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Phylogenetic relationships of *Triticum tauschii* the D genome donor to hexaploid wheat

2. Inheritance and chromosomal mapping of the HMW subunits of glutenin and gliadin gene loci of *T. tauschii*

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Summary. In crosses between *T. tauschii* (D^t) accesions, their polymorphic gliadin forms were inherited as blocks of gliadin components -*Gli-D^{t}1, Gli-D^{t}2* – as single Mendelian characters. From the progeny of four tri-parental crosses (test-crosses), HMW glutenin subunits derived from *T. tauschii* (*Glu-D^{t}1*) segregated as alleles of the *Glu-D1* locus in bread wheat. In three of the tri-parental crosses, a small proportion (2.5%) of the progeny with atypical segregation patterns, were identified through somatic chromosome counts, to be aneuploids (1.9% hypoploids and 0.6% hyperploids). Chromosomal mapping studies revealed that the synteny of genes for HMW glutenin subunits and gliadins in *T. tauschii* are conserved in the D genome 'homologue' (chromosome 1D) of *T. aestivum.* The map distance between the *Glu-D1/-D^{t}1* and *Gli-D1/-D^{t}1* loci was calculated to be 63.5 cM, while a linkage to the centromere of 7.7–9.7 cM was estimated for the *Glu-D1/-D^{t}1* locus.

Key words: *T. tauschii* – Chromosomal mapping – Gliadin – Glutenin – Synthetic hexaploid wheat

Introduction

Gliadin components associated with the D genome of hexaploid wheats (as with those in the A and B genomes- *Gli-A1, -A2, -B1* and *-B2*) are generally inherited as blocks of tightly-linked components coded by the *Gli-D1* and *Gli-D2* loci, distally located on the short arms of chromosomes 1D and 6D respectively (Sosinov and Poperelya 1982; Metakovsky et al. 1984; Payne et al. 1984a). Their high-molecular-weight (HMW) glutenin subunits (*Glu-D1*) are located proximally on the long arm of chromosome 1D and code for multiple allelic forms usually characterised by a pair of subunits as well as rare occurrences of single subunits (Lawrence and Shepherd 1981; Payne et al. 1984a). While the use of wild diploid relatives for hexaploid wheat improvement can be made more efficient through the elucidation of the genetics of their commercially important characters, very few genetic studies of *T. tauschii,* the putative diploid donor of the D genome to hexaploid wheat, have been reported.

In a previous communication (Lagudah and Halloran 1988), polymorphism in HMW glutenin subunits (*Glu-D^{t}1*) and gliadins (*Gli-D^{t}1, Gli-D^{t}2*) was used to assess phylogenetic relationships in the D genome donor. The present study was aimed at establishing the genetic basis of the variants, as well as mapping the *Glu-D^{t}1* and *Gli-D^{t}1* loci in derivatives of *T. tauschii,* presumed to be located on the chromosome 1D 'homologue' of synthetic hexaploid wheat (*T. turgidum* conv. *durum* × *T. tauschii*).

Materials and methods

Hybridisation between (1) T. tauschii accessions, and (2) synthetic and normal hexaploid wheat (T. aestivum)

Segregation for gliadin components were analysed in the following crosses between *T. tauschii* accessions: AUS 18987 × 185-1487-7 (both for *Gli-D^{t}1* and *Gli-D^{t}2*) and KUSE 2144 × KUSE 2135 (*Gli-D^{t}2* blocks).

Five synthetic hexaploids (C2 generation)-'Langdon', ('L'-durum wheat) × 184-1481 (*T. tauschii*), 'L' × 18911, 'L' × 18913, 'L' × 181-1472 and K735 (durum wheat) × 5271 – obtained

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from colchicine treatment of hybrids between *T. turgidum* conv. *durum* and *T. tauschii* were used for the inheritance studies of HMW glutenin subunits. In testing for allelism between the *Glu-D1* subunits and their derivatives from *T. tauschii (Glu-D^{t}1)* use was made of the test-cross procedure (tri-parental cross) which employed the primary cross (as female parent) of 'Chinese Spring' ('CS') or 'CS' (Hope 1D) substitution line (*T. aestivum*)×synthetic hexaploid which was then test crossed to a derivative (63/64) of the bread wheat cultivar 'Gabo' which does not express subunits controlled by the *Glu-D1* locus. (63/64 'Gabo' was kindly supplied by G. J. Lawrence CSIRO, Canberra, Australia). The synthetic hexaploids possessed different HMW glutenin subunit combinations derived from *T. tauschii* (Table 2) and for each primary cross obtained with the *T. aestivum* parent, the latter carried an alternative form of the *Glu-D1* subunits to those of *Glu-D^{t}1* (Table 2).

The tri-parental cross, ['CS' ('Hope' 1D)×'L'/184-1481]× 63/64 'Gabo', was also used in mapping the HMW glutenin subunits relative to the ω-gliadins of 'CS' ('Hope' 1D) and their respective 'allelic' derivatives from the *T. tauschii* parent.

In mapping the distance of the HMW glutenin subunits (*Glu-D1/-D^{t}1*) locus from the centromere, a different kind of cross was used to employ the telocentric mapping method developed by Sears (1966). This was achieved by crossing the synthetic hexaploid, K735/5271 with ditelo-1DL of 'Chinese Spring' (CS1DL) and the F_1 was then backcrossed to 'CS' 1DL (male parent).

The calculation of map distances and their standard deviation in centiMorgans (cM) were based on the Kosambi (1944) Function and adapted for wheat endosperm proteins by Payne et al. (1982).

Endosperm protein markers

Methods used for the extraction and separation of gliadins and HMW glutenins were the same as previously described (Lagudah and Halloran 1988). In the gene mapping studies, endosperm portions from single grains were analysed separately by sodium dodecyl sulphate and acid polyacrylamide gel electrophoresis (SDS-PAGE and APAGE) for their HMW glutenin subunits and gliadins, respectively.

Mitotic and meiotic analysis

Somatic chromosome numbers were determined in root-tips of germinating seed which had been placed in colchicine (10^{-3} M) for 4 h and stained in 1% acetocarmine for 48 h. For the meiotic studies, spikes of K735/5271×CS1DL were collected and fixed in Carnoy's solution for 48 h, stored in 70% ethanol and their anthers were stained in 1% acetocarmine. Pairing between the 'CS' telocentric and its 'homologue' in the synthetic hexaploid K735/5271, was examined at metaphase I of meiosis in pollen mother cells.

Results

Inheritance of gliadins in T. tauschii

The α- and β-gliadin components associated with the *T. tauschii* accessions KUSE 2144 and 2135 did not segregate independently of each other, but occurred as single blocks in the parental phenotypes of the F_2 seed (Fig. 1). However, a dosage effect (1:2 and vice versa) was observed in gliadin components of seeds heterozygous for *Gli-D^{t}2* blocks 35 and 45 of KUSE 2144 and 2135 respectively (Fig. 1).

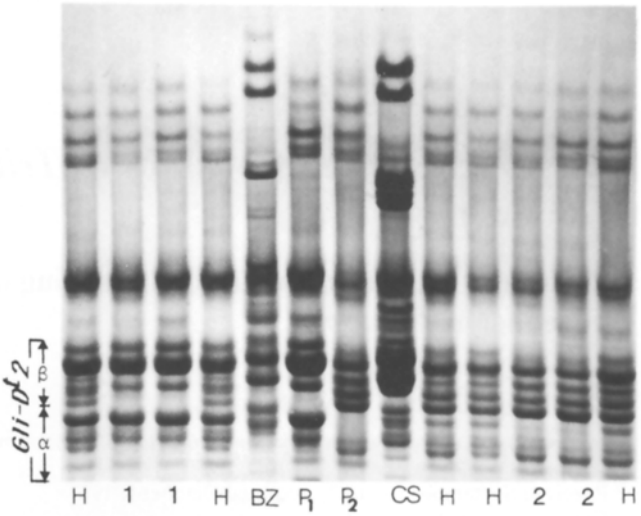

Fig. 1. F2 segregation of *Gli-D^{t}2* blocks in the cross of *T. tauschii* accessions, KUSE 2144×2135 and two hexaploid wheats used as standards in the APAGE runs. P_1 KUSE 2144, P_2 KUSE 2135, *BZ* 'Bezostaya 1', *CS* 'Chinese Spring', *H* heterozygotes, *1 Gli-D^{t}2* block 35, *2 Gli-D^{t}2* block 45

In the cross between AUS 18987 and 185-1487-7 assessments were made on the same gel for both *Gli-D^{t}1* and *Gli-D^{t}2* blocks. AUS 18987 possesses *Gli-D^{t}1* block 26 and *Gli-D^{t}2* block 18, while 185-14587-7 carries blocks 10 and 14 of *Gli-D^{t}1* and *Gli-D^{t}2* respectively (Table 1). The lower number of progeny (85) scored for the *Gli-D^{t}1* blocks in this cross compared with the *Gli-D^{t}2* blocks (130) (Table 1) was due to the weakly-stained bands of the former gliadin blocks in the first set of electrophoretic runs. While segregation ratios of *Gli-D^{t}2* blocks could be scored unequivocally in the first electrophoretic run, this was not possible for the *Gli-D^{t}1* blocks. The use of higher sample concentrations in subsequent electrophoretic runs facilitated the detection of segregants associated with *Gli-D^{t}1*. Each of the blocks associated with *Gli-D^{t}1* (10, 26) and *Gli-D^{t}2* (8, 14, 35, 45) segregated as single Mendelian units in the crosses examined (Table 1).

Segregation of HMW glutenin subunits inherited from T. tauschii derivatives and T. aestivum

The distinctive expression of HMW glutenin subunits inherited from *T. tauschii* in the synthetic hexaploids, coupled with their high crossability with the *T. aestivum* parents, proved to be useful in assessing the allelism of HMW subunits of *T. aestivum* (*Glu-D1*) and derivatives of *T. tauschii* (*Glu-D^{t}1*) in their test-cross progeny. The synthetic hexaploids 'L'/184-1481 and 'L'/18911 pos-

Table 1. F2 segregation of gliadins in *T. tauschii* crosses

Cross	Progeny			χ^2 value (1:2:1)	*P*
		Gli-D^{t}1			
	block 26	blocks 26/10[a]	block 10		
AUS 18987 × 185-1487-7	21	48	16	2.01	0.25–0.50
		Gli-D^{t}2			
AUS 18987 × 185-1487-7	block 8	blocks 8/14[a]	block 14		
	32	71	27	1.49	0.25–0.50
	block 35	blocks 35/45[a]	block 45		
KUSE 2144 × KUSE 2135	36	53	29	2.05	0.25–0.50

[a] Heterozygotes

Table 2. Segregation in the progeny of four testcrosses for HMW glutenin subunits in *T. aestivum* (*Glu-D1*) and derivatives of *T. tauschii* (*Glu-D^{t}1*)

Testcross		No. of progeny, with designated subunits in brackets				
Primary cross	Tester parent	Euploid progeny		Aneuploid	χ^{2a} (1:1)	*P*
		Glu-D1	*Glu-D^{t}1*			
['CS' ('Hope' 1D) × 'L'/184-1481]	× 63/64 'Gabo'	115 (5, 10)	110 (2, 12)	6	0.07	0.90–0.95
['CS' ('Hope' 1D) × 'L'/18913]	× 63/64 'Gabo'	42 (5, 10)	46 (2, T_1, T_2)	0	0.10	0.75–0.90
['CS' × 'L'/18911]	× 63/64 'Gabo'	55 (2, 12)	48 (5, 10)	5	0.35	0.50–0.75
['CS' × 'L'/181-1472]	× 63/64 'Gabo'	58 (2, 12)	38 (2.1, 10.1)	2	3.76	0.05–0.10

[a] χ^2 values calculated from euploid progeny

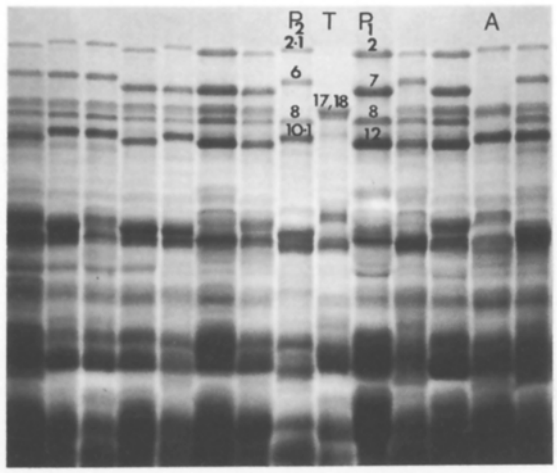

Fig. 2. SDS-PAGE of endosperm proteins from the progeny of the testcross ['CS' × 'L'/184-1472] × 63/64 'Gabo'. Numbered bands represent their HMW subunits of glutenin designations. P_1 'Chinese Spring', P_2 'L'/181-1472, T-tester parent (63/64 'Gabo'), *A* aneuploid seed (2n = 41), absence of HMW subunits controlled by chromosome 1 B of primary parents

sessed the common HMW subunit types 2, 12 and 5, 10 (*Glu-D^{t}1*), while 'L'/18913 and 'L'/181-1472 carried the newly identified HMW subunit combination 2, T_1, T_2 and 2.1, 10.1 (Table 2), respectively. In addition, all the synthetics possessed subunits 6 and 8, derived from their 'Langdon' durum ('L') wheat parent, presumed to be coded for by the *Glu-B1* locus. 'Chinese Spring' and the 'Hope' chromosome 1D substitution line possessed the *Glu-D1* subunits 2, 12 and 5, 10 respectively, while the subunits 7, 8 of the *Glu-B1* locus were common to both cultivars (Figs. 2 and 3 a). Most of the test-cross F_1 seeds (512) examined, carried either the *Glu-D^{t}1* or *Glu-D1* subunits (Table 2) and subunit 6 or 7 from the synthetic hexaploid and *T. aestivum* parents respectively (Figs. 2 and 3 a). The HMW subunits 8 and the combination 17, 18 occurred in all the test-cross progeny, with the latter subunit combination being derived from the tester parent, 63/64 'Gabo' (Figs. 2 and 3 a). The HMW glutenin subunits 2, 12 and 2, T_1, T_2 derived from *T. tauschii* (*Glu-D^{t}1*) segregated as strict alternatives (mutually exclusive) to subunits 5, 10 of the

'Chinese Spring' ('Hope' 1D) substitution line (Table 2). *T. tauschii* HMW subunit derivatives 5, 10 and 2.1, 10.1 also segregated as alternatives to subunits 2, 12 of 'Chinese Spring' consistent with a 1 : 1 ratio (Table 2). *T. tauschii* derivatives of the sub-family of lower mobility HMW subunits (1Dx), 2.1, 2 and 5 were not inherited independently of the faster mobility subunits 10.1, 12 and 10, respectively. Similarly, the triplet subunit combination 2, T_1, T_2, derived from the synthetic hexaploid 'L'/18913, was always inherited as a unit.

However, 13 seeds were characterised by non-parental HMW subunit patterns, although they all possessed the HMW subunit combination 17, 18 of the tester parent in three of the test crosses. These groups of non-parental HMW subunit types occurred in two categories: (i) a major group (10 seeds), characterised by a null expression of HMW glutenin subunits associated with either chromosome 1D or 1B (Fig. 2). (ii) a minor group (3 seeds) characterised by the presence of subunits 6, 7, and 8 of the *Glu-B1* locus as well as a normal expression of subunits located on chromosome 1D. Mitotic examination of root tips of seedlings from these seeds revealed them to be aneuploids (Table 2); those in the latter category possessed 43 chromosomes.. The former category were found to possess predominantly 41 chromosomes while a somatic count of 40 was observed in one seedling.

Chromosomal mapping of HMW glutenin subunits (Glu-D1/-D^{t}1) and ω-gliadins (Gli-D1/-D^{t}1)

1 Glutenin subunits and the ω-gliadins. The tri-parental cross, ['CS' ('Hope'1D)×'L'/184-1481]×63/64 'Gabo', apart from its use in studying 'allelic' segregation for HMW glutenin subunits, (Fig. 3a) was also examined for its ω-gliadins (Fig. 3b). The ω-gliadins of the parents of the primary cross could be distinguished using acid polyacrylamide gel electrophoresis (APAGE). The ω-gliadins used in scoring for the synthetic hexaploid parental type were components of the *Gli-D^{t}1* block 1 derived from *T. tauschii* var. *strangulata* 184-1481 (Fig. 3b). Although there was hardly any qualitative difference in the ω-gliadin region of the *Gli-D1* locus between 'CS' ('Hope' 1D) and the tester parent, it was still possible to classify the 'CS' ('Hope' 1D) parental type in the test-cross progeny. This was made possible by the double dose of its expression expected in the endosperm for gliadins of the 'CS' ('Hope' 1D) parental type, which enabled unequivocal scoring to be made of the 'CS' ('Hope' 1D) parental type as distinct from the synthetic hexaploid pattern. The possibility of aneuploids confounding the distinction between the parental ω-gliadin patterns was eliminated by excluding seed of the six aneuploids of this triparental cross from the analysis.

The segregation frequency of 113 ω-gliadins of *Gli-D1* ('CS' ('Hope' 1D) parental) compared to 112 of the *Gli-D^{t}1* block ('synthetic') in the test-cross fitted a 1 : 1 ratio ($\chi^2 = 0.00$, $P < 0.99$) expected for allelic segregation (Table 3). This observation confirms the expected homology between chromosome 1D of *T. aestivum* and its *T. tauschii* 'homologue' in the synthetic hexaploid. The combined frequency of the parental HMW glutenin subunits and ω-gliadins (5, 10/*Gli-D1* and 2, 12/*Gli-D^{t}1* – in the *T. aestivum* and *T. tauschii* derivatives respectively) was 129 compared with 96 for the recombinants (5, 10/*Gli-D^{t}1* and 2, 12/*Gli-D1*) (Table 3). This represented a recombination percentage of 42.7 ± 3.3 between the HMW glutenin subunits and ω-gliadins located on chromosome 1D from which their map distance apart was calculated to be 63.5 ± 4.5 centiMorgans.

2 Teolocentric mapping of HMW glutenin subunits. The primary cross K735/5271 (synthetic)×'CS' ditelosomic 1DL (CS1DL) when backcrossed to CS1DL (male parent) enabled the recombination frequencies between the HMW subunits, located on the long arm of chromosome 1D and the centromere, to be estimated. The synthetic hexaploid wheat parent, K735/5271 possesses the HMW subunit pair 5, 10 and *Gli-D^{t}1* block 3 derived from *T. tauschii* var. *strangulata,* RL 5271. Despite the overlap of gliadin components of chromosomes 1A and 1B with the *Gli-D^{t}1* block, the ω-gliadins of the latter were unambiguously identified by APAGE. The ditelosomic line of 'Chinese Spring', (CS1DL) lacks its *Gli-D1* locus but carries its HMW subunits 2 and 12, located on the long arm of chromosome 1D. By dual examination of the endosperm portions of single grains on SDS-PAGE and APAGE respectively, the following genotypes were to be expected in the telocentric analysis.

Parentals (i) CS1DL – 3 doses of HMW subunits 2 and 12 (*Glu-D1*) and a null expression for ω-gliadins at the *Gli-D1* locus (detected by the absence of its ω-gliadins) and (ii) 'Synthetic' – 2 doses of HMW subunits 5 and 10 (*Glu-D^{t}1*), 1 dose of the subunit pair 2, 12, and the presence of ω-gliadins of *Gli-D^{t}1* block 3.

Recombinants (i) 3 doses of HMW subunits 2 and 12 and the presence of ω-gliadins of *Gli-D^{t}1* block 3, and (ii) 2 doses of HMW subunits 5 and 10, 1 dose of the subunit pair 2, 12 and the absence of ω-gliadins of the *Glu-D1* locus.

Segregation in the progeny revealed a low recombination percentage of 7.6 ± 1.8 (Table 4). The absence of the short arm of chromosome 1D of 'Chinese Spring' implies that the recombinant seed protein types

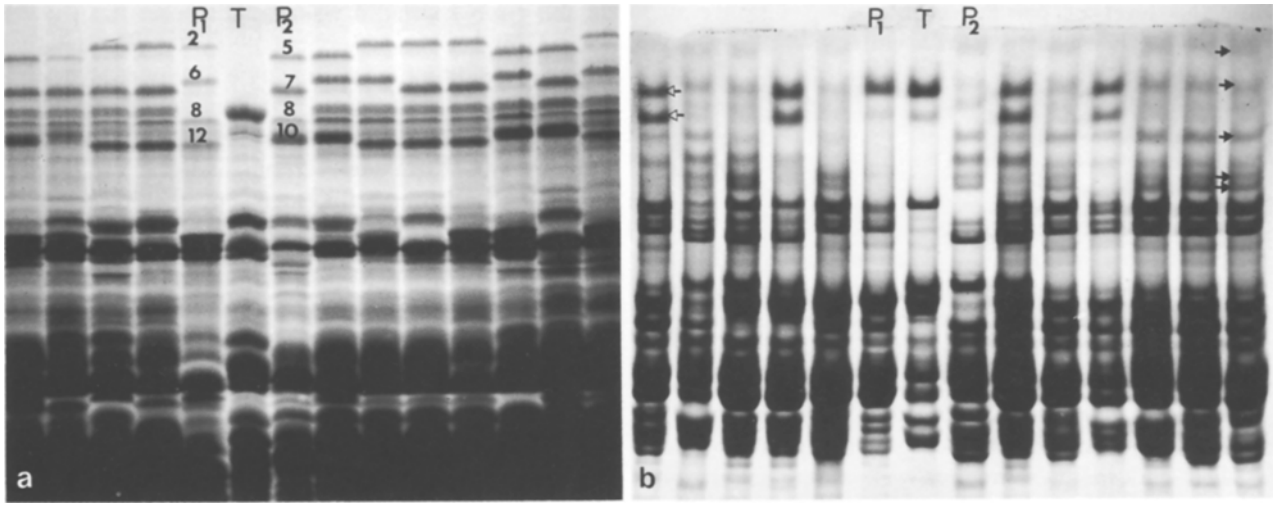

Fig. 3. **a** SDS-PAGE of endosperm proteins from the progeny of the testcross, ['CS' ('Hope' 1D)×'L'/184-1481]×63/64 'Gabo', showing their HMW subunits of glutenin (numbered bands). P_1 'L'/184-1481, P_2 'CS' ('Hope' 1D), *T* tester parent (63/64 'Gabo') **b** APAGE of gliadin proteins from the progeny of the same testcross in **a.** P_1 'CS' (Hope 1D), P_2 'L'/184-1481, *T* tester parent (63/64 'Gabo'). The *arrows* point to the ω-gliadins of *Gli-D1* (⊣▷) and *Gli-D^{t}1* (⊣▶)

Table 3. Segregation of HMW glutenin subunits and ω-gliadins of *T. aestivum* and derivatives of *T. tauschii* in the testcross, ['CS' ('Hope' 1D)×'L'/184-1481]×63/64 'Gabo'

	HMW glutenin subunits	ω-gliadin	Progeny no.	Recombination ±SD	Map distance (cM) (apart) ±SD
Parentals					
'CS' ('Hope' 1D)	*Glu-D1*	*Gli-D1*	66		
'L'/184-1481	*Glu-D^{t}1*	*Gli-D^{t}1*	63		
Recombinants					
	Glu-D1	*Gli-D^{t}1*	49		
	Glu-D^{t}1	*Gli-D1*	47	42.7±3.3	63.5±4.5

Table 4. Frequency of HMW glutenin subunits and ω-gliadins from the telocentric analysis [K735/5271 (synthetic) ×CSDT1DL]×CSDT1DL

Parentals		Recombinants		% Telocentric pairing (T)	Linkage to centromere ±SD		Map distance (cM) (apart) ±SD
Glu-D1 *Gli-D1* (null)	*Glu-D^{t}1* *Gli-D^{t}1*	*Glu-D1* Gli-D^{t}1	*Glu-D^{t}1* Gli-D1 (null)		% R[a]	Adjusted % R[a]	
103	104	10	7	79.5	7.6±1.8	9.6±2.0	9.7±2.1

[a] % R = Recombination percentage; adjusted R = %R × 100/T

could be obtained only through recombination between the long arm and the centromere of 'Chinese Spring' chromosome 1D and the corresponding arm of its 1D 'homologue' of *T. tauschii* in the synthetic hexaploid. Hence from the recombination value, an estimate of the map distance between the HMW subunits located on the long arm of chromosome 1D and the centromere can be calculated. However, a reliable estimate of this map distance is dependent on the degree of pairing between these chromosome arms. The level of pairing based on meiotic analysis of 146 pollen mother cells of the primary cross, were found to be 79.5%. This level of pairing could have underestimated the number of possible recombinants; however, when a complete pairing condition is assumed, an adjusted recombination value (Table 4), which takes into consideration the

observed level of pairing, gave a map distance of 9.7 ± 2.1 cM between the HMW glutenin subunits and the centromere (Table 4).

Discussion

In spite of the complexity of the components within a gliadin block, which is usually characterised by its particular electrophoretic mobilities as well as varying levels of intensity, all the *Gli-D^{t}1* and *-D^{t}2* blocks analysed in this study were inherited as single Mendelian units. In addition, their codominant inheritance, which is influenced by the dosage effect characteristic of their endosperm source, as well as the failure to detect any recombinant forms, are consistent with the observations made in hexaploid wheats (Doekes 1973; Baker and Bushuk 1978; Sosinov and Poperelya 1982; Metakovsky et al. 1984; Payne et al. 1984b). The joint segregation in *T. tauschii* of the ω and γ components of *Gli-D^{t}1* blocks 10 and 26 as well as the α and β components of *Gli-D^{t}2* blocks 8, 14, 35 and 45 are a further indication of their homology with the *Gli-D1* and *-D2* loci located on the short arms of chromosomes 1 and 6, respectively, of hexaploid wheat (Metakovsky et al. 1984).

The segregation pattern in the test-cross progeny for the HMW subunit combinations 5, 10; 2, 12; 2.1, 10.1 and 2, T_1, T_2 of the *T. tauschii* derivatives at the *Glu-D1* locus suggests a similar location on chromosome 1D of hexaploid wheats and its putative diploid donor. The frequency of the parental and recombinant forms of the telocentric analysis is a further indication of their location on the long arm of chromosome 1D. The validity of the homoallelism between the *Glu-D1* and *-D^{t}1* subunits is dependent on the presence in the test-cross progeny of mutually exclusive parental HMW subunit types and the non-occurrence of recombinant forms for the locus in question. The recombinant forms would either be of a null phenotype or would exhibit the presence of both parental HMW subunit types. None of the latter recombinant types, associated with chromosome 1D, was detected in the test-cross progeny. However, as stated in the results, three seeds were found to possess a null expression in the region of the *Glu-D1/-D^{t}1* locus from a total of 512 progeny of the four crosses (Table 2). Each of these seeds was found to be monosomic and it was assumed that the monosomic condition was associated with the critical chromosome 1D from either parents of the primary cross. This assumption was based on the fact that, even in the hemizygous condition, genes coding for HMW subunits are expected to be detected due to their codominant expression in inheritance. Since the tester parent used in this study carried a null phenotype at the *Glu-D1* locus (Lawrence and Shepherd 1981), it is expected that the only condition for producing a null phenotype in a monosomic test-cross progeny would be the absence of chromosome 1D from the female gametes (eggs) of the primary cross. The same argument holds for the ten aneuploid seds found to be deficient in either subunits 6 or 7 and subunit 8 located on chromosome 1B. The three hyperploids, each expressing one parental form of the chromosome 1D HMW subunits possessed both subunits 6 and 7 in addition to subunit 8. Consequently, the female gamete of the primary cross must have carried an extra 1B chromosome. The presence of aneuploids (0, 2.1, 2.7 and 4.9%) was not unexpected since the synthetics used were in only their second generation subsequent to their production.

Lawrence and Shepherd (1981) and Payne et al. (1981) have shown that the 1Dx and 1Dy subfamily of HMW glutenin subunits in hexaploid wheats is not inherited independently. This observation is consistent with the inheritance pattern reported in this study for their corresponding derivatives in their putative diploid donor. Though subunit T_2 occurs outside the recognised HMW range, its joint inheritance with the subunits 2 and T_1 is a further indication that all three subunits represent one allelic form of the *Glu-D^{t}1* locus.

The recombination value of 42.7% between the gliadins and HMW glutenin subnits on chromosome 1D from the cross ['CS' ('Hope' 1D)×'L'/184-1481 ('synthetic')]×63/64 'Gabo' suggests that the *Gli-D1/-D^{t}1* and *Glu-D1/-D^{t}1* loci are widely separated. By using the F_2 selfed progeny from the cross between the wheat variety 'Koga II' and 'Chinese Spring' IBL, Chojecki et al. (1983) obtained a recombination of 48.3% between the *Glu-D1* and *Gli-D1* loci which is quite similar to the value (42.7%) obtained in this study. It can be deduced from these recombination values that the relative location of the *Glu-D1* and *Gli-D1* loci on chromosome 1D of hexaploid wheat reveals a similar spatial relationship between the *Glu-D^{t}1* and *Gli-D^{t}1* loci located on the *T. tauschii* 'homologue'. In addition the map distance of 7.7-9.7 cM of the HMW glutenin subunits from the centromere was comparable with the value of 10.1 cM reported by Payne et al. (1982). A longer map distance of 16.9-28.1 cM was observed by Singh and Shepherd (1984). Nevertheless the results obtained from this study as well as the telocentric mapping results of Payne et al. (1982) and Singh and Shepherd (1984) revealed a close linkage between the centromere and the HMW glutenin subunits located on the long arm of chromosome 1D.

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