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Cytogenetic and molecular mapping of the wheat-*Aegilops longissima* chromatin breakpoints in powdery mildew-resistant introgression lines

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Abstract The amount of alien chromatin introgressed in eight wheat/*Ae. longissima Pm13* recombinant lines, involving breakpoints on the short arms of wheat chromosomes 3B and 3D, was evaluated by cytogenetic and molecular approaches. For each line the residual homologous synaptic ability of the recombinant chromosome in its proximal wheat and distal alien portion was estimated through meiotic analyses. Subsequently, telocentric and RFLP mapping were used to assess the genetic distance from the wheat centromere to the wheat/*Ae. longissima* breakpoints. One 3B recombinant line was distinguished from the other four by the chromosome pairing and telocentric mapping analyses. RFLP analysis succeeded in differentiating the remaining four lines into two groups. Chromosome pairing and telocentric mapping of the three 3D recombinant lines suggested that all had distinct breakpoints. However, the RFLP data could not discriminate between the two more proximal translocations. Physical locations for some RFLP loci were determined by a comparison of genotypes and C-banding karyotypes. This showed a considerable expansion of the genetic map compared to its physical length.

Key words Alien introgression · Homoeologous recombination · Telocentric mapping · RFLP mapping

Introduction

Utilisation of the wild gene resources of wheat represents a major but as yet relatively little exploited opportunity in genetic improvement. Well-established methodologies of "chromosome engineering" (Sears 1972) enable the transfer of chromosomal segments derived from species with homoeologous genomes, and by means of these techniques, various chromosomal segments bearing the gene *Pm13*, which conditions complete resistance to all known races of wheat powdery mildew, have been transferred from the $3S^l$ short arm of *Aegilops longissima* into common wheat, *Triticum aestivum* cv 'Chinese Spring' (Ceoloni et al. 1988). The new chromosomal locations of the introgressed segments were determined by monosomic and C-banding analyses to be on the short arm of chromosomes 3B and 3D (Ceoloni et al. 1992). Although C-banded karyotyping confirmed that a distal wheat segment had been replaced by one from *Ae. longissima* in all transfers, its precision was only sufficient to estimate the size of the alien segment in those involving 3D. A provisional further estimate of the amount of alien chromatin introgressed in the different recombinants was made by measuring the residual pairing ability of the wheat/*Ae. longissima* recombinant chromosomes with their parental homologues (Ceoloni et al. 1992). In the present paper, we describe a fuller cytogenetic characterisation of the recombinant lines, using a combination of chromosome pairing frequency, telocentric mapping and RFLP analysis. These methods have enabled us to distinguish the translocation breakpoints of certain of the lines.

Materials and methods

Genetic stocks

Pm13 carrying wheat/*Ae. longissima* transfers, the isolation and chromosomal localization of which have been previously described (Ceoloni et al. 1988, 1992), were employed in the present investigation. Of a total of eight lines, five (R1A, R4A, R5A, R6A and R1B) involve exchanges between $3S^l$ and 3BS and three (R2A, R2B and R1D) between $3S^l$ and 3DS. A further 3BS recombinant line (R3A) that was thought, on the basis of its C-banding karyotype, to carry zero doses of chromosome 3A and four of chromosome 3B, of which two are recombinant and two normal (unpublished data), was included only in some restriction fragment length polymorphism (RFLP) analyses.

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The 'Chinese Spring' (CS) aneuploid stocks used included ditelosomic (DT) 3BS and 3DS (Sears and Sears 1978) and the nullisomic-tetrasomic stocks N3BT3D and N3DT3B (Sears 1966a). Seeds of the $3S^1$ disomic addition line (TLDAG) and of the corresponding *Ae. longissima* accession (TL01) were obtained from M. Feldman, Rehovot, Israel. The $3S^1$ (3B) and $3S^1$ (3D) substitution lines into 'Chinese Spring' were selected from the self-fertilised progeny of monosomic 3B (or 3D) × TLDAG (C. Ceoloni, unpublished).

DNA probes and RFLP analysis

The wheat homoeologous group-3 RFLP clones employed were those used by Devos et al. (1992) and Devos and Gale (1993). They include: PSR123, PSR305, PSR383, PSR485, PSR547, PSR598, PSR649, PSR689, PSR902, PSR903, PSR907, PSR909, PSR910, PSR926, PSR930, PSR947, PSR968, PSR1060, PSR1158 and PSR1196. In addition, some heterologous group-3 probes were used, namely: barley probes PSB83 and PSB4 (D. A. Laurie, unpublished) and MWG582, MWG584 and MWG595 (Graner et al. 1991); oat probes CDO395 and CDO1174 (Heun et al. 1991); *T. tauschii* probe DO19 (Gill et al. 1991) and the rice chromosome-1 probe C146, which identifies a locus on wheat homoeologous group 3 (Kurata et al. 1994). The RFLP procedures followed those of Devos et al. (1992).

Meiotic pairing analyses and telocentric mapping

Chromosome pairing configurations were analysed in Feulgen-stained metaphase-I PMCs of (recombinant line × wheat DT) and (recombinant line × $3S^1$ substitution line) F_1 plants. The percentage of meiocytes in which the critical pair occurred either as an open bivalent or as two univalents was recorded. Except for one case, anthers were sampled from two to four plants of each given combination. Individual mildew-resistant (hemizygous for *Pm13*) F_1 plants derived from (recombinant line × DT) having 2n=41+t chromosomes were used to pollinate euploid, mildew-susceptible CS. The resulting testcross progenies were tested for both somatic chromosome number and for their reaction to powdery mildew infection. Tests for reaction to the pathogen, performed in a controlled environment, consisted of a first leaf stage infection followed, 10 days later, by the assessment of disease reaction based on a 0–4 scale. Infections were carried out using a mixture of Italian mildew biotypes characterised by their virulence on CS and lack of virulence on TLDAG. Crossover frequencies (%) were converted into genetic map distances using the Kosambi mapping function (Kosambi 1944).

Results

Pairing ability of the recombinant chromosomes

Pairing data from all of the transfer lines except R5A have been presented by Ceoloni et al. (1992). These data have now been extended by further observations and are summarised in Table 1, which also includes those relevant to line R5A. The proximal wheat segments in the 3B recombinants R1A, R4A and R1B supported a relatively similar amount of pairing with the 3BS telosome. R5A exhibited an intermediate value, while R6A showed a considerably lower percentage.

Pairing of the non-critical chromosomes of the complement was regular, except in line R5A, where 5–15% of the PMCs included a trivalent, which probably reflects the presence of a background translocation induced by the absence, earlier in the pedigree, of the pairing control gene *Ph1*. A survey of a sample of such PMCs at anaphase-telophase I revealed a considerable amount of various abnormalities, often present simultaneously. In 20% of these PMCs, misdivision of a complete chromosome was observed. This probably involved either one member of the critical pair or a univalent generated by the trivalent segregation.

A complementary pattern emerged from the pairing behaviour in the hybrids between the recombinants and the $3S^1$ (3B) substitution line. In these plants, the pairing frequency was highest in R6A, and lower, but at similar levels, in R1A, R4A and R1B. In R5A, the level was intermediate. For the 3D transfers, rather dissimilar values char-

Table 1 Percentage of meiotic metaphase I pairing of recombinant chromosomes bearing *Pm13* with wheat telo-3BS or -3DS and with the *Ae. longissima* $3S^1$ complete chromosome

	3B recombinants					
	Pairing with 3BS			Pairing with $3S^1$		
Recombinant line	Number of plants	Number of cells	% pairing	Number of plants	Number of cells	% pairing
R1A	3	186	41.0	1	55	49.1
R4A	4	348	44.8	2	166	45.8
R5A	3	268	33.6	4	260	61.2
R1B	2	195	43.4	3	193	43.5
R6A	2	203	8.6	3	146	69.1
	3D recombinants					
	Pairing with 3BS			Pairing with $3S^1$		
Recombinant line	Number of plants	Number of cells	% pairing	Number of plants	Number of cells	% pairing
R2A	3	175	23.4	2	149	63.5
R2B	2	185	53.5	2	162	32.8
R1D	3	375	38.4	2	108	55.7

Table 2 Telocentric mapping of the breakpoint of eight wheat/*Ae. longissima* introgression lines. Distribution of chromosome number and reaction to powdery mildew infection (*R* resistant; *S* susceptible) of the testcross populations euploid × (recombinant line × DT3BS [or 3DS] F_1). Genetic distances calculated from expected (42R, 41+tS and 42S, 41+tR) genotypes (see text)

Recombinant line	Total plants	Progeny types									% crossing-over	Map distance (cM ± SE)
		A	B	C	D	E	F	G	H	I	C + D	
		42 R	41+t S	42 S	41+t R	41 R	41 S	42+t R	42+t S	43 R	A + B + C + D	
R1A	58	32	3	16	1	3	–	3	–	–	32.7	39.1 ± 7.3
R4A	61	33	2	18	4	–	–	3	–	1	38.6	51.3 ± 7.5
R5A	73	26	6	12	4	1	5	14	5	–	33.3	40.2 ± 7.6
R1B	55	29	2	17	1	2	–	2	1	1	36.7	46.9 ± 7.8
R6A	62	43	4	4	1	1	3	6	–	–	9.6	9.8 ± 4.1
R2A	35	27	1	4	–	1	–	2	–	–	12.5	12.8 ± 5.9
R2B	52	27	4	19	2	–	–	–	–	–	40.4	56.1 ± 8.1
R1D	42	26	3	11	1	–	–	1	–	–	29.3	33.6 ± 7.8

acterised each line in both pairing combinations, with R2A showing the lowest level with 3DS and the highest with $3S^l$, and R2B the opposite.

Telocentric mapping

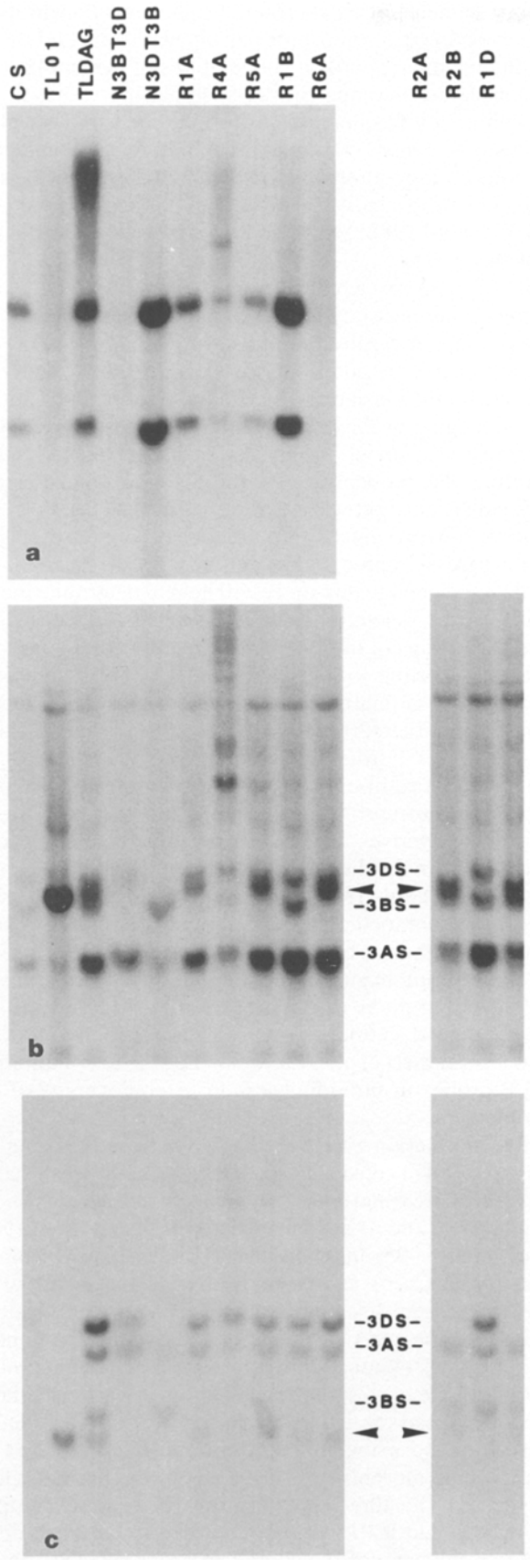
The absolute and relative frequencies of the various testcross progeny types are shown in Table 2. The use of the (recombinant line × DT) monotelodisomic plants as pollen donors evidently caused considerable gametic selection, since there is a prevalence of disomic individuals of both the parental and recombinant type over monotelodisomic ones as well as a noticeable lack of aneuploid types. This pattern was not true for R5A progeny in which chromosome number was more variable. However, this situation can be attributed to its aberrant meiotic pattern. It is also likely that at least some of the telosomes present in the R5A progeny resulted from a misdivision of univalents generated by the trivalent segregation.

Crossover (C.O.) frequency and map distance of the translocation breakpoint from the centromere was obtained from the proportion of recombinant individuals among the expected disomic and monotelodisomic genotypes (i.e. resistant 2n=42 and susceptible 2n=41+t as non-C.O., and susceptible 2n=42 and resistant 2n=41+t as C.O.) (Table 2). On the basis of this calculation, the map distance of the wheat/*Ae. longissima* translocation point from the 3B centromere in line R6A appears to be statistically different from those of the other 3B recombinants. On the other hand, values of R1A, R5A, R4A and R1B show no statistical difference, though exhibiting a two-by-two (R1A/R5A vs. R4A/R1B) closer similarity. Among the 3D recombinant lines, R2A showed the lowest C.O. value and R2B the highest, with that of R1D being intermediate. The R2A and R2B distances are statistically different.

Non-standard types were excluded from the estimate, since attribution of most of them to either the parental or recombinant classes could not be unequivocal. More than one alternative was equally possible to account for the origin of types other than the 2n=41 and 2n=43 resistant individuals, which probably carry a parental chromosome 3B (or 3D) since they lack a telosome in their karyotype. The exclusion of the non-standard types from the calculation of crossover frequency has, however, a negligible effect on map distance estimates, since their occurrence averages just 11% for the 3B recombinants (not including R5A) and only 8% when the 3D recombinants are included. For the R5A estimate, 34% of the population has been excluded, and thus the estimate is less precise.

RFLP analysis

A total of 29 RFLP clones was used in order to detect pattern differences among the recombinants and between these and the control lines. Seven of these probes detected RFLPs between TLDAG and CS, but only the 3 detecting the most distal loci on wheat chromosome arms 3BS and 3DS (Devos et al. 1992) generated a pattern in CS that was different from at least one of the recombinant lines. *Xpsr907-3B* was the most proximal locus at which a polymorphism was found to exist between line R6A, which lacked any hybridisation signal, and CS. PSR 907, a 3BS-specific probe (Devos et al. 1992) also showed no hybridisation with *Ae. longissima*. However, the remaining 3B recombinants gave a profile identical to that of CS (Fig. 1a). The more distally located *Xpsr1196-3B* locus was absent in the 3B recombinant lines R1A, R5A and R6A (Fig. 1b). Among the 3D recombinant lines, R2A and R1D lacked *Xpsr1196-3D*, but line R2B retained it. PSR1196 also detected an *Ae. longissima* locus that was present in the addition line profile (TLDAG) and in those of lines R6A, R1A, R5A, R2A and R1D, but not in lines R4A, R1B and R2B. Finally, the to-date most distally mapped wheat locus *Xpsr305-3B* turned out to be absent in all 3B recombinant lines, while *Xpsr305-3D* was present only in R2B among the 3D lines. *Xpsr305-3S*^{l} was present in all of the recombinant lines except R2B (Fig. 1c). These results locate the breakpoints of 3B and 3D recombinant chromosomes to three and two intervals, respectively (Figs. 2 and 3).



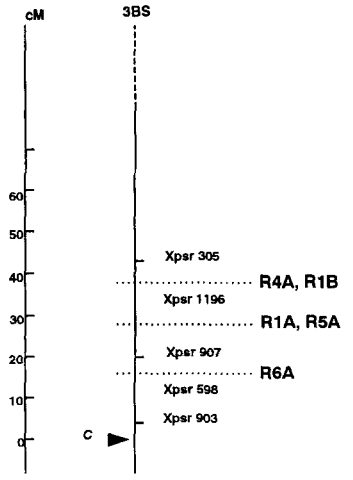


Fig. 2 A RFLP-based map of *Pm13* wheat/*Ae. longissima* 3BS recombinant lines. The breakpoint of each line has been arbitrarily placed (*dotted lines*) within the interval flanked by the discriminating wheat RFLP loci. Genetic map distances (in cM) and relative positions of wheat markers are from Devos and Gale (1993)

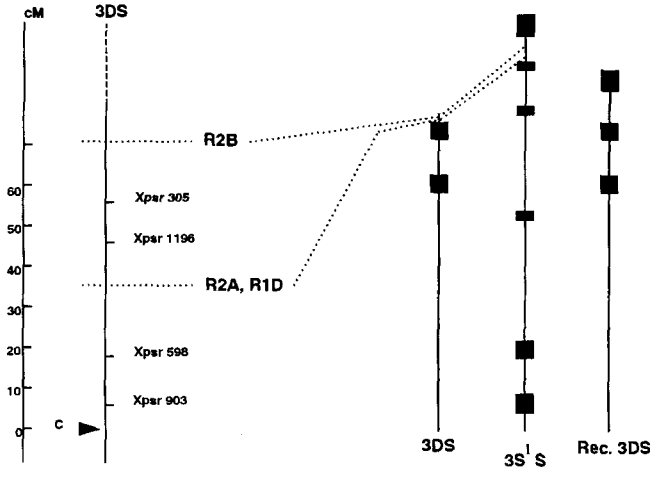


Fig. 3 RFLP mapping (*left*) and C-banding (*right*) of *Pm13* wheat/*Ae. longissima* 3DS recombinant lines. The arbitrary placement of the breakpoint (*dotted lines*) corresponds to an RFLP-based interval for recombinants R2A and R1D and to an unknown position beyond the most distal available RFLP marker (PSR305) for line R2B. A comparison is drawn with a physical map previously obtained by means of C-banding (Ceoloni et al. 1992)

Fig. 1a–c Analysis of short arm group-3 wheat/*Ae. longissima* *Pm13* recombinant lines with RFLP probes. Hybridisation of *Dra*I (**a**)- and *Hin*dIII (**b, c**)-restricted DNA of control and recombinant lines with probe (**a**) PSR907 (a chromosome arm 3BS-specific probe), (**b**) PSR1196 and (**c**) PSR305. Bands mapping to the 3B or 3D chromosomes are shown. $3S^l$ fragments are indicated by arrowheads

Discussion

The three cytogenetic and molecular approaches used here allowed us to draw largely consistent conclusions regarding the position of the wheat/*Ae. longissima* translocation breakpoint in the *Pm13* recombinant lines. The ranking of the amount of residual wheat chromatin among the 3D recombinants produced the same order, R2B>R1D>R2A, from both chromosome pairing and telocentric mapping, while the RFLP analysis could not distinguish between the latter two lines. On the other hand, RFLP was more efficient at discriminating between the breakpoints of the 3B lines R4A/R1B, and R1A/R5A, which were not well-resolved by the other methods. The anomalously high level of pairing between the recombinant R5A chromosome and chromosome $3S^l$ (and correspondingly low level between it and the 3BS telosome) is not readily explicable, given the RFLP-determined location of the translocation breakpoint. Poor correspondence between the levels of metaphase I pairing and recombination frequencies are well-documented (see Fu and Sears 1973; Barlow and Driscoll 1981; Curtis and Lukaszewski 1991; Curtis et al. 1991). Both desynapsis and gametic selection can contribute to the discrepancy. Since the observation of chromosome pairing is normally performed at metaphase I, desynapsis can lead to a misclassification of precociously released associations and thus to an underestimate of the actual pairing frequencies. The occurrence of desynapsis may be favoured by a heterozygosity for homoeologous segments in the distal region of the critical chromosomes (Gillies and Lukaszewski 1989; Curtis et al. 1991), as in the present experiment and in previous ones involving rye (Driscoll and Sears 1965) and *Ae. umbellulata* (Sears 1966b) chromatin transferred into wheat. An estimate of the extent to which desynapsis may have distorted the chromosome pairing values in the (recombinant line × ditelo) F_1s was made by calculating the amount of pairing required to give the observed crossover values (Driscoll and Sears 1965; Sears 1966b), where only those gametes – both parental and recombinant – that received the normal complement of chromosomes are considered. This gives estimates of the percentage of the sporocyte populations in which pairing of the critical chromosome pair had occurred, and these closely resembled the values derived from meiotic observations. However, the expected C.O. frequencies calculated on this basis are generally lower than the observed ones, ranging from about 20% less (R2B) to 60% less (R6A). Similarly, an exact estimate of the amount of gametic selection cannot be made, though its contribution in reducing the spectrum of expected gametic classes, and thus in inflating the recombination frequencies, is probably considerable in telocentric mapping experiments where the aneuploid (41+t) F_1 is used as male in the testcross to the euploid.

The scoring of backcross populations obtained using the F_1s as the female parent may provide estimates of map distances which better reflect the pairing frequency, since in wheat there is usually little selection on the female side against gametes of an aberrant chromosome constitution. However, since chromosome pairing was evaluated by analysing the microsporocyte populations of the 2n=41+t resistant plants, a comparison of such pairing values to the recombination frequencies concerning the same germline seems to be a more correct approach. In fact, conspicuous differences in recombination frequency between the two sexes have repeatedly been shown (Carlson 1977; Singh and Shepherd 1988; Vizir and Korol 1990; De Vicente and Tanksley 1991).

RFLP analyses, which do not suffer from the above limitations inherent to cytogenetic mapping approaches, allowed a higher resolution in discriminating the *Pm13* 3B recombinants. In addition, the identification of RFLP markers for the introgressed *Ae. longissima* segment allows for the tagging of *Pm13* in pyramiding experiments. Alien introgressed segments are conserved as linkage blocks, and therefore the probably large (homologous) genetic and physical distance between resistance gene and marker is unimportant. At present the agronomic effect of even the shortest introgression product has not been fully evaluated, but the data gathered in this study will help to determine the location of any deleterious effect associated with the presence of portions of this alien chromosome arm.

Even resorting to RFLPs, we could only assign each breakpoint to a relatively large interval, spanning, for instance, more than 20 cM in the case of 3D recombinants R2A and R1D. Further resolution is limited at the moment by the lack of additional markers in the critical, distal portion of the chromosomes concerned. This fact, which generally characterises all of the wheat and related species RFLP maps in the distal chromosome regions (Chao et al. 1989; Wang et al. 1991) appears particularly marked for the group-3 homoeologues (Devos and Gale 1993). A non-random distribution of the markers assayed can be one factor contributing to such a picture, but new types of markers, including microsatellites (Devos et al. 1994) and sequence-tagged site polymerase chain reaction (STS PCR) products (Talbert et al. 1994), may be able to complement RFLP probes in providing a more even coverage of the chromosome.

Recombination events are known to be clustered in the distal regions of cereal chromosomes, resulting in the compression of proximal and expansion of distal regions on genetic maps (Linde-Laursen 1982; Dvorak and Chen 1984; Snape et al. 1985; Jampates and Dvorak 1986; Gustafson et al. 1990; Curtis and Lukaszewski 1991; Lukaszewski 1992). The same discrepancy has also emerged in the comparison of the physical maps of the *Pm13* recombinant chromosomes obtained through C-banding (Ceoloni et al. 1992) and the corresponding genetic maps reported here. Such a comparison could be carried out only for the 3D transfers, whose recombinant chromosomes showed C-banding polymorphism with respect to the normal wheat karyotype. The three translocation breakpoints of lines R2A, R1D and R2B were all localised to the most distal euchromatic band of the short arm of wheat 3D (Ceoloni et al. 1992), a segment whose relative size is only a few percent of the total arm length. This segment, which is only

30 cM from the centromere, has a genetic length of at least 40 cM (Fig. 3). Very small variations in the size of the subterminal euchromatic band of the recombinant 3Ds of the three transfer lines were observed, but their quantification, even in a large sample, was not possible (Ceoloni et al. 1992). Nevertheless, these differences result in conspicuous variation in both chromosome pairing (Table 1) and recombination (Table 2 and Fig. 3) frequencies. C-banding could not discriminate between normal and recombinant 3B chromosomes, so other physical mapping strategies need to be resorted to. Genomic *in situ* hybridisation (Schwarzacher et al. 1992) was unsuccessful, due to extensive cross-hybridisation between wheat and *Ae. longissima* DNA. As an alternative, a modified version of the phenol emulsion reassociation technique, recently used for isolating species-specific sequences in plants (Aswidinnoor et al. 1991; Clarke et al. 1992), is being attempted, together with other approaches, to develop probes for physical mapping.

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