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Development and characterisation of a line of bread wheat, *Triticum aestivum*, which lacks the short-arm satellite of chromosome 1B and the *Gli-B1* locus

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Summary. About 360 offspring of a tri-parental cross were screened by gel electrophoresis and unexpectedly one of them did not contain chromosome 1B ω-gliadins derived from either of the primary parents. A line disomic for the ω-gliadin null was developed from the surviving embryo half of the unique grain. Two dimensional electrophoresis revealed that all the storage protein genes at *Gli-B1,* coding for γ-gliadins, β-gliadins and low-molecular-weight subunits of glutenin as well as the ω-gliadin, were not expressed. The nuclei of dividing root-tip cells were shown by light microscopy to lack the normal short-arm satellites of chromosome 1B, indicating that the genes for the missing storage proteins had been lost through a terminal deletion. Using a radioactive ribosomal RNA probe, the deficient 1B chromosomes were shown to contain ribosomal RNA genes demonstrating that at least two-thirds of the short arm was still present. Examination of serial sections of chromosome 1B at metaphase by low-power electron microscopy showed that the point of scission of this chromosome was within the secondary constriction where the ribosomal RNA genes are located. The *Gli-B1* locus must therefore be carried on the short-arm satellite. Transmission of the deficient chromosome from female gametes to progeny was normal (i.e., about 50%) but from pollen it was poor (8.8%). Recombination mapping indicated that the distance from the ribosomal RNA genes (*Nor1*) to *Glu-B1* was 22 cM, equivalent to 13 cM from *Nor1* to the centromere.

Key words: Gliadin – *Triticum* – Polyacrylamide gel-electrophoresis – Light and electron microscopy – Chromosome deficiency

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Introduction

Over the last three decades many aneuploid lines of bread-wheat have been collected (Sears 1954) but relatively few lines are available which contain deletions of parts of chromosome arms. Such lines would be extremely useful for several types of genetical study, for instance in locating structural genes to chromosome segments. One of the best examples of a partial arm deletion was developed in 'Chinese Spring' by Giorgi (1981) which has two thirds of the terminal segment of the long arm of chromosome 6B deleted. Sears (1977) reported a small, interstitial deletion involving the *Ph* locus on the long arm of chromosome 5B. More recently, Miller and Reader (1982) described a line of 'Chinese Spring' which was heterozygous for a major deletion of part of the long arm of chromosome 5A. However, upon selfing, no progeny with disomic deletions were recovered, which the authors attributed to male gametes containing incomplete 5A chromosomes being incapable of competing with normal gametes during pollination.

In this communication, a genetic line is characterised that has a partial deletion of the short arm of chromosome 1B. It was used as a parent in a crossing procedure to estimate recombination between *Glu-B1* on the long arm of chromosome 1B and the ribosomal RNA genes at the secondary constriction on the short arm of the same chromosome.

Materials and methods

The bread-wheat varieties used in this study were taken from the collection held at the Plant Breeding Institute, Cambridge, UK.

1 Sodium dodecyl sulphate, polyacrylamide-gel electrophoresis (SDS-PAGE)

The method used to fractionate the total proteins of wheat endosperm after reduction with 2-mercaptoethanol was described previously (Payne et al. 1980; Payne et al. 1981). The method fractionates proteins mainly according to their molecular weight.

2 Two-dimensional electrophoresis of gliadin

Gliadin was extracted from wheat flour and fractionated by acid, polyacrylamide gel electrophoresis (APAGE) in the first dimension and SDS-PAGE in the second as described previously (Payne et al. 1984a).

3 Two-dimensional electrophoresis of total endosperm protein

Two methods were used, isoelectric focussing (IEF) followed by SDS-PAGE to fractionate acidic and neutral proteins and non-equilibrium pH gradient electrophoresis (NEPHGE) followed by SDS-PAGE to fractionate the more basic proteins. Details of both methods modified for wheat endosperm proteins are given in Holt et al. (1981) and Jackson et al. (1983).

4 Light microscopy of root-tip chromosomes

Root tips were excised from grains germinated for 48 h, incubated in a saturated solution of 1-bromonaphthalene for 4.5 h, fixed in glacial acetic acid and stored at 4 °C. Prior to microscopy, root tips were hydrolysed in 1N HCl at 60 °C for 12 min and then treated with Feulgen stain.

5 In situ hybridisation

Wheat chromosomes were hybridised in situ using the technique described by Hutchinson et al. 1980. The probe used was the tritium-labelled cRNA transcribed from plasmid pTA71 which contains a single wheat ribosomal gene repeating unit (Gerlach and Bedbrook 1979). The photographic emulsion was exposed for 8 weeks when the autoradiographs were developed and the chromosomes stained with Giemsa prior to cytological examination.

6 Electron microscopy

Roots from young seedlings were excised and fixed. Serial sections, 0.1 μM thick, were made and prepared for electron microscopy as described by Bennett et al. (1979). The volumes of chromosomes and of chromosome arms in cells at metaphase were estimated as described by Heslop-Harrison and Bennett (1983).

Results

1 Isolation of a line completely deficient in chromosome 1B ω-gliadins

The development of a line lacking the short-arm satellite of chromosome 1B originated from the analysis, by SDS-PAGE, of progeny from the cross ('Hope' × 'Cappelle-Desprez') ♀ × 'Highbury' ♂. The cross was originally made to estimate recombination between *Glu-B1*, which occurs on the long arm of chromosome 1B and codes for high-molecular-weight (HMW) subunits of glutenin, and *Gli-B1* which occurs on the short arm of the same chromosome and codes for ω-gliadins, γ-gliadins and low-molecular-weight subunits of glutenin (Payne et al. 1984b).

All three parents had therefore been selected to have different allelic blocks of proteins coded at each *Glu-B1* and *Gli-B1* locus. Because of the triploid nature of the endosperm, the grains from this cross would all be expected to contain two doses of chromosome 1B ω-gliadins, either from 'Hope' or from 'Cappelle-Desprez', plus one dose of allelic proteins from the third, male parent, 'Highbury'. However, one grain out of 361 was unique in having neither of the 1B ω-gliadins from the two primary parents (Fig. 1, arrow) although it had the allelic counterpart from 'Highbury'.

To bring the chromosome 1B ω-gliadin null to homozygosity, the embryo half of the unique grain was germinated and the adult plant allowed to self pollinate. Those progeny which were completely lacking 'Highbury' chromosome 1B ω-gliadins were germinated and selfed again to obtain a stock of grains.

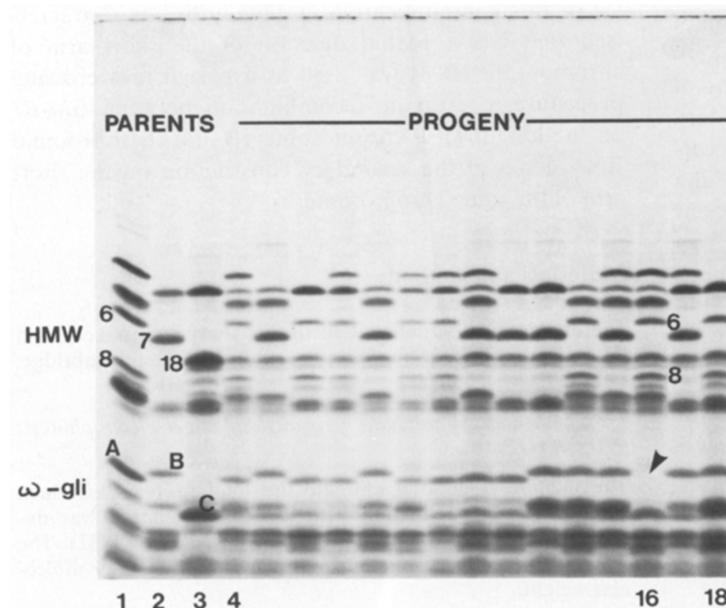

Fig. 1. Analysis by SDS-PAGE of the storage proteins of 'Hope' (*slot 1*), 'Cappelle-Desprez' (*slot 2*), 'Highbury' (*slot 3*) and 15 progeny from a cross between these varieties (*slots 4–18*). The mutant analysed in *slot 16* lacks both ω-gliadins *A* and *B* as indicated by the *arrow* but contains the allelic protein *C* from 'Highbury'. The numbered *HMW* glutenin subunits found in the three parents are all coded by chromosome 1B

2 Analysis by two-dimensional electrophoretic procedures

When a gliadin extract of grain from the null stock was analysed by pH 3.1 × SDS-PAGE and compared to the corresponding patterns for 'Hope' and 'Cappelle-Desprez' (not shown) it was clear that all gliadins coded at *Gli-B1*, one major γ-gliadin and one minor β-gliadin as well as two ω-gliadins were not being expressed (Fig. 2). Similarly, NEPHGE × SDS-PAGE and IEF × SDS-PAGE revealed that several LMW glutenin subunits coded at *Gli-B1* were not expressed either (E. A. Jackson, unpublished). Thus all the genes at this locus must either have been deleted in this stock or, if still present, they must remain repressed during grain development.

3 Characterisation by light microscopy and by in situ hybridisation

The karyotypes of dividing root-tip nuclei from one of the primary parents, 'Hope', and the null stock are shown in Fig. 3. 'Hope' has the normal bread wheat chromosome number of 42. Four of the chromosomes have satellites caused by secondary constrictions at the nucleolar organiser regions, which bear the ribosomal RNA genes; the two satellites which are small relative to the length of the short arms belong to the pair of 1B chromosomes and the two, larger, satellites belong to 6B chromosomes (Riley et al. 1958) as indicated in Fig. 3A. The deletion mutant, whilst having 42 chromosomes, has only two satellites and as they are relatively long, they must belong to chromosome 6B (Fig. 3B, arrows). Otherwise, all the chromosomes appeared to be normal in that they possessed two arms

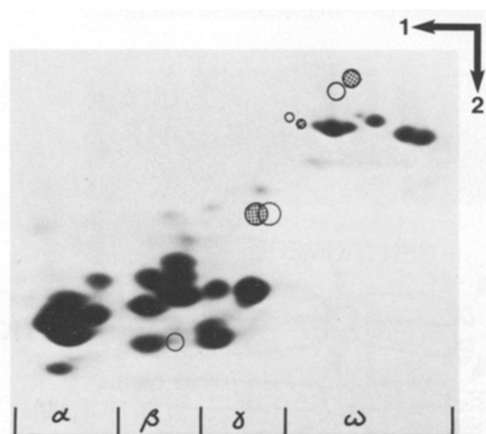

Fig. 2. Two-dimensional fractionation of the gliadin proteins from the chromosome 1BS satellite deletion. The map positions of chromosome 1B- encoded gliadins from the two primary parents, 'Hope' and 'Capelle-Desprez', are shown by *open* and *stippled circles*, respectively. The gliadins have been subdivided into four groups, α-, β-, γ- and ω-, according to their mobilities in the first dimension

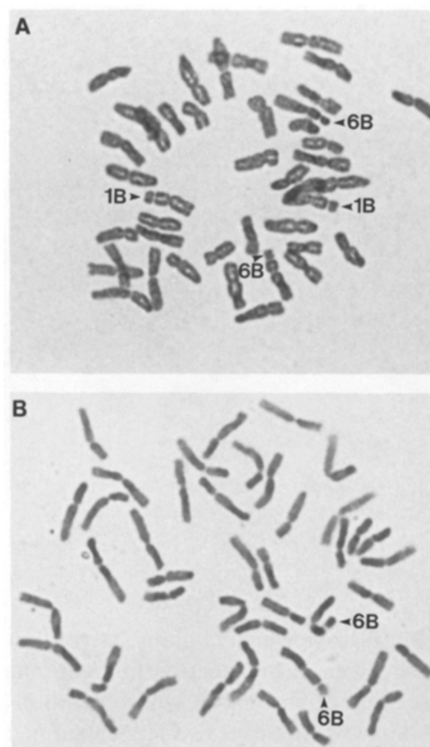

Fig. 3. The karyotypes of (**A**) 'Hope' and (**B**) the chromosome 1BS satellite deletion line revealed by light-microscopy after Feulgen staining. The chromosomes possessing satellites are identified

so it is presumed that the null stock had arisen by the cleavage of chromosome 1B at some point on the short arm with the satellite either completely deleted or too small to be detected by light microscopy. This conclusion is consistent with the electrophoretic evidence shown in Fig. 1 for while the ω-gliadins coded by chromosome 1B are absent in the unique grain, HMW glutenin subunits 6 and 8, whose genes are located on the long arm of chromosome 1B (Payne and Lawrence 1983), are present and are inherited from 'Hope'.

To determine more accurately the location of the chromosome break, tritium-labelled, copy RNA transcribed from a plasmid containing wheat ribosomal RNA gene sequences, was hybridised to root-tip squashes of the deletion mutant. Extensive silver graining, due to the hybridised, radioactive probe was associated with four areas, one on each of four chromosomes (Fig. 4). In two of them, the Giesma-stained satellite could be seen distal to the silver grains and these must be the pair of 6B chromosomes. However, no satellites could be seen clearly for the other two labelled chromosomes which are presumably the 1B chromosomes. Thus it is concluded that chromosome 1B has broken either within the ribosomal RNA genes or just distal to them to produce a very small satellite which cannot be resolved by light microscopy.

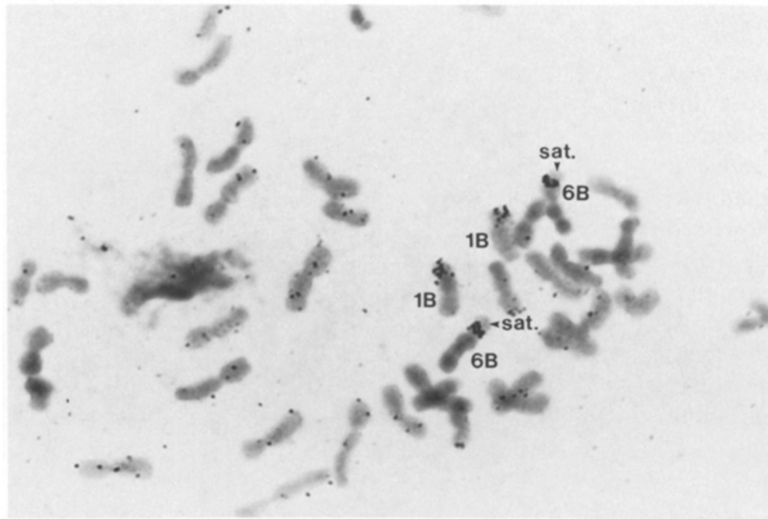

Fig. 4. In situ hybridisation of radioactive ribosomal RNA probes to chromosomes of the 1BS deletion line. The ribosomal RNA genes are revealed by heavy silver-graining. *sat.* is short for satellite

4 Characterisation by electron microscopy

Nucleolar organising regions which contain active ribosomal RNA genes are seen in the electron micrographs as light staining regions of chromatin whose positions relate to the secondary constrictions of Feulgen-stained chromosomes. Consequently, light-staining regions are used as diagnostic features of nucleolus organising chromosomes in serially sectioned metaphase cells (Bennett et al. 1982).

Examination of a completely reconstructed metaphase plate of the chromosome deficiency line showed the presence of two chromosomes with terminal lighter staining regions of chromatin on both chromatids of their short arms. From the work described above with the light microscope it is likely that these are the pair of 1B chromosomes and independent evidence from the measurement of chromosome arm volumes confirms this. The mean ratios of long to short arm volumes for the unusual chromosome pair were 2.56 and 2.38 (mean, 2.47). These values were greater than the long arm, short arm ratios for any of the 21 chromosome types of euploid 'Chinese Spring', the maximum value being 2.21 (2 determinations on each of two cells). For 'Chinese Spring', the mean arm ratio for chromosome 1B was 1.61 but the ratio of long arm to the non-satellited segment only of the short arm was 2.44, which is not significantly different from the volume ratio of the suspected 1B chromosome in the deficiency line.

Electron micrographs of four serial sections of one of the 1B chromosomes are illustrated in Fig. 5. The vertical arrows indicate the position of the centromere and the diagonal arrows the light staining nucleolar organising region. The short arm of chromosome 1B is therefore on the left-hand side of Fig. 5. The long arm, on the right hand side in Fig. 5C and 5D is orientated at right angles to the plane of the photograph and the

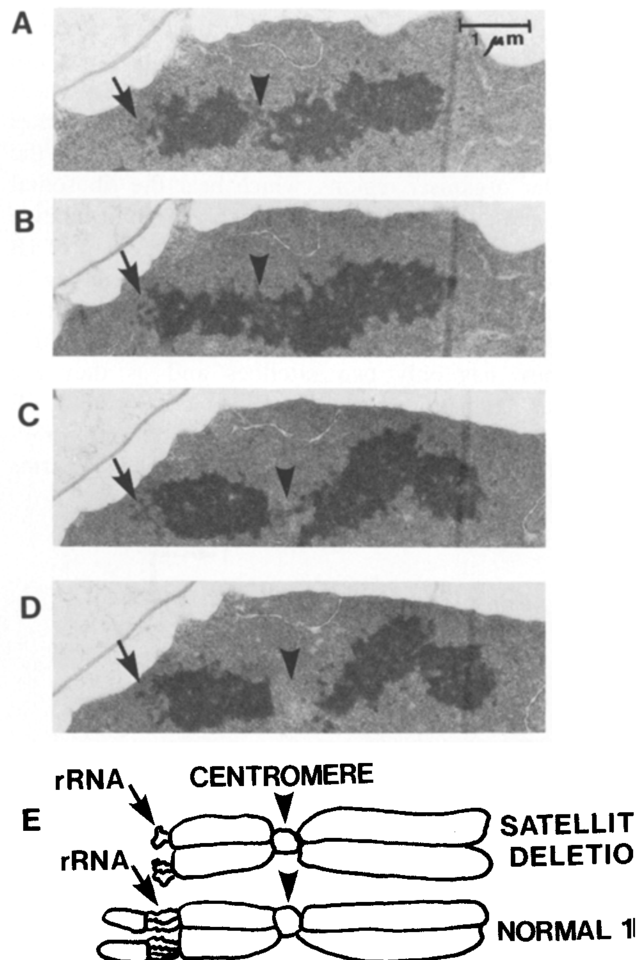

Fig. 5. A–D low-power electron microscopy of four serial sections of chromosome 1B. The position of the centromere is indicated by *vertical arrows* and the position of the nucleolar organiser region (the ribosomal RNA genes) is indicated by *diagonal arrows.* **E** diagrammatic representation of the complete and deficient 1B chromosomes. *rRNA* is short for ribosomal RNA genes

two chromatids are clearly seen in cross section. For one of the 1B chromosomes, seven serial sections contained the nucleolar organising region and the other contained five, but in none of them was there any dark-staining chromatin distal to the region. Furthermore, the total volume of light staining material in this chromosome pair was much less than would be expected for chromosome 1B (normally the major nucleolar organiser site in bread wheat). Two other, larger chromosomes in the same cell identified as 6B on the basis of possessing large satellites and arm ratios close to unity, had a much more pronounced region of light stained chromatin. Similarly in the in situ hybridisation experiment (Fig. 4), silver graining was much more extensively associatd with chromosome 6B than with the satellite-deleted 1B chromosome, whereas the same chromosomes of one of the parents, 'Hope', had similar densities of silver graining. While there can be large variations in the size of the nucleolus organising region, these observations suggest that the cleavage of chromosome 1B occurred within the secondary constriction and probably resulted in a significant reduction in the number of ribosomal RNA genes (Fig. 5 E).

It is therefore concluded that the deletion line arose from the cleavage of chromosome 1B within the ribosomal RNA genes with the loss of the satellite and the *Gli-B1* locus which is carried on this chromosome segment.

5 Transmission frequencies of the deficient 1B chromosome through male and female gametes

When plants heterozygous for the 1BS chromosome deficiency were selfed, only 4 of the 50 progeny were homozygous for this chromosome. The frequency of this homozygous type, 1 to 12.5, was far less than the expected 1 to 3 and indicated difficulties in the transmission of the deficient chromosome. To compare in more detail its transmission frequency, compared to that of a complete 1B chromosome, progeny of the cross (1BS satellite deletion line × 'Sicco') F_1 × 'Highbury' were screened by SDS-PAGE. For male transmission, 'Highbury' was used as the female parent in the second cross and for female transmission, it was used as male.

Those progeny carrying a complete 1B chromosome derived from 'Sicco' contained an ω-gliadin coded by this chromosome which is easily distinguishable by gel electrophoresis (Fig. 6, large arrow). It was assumed that the progeny lacking this gliadin had inherited the deficient 1B chromosome. The ω-gliadin band was much more intense in progeny of the female transmission experiment (Fig. 6 B) compared to the male (Fig. 6 A) because of the triploid nature of the endosperm. Similarly all progeny had either one or two doses of the allelic ω-gliadin from 'Highbury' (Fig. 6, small arrow).

In the male transmission experiment, most of the progeny in the small sample illustrated (Fig. 6 A) and in the total sample (Table 1) contained the 'Sicco' chromosome 1B ω-gliadin. Transmission of the 1B chromosome with the deleted satellite was only 8.8%, showing that male gametes containing this deficient chromosome compete much less effectively than gametes with a normal karyotype in fertilizing the ovule. By contrast, the frequency of transmission of the deficient 1B chromosome by female gametes was very similar to that of the complete chromosome (Fig. 6 B, Table 1).

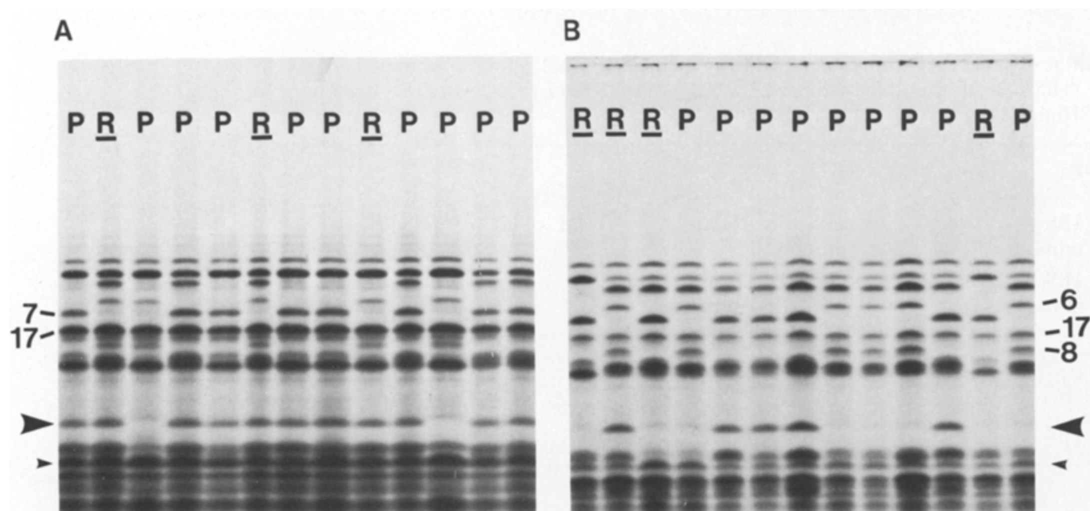

Fig. 6. Transmission of the 1B deficient chromosome by male (**A**) and female (**B**) gametes. The ω-gliadins coded by chromosomes 1B and inherited from 'Sicco' and 'Highbury' are marked by *large* and *small arrows*, respectively. HMW glutenin *subunits 6* and *8* are inherited from the 1B satellite deletion line, *subunit 7* is from 'Sicco' and *17* from 'Highbury'. Progeny with parental classes of chromosome 1B HMW subunits and ω-gliadins are marked *P* and those with recombinant classes, *R*

Table 1. Transmission of the short-arm deficient chromosome through male and female gametes by analysing progeny of the respective crosses (1BS deletion mutant × 'Sicco')♂ × 'Highbury' ♀ and (1BS deletion mutant × 'Sicco') ♀ × 'Highbury' ♂

Chromosome 1B ω-gliadins from:	1BS mutant	'Sicco'	Total	% transmission
1. Female parent	97	88	185	52.4
2. Male parent	12	124	136	8.8

6 Recombination between Glu-B1 and ribosomal RNA genes

Since the three parents in the two crosses described in the previous section had different alleles for *Glu-B1*, the products of which were easily distinguished by SDS-PAGE, the recombination map distance between *Glu-B1* and the ribosomal RNA genes could be estimated (Fig. 6). As in a previous mapping experiment (Payne et al. 1982) mispairing between the long-arm ditelocentric of chromosome 1B and the complete 1B chromosome at meiosis was only 6%, it was assumed that mispairing involving the 1BS satellite deleted chromosome would be even less and so could not significantly affect the results. Consequently, F_1 plants were not examined cytologically for non-pairing.

The ribosomal RNA genes have not so far been given gene symbols, so it is proposed here to adopt *Nor1* for those genes on chromosome 1B. *Nor1* has been added to the collection of wheat gene symbols catalogued by R. A. McIntosh. For the cross set up to estimate transmission of deficient 1B chromosome through female gametes, recombination was 20.5% (Table 2). A similar value of 20.6% was obtained with the reciprocal cross, despite highly distorted ratios for the two parental classes and the two recombinants. The two sets of data were therefore pooled and the overall recombination distance between *Glu-B1* and *Nor1* was calculated to be 21.9 cM. Since the distance between *Glu-B1* and the centromere had previously been shown to be 9.0 cM (Payne et al. 1982), it follows that the distance from the centromere to *Nor1* is only about 13 cM.

Discussion

In this paper, we have described the development and characterisation of a line from the embryo half of a single grain which has a similar karyotype to euploid bread wheat except that it lacks the short-arm satellites of the pair of 1B chromosomes. As the storage proteins coded by genes at *Gli-B1* are not produced in this line, it follows that *Gli-B1* and also *Rg1* genes for red glume colour, which are tightly linked to *Gli-B1* (Leisle et al. 1981) are carried on the satellite. Cytological examination has revealed that chromosome 1B has broken within the ribosomal RNA genes at *Nor1*. Consequently the line can be exploited to map *Nor1* to other gene markers on chromosome 1B by estimating recombination in progeny of crosses between the line and other varieties. Here, *Nor1* has been mapped to *Glu-B1*, which occurs proximally on the long arm of chromosome 1B and codes for HMW subunits of glutenin. The presence or absence of chromosome 1B ω-gliadins by SDS-PAGE determines whether the 1B satellite is present or not in progeny without resort to cytological

Table 2. Recombination distance between *Glu-B1* and the ribosomal RNA genes determined from analysing cross one, (1BS delection mutant × 'Sicco') ♀ × 'Highbury' ♂ and cross two, (1BS deletion mutant × 'Sicco')♂ × 'Highbury' ♀

HMW subunits	P		R		Total	%R	cM
	1BS mutant	'Sicco'	1BS mutant	'Sicco'			
ω-gliadin	1BS mutant	'Sicco'	'Sicco'	1BS mutant			
Cross 1							
Progeny no.	72	75	13	25	185	20.5±3.0[a]	–
Cross 2							
Progeny no.	11	97	27	1	136	20.6±3.5[a]	–
Combined							
Progeny no.	255		66		321	20.6±2.3[a]	21.9±2.7[a]

Map distances in centiMorgans (cM) were calculated from the recombination frequency using the Kosambi function (Kosambi 1944)

[a] SD

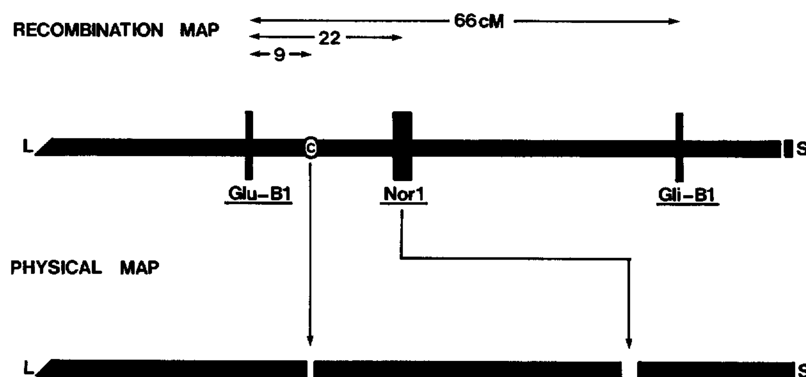

Fig. 7. Comparison of recombination and physical maps of the short arm and part of the long arm of chromosome 1B. The two maps have been aligned at their centromeres (*C*). The *bent arrow* highlights the disparity in the positions of the ribosomal RNA genes on the maps. The *bar* denoting *Nor1* is thicker than the bars for *Glu-B1* and *Gli-B1* and indicates a large locus arising from great re-iteration of the ribosomal RNA genes (Flavell and Smith 1974). *L* is short for long and *S* for short

examination, and the same electrophoretic system also distinguishes allelic variation at *Glu-B1*. The mapping procedure is therefore far less time-consuming than mapping *Nor1* in conventional crosses for here, allelic variants must be distinguished at *Nor1* and this requires restriction-enzyme analysis, agarose-gel electrophoresis and autoradiography.

The screening of over 300 progeny gave recombination between *Nor1* and *Glu-B1* at 21%, or 22 cM (Table 2). In Fig. 7, this estimate has been combined with previous mapping data for storage protein genes and the centromere (Payne et al. 1982) to form a simple recombination map for chromosome 1B. *Nor1* and *Glu-B1,* although occurring on different arms of the chromosome, both lie close to the centromere in terms of recombination units. As *Glu-B1* and *Gli-B1* are only very weakly linked (Payne et al. 1982) the map predicts high recombination between *Nor1* and *Gli-B1*. The results differ greatly from physical measurements of chromosomes at mitosis since the ribosomal RNA genes at *Nor1* occur two-thirds of the length of the short arm away from the centromere (Riley et al. 1958) and by deduction, relatively close to *Gli-B1*. There are several other examples of differences between recombination and physical maps for wheat chromosomes in the literature. For instance, the awn inhibitor gene *B2* occurs on the long arm of chromosome 6B and is tightly linked (1.0% R) to the centromere (Sears 1966). However, Giorgi (1981), working with chromosome deficiency line of chromosome 6B showed that *B2* must occur on the terminal two thirds of 6BL and is therefore physically distant from the centromere. Dvorak and Chen (1983) did not detect any recombinations in 49 progeny between the ribosomal RNA genes on the short arm of chromosome 6B (*Nor2* according to our terminology) and the centromere even though the distance between them when measured by microscopy at metaphase amounted to 68% of the entire chromosome arm. There was, however, a 20% recombination between *Nor2* and the more distal *Gli-B2* even though the physical distance between them was relatively small. These results imply that chiasma formation occurs non-randomly on wheat chromosomes, being low in long chromosome segments adjacent to centromeres and high elsewhere.

The 1B chromosome with the deleted satellite is only about 15% shorter than a complete 1B chromosome (Riley et al. 1958; Sears 1954). In spite of this, male gametes containing the deficient chromosome only succeed in fertilizing 1 out of every 11 female gametes when they have to compete with male gametes containing the normal semikaryotype. However, male gametes lacking the entire 1B chromosome are even less effective compared to normal gametes and only 1 out of 31 grains produced will be monosomic for chromosome 1B (Sears 1954). Because of poor transmission frequencies the deletion line cannot be used directly in wheat breeding programmes although its effect, in the homozygous state, on bread-making quality is currently being determined. The line will probably be most useful in genetical analysis to determine whether genes on the short arm of chromosome 1B are located on the satellite or the non-satellited segment.

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References

Bennett MD, Smith JB, Simpson S, Wells B (1979) Intranuclear fibrillar material in cereal pollen mother cells. Chromosoma 71:289–332

Bennett MD, Smith JB, Ward JP, Finch RA (1982) The relationship between chromosome volume and DNA content in unsquashed metaphase cells of barley, *Hordeum vulgare* cv. 'Tuleen 346'. J Cell Sci 56:101–111

Dvorak J, Chen K-C (1983) Distribution of nonstructural variation between wheat cultivars along chromosome arm 6Bp: evidence from the linkage map and physical map of the arm. Genetics 106:325–333

Flavell RB, Smith DB (1974) The role of homoeologous group 1 chromosomes in the control of rRNA genes in wheat. Biochem Genet 12:271–279

Gerlach WL, Bedbrook J (1979) Cloning and characterisation of ribosomal RNA genes from wheat and barley. Nucleic Acids Res 7:1869–1886

Giorgi B (1981) A line with a deletion on the long arm of chromosome 6B isolated in *Triticum aestivum* cv. 'Chinese Spring'. Wheat Inf Serv 50:22–23

Heslop-Harrison JS, Bennett MD (1983) The spacial order of chromosomes in root-tip metaphases of *Aegilops umbellulata.* Proc R Soc London, Ser B 218:225–239

Holt LM, Astin R, Payne PI (1981) Structural and genetical studies on the high-molecular-weight subunits of wheat glutenin. 2. Relative isoelectric points determined by two-dimensional fractionation in polyacrylamide gels. Theor Appl Genet 60:237–243

Hutchinson J, Chapman V, Miller TE (1980) Chromosome pairing at meiosis in hybrids between *Aegilops* and *Secale* species: a study by in situ hybridisation using cloned DNA. Heredity 45:245–254

Jackson EA, Holt LM, Payne PI (1983) Characterisation of high molecular weight gliadin and low-molecular-weight glutenin subunits of wheat endosperm by two-dimensional electrophoresis and the chromosomal localisation of their controlling genes. Theor Appl Genet 66:29–37

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Leisle D, Kosmolak FG, Kovacs M (1981) Association of glume colour with gluten strength and gliadin proteins in durum wheat. Can J Plant Sci 61:149–151

Miller TE, Reader SM (1982) A major deletion of part of chromosome 5A of *Triticum aestivum.* Wheat Inf Serv 55:10–12

Payne PI, Law CN, Mudd EE (1980) Control by homoeologous group 1 chromosomes of the high-molecular-weight subunits of glutenin, a major protein of wheat endosperm. Theor Appl Genet 58:113–120

Payne PI, Corfield KG, Holt LM, Blackman JA (1981) Correlations between the inheritance of certain high-molecular-weight subunits of glutenin and bread-making quality in progenies of six crosses of bread wheat. J Sci Food Agric 32:51–60

Payne PI, Holt LM, Worland AJ, Law CN (1982) Structural and genetical studies on the high-molecular-weight subunits of wheat glutenin. 3. Telocentric mapping of the subunit genes on the long arms of the homoeologous group 1 chromosomes. Theor Appl Genet 63:129–138

Payne PI, Jackson EA, Holt LM, Law CN (1984a) Genetic linkage between endosperm storage protein genes on each of the short arms of chromosomes 1A and 1B in wheat. Theor Appl Genet 67:235–243

Payne PI, Holt LM, Jackson EA, Law CN (1984b) Wheat storage proteins: their genetics and their potential for manipulation by plant breeding. Philos Trans R Soc London, Ser B 304:359–371

Payne PI, Lawrence GJ (1983) Catalogue of alleles for the complex gene loci, *Glu-A1, Glu-B1,* and *Glu-D1* which code for the high-molecular-weight subunits of glutenin in hexaploid wheat. Cereal Res Commun 11:29–35

Riley R, Unrau J, Chapman V (1958) Evidence on the origin of the B genome of wheat. J Hered 3:91–98

Sears ER (1954) The aneuploids of wheat. Res Bull Mo Coll Agric Exp Stan 572:1–59

Sears ER (1966) Chromosome mapping with the aid of telocentrics. Proc 2nd Int Wheat Genet Symp, Lund 1963. Hereditas (Suppl) 2:370–381

Sears ER (1977) An induced mutant with homoeologous pairing in common wheat. Can J Genet Cytol 19:585–593