultivars, both Lennox and Vernon have high *Glu-1* scores of 9 yet are placed in the lowest bread-quality category. It is universally recognised that bread-making quality is very complex, and it is presumed that these two varieties are simply deficient in one or more unidentified quality factors, factors which contribute between 31 and 41% of the quality variation in these wheats (Table 5).

The high *Glu-1* score of Canadian-grown wheat cultivars, particularly those found in the top bread-making rank, parallels their international status as high-quality bread wheats. Indeed, the mean *Glu-1* score of the varieties listed in Table 2 (8·7) is substantially higher than the mean scores of Western European cultivars (Table 7) and comparable to those of various other countries. Canadian wheat currently imported into the UK for bread-grist improvement will probably consist of three principal cultivars, Columbus, Katepwa and Neepawa. All have *Glu-1* scores of 9 (Table 2). Traditional cereal quality screening tests have thus succeeded in producing bread wheat cultivars with high *Glu-1* scores. Results presented in this study suggest that the *Glu-1* score could be used to supplement the cereal quality testing regime to permit easy and rapid screening of early generation material in wheat breeding programmes. This would then allow the utilisation of a wider range of parental germplasm since the *Glu-1* score provides a method of identifying the low-frequency, high-bread-making-quality lines from such crosses.

It is clear from previous studies (Payne 1987; Payne *et al* 1979, 1981, 1988) that *Glu-1* quality score is a direct measure of dough mixing strength. Therefore, the optimal *Glu-1* score for bread-making will depend absolutely on the particular type of bread to be made and the process to be used.

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