

Statistical Correlations Between Quality Attributes and Grain-Protein Composition for 71 Hexaploid Wheats Used as Breeding Parents

W. P. CAMPBELL,¹ C. W. WRIGLEY,¹ P. J. CRESSEY,² and C. R. SLACK³

ABSTRACT

Cereal Chem. 64(4):293-299

Seventy one wheat lines of diverse quality and protein composition were grown under the same conditions to produce over a kilogram of grain, which was milled into flour for extensive quality testing (farinograph, extensigraph, grain hardness, baking, residue protein, and sodium dodecyl sulfate sedimentation). In statistical correlations between these results and gluten composition, no protein components were found to be related to dough extensibility or development time, but very highly significant

relationships were obtained between other measures of grain quality (especially resistance to dough extension) and specific gliadins and high molecular weight glutenin subunits. The protein components most consistently implicated were high molecular weight glutenin subunits 5 and 10 and gliadin 59 (with high resistance) and glutenin subunits 2 and 12 and gliadin 58 (with dough weakness).

Several studies have indicated that specific gluten proteins correlate with desirable grain-quality attributes, mainly dough properties. If these indications were established to hold generally, then the possibility of major genes for grain quality being manipulated by conventional breeding and by genetic engineering could be realized, leading to simple testing of minute samples for quality type. Such testing could involve detecting these quality-related proteins by electrophoresis or high-performance liquid chromatography, or with specific antibodies.

Early indications of such relationships were provided by studies of durum wheat (Damidaux et al 1980, Kosmolak et al 1980, duCros et al 1982), for which groups of gliadin components, genetically linked to either gliadin 45 or gliadin 42, were statistically correlated with strength or weakness of dough, respectively. In durums, the high molecular weight (HMW) glutenin subunits do not appear to be related to grain quality, but low molecular weight glutenin subunits do, presumably because of the genetic linkage of the genes for their synthesis to those for the above gliadins (duCros 1987).

Similar information concerning protein-quality associations in hexaploid wheats has been accumulating, with attention focusing on specific HMW glutenin subunits, the presence of 5 and 10 being associated with dough strength and of 2 and 12 with weakness (Payne et al 1981; Paradies and Ohms 1984; Moonen and Zeven 1985; Burnouf and Bouriquet 1983; Branlard and Dardevet 1985a,b).

Other studies have concentrated on gliadin proteins or have attempted to examine both classes of proteins (Wrigley et al 1982, Sozinov and Poperelya 1980, Peruffo et al 1985, Branlard and Dardevet 1985a, Sasek et al 1986), with indications that the presence of specific gliadin proteins also correlates with dough properties.

However, most of these studies on hexaploid wheats are inadequate in some respect, e.g., a restricted range of genotypes was examined, quality testing was inadequate (being based on small-scale tests), or the range of proteins examined was restricted to either gliadins or HMW glutenin subunits. Furthermore, in studies of commercially acceptable varieties, particularly poor quality types have already been eliminated, making the study nonrepresentative of a breeding situation.

The study described in this article was designed to overcome some of these problems. In particular, it involved a wide range of quality types, with many genotypes being grown together to

eliminate environmental factors, and producing sufficient grain (over a kilogram) to permit a range of conventional quality tests to be applied. Two types of electrophoretic analyses were applied, so that protein composition could be defined according to both gliadins and HMW glutenin components.

The wheats for this study were a set of parent lines chosen for the wheat-breeding program conducted at the Waite Agricultural Research Institute (South Australia) by A. J. Rathjen. The basis of choice was mainly agronomic, rather than grain quality. Consequently, the set represents a very wide range of quality types and is deemed to be typical of the full range of qualities encountered in a breeding program. In the article accompanying this one (Cressey et al 1987), the conclusions derived from this study of parent lines are compared with those obtained for unselected fixed lines from a very different breeding program. These complementary studies indicated the same proteins were useful markers of high (or low) resistance to dough stretching.

MATERIALS AND METHODS

Grain Samples

The set of samples analyzed involved 71 wheats collected from many countries by A. J. Rathjen (Waite Agricultural Research Institute, South Australia). They were all grown at Strathalbyn in South Australia during 1982. Although many are named cultivars, the wheats were diverse with respect to quality (Table I), the main criterion for their selection and maintenance as parental stock for breeding purposes being agronomic attributes. They are listed below according to country of origin.

Argentina. Gaboto, Klein Petiso Raf, Pato Argentino, Son 64*Kl.Rend.

Australia. Bencubbin, Currawa, Dirk, Free Gallipoli, Gluyas,

TABLE I
Range of Quality Values for the Set of 71 Wheat Lines Examined

Attribute	Units	Range	Mean	Standard Deviation
Resistance (5 cm)	BU	110-400	232	69
Resistance (max)	BU	120-770	350	161
Extensibility	cm	16-26	21.5	2.2
Development time	min	2-8	4.6	1.7
Loaf volume	ml	684-936	816	57
Work input	Whr/kg	2.8-23.7	9.2	4.3
SDS volume	ml	43-87	71.1	8.4
Residue protein	%	25.9-38.1	31.7	3.4
Particle size	...	7-29	17.8	5.3
Water retention capacity	%	59-89	72.8	8.3
Water absorption	%	56-69	61.0	3.4
Color grade	...	-0.8 to 2.4	0.4	0.7
Protein content	%	10.0-14.1	12.1	1.0

¹CSIRO Wheat Research Unit, North Ryde (Sydney) NSW 2113, Australia.

²DSIR Wheat Research Institute, Christchurch, New Zealand.

³DSIR Plant Physiology Division, Palmerston North, New Zealand.

This manuscript was prepared for electronic processing.

Heron, Insignia, MH3* Warimba, Nabawa, Pinnacle, Ranee, Reldep, Teal, Ward's Prolific.

Belgium. Jufy 1.

Brazil. Carazinho.

Canada. Manitou (Insens), Marquis, Selkirk, Thatcher.

Chile. Huelquen, Mara*Seprem-Mentara-MCM.

Columbia. Toquifen*S*, Crespo.

Egypt. Giza 160.

Guatemala. Xelaja 66.

India. Chhoti Lerma, C-271, C-273, C-306, C-518, Hira, Kalyansona 227, Sonalika.

Israel. Hezera 2152.

Italy. Victor 1.

Japan. Haruhikari.

Kenya. Kenya Leopard.

Mexico. BB-Inia, Calidad, Ciano 'S', Inia 66, Lerma Rojo 64A, Potam 70, Roque 66, Sondra 64A, Tanori 71, Tobari 66, Vicam 71, 8156.

Netherlands. Opal.

New Zealand. Tainui.

Pakistan. Chanab 70.

Portugal. Mexicana 1481.

South Africa. Red Egyptian, Turpin 7.

Tunisia. Ariana 66, BT-2288, T-64-2W.

United States. Chris, Crim, Era, Hope, Justin.

Zimbabwe. Jaral*S*/Lee-SK-MANA, Lundi, Zambezi.

and Martin series 3 color grader according to the instructions of the manufacturer (INS 43C, Henry Simon Ltd).

Predictive test. Alkaline water retention capacity was determined by the method of Yamazaki et al (1953) and, employing an established calibration, was used to predict farinograph water absorptions.

Small-scale quality tests. Percentage residue protein was determined as the proportion of flour protein insoluble in 0.05M acetic acid according to Orth and O'Brien (1976). The sodium dodecyl sulfate (SDS) sedimentation volume was estimated by the method of Axford et al (1978).

Full-scale quality tests. Farinograph development time and water absorption were determined by a modification of AACC method 54-21 (H. J. Moss, *personal communication*). For this modification, water absorptions were initially estimated from alkali water retention capacity and flour color grade through an established calibration. A dough was mixed from 50 g of flour using this water absorption, with any further additions of water dispensed by an automatic titrator (Mitchell and Meredith 1966). Doughs were mixed to just past peak, then removed and stored in a sealed container. A second dough was mixed with the corrected water absorption to peak and combined with the first dough piece. A 150-g sample was weighed off for extensigraph testing. Resistance to extension measured at 5 cm or at maximum height and extensibility were determined with a Brabender Extensograph (AACC 1983) on the dough piece after a 45 min rest. Mechanical dough development, water absorption, and work input were determined by mixing a dough from 125 g of flour according to the method described by Mitchell (1984). A second dough was mixed using these optimized parameters and test baked. The resulting loaves were assessed for loaf volume by rapeseed displacement.

Assessment of Quality

Grain (about 1 kg) of each line was milled to an extraction rate of 72% on a Buhler type MLU-202 laboratory mill, fitted with entoleters to further reduce endosperm particles in size. Grain hardness was measured as particle size index (PSI) (Symes 1961). The following range of quality tests was applied to the flour samples.

Tests to screen for flour defects. Several tests were carried out to ensure that flour samples were as uniform as possible with respect to environmental and processing factors. Protein content was determined by the boric acid modification of the Kjeldahl method (AACC 1983). Falling number was determined on 5 g of flour (AACC 1983). Flour color grade was determined on a Kent-Jones

Grain Protein Composition

Gliadin proteins were extracted with 1M urea (6 µl/mg flour) and fractionated by gel electrophoresis in sodium lactate buffer (pH 3.1) in gels containing a 2.5 to 13% gradient of polyacrylamide (duCros and Wrigley 1979). In order to allow computer analysis, electrophoretic bands were assigned mobilities relative to that of Marquis band 50 (Bushuk and Zillman 1978), as shown in Figure 1. In all, 49 possible band positions were allocated. For each wheat,

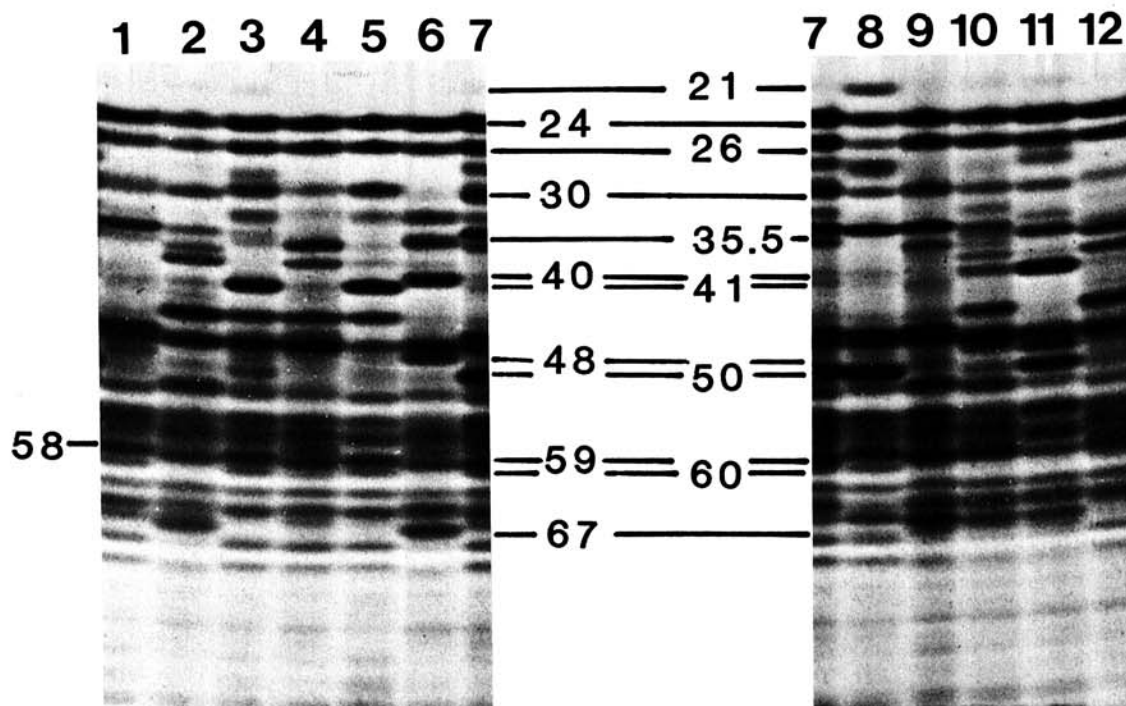


Fig. 1. Electrophoretic patterns for gliadin proteins separated in a 2.5 (top) to 13% gradient of polyacrylamide at pH 3.1 (cathode at bottom). Designations for some components are given according to the nomenclature of Bushuk and Zillman (1978). Samples were 1, Opal; 2, Pato Argentino; 3, Pinnacle; 4, Potam 70; 5, Ranee; 6, Red Egyptian; 7, Marquis; 8, Reldep; 9, Roque 66; 10, Selkirk; 11, Son 64* K1 Rend; 12, Sonalika.

TABLE II
Correlation Coefficients Between Qualities of the Set of 71 Wheat Lines Examined^a

Attribute	R5	Rmax	Ext	DT	LV	WI	SDS	Res	PSI
Resistance (5 cm), R5	1.00	...							
Resistance (max), Rmax	0.97	1.00	...						
Extensibility, Ext	0.10	0.24	1.00	...					
Development time, DT	0.38	0.51	0.06	1.00	...				
Loaf volume, LV	0.48	0.53	0.43	0.47	1.00	...			
Work input, WI	0.84	0.90	0.28	0.48	0.53	1.00	...		
SDS volume, SDS	0.68	0.71	0.47	0.45	0.69	0.67	1.00	...	
Residue protein, Res	0.75	0.77	0.16	0.37	0.49	0.72	0.60	1.00	...
Particle size, PSI	-0.59	-0.53	0.06	-0.21	-0.17	-0.56	-0.24	-0.48	1.00
Protein content, Prot	0.43	0.47	0.36	0.38	0.39	0.42	0.52	0.23	-0.23

^a Correlation coefficients above 0.47 are italicized as being very highly significant ($***P < 0.001$), those over 0.41 are highly significant ($**P < 0.01$), and those over 0.37 are significant ($*P < 0.05$).

the band intensities at each position were graded subjectively from 1 to 4 (1, absent; 2-4, increasing intensity). In this way each line could be represented by an electrophoretic profile of 49 digits, with each varying from 1 to 4. However on statistical analysis, no aspect of band intensity correlated with quality in any case. Presence or absence of gliadin components was thus the important parameter.

HMW-glutenin composition was determined by extracting flour samples with SDS and mercaptoethanol, and by electrophoresis in an SDS-polyacrylamide gel using the method of Laemmli (1970), as modified by Payne et al (1981). Subunit composition was described as a profile indicating the presence or absence of components in 20 positions (Payne and Lawrence 1983). Other faint bands were not recorded.

Computer Methods

All quality results and electrophoretic profiles were compared using a Genstat program to obtain similarity indices for all combinations, as described by duCros (1987). The bands with either high (significantly positive) or low (significantly negative) similarity indexes were then tested by the chi-squared method to determine the levels of significance. Correlation coefficients (as an alternative approach) provided the same quality-band associations and the same levels of significance.

RESULTS

Grain Quality Range

Examination of the ranges and standard deviations of the results of the specific quality tests applied to the 71 wheats indicates the broad spread of quality in this set of genotypes, justifying the claim that it represents a broader genetic base (with respect to dough properties and baking quality) than genotypes in many other studies (Table I). Some of the tests listed in Table I were designed to identify samples for which environmental or processing effects would confuse the interpretation of genetic differences. However, none was considered to be so extreme as to warrant omission. The results of falling number testing indicated that all samples were sound. Table II shows the extent to which variations in protein content interacted with other attributes.

Relationships are shown in Table II between those aspects of quality considered to particularly relate to genotype, and thus studied with respect to protein composition. Resistances of dough to extension, measured at 5 cm or at maximum height, correlated strongly with one another and with work input, which measures similar characteristics in the dough. They also correlated quite highly with most other quality attributes except dough extensibility. All these correlations were positive except that with PSI, reflecting the common observation that hard wheats (low PSI) have strong dough.

Protein Composition Range

Diverse gluten compositions were revealed in flour extracts of the 71 wheats, according to gliadin composition (Fig. 1; bands allocated to 49 possible positions), as well as for HMW glutenin polypeptides (20 positions). None of the wheats had the same overall protein composition, again indicating that a broad range of

TABLE III
Frequencies of Occurrence Together
of Certain High Molecular Weight Glutenin and Gliadin Components

Component	Glutenin Subunits				Gliadins					
	2	5	10	12	20	24	25	26	58	59
...										
Glu 2	31	...								
Glu 5	1	41	...							
Glu 10	1	41	41	...						
Glu 12	31	1	1	31	...					
Gli 20	0	8	8	0	8	...				
Gli 24	30	34	34	30	0	63	...			
Gli 25	0	8	8	0	8	0	8	...		
Gli 26	30	34	34	30	0	63	0	63	...	
Gli 58	8	9	9	8	0	18	0	18	18	...
Gli 59	20	33	33	20	8	43	8	43	0	51

^a Numbers indicate how many of the wheats had the band combination indicated.

genotypes was studied. Each had a unique gliadin composition. There were 26 different patterns of HMW glutenin subunits distributed between the 71 wheats. The most common combination occurred in 10 of the wheats; it consisted of HMW bands 2*, 5, 7, 9, and 10.

There were some consistent patterns of band distribution between genotypes. Some of these are illustrated in Table III, where gliadin and HMW glutenin subunits of particular interest are abbreviated to Gli and Glu, respectively, followed by the component number. For example, Glu 5 and Glu 10 appeared together in 40 wheats and also in one of the 31 that had glutenins 2 and 12. These combinations are consistent with previous observations (Payne and Lawrence 1983) that these proteins are coded by allelic pairs of genes; one wheat presumably contained a mixture of these two genotypes.

Similar tight linkages would explain the consistent pairings of Glu 14 with Glu 15 (Table IV), of Gli 20 with Gli 25, and of Gli 24 with Gli 26 (Table III). On the other hand, Gli 58 and Gli 59 occurred on a mutually exclusive basis in nearly all wheats, presumably because genes controlling their synthesis are allelic (Table III). Similarly, Gli 20 always occurred together with Gli 25, and Gli 24 with Gli 26, but Gli 20+25 never occurred together with Gli 24+26.

Table IV was compiled assuming the genetic relationships between glutenin subunits described by Payne and Lawrence (1983), the total pattern for any one wheat consisting of a selection of one allele from each locus of the three wheat genomes (A, B, and D). One allele from the Glu-A1 locus appeared in each sample, and one in each for the Glu-D1 locus (including one sample as a mixture of both 1D alleles), but many of the wheats appeared to be mixed for the 1B subunits, particularly for alleles involving subunits 7, 7+8, and 7+9.

Protein-Quality Associations

A similarity matrix was obtained relating the presence of all electrophoretic components with all quality attributes, so the

TABLE IV
Frequencies of Occurrence of Allelic Variants
of High Molecular Weight Glutenin Subunits in the 71 Wheats

Allele	Number
Glu-A1 locus	
1	29
2*	31
Null	11
Glu-B1 locus	
6 + 8	3
7	9
7 + 8	20
7 + 9	24
17 + 18	11
13 + 19	1
13 + 16	4
14 + 15	11
20	2
Glu-D1 locus	
5 + 10	41
2 + 12	31

individual proteins could be identified that most strongly related to a quality attribute being high or low. These are listed in Table V in decreasing order of similarity index, with the addition of significance of relationship based on chi-squared determinations.

No significant correlations were found between the presence of any protein component and extensibility or dough development time. However, many proteins were correlated (some very highly significantly) with other aspects of quality, particularly with resistance to extension. Glutenin subunits 5 and 10 and gliadin 59 correlated with high values for these aspects of quality, and low values were associated with the (allelic) glutenins 2 and 12 and gliadin 58. These combinations were most evident for resistance at 5 cm; their involvement in other qualities is presumably, at least partly, attributable to correlations between the quality attributes themselves (Table II). Protein content presumably played a part, because the mean protein content of lines having Glu 5+10 was slightly higher (12.5 ± 0.9) than those with Glu 2+12 (11.7%, with a standard deviation of 0.8).

Figure 2 focuses attention on the components mentioned above with respect to 69 of the wheats, omitting two in which these

A. First split according to glutenins.

No. wheats	Glu 2+12		Glu 5+10	
	29		40	
R5	188.3 ± 50.2	***	266.5 ± 63.8	
Rmax	239.6 ± 95.1	***	436.0 ± 149.5	
LV	786.6 ± 61.2	***	835.2 ± 45.0	
WI	6.9 ± 2.4	***	11.1 ± 4.6	
PSI	18.0 ± 5.7	NS	17.5 ± 5.1	

No. wheats	Gli 58		Gli 59		No. wheats	Gli 58		Gli 59	
	9		20			9		31	
R5	181.1 ± 28.5	NS	191.5 ± 57.8		197.8 ± 38.7	***	286.4 ± 55.4		
Rmax	216.7 ± 55.2	NS	250.0 ± 110.2		282.2 ± 104.1	***	480.7 ± 130.5		
LV	768.6 ± 43.2	NS	795.6 ± 66.6		824.4 ± 55.8	NS	838.8 ± 41.4		
WI	5.8 ± 1.1	NS	7.3 ± 2.7		7.1 ± 2.7	**	12.3 ± 4.4		
PSI	20.2 ± 3.7	NS	17.0 ± 6.3		22.2 ± 3.8	**	16.1 ± 4.6		

B. First split according to gliadins.

No. wheats	Gli 58		Gli 59	
	18		51	
R5	189.4 ± 34.0	**	249.2 ± 72.8	
Rmax	249.4 ± 87.6	**	390.2 ± 166.6	
LV	795.6 ± 55.8	NS	822.6 ± 55.8	
WI	6.4 ± 2.1	***	10.3 ± 4.5	
PSI	21.2 ± 3.8	***	16.4 ± 5.3	

No. wheats	Glu 2+12		Glu 5+10		No. wheats	Glu 2+12		Glu 5+10	
	9		9			20		31	
R5	181.1 ± 28.5	NS	197.8 ± 38.7		191.5 ± 57.8	***	286.4 ± 55.4		
Rmax	216.7 ± 58.2	NS	282.2 ± 104.1		250.0 ± 110.2	***	480.7 ± 130.5		
LV	768.6 ± 43.2	*	824.4 ± 55.8		795.6 ± 66.6	**	838.8 ± 42.4		
WI	5.8 ± 1.1	NS	7.1 ± 2.7		7.3 ± 2.7	***	12.3 ± 4.4		
PSI	20.2 ± 3.7	NS	22.2 ± 3.8		17.0 ± 6.3	NS	16.1 ± 4.6		

Fig. 2. Classification of 69 wheats examined according to the presence of gliadins 58 and 59 or of high molecular weight glutenins 2+12 and 5+10, giving means and standard deviations for the resulting groups and indicating degree of significance (*t* test) of differences between group results. **R5** = resistance at 5 cm on extensigram, **Rmax** = maximum resistance, **LV** = loaf volume (by mechanical dough development), **WI** = work input (by mechanical dough development), **PSI** = particle size index. Significance levels: ****P* < 0.001, ***P* < 0.01, **P* < 0.05, and NS, not significant. Wheats excluded from this comparison contained either both glutenins 2+12 and 5+10 or neither gliadins 58 or 59.

components were either mixed or absent. The aim of this exercise was to see how effectively quality attributes could be predicted according to the presence of these components. Classification of the wheats according to the Glu 2+12/Glu 5+10 groupings was extremely effective for dough resistance (at 5 cm or maximum height), for loaf volume, and for work input, but not for PSI. Subsequent classification for the presence of gliadins 58 and 59 was only effective in separating out the wheats with the highest values of the attributes.

Classification according to these gliadins was less effective than by glutenin components when used as the first step in segregation.

DISCUSSION

Evidence is provided above for the existence of statistically based associations between quality and specific protein components. Such evidence has been reported by others for small-scale quality tests and for different sets of wheats. The value of such associations is likely to be their universal applicability to any combination of wheats, rather than merely to the wheats studied. It was for this reason that a broad genetic base was sought in choosing the genotypes for this study; there are various indications that this aim was achieved.

Better still, however, is the possibility that independent studies in many places might identify similar associations for the same protein components. Such general agreement has been reached, for example, on the importance of gliadins 45 and 42 and associated proteins for durum wheats.

HMW Glutenin Subunits

In an attempt to summarize several previous studies of hexaploid wheats, Tables VI and VII were compiled to compare quality-related proteins on a consistent basis. Immediately, however, problems arise of inconsistent nomenclature and of different electrophoretic procedures. The nomenclature of Payne and Lawrence (1983) for HMW glutenin bands was used in this biochemical study in preference to their allele classification,

TABLE V
Electrophoretic Components that Correlate Best with Quality Attributes in the 71 Wheats Examined When the Attribute is Either at a High or a Low Value^a

Attribute	Value	Electrophoretic Components in Decreasing Order of Significance
Resistance (5 cm)	High	Glu 5+10***, Gli 59***, Gli 67**, Gli 20+25*, Gli 35.5*, Gli 48*
	Low	Glu 2+12***, Gli 58***, Gli 14+15**, Gli 24+26*, Gli 41*, Gli 60*, Gli 30*
Resistance (max)	High	Glu 5+10***, Gli 48**, Gli 20+25**, Gli 67**, Gli 23**, Gli 59**, Gli 40*, Gli 35.5*
	Low	Glu 2+12***, Gli 60***, Gli 24+26**, Gli 58**, Gli 14+15*, Gli null*
Extensibility	High	No proteins correlate
	Low	No proteins correlate
Development time	High	No proteins correlate
	Low	No proteins correlate
Loaf volume	High	Glu 5+10***
	Low	Glu 2+12***, Gli 60*, Gli 14+15*
Work input	High	Gli 20+25***, Gli 23***, Gli 5+10**, Gli 7**, Gli 48**, Gli 59**, Gli 67*
	Low	Gli 24+26***, Gli 2+12**, Gli 14+15**, Gli 58*
SDS ^b volume	High	Glu 5+10**, Gli 37*, Gli 59*
	Low	Glu 2+12**, Gli 14+15**
Residue protein	High	Gli 37**, Gli 63**, Gli 5+10*
	Low	Glu 2+12*
Particle size	High	Gli 58**, Gli 60**, Gli 24+26*, Gli 14+15*, Gli 2+12*, Gli 41*
	Low	Gli 59**, Gli 67**

^a Extent of correlation is shown as very highly significant (***), highly significant (**), or significant (*).

^b SDS = Sodium dodecyl sulfate.

although this is also listed in Table VI.

The consistent prominence of Glu 5+10 and Glu 2+12 among the HMW glutenin subunits is most striking in Tables V and VI and is consistent with studies on several other sets of wheats; some of these studies are mentioned in Table VI. It is significant that these proteins are associated with the D-genome, the one that distinguishes bread wheats from durum. This probably explains why HMW glutenin subunits have not been found to be associated in any way with dough properties in durum wheats (duCros 1987).

The correlation of these components to quality was not, however, shown to the same extent in studies of Australian wheats by Wrigley et al (1982) or more recently by Lawrence (1986). This may result from another HMW glutenin combination, bands 17+18 (allele Bli) which is particularly prominent in strong Australian wheats, appearing in 34% of the 106 cultivars examined by Lawrence (1986), but encountered in only 4% of 300 cultivars from a world collection (Payne and Lawrence 1983). It may thus provide a further opportunity not yet generally exploited. This allele was shown to be related to high SDS volume by Payne et al (1984) and Branlard and Dardevet (1985b).

The association between Glu 14+15 and low resistance may be the result of pedigree associations, as all but two of the wheats with these components were Australian (Currawa, Free Gallipoli, Gluyas, Heron, Pinnacle, Ranee, Teal, and Ward's Prolific).

Gliadins

Table VII also compares gliadin components studied in quality associations. The four studies quoted agreed on involvement of the ω -gliadins (of low mobility) coded by genes on chromosomes 1D and 1B (see Sozinov gene-block designations).

These gliadins have mobilities in the same general region as some of the components genetically linked to gliadins 42 and 45 in durum wheat (duCros et al 1982), but none of the studies on hexaploid wheats listed in Table VII showed strong quality associations with gliadins in the region of 42-45. On the other hand, gliadins in this mobility region are implicated by the studies

TABLE VI
Likely Correspondence Between Gluten Protein High Molecular Weight Glutenin Components Implicated by Certain Authors in Associations with Wheat Quality

This Study	Payne et al (1981)	Payne and Lawrence (1983)	Moonen et al (1982, 1983)	Chromosomal Location
Glu 5+10	5+10	Glu-D1d	3+10	1D
Glu 2+12	2+12	Glu-D1a	2+11	1D
Glu 14+15	(14+15)	(Glu-B1h)	...	1B
Glu null	null	Glu-A1c	1 absent	1A
Glu 7	7	Glu-B1a	5	1B

TABLE VII
Likely Correspondence Between Gluten Protein Gliadin Components Implicated by Certain Authors in Association with Wheat Quality^a

This Study	Wrigley et al (1982)	Sozinov and Poperelya (1980)	Branlard and Dardevet (1985)
Gli 20+25	(1+3)	1D4	11+16
Gli 23	2	1D4	13.5
Gli 24+26	2+4	1D1	14.5+17
Gli 30	(9)	(1A/1D)	(23.5?)
Gli 35.5	(32)	1B2	32
Gli 40	16?	1B2	37?
Gli 41	(17)	(1B11)	(39.5?)
Gli 48	(20)	1B2	49
Gli 58	34?	(6B/6D)	(64?)
Gli 59	34?	(6B/6D)	(67?)
Gli 60	34?	(6A/6D)	(68?)
Gli 67	...	(6A)	(78?)

^a Tentative assignments are indicated by a ?. For some attempts to provide correspondence to the Sozinov-Poperelya nomenclature it was possible to indicate only chromosomal location. Band numbers in brackets were not indicated by those authors to be quality related.

of Peruffo et al (1985) and of Wrigley et al (1982) (gliadin 19). Presumably these differences in associations relate particularly to the range of genotypes studied.

The gliadin bands most strongly associated with dough resistance in the present study (58, 59, 60, 67) have not previously received particular attention in this respect, but they probably correspond to components of the compound gliadin 34 of Wrigley et al (1982). They are presumably coded by genes on homoeologous group 6 chromosomes. Unfortunately they lie in a part of the electrophoretic pattern where they are not clearly discernible by most electrophoretic procedures, explaining perhaps why they have gone largely unnoticed previously.

Most notable about the gliadins, however, is that many more gliadins were implicated in quality associations in Table V than HMW glutenins. This may be because of further genetic linkages that were not detected in the statistical approach (up to seven bands have been reported in a gliadin gene block by Sozinov and co-workers).

The Basis of Protein-Quality Associations

It would be very useful to know the cause for the emerging associations between certain gluten proteins and specific aspects of quality. Presumably the associations have a strong genetic basis and are thus valuable in breeding. However, there may not be a cause-and-effect relationship between the protein component(s) and the observed quality attribute (e.g., resistance of dough to extension). It is possible that a dough-modifying compound may be the product of another gene, closely linked to the protein gene. Perhaps this problem can only be resolved by molecular genetics studies.

The problem remains that the main accent has so far been on statistical studies, which can be misleading due to unconsidered factors. However, evidence for the value of such bands as markers of quality is starting to be provided by actual breeding experiments. For example, evidence that Glu 5+10 produces "stronger" wheats than Glu 2+12 has recently come from producing reconstituted hexaploids (Lagudah et al 1987) and from quality evaluation of contrasting biotypes of Australian wheats (Lawrence et al 1987).

At this stage, attention has focused particularly on the most extreme effects, but all these studies also point to components whose presence appears to modify dough properties to a lesser extent. These could be valuable in the most common breeding situations where extremes of strength or weakness are not desired.

As grain quality (even dough resistance to extension) is known to be modified by genetic factors other than protein composition, it is over simplistic to suggest that quality differences can be explained merely in terms of quality-associated protein components. However, evidence is accumulating to support the view that this approach can indicate the existence of major genes that can simplify breeding for grain quality by conventional means. Such evidence also opens new possibilities for genetic engineering. This, and related studies, indicate gluten components whose incorporation through breeding might be expected to raise or lower resistance to extension (depending on the aims of breeding). The extent of these effects might be expected to vary with the degree of correlation of the specific component to dough properties and with its interaction to the new genetic background. Breeding studies to test these possibilities are in progress in several centers.

ACKNOWLEDGMENTS

We wish to thank A. J. Rathjen for providing the wheat samples studied, H. J. Moss for assisting with and advising on quality evaluation, and W. B. Griffin for SDS-sedimentation and SDS-PAGE analyses.

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[Received September 9, 1986. Revision received April 1, 1987. Accepted April 6, 1987.]