Statistical Relationships Between High Molecular Weight Subunits of Glutenin and Breadmaking Quality of Canadian-Grown Wheats[1]

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ABSTRACT

The relationship between the presence or absence of certain high molecular weight (HMW) subunits of glutenin and breadmaking potential was investigated using 26 diverse bread wheat varieties grown in Canada. Subunit composition was determined by polyacrylamide gel electrophoresis in the presence of sodium dodecyl sulfate (SDS-PAGE), and the subunits were identified by their relative molecular weights in kilodaltons (kDa). Thirteen different subunits were observed in the 26 varieties. The main criterion of baking quality was the baking strength index. We found that high-quality varieties have a predominance of specific subunits. Stepwise multiple regression analysis was used to generate the prediction equation for baking strength index from eight HMW subunits in the range of 96.3 to 147.4 kDa ($r^2 = 0.675$; $P < 0.01$). For a different set of eight varieties, the predicted values agreed with actual values within the 95% confidence limit. These findings indicate that selection on the basis of HMW subunit composition should be useful in breeding programs for screening genotypes for breadmaking quality.

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Breadmaking potential (loaf volume) of bread flours of a wheat variety is directly proportional to the protein content of the flour (Finney and Barmore 1948, Bushuk et al 1969). The slope of that relationship depends on variety, i.e., it is a genotypic trait. There is now substantial evidence that most of the intervarietal difference in breadmaking potential results from quantitative and qualitative differences in glutenin proteins (Branlard and Dardevet 1985, Burnouf and Bouriquet 1980, Orth and Bushuk 1972). Apparently, several structural features contribute to the observed variation in functionality (reviewed in Bushuk and MacRitchie 1988). Among the molecular features, subunit composition (electrophoretic bands of reduced glutenin), especially that of the high molecular weight (HMW) components, has been strongly implicated on the basis of statistical evidence (Branlard and Dardevet 1985; Campbell et al 1987; Cressey et al 1987; Lawrence et al 1987; Lorenzo and Kronstad 1987; Payne et al 1980a, 1981a, 1987).

This article examines further the interrelationship between HMW subunit composition and breadmaking potential using a group of widely different bread wheat varieties grown in Western Canada.

MATERIALS AND METHODS

Chemicals

Glycine, Tris, glycerol, potassium hydroxide, and Coomassie Brilliant Blue G-250 were obtained from Sigma Chemical Company (St. Louis, MO). Acrylamide, bisacrylamide, and sodium dodecyl sulfate (SDS) were of electrophoretic grade and were obtained from Bio-Rad (Richmond, CA). All other chemicals used were of analytical reagent grade.

Wheat Samples

Grain of 26 wheat varieties grown in 1983 at four locations (Lethbridge, Regina, Saskatoon, and Swift Current) was provided by A. B. Campbell of the Agriculture Canada Winnipeg Research Station (Table I). Grain of eight cultivars (registered varieties) of the Canada Western Red Spring wheat class was from the 1985 Bread Wheat Cooperative Test provided by the Agriculture Canada Winnipeg Research Station (Table VI). Grain of the Canadian bread wheat Marquis was used as the reference standard (Bushuk and Zillman 1978).

Sample Preparation

In order to have sufficient grain for the technological tests, it was necessary to combine the samples from the four locations for each variety. Before this was done, the identity of each of the 104 samples was verified by polyacrylamide gel electrophoresis (PAGE) (Sapirstein and Bushuk 1985). One sample was found to be a mixture of varieties and was discarded.

Three different starting materials—whole wheat meal, flour, and extracted glutenin—from four varieties of widely different breadmaking quality were examined as the source of glutenin. No intravarietal differences for the three starting materials were observed; accordingly, flour was used as the starting material for all electrophoretic analyses.

To confirm that the electrophoretic patterns were not affected by location, grain of six varieties from each of the four locations was examined by electrophoresis; no intravarietal differences were found. On the basis of the results of the three preliminary experiments, it was concluded that the four samples of each variety could be composited into a single larger sample that would be representative of the variety.

For milling, the wheat was tempered to 15.5% moisture for 24 hr at 21°C. The grain was milled into straight-grade flour (ash content, 0.38–0.49% at 14% moisture basis) on a Buhler pneumatic laboratory mill.

Grain used in the preliminary experiments and that of the eight cultivars of the Bread Wheat Cooperative Test was milled on a Brabender Quadrumat Junior laboratory mill (Brabender Instruments Inc., South Hackensack, NJ). Whole wheat meal samples were prepared on a Udy cyclone mill (Udy Analyzer Co., Boulder, CO).

Preparation of Glutenin Extracts and Electrophoresis

Glutenin extracts were prepared according to Ng and Bushuk

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TABLE I
High Molecular Weight Subunits of 26 Wheat Varieties

Variety[a]	Subunit (kDa)												
	147.4	141.0	135.8	133.1	128.1	121.1	114.7	113.6	105.5	100.2	96.3	91.6	90.0
1 Cypress	−	+	−	−	+	−	+	−	−	−	+	+	−
2 Neepawa	−	−	+	−	+	−	+	−	−	−	+	+	−
3 Kenya	+	−	−	+	−	+	−	−	−	+	−	−	+
4 Columbus	−	−	+	−	+	−	+	−	−	−	+	+	−
5 Cook	+	−	−	+	−	−	+	−	−	+	−	−	+
6 Tobari 66/Romany	+	−	−	+	−	−	+	−	−	+	−	−	+
7 Neelkant sib	+	−	−	+	−	−	−	−	+	−	−	−	+
8 Veery #4	−	−	+	−	+	−	+	−	−	−	+	+	−
9 Veery #5	+	−	−	−	+	−	+	−	−	−	+	+	−
10 Nacozari 76	−	−	+	+	−	−	−	−	+	−	−	−	+
11 Veery #1	+	−	−	−	+	−	+	−	−	−	+	+	−
12 Veery #2	−	−	+	−	+	−	+	−	−	−	+	+	−
13 Veery #3	+	−	−	−	+	−	+	−	−	−	+	+	−
14 Bobwhite sib	−	−	+	−	+	−	+	−	−	−	+	+	−
15 Hopps/Robin//Kalyan	−	−	+	−	+	−	−	−	+	−	−	+	−
16 Veery sib	−	−	+	−	+	−	+	−	−	−	+	+	−
17 G11-AustII61-157// Cno/No/3/Rm "S"	−	−	+	−	+	−	−	+	+	−	−	+	−
18 Pavon 76	−	−	+	−	+	−	−	−	+	−	−	+	−
19 Oxley	−	−	+	−	−	−	+	−	−	+	−	−	+
20 Olympic	+	−	−	−	+	−	+	−	−	−	−	+	−
21 Halberd	+	−	−	−	+	−	+	−	−	−	+	+	−
22 Condor	−	−	+	−	−	−	+	−	−	+	−	−	+
23 Chile	−	−	+	−	−	−	+	−	−	+	−	−	+
24 HY 334	+	−	+	−	−	−	+	−	−	+	−	−	+
25 IAS 5	−	−	+	−	−	−	−	+	+	−	−	−	+
26 SUN 43A	+	−	−	−	+	−	−	+	+	−	−	+	−

[a] Grown in 1983 at four locations.

(1987). Polyacrylamide gel electrophoresis in the presence of sodium dodecyl sulfate (SDS-PAGE) was done on an LKB 2001 electrophoresis unit (Ng and Bushuk 1987).

Determination of Molecular Weights

To examine the relationship between HMW glutenin subunits and breadmaking quality, it is necessary to identify the subunits by some numerical parameter. In our previous paper (Ng and Bushuk 1987), we discussed some limitations of the numerical nomenclature used by Payne et al (1981b) and Payne and Lawrence (1983) and proposed an open system using relative molecular weights expressed in kilodaltons (kDa) to identify the subunits; this system of nomenclature will be used.

Technological Tests

Approved methods of the AACC (1983) were used for evaluation of milling and breadmaking quality. The remix baking test for 100 g of flour was carried out according to Kilborn and Tipples (1981). Volumes of the resulting loaves were measured using a pup loaf volumeter (National Mfg. Co., Lincoln, NB). Loaf volume values were used to calculate the baking strength index (BSI) according to Tipples and Kilborn (1974), which was used as the index of protein "quality" at a constant protein content.

Statistical Analyses

Data were analyzed by standard statistical methods. For the statistical comparison of glutenin subunit patterns, 1 and 0 were used to indicate presence and absence of a subunit, respectively. Data designated as 1 and 0 are considered as indicator or binary variables (Neter and Wasserman 1974). Correlation analyses were executed on an Amdahl 5870 computer system using the Statistical Analysis System (SAS 1985) program package with procedure CORR (correlation analysis).

To generate a prediction equation for a dependent variable (a technological parameter) using independent variables (HMW glutenin subunits), the STEPWISE (stepwise multiple regression) procedure from SAS (1985) was used with the maximum r^2 improvement option to select the best set of independent variables for the prediction equation. To use this equation to predict another set of data from selected independent variables, the REG (linear regression) procedure from SAS (1985) was used with the option of 95% confidence limits for an individual predicted value.

RESULTS AND DISCUSSION

High Molecular Weight Glutenin Subunit Composition

The SDS-PAGE patterns for 13 of the 26 varieties are shown in

TABLE II
Means and Standard Deviations (SD) for Molecular Weights of High Molecular Weight Glutenin Subunits of the 26 Varieties

Mean (kDa)		SD	n[a]	t[b]
147.4	±	1.6	33	
				6.72***[c]
141.0	±	1.6	3	
				6.51***
135.8	±	1.3	45	
				6.62***
133.1	±	1.5	15	
				12.26***
128.1	±	1.3	48	
				9.26***
121.1	±	0.6	3	
				11.13***
114.7	±	1.0	54	
				3.09**
113.6	±	1.1	9	
				17.37***
105.5	±	1.2	21	
				17.57***
100.2	±	0.7	21	
				17.66***
96.3	±	0.8	33	
				24.34***
91.6	±	0.9	48	
				9.14***
90.0	±	0.6	30	

[a] n, Total number of observations in three replicates.
[b] t, Student's t test between two means.
[c] **, ***, Significant at 1% and 0.1%, respectively.

Figure 1. The molecular weights listed on the left-hand side are for the Marquis wheat glutenin subunits that are used as reference proteins. The HMW region includes subunits from 90.0 to 147.4 kDa. This range covers HMW subunits 1 to 12 of Payne et al (1980b), which have MWs of 145.0 to 95.0 kDa. In the present study, the 26 varieties contained a total of 13 statistically different HMW glutenin subunits in the HMW region (Table II).

Intervarietal Relationship Between HMW Glutenin Subunits

Table I shows the distribution of the HMW glutenin subunits for the 26 varieties (presence is indicated by a plus). Each variety has four or five subunits. This observation is in general agreement with published data by Payne et al (1981b). The present study showed subunit 114.7 occurring in highest frequency (69.2%), whereas subunits 141.0 and 121.1 occurred only once each in two of the 26 varieties. These latter two subunits were not used in the statistical analyses because their frequency of occurrence was too low to justify relating them to intervarietal variation of breadmaking quality.

It was noted that subunits 128.1 and 90.0 never occurred together in the same variety; the same was true for subunits 147.4 and 135.8, except for variety 24, which has both of them. On the other hand, subunits 128.1 and 91.6 always appeared together.

The analysis of the relationship between HMW glutenin subunits and breadmaking quality is based on presence and absence of specific subunits. The amount of protein in a specific band, as indicated by the intensity, was not part of the analysis, because quantification requires an accurate and sensitive instrument for measuring band intensity and relating to the amount of protein. Furthermore, this estimation assumes that a similar amount of protein enters the gel for each variety, which may not be the case.

Simple correlation was used first to determine intersubunit relationships for the 26 varieties (Table III). Because subunits 128.1 and 91.6 always appeared together, the correlation coefficient of these was perfect ($r = 1.000$). On the other hand, subunits 128.1 and 90.0 or subunits 91.6 and 90.0 never appeared together in the 26 varieties ($r = -1.000$). Several subunits were positively or negatively correlated to each other at high levels of significance.

The number in parentheses under each subunit column heading in Table III is the identity, as far as can be ascertained, of the subunit according to the numerical nomenclature of Payne et al (1980b, 1981a,b). Studies are in progress to reconcile the two nomenclatures for all the numbered subunits reported by Payne and co-workers. Assuming that the match of the subunit numbers by Payne et al (1980b, 1981a,b) with the identities of the subunits reported in the present study was correct, subunits 147.4, 128.1,

TABLE III
Correlations Between High Molecular Weight Glutenin Subunits

Subunit (kDa)	147.4 (1)[a]	135.8 (2)	133.1 (2*)	128.1 (5)	114.7 (7)	113.6 (13–16)	105.5 (17–18)	100.2 (8)	96.3 (9)	91.6 (10)	90.0 (12)
147.4	1.0										
135.8	−0.842***[b]	1.0									
133.1	0.372	−0.372	1.0								
128.1	−0.123	−0.037	−0.617***	1.0							
114.7	0.065	−0.065	−0.309	0.158	1.0						
113.6	−0.066	0.066	−0.176	0.038	0.542**	1.0					
105.5	−0.169	0.169	0.144	−0.055	−0.910***	0.595**	1.0				
100.2	0.182	−0.007	0.364	−0.768***	0.217	−0.219	−0.368	1.0			
96.3	−0.103	−0.055	−0.418*	0.677***	0.571**	−0.309	−0.520**	−0.520**	1.0		
91.6	−0.123	−0.037	−0.617***	1.0***	0.158	0.038	−0.055	−0.768***	0.677***	1.0	
90.0	0.123	0.037	0.617***	−1.0***	−0.158	−0.038	0.055	0.768***	−0.677***	−1.0***	1

[a] Nomenclature of Payne et al (1980b, 1981a, 1981b); see text for details.
[b] *, **, ***, Significantly correlated at 5%, 1%, 0.1%, respectively.

TABLE IV
Correlations Between Technological Data and High Molecular Weight Glutenin Subunits

	Subunit (kDa)										
Parameter[a]	147.4	135.8	133.1	128.1	114.7	113.6	105.5	100.2	96.3	91.6	90.0
FA	−0.160	0.297	−0.141	0.232	−0.074	−0.073	0.191	−0.247	0.257	0.232	−0.232
DT	−0.192	0.059	−0.149	0.579**[b]	−0.056	−0.043	0.192	−0.511**	0.340	0.579**	−0.579**
MTI	0.051	−0.051	0.052	−0.565**	−0.023	0.123	0.080	0.531**	−0.498**	−0.565**	0.565**
E	0.330	−0.264	0.288	−0.561**	−0.059	0.159	0.015	0.548**	−0.574**	−0.561**	0.561**
R	−0.079	−0.093	−0.053	0.526**	−0.151	0.001	0.288	−0.525**	0.249	0.526**	−0.526**
R/E	−0.205	0.057	−0.150	0.598**	−0.084	−0.067	0.205	−0.586**	0.393*	0.598**	−0.598**
A	0.140	−0.290	0.071	0.335	−0.181	0.094	0.316	−0.333	−0.025	0.335	−0.335
LV	−0.086	−0.012	−0.153	0.522**	0.023	−0.050	0.133	−0.418*	0.362	0.522**	−0.522**
BSI	0.008	−0.037	−0.124	0.516**	0.042	−0.170	0.104	−0.355	0.308	0.516**	−0.516**

[a] FA = Farinograph absorption (%); DT = farinograph development time (min); MTI = farinograph mixing tolerance index (BU); E = extensibility (mm); R = maximum resistance (BU); R/E = ratio of R and E; A = area under the curve (cm^2); LV = remix loaf volume (cm^3); BSI = remix baking strength index.
[b] *, **, Significantly correlated at 5% and 1%, respectively.

TABLE V
Coefficients of High Molecular Weight Glutenin Subunits, Intercept, r^2, F, and Probability of F of the Prediction Equations for Six Breadmaking Quality Parameters

	Subunit (kDa)														
Parameter[a]	147.4	135.8	133.1	128.1	114.7	113.6	105.5	100.2	96.3	91.6	90.0	Intercept	r^2	F	Prob > F
DT	−1.10	···	3.57	5.54	3.74	···	4.98	2.02	···	···	···	−1.99	0.565	4.111	0.0082
MTI	−15.45	−20.87	−29.35	···	−19.21	3.22	−43.01	−22.43	−26.17	···	32.57	84.66	0.738	4.995	0.0026
E	···	−17.08	−9.69	···	17.34	13.20	···	···	−26.67	···	17.27	185.10	0.576	4.304	0.0066
R	···	···	323.33	479.31	384.72	···	708.47	305.69	169.85	···	···	−329.03	0.576	4.295	0.0067
R/E	−0.60	···	1.66	2.57	1.44	−0.96	2.31	···	···	···	···	0.48	0.576	4.295	0.0067
BSI	3.98	···	11.78	34.47	27.85	−15.69	65.68	41.53	21.99	···	···	7.70	0.675	4.416	0.0049

[a] Breadmaking quality parameters: DT = farinograph development time (min); MTI = farinograph mixing tolerance index (BU); E = extensibility (mm); R = maximum resistance (BU); R/E = ratio of R and E; BSI = remix baking strength index.

91.6, and 90.0 are subunits 1, 5, 10, and 12, respectively, reported by Payne and co-workers.

Relationships Between HMW Glutenin Subunits and Technological Parameters

Subunits 128.1 and 91.6 correlated significantly to the strength of the flour, as based on relationships between farinograph development time (DT) and subunit 128.1 ($r = 0.579$, $P < 0.01$), mixing tolerance index (MTI), and subunits 128.1 ($r = -0.565$, $P < 0.01$) (Table IV). The coefficients between DT and subunit 128.1, and subunit 91.6 were the same, as expected, since subunits 128.1 and 91.6 were perfectly correlated (Table III). If, as suspected, subunit 128.1 is indeed subunit 5, and subunit 91.6 is subunit 10 of Payne et al (1980b, 1981a,b), then the results of this study are in agreement with Branlard and Dardevet (1985), who reported that subunits 5 and 10 were significantly correlated with dough strength as measured by the Chopin Alveograph.

Payne et al (1981a) reported that subunits 2 and 12 (subunits 135.8 and 90.0 in this study) were associated with poor breadmaking quality. The results obtained in the present study also indicated a similar trend although not as clearly as reported by Payne et al (1981a) for English wheats. Subunit 90.0 correlated significantly with DT (negative correlation) and MTI (positive correlation). However, for the set of the varieties used in the present study, subunit 135.8 did not correlate with any of these parameters.

Analogous correlations were observed between HMW subunit composition and extensigraph parameters. Subunit 100.2 was significantly and positively correlated to extensibility (E) and negatively to maximum resistance (R). Likewise, subunit 90.0 was also significantly correlated to E and R. This is in general agreement with Branlard and Dardevet's findings (1985), which showed that their subunit 12 (subunit 90.0 in the present study) was significantly correlated to tenacity measured by the alveograph.

Our results indicate that, for the varieties investigated, subunits 100.2 and 90.0 are related to poor rheological properties as measured with the extensigraph. On the other hand, the correlation coefficients of subunits 128.1 and 91.6 to E and R showed that these two subunits were definitely associated with good rheological properties. These findings are also in general agreement with the published data of Branlard and Dardevet (1985) and Campbell et al (1987).

By definition, any of the HMW glutenin subunits that are related to breadmaking quality should correlate with loaf volume (LV). Indeed, the subunits significantly correlated to parameters from farinograph and extensigraph were also significantly correlated with LV (Table IV). As mentioned above, because LV is affected by protein content, it is more appropriate to use the baking strength index (BSI) for examining the relationship between HMW glutenin subunits and breadmaking quality because this index removes the effect of protein content per se. The subunits 128.1 and 91.6 showed highly significant positive correlations with both BSI and LV, whereas subunit 90.0 was negatively correlated. These findings are in general agreement with data published by Payne et al (1981a), Branlard and Dardevet (1985), Campbell et al (1987), and Lawrence et al (1987).

Based on the above findings, it was concluded that subunits 128.1, 91.6, and 90.0 are important to breadmaking quality; the first two contribute positively and the third, negatively.

Predicting Breadmaking Quality on the Basis of HMW Glutenin Subunit Composition

Stepwise multiple regression technique was used to generate equations for predicting certain breadmaking quality parameters from the HMW glutenin subunit composition. All of the 11 HMW subunits of the 26 varieties were used in stepwise multiple regression analysis as independent variables. Farinograph DT and MTI, extensigraph E, R, and R/E, and remix baking test BSI were each used as dependent variables in the regression analyses (Table V).

It can be seen that all r^2 values were significant below the 1% level (Table V, last column). Furthermore, not all of the 11 subunits were selected by statistical analysis for any one of the prediction equations. As mentioned before, some subunits were present or absent together with another subunit; both subunits of such pairs would not be selected for the prediction equation by the stepwise multiple regression analysis.

The range of r^2 values for the six prediction equations was 0.565 for DT to 0.738 for MTI. This means that 56.5% of the variation for DT is explained by six subunits, and that nine subunits account for 73.8% of the variation in MTI. For the BSI, 67.5% of the variation is explained by eight subunits in the range from 96.3 to 147.4 kDa. The prediction equation for BSI is as follows:

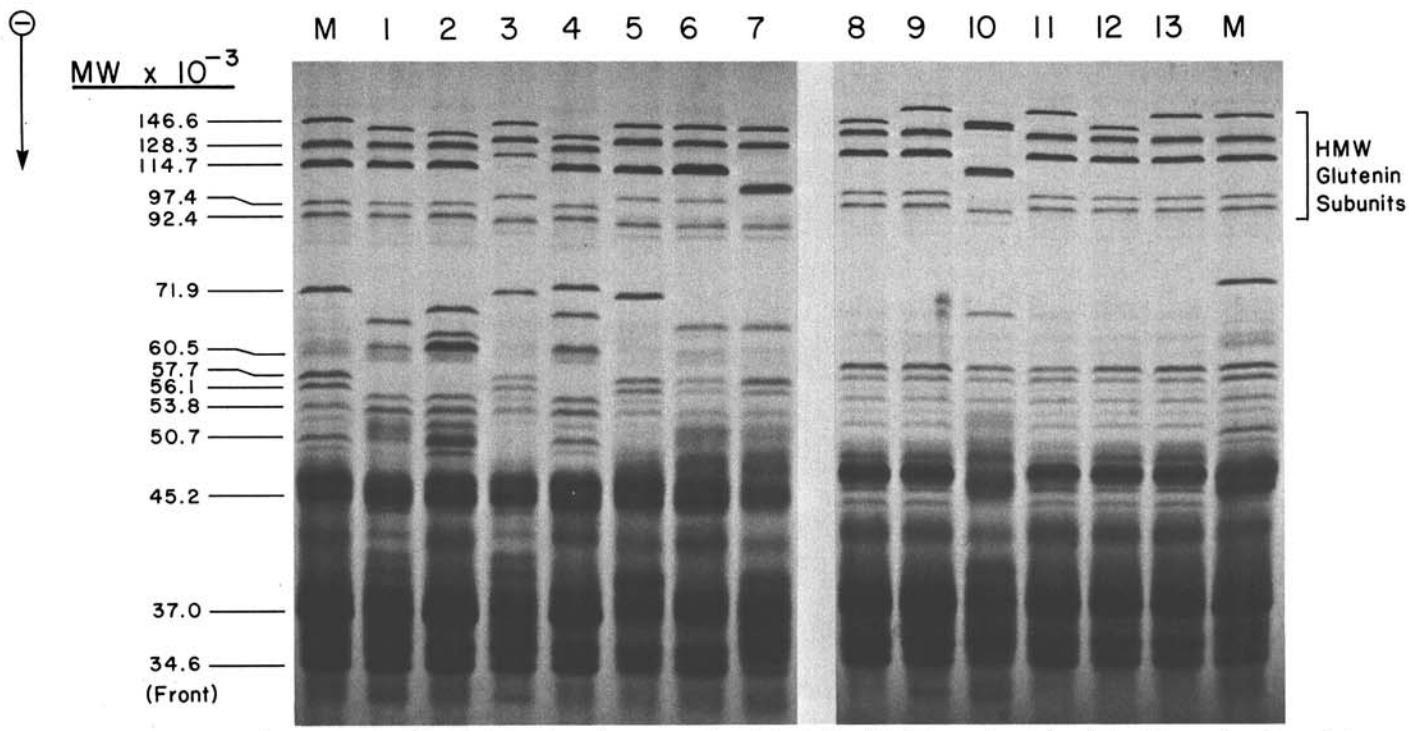

Fig. 1. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis patterns of varieties 1–13 of the 26 experimental varieties. **M** = variety Marquis; lane number corresponds to variety number listed in Table I. Molecular weights (**MW**) shown on left are for Marquis reference subunits.

$$BSI = 7.70 + 65.68\,[105.5] + 41.53\,[100.2] + 34.47\,[128.1] + 27.85\,[114.7] + 21.99\,[96.3] + 11.78\,[133.1] + 3.98\,[147.4] - 15.69\,[113.6]$$

To use this equation for a specific variety, the subunit identified by its MW shown in brackets is replaced by the number 1 (one) if it is present and by 0 (zero) if the subunit is absent in the SDS-PAGE pattern.

The predictive power of the equations generated by stepwise multiple regression analyses was tested by comparing predicted and actual values for a separate set of eight different cultivars from the 1985 Bread Wheat Cooperative Test (Tables V and VI). The SDS-PAGE patterns of these cultivars are shown in Figure 2. It should be pointed out that all eight cultivars are known to have high breadmaking quality as required by the Canada Western Red Spring wheat class. Detailed technological data for these varieties is published in the minutes of the 1986 meeting of the Expert Committee in Grain Quality (Anonymous 1986).

For all eight cultivars, DT and R were predicted within 95% confidence limits. Some predicted values were outside the 95% confidence limits, including MTI of one cultivar, R/E of two cultivars, and E of all eight cultivars. Obviously, factors other than HMW glutenin subunit composition contribute substantially to some of these parameters. Results presented here suggest that the contribution varies among varieties. All of the predicted values of BSI agree with actual values within the 95% confidence limit (Table VI).

TABLE VI
Predicted and Actual Baking Strength Index Values

Variety[a]	Predicted Value	Actual Value	95% Confidence Interval	
			Lower	Upper
C 1 Marquis	96.0	97.7	73.7	118.3
C 2 Neepawa	92.0	99.1	70.3	113.7
C 3 Sinton	92.0	101.4	70.3	113.7
C 4 Benito	92.0	97.5	70.3	113.7
C 5 Columbus	92.0	104.0	70.3	113.7
W1 Katepwa	92.0	102.3	70.3	113.7
W2 Leader	111.5	99.3	83.3	139.8
W3 Lancer	111.5	110.7	83.3	139.8

[a]Grain of the Canada Western Red Spring wheat class from the 1985 Bread Wheat Cooperative Test.
[b]Values obtained from the minutes of the 1986 meeting of the Expert Committee in Grain Quality (Anonymous 1986).

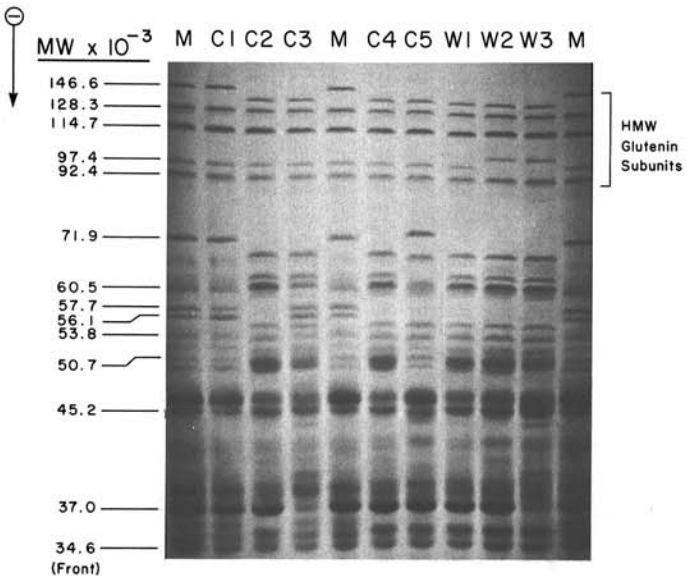

Fig. 2. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis patterns of Canada Western Red Spring wheat cultivars. M = variety Marquis; lane number corresponds to variety number listed in Table VI. Molecular weights (**MW**) shown on left are for Marquis reference subunits.

On the basis of the evidence presented, it was concluded that for a fairly narrow group of bread wheat varieties grown under reasonably uniform environments, about 67% of the intervarietal variation in BSI can be explained on the basis of differences in composition of the HMW subunits of glutenin. The results obtained here cannot be generalized for all bread wheats, since the prediction equations were generated from data for a limited number of varieties (26). However this study showed that the HMW glutenin subunit composition may have some potential for selecting varieties for breadmaking quality in wheat breeding programs. Precise details of the relationship of glutenin structure to its functional role in breadmaking remain to be worked out.

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