Theor Appl Genet (2002) 105:43–49
DOI 10.1007/s00122-001-0826-8

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Identification of novel low M_r glutenin subunits in the high quality bread wheat cv Salmone and their effects on gluten quality

Received: 25 June 2001 / Accepted: 29 September 2001 / Published online: 18 May 2002

Abstract Southern-blot hybridization with a probe specific for genes encoding for low M_r glutenin subunits showed that the high quality bread wheat cv Salmone contains two DNA fragments designated as SF720 and SF750. These fragments were found to occur on the chromosome-1B satellite, and to be associated with the presence of two strongly staining low M_r glutenin subunits in the two-dimensional A-PAGE × SDS-PAGE pattern of cv Salmone. Comparison of 65 F_6 random lines derived from the cross between cv Salmone and the medium quality line FAP74809 revealed that the presence of fragments SF720 and SF750 had significant positive effects on several quality related parameters such as SDS sedimentation volume, Farinograph stability and Alveograph strength (W), tenacity (P) and elasticity (L). Additive effects of high M_r glutenin subunits 1 and 7+9 on gluten quality were found as well. Fragments SF720 and SF750 were suggested to occur at a locus other than *Glu-B3*, as indicated by their relatively high frequency of recombination with the *Gli-B1* locus.

Keywords Low M_r glutenin subunits · Gluten quality · Bread wheat · Random lines

Communicated by J.W. Snape

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Introduction

The viscoelastic properties of dough are strongly affected by wheat storage proteins, gliadins and glutenins (Bushuk and MacRitchie 1989; Gupta and MacRitchie 1994). The latter proteins are polymers in which two types of subunits are cross-linked by disulphide bonds: high M_r subunits, which are encoded by genes at the *Glu-1* loci on the long arms of group-1 chromosomes, and low M_r subunits, which are encoded by genes on the short arms of the same chromosomes at the *Glu-3* loci (Payne 1987; Singh and Shepherd 1988). Ruiz and Carrillo (1993), showed that certain low M_r glutenin subunits in durum wheat are encoded by the *Gli-B3* locus, a classical gliadin coding locus (Payne et al. 1988) located on the short arm of chromosome 1B at about 18 cM from *Glu-B3*.

The role of high M_r subunits in determining gluten strength is well-known and documented, so that the commonly occurring high M_r subunits encoded by the *Glu-A1*, *Glu-B1* and *Glu-D1* loci were ranked according to their influence on breadmaking quality (Payne et al. 1987; Pogna et al. 1989).

The contribution of low M_r subunits to gluten strength has become evident in the last few years. In fact, variation in high M_r subunit composition has been found to be insufficient to account for varietal differences in breadmaking quality, which can be better explained as a result of additive and interaction effects of high M_r and low M_r subunits (Gupta et al. 1994). The role of glutenin subunits in dough strength lies in their capacity to form polymers through intermolecular disulphide linkages. Dough strength was shown to be largely determined by the relative size distribution of the polymers, the larger sized ones, named macropolymers, positively affecting it. Furthermore, Gupta and MacRitchie (1994) suggested that the quantity and the size distribution of glutenin polymers can be affected by allelic variation at the *Glu-1* and *Glu-3* loci.

The use of near-isogenic or recombinant inbred lines is extremely helpful in investigating the effects of individual subunits on gluten quality. Unfortunately, few combined studies of glutenin subunits and gliadins on

dough properties have been reported. In particular, in a set of 74 recombinant inbred lines (RILs) Gupta et al. (1994) showed that both low M_r and high M_r glutenin subunits have strong effects on dough resistance (R_{max}) and that the effects of allelic variation at the *Glu-3* and *Glu-1* loci are largely additive. They also ranked different *Glu-3* loci depending on their effects on dough strength, stating the superiority of chromosome 1B-encoded subunits. It was also found that the interaction between the *Glu-3* and *Glu-1* loci accounted for 10% of the variation in dough resistance. Moreover, Nieto-Taladriz et al. (1994) showed that allelic variation at the *Gli-B1* locus has a significant effect on all rheological parameters, whereas *Glu-A3* and *Glu-D3* have no influence on dough characteristics.

In the present work, a group of F_6 bread wheat lines from the cross between cv Salmone and cv FAP 74809 were analysed for the occurrence of two DNA fragments coding for two strong low M_r glutenin subunits, and for the relationships between the presence of these fragments and superior gluten characteristics as determined by Farinograph, Alveograph and SDS sedimentation tests.

Materials and methods

Plant material

The experimental material consisted of 65 F_6 random lines derived from the cross Salmone × FAP 74809. Cv Salmone is an Italian bread wheat cultivar with superior breadmaking quality, whereas cv FAP 74809 is a Swiss bread wheat cultivar with medium breadmaking quality. The lines and the parents were grown in a plot trial (10 m^2) without replications according to the agronomic practices recommended for high yields in the Po valley, including sowing 400 germinating kernels m^{-2}, seed dressing, chemical control of weeds, 150 kg/ha of nitrogen applied in three top-dressings, no application of growth regulators, fungicides and pesticides. Moreover, 90 bread wheat cultivars or lines including the nulli-tetrasomic lines for group-1 chromosomes in cv Chinese Spring were submitted to protein and DNA fractionation.

Protein and DNA analysis

High M_r glutenin subunits were fractionated by SDS-PAGE according to Pogna et al. (1989) using 12.5% acrylamide gels. Gliadin composition was determined by A-PAGE (pH 3.1) according to Metakovsky and Novoselskaya (1991). High M_r glutenin subunits and gliadins were identified according to Payne and Lawrence (1983) and Metakovsky (1991), respectively. Two-dimensional fractionation (A-PAGE × SDS-PAGE) of glutenin subunits was carried out according to Redaelli et al. (1995).

DNA was extracted from 7-day old seedlings according to a modified CTAB procedure (Murray and Thompson 1980), digested with the four-cutter restriction enzyme *Rsa*I and hybridized to the pLMWTG2 probe, a genomic clone coding for a low M_r glutenin subunit from chromosome 1D (Sabelli and Shewry 1991), kindly provided by P. Shewry (Bristol University, AFRC IACR, Long Ashton, Bristol, UK). DNA digestion, gel electrophoresis, blotting and hybridization were performed according to Gebhardt et al. (1991). Washes were carried out as described by Vaccino and Metakovsky (1995).

Qualitative analysis

Flour protein content was determined with the NIR method according to AACC 39-10 (1995) using an InfraAlyzer 500 (Bran+Luebbe). The SDS sedimentation test was performed according to Preston et al. (1982) with minor modifications. The rheological tests were performed with the Chopin Alveograph with ICC method 121 and with the Brabender Farinograph using a 50-g mixer according to ICC 115-D (1992).

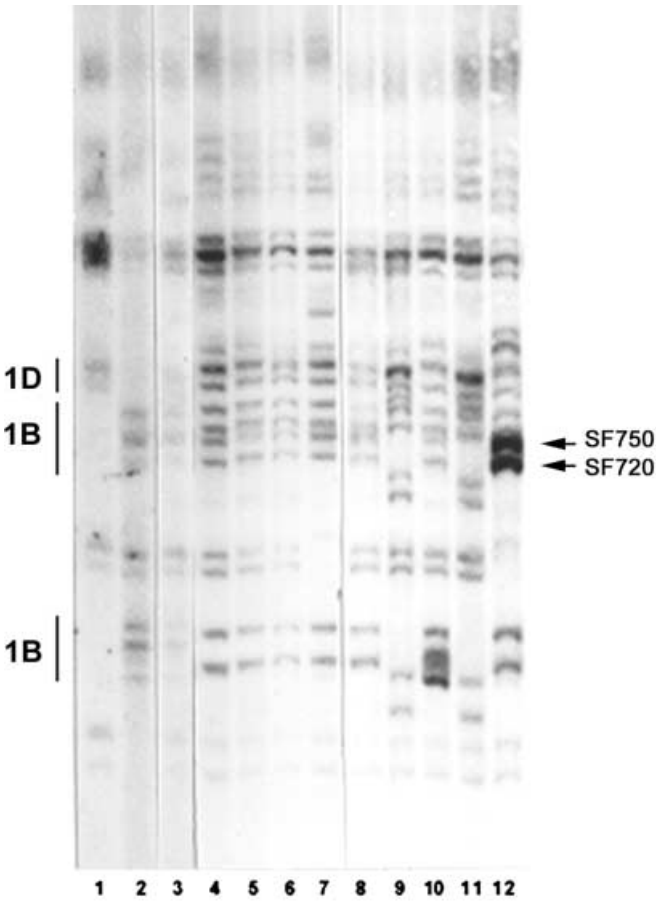

Fig. 1 RFLP patterns of DNAs digested with *Rsa*I and hybridized to the clone pLMWTG2. *Lanes 1 to 12*: Chinese Spring N1BT1D, Chinese Spring N1DT1B, Chinese Spring, Granarolo, Manital, Kosutka, MV 2/24/28, Salvia, Costantino, Gemini, Leopardo and Salmone. The restriction fragments from the *Glu-B3* and *Glu-D3* loci are indicated. *Arrows* show fragments SF720 and SF750

Statistical analysis

Standard ANOVA (analysis of variance) and the *t* test for the comparison of the means were performed with the MSTAT-C (1991) software package.

Results and discussion

Southern-blot analysis and storage protein composition

DNA was extracted from a collection of 90 bread wheat cultivars and digested with the four-cutter restriction enzyme *Rsa*I. Hybridization with the pLMWTG2 probe specific for low M_r subunit genes revealed DNA fragments SF720 and SF750, approximately 720 and 750 bp in size, with a several times greater intensity in cv Salmone than in the remaining genotypes (Fig. 1). These

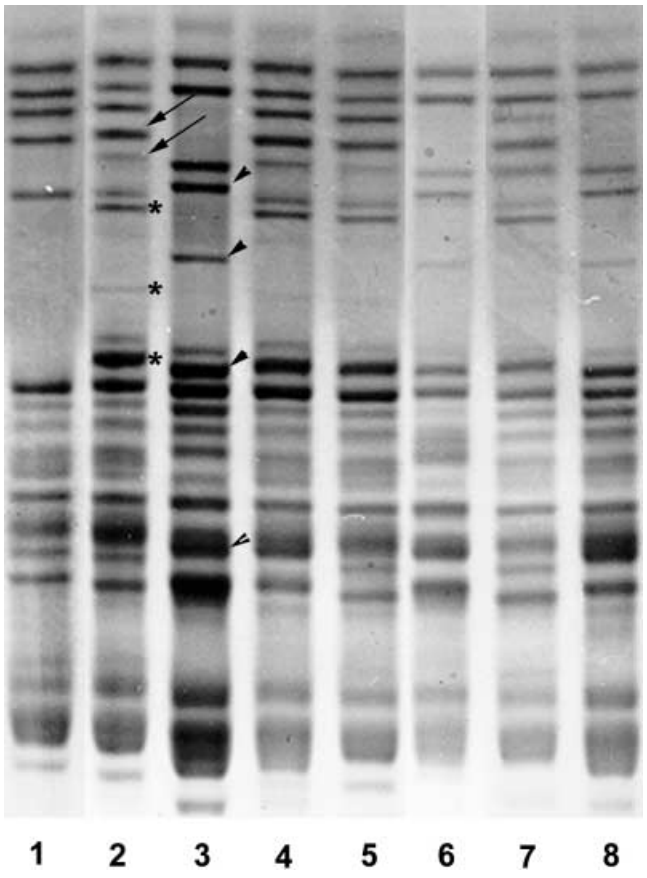

Fig. 2 A-PAGE fractionation of gliadins from cv Salmone 2 (*lane 1*), Salmone (*2*), FAP74809 (*3*) and some F_6 random lines of the cross Salmone × FAP74809. *Asterisks* represent the polypeptides coded for by the *Gli-B1s* allele, whereas *arrowheads* represent the subunits coded for by the *Gli-B1f* allele, and *arrows* indicate the fragments coded for by the *Gli-B5* locus

sequences occurred in the region of the gel occupied by DNA fragments from chromosome 1B, as demonstrated by their absence in the Chinese Spring nulli 1B-tetra 1D line (Fig. 1, lane 1), and by their increased intensity in the nulli 1D-tetra 1B line (lane 2). Cv Salmone inherited the SF720 and SF750 sequences from cv Glutinoso as revealed by their presence in this genotype and by their absence in the other parental cv Bezostaja1. Moreover, fragments SF720 and SF750 occurred as strong bands in cvs Resistente and Mottin, which are related genetically to cv Glutinoso. In particular, cv Resistente was obtained from the cross Glutinoso × Salto, whereas cv Mottin occurs in the cross combination Ardito × (Mottin × Norin 2) from which cv Glutinoso was selected.

Fragments SF720 and SF750, along with a few chromosome-1B-derived sequences, were also absent in the spontaneous mutant line Salmone 2 (data not shown). This white-glumed genotype was isolated from a headrow of the red-glumed cv Salmone and found to lack the chromosome-1B satellite and, therefore, the *Rg1* locus for glume color as well as the prolamin-encoding loci *Gli-B1*/*Glu-B3* and *Gli-B5* (Fig. 2). This result suggests

Table 1 Storage protein compositions and average values of quality characteristics of cvs Salmone and FAP 74809

Item	Salmone	FAP74809
Locus (and storage protein)		
Glu-A1 (high M_r glutenin subunits)	1	*Null*
Glu-B1 (high M_r glutenin subunits)	7+9	7+8
Glu-D1 (high M_r glutenin subunits)	2+12	2+12
Gli-B1 (gliadins)	Allele *s*	Allele *f*
Glu-B3 (low M_r glutenin subunits)	Allele *s*	Allele *f*
Qualitative traits		
Protein content (%)	13.1	12.1
SDS sedimentation volume (ml)	84	54
Chopin Alveograph		
P (mm)	97	61
L (mm)	131	102
P/L	0.74	0.60
W ($\times 10^{-4}$ J)	381	174
Brabender Farinograph		
Water absorption (%)	64.2	59.5
Stability (sec)	516	315
Degree of softening (BU)	52	78

that fragments SF720 and SF750 belong to a linkage group occurring on the chromosome -1B satellite.

Reduced and alkylated glutenins from cvs Salmone, Salmone 2, Glutinoso, Bezostaja1, Resistente and Manital were fractionated by two-dimensional A-PAGE × SDS-PAGE. Five B-group low M_r subunits in cv Salmone (Fig. 3A, arrows) were attributed to the chromosome -1B satellite, as deduced from their absence in line Salmone 2 (Fig. 3B, rectangle). Comparison of cv Salmone with the parental cvs Glutinoso (C) and Bezostaja1 (D) confirmed the derivation of these subunits from the former parent.

Cvs Salmone, Glutinoso and Resistente (E) were also compared with several cultivars showing two-dimensional patterns of chromosome 1B-encoded subunits similar to that of cv Salmone. As an example, Fig. 3F shows the two-dimensional map of cv Manital. In this context it is noteworthy that two out of the five low M_r subunits, marked by ≫ in Fig. 3 (A, C and E), occurred as stronger spots in cvs Salmone, Glutinoso and Resistente than in cv Manital (Fig. 3F). These subunits were tentatively assumed to be encoded by genes containing fragments SF720 and SF750.

Quality analysis of the F_6 RILs

In order to determine whether the presence of fragments SF720 and SF750 has a positive effect on the quality characteristics of cv Salmone, a group of F_6 lines from the cross Salmone × FAP74809 were screened for their Southern-blotting patterns. Based on their HMW glutenin subunit compositions, Salmone and FAP74809 were given a quality score of 10 and 8, respectively (Pogna et al. 1989). In spite of this small difference, the values of all the main technological parameters are significantly higher in cv Salmone than in cv FAP 74809 (Table 1).

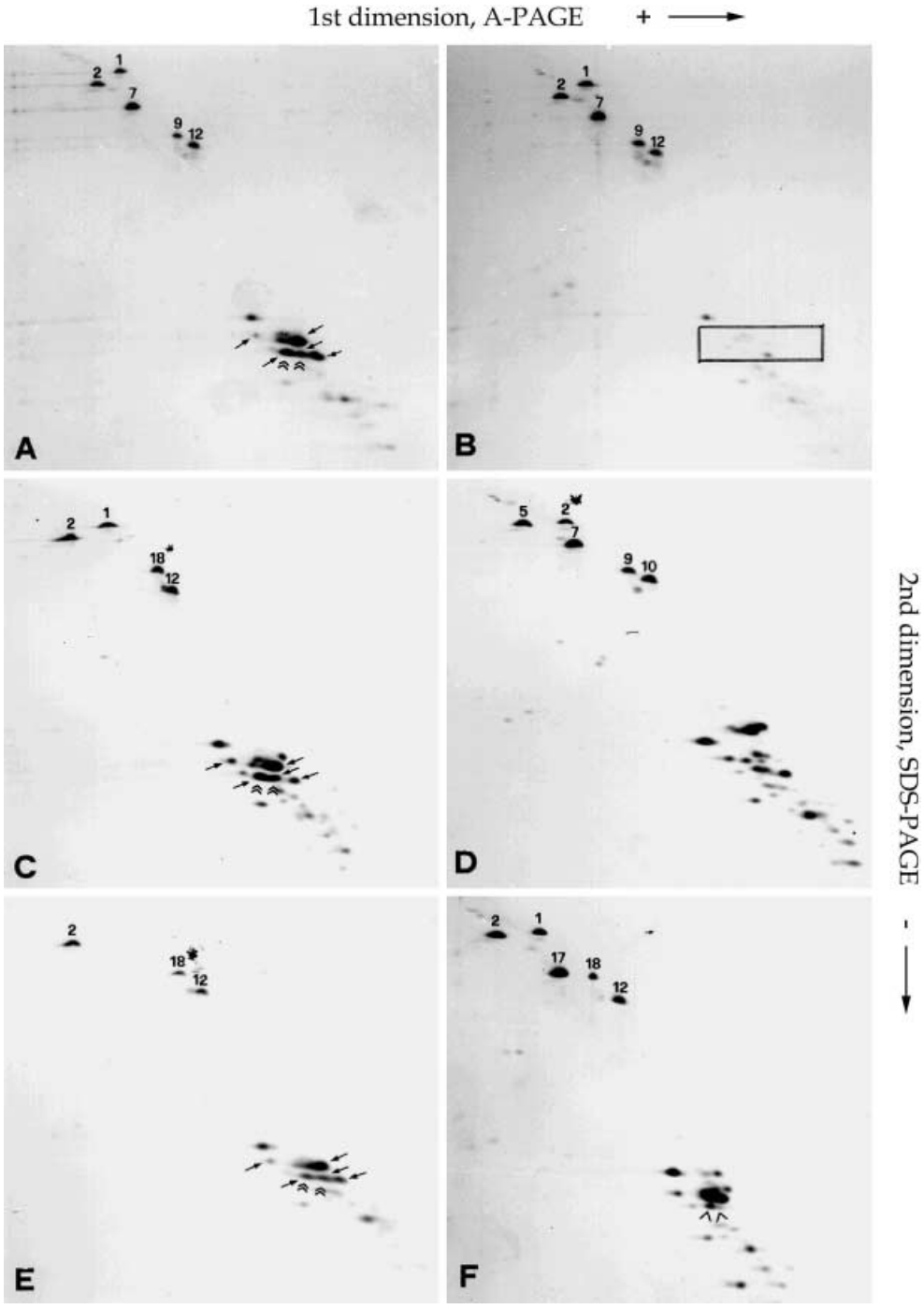

Fig. 3 Two-dimensional A-PAGE × SDS-PAGE of glutenin subunits from cv Salmone (**A**), line Salmone 2 (**B**), cv Glutinoso (**C**), cv Bezostaja1 (**D**), cv Resistente (**E**) and cv Manital (**F**). *Arrows* indicate low M_r subunits encoded by the *Glu-B3* locus. The region of the map containing these subunits in line Salmone 2 (**B**) is indicated by a *rectangle*. Over-produced low M_r subunits are indicated by ≫, whereas their normal counterpart in cv Manital (**F**) are indicated by >. High M_r glutenin subunits are *numbered*

The average values for the main technological parameters of the F_6 lines were analysed by means of a *t* test (Table 2). The superiority of high M_r subunits 1 and 7+9 encoded by *Glu-A1* and *Glu-B1* respectively, was confirmed. Moreover, the presence of fragments SF720 and SF750 had a significant effect on several quality parameters (Table 3). In particular, the SDS sedimentation volume and the Alveograph parameters dough strength (W), tenacity (P) and elasticity (L) were significantly higher in lines possessing SF720 and SF750 as compared with those lacking these fragments. In addition, the Farinograph parameter stability was increased by more than 35% in the former lines, while the degree of softening decreased from 62 to 45 BU.

The positive influence of low M_r subunits associated with fragments SF720 and SF750 in the presence of the different high M_r glutenin subunits was evident as well (Table 4). The progeny with high M_r subunits 1 and 7+9 had the highest W value, thus confirming the additive effect of individual high M_r and low M_r glutenin subunits on gluten quality.

Table 2 Average values of qualitative parameters in the F_6 random lines from the cross Salmone × FAP 74809. Lines are grouped according to their high M_r glutenin subunit compositions

Qualitative parameters	High M_r glutenin subunits		t[b]	High M_r glutenin subunits		t[b]
	1 (34)[a]	**Null** (20)[a]		**7+8** (18)[a]	**7+9** (35)[a]	
Protein content (%)	12.0	11.5	*	11.4	11.9	ns
SDS sedimentation volume (ml)	73	62	**	65	69	ns
Chopin Alveograph						
P (mm)	95	89	ns	88	97	ns
L (mm)	109	91	**	95	103	ns
P/L	0.89	1.05	ns	0.95	0.99	ns
W (×10^{-4} J)	311	233	***	238	302	**
Brabender Farinograph						
Water absorption (%)	61	59	ns	60	61	ns
Stability (sec)	519	386	**	378	489	*
Degree of softening (BU)	49	59	*	60	52	ns

[a] Number of lines analysed; [b]ns = not significant; significant at *$P \leq 0.05$, **$P \leq 0.01$ and ***$P \leq 0.001$

Table 3 Average values of qualitative parameters in F_6 random lines from the cross Salmone × FAP 74809 and level of significance of the *t* test

Qualitative parameters	Fragments SF720 and SF750		t[b]
	Present (37)[a]	Absent (28)[a]	
Protein content (%)	11.9	11.4	*
SDS sedimentation volume (ml)	71	62	**
Chopin Alveograph			
P (mm)	98	86	**
L (mm)	105	95	*
P/L	0.98	0.94	ns
W (×10^{-4} J)	310	234	**
Brabender Farinograph			
Water absorption (%)	60.6	59.2	*
Stability (sec)	531	382	**
Degree of softening (BU)	45	62	**

[a] Number of lines analysed; [b] ns = not significant; significant at *$P \leq 0.05$, **$P \leq 0.01$

Table 4 Average values of qualitative parameters in the F_6 lines from the cross Salmone × FAP 74809. Lines are grouped according to their high M_r glutenin subunit compositions and the presence (+) or absence (–) of fragments SF720 and SF750

Qualitative parameters	High M_r glutenin subunits						High M_r glutenin subunits					
	1		t[b]	**Null**		t[b]	**7+8**		t[b]	**7+9**		t[b]
	+ (22)[a]	– (11)[a]		+ (10)[a]	– (15)[a]		+ (9)[a]	– (8)[a]		+ (21)[a]	– (13)[a]	
Protein content (%)	12.3	11.4	ns	11.3	11.5	ns	11.8	10.8	ns	12.0	11.6	ns
SDS sedimentation volume (ml)	75	66	*	65	60	ns	69	62	ns	73	63	*
Chopin Alveograph												
P (mm)	99	86	*	98	85	ns	92	86	ns	102	89	*
L (mm)	113	100	*	88	92	ns	98	91	ns	107	94	ns
P/L	0.89	0.89	ns	1.19	0.99	ns	0.96	1.03	ns	1.02	0.98	ns
W (×10^{-4} J)	335	257	**	266	215	*	264	216	*	332	248	**
Brabender Farinograph												
Water absorption (%)	61.3	59.2	*	59.3	59.7	ns	60.4	58.8	ns	61.1	59.5	ns
Stability (sec)	564	431	*	456	348	ns	432	325	*	514	409	ns
Degree of softening (BU)	44	56	*	46	65	**	51	67	**	46	62	**

[a] Number of lines analysed; [b]ns = not significant; significant at *$P \leq 0.05$, **$P \leq 0.01$

Table 5 Percentage of the total sum of squares for rheological parameters in the F_6 random lines from the cross Salmone × FAP 74809

Source	SDS sedimentation volume (46)[a]	Alveograph (46)[a]				Farinograph (41)[a]		
		P	L	P/L	W	Water absorption	Stability	Degree of softening
Glu-A1 (subunit 1 *vs Null*)	13	0	18	15	10	3	5	2
Glu-B1 (subunits 7+8 *vs* 7+9)	3	8	0	3	11	2	17	7
SF720 + SF750 (presence *vs* absence)	8	11	0	2	14	3	18	32
Interaction								
Glu-A1 × *Glu-B1*	16	1	7	2	9	5	0	0
Glu-A1 × (SF720 + SF750)	0	1	9	4	1	10	0	3
Glu-B1 × (SF720 + SF750)	2	0	1	2	0	4	0	0
Glu-A1 × *Glu-B1* × (SF720 + SF750)	8	7	0	3	4	3	15	6

[a] Number of lines analysed

The interaction between high M_r glutenin subunits and low M_r glutenin subunits associated with fragments SF720 and SF750 in determining the breadmaking quality of the lines analysed was also calculated (Table 5). The percentages of the total sum of squares for both Alveograph W and Farinograph "Degree of softening" due to the presence of fragments SF720 and SF750 were found to be high compared with those of *Glu-A1*- and *Glu-B1*-encoded high M_r glutenin subunits, suggesting that a strong correlation occurs between the presence of fragments SF720 and SF750 and the rheological properties of dough. Therefore, fragments SF720 and SF750 can be considered as molecular markers of breadmaking quality.

Cv Salmone has been considered for many years as the top quality bread wheat cultivar grown in Italy, and is still commercialized in a separate class at higher prices. Its average Alveograph W value is about 330×10^{-4}J, with maximum values as high as 550×10^{-4}J (Borghi et al. 1985). These strong-gluten properties could not be explained solely in terms of high M_r subunit composition and quality score. In fact, cv Salmone contains subunits 1 (encoded by *Glu-A1*), 7+9 (*Glu-B1*) and 2+12 (*Glu-D1*), which correspond to an intermediate quality score of 7, according to Payne (1986), or 10, according to Pogna et al. (1989).

Figure 2 shows typical A-PAGE patterns of seeds from single F_6 lines of the cross Salmone × FAP 74809. Amongst the 65 progeny analysed, 37 lines contained fragments SF720 and SF750 along with gliadins encoded by allele *Gli-B1*s from cv Salmone (Fig. 2, asterisks), whereas 21 lines contained gliadins encoded by allele *Gli-B1f* from cv FAP 74809 (Fig. 2, arrowheads) in the absence of fragments SF720 and SF750. This indicates that a significant linkage exists between SF720 and SF750 and the *Gli-B1* locus on chromosome 1B. However, seven recombinant lines showed allele *Gli-B1*s in the absence of SF720 and SF750. This frequency of recombination is significantly higher than that (1.4–2.0%) calculated between *Gli-B1* and *Glu-B3* (Singh and Shepherd 1988; Pogna et al. 1990), suggesting that fragments SF720 and SF750 could be located at a locus other than *Glu-B3*. In this context it is noteworthy that a few low M_r glutenin subunits have been found to be encoded by genes at the *Gli-B3* locus on chromosome 1B in durum wheat (Ruiz and Carrillo 1993; Liu and Shepherd 1995), this locus being located 18 cM from *Gli-B1*. During the analysis of near-isogenic lines of cv Alpe (Pogna et al. 1995) and of mutant lines lacking the *Glu-B3* locus (Redaelli et al. 1995), some subunits belonging to the B group of low M_r glutenins could not be assigned to the *Glu-B3*s. Moreover, Metakovsky et al. (1997) described a B-type low M_r glutenin subunit encoded by a locus recombining with *Gli-B1/Glu-B3* at a frequency of 24.8%, this locus being designated as *Glu-B2* according to Liu and Shepherd (1995).

Aknowledgments This work was supported by Ministero delle Politiche Agricole e Forestali (MiPAF), special grant "Mappe genomiche". The critical reading of the manuscript by Prof. Perry NG is gratefully acknowledged. The authors state that the experiments comply with the current laws of the country in which the experiments were performed.

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