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Pairing and recombination between individual chromosomes of wheat and rye in hybrids carrying the *ph1b* mutation

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Abstract Wheat-rye chromosome associations at metaphase I studied by Naranjo and Fernández-Rueda (1991) in *ph1b* ABDR hybrids have been reanalysed to establish the frequency of pairing between individual chromosomes of wheat and rye. Wheat chromosomes, except for 2A and 2D, and their arms were identified by C-banding. Diagnostic C-bands and other cytological markers such as telocentrics or translocations were used to identify each one of the rye chromosomes and their arms. Both the amount of telomeric C-heterochromatin and the structure of the rye chromosomes relative to wheat affected the level of wheat-rye pairing. The degree to which rye chromosomes paired with their wheat homoeologues varied with each of the three wheat genomes; in most groups, the B-R association was more frequent than the A-R or D-R associations. Recombination between arms 1RL and 2RL and their homoeologues of wheat possessing a different telomeric C-banding pattern was detected and quantified at anaphase I. The frequency of recombinant chromosomes obtained supports the premise that recombination between wheat and rye chromosomes may be estimated from wheat-rye pairing.

Key words Homoeologous pairing · Recombination · Wheat · Rye · C-banding

Introduction

Suppression of homoeologous pairing in wheat is largely under the control of the *Ph1* gene located on chromosome 5B (Sears and Okamoto 1958; Riley and Chapman 1958). In the absence of *Ph1*, as a result of either nullisomy for chromosome 5B or the presence of the *ph1b* mutation (Sears 1977), pairing can occur between the homoeologous chromosomes of the three wheat genomes. Similarly, also in the absence of *Ph1*, homoeologous pairing between wheat and alien chromosomes can occur in hybrids between wheat and related species or derivatives from hybrids carrying one or more alien chromosomes. Recombination following the genetic induction of homoeologous pairing has been used often to transfer useful genetic material from alien species into wheat chromosomes (see reviews by Gale and Miller 1987; Islam and Shepherd 1991). The expected frequency of recombination between wheat and alien chromosomes is of direct interest for those breeding programmes since it will imply the likelihood of success in achieving the transfer of useful traits from those related species.

The recent introduction of genomic in situ hybridization (GISH) has enabled the degree of overall pairing between wheat and rye chromosomes in different wheat-rye combinations to be recognized (King et al. 1994; Miller et al. 1994; Fernández-Calvín et al. 1995). A major disadvantage of GISH is that individual chromosomes cannot be distinguished.

Naranjo et al. (1987, 1988a,b) have shown that C-banding can be used to identify all of the wheat chromosomes, and their arms, except for 2A and 2D, at meiosis in hybrids between wheat and rye. Subsequently, Naranjo and Fernández-Rueda (1991), using stocks of rye with cytological markers such as diagnostic C-bands, telocentrics and translocations, also identified all of the rye chromosomes in the wheat-rye hybrids. This enabled them to examine in detail the degree of pairing between individual rye chromosomes and individual wheat chromosomes. The results provided very useful information on the homoeologous relationships of rye chromosomes and those of wheat and also provided evidence of the occurrence of several translocations during the evolution of the rye genome, which were subsequently confirmed by molecular marker analysis (Devos et al. 1993).

Given the recent interest in rye introgression and extent of rye chromosome pairing studied using GISH, we have reanalysed the original pairing data of Naranjo and Fernández-Rueda (1991), which were reported summed

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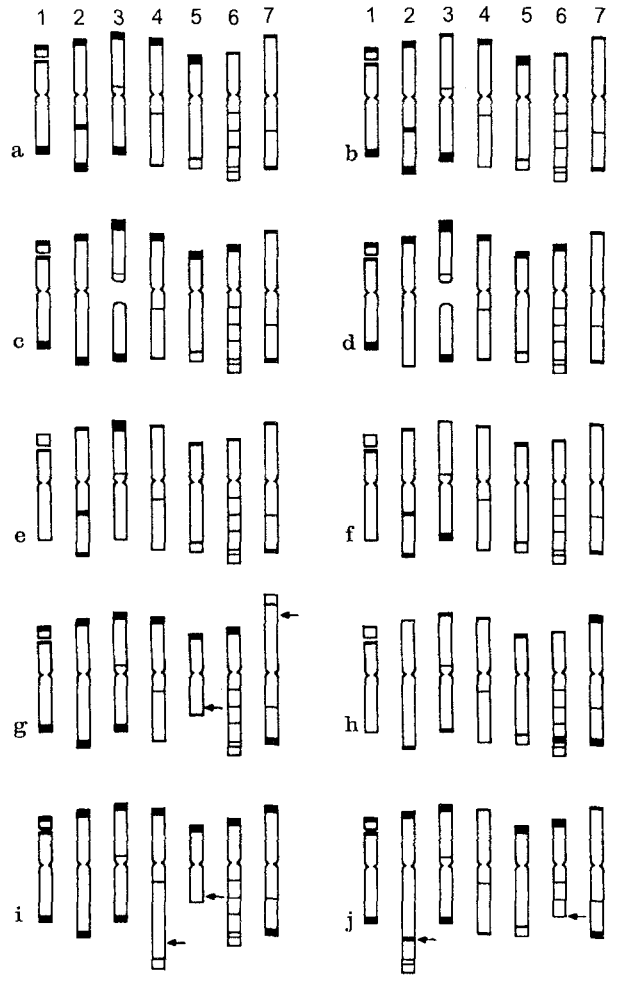

Fig. 1a–j C-banding pattern of the rye chromosomes present in ten *ph1b* ABDR hybrid types. **a, b, e, f** and **h** hybrids with normal chromosome structure. **c–d** hybrids with telocentrics 3RS and 3RL. **g, i** and **j** hybrids with translocation T282 W (5RL/7RS), T501 W (4RL/5RL) and T242 W (2RL/6RL), respectively. *Arrows* indicate translocation points

over all chromosomes within a homoeologous group, in order to determine the pattern of pairing between rye chromosomes and individual wheat chromosome of each genome. Also, where pairing has been observed to be frequent, and parental and recombinant chromosomes of wheat and rye can be cytologically distinguished by C-banding at anaphase I, the degree of recombination between the rye chromosome and its wheat homoeologues has been determined and these results have been compared with metaphase I pairing frequencies.

Material and methods

The ten different types of *ph1b* ABDR hybrids, denominated *a-j*, that were obtained by Naranjo and Fernández-Rueda (1991) were reanalysed.

The C-banding procedure and the criteria used to identify the arms of individual chromosomes of wheat and rye at meiosis are also described in Naranjo and Fernández-Rueda (1991). Figure 1 gives a diagrammatic representation of both the structure and C-banding pattern of the rye chromosomes present in the ten types of hybrids analysed. Both arms of each rye chromosome could be positively identified in all pollen mother cells (PMCs) analysed in the following types of hybrids: chromosomes 1R and 5R in all hybrids, chromosome 2R in hybrids *a, b, d, e, f, h* and *j*, chromosome 3R in hybrids *b, c, d, e* and *f*, chromosomes 4R and 6R in hybrids *a, h, i* and *j*, and chromosome 7R in hybrids *a, b, c, d, e, f, g* and *j*.

One to three plants were analysed for each type of hybrid. Wheat-rye associations were scored in a sample of generally more than 500 PMCs for each type of hybrid. All of the chromosome associations present in a PMC, including wheat-wheat, wheat-rye and rye-rye, were only scored in 100 PMCs of each hybrid. Anaphase I was analysed in all of the hybrids except for type *h*, and a total number of 747 PMCs were scored.

Results

Pairing at metaphase I occurred between chromosomes of wheat, between chromosomes of wheat and rye (Fig. 2a, b), and occasionally between non-homologous chromosomes of rye. The frequency of pairing between arms of individual chromosomes of wheat and rye is shown in Table 1. The type of hybrids where such chromosome associations could be identified is also indicated in Table 1. In group 2 the A-R and D-R associations could not be distinguished from one another and were pooled. As reported earlier (Naranjo and Fernández-Rueda 1991), the degree of pairing shown by a given rye chromosome depended on its telomeric C-banding. Thick telomeric blocks strongly reduced the level of pairing with the exception of the 1RL-1BL association, which was probably due to the presence of a medium-sized C-band in the telomere of 1BL.

Rye chromosomes paired on average with the B genome chromosomes more frequently than with those of the A and D genomes. The frequency of B-R associations was approximately the sum of A-R plus D-R association frequencies for the arms 1RL, 2RL and 3RS, which in addition to 4RS and 5RL showed the highest pairing frequencies. Associations 1RL-1BL, 2RL-2BL and 5RL-4BL exceeded 10% in some plants. Chromosome arm 4AS preserves no genetic colinearity with 4RS because of the existence of a pericentric inversion on chromosome 4A (Naranjo 1990; Liu et al. 1992). This structural difference accounts for the lack of pairing between these two arms. The 5RL arm carries a translocated segment from 4RL; its structure is therefore similar to that of 5AL that carries a translocated segment from 4AL (Naranjo et al. 1987; 1988a,b; Liu et al. 1992). The constitution of 5RL and 5AL may explain why the frequency of the 5RL-5AL association was not much lower than that of 5RL-4BL association. Pairing between the remaining arms of rye and any of their wheat homoeologues showed a frequency lower than 2%.

The average number of wheat-wheat, wheat-rye and rye-rye associations per cell is given in Table 2. The A-B and B-D associations were pooled because they could not be distinguished from one another in group 2 chromosomes. Chromosome arms 4AL, 5AL and 7BS are known to be involved in two interchanges in such a way that 5AL

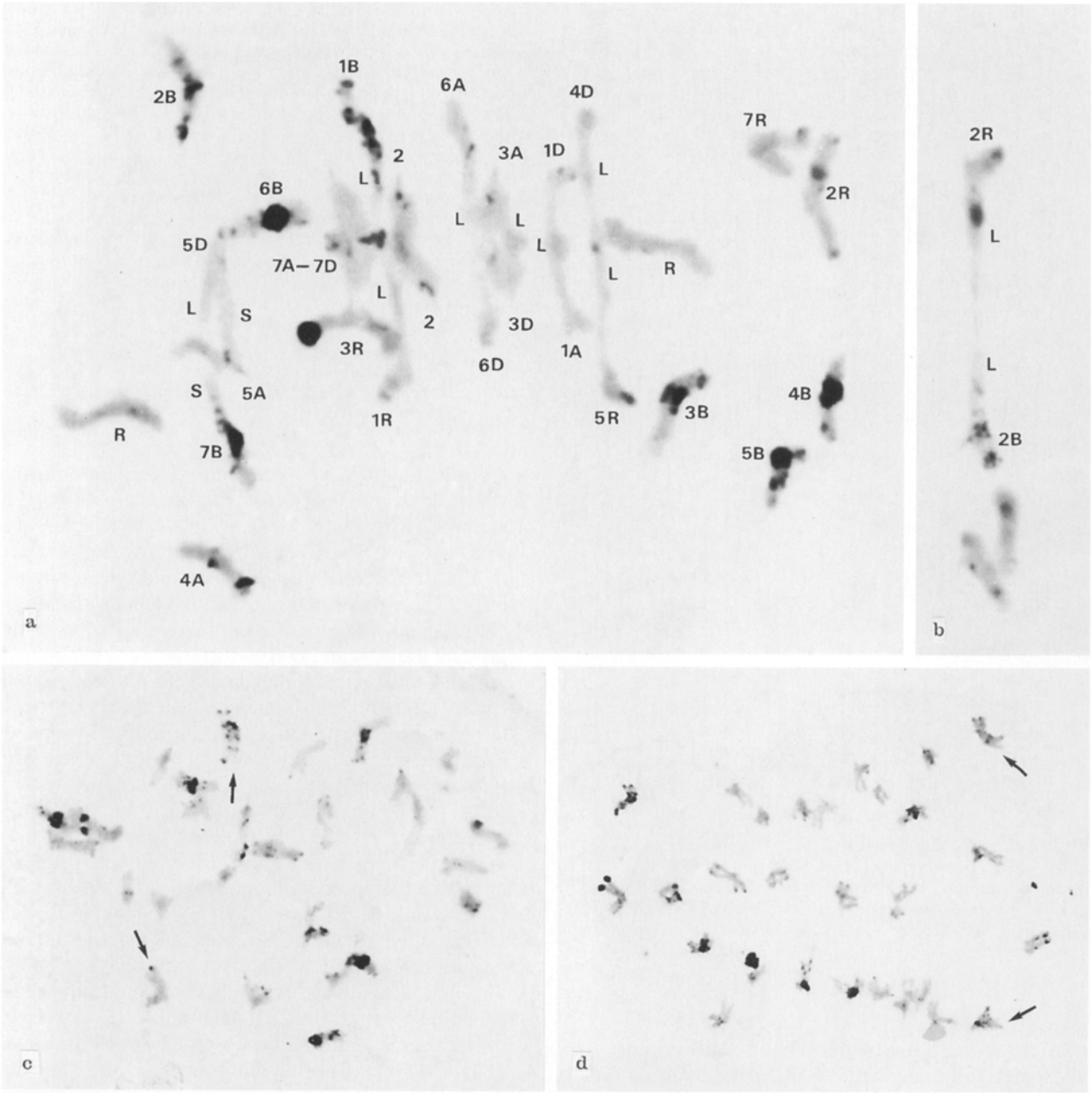

Fig. 2a–d C-banding of chromosomes at metaphase I and anaphase I in *ph1b* ABDR hybrids of types *e* and *f*. **a** Metaphase I cell showing different wheat-wheat associations and wheat-rye associations 1BL-1RL and 4DL-5RL. Chromosomes 2A and 2D (2), as well as 4R and 6R, could not be distinguished from one another. In the ring bivalent 7A-7D individual chromosomes 7A and 7D could not be identified. **b** Association between the arms 2BL and 2RL. **c–d** Anaphase I cells with single recombinant chromosomes between 1BL and 1RL and between 2BL and 2RL, respectively. *Arrows* point to the telomere of the exchanged chromatids

carries a translocated segment from 4AL, 4AL carries a translocated segment from 7BS and 7BS carries a translocated segment from 5AL (Naranjo et al. 1987, 1988a,b; Liu et al. 1992; Anderson et al. 1992). Consequently, 5AL-4DL and 7BS-5DL associations were included in the type A-D group, 5AL-4BL, 7BS-5BL and 7AS-4AL, in the type A-B, and 4AL-7DS in the type B-D. Some rare associations between wheat chromosomes without any known genetic affinity were also observed (mean, 0.02 per cell). These were not included in any of the wheat-wheat combinations of Table 2. The frequency of the different pairing types varied between hybrids, as shown in Table 1. The number of wheat-rye associations correlated positively with the total number of associations per cell, but the *r* value was not significant at the 5% level of significance ($r=0.61$, $0.05<P<0.10$, $df=8$).

To establish whether or not there is a close correspondence between the frequency of wheat-rye pairing at metaphase I and the frequency of recombination between chromosomes of wheat and rye, we determined the frequency of wheat-rye recombinant chromosomes at anaphase I for

Table 1 Frequency (%) of pairing between chromosome arms of wheat and rye in *ph1b* ABDR hybrids with C-banding polymorphism for the R genome

Rye arm	Telomere C-band[a]	Hybrids	Wheat chromosome arm									
			1AS	1DS	1BS	Others						
1RS	++	*a+b+c+d+g+i+j*	0.2	0.1	0.4	0.1						
	–	*e+f+h*	1.6	0.7	0.2	0.0						
			1AL	1DL	1BL	Others						
1RL	++	*a+b+c+d+g+i+j*	0.7	0.6	9.2	0.0						
	–	*e+f+h*	6.4	4.8	13.7	0.0						
			2AS +2DS	2BS	Others							
2RS	++	*a+b+d+j*	0.0	0.0	0.0							
	+	*e+f*	0.2	0.0	0.2							
	–	*h*	0.1	0.1	0.3							
			2AL +2DL	2BL	Others							
2RL	++	*a+b*	1.1	0.7	0.1							
	+	*e+f+h*	5.5	3.6	0.1							
	–	*d*	13.4	12.2	0.2							
			3AS	3DS	3BS	Others						
3RS	++	*c+d+e*	0.0	0.0	0.0	0.4						
	+	*b*	0.4	0.7	1.3	0.2						
	–	*f*	1.3	1.2	2.8	0.2						
			3AL	3DL	3BL	6AL	6DL	6BL	Others			
3RL	++	*b+c+d+f*	0.0	0.0	0.3	0.0	0.0	0.1	0.1			
	–	*e*	0.2	0.0	0.2	0.2	0.0	1.8	0.0			
			4AS	4DS	4BS	Others						
4RS	++	*a + i*	0.0	0.0	0.1	0.0						
	+	*h+j*	0.0	2.3	3.0	0.0						
			4AL	4DL	4BL	6AS	6DS	6BS	Others			
4RL	+	*a + j*	0.0	0.0	0.1	0.1	0.1	1.6	0.2			
	–	*h*	0.0	0.0	0.0	0.1	0.1	1.5	0.1			
	–	*i*[b]	0.0	0.2	0.0	0.0	0.0	0.5	0.2			
			5AS	5DS	5BS	Others						
5RS	++	*a+b+c+d+g+i+j*	0.0	0.1	0.1	0.0						
	+	*e+f+h*	0.2	0.4	0.4	0.0						
			5DL	5BL	5AL	4DL	4BL	Others				
5RL	–	*a+b+c+d+e+f+h*	0.0	0.3	8.6	6.1	10.4	0.0				
	–	*g*[c]	0.1	1.1	8.5	5.9	12.2	0.1				
	–	*i*[b]	0.2	0.5	4.3	6.2	6.9	0.7				
			6AS	6DS	6BS	Others						
6RS	++	*i + j*	0.0	0.0	0.1	0.0						
	+	*a + h*	0.0	0.0	0.0	0.0						
			6AL	6DL	6BL	3AL	3DL	3BL	7AL	7DL	7BL	Others
6RL	–	*a + h + i*	0.0	0.0	0.1	0.2	0.0	0.0	0.2	0.1	0.6	0.2
	–	*j*[d]	0.0	0.0	0.8	0.0	0.0	0.8	0.0	0.0	0.8	0.5
			7AS	7DS	7BS	5DL	5BL	Others				
7RS	+	*a+b+c+d+e+f+j*	0.0	0.0	0.2	1.5	1.5	0.1				
	–	*g*[c]	0.0	0.0	0.5	0.1	0.2	0.1				
			7AL	7DL	7BL	2AS + 2DS	2BS	Others				
7RL	++	*g+j*	0.0	0.0	0.0	0.0	0.3	0.2				
	+	*a+b+c+d+e+f*	0.0	0.1	0.0	0.4	0.4	0.2				

[a]++, Prominent C-band; +, medium-sized or thin C-band; –, no C-band
[b, c, d]Pairing involved the translocated segment of the corresponding arm of translocation 4RL/5RL, 5RL/7RS, 2RL/6RL, respectively

Table 2 Mean number of wheat-wheat, wheat-rye, rye-rye and total chromosome arm associations at metaphase I and range of variation in PMCs from wheat-rye hybrids carrying the *ph1b* mutation

Association type	Mean	Range between hybrids
Wheat-wheat (A–B–D)	0.59 ± 0.02	0.27–1.02
(A–D)	6.80 ± 0.06	5.75–7.70
(A–B+B–D)	2.83 ± 0.05	2.19–3.45
Wheat-rye	0.67 ± 0.02	0.45–0.91
Rye-rye	0.04 ± 0.01	0.02–0.08
Total	11.52 ± 0.08	10.01–13.25

the long arms of chromosomes of groups 1 and 2. The frequency of recombination obtained in this way was compared with the frequency of wheat-rye pairing. Arms 1RL and 2RL, which paired with a relatively high frequency, bore a different telomeric heterochromatin constitution than that of their wheat homoeologues in some plants. This allowed us to detect cytologically wheat-rye recombination at anaphase I, which should involve distal chromosome regions as deduced from the position of most of the metaphase I bonds.

Wheat chromosome arms 1AL and 1DL are unmarked at the telomere. In hybrids *a, b, c, d, g, i* and *j*, the telomeric heterochromatin block of 1RL (Fig. 1) was more prominent than that of 1BL. Therefore, recombination between 1RL and 1AL or 1DL and between 1RL and 1BL could be cytologically observed at anaphase I. Single recombinant chromosomes with different telomeric C-banding in the two chromatids and double recombinants that had exchanged both chromatids could be distinguished from the parental chromosome type. In hybrids *e, f* and *h* the telomere of 1RL was unbanded. Anaphase I was analysed in plants *e* and *f*. Single recombinants between 1RL and 1BL were detected by the presence of a telomeric C-band on only one of the two chromatids (Fig. 2c).

Chromosome arm 2RL with an intercalary C-band could be distinguished unambiguously at anaphase I in hybrids *a, b, e,* and *f* (Fig. 1). In these plants 2RL also carried a telomeric C-band. Wheat arms 2AL, 2DL and 2BL are unbanded at the telomere. Single and double recombinants between 2RL and 2AL or 2DL, as well as single recombinants between 2RL and 2BL, were detected in these plants by segregation for the telomeric C-banding pattern (Fig. 2d).

The frequencies of wheat-rye recombination detected at anaphase I between the long arms of chromosomes of groups 1 and 2 are given in Table 3. As expected, the double recombinant chromosomes appeared at a much lower frequency than single recombinants. The length of the exchanged segment could not be determined.

The metaphase I pairing frequencies were compared with the frequencies of recombination measured at anaphase I using a contingency χ^2 test as it is shown in Table 4. Differences between pairing and recombination frequencies were not significant.

Discussion

The hybrids analysed here displayed a higher level of homoeologous pairing between chromosomes of wheat and between chromosomes of wheat and rye than that observed by Miller et al. (1994) in 5B-deficient ABDR hybrids. The presence of the pairing promoter gene located on 5BS in the *ph1b* hybrids and its absence in hybrids lacking chromosome 5B could account for such a difference (Naranjo et al. 1988b). Between hybrids variation in the degree of pairing (Table 2) may be attributable at least in part to differences in the parental rye genotypes used. We found that the frequency of the wheat-rye association was not closely correlated to the total number of bonds per cell; this may be derived from the existence of polymorphism for telomeric C-bands, since it was apparent that telomeric heterochromatin had a negative effect on wheat-rye pairing (Table 1). The occurrence of non-homologous pairing between rye chromosomes could be due to the presence of dupli-

Table 3 Frequency (%) of recombination between the arms 1RL and 2RL and their wheat homoeologues detected at anaphase I in *ph1b* ABDR hybrids

Rye arm	Hybrids (Telomere C-band[a])	Recombinant type	Wheat arm[b]		Number of PMCs
			1AL or 1DL	1BL	
1RL	*a+b+c+d+g+i+j*	Single	1.3	11.2	547
	(++)	Double	0.0	0.9	
	e+f	Single	–	11.5	200
	(–)	Double	–	0.0	
			2AL or 2DL	2BL	
2RL	*a+b*	Single	1.6	0.5	186
	(++)	Double	0.0	0.0	
	e+f	Single	4.5	6.0	200
	(+)	Double	0.5	0.0	

[a] As in Table 1
[b] –, Recombinants could not be detected

Table 4 Values of pairing at metaphase I between the arms 1RL and 2RL and their wheat homoeologues are compared with the observed numbers of 1RL-wheat and 2RL-wheat recombinants at anaphase I in *ph1b* ABDR hybrids

Rye-wheat pairing or recombination	Number of PMCs		Contingency χ^2 (Hybrids)
	Metaphase I	Anaphase I	
1RL-(1AL/1DL)	47	7	$\chi^2_2 = 4.57$
1RL-1BL	341	66	$(a+b+c+d+g+i+j)$
Not observed	3321	474	
1RL-1BL	262	23	$\chi^2_1 = 0.72$
1RL-(1AL/1DL)+Not observed	1656	177	$(e+f)$
2RL-(2AL/2DL)	12	3	
2RL-2BL	8	1	$(a+b)$
Not observed	1123	182	
2RL-(2AL/2DL)	105	10	$\chi^2_2 = 2.92$
2RL-2BL	69	12	$(e+f)$
Not observed	1744	178	

cated segments, the occurrence of which has been postulated in haploids of rye (de Jong et al. 1991; Santos et al. 1994; and references therein).

The homoeologous relationships of rye chromosome arms to wheat arms as deduced from pooled frequencies of A-R, B-R and D-R pairing associations (Naranjo and Fernández-Rueda 1991) were subsequently confirmed by comparing the genetic maps of wheat and rye constructed from restriction fragment length polymorphism (RFLP)-markers (Devos et al. 1993). The only disagreement concerned the proposal of Naranjo and Fernández-Rueda (1991) that chromosome 4R carried a pericentric inversion. This had been deduced from earlier reports on the location of loci *Amp-2* (Koebner and Martin 1989) and *Xpsr144* (Sharp et al. 1989) in wheat and rye chromosomes. However, later, Liu et al. (1992) reported that *Amp-R2* is located on 4RS instead of 4RL, and that the location of *Xpsr144* had not been determined in rye. Hence, there is now no evidence supporting the existence of such a pericentric inversion on chromosome 4R. Thus, the efficiency of C-banding to carry out a correct identification of chromosomes involved in wheat-rye associations was demonstrated.

Chromosomes of rye paired with chromosomes of the B genome of wheat more frequently than with chromosomes of the A and D genomes except in the short arm of group 1 and 5 chromosomes (Table 1). The associations between arms of different homoeologous groups that are indicated in Table 1 occurred between homoeologous segments that had undergone some rearrangement in the evolution of rye (Naranjo and Fernández-Rueda 1991; Devos et al. 1993). In these associations, B-R pairing was also more frequent than A-R or D-R pairing. Among wheat chromosomes, homoeologues of the A and D genomes showed preferences to pair with each other (Table 2). This preferential pairing between chromosomes of the A and D genome probably results in such chromosomes having fewer opportunities to pair with rye chromosomes than chromosomes of the B genome. Moreover, the possibility exists that the R genome is related more closely to the B than to the A or D genomes. The arms 2RS, 3RS, 4RL, 6RS, 6RL, 7RS and 7RL, which are involved in evolutionary translocations, showed a very low frequency of pairing with wheat chromosomes. Chromosome arm 5RL carries a translocated segment from 4RL and paired at a relatively high frequency, however. This behaviour suggests that the translocated segment of 5RL may be quite long.

Among the rye arms 1RS, 1RL, 2RL, 3RS, 4RS and 5RS, all of which seem to have a comparable structure to that of their wheat homoeologues, 1RL and 2RL paired much more frequently than the others. Frequencies of 1RL-wheat and 2RL-wheat associations at metaphase I (Table 1) closely paralleled the frequencies of recombinants detected at anaphase I (Table 3). This result is in agreement with an earlier study of Naranjo et al. (1989) that showed a good correspondence between homoeologous pairing and recombination for the long arm of group 1 chromosomes in different wheat-rye hybrids. Thus, the frequency of wheat-rye pairing may be used as an estimate of the recombination between chromosomes of rye and wheat.

The results from the present work have two main implications for the use of controlled introgression of useful genes from alien chromosomes by induction of homoeologous pairing. First, the existence of structural modifications in the alien chromosome from which chromatin should be transferred to wheat may strongly reduce the possibility of recovering the desired recombinants. Second, the probability of achieving the desired transfer of genes depends on which genome of wheat the alien genes are being introduced into.

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