Prediction of Physical Dough Properties from Glutenin Subunit Composition in Bread Wheats: Correlation Studies

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ABSTRACT

The low and high molecular weight (LMW and HMW) subunit allelic composition of two sets of bread wheat genotypes (48 Australian cultivars and 53 genotypes from around the world) were compared according to the quality parameters of their dough as measured by extensigraph. The HMW subunits correlated more strongly ($r = 0.75$, $P < 0.001$) with maximum dough resistance (*R*max) than did the LMW subunits of glutenin ($r = 0.56$, $P < 0.001$) in the world wheat set. Conversely, the LMW subunits in the Australian wheats correlated more strongly ($r = 0.72$, $P < 0.001$) with *R*max than did the HMW subunits of glutenin ($r = 0.48$, $P < 0.01$). Dough extensibility (Ext) correlated equally with LMW ($r = 0.44$, $P < 0.001$) or HMW ($r = 0.43$, $P < 0.01$) glutenin subunits in the world set, but in the Australian wheat set, it showed significant correlation only with LMW subunits ($r = 0.54$, $P < 0.001$). However, in both sets of wheat, the highest correlation coefficients between predicted and actual *R*max and Ext were obtained when predictions were based on LMW and HMW subunits together. An effective predictive model of dough properties should therefore be based on the composition of both LMW and HMW glutenin subunits. Predictive formulas are presented, based on the wheat sets examined, to estimate *R*max and Ext; the factors involved for each locus provide a measure of the predictive value of the six glutenin subunit loci. The HMW glutenin subunits loci generally made a bigger contribution to *R*max values than did the LMW glutenin loci.

Recent years have brought advances in our understanding of the genetics and relationship to dough quality of the low molecular weight (LMW) subunits of glutenin in bread and durum wheats. Most of these subunits are controlled by *Glu-3* loci on the short arms of group 1 chromosomes in bread wheat (Jackson et al 1983, Gupta and Shepherd 1987), i.e., *Glu-A3*, *Glu-B3*, and *Glu-D3* loci (Singh and Shepherd 1988). In a survey of 220 bread wheat cultivars, six, nine, and five alleles, respectively, have been detected at these three loci (Gupta and Shepherd 1990). Considerable variation at the *Glu-A3* and *Glu-B3* loci in durum wheat has also been recorded (Gupta and Shepherd 1988). Allelic variation at these loci has been associated with significant differences in dough quality in bread (Gupta and Shepherd 1988, Gupta et al 1989) and durum wheat (Pogna et al 1990). In this respect, the LMW subunits appear to be similar to the high molecular weight (HMW) subunits. The latter, which are coded by genes at the *Glu-1* loci on the long arms of group 1 chromosomes, have been extensively studied (see reviews by Payne 1987, MacRitchie et al 1990). However, little has been published about the relative contributions to dough properties of these two groups of glutenin polypeptides.

The LMW subunits of glutenin had a much stronger correlation than had the HMW subunits of glutenin with the dough quality (as determined by extensigraph) in a set of 28 Australian bread wheats (Metakovsky et al 1990). In this study, only a small proportion of dough quality variation could be explained by HMW glutenin subunit composition, in contrast to the very high correlation between these subunits and wheat quality in genotypes from other countries, e.g., Britain, Spain, and Canada (Payne et al 1987, MacRitchie et al 1990).

Perhaps the most important information about these polypeptides from a breeding point of view is that the effects of the LMW and HMW glutenin subunits on dough quality appear to be additive (Gupta et al 1989, Pogna et al 1990). This enhances their value for predicting dough properties. However, the information available on the effects of LMW glutenin subunits is much more limited than for the HMW subunits; thus, further analysis is needed of the relationship between the LMW glutenin alleles and dough properties so that LMW and HMW subunits can be considered together so as to better predict flour quality.

Hence, in this study we compared the LMW and HMW subunit composition of two sets of bread wheat genotypes (48 Australian cultivars and 53 wheat genotypes from around the world) with their dough properties (resistance and extensibility) as determined by extensigraph. As a result, the LMW glutenin alleles were ranked with respect to their effects in predicting these dough properties.

MATERIALS AND METHODS

Genotypes Studied

The genotypes examined included 48 Australian cultivars and 53 cultivars or breeding lines from about 22 countries (referred to as the "world wheat" set). The two sets of wheats were listed in Lawrence (1986) and Campbell et al (1987), respectively. Details of these wheat genotypes and their glutenin subunit composition and dough quality estimates are provided in Gupta et al (1990).

Flour Quality Data

Dough properties were determined by the Brabender extensigraph (AACC 1983), using a 150-g piece of dough, and were indicated as resistance to extension (*R*max = the height of the extensigram at its maximum) and extensibility (Ext = the length of the extensigram). Campbell et al (1987) reported on the quality data for the world wheat set. *R*max and Ext values for the Australian wheats are based on regressions from many analyses of annual variety trials conducted at various sites over several years. The estimates are given for a flour protein content of 11-12% as listed by Gore et al (1989).

Glutenin Subunit Composition

The LMW glutenin subunit (Glu-3) composition of proteins, extracted with hot (>50°C) 70% ethanol from at least four seeds from each line was determined by the two-step, one-dimensional gel electrophoretic procedure of Gupta and Shepherd (1990), whose LMW-glutenin-allele symbols were adopted to express LMW glutenin composition. The electrophoretic procedure and the nomenclature for HMW subunit (Glu-1) composition were as described by Lawrence (1986).

Statistical Analysis

The relationships between *Glu-1* and/or *Glu-3* allelic composition and dough quality parameters (*R*max and Ext) were studied by regression analysis according to the MSUSTAT statistical program package (Lund 1986). The mean *R*max and Ext values for each HMW and LMW glutenin allele were subjected to multiple comparisons using Student's *t* test. In a multiple regression analysis, estimated *R*max and Ext were obtained using the actual means for the *Glu-1* and/or *Glu-3* alleles. The relationships between actual and estimated quality data were determined by linear correlation coefficients.

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RESULTS

Dough Quality and Glutenin Subunit Composition

The set of 53 world wheats showed a broad range of flour quality parameters (Table I) and glutenin composition, indicating that the set represents a broad genetic base. Of six, nine, and five LMW glutenin subunit alleles detected at *Glu-A3*, *Glu-B3*, and *Glu-D3* loci, respectively, among 220 bread wheat cultivars (Gupta and Shepherd 1990), four, seven, and five were present at the respective loci in the 53 wheat genotypes (Table II).

In comparison, variation in the 48 Australian wheat cultivars for dough properties and glutenin composition was relatively smaller (Tables I and III). This set represented three, four, and three alleles coded by *Glu-A3*, *Glu-B3*, and *Glu-D3* loci, respectively (Table III). Similarly, the HMW glutenin loci (*Glu-A1* and *Glu-B1*) were more variable in the world wheat set than in the Australian set. However, both sets of wheats contained the same number of *Glu-D1* alleles (Tables II and III). Frequencies of occurrence of the different *Glu-1* and *Glu-3* alleles in these two sets of wheats are given in Tables II and III. The glutenin composition of these genotypes is based on the analysis of at least four seeds. The cultivars we studied were pure with respect to their glutenin composition or contained another biotype at a very low frequency.

Relationship Between HMW Glutenin Score and *R*max

Linear regression analysis between the HMW glutenin (Glu-1) score based on Payne et al (1987) and the *R*max in a set of 69 wheats including 53 wheats from around the world showed a high correlation coefficient ($r = 0.65$, $P < 0.001$), indicating that the Glu-1 score accounted for about 42% of the variation in *R*max. A quality score of 1 for *Glu-B1h* (HMW subunits 14 and 15) allele was assigned, based on the relative mean *R*max value (Table II). High correlations between the Glu-1 score and various estimates of dough strength also have been reported for national wheat sets from many countries (for a review, see MacRitchie et al 1990).

A general trend of increasing *R*max with HMW glutenin score in the set of 48 Australian wheats was noted, but the Glu-1 score accounted for only about 19% of the variation in the *R*max ($r = 0.44$, $P < 0.01$). In a larger set of 102 Australian cultivars, the correlation was even lower ($r = 0.39$, $P < 0.001$). The inadequacy of HMW glutenin composition to explain the variation in dough quality in such cases (especially for Australian wheats) suggests that additional aspects of gluten composition (particularly LMW subunits of glutenin) must be examined to provide a more complete explanation.

Relating *Glu-3* and *Glu-1* Alleles to *R*max and Ext

The 53 world wheats and the 48 Australian wheats were also analyzed for their LMW glutenin (Glu-3) composition. Comparing

TABLE I
Flour Quality Values for Wheat Genotypes Examined for Low and High Molecular Weight Glutenin Subunit Composition[a]

Attribute	Units	Range	Mean	SD
World wheats (53)				
Maximum resistance	BU	120–770	351	169
Extensibility	cm	16–26	21.5	2.2
Australian wheats (48)				
Maximum resistance	BU	190–392	294	46.4
Extensibility	cm	19.5–25	22.4	1.0

[a] Protein content varied from 10 to 14.1% (mean = 12.1, SD = 1.0) for world wheat sets and 11–12% for Australian sets. (See also materials and methods section.)

TABLE II
Mean Maximum Dough Resistance (in BU) for 53 World Wheats Grouped According to Low Molecular Weight (*Glu-3*) and High Molecular Weight (*Glu-1*) Alleles and Comparison of Mean Values Using Student's Multiple *t* Test

	Allele					
Locus	*Glu-A3*	*Glu-B3*	*Glu-D3*	*Glu-A1*	*Glu-B1*	*Glu-D1*
a	...	...	356 b (15)	359 a (25)	490 d (3)	231 a (18)
b	402 b[a] (6)[b]	421 c (15)	381 b (15)	381 a (20)	419 d (13)	...
c	310 a (14)	191 a (7)	307 ab (18)	250 a (8)	376 c (15)	...
d	373 ab (6)	450 c (3)	215 a (2)	...	427 d (3)	412 b (35)
e	355 ab (27)	...	423 c (3)	...	260 b (2)	...
f	...	285 b (2)	...	...	...	...
g	...	337 b (11)	...	...	...	...
h	...	324 b (10)	...	...	203 a (12)	...
i	...	410 c (5)	...	...	360 c (7)	...
SEM[c]	75	57	59	60	54	52

[a] Letters following the resistance values are the ranking for each allele at the respective locus.
[b] Figures within parentheses indicate frequencies of occurrence of the respective alleles.
[c] Standard error of the means.

TABLE III
Mean Maximum Dough Resistance (in BU) for 48 Australian Wheats Grouped According to Low Molecular Weight (*Glu-3*) and High Molecular Weight (*Glu-1*) Alleles and Comparison of Mean Values Using Student's Multiple *t* Test

	Allele					
Locus	*Glu-A3*	*Glu-B3*	*Glu-D3*	*Glu-A1*	*Glu-B1*	*Glu-D1*
a	...	...	291 b (7)	291 a (19)	...	299 a (25)
b	321 b[a] (12)[b]	322 d (29)	309 b (33)	302 a (29)	305 ab (7)	...
c	285 a (8)	258 b (11)	257 a (8)	...	300 ab (11)	...
d	...	209 a (2)	...	...	...	297 a (23)
e	292 a (28)	...	...	...	273 a (15)	...
f	...	...	...	...	...	...
g	...	286 c (6)	...	...	...	...
i	...	...	...	...	318 b (15)	...
SEM[c]	20	14	17	19	18	19

[a] Letters following the resistance values are the ranking for each allele at the respective locus.
[b] Figures within parentheses indicate frequencies of occurrence of the respective alleles.
[c] Standard error of the means.

the mean *R*max values for different LMW glutenin alleles by Student's *t* test revealed that certain alleles at all the *Glu-3* loci (i.e., *Glu-A3*, *Glu-B3*, *Glu-D3*) showed significant differences with respect to the *R*max in both sets of wheats (Tables II and III). Alleles at the *Glu-A3* locus could be arranged into two ranks, and the allele *b* was superior to the other alleles (e.g., *c* and *e*). Similarly, the alleles at the *Glu-B3* locus occurring at a frequency of five or more showed three *R*max ranks. The allele *b* had the highest *R*max values, whereas the allele *c* had the lowest. The other alleles at this locus did not show consistent differences across sets, probably because they occurred in very low frequencies i.e., three or less. Results for the *Glu-D3* locus were also comparable between sets but were statistically significant only in Australian wheats; alleles *b* and *a* were superior to allele *c* (Table III).

Regarding the *Glu-1* (HMW) loci, alleles at the *Glu-A1* locus did not reveal significantly different mean *R*max values in either wheat set, although the trend of ranking was in accordance with their quality scores (Payne et al 1987). Alleles at the *Glu-B1* locus showed significantly different *R*max values in both sets, but allele *i* (bands 17 + 18) had significantly lower *R*max value than did allele *b* (bands 7 + 8) in world wheat sets, whereas they ranked equally in the Australian wheat set. The data also indicated that bands 17 + 18 were superior to bands 14 + 15 (allele *h*) and band 20 (allele *e*). Only two alleles were noted at *Glu-D1* locus in either wheat set, and both occurred in high frequencies (Tables II and III). However, the relative ranking of the alleles was not consistent between sets. In the world wheat set (Table II), allele *d* (bands 5 + 10) had significantly higher *R*max value than did allele *a* (bands 2 + 12). On the other hand, they did not give different *R*max values in the Australian wheat set (Table III).

TABLE IV
Mean Dough Extensibility (in cm) for 53 World Wheats Grouped According to Low Molecular Weight (*Glu-3*) and High Molecular Weight (*Glu-1*) Alleles and Comparison of Mean Values Using Student's Multiple *t* Test

	Allele					
Locus	*Glu-A3*	*Glu-B3*	*Glu-D3*	*Glu-A1*	*Glu-B1*	*Glu-D1*
a	···	···	21.1 a	21.9 b	21.3 a	20.7 a
b	22.0 ab[a]	20.8 a	21.1 a	21.5 ab	22.0 a	···
c	20.4 a	22.6 a	21.7 ab	20.0 a	21.9 a	···
d	22.3 b	20.3 a	20.0 a	···	20.7 a	21.8 a
e	21.7 a	···	24.0 b	···	19.0 a	···
f	···	22.0 a	···	···	···	···
g	···	21.3 a	···	···	···	···
h	···	21.7 a	···	···	21.3 a	···
i	···	22.2 a	···	···	21.4 a	···
SEM[b]	0.90	1.16	0.95	0.94	1.18	0.95

[a]Letters following the extensibility values are the ranking for each allele at the respective locus.
[b]Standard error of the means.

TABLE V
Mean Dough Extensibility (in cm) for 48 Australian Wheats Grouped According to Low Molecular Weight (*Glu-3*) and High Molecular Weight (*Glu-1*) Alleles and Comparison of Mean Values Using Student's Multiple *t* Test

	Allele					
Locus	*Glu-A3*	*Glu-B3*	*Glu-D3*	*Glu-A1*	*Glu-B1*	*Glu-D1*
a	···	···	22.3 a	22.3 a	···	22.6 a
b	23.1 b[a]	22.6 a	22.5 a	22.3 a	23.7 b	···
c	22.5 ab	22.1 a	22.0 a	···	22.0 a	···
d	···	21.6 a	···	···	···	22.1 a
e	21.9 a	···	···	···	22.1 a	···
f	···	···	···	···	···	···
g	···	22.0 a	···	···	···	···
i	···	···	···	···	22.2 a	···
SEM[b]	0.84	1.18	1.11	1.11	0.85	1.05

[a]Letters following the extensibility values are the ranking for each allele at the respective locus.
[b]Standard error of the means.

Regarding Ext, LMW *Glu-A3* locus showed significant differences in values in both wheat sets, and allele *b* and/or *d* were associated with greater Ext values than were alleles *c* and/or *e* (Tables IV and V). Two ranks were found in the Ext values for *Glu-D3* alleles in world wheats (Table IV). Allele *e* was better than alleles *a, b,* or *d.* This ranking could not be confirmed in the Australian set because the allele *e* was absent. Among HMW glutenin loci, allele *a* (band 1) at the *Glu-A1* locus had a higher Ext value than did the null allele *c* in world wheats. The latter allele was not present in the Australian wheat set, however. The *Glu-B1* locus gave conflicting results between the sets. In the Australian wheat set, allele *b* (bands 7 + 8) was superior to others (alleles *c, e, i*), whereas it ranked equally with the others in the world wheat set. Overall, these data indicate that variation in LMW subunits of glutenin is also needed to provide a better explanation of differences in dough properties.

Predictability of Dough Quality Using *Glu-1* and/or *Glu-3* Alleles

The dough quality data from the two sets of wheats were used to develop predictive equations to estimate *R*max and Ext, based on allocating a factor for each of the three LMW glutenin loci (*Glu-A3*, *Glu-B3*, *Glu-D3*) alone, or to each of the three HMW glutenin loci (*Glu-A1*, *Glu-B1*, *Glu-D1*) alone, or to all six loci together. For instance, the predictive equations for *R*max took this form: $R\text{max}_{est} = a_O + \Sigma(a_i \times \overline{R\text{max}}_i)$, where a_O is the intercept, a_i is the slope or factor for each individual locus, and $\overline{R\text{max}}_i$ is the mean value of *R*max for the individual alleles (Tables II and III). Thus, the factors used in the predictive equation for *R*max based on *Glu-3* loci only in the world wheat set were: $R\text{max}_{est} = -475 + (0.73\ \overline{A3} + 0.90\ \overline{B3} + 0.74\ \overline{D3})$. The *A3, B3,* and *D3* represent the three *Glu-3* loci. The equations for predicting *R*max values in world or Australian wheats are given in the captions for Figures 1 and 2. However, for Ext of world wheats, the factors were: Ext_{est} based on *Glu-3* loci $= -16.9 + (0.06\ \overline{A3} + 0.85\ \overline{B3} + 0.39\ \overline{D3})$; Ext_{est} based on *Glu-1* loci $= -28.7 + (0.92\ \overline{A1} + 0.97\ \overline{B1} + 0.43\ \overline{D1})$; Ext_{est} based on both Glu-3 and *Glu-1* loci $= -51.3 + (0.03\ \overline{A3} + 0.94\ \overline{B3} + 0.47\ \overline{D3} + 0.62\ \overline{A1} + 0.82\ \overline{B1} + 0.53\ \overline{D1})$. Similarly, factors for Ext in Australian wheats were: Ext_{est} based on *Glu-3* loci $= -24.9 + (1.0\ \overline{A3} + 0.03\ \overline{B3} + 0.08\ \overline{D3})$; Ext_{est} based on *Glu-1* loci $= -26.4 + (0.61\ \overline{A1} + 0.89\ \overline{B1} + 0.64$ D1); Ext_{est} based on both *Glu-3* and *Glu-1* loci $= -32.7 + (0.80\ \overline{A3} + 0.18\ \overline{B3} + 0.18\ \overline{D3} + 0.07\ \overline{A1} + 0.68\ \overline{B1} + 0.03\ \overline{D1})$.

Using these prediction equations, estimated values for *R*max and Ext were obtained on the basis of LMW alone, HMW alone, or LMW and HMW loci together, for all wheats of each set. The estimated values were subsequently compared with the corresponding actual mean *R*max and Ext values by using multiple linear regression analysis to determine the predictive value of *Glu-3* and *Glu-1* loci separately and together. In world wheats, alleles at the *Glu-1* loci gave better predictions of *R*max than did the *Glu-3* alleles (Fig. 1). On the other hand, in the Australian wheat set, alleles at the *Glu-3* loci provided higher predictions for *R*max than did the *Glu-1* alleles (Fig. 2). The *Glu-3* alleles also gave a better prediction of Ext in the Australian set than did the *Glu-1* loci (Table VI).

The predictive value of *Glu-3* loci was further checked by applying the prediction values of these loci from the world wheat set (the general case) to estimate the *R*max and Ext values in Australian wheat set (a different, specific case). The results (Table VI) show that the *Glu-3* alleles were good predictors of *R*max ($r = 0.59$***) and Ext ($r = 049$***). Similar application of the *Glu-1* loci indicated that they were not as good predictors, especially of *R*max ($r = 0.33$*) in Australian wheats. These data once more highlight the importance of the *Glu-3* alleles in predicting *R*max and Ext in a range of wheat genotypes. However, the best prediction of these values was obtained when it was based on both LMW and HMW subunits together (Table VI), despite notable discrepancies in the predictive value of these two groups of glutenin subunits separately between sets. These results probably indicate that these subunits acted in a complementary

fashion (i.e., a synergistic effect). Hence, both *Glu-1* and *Glu-3* alleles should be considered for a maximum predictive value for dough quality.

Ranking Glutenin Loci and Alleles for *R*max

Figure 3 illustrates the ranking of *Glu-3* and *Glu-1* loci and alleles with respect to *R*max for world and Australian wheat sets (Fig. 3A and 3B, respectively). It shows the relative ranking of alleles within each locus, but equally important, it gives a preliminary indication of the relative contribution of different *Glu-1* and *Glu-3* loci. Values for each allele in the figure are based on $a_i \times \overline{Rmax}_i$ obtained using multiple regression analysis.

The results were generally comparable between sets. The HMW subunits (Glu-1) appeared to make relatively bigger contributions to *R*max than did the LMW subunits (Glu-3). However, in the Australian wheat set, alleles at the *Glu-3* loci were associated with relatively larger *R*max differences than were the *Glu-1* alleles, thus accounting for a greater amount of variation. Among the *Glu-3* loci, the *Glu-B3* locus made the maximum contribution to *R*max in both sets. Relative ranking of the alleles, occurring at a frequency of five or more at each LMW glutenin locus, was almost identical between sets; thus, they were summarized as follows with respect to their effects on *R*max: *Glu-A3*, $b > [d = e] > c$; *Glu-B3*, $b = i >> g = h >> c$; and *Glu-D3*, $b = a >> c$. Similarly, these alleles can be ranked with respect to their effect on Ext: *Glu-A3*, $d > b > c \geq e$ and *Glu-D3*, $e > c > b = a = d$.

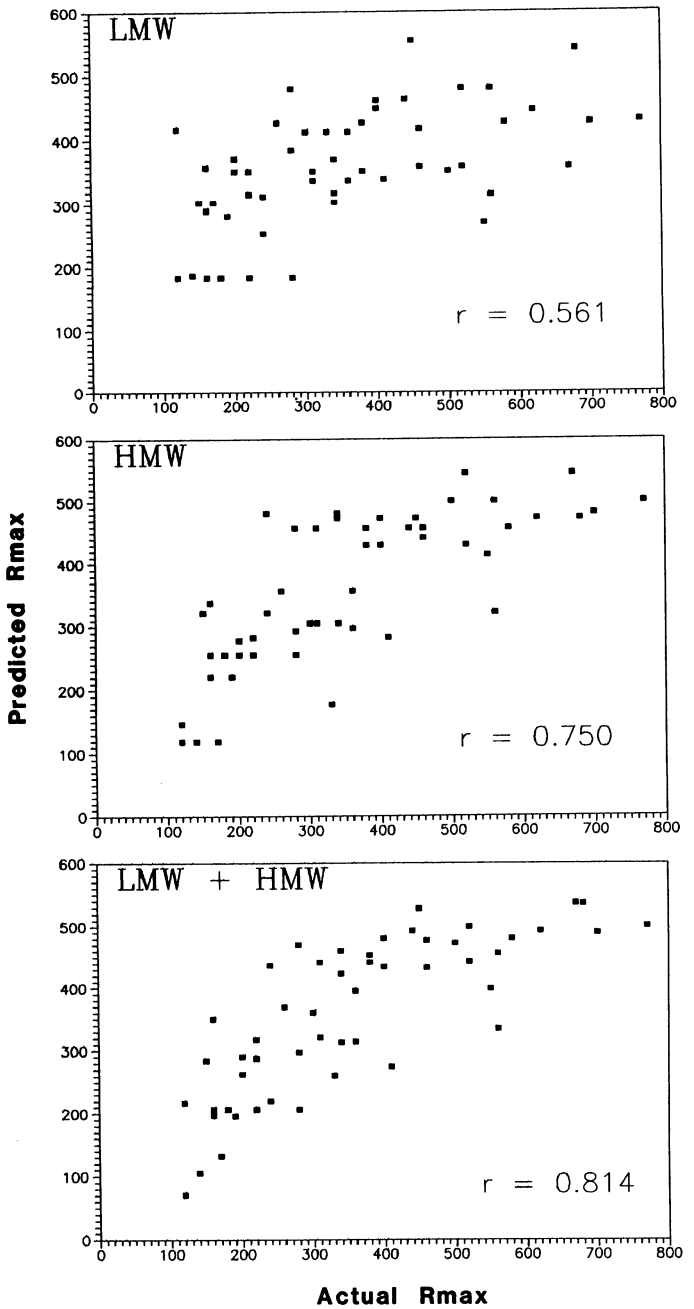

Fig. 1. Relationship between predicted and actual mean maximum dough resistance values calculated by using low and high molecular weight (LMW and HMW, respectively) subunits of glutenin separately and together for 53 world wheats. The factors used in the predictive equations were: $R\text{max}_{est}$ based on *Glu-3* loci = $-475 + (0.73\ \overline{A3} + 0.90\ \overline{B3} + 0.74\overline{D3})$; $R\text{max}_{est}$ based on *Glu-1* loci = $-651 + (1.10\ \overline{A1} + 1.01\ \overline{B1} + 0.75\overline{D1})$; $R\text{max}_{est}$ based on both *Glu-3* and *Glu-1* loci = $-806 + (0.17\ \overline{A3} + 0.46\ \overline{B3} + 0.34\ \overline{D3} + 1.09\ \overline{A1} + 0.72\overline{B1} + 0.75\ \overline{D1})$.

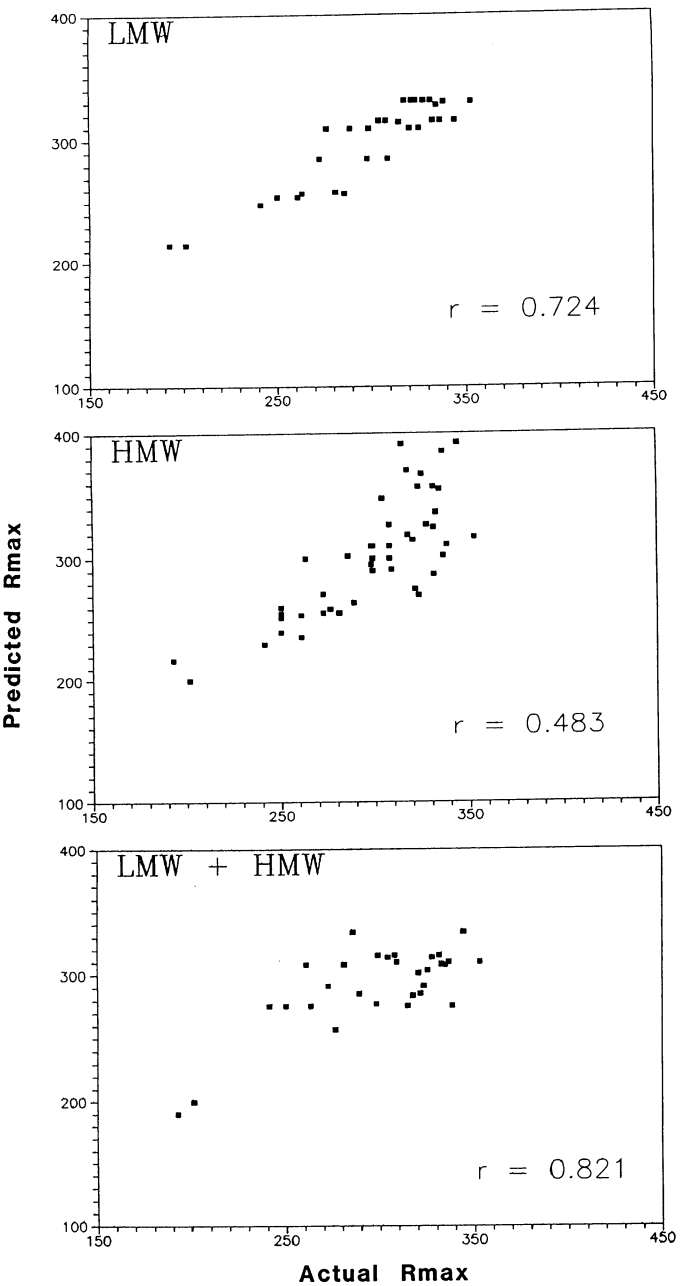

Fig. 2. Relationship between predicted and actual mean maximum dough resistance values calculated by using low and high molecular weight (LMW and HMW, respectively) subunits of glutenin separately and together for 48 Australian wheats. The factors used in the predictive equations were: $R\text{max}_{est}$ based on *Glu-3* loci = $-131 + (0.45\ \overline{A3} + 0.91\ \overline{B3} + 0.07\overline{D3})$; $R\text{max}_{est}$ based on *Glu-1* loci = $-430 + (0.15\ \overline{A1} + 1.1\ \overline{B1} + 0.94\overline{D1})$; $R\text{max}_{est}$ based on both *Glu-3* and *Glu-1* loci = $-632 + (0.61\ \overline{A3} + 0.81\ \overline{B3} + 0.39\ \overline{D3} + 0.37\ \overline{A1} + 0.40\overline{B1} + 0.10\ \overline{D1})$.

DISCUSSION

Previous work has demonstrated that the *Glu-1* score accounts for a substantial proportion (50–70%) of the variation in bread-making quality for wheats from many countries (for a review, see MacRitchie et al 1990). The data obtained in the present study on a set of 53 wheats from around the world also supported this observation. The results for Australian wheats, however, gave contrasting results, showing that the Glu-1 score accounted for very little of the variation in *R*max (19%). Similarly, Wrigley et al (1989) found that the *Glu-1* score accounted for only 15% of the variation in *R*max in a set of 102 Australian cultivars. In particular, alleles at the *Glu-D1* locus showed no relationship to *R*max or Ext (Tables III and IV), despite their predictive value for many other sets of wheat. The *Glu-D1d* allele (representing HMW subunits 5 + 10) is associated with greater dough strength than is its counterpart, *Glu-D1a* (coding for subunits 2 + 12) in several studies of genetic lines (e.g., Lawrence et al 1987) and in many analyses of sets of varieties (e.g., Branlard and Dardevet 1985, Campbell et al 1987, Payne et al 1987). This generally claimed superiority of subunits 5 + 10 to subunits 2 + 12 was not seen in the set of Australian wheats studied here. Part of the explanation for the difficulties in assessing the relevance of Glu-1 composition for Australian wheats having a relatively high average Glu-1 score (8.6, see MacRitchie et al 1990) lies in their Glu-3 composition. The Glu-3 LMW subunits of glutenin accounted for much greater variation (42%) than did the Glu-1 score in the set of 48 Australian wheats. Several of the Australian wheat cultivars, which have very high Glu-1 scores, were found to carry the *Glu-3* alleles of low ranks; e.g., Halberd, Insignia, and Egret. These cultivars have low to average *R*max and Ext. These data thus emphasize the previously little-recognized importance of the LMW subunits of glutenin as significant components contributing to the assessment of the breadmaking potential of wheat flour.

TABLE VI
Correlation Coefficients Between Measured and Estimated Maximum Dough Resistance (*R*max) and Extensibility (Ext) Using Glutenin Loci in 53 World and 48 Australian Wheats

Glutenin Loci	World Wheat Set		Australian Wheat Set		Australian Set[a]	
	*R*max	Ext	*R*max	Ext	*R*max	Ext
Glu-1	0.75***[b]	0.43**	0.48**	0.26	0.33*	0.42**
Glu-3	0.56***	0.44***	0.72***	0.54***	0.59***	0.49***
Glu-1 and *Glu-3*	0.81***	0.54***	0.82***	0.57***	0.70***	0.53***

[a] Based on world predictions.
[b] *, **, and *** = Correlation values were significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

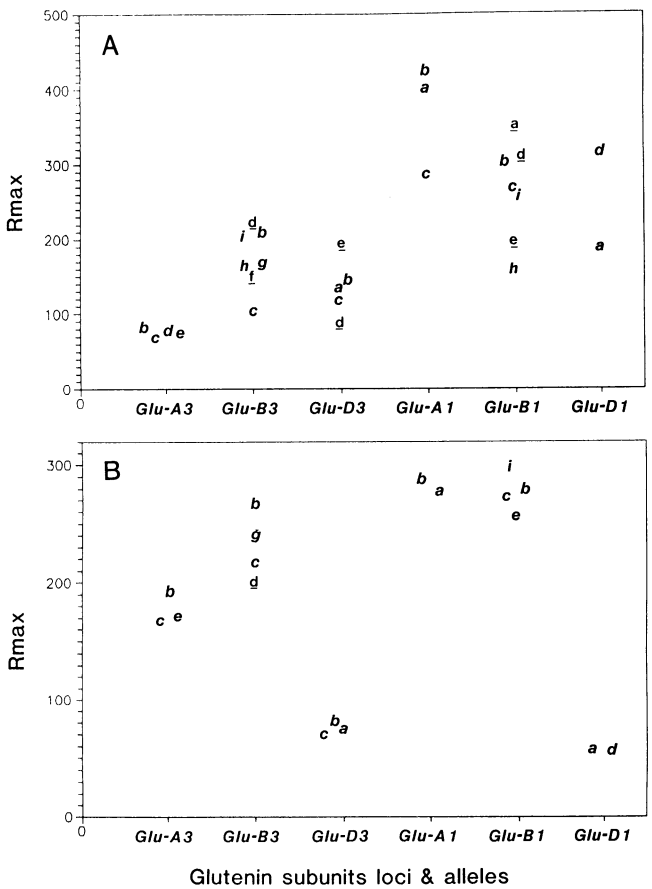

Fig. 3. Relative contribution to maximum dough resistance of low molecular weight glutenin alleles at the *Glu-A3*, *Glu-B3*, and *Glu-D3* loci and of HMW glutenin alleles at the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci in 53 world wheats (**A**) and 48 Australian wheats (**B**). Values for each allele are based on $a_i \times \overline{Rmax_i}$ obtained using multiple regression analysis. The underlined alleles had a frequency of ≤3; the others had a frequency of ≥5.

Each of the three *Glu-3* loci showed significant differences in the *R*max and Ext values in both wheat sets. The *Glu-B3* locus accounted for the maximum variation in *R*max (Fig. 1), possibly because the greatest allelic variation occurred at this locus. Variation at the *Glu-A3* locus also showed a significant relationship with Ext; this is consistent with our previous findings for Australian wheats using biotypes (Gupta and Shepherd 1988) or progeny lines derived from F2 (Gupta et al 1989). However, the null *Glu-A3e* allele ranked almost equally with the *Glu-A3c* allele, contrary to its inferior ranking in our previous results (Gupta et al 1989). This can be partly accounted for by a greater background variation at the varietal level in this study. Since in assessing the relationships between these glutenin alleles and dough properties using different cultivars or breeding lines the same *R*max or Ext value was allocated to each of the six glutenin loci in a given variety, it is quite possible that each of the six loci may not show the same effect in an isogenic background for given alleles. Hence, direct testing of the effects of different *Glu-3* alleles is required for more precise comparisons of different alleles or loci using isogenic lines or biotypes. Although it will take time to develop these lines, the results indicate that it should be worth the effort of repeating what has already been done fairly thoroughly for the *Glu-1* alleles (see review by MacRitchie et al 1990). The potential value of further study of the *Glu-3* alleles is also indicated by the finding that flour quality can be improved much more efficiently by selecting for both Glu-1 and Glu-3 subunits than for either group alone (Table VI). This is supported by evidence that some of the *Glu-A1* and *Glu-A3* alleles in bread wheats (Gupta et al 1989) and, similarly, that some *Glu-B1* and *Glu-B3* alleles in durum wheat (Pogna et al 1990) exert cumulative effects on flour quality.

The positive synergystic effects associated with the inclusion of the LMW glutenin subunits in predictive equations are most likely due to an increase in the amount of the glutenin and/or to the incorporation of different types of subunits. Either situation can lead to an improvement in the elastic properties of glutenin, hence *R*max and Ext. The amount and composition of the glutenin have significant effects on *R*max, whereas Ext largely depends on the amount (Gupta et al 1991, Singh et al 1991). In the present study, no attempt was made to measure the difference in amounts of the LMW or HMW subunits of glutenin coded by different alleles, but our visual observations suggest that the LMW alleles with high ranks are generally associated with a greater number and/or intensity of bands (Gupta and Shepherd 1990). However, the quality predictions based on the glutenin composition are likely to be influenced by variation in the amount of the glutenin subunits coded by the same alleles, which, in turn, are governed by the level of the protein in the grain or flour sample. Other protein factors (gliadins, albumins-globulins) and nonprotein factors (lipids, starch) could also be responsible for some variation in the dough properties of the cultivars analyzed

here. Of particular interest are the aggregating HMW albumins (Gupta and Shepherd 1987) and globulins or triticins (Singh and Shepherd 1988) that are present in the glutenin complex. These may also have some influence on the functionality of glutenin and thus on flour quality (MacRitchie 1987).

The HMW glutenin subunits generally appeared to make a larger contribution to *R*max than did the LMW glutenin subunits (Fig. 3), although the latter types accounted for more variation in the *R*max values of Australian wheats. Results obtained from analyzing genetic lines deficient in varying numbers or amounts of LMW or HMW glutenin subunits also indicate that HMW glutenin subunits, on a constant weight basis, have more pronounced effects on dough resistance than do the LMW subunits of glutenin (Gupta et al 1991). On the other hand, Ext was equally affected by both groups of subunits. Since LMW subunits are quantitatively the major group of glutenin subunits, contributing considerably more than do the HMW subunits to total glutenin, they are still expected to play quite an important role in determining both *R*max and Ext of bread wheats. Perhaps greater amounts of LMW subunits in total glutenin might account for their generally stronger correlation with Ext, as observed in this study.

Finally, since this study was based on only two sets of genotypes, the factors obtained in the predictive equations must be regarded as interim indications of predictive value. However, the results clearly indicate the value of continuing to study the LMW subunits of a broader range of wheats, so that more comprehensive results can be obtained for use in predicting dough properties. LMW subunits of glutenin certainly have potential application in wheat breeding programs. However, a rapid screening method is needed for detecting different LMW alleles in segregating progeny because the current electrophoretic method, i.e., two-step sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE), is tedious and time-consuming. Thus, we recently developed a one-step SDS-PAGE method that is much more efficient for routine screening of LMW and HMW glutenin alleles in breeding programs (Gupta, *unpublished data*).

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