

Use of Near-Isogenic Wheat Lines to Determine Protein Composition-Functionality Relationships

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ABSTRACT

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Nine and six major loci control the synthesis of the gluten proteins that are responsible for many of the physical and technological properties of hexaploid and tetraploid wheats, respectively. For hexaploid wheats, these are the three *Glu-1* and three *Gli-1/Glu-3* loci on group 1 chromosomes, and the three *Gli-2* loci on group 6 chromosomes. Lines in which

genes at one or more of these loci are absent or silent are available and have been used to assist in deducing the effects on functional properties of deleting or substituting specific proteins or subunits, while maintaining a constant genetic background. The lines that are available and the information they have provided are summarized.

One of several approaches that can be used to elucidate relationships between wheat protein composition and functional properties is to use near-isogenic wheat lines that differ at one or more loci coding for proteins. In this way, the effects of specific proteins can be deduced without the confounding effects of differing genetic backgrounds that are usually present when surveying different cultivars. Deletions of part or whole chromosomes in wheat occur spontaneously in nature and these lines have been used by cytogeneticists to produce valuable experimental materials. The foundations for these developments were laid by the pioneering work of Sears (1954, 1966), who created a series of lines in the cultivar Chinese Spring. The resulting stocks include monosomic (one chromosome missing), nullisomic-tetrasomic (missing one chromosome but with a double dosage of another), and ditelosomic (missing one arm of the chromosome) lines. There are lines available with deletions, additions, or differences in allelic expression at specific loci. Some have arisen by natural mutation, while others have been created by chromosomal engineering. As well as providing excellent materials for composition, structure, and function studies, these lines can be used to manipulate functional properties predictably in breeding situations. This article will review some of the interesting germplasm presently available, how it may be used to gain knowledge about composition-functionality, and how it may be used to target certain properties in breeding programs.

Chromosomal Location of Genes Coding for Gluten Proteins

The use of the aneuploid lines, in combination with electrophoresis, has enabled location of genes coding for different wheat proteins. This breakthrough has resulted from the efforts of a number of researchers but in particular, Shepherd (1968), Wrigley and Shepherd (1973), Bietz et al (1975) and Payne (1987).

There are roughly nine major loci that code for gluten proteins, the main proteins that contribute to flour functionality: the three *Glu-1* loci (*Glu-A1*, *Glu-B1*, *Glu-D1*) on the long arms of chromosomes 1A, 1B, and 1D, respectively, coding for high molecular weight glutenin subunits (HMW-GS); the three complex *Gli-1/Glu-3* loci (*Gli-A1/Glu-A3*, *Gli-B1/Glu-B3*, *Gli-D1/Glu-D3*) on the short arms of chromosomes 1A, 1B, and 1D with tightly linked genes coding for ω - and γ -gliadins and low molecular weight glutenin subunits (LMW-GS); and the three *Gli-2* loci (*Gli-A2*, *Gli-B2*, *Gli-D2*) coding for α - and β -gliadins. The chromosomal location of the genes is illustrated in Fig. 1. All these loci exhibit allelic

variation. Thus, there are available a large number of alleles on which to base systematic studies. It should be noted, however, that Fig. 1 is a simplification of the loci. A number of other minor loci have been identified on these chromosomes (Payne et al 1988; Ruiz and Carrillo 1993; Pogna et al 1995) as well as on other chromosomes (Sreeramulu and Singh 1997).

GLU-1 Loci

HMW-GS Null Lines

Lawrence et al (1988) developed a set of lines in which the number of HMW-GS varied progressively from a full complement of five down to zero. This was achieved by crossing a mutant line of the cultivar Olympic, null at the *Glu-B1* locus, and an isogenic line of the cultivar Gabo, null at the *Glu-A1* and *Glu-D1* loci. SDS-PAGE patterns of all these lines are shown in Fig. 2. A similar set of lines based on the cultivar Sicco was developed by Payne et al (1987a), in which the number of HMW-GS varied from five to two. Studies of these two sets of lines confirmed that the HMW-GS proteins of wheat make the greatest contribution to functionality on a weight basis. This had been suggested by the earlier research on this group of protein subunits (Payne et al 1981).

Two important pieces of information come from studies of HMW-GS null lines. One is that properties such as dough mixing strength and breadmaking quality decrease dramatically as HMW-GS are deleted (Table I). The other is that the total quantity of HMW-GS decreases approximately linearly with decreasing number of subunits (Fig. 3). This result suggests that the quantity of a given group of proteins in a wheat or flour sample is closely related to the number of individual proteins and therefore the number of genes coding for those proteins.

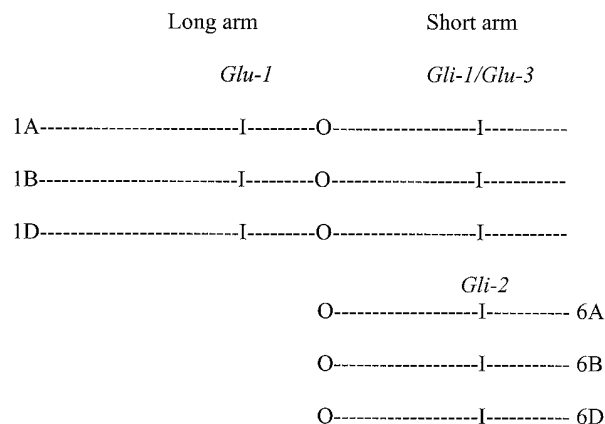


Fig. 1. Chromosomal location of genes coding for gluten proteins.

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Allelic Variation at One *Glu-1* Locus

The work of Payne et al (1987b) established that different HMW-GS arising from allelic variation at *Glu-1* were related to dough strength and breadmaking quality. Two pairs of subunits in particular had contrasting effects. These were the allelic pairs 5+10 and 2+12 coded at the *Glu-D1* locus. Subunits 5+10 were associated with strength and 2+12 were associated with lack of strength. Use of near-isogenic lines differing in allelic expression of these two pairs of subunits at *Glu-D1* have been used to explain the reasons for the observed differences. Figure 4 summarizes some compositional data for three pairs of lines differing at *Glu-D1* and compares the data with dough strength of each line, assessed by mixograph peak dough development time (MDDT). MDDT shows no obvious relation to either flour protein content or the percentage of polymeric protein in the total protein (PPP). However, the unextractable polymeric protein (UPP) appears to match the MDDT quite well. UPP is a parameter that gives a relative measure of the molecular weight distribution of the polymeric protein, based on solubility

(Gupta et al 1993). A greater amount of unextractable polymeric protein (and therefore molecular weight distributions shifted to higher molecular weights) thus appears to be associated with the presence of HMW-GS 5+10 and gives a plausible explanation of greater dough strength of these lines over the lines with HMW-GS 2+12. Studies of the protein composition of allelic variants of cultivar Lance at different stages of grain filling showed that, in the line with HMW-GS 5+10, the UPP began to increase steeply at an earlier time than the UPP of the line with 2+12 subunits (Gupta et al 1996). This difference was maintained up to maturity, although the amounts of polymeric protein in the two lines were not significantly different. The reason behind this temporal difference in polymerization of polymeric subunits is of great interest, but so far has not been explained. It has been suggested that it may be related to differences in the number of cysteine residues in the HMW-GS (Shewry et al 1992).

Translocation of HMW-GS

Application of cytogenetic techniques has produced valuable wheat lines for composition-functionality studies. These include the tetraploid aneuploids developed by Joppa (Joppa and Williams 1988; Joppa et al 1983), and the translocations of Lukaszewski (Ammar et al 1997).

Among the interesting lines produced by Lukaszewski using chromosomal engineering techniques (Ammar et al 1997), lines have been created in which HMW-GS normally associated with hexaploid wheats have been translocated on to chromosome 1A of a tetraploid (durum) line, replacing the widespread null allele present at the *Glu-A1* locus. The effect of this translocation on protein composition and MDDT is summarized in Table II. There is a dramatic increase in MDDT from 5 to 15 min as a result of introduction of the extra HMW-GS. There is an increase in PPP of 2.6%, but what is probably more relevant to the increase in MDDT is the large increase in UPP. The presumed shift of the molecular weights to higher values are the result of introduction of strength-contributing HMW-GS 5+10.

TABLE I
Mixograph Dough Development Times (MDDT)
and Bake Test Loaf Volume (LV)^a for lines Varying in HMW-GS^b

HMW-GS			MDDT (min)	LV (mL)
<i>Glu-A1</i>	<i>Glu-B1</i>	<i>Glu-D1</i>		
1	17+18	5+10	5.9	48
Null	17+18	5+10	4.6	46
1	Null	5+10	3.4	41
1	17+18	Null	2.7	na ^c
Null	17+18	Null	3.3	46
Null	Null	5+10	2.4	40
1	Null	Null	1.7	34
Null	Null	Null	0.7	32

^a Bake test used 10 g of flour.

^b Lawrence et al (1988).

^c Not available.

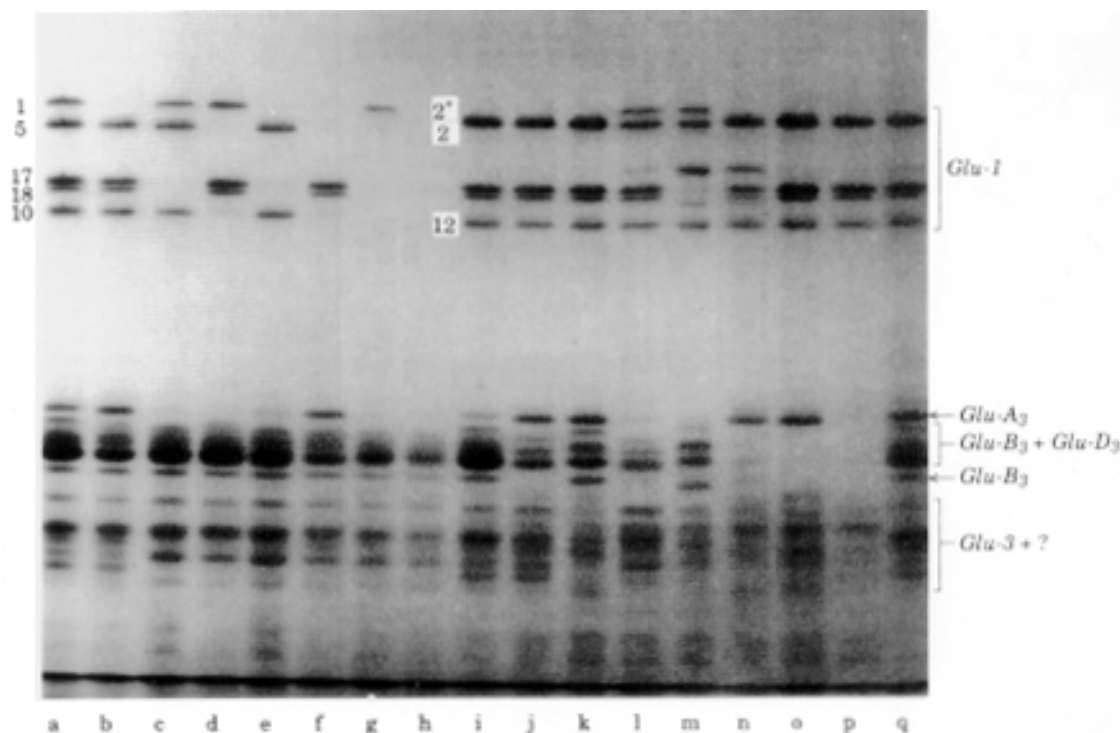


Fig. 2. SDS-PAGE of glutenin subunits in sets of HMW-GS null lines (a–h) and wheat/rye translocation lines (i–q). a) parent line carrying *Glu-A1*, *Glu-B1* and *Glu-D1*; b) null at *Glu-A1*; c) null at *Glu-B1*; d) null at *Glu-D1*; e) null at *Glu-A1*, *Glu-B1*; f) null at *Glu-A1*, *Glu-D1*; g) null at *Glu-B1*, *Glu-D1*; h) null at *Glu-A1*, *Glu-B1*, *Glu-D1*; i) parent line Gabo; j) null at *Glu-B3*; k) null at *Glu-D3*; l) null at *Glu-A3*, *Glu-B3*; m) Null at *Glu-A3*, *Glu-D3*; n and o) null at *Glu-B3*, *Glu-D3*; p) null at *Glu-A3*, *Glu-B3*, *Glu-D3*; q) parent line Gabo (Gupta et al 1995).

Wheat/Rye Translocation Lines

There are no equivalent lines to the HMW-GS nulls with a gradation of LMW-GS. Such lines are difficult to attain because of the tight linkage between the *Gli-1* and *Glu-3* loci. The ditelosomic materials with deletions of chromosome 1 short arms are one alternative, but the closest materials to the HMW-GS null lines may be the wheat/rye translocation lines developed by Gupta and Shepherd (1993). In these lines, one, two, or all three short arms of the group 1 chromosomes of wheat have been replaced by the short arm of chromosome 1 of the diploid rye. The effect is illustrated in Fig. 5 for a single translocation on chromosome 1B, the most common rye translocation. The *Gli-B1/Glu-B3* locus is deleted and the *Sec-1* locus, coding for secalins (single-chain rye proteins similar to gliadins) is substituted. The 1B/1R lines have been of interest because they introduce a range of pathogen-resistant genes from the 1R short arm (Graybosch 2001), as depicted in Fig. 5.

The single, double, and triple wheat/rye translocation lines therefore form a set that is closely analogous to the HMW-GS lines. LMW-GS are progressively deleted; in addition, γ - and ω -gliadins are removed and replaced by secalins. SDS-PAGE patterns for single, double, and triple wheat/rye translocations are shown in Fig. 2. Figure 6 shows plots of extensigraph maximum resistance (R_{max}) as a function of the percentage of polymeric protein (PPP) evaluated from Peak 1 of the SE-HPLC for the two sets of lines: the HMW-GS null series and the wheat/rye translocation lines (single, double, and triple). The regression lines for the two sets of data show markedly different slopes; that for the HMW-GS null set is much steeper. This can be interpreted to mean that contributions to dough strength are greater for variation of HMW-GS than for LMW-GS on an equal weight basis, a direct confirmation of what has been suggested previously with more indirect evidence. Figure 7 shows extensigrams from parent lines for both the HMW-GS null set and the rye translocation set, together with corresponding extensigrams for the triple HMW-GS null line and the triple rye translocation line. It shows, in both cases, a dramatic reduction in dough strength as a

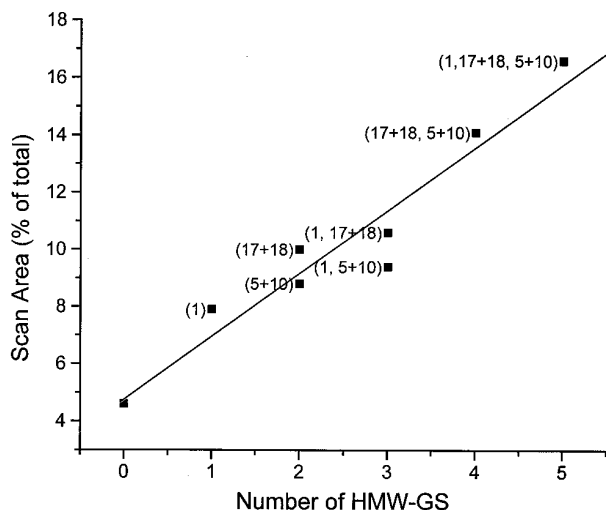


Fig. 3. Total quantity of HMW-GS (measured by densitometry of SDS-PAGE patterns) as a function of the number of HMW-GS. Nonextrapolation of the line to zero is due to background staining (Lawrence et al 1988).

result of deletion of each full set of glutenin subunits. The relative reduction appears to be less for full deletion of LMW-GS (triple rye translocation), even though the reduction in quantity of glutenin is much greater (LMW-GS are usually in excess of HMW-GS by a factor of two to three). Again, this is consistent with the greater contribution per unit weight of the HMW-GS; however, it shows that LMW-GS also play an important role.

***Gli-1/Glu-3* Deletions**

Lines are available in which a whole *Gli-1/Glu-3* locus is missing. So far, the most common is the *Gli-B1/Glu-B3* deletion. Table III summarizes some data for protein composition and MDDT for three lines with *Gli-B1/Glu-B3* deletions, comparing them with their normal parent lines (Gianibelli et al 1998). For each of the deletion lines, there is a reduction of the percentage of polymeric protein in the total protein (PPP) and a corresponding decrease in the MDDT. What may be deduced from this data is that there is a greater amount of LMW-GS than gliadins expressed at the *Gli-B1/Glu-B3* locus in the parent lines. Thus, when this locus is deleted, the glutenin-to-gliadin ratio is shifted to lower values, leading to reduced dough strength. Of course, this is not necessarily a general result for all *Gli-1/Glu-3* deletions. It seems likely that at other loci, and even at certain *Gli-B1/Glu-B3* loci in other cultivars, there could be a greater expression of gliadins than LMW-GS. In those cases, deletion of the *Gli-1/Glu-3* locus would shift the glutenin-to-gliadin ratio to higher values and lead to increased strength. Thus, depending on the relative amounts of LMW-GS and gliadins expressed at this locus, deletion of the locus could be used to increase or decrease the strength of cultivars.

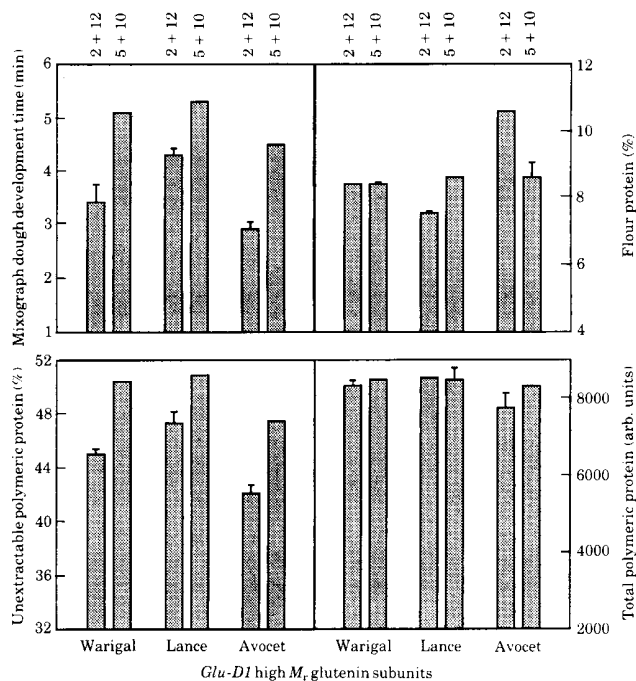


Fig. 4. Mixograph dough development time and several measures of protein composition for three pairs of wheat lines, individual lines in each pair differing at *Glu-D1* (Gupta and MacRitchie 1994).

TABLE II
Protein Composition and Mixograph Dough Development Times for Near-Isogenic Lines (NIL) of Tetraploid (Durum) Wheat Cultivar Svevo^a

Line	<i>Glu-A1</i>	<i>Glu-B1</i>	MDDT (min)	PPP (%)	UPP (%)
Svevo	Null	7+8	5.1	47.2	54.1
Svevo NIL	5+10	7+8	15.0	49.8	62.1

^a MDDT, mixograph dough development time; PPP, percent polymeric protein in total protein; UPP, unextractable polymeric protein (Lafiandra et al 2000).

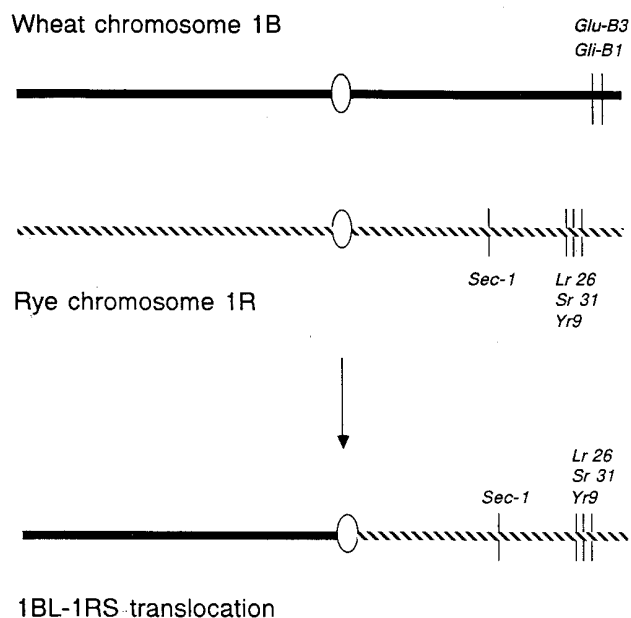


Fig. 5. 1BL-1RS translocation showing replacement of *Gli-B1/Glu-B3* locus by *Sec-1* and introduction of genes for leaf, stem, and stripe rusts, *Lr 26*, *Sr 31*, and *Yr 9*, respectively.

TABLE III
Effect of Deletion of *Gli-B1/Glu-B3* Locus on Percent Polymeric Protein in Total Protein (PPP) and Mixograph Dough Development Time (MDDT)^a

Line	<i>Gli-B1/Glu-B3</i>	PPP (%)	MDDT (min)
Oderzo	+	51.1	4.9
Null	-	45.4	4.2
San Pastore	+	50.5	2.6
Null	-	42.5	2.2
Spada	+	52.2	4.5
Null	-	46.6	3.6

^a Gianibelli et al 1998.

TABLE IV
Protein Composition and Mixograph Dough Development Times (MDDT) for Flours from Lines Varying at *Gli-D1/Glu-D3*^a

Line	<i>Gli-D1/Glu-D3</i>	PPP (%)	UPP (%)	MDDT (min)
Oasis	CS	46.7	47.7	4.4
	CNN	42.7	51.3	5.3
Thomas	CS	54.7	49.4	4.7
	CNN	53.2	52.6	5.6

^a PPP = percent polymeric protein in total protein, UPP = percent unextractable polymeric protein (Gianibelli et al 1998). CS = Chinese Spring allele; CNN = Cheyenne allele.

Allelic Variation at One *Gli-1/Glu-3* Locus

As in the case of *Glu-1*, sister lines differing in allelic expression at one *Gli-1/Glu-3* locus can occur naturally. Table IV summarizes data for two cultivars exhibiting allelic variation at *Gli-D1/Glu-D3*. Each cultivar has two allelic variants, one corresponding to that of the cultivar Chinese Spring and the other to the cultivar Cheyenne. The results in Table IV show that the lines with the Cheyenne-type allele have greater dough strength as measured by MDDT. This does not appear to be related to a greater amount of polymeric protein as this is less for both Cheyenne-type lines. However, UPP is significantly greater for the two lines with the Cheyenne-type alleles. The Chinese Spring allele expresses two D-type subunits. These are modified ω-gliadins containing one cysteine residue and therefore they are able to act as chain terminators (Masci et al 1999). This effect is consistent with the lower UPP for lines with the

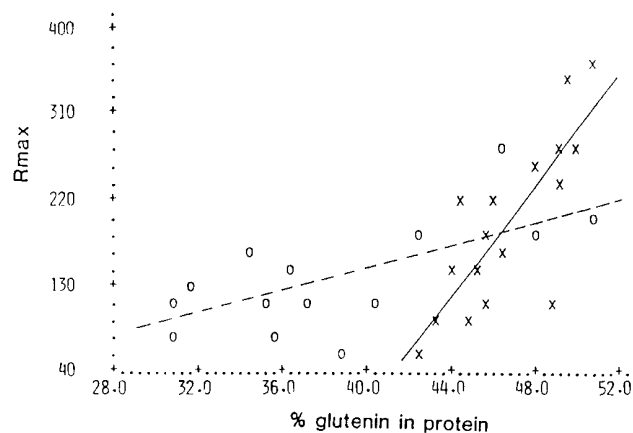


Fig. 6. Maximum extensigraph resistance (R_{max}) as a function of the percentage of glutenin in protein for two sets of lines. x = HMW-GS null series; o = wheat/rye translocation lines (single, double, triple) (Gupta et al 1991).

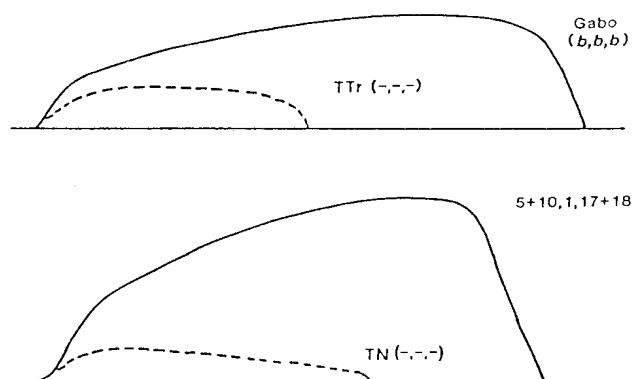


Fig. 7. Extensigrams of parent lines compared with those for corresponding triple HMW-GS null line and triple wheat/rye translocation line. Top, parent line Gabo and triple rye translocation line; bottom, parent line for HMW-GS series and triple HMW-GS null line (Gupta et al 1991).

Chinese Spring allele, suggesting a molecular weight distribution of polymeric protein shifted to lower molecular weights than for the Cheyenne allele.

GLI-2 Loci

Gli-2 loci code only for α- and β-gliadins and are not linked to LMW-GS as are the gliadins on chromosome 1. Single chromosome intercultural substitution lines are available. Among these are lines in which chromosomes from the good quality cultivar Cheyenne (CNN) have been substituted for chromosomes from the poorer quality Chinese Spring (CS), including lines with substitutions on chromosome 6 (substitution of *Gli-2* loci) (Mansur et al 1990). Lines with single chromosomes from the good quality Bezostaya 1 substituted for chromosomes of the poorer quality Capelle-Desprez have also been evaluated and showed highly significant positive effects of Bezostaya 1 chromosomes 1A, 1D, and 6D on baking performances (Krattiger et al 1987). The Russian cultivar Saratovskaja has mutant lines with deletions of *Gli-A2* and *Gli-D2*. Results of MDDT and PPP for these lines are shown in Table V in comparison with the normal parent line. Both deletion lines exhibit increased dough strength (MDDT) and increased PPP. This shows that the proportion of glutenin in a line can be increased by deletion of gliadins and that *Gli-2* deletion lines therefore have potential for manipulating the glutenin-to-gliadin ratio. One possible application is in modifying the protein composition of wheat/rye translocation lines to make them acceptable for use as bread wheats. Rye translocation lines are attractive because they have resistance to

TABLE V
Effect of Deletion of *Gli-2* Locus on Percent Polymeric Protein (PPP)
and Mixograph Dough Development Time (MDDT)^a

	<i>Gli-A2</i>	<i>Gli-D2</i>	PPP (%)	MDDT (min)
Saratovskaja				
Normal	+	+	56.5	4.9
<i>Gli-A2</i> null	-	+	60.5	5.7
<i>Gli-D2</i> null	+	-	59.6	5.9

^a Gianibelli et al 1998.

a wide range of pathogens but their use has been curtailed because of their inherent weak and sticky dough properties. Some strategies have been suggested to bolster their strength such as introducing strength-contributing HMW-GS 5+10. However, the problem is that the removal of the LMW-GS coded at the *Gli-1/Glu-3* loci (most commonly the *Gli-B1/Glu-B3* locus for 1B/1R translocations) has two effects that need to be taken into account. One, it considerably depletes the amount of glutenin present because LMW-GS are more abundant than HMW-GS. This reduction in glutenin is possibly the major cause of dough stickiness because an optimum balance of polymeric and monomeric proteins is necessary for good dough properties. Second, as a result of loss of an appreciable proportion of LMW-GS, the dough properties are already shifted toward greater strength due to the increase in the HMW/LMW GS ratio. Any further action to increase dough strength further in the wrong direction would exacerbate the situation, likely leading to excessive dough mixing requirements and impaired dough extensibility. What is required is to recover the glutenin content of the protein without further exacerbating the protein balance. This is where lines with *Gli-2* deletions may be useful, as the removal of an appreciable amount of gliadins has the effect of shifting the balance toward higher glutenin content.

CONCLUSIONS

The development of near-isogenic lines differing at one or more loci has helped in understanding the complex relationships between protein composition and parameters that measure end-use functionality of wheat flours. It would be valuable to have more of these test materials. For example, lines with deletions at *Gli-1/Glu-3* loci that show increased glutenin content; thus, increased strength would be useful in addition to the lines described here that decrease dough strength. By careful selection of such deletion lines, it would be possible to manipulate dough properties to increase or decrease dough strength as required in breeding programs. Other lines that would be valuable are the *Gli-2* nulls. Availability of single, double, and triple *Gli-2* nulls is a worthy goal. Such material could be used for increasing glutenin content of cultivars. The molecular weight distribution is a parameter known to control dough properties. For example, dough strength as measured by MDDT and R_{max} is related to the proportion of polymeric protein above a critical molecular weight (Bangur et al 1997). Extensibility appears to relate to the proportion of polymeric protein in the flour and does not require too high molecular weights. Therefore, it may be possible to produce doughs with moderate strength but high extensibility, based on these criteria, using a suitable combination of *Gli-2* nulls and lines with alleles expressing high amounts of chain terminators. The aim would be to develop lines of exceptionally high glutenin content but with the molecular weight distribution of the glutenin shifted to relatively low molecular weights. This is just one example of how these special lines may be used in formulating specific end-use properties.

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