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Molecular linkage map of Einkorn wheat: mapping of storage-protein and soft-glume genes and bread-making quality QTLs

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Summary

Two molecular maps of *Triticum monococcum* L were produced and integrated. The integrated map includes a total of 477 markers, 32 RFLPs, 438 AFLPs, one morphological (*soft glume* (*Sog*)) and six storage-protein markers, and covers 856 cM. The trait *Sog* with the recessive allele *sog* maps to linkage group 2S. Probably, this is the *T. monococcum* homologue of *Tg* and *Tg2* in hexaploid and tetraploid wheats, respectively. Loci coding for seed storage proteins were allocated to chromosomes 1L (*HMW GLU1,2* and *Glu1*), 1S (*LMW GLU6,7*, *LMW GLU1-4*, *ωGLI1-4*, *γGLI5* and *Gli-1*) and 6L (*α/βGLI7-14*). Parameters related to bread-making quality (SDS sedimentation volume, specific sedimentation volume (SSV) and total protein content) were studied in one of the two populations. A QTL that is consistently present across environments was detected for SDS sedimentation volume and for SSV. The position of the QTL on chromosome 1S was in close agreement with the map positions of storage-protein loci. A second QTL was mapped on chromosome 5. For protein content, two significant QTLs were mapped to linkage groups 1 and 5.

1. Introduction

The importance of wheat in human nutrition stems from the peculiar properties of its gluten, a network of endosperm proteins that expands when dough is fermenting. The viscoelastic properties of the dough mainly depend on two classes of wheat storage proteins: glutenins and gliadins. For bread wheat, the significance of high-molecular-weight (HMW) glutenins for bread-making quality (BMQ), originally demonstrated by Payne *et al.* (1979), has been documented by several authors. The contribution of low-molecular-weight (LMW) glutenins to the BMQ of hexaploid wheat has been recognized only recently (Gupta *et al.*, 1994; Nieto-Taladriz *et al.*, 1994). The monomeric gliadins contribute mainly to the viscosity of the dough (Shewry & Tatham, 1997). In bread wheat, genes controlling storage-protein subunits have been localized to the long arms of chromosomes 1A, 1B and 1D (HMW glutenins), the short arms of the same chromosomes (LMW glutenins, γ- and ω-gliadins) and the short arms of chromosomes 6A, 6B and 6D (α- and β-gliadins) (Payne, 1987).

Triticum monococcum L, the first wheat to be domesticated in the Near East (Heun *et al.*, 1997; Nesbitt & Samuel, 1996), is a close relative of durum and bread wheat. The diploid nature of its genome (chromosome no. = 14), the broad range of variation for agronomic, physiological, biochemical and morphological traits, and the homology of its genome with those of the polyploid wheats (Dvorak *et al.*, 1993; Dubcovsky *et al.*, 1996), indicate that Einkorn might be a valuable source of promising genes. Hence, it is also a good candidate for quantitative trait locus (QTL) identification and mapping in *Triticum*, with a view to cloning the corresponding genes.

The poor baking quality of Einkorn flour has been described by D'Egidio *et al.* (1993) and Abdel-Aal *et al.* (1997). Recently, however, Borghi *et al.* (1996) and

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Corbellini *et al.* (1999) identified several *T. monococcum* accessions with high BMQ. By analysing the storage-protein composition of good and poor lines, they reported a strong association between BMQ and specific LMW glutenin subunits, and a very high and significant correlation between the SDS sedimentation volumes of Einkorn flours and rheological parameters contributing to BMQ, particularly bread volume (Borghi *et al.*, 1997; Corbellini *et al.*, 1999).

In this paper, we report BMQ parameters in a segregating population obtained from a cross between Einkorn lines that differ in storage-protein composition and SDS sedimentation volume. While storage protein loci from bread wheat are located on the long arms of chromosomes 1A, 1B and 1D, and have alternative alleles controlling BMQ, in Einkorn wheat it is the short arm of chromosome 1 that plays the major role.

2. Materials and methods

(i) *Plant materials*

Mapping was based on two populations of 117 and 168 F_2 plants, respectively, from which F_3 families were derived. Population 1 (117 progenies) derived from a cross between ID 49, a wild Einkorn line (*T. monococcum* subsp. *boeoticum*; this nomenclature follows Zohary & Hopf (1993); in the other parts of the text, a simplified nomenclature is used) and ID 69, a free-threshing cultivated Einkorn (*T. monococcum* subsp. *monococcum* var. *sinskajae*). Population 2 (168 progenies) was derived from a cross between two cultivated Einkorn lines (*T. monococcum* subsp. *monococcum*) that vary in BMQ, ID 362 (poor baking quality) and ID 1331 (good baking quality). Additional F_2 populations segregating the *soft glume* (*Sog*) traits were from the Einkorn wheat breeding program carried out at Max-Planck-Institut fuer Zuechtungsforschung (MPIZ) Cologne, Germany.

(ii) *Field activity and parameter analysis*

To assess BMQ parameters, F_3 families of Population 2 were grown at the Istituto Sperimentale per la Cerealicoltua, Sant'Angelo Lodigiano (Italy) in 1998 (S98) and in Cologne (Germany) in 1996, 1997 and 1998 (K96, K97 and K98, respectively) with two replications, under the conditions described by Castagna *et al.* (1995). After harvest, seeds of the two replicates were combined, mechanically dehulled (FC4S, Otake, Satake, Japan) and milled with an experimental mill (Bona 4RB, Bona, Italy). Total protein content of the seed (expressed as a percentage of dry matter) was determined by near-infrared reflectance (NIR) according to AACC Method 39-10 (1995). The SDS sedimentation volume (expressed as height in mm of a standard column) was determined according to Preston *et al.* (1982) with minor modifications. The ratio of SDS sedimentation volume to protein content yields the specific sedimentation volume (SSV). Data obtained for F_3 families were taken as indicators of values for individual F_2 plants.

To assess the free-threshing character, field-grown F_2 plants of Population 1 were harvested by hand and ears were scored for the *sinskajae*-type shape of the glume (allele *sog*), as well as for manual threshability.

(iii) *Characterization of storage proteins*

Gliadins were extracted from 30 mg aliquots of flour by incubation in 100 μl of 70% ethanol for 60 min at room temperature. After centrifugation at 12,000 rpm for 5 min (S45-24-11 rotor, Eppendorf 5415G), the supernatant was mixed with an equal volume of a solution containing 60% (w/v) glycerol and 0·005% (w/v) pyronin G, and fractionated by A-PAGE electrophoresis, according to Pogna *et al.* (1990).

Glutenins were extracted as described by Morel (1994): 30 mg samples of flour were washed three times with 50% (v/v) 2-propanol at 60 °C for 30 min to remove the gliadin fraction. The residue was reduced with 20 mM dithiothreitol, alkylated with 40 mM 4-vinylpyridine and precipitated with cold acetone. The pellet was resuspended in a loading buffer containing 2% SDS, 20% glycerol, 80 mM Tris-HCl pH 8·0 and 0·02% bromophenol blue, and fractionated by SDS-PAGE electrophoresis as described by Pogna *et al.* (1989), using a 12·5% separating gel.

(iv) *DNA isolation*

The DNA was isolated from freeze-dried leaf samples of 30 F_3 plants per progeny, following the QIAtip 100 protocol for genomic DNA (Qiagen, Hilden, Germany). DNA concentrations were estimated by agarose gel electrophoresis (0·8% w/v) using known concentrations (50–500 ng) of undigested λ DNA.

(v) *AFLPs*

The AFLP analysis was performed according to the original protocol of Vos *et al.* (1995). In the AFLP autoradiograms, amplified fragments were numbered successively, starting from the one with the lowest mobility.

(vi) *RFLPs*

DNA digestion with *Eco*RI, *Eco*RV and *Xba*I, gel electrophoresis, blotting onto Hybond N+ nylon membranes (Amersham Pharmacia Biotech AB,

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Table 1. *RFLP probes used to assign the chromosome number to linkage groups of Einkorn.*

Probe	Mapped in other *Triticeae*	Reference	Mapping population	Linkage group in Einkorn
Gli 1	1S	Bartels *et al.* (1986)	1	1
PSR 601	1L	Boyko *et al.* (1999), Van Deynze *et al.* (1995)	2	
WG 983	1L	Becker *et al.* (1995), Dubcovsky *et al.* (1995*a*)	1, 2	
Glu 1	1L	Thompson *et al.* (1983)	1	
PSR 305	1L	Bezant *et al.* (1997)	1, 2	
WG 996	2L	Dubcovsky *et al.* (1995*a*), Nelson *et al.* (1995*b*)	1	2
PSR 102	2L	Boyko *et al.* (1999), Dubcovsky *et al.* (1996)	2	
PSR 934	2L	Blanco *et al.* (1998), Dubcovsky *et al.* (1996), Nelson *et al.* (1995*b*)	2	
PSR 910	3S	Boyko *et al.* (1999)	1	3
WG 178	3L	Becker *et al.* (1995), Boyko *et al.* (1999)	1, 2	
PSR 931	3L	Bezant *et al.* (1997), Blanco *et al.* (1998), Boyko *et al.* (1999)	1, 2	
WG 464	4L	Becker *et al.* (1995), Dubcovsky *et al.* (1996)	1	4
PSR 1051	4L	Bezant *et al.* (1997), Blanco *et al.* (1998), Boyko *et al.* (1999), Dubcovsky *et al.* (1996)	1, 2	
PSR 1316	4L	Blanco *et al.* (1998), Dubcovsky *et al.* (1996)	2	
WG 1026	5L	Becker *et al.* (1995), Boyko *et al.* (1999), Dubcovsky *et al.* (1996)	1	5
PSR 637	5L	Blanco *et al.* (1998), Boyko *et al.* (1999)	1, 2	
WG 364	5L	Becker *et al.* (1995)	1	
WG 644	5L	Becker *et al.* (1995), Bezant *et al.* (1997), Boyko *et al.* (1999), Dubcovsky *et al.* (1996)	1	
CDO 412	5L	Blanco *et al.* (1998), Boyko *et al.* (1999), Nelson *et al.* (1995*a*), Van Deynze *et al.* (1998)	2	
CDO 590	5L	Van Deynze *et al.* (1998)	2	
PSR 604	5L	Bezant *et al.* (1997)	1, 2	
WG 199	5L	Dubcovsky *et al.* (1996)	2	
WG 114	5L	Dubcovsky *et al.* (1996), Nelson *et al.* (1995*a*)	1	
PSR 164	5L	Blanco *et al.* (1998), Dubcovsky *et al.* (1996)	1, 2	
WG 223	6S	Boyko *et al.* (1999)	2	6
PSR 627	6S	Blanco *et al.* (1998), Boyko *et al.* (1999)	1	
PSR 113	6S	Dubcovsky *et al.* (1996)	2	
WG 420	7L	Becker *et al.* (1995), Bezant *et al.* (1997), Dubcovsky *et al.* (1996)	1, 2	7
WG 380	7L	Becker *et al.* (1995), Boyko *et al.* (1999), Dubcovsky *et al.* (1996)	1, 2	
Probes with inconsistent mapping				
PSR 128	5L	Bezant *et al.* (1997), Boyko *et al.* (1999)	1	1
WG 341	5S, 6, 7	Dubcovsky *et al.* (1996)	1	1
WG 282	6L	Becker *et al.* (1995)	1	4

Uppsala, Sweden) and hybridization with ^{32}P were performed as described by Heun *et al.* (1991). Probes specific for wheat and oat were utilized as reported in Table 1. The CDO probes (oat cDNA clones) were obtained from M. Sorrells (Cornell University, Ithaca, New York, USA). The WG genomic probes were also from Cornell University (S. Tanksley and M. Sorrells, Cornell University, Ithaca, New York, USA). The PSR probes were from M. Gale (John Innes Centre, Norwich, UK). The probes Glu-1 and Gli-1 were from R. Thompson (MPIZ Köln, Germany). Autoradiograms were produced by exposing GP SO-230 Phosphorfilm screens to the hybridized membrane, and were analysed with the Phosphorimager Storm 860 and ImageQuant software (Molecular Dynamics, Sunnyvale, USA).

(vii) *Map construction*

Maps based on the two crosses were built with the computer programme MAPMAKER/EXP version 3.0 (Lincoln *et al.*, 1993), using the Kosambi function (Kosambi, 1944). The markers were assigned to seven groups, based on the χ^2 test for independence of segregation, at LOD scores $\geqslant 3{\cdot}0$. A LOD score value between 2 and 3 was only accepted for the genetic locus *γGLI5* on chromosome 1S. The pairwise data were then used as input for the construction of linkage maps, and the chromosomes were numbered based on the map positions of RFLP probes whose locations are known in other *Triticeae*. As a final step, an integrated map based on the data sets for both populations was assembled using JoinMap version 2.0

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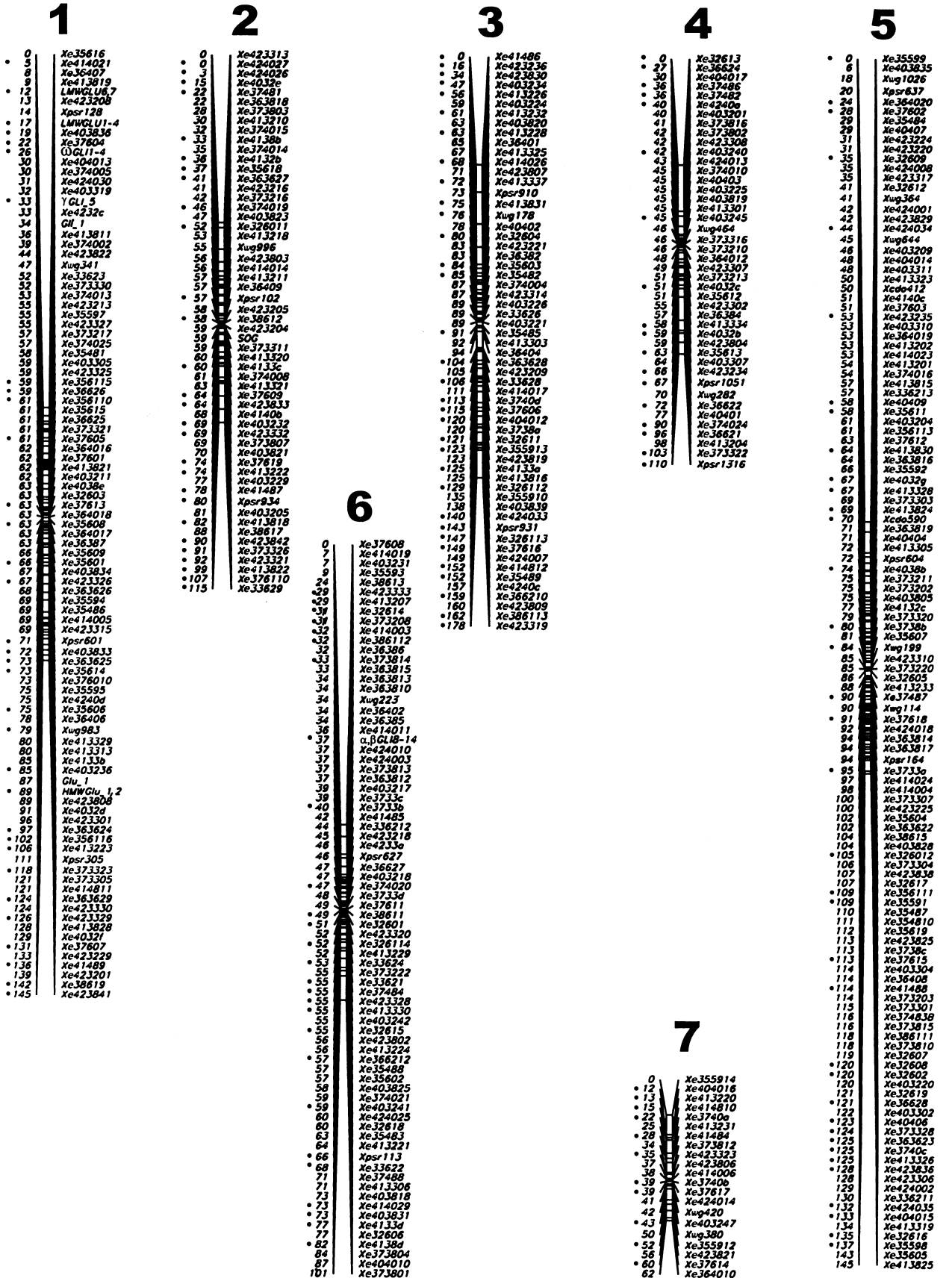

Fig. 1. Linkage map of Einkorn wheat derived by the combination of markers mapped in Populations 1 and 2. The map was produced by the JoinMap program version 2.0 as specified in Materials and Methods. The assignment of a specific number to each Einkorn linkage group was based on the RFLP probes listed in Table 1. Dots to the left of each linkage group indicate markers used in the composite interval QTL mapping procedure.

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(Stam & Van Ooijen, 1995). For molecular markers, the nomenclature of McIntosh *et al.* (1998) was followed: marker loci corresponding to unknown DNA probes are indicated by *X* followed by the probe symbol in italics; the letter *e* indicates AFLP probes.

(viii) *QTL analysis*

To localize QTLs responsible for BMQ parameters, the chromosome marker order determined by JoinMap was transferred to the computer program PLABQTL (Utz & Melchinger, 1996), together with laboratory data of Population 2 (protein content, SDS sedimentation volume and SSV). The numbers of markers mapped in Population 2 and considered in QTL analysis for linkage groups 1–7 were 33, 28, 33, 18, 37, 27 and 11, respectively. In Fig. 1, these markers are indicated by dots to the left of the linkage maps. QTLs were identified by composite-interval mapping (Zeng, 1993, 1994), using a LOD threshold derived from 1000 random permutations of observations (Churchill & Doerge, 1994). Allelic substitution value of chromosome fragment 1S was determined by halving the difference between the average SSV values of the F_3 lines homozygous for good BMQ alleles (34) and those homozygous for poor alleles (30).

3. Results

(i) *Production of an integrated map*

Molecular polymorphisms were present in Populations 1 and 2. When analysed using the χ^2 test, the segregation behaviour of several AFLP fragments was found to deviate significantly from the expected 3:1 ratio. These polymorphisms were not used in mapping. Moreover, at the end of the mapping procedure, several polymorphisms had not been allocated to linkage groups with a LOD value of 3 or better. These markers were also disregarded. In Population 1, 23 RFLP markers were mapped together with 182 AFLP fragments. These were generated by 20 primer combinations. Because one morphological marker (*soft glume* (*Sog*)) was also scored, a total of 206 polymorphisms were mapped in this population. In the paper by Dorofeev & Navruzbekov (1982), the soft-glume trait is indicated by the symbol *sr* (*scariosus*).

In Population 2, 19 RFLP markers and 289 AFLPs were mapped. AFLPs were identified among the products of 29 primer combinations (9·9 polymorphic bands per combination). Alleles of six polymorphic storage-protein loci were also recorded, for a total of 314 markers.

The map shown in Fig. 1 combines the data from two populations and includes 477 markers, including 32 RFLPs (ten are common to both populations), 438 AFLPs (33 common), one morphological marker (*Sog*) and six storage-protein markers. The integrated map has a length of 856 cM, with an average distance of 1·8 cM between markers. A total of 97 markers were mapped to chromosome 1, spanning 145 cM. Five RFLP markers had a linkage-group assignment on chromosome 1 consistent with their homologous positions in other wheats (Table 1). Probes PSR 128 and WG 341, which were initially expected to reveal loci mapping to linkage group 5, defined polymorphic loci mapping to chromosome 1. Linkage group 2 was equated with chromosome 2 because it includes loci revealed by the RFLP probes PSR 102, 934 and WG 996. This linkage group included 55 DNA marker loci and the *Sog* gene, and covered a total of 115 cM. Linkage group 3 included 59 markers distributed over 178 cM, with RFLP probes WG 178, PSR 931 and PSR 910 supporting its identification as chromosome 3. Linkage group 4 comprised 43 markers in a total length of 110 cM; group-specific RFLP marker loci were revealed by probes PSR 1051, PSR 1316 and WG 464. The locus revealed by probe WG 282 was also assigned to this linkage group; in other *Triticum* species, the same locus maps to chromosome 6 (Table 1). Linkage group 5 included the largest number of marker loci (125) and covered 145 cM; chromosome-5-specific RFLP markers are listed in Table 1. Linkage group 6 was 101 cM long and included 76 marker loci, of which the RFLP probes WG 223, PSR 113 and 627 were chromosome specific. Only 21 markers could be assigned to linkage group 7 (62 cM), and the RFLP probes WG420 and 380 were specific for this chromosome. The positions of the RFLP markers listed in Table 1 allowed us to orient the Einkorn linkage groups shown in Fig. 1 with the short (above) and long (below) chromosome arms.

(ii) *Monogenic traits*

The trait *soft glume* is typical of *T. monococcum sinskajae* accessions. In the mutant form (*sog*), the glumes are soft, longer and broader than in normal Einkorn (Fig. 2*a*). The kernel is loosely covered and it can be easily threshed. The *sog* allele is also associated with a compact structure of the spike: in all of its F_2 progenies, this pleiotropic effect of the *sog* allele was always noted (Fig. 2*b*). The analysis of the F_2 segregation of Population 1 allocated the *Sog* gene to chromosome 2, co-segregating, without recombination, with AFLP loci *Xe423204* and *Xe373311*.

The parents of Population 2 differed in the electrophoretic pattern of their storage-protein subunits (Fig. 3). Six loci were mapped for which different alleles could be recognized by gel electrophoresis of their products (Fig. 1). The gene *HMW GLU1,2* was

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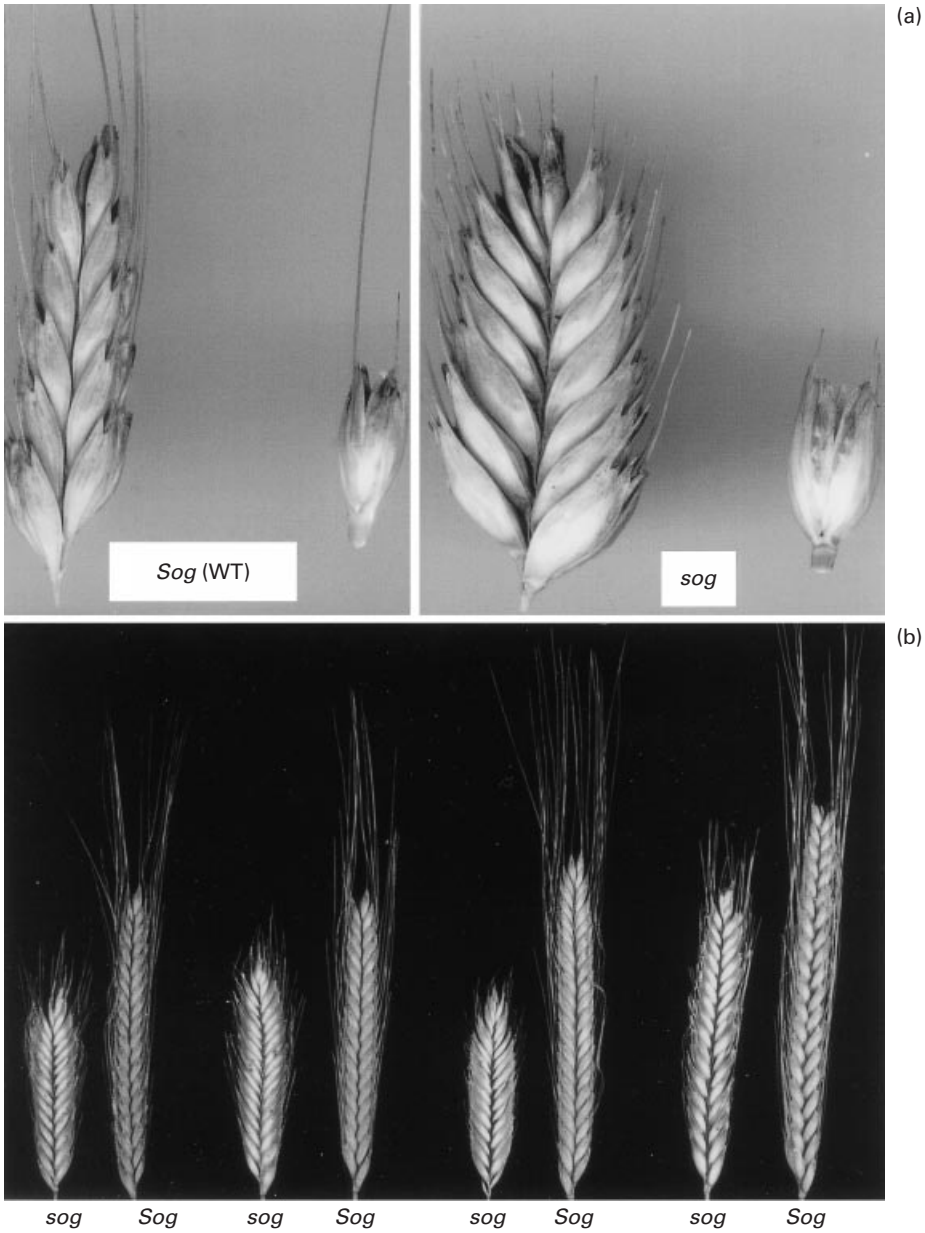

Fig. 2. Phenotypes of the two alleles of the *Sog* locus (*soft glume*) mapped in Population 1 to linkage group 2. (*a*) Ear and spikelets. (*b*) Ears representative of *sog* and *Sog* phenotypes segregating in four different F_2 populations.

allocated to the long arm of chromosome 1 and the two genes for LMW glutenins (*LMW GLU6,7* and *LMW GLU1-4*) were on the short arm of the same chromosome. In Population 1, the position of the locus *Glu1*, which codes for HMW glutenins, was assigned to chromosome 1L using a molecular probe (Table 1) and corresponded to the position of *HMW GLU1,2* in Population 2. One gene for gliadins (*ωGLI1-4*) was also mapped to the short arm of chromosome 1 (Fig. 1): this locus codes for ω-type gliadins (Fig. 3). In population 1, the genetic locus *Gli1* (coding for γ-gliadins) was mapped with a molecular probe to position 34 on linkage group 1 (Fig. 1). The *γGLI5* locus was mapped almost at a corresponding position in Population 2, albeit with a low LOD score, owing to the difficulty of classifying this γ-gliadin band in some genotypes (Fig. 3). Finally, a locus coding for α/β gliadins was detected on the short arm of chromosome 6 (*α/βGLI7-14*).

(iii) *QTL analysis of traits related to BMQ*

Three parameters correlated with BMQ were analysed in Population 2. The total protein content (%) and SDS sedimentation volume were determined, and the SSV was calculated, for four mapping environments: K96, K97, K98 and S98 (Table 2). The poor-quality parent ID 362 showed an average protein content of

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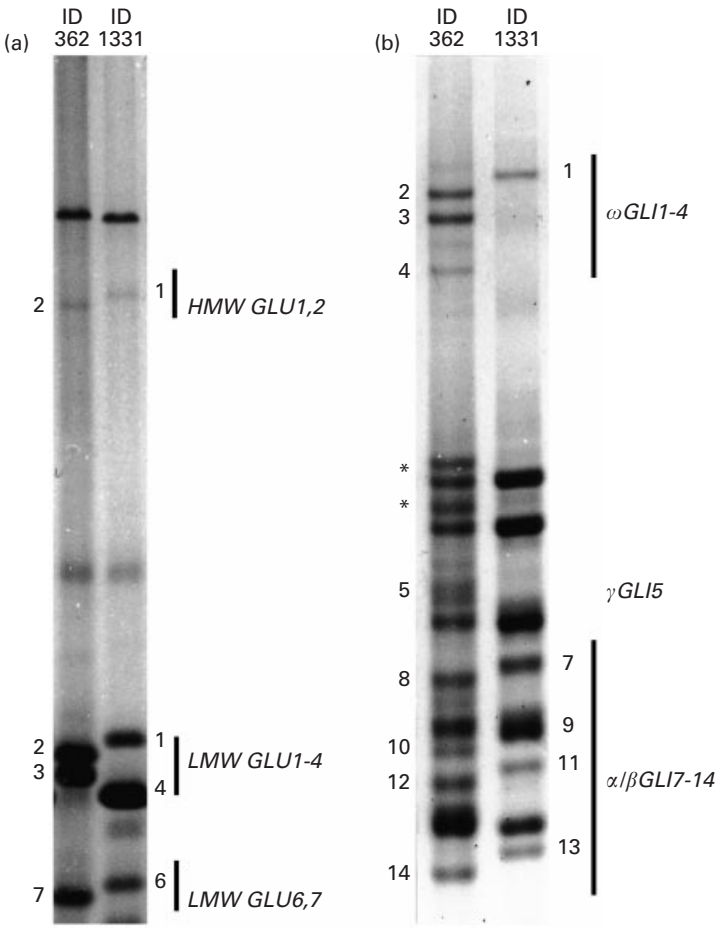

Fig. 3. Storage-protein subunits revealed by SDS-PAGE (*a*) and A-PAGE (*b*). Genes controlling low and high molecular weight glutenin (LMW GLU and HMW GLU, respectively) and gliadin (GLI) subunits are indicated for parents 1 and 2 of Population 2. Asterisks indicate bands not scored in the segregating population.

Table 2. *Average values* (± *standard error*) *recorded for Population* 2 (*parents and* F_3 *progeny*) *for total protein content* (*% of dry matter*), *SDS sedimentation volume and SSV. For* F_3 *progeny, in addition to average values, the field of variation covered by single progenies is reported*

		Location				
Character	Genotype	K96	K97	K98	S98	Average
Protein content (%)	ID 1331	17·4 ± 0·00	17·2 ± 0·30	18·6 ± 0·55	20·0 ± 0·90	18·3 ± 0·44
	ID 362	21·9 ± 0·05	24·7 ± 0·15	24·1 ± 0·25	21·7 ± 0·10	23·1 ± 0·14
	F_3	15·9 ± 0·13	20·0 ± 0·10	21·3 ± 0·08	20·9 ± 0·09	19·5 ± 0·09
	Range	12·5–19·8	16–23·9	18·8–24·7	17·8–24·6	13·4–21·6
SDS sedimentation volume (mm)	ID 1331	40·0 ± 0·50	35·0 ± 2·50	38·0 ± 2·00	56·0 ± 4·00	42·3 ± 2·25
	ID 362	15·0 ± 1·00	14·0 ± 1·00	14·0 ± 0·00	22·0 ± 2·00	16·3 ± 1·00
	F_3	25·6 ± 0·94	20·4 ± 0·68	22·7 ± 0·81	31·1 ± 1·07	24·8 ± 0·77
	Range	10·0–80·0	11·0–50·0	11·0–59·0	12·0–63·0	12·3–63·0
SSV	ID 1331	2·30 ± 0·03	2·04 ± 0·11	2·04 ± 0·05	2·80 ± 0·07	2·30 ± 0·06
	ID 362	0·68 ± 0·04	0·57 ± 0·04	0·58 ± 0·01	1·01 ± 0·10	0·71 ± 0·05
	F_3	1·60 ± 0·06	1·03 ± 0·04	1·06 ± 0·04	1·49 ± 0·05	1·29 ± 0·04
	Range	0·64–4·30	0·48–2·62	0·52–2·67	0·52–3·13	0·60–2·91

23·1 % and an SDS sedimentation volume of 16·3 mm, whereas the good-quality parent ID 1331 had 18·3 % protein content and an SDS volume of 42·3 mm. The four environments showed different mean values ranging from 15·9 % (K96) to 21·3 % (K98) for protein content and from 20·4 mm (K97) to 31·1 mm

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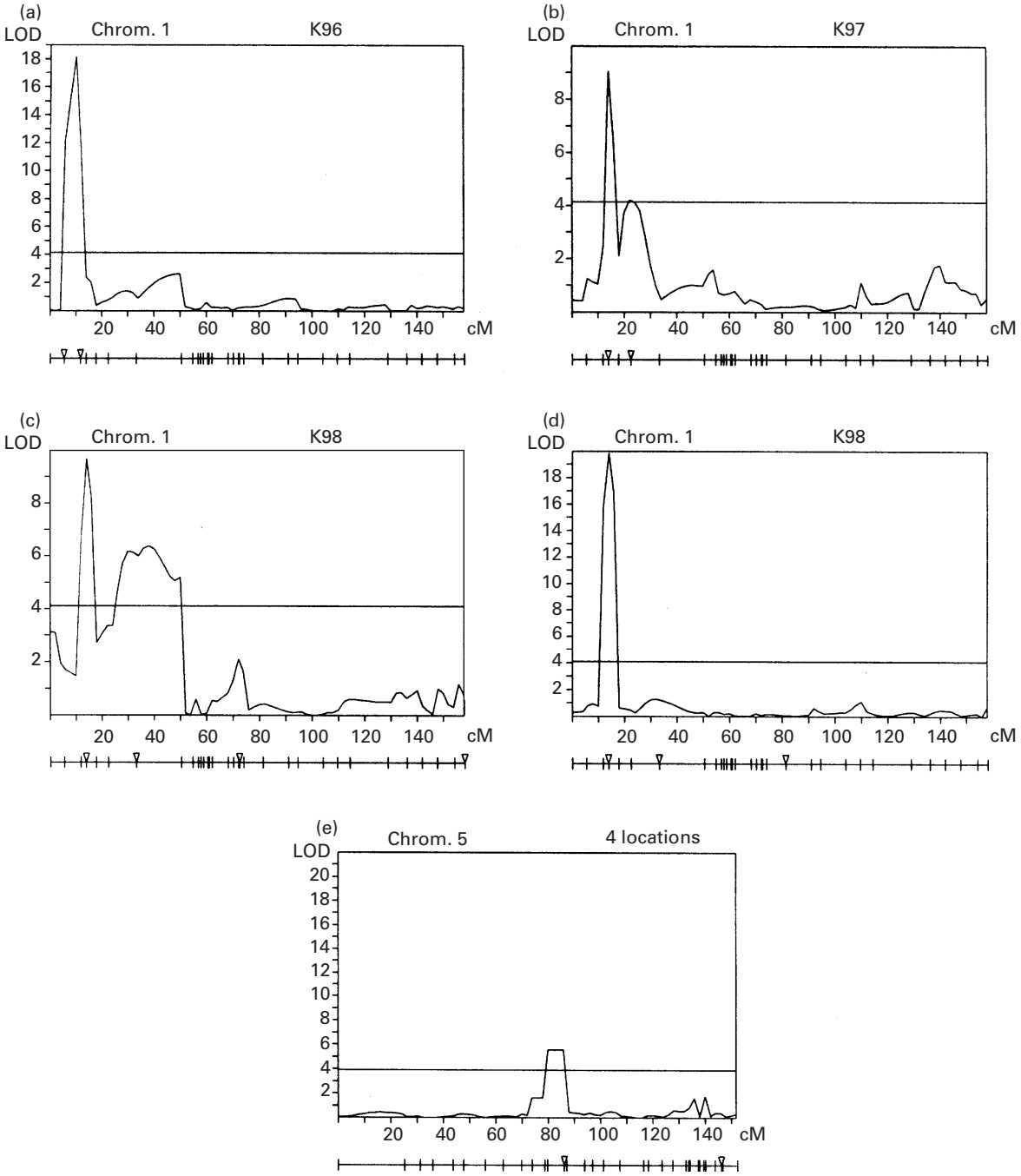

Fig. 4. Assignment to chromosomes of Einkorn wheat of QTLs controlling baking quality, as measured by the SSV parameter (SDS sedimentation volume of gluten divided by total % protein content) in four different experiments (chromosome 1, locations K96 (*a*), K97 (*b*), K98 (*c*) and S98 (*d*)) and using pooled data from the four locations (chromosome 5 (*e*)). LOD thresholds reported graphically (transversal lines) were determined as described in Materials and Methods, and correspond to 4·12 (K96), 4·14 (K97), 4·11 (K98), 4·08 (S98) and to 3·9 (average of 4 locations).

(S98) for SDS sedimentation volume. SSV values were 2·30 units in ID I331 and 0·71 in ID 362; average values for the F_3 progeny were 1·60, 1·03, 1·06 and 1·49 units, respectively for K96, K97, K98 and S98.

In QTL analyses, for all traits considered, a LOD score threshold between 3·9 and 4·14 was estimated. SDS volume and SSV gave similar QTL results, indicating that protein content did not influence the SDS sedimentation volume. Both analyses revealed the existence of a large QTL consistently present across environments and mapping to the short arm of chromosome 1. In two locations (K96 and K98), this QTL consisted of 1–4 peaks. In locations K97 and S98, only the first peak was highly significant. For SSV, a second QTL was detected on chromosome 5 (Fig. 4*e*) when the analysis was carried out with the average SSV data of four locations. At a LOD score of 3·9, this QTL was significant in one out of four

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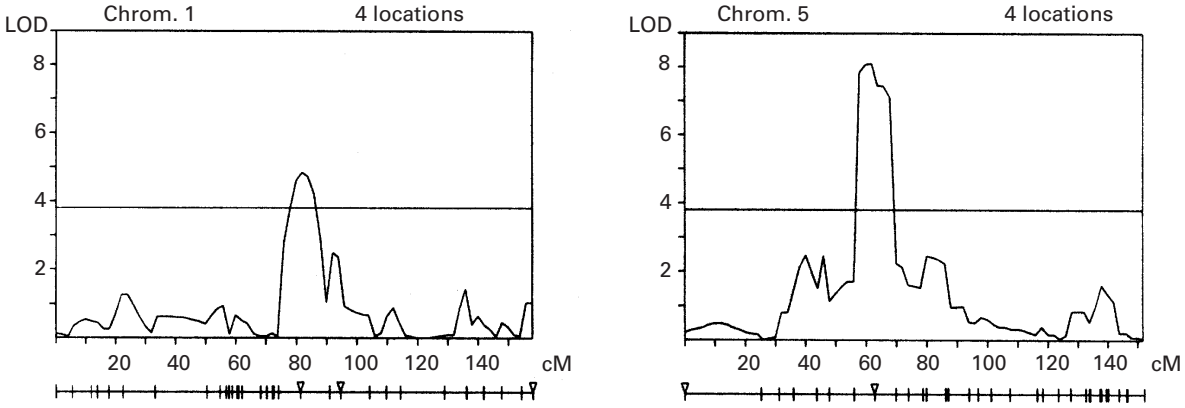

Fig. 5. Localization on chromosomes 1 and 5 of Einkorn wheat of QTLs controlling total protein content (% of dry matter). The analysis reported is based on the average protein content of four locations. The LOD thresholds correspond to 3·8 for both chromosomes.

locations and, at a LOD score of 3, in three of the four.

The locations of the four peaks of the major QTL of chromosome 1S in K98 and in K97 were in agreement with the map positions of *LMW GLU6,7*, *LMW GLU1-4* and *ωGLI1-4*, with less probable contribution of the more proximal locus *γGLI5*. This locus mapped proximally to *ωGLI1-4* (Fig. 1). The linkage between the storage protein loci on chromosome 1S did not allow the determination of the specific contribution of each locus to the BMQ QTL. However, loci *LMW GLU6,7* and *LMW GLU1,4* had a better probability of representing the major QTL, at least based on peak positions in K96 and S98. Alleles of the loci *LMWGLU6,7*, *LMWGLU1-4* and *ωGLI1-4* originating from ID 1331 had a substitution SSV value of +0·58. This indicates that the allelic segment encompassing the region of the three storage protein loci in ID 1331 induces in an increase of 0·58 units in the SSV value compared with the same allelic segment from ID 362 (SSV was 2·30 in ID 1231 and 0·71 in ID 362).

The γ-gliadin subunit GLI5 was represented in ID 362 by a faint band absent in ID 1331 (Fig. 3). F_2 progeny homozygous for the absence of the band had an SSV value higher than other progeny. This supports the conclusion that the storage-protein band encoded by the locus *γGLI5* originating from ID 362 had a negative effect on BMQ.

Total seed protein content (percentage of dry matter) was analysed to test for the existence of QTLs. One significant QTL was found to map to linkage group 5, between 30 cM and 60 cM from the tip of the short arm of the chromosome. The LOD score for the QTL was significantly higher than the LOD threshold when the average data of four locations were considered (Fig. 4). A second minor QTL was mapped on chromosome 1 (position between 75 cM and 85 cM from the end of the short arm).

4. Discussion

The results presented provide evidence that, in Einkorn wheat, allelic variation at linked loci on the short arm of chromosome 1 explains the variability in bread loaf volume among Einkorn wheat lines first observed by Borghi *et al.* (1996). Saponaro *et al.* (1995) had already reported that gliadin-encoding loci located on chromosome 1 of Einkorn were putatively associated with high values of the SDS sedimentation volume. Later, Borghi *et al.* (1997) and Corbellini *et al.* (1999) reported that LMW glutenins also had a significant influence on the same trait. Now, we have found that the loci on the short arm of chromosome 1 affect SDS sedimentation volume and SSV. Moreover, the QTL analysis reveals that almost all detectable genetic variation influencing BMQ is restricted to chromosome 1S, with a minor contribution from chromosome 5. In polyploid wheats, QTLs for BMQ have been mapped to chromosome 1AL (Sourdille *et al.*, 1999; Garland Campbell *et al.* 2001). Payne *et al.* (1987) suspected that, in hexaploid wheats, the effect on dough of the *GliA1* locus located on chromosome 1AS was due to LMW glutenin subunits encoded by the closely linked gene *Glu-A3*. More recently, in hexaploid wheats, genes for LMW glutenins have also been credited with an effect on BMQ (Gupta *et al.*, 1994; Nieto-Taladriz *et al.*, 1994).

Our data derive from a cross between two Einkorn lines only. However, the available data (Borghi *et al.*, 1997; Corbellini *et al.*, 1999) indicate that all good-quality lines considered to date have very similar storage-protein profiles for the loci mapping to chromosome 1S. Thus, the chromosomal segment hosting these loci seems to exist in alternative haplotypes spanning a relatively large recombination distance. The haplotype present in ID 1331 is of particular value because of the combined effects of

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alleles of the loci *LMW GLU6,7*, *LMW GLU1-4* and *ωGLI1-4*. Our observations of the positive influence of LMW glutenin and of gliadin subunits on BMQ contradict the results of Tranquilli *et al*. (1998). Using hexaploid substitution lines differing for segments of chromosomes 1A and $1A^m$, they reported a low BMQ value for Einkorn LMW glutenins. Their finding can, however, be explained in light of the contrasting effects on BMQ of different Einkorn genotypes. Further support stems from the work of Wieser (2000), who demonstrated that Einkorn storage-protein subunits are, in general, quite different from those of tetra- and hexaploid wheats.

A surprising aspect of our results is the finding that also a second, minor QTL has a detectable effect on the SDS sedimentation volume or SSV. Even the role on BMQ of total protein content can be considered to be marginal, because the parent with poor BMQ (ID 362) actually had a higher protein content than the good-quality line ID 1331. Even though the difference in protein content between parents was high, only two QTLs for this trait emerged as significant. Similar QTLs, always explaining only a small part of the total phenotypic variance, have been described in hexaploid (Sourdille *et al*., 1999; Zanetti *et al*., 1999) and tetraploid (Blanco *et al*., 1998; Joppa & Cantrell, 1990; Steiger *et al*., 1996; Gonzalez-Hernandez *et al*., 1998) wheats.

Enough RFLP loci were mapped with probes common to the chromosomes of other *Triticeae* to allow linkage-number assignment and linkage-group orientation. It has, moreover, already been established that the marker order in Einkorn genetic maps is consistent with those of other wheat A chromosomes (Kojima & Ojihara, 1998; Kojima *et al*., 1998; Dubcovsky *et al*., 1995*a*, *b*, 1996). However, because *T. monococcum* and *T. urartu* (the putative progenitor of genome A of polyploid wheats) differ extensively in their restriction profiles, the genome of *T. monococcum* has been redesignated A^m (Dvorák *et al*., 1993; Dubcovsky *et al*., 1995*b*). In our map, discrepancies in RFLP mapping (Table 1) concerned three probes assigned to chromosomes 5L, 5S and 6L in other *Triticeae*; these mapped on chromosomes $1A^m$, $1A^m$ and $4A^m$, respectively. The most probable explanation for the differences is that, in Einkorn, polymorphisms detected by genomic probes have a 34·4% probability of being duplicated (Dubcovsky *et al*., 1996).

In the map shown in Fig. 1, the order of storage protein genes and the homology to gene loci of other *Triticeae* are of particular interest. The molecular probe *Gli-1* can, almost certainly, be identified with the *Gli-1* multigene locus, which encodes most γ- and ω-gliadins, and maps to the short arm of chromosomes 1A, 1B and 1D in polyploid wheats (Payne, 1987). The tight linkage with the locus defined by the gliadin band γGLI5 supports this hypothesis. With regard to diploid wheats, the locus could correspond to the *XGli1* of the maps of Dubkovsky *et al*. (1997) and Van Deynze *et al*. (1995). The *ωGLI1-4* locus cannot be identified unequivocally with loci already described. Candidates could be *Gli-5* and *Gli-6*, two minor loci coding for ω-gliadin components observed in common wheat by Pogna *et al*. (1993) and Metakovsky *et al*. (1996), respectively, and mapped on chromosome 1A, about 2–5 cM from *Gli-1* and distal to it with respect to the centromere. The more distal loci *LMWGLU6,7* and *LMWGLU1-4* might have a candidate homologue in *Gli-3*, mapping 25–36 cM from *Gli-1* (Galili & Feldman, 1984; Sobko *et al*., 1986; Metakovsky *et al*., 1996). However, in both polyploid wheats and the diploid maps of Dubkovsky *et al*. (1997) and Van Deynze *et al*. (1995), *Gli3* is halfway between *Gli-1* and the centromere, whereas, in our map, the locus in question is distal to *Gli1*. The presence of an inversion in at least one of the parents of the two mapping populations cannot be excluded.

Free threshing (FT) is important in mechanically harvested hexaploid wheats. In all FT varieties of this species, the dominant allele *Q*, located on chromosome 5AL, is essential for free threshing. Kerber & Dyck (1969) uncovered a second system governing threshability associated with the D genome. Later, Kerber & Rowland (1974) showed that the D genome effect was due to a dominant allele at the locus *Tenacious glumes* (*Tg*), to which the soft-glume allele *tg* is recessive. The gene was mapped to chromosome 2D, with the *Tg* allele inhibiting the expression of the *Q* allele, which maps to chromosome 5 (Luo *et al*., 2000). In tetraploid wheat, FT varieties have the *Q* allele on chromosome 5AL (Muramatsu, 1986). A recent study by Simonetti *et al*. (1999) proved that both *Tg* and *Q* are active in the tetraploid, as in the hexaploid wheat, and that they occupy homologous loci on chromosomes 2BS (= *Tg2*) and 5AL (= *Q2*). The same authors indicate the existence of two further loci on chromosomes 5AS and 6AS that might play an additional role in FT.

In *T. monococcum sinskajae*, the *soft-glume* character is controlled by a single gene (Dorofeev & Navruzlekov, 1982). We have mapped the same trait with a very high LOD score (*Sog* vs *sog* alleles in this paper) to the short arm of chromosome 2. Given the locations of *Tg*, *Tg2* and *Sog* in homologous chromosomes of hexaploid, tetraploid and diploid wheats, respectively, the three loci can, in all probability, be considered to be homologous. As in the case of *Tg*, *Tg2*, *Q* and *Q2*, the *sog* allele is tightly associated with very compact ears.

References

American Association of Cereal Chemists (1995). Method 39-10. Final approval 10-27-82; revised 10-8-86 and 11-1-89; reviewed 10-26-94. In *Approved Methods of the*

https://doi.org/10.1017/S001667230200575X Published online by Cambridge University Press

American Association of Cereal Chemists, 9th edn. St Paul, MN, USA: American Association of Cereal Chemists.

Abdel-Aal, E.-S. M., Hucl, P., Sosulski, F. W. & Bhirud, P. R. (1997). Kernel, milling and baking quality of spring-type spelt and einkorn wheats. *Journal of Cereal Science* **26**, 363–370.

Bartels, D., Altosaar, I., Harberd, N. P., Barker, R. F. & Thompson, R. D. (1986). Molecular analysis of γ-gliadin gene families of the complex *GLI-1* locus of bread wheat (*T. aestivum* L.). *Theoretical and Applied Genetics* **72**, 845–853.

Becker, J., Vos, P., Kuiper, M, Salamini, F. & Heun, M. (1995). Combined mapping of AFLP and RFLP markers in barley. *Molecular and General Genetics* **249**, 65–73.

Bezant, J. H., Laurie, D. A., Pratchett, N., Chojecki, J. & Kearsey, M. J. (1997). Mapping of QTL controlling NIR predicted hot water extract and grain nitrogen content in a spring barley cross using marker-regression. *Plant Breeding* **116**, 141–145.

Blanco, A., Bellomo, M. P., Cenci, A., De Giovanni, C., D'Ovidio, R., Iacono, E., Laddomada, B., Pagnotta, M. A., Porceddu, E., Sciancalepore, A., Simeone, R. & Tanzarella, O. A. (1998). A genetic linkage map of durum wheat. *Theoretical and Applied Genetics* **97**, 721–728.

Borghi, B., Castagna, R., Corbellini, M., Heun, M. & Salamini, F. (1996). Breadmaking quality of einkorn wheat (*Triticum monococcum* ssp. *monococcum*). *Cereal Chemistry* **73**, 208–214.

Borghi, B., Castagna, R., Corbellini, M., Empilli, S., Brandolini, A., Vaccino, P., Oleimeulen, B., Salamini, F. & Heun, M. (1997). Variability and genetic control of breadmaking quality in Einkorn (*Triticum monococcum*). In *Summary Proceedings International Triticeae Symposium* (ed. A. Bari & A. A. Jaradat), pp. 53. IPGRI–ICARDA, Aleppo, Syria.

Boyko, E. V., Gill, K. S., Mickelson-Young, L., Nasuda, S., Raupp, W. J., Ziegle, J. N., Singh, S., Hassawi, D. S., Fritz, A. K., Namuth, D., Lapitan, N. L. V. & Gill, B. S. (1999). A high-density linkage map of *Aegilops tauschii*, the D-genome progenitor of bread wheat. *Theoretical and Applied Genetics* **99**, 16–26.

Castagna, R., Borghi, B., Di Fonzo, N., Heun, M. & Salamini, F. (1995). Yield and related traits of Einkorn (*Triticum monococcum* ssp. *monococcum*) in different environments. *European Journal of Agronomy* **4**, 371–378.

Churchill, G. A. & Doerge, R. W. (1994). Empirical threshold values for quantitative trait mapping. *Genetics* **138**, 963–971.

Corbellini, M., Empilli, S., Vaccino, P., Brandolini, A., Borghi, B., Heun, M. & Salamini, F. (1999). Einkorn characterization for bread and cookie production in relation to protein subunit composition. *Cereal Chemistry* **76**, 727–733.

D'Egidio, M. G., Nardi, S. & Vallega, V. (1993). Grain, flour and dough characteristics of selected strains of diploid wheat, *Triticum monococcum* L. *Cereal Chemistry* **70**, 298–303.

Dorofeev, V. F. & Navruzbekov, N. A. (1982). Genetic aspects of easy threshing and rachis strength in naked-grained wheats. [Russian]. *Doklady Vsesoyuznoi Ordena Lenina i Ordena Trudovogo Krasnogo Znameni Akademii Sel'skokhozyaistvennykh Nauk Imeni V. I. Lenina* **2**, 3–6.

Dubcovsky, J., Luo, M. C. & Dvorak, J. (1995*a*). Differentiation between homoeologous chromosomes 1A of wheat and 1 A^m of *Triticum monococcum* and its recognition by the wheat *Ph1* locus. *Proceedings of the National Academy of Sciences of the USA* **92**, 6645–6649.

Dubcovsky, J., Luo, M. C. & Dvorak, J. (1995*b*). Linkage relationship among stress-induced genes in wheat. *Theoretical and Applied Genetics* **91**, 795–801.

Dubcovsky, J., Luo, M. C., Zhing, G. Y., Bainsteitter, R., Desai, A., Kilian, A., Kleinhofs, A. & Dvorak, J. (1996). Genetic map of diploid wheat, *T. monococcum* L., and its comparison with maps of *H. vulgare* L. *Genetics* **143**, 983–999.

Dubcovsky, J., Echaide, M., Giancola, S., Rousset, M., Luo, M. C., Joppa, L. R. & Dvorak, J. (1997). Seed storage protein loci in RFLP maps of diploid, tetraploid and hexaploid wheats. *Theoretical and Applied Genetics* **95**, 1169–1180.

Dvorák, J., Di Terlizzi, P., Zhang, H. B. & Resta, P. (1993). The evolution of polyploid wheats: identification of the A genome donor species. *Genome* **36**, 21–31.

Galili, G. & Feldman, M. (1984). Mapping of glutenin and gliadin genes located on chromosome 1B of common wheat. *Molecular and General Genetics* **193**, 293–298.

Garland Campbell, K., Finney, P. L., Bergman, C. J., Gualberto, D. G., Anderson, J. A., Giroux, M. J., Sititunga, D., Zhu, J., Gendre, F., Roué, C., Vérel, A. & Sorrels, M. E. (2001). Quantitative trait loci associated with milling and baking quality in a soft × hard wheat cross. *Crop Science* **41**, 1275–1285.

Gonzalez-Hernandez, J. L., Kianian, S. & Elias, E. M. (1998) Grain protein content and 1000-kernel weight QTL mapping on chromosome 5B of *Triticum dicoccoides Proceedings of the 9th International Wheat Genetics Symposium* (ed. A. E. Slinkard), Vol. 2, pp. 47–49. University Extension Press, University of Saskatchewan, Saskatoon, Canada.

Gupta, R. B., Paul, J. G., Cornish, G. B., Palmer, G. A., Bekes, F. & Rathjen, A. J. (1994). Allelic variation at glutenin subunit and gliadin loci, Glu-1, Glu-3 and Gli-1 of common wheats. I. Its additive and interaction effects on dough properties. *Journal of Cereal Science* **19**, 9–17.

Heun, M., Kennedy, A. E., Anderson, J. A., Lapitan, N. L. V., Sorrells, M. E. & Tanksley, D. (1991). Construction of a restriction fragment length polymorphism map for barley (*Hordeum vulgare*). *Genome* **34**, 437–447.

Heun, M., Schaefer-Pregl, R., Klawan, D., Castagna, R., Accerbi, M., Borghi, B. & Salamini, F. (1997). Site of Einkorn wheat domestication identified by DNA fingerprinting. *Science* **278**, 1312–1314.

Joppa, L. R. & Cantrell, R. G. (1990). Chromosomal location of genes for grain protein content of wild tetraploid wheat. *Crop Science* **30**, 1059–1064.

Kerber, E. R. & Dyck, P. L. (1969). Inheritance in hexaploid wheat of leaf rust resistance and other characters derived from *Aegilops squarrosa*. *Canadian Journal of Genetic Cytology* **11**, 639–647.

Kerber, E. R. & Rowland, G. G. (1974). Origin of the free threshing character in hexaploid wheat. *Canadian Journal of Genetic Cytology* **16**, 145–154.

Kojima, T. & Ogihara, Y. (1998). High-resolution RFLP map of the long arm of chromosome 5A in wheats and its synteny among cereals. *Genes and Genetic Systems* **73**, 51–58.

Kojima, T., Nagaoka, T., Noda, K. & Ogihara, Y. (1998). Genetic linkage map of ISSR and RAPD markers in Einkorn wheat in relation to that of RFLP markers. *Theoretical and Applied Genetics* **96**, 37–45.

Kosambi, D. D. (1944). The estimation of map distances from recombination values. *Annual Eugenics* **12**, 172–175.

Lincoln, S. E., Daly, M. J. & Lander, E. S. (1993). *Constructing genetic linkage maps with MAPMAKER/EXP Version 3.0: a tutorial and reference manual*. USA:

https://doi.org/10.1017/S001667230200575X Published online by Cambridge University Press

Whitehead Institute for Biomedical Research, Cambridge, MA.

Luo, M. C., Yang, Z. L. & Dvoràk, J. (2000). The Q locus of Iranian and European spelt wheat. *Theoretical and Applied Genetics* **100**, 602–606.

McIntosh, R. A., Hart, G. E., Devos, K. M., Gale, M. D. & Rogers, W. J. (1998). Volume 5 – catalogue of gene symbols for wheat. *Proceedings of the 9th International Wheat Genetics Symposium*. University Extension Press, University of Saskatchewan, Saskatoon, Canada.

McKey, J. (1954). Neutron and X-ray experiments in wheat and a revision of the speltoid problem. *Hereditas* **40**, 65–180.

Metakovsky, E. V., Chernakov, V. M., Upelniek, V. P., Redaelli, R., Dardevet, M., Branlard, G. & Pogna, N. E. (1996). Recombination mapping of minor γ-gliadin-coding loci on chromosome 1A of common wheat: a revision. *Journal of Genetics and Breeding* **50**, 277–286.

Morel, M. H. (1994). Acid–polyacrylamide gel electrophoresis of wheat glutenins: a new tool for the separation of high and low molecular weight subunits. *Cereal Chemistry* **71**, 238–242.

Muramatsu, M. (1986). The vulgare super gene, *Q*: its universality in durum wheat and its phenotypic effects in tetraploid and hexaploid wheats. *Canadian Journal of Genetic Cytology* **28**, 30–41.

Nelson, J. C., Sorrells, M. E., Van Deynze, A. E., Lu, Y. H., Atkinson, M., Bernard, M., Leroy, P., Faris, J. D. & Anderson, J. A. (1995*a*). Molecular mapping of wheat. Major genes and rearrangements in homoeologous groups 4, 5 and 7. *Genetics* **141**, 721–731.

Nelson, J. C., Van Deynze, A. E., Autrique, E., Sorrells, M. E., Lu, Y. H., Merlino, M., Atkinsons, M. & Leroy, P. (1995*b*). Molecular mapping of wheat. Homoeologous group 2. *Genome* **38**, 516–524.

Nesbitt, M. & Samuel, D. (1996). From staple crop to extinction? The archaeology and history of the hulled wheats. In *Hulled Wheats* (Proceedings of the First International Workshop on Hulled Wheats, 21–22 July 1995, Castelvecchio Pascoli, Italy (ed. S. Padulosi, K. Hammer & J. Heller), pp. 41–100. Rome, Italy: International Plant Genetic Resources Institute.

Nieto-Taladriz, M. T., Perretant, M. R. & Rousset, M. (1994). Effect of gliadin and HMW and LMW subunits of glutenin on dough properties in the F_6 recombinant inbred lines from a bread wheat cross. *Theoretical and Applied Genetics* **88**, 81–88.

Payne, P. I. (1987). Genetics of wheat storage proteins and the effect of allelic variation on breadmaking quality. *Annual Review of Plant Physiology* **38**, 141–153.

Payne, P. I., Corfield, K. G. & Blackman, J. A. (1979). Identification of a high molecular weight subunit of glutenin whose presence correlates with breadmaking quality in wheats of related pedigree. *Theoretical and Applied Genetics* **55**, 153–159.

Payne, P. I., Nightingale, M. A., Krattiger, A. F. & Holt, L. M. (1987). The relationship between HMW glutenin subunit composition and the breadmaking quality of British grown wheat varieties. *Journal of Science Food Agriculture* **40**, 51–65.

Pogna, N. E., Autran, J. C., Mellini, F., Lafiandra, D. & Feillet, P. (1990). Chromosome 1B-encoded gliadins and glutenin subunits in durum wheat: genetics and relationships to gluten strength. *Journal of Cereal Science* **11**, 15–34.

Pogna, N. E., Mellini, F., Beretta, A. Dal Belin & Peruffo, A. (1989). The high-molecular-weight glutenin subunits of common wheat cultivars grown in Italy. *Journal of Genetics and Breeding* **43**, 17–24.

Pogna, N. E., Metakovsky, E. V., Redaelli, R., Raineri, F. & Dachkevitch, T. (1993). Recombination mapping of *Gli-5*, a new gliadin-coding locus on chromosomes 1A and 1B in common wheat. *Theoretical and Applied Genetics* **87**, 113–121.

Preston, K. R., March, P. R. & Tipples, K. H. (1982). An assessment of the SDS sedimentation test for the prediction of Canadian bread wheat quality. *Canadian Journal of Plant Science* **62**, 545–553.

Saponaro, C., Pogna, N. E., Castagna, R., Pasquini, M., Cacciatori, P. & Redaelli, R. (1995). Allelic variation at the *Gli-A1m*, *Gli-A2m* and *GluA1m* loci and breadmaking quality in diploid wheat *Triticum monococcum*. *Genetical Research* **66**, 127–137.

Shewry, P. R. & Tatham, A. S. (1997). Disulphide bonds in wheat glutin proteins. *Journal of Cereal Science* **25**, 207–227.

Simonetti, M. C., Bellomo, M. P., Laghetti, G., Perrino, P., Simeone, R. & Blanco, A. (1999). Quantitative trait loci influencing free-threshing habit in tetraploid wheats. *Genetic Resources and Crop Evolution* **46**, 267–271.

Sobko, T. A., Poperelya, F. A., Ribalka, A. I. & Sozinov, A. A. (1986). Inheritance and mapping of genes encoding storage protein biosynthesis on the chromosome 1A of common wheat. *Tsitologiya I Genetika* **20**, 372–376.

Sourdille, P., Perretant, M. R., Charmet, G., Cadalen, T., Tixier, M. H., Joudrier, P., Gautier, M. F., Branlard, G., Bernard, S., Boeuf, C. & Bernard, M. (1999). Detection of QTL for bread-making quality in wheat using molecular markers. In *Genetics and Breeding for Crop Quality and Resistance* (ed. G. T. Scarascia-Mugnozza, E. Porceddu & M. A. Pagnotta), pp. 361–366. Kluwer Academic Press, Dordrecht, The Netherlands.

Stam, P. & Van Ooijen, J. W. (1995). *JoinMap Version 2.0. Software for the calculation of genetic linkage maps*. Wageningen, The Netherlands: CPRO–DLO.

Steiger, D. K., Elias, E. M. & Cantrell, R. G. (1996). Evaluation of lines derived from wild emmer chromosome substitutions: I. Quality traits. *Crop Science* **36**, 223–227.

Thompson, R. D., Bartels, D., Harberd, N. D. & Flavell, R. B. (1983). Characterization of the multigene family coding for HMW glutenin subunits in wheat using cDNA clones. *Theoretical and Applied Genetics* **67**, 87–96.

Tranquilli, G., Cuniberti, M., Gianibelli, C., Bullrich, L., Larroque, O., MacRitchie, F. & Dubcovsky, J. (1998). Effect of *T. monococcum* glutenin loci on bread making quality. In *Proceedings of the 9th International Wheat Genetics Symposium* (ed. A. E. Slinkard), pp. 282–284. University Extension Press, University of Saskatchewan, Saskatoon, Canada.

Utz, H. F. & Melchinger, A. E. (1996). PLABQTL: a program for composite interval mapping of QTL. *Journal of Quantitative Trait Loci* **2**, 1.

Van Deynze, A. E., Dubcovsky, J., Gill, K. S., Nelson, J. C., Sorrels, J. E., Dvorák, J., Gill, B. S., Lagudah, E. S., McConch, S. R. & Appels, R. (1995). Molecular-genetic maps for group 1 chromosomes of *Triticeae* species and their relation to chromosomes in rice and wheat. *Genome* **38**, 45–59.

Van Deynze, A. E., Sorrells, M. E., Park, W. D., Ayres, N. M., Fu, H., Cartinhour, S. W., Paul, E. & McCouch, S. R. (1998). Anchor probes for comparative mapping of grass genera. *Theoretical and Applied Genetics* **97**, 356–369.

https://doi.org/10.1017/S001667230200575X Published online by Cambridge University Press

Vos, P., Hogers, R., Bleeker, M., Rijans, M., Van Der Lee, T., Hornes, M., Frijters, A., Pot, J., Peleman, J., Kuiper, M. & Zabeau, M. (1995). AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research* **23**, 4407–4414.

Wieser, H. (2000). Comparative investigations of gluten protein from different wheat species. I. Qualitative and quantitative composition of gluten protein types. *European Food Research Technology* **211**, 262–268.

Zanetti, S., Keller, M., Winzeler, M., Saurer, W., Keller, B. & Messmer, M. (1999). QTL for quality parameters for bread-making in a segregating wheat by spelt population. In *Genetics and Breeding for Crop Quality and Resistance* (ed. G. T. Scarascia-Mugnozza, E. Porceddu & M. A. Pagnotta), pp. 357–360. Kluwer Academic Press, Dordrecht, The Netherlands.

Zeng, Z.-B. (1993). Theoretical basis of separation of multiple linked gene effects on mapping quantitative trait loci. *Proceedings of the National Academy of Sciences of the USA* **90**, 10, 972–10, 976.

Zeng, Z.-B. (1994). Precision mapping of quantitative trait loci. *Genetics* **136**, 1457–1468.

Zohary, D. & Hopf, M. (1993). *Domestication of Plants in the Old World*, 2nd edn. Oxford: Clarendon Press.

https://doi.org/10.1017/S001667230200575X Published online by Cambridge University Press