

Effects of Prolamins Encoded by Chromosomes 1B and 1D on the Rheological Properties of Dough in Near-Isogenic Lines of Bread Wheat

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ABSTRACT

Cereal Chem. 74(2):102–107

Fourteen bread wheat near-isogenic lines (NILs) with different alleles at 1B- and 1D-chromosome loci *Glu-1*, *Glu-3* and *Gli-1* coding for high molecular weight glutenin subunits (HMW-GS), low molecular weight-GS, and gliadins, respectively, were grown in replicated plots to investigate the individual and combined effects of glutenin and gliadin components on the rheological properties of dough as determined by the Chopin alveograph. NILs did not reveal significant differences in seed yield, protein content, kernel weight, test weight, flour yield, and starch damage. On the contrary, they had a large variation in alveograph dough tenacity *P* (55–93 mm), swelling *G* (17–26 mL) and strength *W* (140–252 J × 10⁻⁴). The null alleles at the *Gli-D1/Glu-D3* loci, and allele *Glu-D1d* (HMW-GS 5+10) were found to have a strong positive influence on dough tenacity and a remarkable negative influence on dough swelling

(extensibility) when compared to alleles *Gli-D1/Glu-D3b* and *Glu-D1a* (HMW-GS 2+12), respectively. On the other hand, alleles *Glu-B1c* (HMW-GS 7+9) and *Gli-B1/Glu-B3k* gave greater *G* values than alleles *Glu-B1u* (HMW-GS 7*+8) and *Gli-B1/Glu-B3b*. The effects of individual *Glu-1*, *Gli-1*, or *Glu-3* alleles on *P* and *G* values were largely additive. The impact of the null allele at *Gli-D1/Glu-D3* on gluten strength was highly positive in NILs possessing HMW-GS 2+12, and negligible or negative in NILs containing HMW-GS 5+10, suggesting that there is scope for improving dough quality by utilizing this allele in combination with HMW-GS 2+12. *Gli-D1/Glu-D3*-encoded prolamins were shown to play a major role in conferring extensibility to dough, and could account for the superior breadmaking characteristics of bread wheat as compared to durum wheat.

Various sets of wheat cultivars, recombinant inbred lines, biotypes, intervarietal substitution lines, and F₂ or more advanced progeny have been used to study relationships between individual alleles coding for gliadins, high molecular weight (HMW) or low molecular weight (LMW) glutenin subunits (GS) and dough viscoelastic properties (Sozinov and Poperelya 1980; Payne et al 1979, 1987; Branlard and Dardevet 1985a,b; Gupta and Shepherd 1987, 1988; Gupta et al 1989; Carrillo et al 1990; Gupta and MacRitchie 1994). The relative ranking of several alleles at gliadin loci (*Gli-1* and *Gli-2*), HMW-GS loci (*Glu-1*) and LMW-GS loci (*Glu-3*) with respect to dough resistance and extensibility has been determined based on these studies. Furthermore, two important findings from a breeding point of view have been obtained from these and other studies (Pogna et al 1990): 1) gliadin alleles at the *Gli-1* loci are useful genetic markers for dough quality because of their close linkage with *Glu-3* alleles, which are the likely cause of flour quality variation; and 2) the effects of glutenin subunits alleles at *Glu-1* and *Glu-3* loci on dough resistance and extensibility are largely cumulative. Precise evaluation of individual and combined effects of glutenin alleles on dough elasticity and extensibility requires special genotypes such as recombinant inbred lines or near-isogenic lines (NILs), especially when alleles with minor but significant effects are compared. Therefore, a set of NILs with contrasting allelic compositions at gliadin and glutenin loci on chromosomes 1B and 1D have been developed in the Italian bread wheat cv. Alpe. The objective of this study was to determine the effects of these NILs on dough quality. This presented an opportunity to determine the relative contribution of some of the most common alleles coding for storage proteins as well as that of the presence or absence of *Gli-D1/Glu-D3* loci, whose impact on dough quality has been stressed in recent works (Masci et al 1991, Branlard and Dardevet 1994, Popineau et al 1994).

MATERIALS AND METHODS

Plant Materials

Fourteen near-isogenic lines (NILs) were produced in the Italian bread wheat cv. Alpe and grown in the Po Valley at S. Angelo Lodigiano (Lodi, Italy) on sandy soil under husbandry conditions similar to those used for commercial production. The experimental design was a randomized block with three replicates. The elementary plot of 10 m² consisted of eight rows, 17 cm apart, sown with 400 germinating kernels/m². Cultivar Chinese Spring and Chinese Spring ditelosomic DT-1DL were used as references in electrophoresis.

Electrophoretic Analyses

Reduced total protein and unreduced alcohol-soluble proteins were fractionated by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) and acid PAGE (A-PAGE), respectively, as described previously (Pogna et al 1990).

Quality Evaluation

Grain yield, 1,000-kernel weight and hectolitre weight were measured on each plot. After harvesting, the seeds from the three replicates of each NIL were blended and 3-kg samples were tempered to a moisture of 16% and milled with the MLU 202 Buhler experimental mill. The α -amylase activities of all the flour samples were low (Falling Number >300 sec). Flour samples were analyzed for protein content (N × 5.7, dwb) by the micro-Kjeldahl method (AACC 1995), and for starch damage levels by method 76-31 (AACC 1995). For dough properties, flour samples were analyzed with a Chopin alveograph according to the manufacturer's instructions. Standard analysis of variance was applied to all data.

RESULTS

Seed Characteristics and Storage Protein Compositions of NILs

The 14 NILs analyzed here were selected from the cross between biotypes 2II and 1I⁻ in the bread wheat cultivar Alpe (Pogna et al 1995). Yield and seed characteristics of these lines are listed in Table I. The analysis of variance showed no significant difference in seed yield, kernel weight, test weight, and pro-

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tein content amongst the 14 NILs grown in replicated plots. The A-PAGE and SDS-PAGE fractionations of storage proteins (Fig. 1) showed that these NILs share the same alleles at the *Gli-A1*, *Gli-2* and *Glu-A3* loci coding for gliadins or LMW-GS, and at the *Glu-A1* locus coding for HMW glutenin band 2*. However, they differ from each other in the allele compositions at *Gli-B1/Glu-B3* (allele *k* vs. *b*), *Gli-B5* (*a* vs. "null"), *Gli-D1/Glu-D3* (*b* vs. "null"), *Glu-B1* (*c* vs. *u*, coding for HMW-GS 7+9 and 7*+8, respectively) and *Glu-D1* (*a* vs. *d*, HMW-GS 2+12 vs. 5+10) (Table II). In particular, the seven NILs marked with "minus" lack the *Gli-D1* and *Glu-D3* loci because of deletion of a small segment in the short arm of chromosome 1D (Pogna et al 1995). The missing segment also contains the *Glo-D1* locus encoding for the 25-kDa globulins described by Gomez et al (1988), as suggested by the absence of these proteins in the *Gli-D1/Glu-D3*-null NILs (Fig. 2). Results of the seed characteristics (Table I) suggest that these allelic variations at the storage protein loci did not affect the agronomic performances of the genotypes.

Alveograph Parameters of NILs

The flour extraction rates of the 14 NILs milled by the MLU 202 Buhler experimental mill were 62–63% (w/w). All flour sam-

ples showed a low level of starch damage (3.5–3.7%). On the contrary, there were remarkable differences on the alveograph parameters of tenacity (*P*), swelling (*G*), tenacity/extensibility ratio (*P/L*), and strength (*W*) of the flours (Table II). In particular, the *P* and *G* values varied between 55 and 93 mm, and between 16.7 and 25.5 mL, respectively, resulting in a wide variation of the *P/L* ratio (0.36–1.64). Dough strength varied between 140 and 252 J × 10⁻⁴. Consequently, the effects of allelic variation at each storage protein locus on the alveograph parameters were investigated by comparison of appropriate pairs of NILs.

Effects of Alleles at the *Glu-D1* Locus

Six comparisons (2I vs. 4I, 2I⁻ vs. 4I⁻, 2II⁻ vs. 4II⁻, 1I vs. 3I, 1II vs. 3II, and 1II⁻ vs. 3II⁻) were made to determine the effects

TABLE I
Yield and Seed Characteristics of 14 Near-Isogenic Lines of Bread Wheat cv. Alpe^a

Genotype	Yield (t/ha)	1,000-Kernel Weight (g)	Hectolitre Weight (kg)	Protein Content (%)
1I	6.3	42.6	74.6	11.3
1II	6.2	42.5	74.5	11.1
2I	6.0	42.5	73.9	11.5
2II	6.1	42.4	74.1	10.9
3I	6.2	42.1	74.0	11.2
3II	6.3	42.1	73.8	11.0
4I	6.4	42.5	73.7	11.1
1I ⁻	6.0	42.0	72.6	11.3
1II ⁻	6.2	42.5	74.5	11.3
2I ⁻	6.1	42.3	73.9	11.4
2II ⁻	6.1	42.4	73.0	11.4
3II ⁻	6.3	42.3	74.4	11.5
4I ⁻	6.3	42.5	74.0	11.4
4II ⁻	6.0	42.1	73.8	11.2
LSD ^b	0.6	1.0	3.2	0.9

^a Mean of three replicates.

^b Least significant difference at *P* = 0.05.

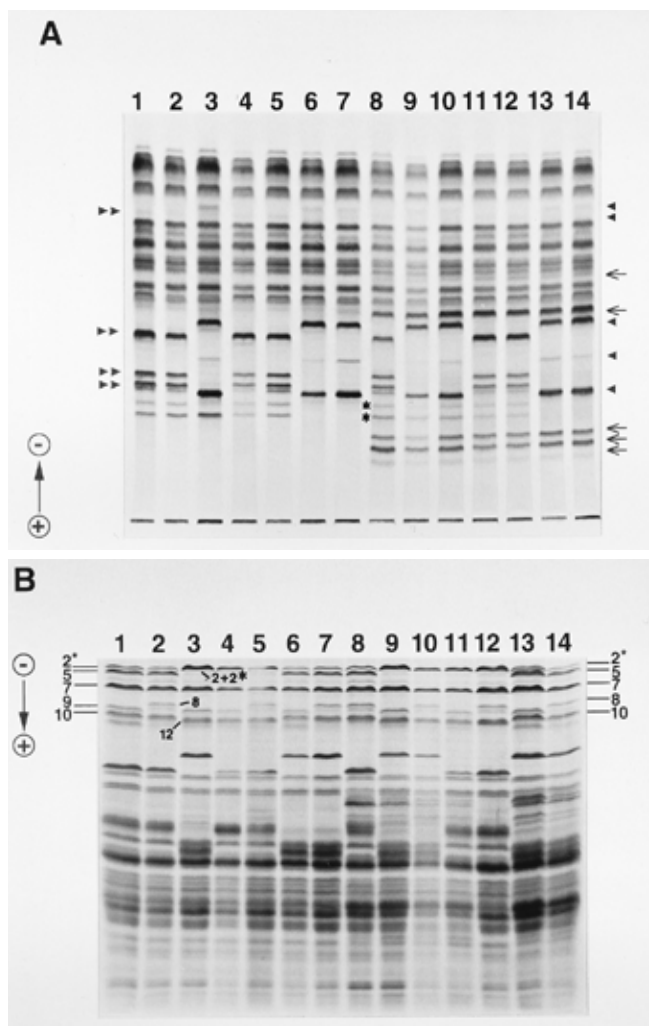


Fig. 1. Acid polyacrylamide gel electrophoresis (A-PAGE) fractionation of gliadins (A) and sodium dodecyl sulfate (SDS-PAGE) fractionation of total reduced proteins (B) from near-isogenic lines of bread wheat cv. Alpe. Lanes 1–14: 4I⁻, 4I⁻, 3II⁻, 2II⁻, 2I⁻, 1II⁻, 1I⁻, 4I, 3II, 3I, 2II, 2I, 1II, 1I. Gliadin bands encoded by alleles *Gli-B1k* (double arrowheads), *Gli-B1b* (arrowheads), *Gli-D1b* (arrows), and *Gli-B5a* (asterisks) are indicated in A. High molecular weight glutenin subunits are numbered in B.

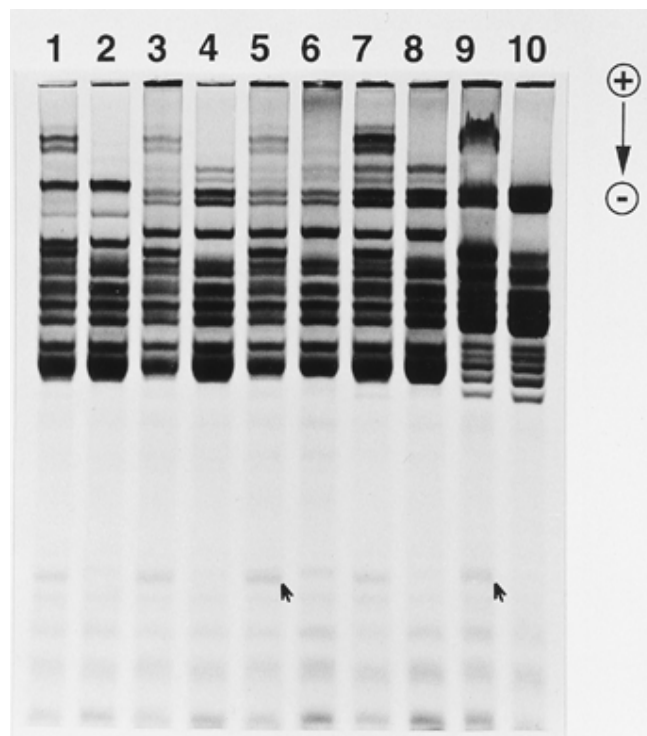


Fig. 2. Acid polyacrylamide gel electrophoresis (A-PAGE) fractionation of alcohol-soluble proteins from near-isogenic lines of bread wheat cv. Alpe. Lanes 1–10: 1I, 1I⁻, 2I, 2I⁻, 2II, 2II⁻, 4I, 4I⁻, cv. Chinese Spring, and Chinese Spring ditelosomic DT-1DL. Arrows indicate 25-kDa globulins.

of alleles *Glu-D1a* (coding for HMW-GS 2+12) and *Glu-D1d* (HMW-GS 5+10) on the alveograph parameters. The last three pairs of NILs were considered in this analysis because of the small effects of the *Gli-B5a* allele on the rheological properties of dough (see below). In each of the six comparisons, a NIL containing subunits 5+10 showed higher *P* and *P/L* values and lower *G* values than its counterpart possessing subunits 2+12. The *P* and *P/L* mean values attributed to allele *d* were larger than those of allele *a* by 27 and 55%, respectively, whereas the reduction of the *G* mean value due to the allele *d* was 9% (Table III). Furthermore, allele *d* was associated with higher dough strength than allele *a* in all the comparisons except 2II⁻ vs. 4II⁻, which showed similar *W* values. The mean increase in gluten strength attributed to allele *d* was as high as 25%.

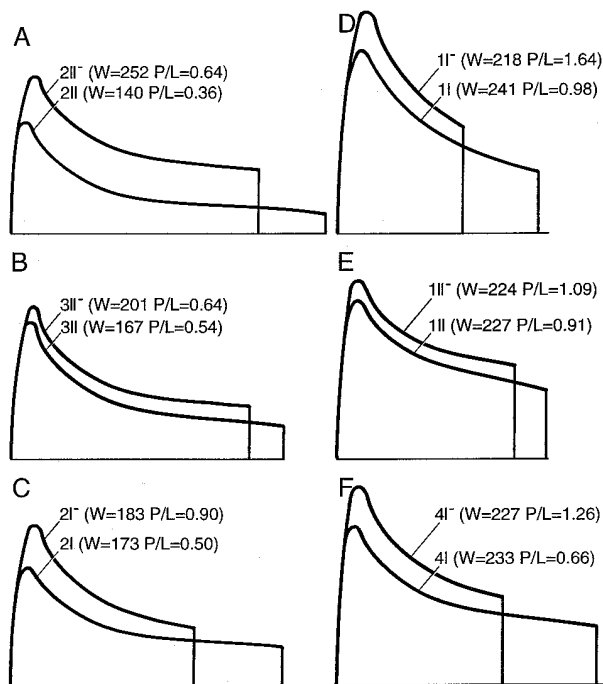


Fig. 3. Alveograms of 12 near-isogenic lines of bread wheat cv. Alpe. Near-isogenic lines containing high molecular weight glutenin subunits 2+12 (A–C) and 5+10 (D–F). *W* = strength ($J \times 10^{-4}$), *P/L* = tenacity/extensibility ratio.

Effects of Alleles at the *Glu-B1* Locus

The presence of allele *Glu-B1u* coding for HMW-GS 7*+8 was associated with a larger value of *P* and *P/L* than the presence of allele *Glu-B1c* (HMW-GS 7+9) in five out of six comparisons (1I vs. 1II, 2I vs. 2II, 3I vs. 3II, 1I⁻ vs. 1II⁻, 2I⁻ vs. 2II⁻, and 4I⁻ vs. 4II⁻). On the contrary, NILs possessing allele *u* gave *G* values equal to or lower than those of their counterparts with allele *c*. The mean increases of *P* and *P/L* values attributed to allele *u* were calculated to be 10 and 33%, respectively, whereas the mean reduction of *G* value was 8.1% (Table III). Contrasting results were obtained for gluten strength: lines 1I, 2I, and 3I, which contain allele *u* along with allele *b* at the *Gli-D1/Glu-D3* loci, showed high *W* values compared to their *Glu-B1c* counterparts 1II, 2II, and 3II, whereas the converse occurred in the three NIL pairs possessing the null allele at *Gli-D1/Glu-D3*. However, the mean *W* values attributed to alleles *c* and *u* were very similar (Table III).

Effects of Alleles at the *Gli-D1/Glu-D3* Loci

Comparisons of six NIL pairs (1I vs. 1I⁻, 1II vs. 1II⁻, 2I vs. 2I⁻, 2II vs. 2II⁻, 3I vs. 3I⁻, and 4I vs. 4I⁻) showed that NILs having the null allele at the *Gli-D1/Glu-D3* loci were characterized by larger *P* and *P/L* values and lower *G* values than those of their counterparts with allele *b*, the mean variations of *P*, *P/L*, and *G* values due to the null allele being 18, 56, and -12%, respectively (Table III). Furthermore, the null allele was associated with a significant increase in the *W* value in the three NIL pairs possessing HMW glutenin subunits 2+12 (2I vs. 2I⁻, 2II vs. 2II⁻ and 3II vs. 3I⁻). On the contrary, this allele showed negligible or even adverse effects on dough strength in NIL pairs containing HMW subunits 5+10. The effects of the absence of the storage proteins encoded by the *Gli-D1/Glu-D3* loci on the rheological properties of the 2+12 or 5+10 NILs are illustrated by the alveograms in Figure 3.

Effects of Alleles at the *Gli-B1/Glu-B3* and *Gli-B5* Loci

Only three pairs of NILs (2I vs. 3I, 2II vs. 3II, and 2II⁻ vs. 3II⁻) were available to investigate the effects of alleles *b* and *k* at the *Gli-B1/Glu-B3* loci on dough viscoelastic properties, all six genotypes containing HMW subunits 2+12. Allele *k* was associated with increased *G* values and, therefore, with a small decrease in the *P/L* ratio (Table III). Allelic variation at these loci did not affect significantly dough tenacity and strength. There were no valid pairs of NILs to determine the effects of allele *Gli-B5a* on the dough parameters. However, comparison of the dough quality of NIL pairs 1I vs. 4I, 1I⁻ vs. 4I⁻, and 1II⁻ vs. 4II⁻ indicated that the combined effects of alleles *k* and *a* at *Gli-B1/Glu-B3* and *Gli-B5*, respectively, on *G* and *W* values did not differ significantly

TABLE II
Storage Protein Compositions and Alveograph Parameters of 14 Near-Isogenic Lines of Bread Wheat cv. Alpe

Genotype	Storage Protein Allele ^a					Alveograph Parameter ^b			
	<i>Gli-B1/Glu-B3</i>	<i>Gli-B5</i>	<i>Gli-D1/Glu-D3</i>	<i>Glu-B1</i>	<i>Glu-D1</i>	<i>P</i>	<i>G</i>	<i>P/L</i>	<i>W</i>
1I	b	null	b	u	d	82	20.4	0.98	241
1II	b	null	b	c	d	77	20.4	0.91	227
2I	k	a	b	u	a	55	23.2	0.50	173
2II	k	a	b	c	a	47	25.5	0.36	140
3I	b	a	b	u	a	57	23.1	0.52	172
3II	b	a	b	c	a	59	23.1	0.54	167
4I	k	a	b	u	d	69	22.8	0.66	233
1I ⁻	b	null	null	u	d	93	16.7	1.64	218
1II ⁻	b	null	null	c	d	79	18.8	1.09	224
2I ⁻	k	a	null	u	a	71	19.8	0.90	183
2II ⁻	k	a	null	c	a	70	23.8	0.64	252
3II ⁻	b	a	null	c	a	62	21.8	0.64	201
4I ⁻	k	a	null	u	d	86	18.4	1.26	227
4II ⁻	k	a	null	c	d	72	20.8	0.87	244

^a Alleles *Glu-B1c* and *Glu-B1u* code for HMW-GS 7+9 and 7*+8, respectively; alleles *Glu-D1a* and *Glu-D1d* code for HMW-GS 2+12 and 5+10, respectively.

^b *P* = tenacity (mm), *G* = swelling (mL), *P/L* = tenacity/extensibility ratio, *W* = strength ($J \times 10^{-4}$).

from the individual effect of allele *k* (Table III), suggesting a minor influence, if any, of allele *Gli-B5a* on these alveograph parameters. These indirect comparisons also revealed that allele *Gli-B5a* was associated with a slight decrease of *P* and *P/L* values.

Combined Effects of Alleles at Different Storage Protein Loci

In general, alleles at the *Glu-D1*, *Glu-B1*, *Gli-D1/Glu-D3*, and *Gli-B1/Glu-B3* loci acted in an additive manner on alveograph parameters *P* and *G*, the combined effects of alleles being not very different from the simple sum of their individual effects on dough tenacity and swelling (Fig. 4). Allelic variation at the *Gli-B5* locus was not considered in this analysis because of the small number of NILs for a valid comparison. On the contrary, the mean *W* values of allele compositions *Gli-D1/Glu-D3null* plus *Glu-D1d*, *Gli-D1/Glu-D3null* plus *Glu-B1u* and *Gli-D1/Glu-D3null* plus *Gli-B1b* were much lower than those expected on the basis of the individual effect of each allele on dough strength.

DISCUSSION

An isogenic line approach was adopted in the present study to relate individual alleles coding for storage proteins to dough rheological properties. The Alpe NILs used here were very similar agronomically and were not significantly different from each other in terms of seed yield, kernel weight, test weight, and protein content. Furthermore, they showed no differences in gliadins, LMW-GS, and HMW-GS other than those already described. One major difference in globulin components controlled by the short arm of chromosome 1D was noted between *Gli-D1/Glu-D3b* and *Gli-D1/Glu-D3null* lines (Fig. 2). Based on their solubility in dilute saline solutions and two-dimensional IEF × SGE patterns (data not shown), these components were identified as the 25-kDa

globulins described by Gomez et al (1988). It is not known whether these globulins have any effect on dough quality. However, they do not form disulfide-linked polymers (Gomez et al 1988), thus they would have no major effects on strength properties of wheat flours (Singh et al 1990, Gupta and MacRitchie 1994).

Allelic variation at the storage protein loci on chromosomes 1B and 1D had significant effects on dough tenacity, swelling and strength. Furthermore, the effects of individual alleles on alveograph *P* and *G* values were largely cumulative, so that different allele combinations in the same wheat genotype showed contrasting dough properties (Fig. 3), confirming that wheat quality can be modified genetically without affecting the grain protein level. In particular, allele *Glu-D1d* coding for HMW-GS 5+10 and the null allele at the *Gli-D1/Glu-D3* loci had a positive effect on dough tenacity and a strong negative impact on dough extensibility compared to alleles *Glu-D1a* (HMW-GS 2+12) and *Gli-D1/Glu-D3b*, respectively. The superiority of the former alleles for dough tenacity has been associated with their capacity to form larger size polymers (Gupta and MacRitchie 1994, Popineau et al 1995). The contrasting effects of HMW-GS 5+10 and 2+12 have been accounted for by basic differences in their structures (Anderson et al 1989), whereas the reduced strength tenacity attributed to the active *Gli-D1/Glu-D3b* allele is possibly due to altered polymer formation of the encoded proteins. Masci et al (1993) recently showed D-group LMW-GS encoded by *Gli-D1/Glu-D3* to have cysteine in their primary structures and suggested that they originated from a single codon mutation occurring in an ω-gliadin gene. According to these authors, mutated ω-gliadins would act as “chain terminators” during glutenin polymer growth, affecting negatively dough tenacity and strength as a result of the reduced sizes of the overall glutenin polymers.

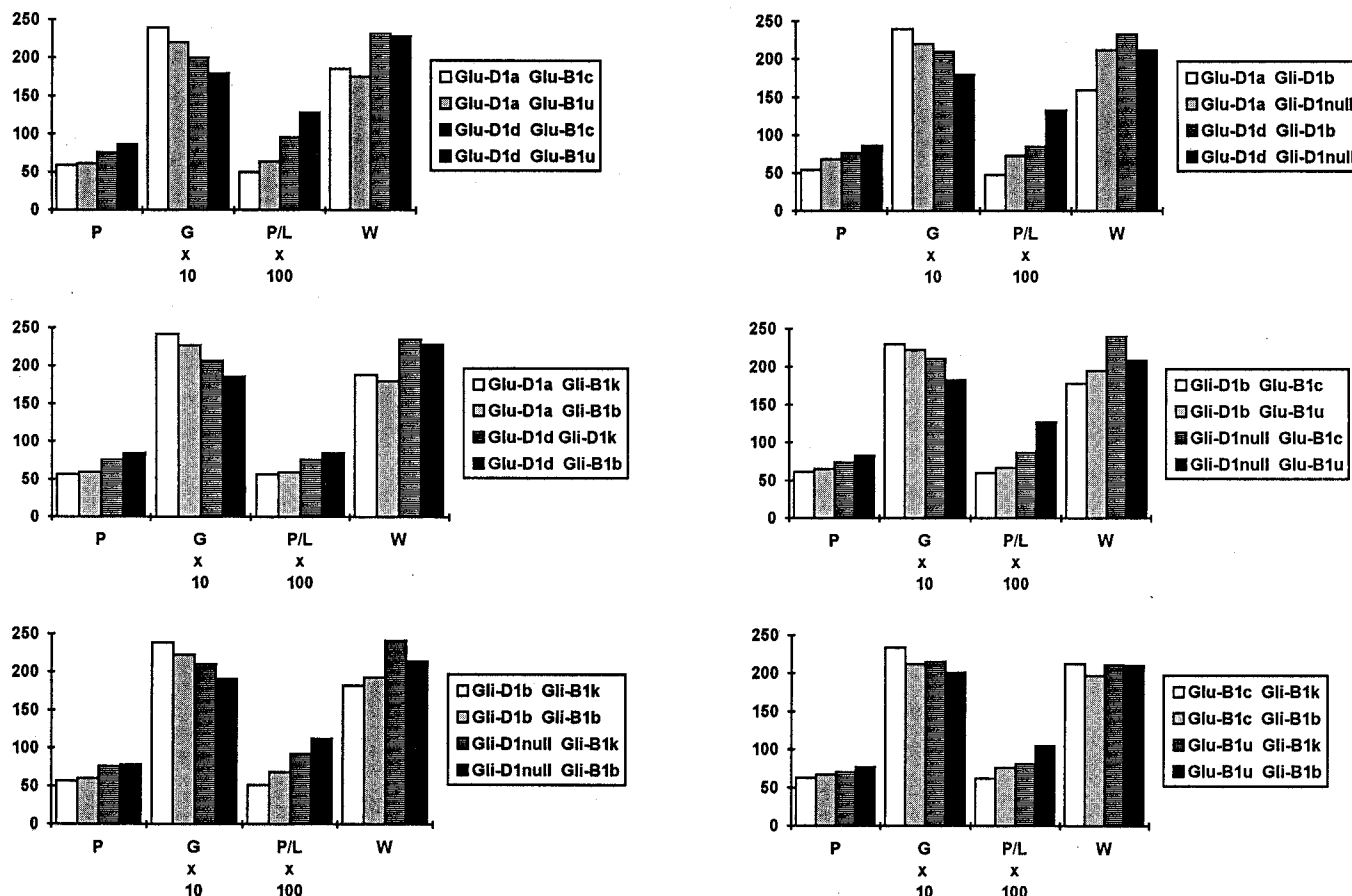


Fig. 4. Mean values for alveograph tenacity (*P*, mm), swelling (*G*, mL), *P/L* ratio, and strength (*W*, $J \times 10^{-4}$) attributed to allele combinations in near-isogenic lines of bread wheat cv. Alpe.

TABLE III
Mean Alveograph Values Attributed to Different Alleles Coding for Storage Proteins in Near-Isogenic Lines of Bread Wheat cv. Alpe and the Differences Between the Means (%)^a

Parameter ^b	<i>Glu-D1</i>			<i>Glu-B1</i>			<i>Gli-D1/Glu-D3</i>			<i>Gli-B1/Glu-B3</i>			<i>Gli-B1/Glu-B3/Gli-B5</i>		
	d	a	%	u	c	%	null	b	%	b	k	%	b/null	k/a	%
<i>P</i>	79	62	+27.4	74	67	+10.4	77	65	+18.5	59	57	+3.5	85	76	+11.8
<i>G</i>	20.5	22.5	-8.9	20.3	22.1	-8.1	19.9	22.6	-11.9	22.7	24.2	-6.2	18.6	20.7	-10.1
<i>P/L</i>	0.96	0.62	+54.8	0.97	0.73	+32.9	1.03	0.66	+56.1	0.57	0.50	+14.0	1.24	0.93	+33.3
<i>W</i>	240	191	+25.7	202	209	-3.3	218	197	+10.7	180	188	-4.3	228	235	-3.0

^a Sample calculation: *Glu-D1*, $(79 - 62)/62 \times 100 = 27.4\%$.

^b *P* = tenacity (mm), *G* = swelling (mL), *P/L* = tenacity/extensibility ratio, *W* = strength ($J \times 10^{-4}$).

Alveograph Parameter	Decreasing effect ⇒⇒⇒⇒
P	<i>Glu-D1</i> : <i>d</i> > <i>a</i> <i>Gli-D1/Glu-D3</i> : null > <i>b</i> <i>Gli-B1/Glu-B3b</i> + <i>Gli-B5</i> : null > <i>k</i> + <i>a</i> <i>Glu-B1</i> : <i>u</i> > <i>c</i>
G	<i>Gli-D1/Glu-D3</i> : <i>b</i> > null <i>Gli-B1/Glu-B3k</i> + <i>Gli-B5</i> : <i>a</i> > <i>b</i> + null <i>Glu-D1</i> : <i>a</i> > <i>d</i> <i>Glu-B1c</i> > <i>u</i>
W	<i>Glu-D1</i> : <i>d</i> > <i>a</i> <i>Gli-D1/Glu-D3</i> : null > <i>b</i>

Fig. 5. Relative performance of various prolamin alleles for alveograph tenacity (*P*, mm), swelling (*G*, mL) and strength (*W*, $J \times 10^{-4}$).

On the other hand, allele *Gli-D1/Glu-D3b* revealed strong positive effects on dough extensibility, suggesting that the greater extensibility of bread wheat dough as compared to that of durum wheat could primarily be attributed to the presence of *Gli-D1/Glu-D3*-encoded proteins in hexaploid wheat. Near-isogenic durum wheat lines differing from each other in the presence or absence of *Gli-D1/Glu-D3*-encoded prolamins are currently being produced to confirm this conclusion and develop durum wheat genotypes with improved breadmaking quality (Redaelli et al 1992). LMW-GS have been reported to affect dough extensibility and swelling (Gupta et al 1989, 1994; Khelifi and Branlard 1992; Brett et al 1993). This suggests that the effects on dough extensibility attributed to *Gli-D1/Glu-D3* may be largely due to LMW-GS encoded at *Glu-D3*, gliadins encoded by the linked *Gli-D1* locus having only minor effects, if any.

The present results agree with those of Branlard and Dardevet (1994) showing the positive effects of the null allele at *Gli-D1* from cv. Darius on dough strength of wheat lines containing HMW-GS 2+12 or 3+12. However, clear evidence is provided here that, when compared with allele *Gli-D1b*, the null allele had negligible or negative effects on dough strength in Alpe lines containing HMW-GS 5+10 (Figs. 3 and 4). Moreover, these lines showed *P/L* > 1, with deleterious effects on breadmaking quality.

The effects of allelic variation at the *Glu-B1*, *Gli-B1/Glu-B3* and *Gli-B5* loci on dough tenacity and strength were much smaller. On the contrary, alleles *Glu-B1c* and *Gli-B1k* were positively correlated with dough extensibility and, therefore, with reduced *P/L* ratio, suggesting that there is scope for improving dough quality by utilizing these alleles. Based on their relative performances, the storage protein alleles analyzed here can be ranked as shown in Figure 5.

One of the key findings of the present study is that chromosome 1D exerts a strong influence on the viscoelastic properties (elasticity and extensibility) of dough. In particular, deletion of the *Gli-D1/Glu-D3* loci may have application in breeding programs for dough strength improvement (in combination with HMW-GS 2+12). On the other hand, selection based on alleles *Glu-B1c* and *Gli-B1/Glu-B3k* can lead to extensible and balanced (*P/L* ≤ 0.5) dough without significant negative effects on dough tenacity.

ACKNOWLEDGMENTS

This project has been supported by a grant from the Commission of the European Communities, ECLAIR program, Contract AGRE 0052.

LITERATURE CITED

- ANDERSON, O. D., GREEN, F. C., RYAN, E. Y., HALFORD, N. G., SHEWRY, P. R., and MALPICA-ROMERO, J. M. 1989. Nucleotide sequences of the two high molecular weight glutenin subunit genes from the D genome of a hexaploid wheat, *Triticum aestivum* L. cv. Chejenne. *Nucl. Acids Res.* 17:461-462.
- BRANLARD, G., and DARDEVET, M. 1985a. Diversity of grain proteins and bread wheat quality. I. Correlation between gliadin bands and flour quality characteristics. *J. Cereal Sci.* 3:329-343.
- BRANLARD, G., and DARDEVET, M. 1985b. Diversity of grain proteins and bread wheat quality. II. Correlation between high molecular weight subunits of glutenin and flour quality characteristics. *J. Cereal Sci.* 3:345-354.
- BRANLARD, G., and DARDEVET, M. 1994. A null *Gli-D1* allele with a positive effect on bread wheat quality. *J. Cereal Sci.* 20:235-244.
- BRETT, G. M., MILLS, E. N. C., TATHAM, A. S., FIDO, R. J., SHEWRY, P. R., and MORGAN, M. R. A. 1993. Immunochromatological identification of LMW subunits of glutenin associated with bread-making quality of wheat flour. *Theor. Appl. Genet.* 86:442-448.
- CARRILLO, J. M., ROUSSET, M., QUALSET, C. O. and KASARDA, D. D. 1990. Use of recombinant inbred lines of wheat for the study of association of high-molecular-weight glutenin subunit alleles to quantitative traits. I. Grain yield and quality prediction tests. *Theor. Appl. Genet.* 79:321-330.
- GOMEZ, L., SANCHEZ-MONGE, R., and SALCEDO, G. 1988. A family of endosperm globulins encoded by genes in group 1 chromosomes of wheat and related species. *Mol. Gen. Genet.* 214:541-546.
- GUPTA, R. B., and MacRITCHIE, F. 1994. Allelic variation at glutenin subunit and gliadin loci, *Glu-1*, *Glu-3*, and *Gli-1*, of common wheats. II. Biochemical basis of the allelic effects on dough properties. *J. Cereal Sci.* 19:19-29.
- GUPTA, R. B., and SHEPHERD, K. W. 1987. Genetic control of LMW glutenin subunits in bread wheat and association with physical dough properties. Page 13 in: Proc. 3rd Int. Workshop Gluten Proteins. R. Laszity and Bekes eds. World Scientific Publishing: Singapore.
- GUPTA, R. B., and SHEPHERD, K. W. 1988. Low-molecular-weight glutenin subunits in wheat: Their variation, inheritance and association with bread-making quality. Page 943 in: T. E., Miller R. M. D. Koebner, eds. Proc. 7th Int. Wheat Genet. Symp. Inst. Plant Sci. Res.: Cambridge, England.
- GUPTA, R. B., SINGH, N. K., and SHEPHERD, K. W. 1989. The cumulative effects of allelic variation in LMW and HMW glutenin subunits on physical dough properties in the progeny of two bread wheats. *Theor. Appl. Genet.* 77:57-62.
- GUPTA, R. B., PAUL, J. G., CORNISH, G. B., PALMER, G. A., BEKES, F., and RATTIJEN, A. J. 1994. Allelic variation at glutenin subunit and gliadin loci, *Glu-1*, *Glu-3* and *Gli-1*, of common wheat. 1. Its additive and interaction effects on dough properties. *J. Cereal Sci.* 19:9-18.
- KHELIFI, D., and BRANLARD, G. 1992. The effects of HMW and LMW subunits of glutenin and of gliadins on the technological quality of progeny from four crosses between poor breadmaking quality and strong wheat cultivars. *J. Cereal Sci.* 16:195-209.
- MASCI, S. M., PORCEDDU, E., COLAPRICO, G., and LAFIANDRA, D. 1991. Comparison of the B and D subunits of glutenin encoded at the *Glu-D3* locus in two biotypes of the common wheat cultivar Newton with different technological characteristics. *J. Cereal Sci.* 14:35-46.
- MASCI, S. M., LAFIANDRA, D., PORCEDDU, E., LEW, E. J.-L., TAO, M. P., and KASARDA, D. D. 1993. D-glutenin subunits: N-terminal sequences and evidence for the presence of cysteine. *Cereal Chem.* 70:581-585.

- PAYNE, P. I., CORFIELD, K. G., and BLACKMAN, J. A. 1979. Identification of a high-molecular weight subunit of glutenin whose presence correlates with bread-making quality in wheats of related pedigree. *Theor. Appl. Genet.* 55:153-159.
- PAYNE, P. I., SEEKINGS, J. A., WORLAND, A. J., JARVIS, M. G., and HOLT, L. M. 1987. Allelic variation of glutenin subunits and gliadins and its effect on bread making quality in wheat: Analysis of F₅ progeny from Chinese Spring × Chinese Spring (Hope 1A). *J. Cereal Sci.* 6:103-118.
- POGNA, N. E., AUTRAN, J.-C., MELLINI, F., LAFIANDRA, D., and FEILLET, P. 1990. Chromosome 1B-encoded gliadins and glutenin subunits in durum wheat: genetics and relationship to gluten strength. *J. Cereal Sci.* 11:15-34.
- POGNA, N. E., REDAELLI, R., VACCINO, P., PERUFFO, A. D. B., CURIONI, A., METAKOVSKY, E. V., and PAGLIARICCI, S. 1995. Production and genetic characterization of near-isogenic lines in the bread wheat cultivar Alpe. *Theor. Appl. Genet.* 90:650-688.
- POPINEAU, Y., POGNA, N. E., and LEFEBVRE, J. 1995. Rheological properties of glens differing by their glutenin subunit compositions. Pages 129-134 in: *Wheat Kernel Proteins. Molecular and Functional Aspects.* University of Tuscia: Viterbo, Italy.
- REDAELLI, R., POGNA, N. E., DACHKEVITCH, T., CACCIATORI, P., BIANCARDI, A. M., and METAKOVSKY, E. V. 1992. Inheritance studies of the 1AS/1DS chromosome translocation in the bread wheat variety Perzivan-1. *J. Genet. Breed.* 46:253-262.
- SINGH, N. K., DONOVAN, G. R., and MacRITCHIE, F. 1990. Use of sonication and size-exclusion high-performance liquid chromatography in the study of wheat flour proteins. II. Relative quantity of glutenin as a measure of breadmaking quality. *Cereal Chem.* 67:161-170.
- SOZINOV, A. A., and POPERELYA, F. A. 1980. Genetic classification of prolamins and its use for plant breeding. *Ann. Technol. Agric.* 29:229-248.

[Received June 7, 1996. Accepted December 20, 1996.]