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The cumulative effect of allelic variation in LMW and HMW glutenin subunits on dough properties in the progeny of two bread wheats

R.B. Gupta, N.K. Singh and K.W. Shepherd*

Department of Agronomy, Waite Agricultural Research Institute, Glen Osmond, South Australia 5064, Australia

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Summary. The effects of allelic variation at *Gli-A1, Glu-A3* and *Glu-A1* loci coding for gliadins, LMW glutenin subunits and HMW glutenin subunits on dough resistance and extensibility was analysed in 56 F_2-derived F_6 families from a cross between bread wheats MKR(111/8) and 'Kite'. Extensograph data from two sites giving widely different flour protein levels (approximately 7% and 14%) revealed that the *Glu-A3m* and *Glu-A1b* alleles were associated with larger effects on dough resistance and extensibility than the null alleles *Glu-A3k* and *Glu-A1c*, respectively, and moreover, their effects were additive at both protein levels. The effect of the LMW glutenin allele *Glu-A3m* on both dough resistance and dough extensibility was relatively larger than that of the HMW glutenin allele *Glu-A1b* at both sites. Variation at the *Gli-A1* locus did not appear to contribute towards dough strength. The results also showed the large effect of flour protein content on dough properties.

Key words: Wheat flour protein content – Gliadins – Glutenins – Extensograph tests – Bread-making quality

Introduction

It has long been recognized that the gluten protein fraction (gliadins and glutenins) is the main determinant of the viscoelastic property of doughs made from wheat flours (Dimler 1965), but it is only in the last 10 years that it has been possible to associate specific components of these seed proteins with the functional properties of dough. Damidaux et al. (1978) and Kosmolak et al. (1980) showed that gliadin bands 45 and 42 are correlated with good and poor pasta quality, respectively, in durum wheats, while Sozinov and Poperelya (1980) and Wrigley et al. (1981) demonstrated associations between certain gliadin bands and bread-making quality in bread wheats. Payne et al. (1979) were the first to correlate individual high-molecular-weight (HMW) glutenin subunits and wheat flour quality. Subsequently, several other groups (Burnouf and Bouriquet 1980; Moonen et al. 1983; Branlard and Dardevet 1985b; Lawrence et al. 1987) have confirmed and extended these correlations.

In contrast to these extensive studies on HMW glutenin subunits, much less is known about the association of specific low-molecular-weight (LMW) glutenin subunits with dough quality characters, even though it is known that these LMW subunits form disulphide-linked aggregates and make up a large proportion (about 30%) of the total endosperm proteins. Recent genetic studies have shown that genes coding for gliadin bands 42 or 45 in durum wheat are linked with those coding for different LMW glutenin subunits, and chemical studies have shown that differences in the amount of these LMW glutenin subunits might instead be the cause of differences in pasta-quality (Payne et al. 1984; Autran and Berrier 1984; Autran et al. 1987). These positive effects of LMW glutenin subunits point to the need for much further work on determining their influence on the flour quality of both durum and bread wheats.

The main aim of the present investigation was to assess the relative importance of LMW and HMW glutenin subunits on the physical dough properties of flour from bread wheats. An opportunity to investigate this question arose from observations of wheat breeders at the Waite Agricultural Research Institute (A. J. Rathjen personal communication) who found that several bread wheat progeny lines selected from a particular cross ('Kite' × MKR 111/8) gave high grain yield, but pro-

* To whom correspondence should be addressed

duced flour with low dough strength. When the protein patterns of these lines were analysed by SDS-PAGE, it was found that the lines with low strength lacked a particular LMW glutenin subunit from one parent and/or a HMW glutenin subunit from the other. Thus, in the present study, a large number of F_2-derived families from this cross, with all combinations of these parental protein band differences, were selected and multiplied to test for associations between the bands and dough quality.

Some early results from this investigation were presented at the Third International Workshop on Gluten Proteins held at Budapest (Gupta and Shepherd 1987). Concurrently, Payne et al. (1987) reported the results from a similar study on the effect of a different LMW and a HMW glutenin subunit on bread-making quality in the progeny from a cross between 'Chinese Spring' and 'Chinese Spring (Hope 1A)' substitution line, and their results are compared with ours in the discussion.

Materials and methods

1 Experimental materials

The primary experimental material was obtained from the F_2 progeny of a cross between a breeding line MKR-111/8 = {(('Mexico 120' × 'Koda') × 'Raven') – selection 111/8} and the Australian bread wheat cultivar 'Kite'. The parents possess poor and medium bread-making qualities, respectively, and they possess different gliadins, and HMW and LMW glutenin subunit components (Table 1). The protein phenotypes of the parents and the detailed procedure for selecting and multiplying the F_2-derived lines are given in the Results section (Fig. 2). In brief, the F_2 seeds were screened by SDS-PAGE to select 20 individuals for each of the four phenotypic classes representing all combinations of presence and absence of specific bands at the *Glu-A3* (LMW subunit) and *Glu-A1* (HMW subunit) loci. After further testing of their protein patterns during multiplication, the number of isolates in each family (phenotypic class) was reduced from 20 to 14, and these were included in the field trials along with the parents.

2 Field experiments

The experimental layout consisted of 14 randomized sub-blocks each containing six plots, allocated to one line from each of the four selected protein patterns and the two parents, planted in two replicates at two different wheat growing sites in South Australia [Roseworthy Agricultural College (RAC) and Bordertown (BTN)]. The seeds were planted at normal field sowing rates by a semi-automatic seeder into four-row plots with overall dimensions 0.6 m × 4 m.

3 Quality testing

3.1 Milling. Seed samples of 250 gm from each family and the two parental lines were tempered to 14% moisture content and milled to an approximate 70% extraction rate using a Brabender Quadrumat Junior Experimental Mill fitted with a 0.255 mm aperture sieve.

3.2 Flour protein content. The flour protein percentage was determined using a standard micro-Kjeldahl method and was expressed on flour dry weight basis (N × 5.7).

3.3 Extensograph tests. Dough was prepared by mixing 50 gm of flour in a Brabender farinograph with the required amount of distilled water at 30 °C containing 1 gm of common salt (NaCl), to give a final consistency of 500 Brabender units (BU) after 5 min of mixing. A measured amount (75 gm) of this dough was formed into a ball, then rolled and stored in a dough fermentation cabinet for 45 min at 30 °C. The dough was then stretched with a constant speed until the breaking point was reached. The maximum resistance to extension (R_{max}) in BU was obtained by measuring the maximum height of the extensograph curve (extensogram) while the extensibility (E) in cm was given by the length of the extensogram. The area (cm^2) under the curve reflects both dough resistance and extensibility and is a measure of dough strength (energy).

4 Electrophoresis

4.1 Extraction of seed proteins. The unreduced endosperm proteins were extracted in TRIS-HCl buffer containing SDS as described by Lawrence and Shepherd (1980) except that 2-mercaptoethanol was excluded (Singh and Shepherd 1988).

4.2 One-dimensional (1-D) SDS-PAGE. The 1-D SDS-PAGE of unreduced extracts of endosperm proteins was performed according to the method of Lawrence and Shepherd (1980) except that the gels were thinner (1.2 mm thick) and more concentrated (10% acrylamide). Electrophoresis was carried out at a constant current of 40 mA/gel for about 2 h.

4.3 Two-step 1-D SDS-PAGE. The two-step 1-D SDS-PAGE procedure used to separate the LMW and HMW glutenin subunits under study was as described by Singh and Shepherd (1988) except that the gels were thinner (1.2 mm for the 1st step, 1.5 mm for the 2nd step) and the tracking dye was added directly into the equilibration solution. The second step of electrophoresis was carried out in a gradient gel (7.5% – 15% acrylamide) at a constant current of 25 mA/gel for 6 h.

4.4 Staining and destaining. Gels were stained with Coomassie Blue R-250 for about 16 h as described by Lawrence and Shepherd (1980). The two-step gels were first soaked in de-ionised water for 16 h and then treated with destaining solution (containing glacial acetic acid, methanol and water in 1 : 6 : 14 ratio) for about 4 h to obtain maximum band contrasts. However, enhanced band appearance was obtained in 1-D gels simply by soaking in de-ionised water for about 48 h (Singh and Shepherd 1988). The two-step gels were frozen to sharpen the bands for photography.

5 Statistical analysis

Since extensograph tests require much labour, only one replicate from each site was analysed for R_{max} and E. The analyses of variance (ANOVA) were performed on both individual site data and the pooled data. The 14 different sub-blocks containing isolates of each of the four protein phenotypes were treated as replicates in the single-site analysis of variance.

Results

Isolation and characterization of experimental lines

The protein phenotypes of parents MKR-111/8 and 'Kite' are shown in Fig. 1, and the allelic differences for gliadins, LMW glutenin subunits and HMW glutenin

Table 1. Allelic differences between parents for storage proteins and the location of genes controlling them

Protein class	Locus	Protein band differences in parents	
		MKR (111/8)	Kite
Gliadins	*Gli-A1*	Gli-A1m	Gli-A1k
LMW glutenin subunits	*Glu-A3*	Glu-A3m	Glu-A3k (null)
HMW glutenin subunits	*Glu-A1*	Glu-A1c (null)	Glu-A1b (2*)
HMW glutenin subunits	*Glu-B1*	Glu-B1b (7+8)	Glu-B1i (17+18)

The symbols for HMW glutenin bands and the designations *Glu-A1*, *Glu-B1*, *Glu-D1* and *Gli-A1* are according to Payne and Lawrence (1983). The symbol *Glu-A3* was introduced by Singh and Shepherd (1988). The designations for protein bands coded by *Gli-A1* and *Glu-A3* loci are new

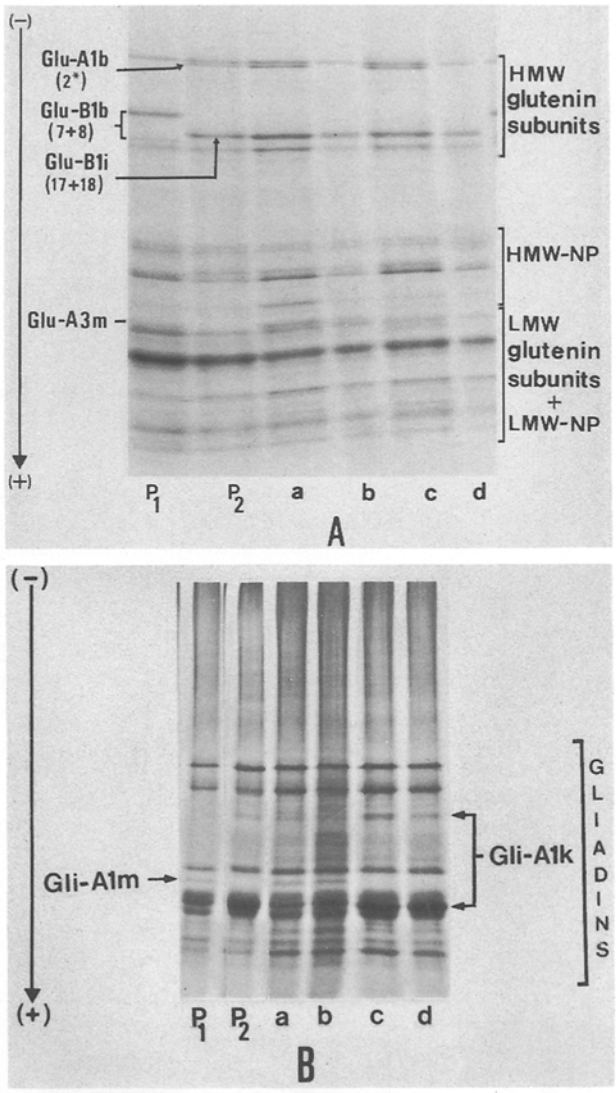

Fig. 1 A and B. SDS-PAGE patterns of parents MKR (111/8) (P_1) and 'Kite' (P_2) and F_6 families (*a, b, c, d*) showing the four main phenotypic classes. **A** 2-step SDS-PAGE patterns of protein extracts; **B** 1-D SDS-PAGE patterns of unreduced protein extracts of the same seeds. The *arrow* indicates the direction of protein migration. *NP*, non-prolamins

subunits are summarized in Table 1. The LMW and HMW glutenin subunits were scored in two-step SDS-PAGE whereas the gliadins were examined by 1-D SDS-PAGE. Since 'Kite' did not possess an alternative band to Glu-A3m of MKR (111/8), and similarly MKR (111/8) had no obvious band equivalent to the Glu-A1b of 'Kite', it was assumed that they possess null alleles (*Glu-A3k* and *Glu-A1c*, respectively) at these loci (Fig. 1 A).

In the analysis of F_2 seeds, the Glu-A3m band was always associated with Gli-A1m, and similarly null Glu-A3k with Gli-A1k (Fig. 1 B) indicating complete or close linkage between *Glu-A3* and *Gli-A1* loci (Singh and Shepherd 1988). The Gli-A1 and Glu-A3 bands were found to be loosely linked (43.5% recombination) with the 2* band, which is known to be controlled by a locus on the long arm of chromosome 1A (Payne and Lawrence 1983), and thus it was concluded that all three of these loci are located on chromosome 1A.

There was no difficulty in selecting F_2 seeds homozygous for the Glu-A3, Gli-A1 and Glu-B1 bands (7+8 and 17+18) due to the co-dominant expression of alleles. However, the homozygosity for Glu-A1b (band 2*) could only be determined by progeny testing because there was no detectable band allelic to it. The linked gliadins were used to select seeds homozygous for the Glu-A3m band. For simplicity, only the detectable bands are referred to in the tables, figures and diagrams.

The main objective of the study was to investigate the effects of the Glu-A3m and Glu-A1b bands on physical dough properties; consequently, the F_2 seeds were classified into the four main phenotypic classes: Glu-A3m$^+$ Glu-A1b$^+$; Glu-A3m$^+$ Glu-A1b$^-$; Glu-A3m$^-$ Glu-A1b$^+$; Glu-A3m$^-$ Glu-A1b$^-$. To minimize possible effects from the co-segregation of Glu-B1 bands, all combinations of these phenotypes (Glu-B1b, Glu-B1i and Glu-B1b/Glu-B1i) were included within each of the four main classifications as shown in Fig. 2. The 80 selected F_2 seeds were individually multiplied for two further generations to produce F_4 families (Fig. 2), and the phenotypes of these families were checked on gels. Finally, 56 verified F_4 families (14 in each main class) were chosen and multiplied to develop 56 F_5 families which were then planted in the field along with 14 lines of each parent for quality testing.

Effect of flour protein level on dough properties

The flour protein content of the parents and families was very different at the two sites, with an average value of

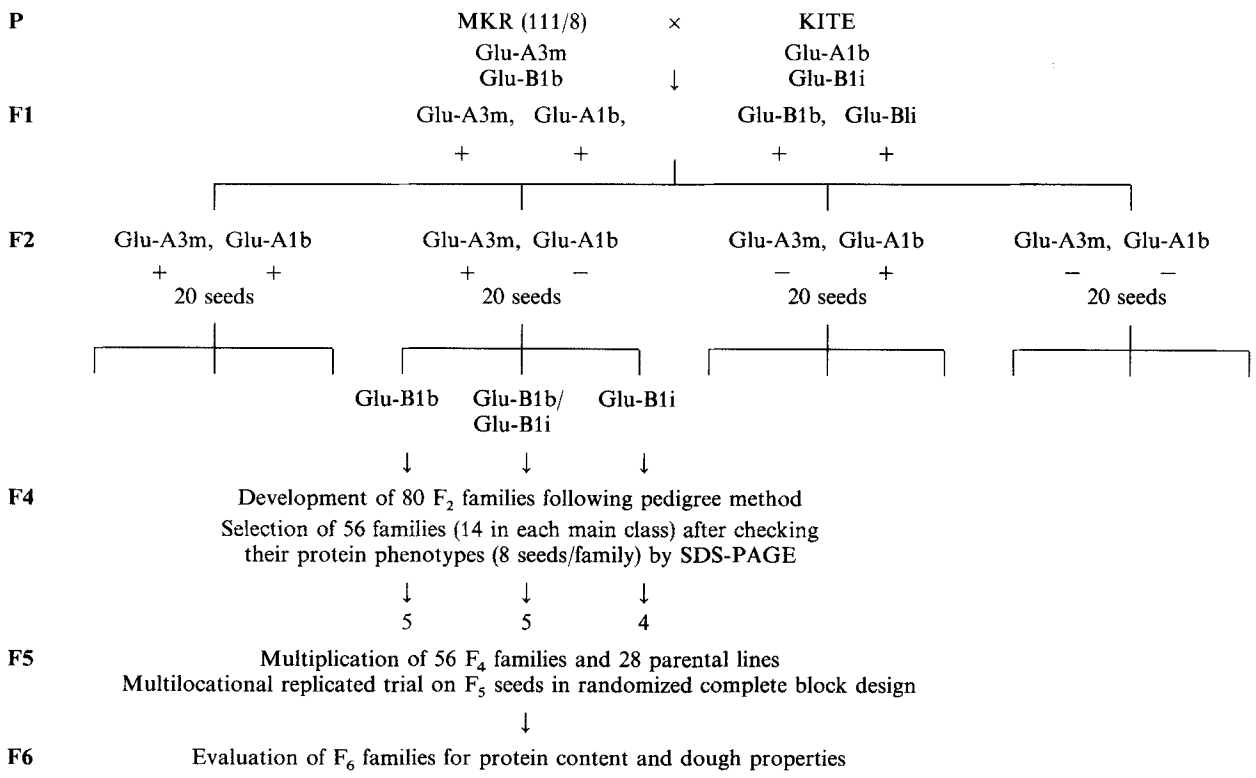

Fig. 2. Procedure used to develop 56 F_6 families from a cross between parents MKR (111/8) and 'Kite'. The same procedure for selecting F_2 seeds – dividing them into Glu-B1 subgroups and multiplying them – was used for all groups, but is only shown in detail for the Glu-A3m$^+$ Glu-A1b$^-$ group

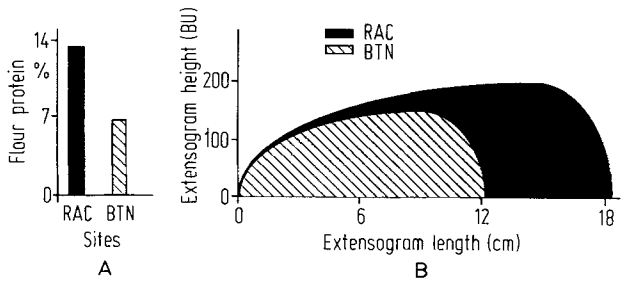

Fig. 3 A and B. Overall mean values for quality characters of 56 F_6 families and 28 parental lines grown at two sites (*RAC*, Roseworthy Agricultural College; *BTN*, Bordertown). **A** Flour protein content; **B** dough strength measured as dough resistance (extensogram height) and extensibility (extensogram length)

approximately 14% at RAC and 7% at BTN (Fig. 3 A). Similarly, the average dough strength (both dough resistance and extensibility) of these parents and families was very different between the two sites, reflecting the differences in flour protein content (Fig. 3 B). The effect of protein content on dough extensibility was relatively greater than on dough resistance, however (Fig. 3 B).

Effect of allelic variation in protein bands on dough properties

The pooled ANOVA including all treatments (parents and F_6 families) showed significant interaction between treatments and sites for R_{max} ($F=3.49$; $P=0.005$) and E ($F=2.70$, $P=0.023$). However, when the parents were excluded from the analysis, there was no interaction ($F<1.5$, $P>0.2$). Similarly, there was a significant difference ($F=3.73$, $P=0.005$) in the protein content of treatments at RAC due to differences between the parents but not between the F_6 families (Table 2). These differences in response shown by the parents are assumed to result from their different genetic backgrounds. Because of the statistical problems introduced by including the parents and since the only valid comparisons are those within a common background, the data pertaining to parents are considered to be reference material only.

There were highly significant differences in the R_{max} and E values for the different F_6 families at both locations (Table 3), and these could not be assigned to differences in the protein content (Tables 2 and 3). The families lacking both the Glu-A3m and Glu-A1b bands had the lowest mean values for R_{max} (Fig. 4 A) and E (Fig. 4 B),

Table 2. Average flour protein content (mean of 14 entries) of parents and four types of families at two sites (RAC and BTN)

Phenotypic classes	Flour protein content (%)	
	RAC	BTN
Parents		
MKR (111/8)	13.26	6.64
'Kite'	14.20	6.95
Families		
Glu-A3m$^+$Glu-A1b$^+$	13.70	6.66
Glu-A3m$^+$Glu-A1b$^-$	13.40	6.75
Glu-A3m$^-$Glu-A1b$^+$	13.49	6.58
Glu-A3m$^-$Glu-A1b$^-$	13.70	6.84
SED	0.24	0.16

Table 3. Between family variance ratios (*F* values) in ANOVA for flour protein %, maximum resistance (R_{max}) and extensibility (E) among 56 F_6 families at two sites (RAC and BTN)

Character	RAC		BTN	
	F value	*P*	*F* value	*P*
Protein %	0.79	0.50	0.88	0.46
R_{max}	21.07	<0.001	19.97	<0.001
E	11.13	<0.001	4.6	<0.001

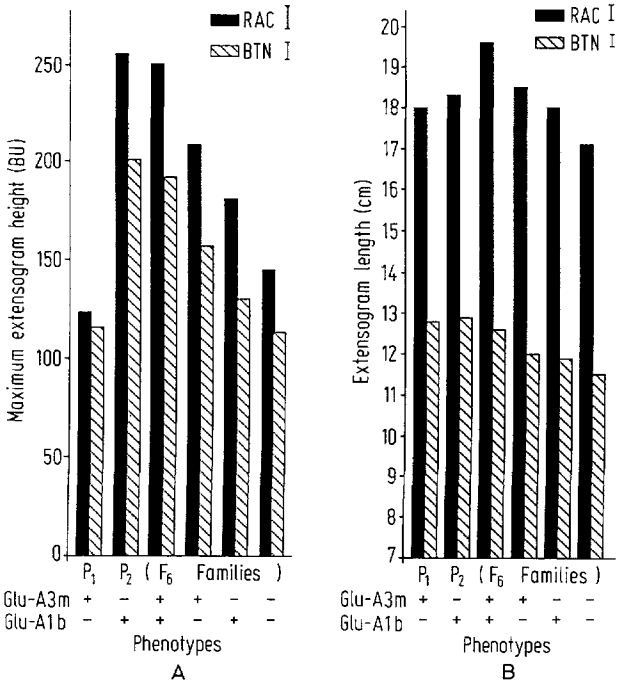

Fig. 4 A and B. Mean values (average of 14 entries) for maximum extensogram height **A** and extensogram length **B** for both parents (P_1, MKR (111/8); P_2, 'Kite') and 56 F_6 families grown at two sites (*RAC*, Roseworthy Agricultural College; *BTN*, Bordertown). The standard error of differences (SED) are shown as *bars*

whereas families having both of these bands had the highest values for these characters. The families with just one of the bands had intermediate values indicating the additive effects of these bands on the dough parameters. Interestingly, families with LMW band Glu-A3m gave significantly higher values for R_{max} at both sites and for E at RAC than those with HMW band Glu-A1b.

The families with the lowest dough strength (phenotype Glu-A3m$^-$ Glu-A1b$^-$) possess the null alleles *Glu-A3k* and *Glu-A1c* but have two prominent gliadin bands controlled by the *Gli-A1k* allele (slot d, Fig. 1 B). The families with phenotype Glu-A3m$^+$ Glu-A1b$^-$ differ from the above by two extra bands (LMW glutenin band Glu-A3m and gliadin band Gli-A1m) and have much higher dough resistance and extensibility. Although, we cannot be certain from these data, we believe that it is the LMW glutenin subunit rather than the extra gliadin band which is mainly responsible for the improved dough properties. We also believe that allele *Glu-A3m* is better than its null allele *Glu-A3k* for dough quality. Similarly, comparison of the dough quality of families possessing the *Glu-A1b* allele (phenotype Glu-A3m$^-$ Glu-A1b$^+$) and those having allele *Glu-A1c* (phenotype Glu-A3m$^-$ Glu-A1b$^-$) indicated that *Glu-A1b* is associated with higher dough strength than the null allele *Glu-A1c*.

Relative effects of Glu-A3m and Glu-A1b on dough quality

As shown in Table 4, the presence of LMW allele *Glu-A3m* was associated with a larger value of R_{max} and E than the presence of HMW allele *Glu-A1b* at both sites. However, the presence of both alleles together gave higher R_{max} and E values than the presence of each one separately, suggesting that these alleles at the *Glu-A3* and *Glu-A1* loci act in an additive manner on quality attributes at both high and low levels of flour protein (Fig. 4 A, B). The combined effect of these alleles did not differ significantly from the simple sum of their individual effects ($F<2.05$, $P>0.16$), confirming their additive behaviour (Table 4).

Discussion

An F_2 progeny method was adopted in the present study to relate individual protein bands to dough quality. This procedure has the advantage of analysing the association between two traits over a wide range of genetic backgrounds, and thus any correlations detected are likely to be real. Its main disadvantage is the necessity to produce and test a large number of progeny lines for each genotype. Although, the alternative isogenic line approach requires only one or a few isolates of each genotype for comparison, these lines are very time consuming to produce.

Table 4. Average effects of bands Glu-A3m and Glu-A1b on R_{max} and E at two sites (RAC and BTN)

Type of effect	Protein bands	R_{max}		E_{total}	
		RAC	BTN	RAC	BTN
Individual[a]	Glu-A3m	63.8	44.0	1.4	0.5
	Glu-A1b	35.5	17.1	0.8	0.4
Observed combined	Glu-A3m &Glu-A1b	109.3	79.1	2.6	1.2
Interaction[b]	Glu-A3m &Glu-A1b	10.0	18.0	0.4	0.3

[a] Individual effects were highly significant ($F > 5.53$, $P < 0.024$)
[b] Interactions were not significant ($F < 2.05$, $P > 0.16$). The interaction represents the difference between the observed combined effect and the sum of individual effect of both bands

The parents used in this study were similar agronomically and had no major differences in gliadins, LMW glutenin subunits and HMW glutenin subunits other than those already considered. Efforts were made to minimize the effects due to differences in Glu-B1 bands (7 + 8 and 17 + 18), by grouping the progeny according to their Glu-B1 phenotype (Fig. 2). Further, these bands do not normally have significantly different effects on dough quality (Lawrence et al. 1987), and therefore it is unlikely that these bands had any significant effect on the results. Some differences in albumin components, possibly controlled by chromosome arm 5BL (Gupta and Shepherd 1987), were also noted (Fig. 1 A), but it is not known whether they have any effect on dough quality. Nevertheless, since they were randomly distributed among the selected F_6 families, it is unlikely that they would have contributed to the associations observed.

The amounts of flour protein at the two sites (RAC and BTN) were very different, allowing the effects of allelic variation at the *Gli-A1*, *Glu-A3* and *Glu-A1* loci on dough quality to be tested at two extremes of flour protein. The LMW glutenin allele *Glu-A3m* and HMW glutenin allele *Glu-A1b* were associated with larger effects on dough parameters than the null alleles *Glu-A3k* and *Glu-A1c*; this was possibly due to the formation of a greater amount of glutenin. Moreover, they had cumulative effects on R_{max} and E at both protein levels which suggested that the bands coded by these alleles act on dough viscoelasticity independently of the level of flour protein. These results support the recent work of Payne et al. (1987) who showed that a different LMW glutenin band (corresponding to band Glu-A3a of Gupta and Shepherd 1988) and a HMW glutenin subunit (band 1 of Payne and Lawrence 1983) acted additively on bread-making quality, as measured by sedimentation test and extensometer, in the progeny of a cross between 'Chinese Spring' and 'Chinese Spring (Hope 1A)' substitution line. According to our recent designations, band Glu-A3m corresponds to the Glu-A3c band (Gupta and Shepherd 1988). Since cumulative effects were observed in these two studies with different alleles (at the same loci) and different genetic backgrounds, these results highlight the combined role of LMW and HMW glutenin subunits in improving bread-making quality.

The most interesting finding of the present study is that LMW glutenin band (Glu-A3m) was associated with greater dough resistance and extensibility than the HMW glutenin band (Glu-A1b). However, Payne et al. (1987) did not detect any difference in the relative effects of the LMW and HMW glutenin band (Glu-A3a and Glu-A1a) on sedimentation volume and dough elasticity in their study, possibly because the comparison was made in the poor quality background of 'Chinese Spring'. Visual assessment of the staining intensity of the Glu-A3m and Glu-A1b bands did not reveal any major difference between them, therefore, it is speculated that differences in the number and positions of cysteine residues (Moonen et al. 1985) in their polypeptide chains could be responsible for the observed differences in dough viscoelasticity. Clearly, the biochemical basis of the greater effect associated with LMW glutenin band Glu-A3m on dough quality needs to be investigated. These studies also point to the need for more detailed analyses of the associations between the extensive allelic variation detected in LMW glutenin subunits (Gupta and Shepherd 1988) and bread-making quality.

The close genetic linkage between Glu-A3m and Gli-A1m makes it difficult to interpret whether the observed effects on quality are due to the LMW glutenin band or the gliadin bands. However, Pogna et al. (1988) recently detected a durum wheat which possessed gliadin band 42 and LMW glutenin bands of LMW-2, and showed that the gluten elasticity of this naturally occurring recombinant line was equal to high quality durum wheats having gliadin bands 45 and LMW-2, thus providing evidence for a causal relationship between the LMW glutenin bands and the gluten elasticity. These observations suggest that associations found between certain gliadins and bread wheat quality by other groups (Sozinov and Poperelya 1980; Wrigley et al. 1981; Branlard and Dardevet 1985a; Payne et al. 1987) are also due to the linked LMW glutenin subunits.

The observed strong positive effect of flour protein quantity on physical dough properties is in accordance with its positive effect on other quality parameters, viz. bread loaf volume and sedimentation volume (Bailey and Sherwood 1926; Finney and Barmore 1948; Bushuk et al. 1969). Although this indicates that bread-making quality can be improved by increasing grain protein level, the well known inverse relationship between grain protein and grain yield makes increasing grain protein level difficult to achieve. Moreover, increasing the level of grain

protein does not assure good dough resistance in the absence of suitable alleles for glutenin bands; for example, the progeny having alleles LMW *Glu-A3*^{c} and HMW *Glu-A1c* (phenotype Glu-A3m$^-$ Glu-A1b$^-$) at the 14% protein level had a much lower dough resistance than that having alleles *Glu-A3m* and *Glu-A1b* (phenotype Glu-A3m$^+$ Glu-A1b$^+$) at the 7% protein level (Fig. 4A). Thus, these results suggest that favourable alleles for glutenin bands are required for good dough resistance. Moreover, since these alleles (*Glu-A3m* and *Glu-A1b*) were associated with large positive effects on dough resistance at two given protein levels (7% and 14%), selection of such alleles will help improve dough quality irrespective of grain protein level.

The allelic variations at these loci also were significantly correlated with dough extensibility at both sites (Table 4). The LMW glutenin/gliadin allele *Glu-A3m*/*Gli-A1m* had significantly larger effect than the HMW allele *Glu-A1b* at RAC, however. Some other LMW glutenin alleles (e.g. *Glu-A3b*) and associated gliadins have also been found to be positively correlated with dough extensibility in biotypes of bread wheats (Gupta and Shepherd 1988). The information available on the relative performance of various alleles at the *Glu-A3* locus for dough extensibility can be summarized as follows: *Glu-A3a* > *Glu-A3e* (Payne et al. 1987), *Glu-A3b* > *Glu-A3c* (Gupta and Shepherd 1988) and *Glu-A3c* > *Glu-A3e* (this study). These allele symbols are adopted from Gupta and Shepherd (1988). The symbol *Glu-A3e* represents a null allele and corresponds to the *Glu-A3k* allele of 'Kite' (this paper) and to the null allele of 'Hope' (Payne et al. 1987). These results suggest that there is scope for improving dough extensibility by utilizing allelic variation in LMW glutenin subunits. Although the total quantity of flour protein had a larger effect on dough extensibility than the alleles at these loci (Fig. 4B), the results indicate that selection based on alleles associated with positive and cumulative effects can improve dough extensibility regardless of the level of grain protein. This is illustrated by progeny carrying *Glu-A3m* and *Glu-A1b* alleles having the largest dough extensibility while progeny with *Glu-A3k* and *Glu-A1c* alleles have the lowest dough extensibility at both protein levels (Fig. 4B).

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