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Preferential Occurrence of Wheat-Rye Meiotic Pairing Between Chromosomes of Homoeologous Group 1

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Summary. Wheat-rye homoeologous pairing in both ABRR and (0–7)A(0–7)BRR plants takes place preferentially between homoeologous chromosomes of group 1. This suggests either a much greater affinity between wheat and rye chromosomes for this group or more efficient pairing initiation because of common nucleolar organizer activities. 1A–1R associations were more frequent than 1B–1R associations though in both cases pairing was restricted mostly to the long arms. From the variation in these particular chromosome arms the three following factors might hinder the wheat-rye pairing: regular homologous pairing of rye chromosomes, presence of prominent telomeric C-bands in rye chromosomes or occurrence of wheat-wheat homoeologous pairing.

Key words: Wheat-rye – Pairing – Homoeologues – Group 1 – C-banding

Introduction

Studies performed in different wheat-rye chromosome combinations have made clear that rye chromosomes induce homoeologous pairing (Miller and Riley 1972; Riley et al. 1973; Lelley 1976a; Bernard and Bernard 1978; Jouve and Montalvo 1978; Naranjo et al. 1979; Jouve et al. 1980; Naranjo and Palla 1982). This promoter activity seems to affect both wheat-wheat and wheat-rye pairing. The C-banding technique allows the distinction of wheat and rye chromosomes and both homoeologous pairing types have been observed, although the wheat-rye pairing frequency is low. (Lelley 1976b; Mettin et al. 1976; Schlegel 1977; Dhaliwal et al. 1977; Naranjo et al. 1979; Naranjo and Lacadena 1980; Jouve et al. 1980; Naranjo and Palla 1982). By comparing the results obtained by Naranjo et al. (1979) in ABRR and ABRRR hybrids and those of Mettin et al. (1976) and Schlegel (1977) in ABDR hybrids, a dosage effect of rye genomes on wheat-rye pairing is suggested. However, significant variation of wheat-rye pairing frequencies has also been detected in different genotypes with the same genome constitution ABRR (Jouve et al. 1980; Naranjo and Palla 1982) as well as in plants with the constitution (0–7)A(0–7)BRR (two sets of rye chromosomes and a variable number (6, 7 or 8) of wheat chromosomes, in which the percentage of PMCs showing wheat-rye pairing ranged from 0.67 to 19.33 (Naranjo and Lacadena 1980). Such a variation indicates that in addition to the number of rye genomes other factors greatly influence wheat-rye pairing levels.

It is obvious that finding conditions under which more wheat-rye recombination can be obtained is important for breeding-related programs. In this study, wheat-rye pairing is analyzed using a C-banding procedure in plants with the genome constitutions ABRR and (0–7)A(0–7)BRR and includes some of the factors affecting it.

Materials and Methods

Two series of plants were used: i) Three plants belonging to the offspring of the cross "Cachirulo" triticale (AABBRR)× *Secale cereale* cv. "Ailés" (RR) with genome constitution ABRR (2n=28). ii) Seven plants from the backcross of ABRR hybrids (sisters of the afore mentioned three plants)× *S. cereale* cv. "Ailés". These plants, with chromosome constitution (0–7)A(0–7)BRR, had the chromosome numbers 2n=20 (plant 2E16-2), 2n=21 (plants 2E15-1, 2E2, 2E1, 2E11-1 and 2E6-1) and 2n=22 (plant 2E10); that is, 14 rye chromosomes as recognized by their C-banding pattern, plus 6, 7 or 8 A and/or B wheat chromosomes. This material has also been studied by Naranjo and Lacadena (1980) for other purposes, and the present study is based on a re-examination of their slides.

Meiotic observations were made on PMCs from anthers fixed in 1:3 acetic alcohol and passed to 70% alcohol for 6–8 h before squashing. C-banding was applied according to Giráldez et al. (1979).

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Results

Identification of Chromosomes of Homoeologous Group 1

Chromosomes 1R, 1A and 1B were identified at metaphase I by means of C-banding. Chromosome 1R carries the nucleolar organizer and has a faint heterochromatic band proximal to the NOR. When the presence or absence of large telomeric C-bands in the short and the long arm is indicated by SH, Sh, LH and Lh respectively, the constitution of chromosome pair 1R in all three ABRR plants can be described as SHLH/ShLh. Chromosome SHLH derives from "Cachirulo" triticale (Naranjo and Lacadena 1982) and chromosome ShLh from rye (Ailés). In the seven (0–7)A(0–7)BRR plants the constitution was: ShLh/ShLh in plant 2E15-1, SHLh/ShLh in plants 2E2 and 2E1, ShLH/ShLh in plants 2E11-1 and 2E10, SHLH/ShLh in plant 2E6-1, and SHLH/Sh'LH in plant 2E16-2 (h' represents a band of intermediate width) (see Naranjo and Lacadena, 1980).

Chromosome 1A is submetacentric and shows the centromere faintly C-banded (Fig. 1a). Chromosome 1B (Fig. 1b) is one SAT chromosome and has a characteristic medium-sized band (thinner than that of the 1RLH arm, Fig. 1f) at the telomere of the long arm. Four faint bands in its pericentromeric region, two more faint bands, one at the satellite and the other approximately in the middle of the long arm, were also frequently observed. Both chromosomes were easily recognized and were present in the ABRR and in three (0–7)A(0–7)BRR plants (chromosome 1A in plant 2E11-1 and chromosome 1B in plants 2E15-1 and 2E10). Conclusions on their homoeology relation were based on the two following observations: i) When they did not pair with rye chromosomes in ABRR hybrids they appeared as univalents or formed an open (homoeologous) bivalent (Fig. 1e). In (0–7)A(0–7)BRR plants no 1A–1B bivalent could be observed because each plant only carried one wheat chromosome of group 1. ii) The rye chromosome taking part in the wheat-rye associations could be recognized as 1R in both ABRR and (0–7)A(0–7)BRR plants. The C-banding patterns described above are very similar to those described for these chromosomes by Gill and Kimber (1974) in *Triticum aestivum* cv. "Chinese Spring", and have also been identified by Gustafson and Krolow (1978) in tetraploid triticales.

Two translocated chromosomes belonging to group 1 and designated 1At and 1Bt were observed in four (0–7)A(0–7)BRR plants. Such chromosomes showing novel C-banding patterns arose by recombination between homoeologous chromosomes (1A–1B, 1A–1R, or 1B–1R) in ABRR plants (Fig. 1e). It is not likely that any of them were already present in the

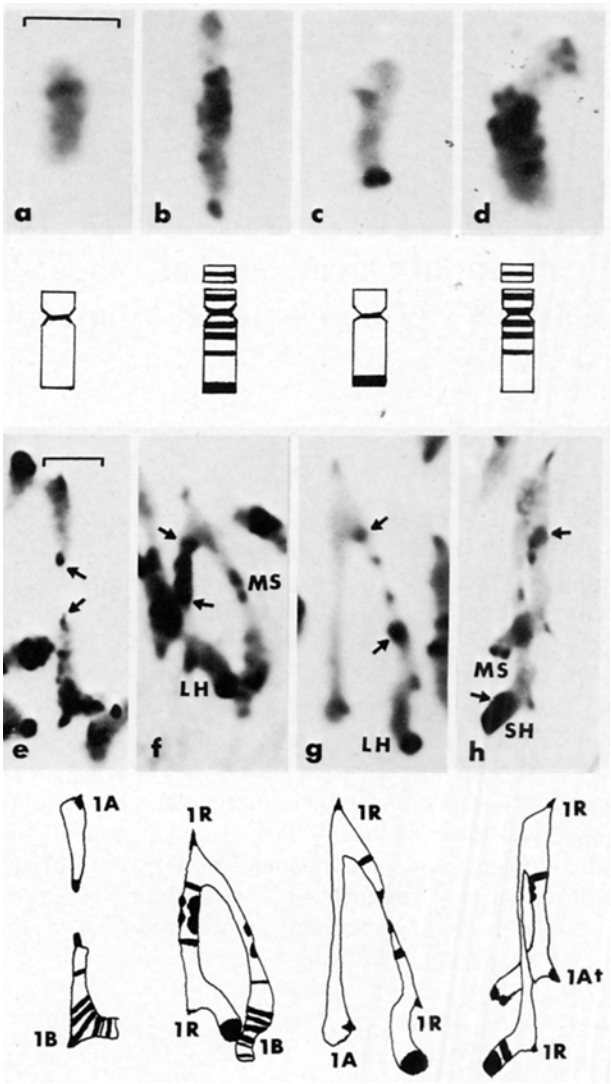

Fig. 1a–h. C-banding pattern and meiotic pairing of homoeologous group 1 chromosomes in ABRR and (0–7)A(0–7)BRR plants. **a** Chromosome 1A. **b** Chromosome 1B. **c** Chromosome 1At: the translocated terminal segment of 1BL in the long arm recognized by medium-sized telomeric band. **d** Chromosome 1Bt: unmarked terminal segment of 1AL at the end of its long arm. **e** Homoeologous bivalent 1A–1B (plants ABRR), chromosomes already separated and showing one C-banded chromatid at the telomere of the long arm (arrows) as a result of recombination. **f** Wheat-rye trivalent made up of chromosome 1B and chromosome pair 1R (1RSHLH and 1RShLh) in plant ABRR14, the bound arms being 1BL-1RLhSh-1RSH. The telomeric band of the long arm (LH) of chromosome 1RSHLH from "Cachirulo" triticale is more prominent than the telomeric medium-sized band (MS) of the 1BL arm. **g** Wheat-rye trivalent involving chromosome 1A and chromosome pair 1R (1RShLh and 1RShLH), bound arms 1AL-1RLhSh-1RSh (plant 2E11-1); unpaired 1RL arm with prominent telomeric band (LH). **h** Wheat-rye trivalent involving chromosome 1At and chromosome pair 1R (1RShLh and 1RSHLh), bound arms 1AS-1RShLh-1RLh (plant 2E2). Medium-sized band (MS) of unpaired 1AtL arm and prominent telomeric band (SH) of unpaired 1RSH shown. **f–h** arrows indicate interstitial bands proximal to the NOR of 1R chromosomes. Bars represent 5 μm

parental material as none was detected in the ABRR hybrids obtained from "Cachirulo" triticale and checked in this and in previous work (Naranjo et al. 1979; Naranjo and Palla 1982). Chromosome 1At (present in plant 2E2) shows two typical characteristics of chromosome 1A, that is, the arm ratio and the centromeric faint band, plus a medium-sized band at the end of the long arm which reveals the translocation (Fig. 1c). This translocated chromosome paired by the short arm with chromosome 1R (Fig. 1h) in three PMCs, which suggests it is a 1A/1B or 1A/1R translocation. Since only one wheat chromosome, chromosome 1B, carries a medium-sized telomeric band, and since wheat-rye associations between the chromosomes of the groups 2 to 7 were scarce plus the fact that none of the characteristics of other wheat chromosomes were recognized in chromosome 1At, it is unlikely that this chromosome had originated by translocation between chromosomes belonging to other groups. Chromosome 1Bt (plants 2E1, 2E6-1 and 2E16-2) only carried the six faint bands of chromosome 1B: one in the satellite, four in the pericentromeric region and one in the center of the long arm. The unmarked telomere of the long arm carried the translocation (Fig. 1d). Distinguishing chromosome 1Bt as well as chromosome 6B (the other SAT chromosome present in plants 2E6-1, 2E11-1 and 2E16-2) was no major problem as chromosome 6B is more metacentric and its bands, located in the pericentromeric region, are thicker than those of chromosome 1Bt. Chromosome 1Bt paired by the long arm with chromosome 1R in some PMCs of plants 2E6-1 and 2E16-2, which supports its identification as a 1B/1A or 1B/1R translocation.

ABRR Plants

The results of pairing at metaphase I between homologous chromosomes (rye-rye associations) and homoeologous chromosomes (wheat-wheat and wheat-rye associations) of group 1 as well as of the six remaining groups in the three plants studied are shown in Table 1. In PMCs without wheat-rye associations, chromosome pair 1R could form a ring bivalent (R) or an open bivalent with the short arm bound (OS) or an open bivalent with the long arm bound (OL) or even a pair of univalents (U). The long arm paired more frequently than the short arm. In these three plants the average number of bound arms per chromosome pair was lower for 1R than for the other chromosome pairs. This does not necessarily mean that chromosome pair 1R showed the

Table 1. Frequencies of three types of meiotic pairing (rye-rye, wheat-wheat and wheat-rye) observed at metaphase I for homoeologous group 1 as well as for remaining groups in three ABRR plants. 100 PMCs per plant in plants ABRR9 and ABRR14 and 80 PMCs in plant ABRR15. (R = ring bivalent, OS = open bivalent with the short arm bound, OL = open bivalent with the long arm bound, U = pair of univalents)

Pairing type	Plant	Group 1					Groups 2 – 7
Rye-rye[a]		*Homologous pair 1R*					*Bound arms per chromosome pair*
		R	OS	OL	U	*Bound arms*	
	ABRR9	29	15	27	15	1.16±0.15	1.67±0.05
	ABRR14	24	8	42	17	1.08±0.14	1.70±0.05
	ABRR15	7	7	36	18	0.84±0.14	1.63±0.05
Wheat-wheat[a]		*Homoeologous pair 1A – 1B*					
	ABRR9			20	66	0.23±0.09	0.28±0.04
	ABRR14		1	19	71	0.22±0.09	0.26±0.04
	ABRR15		1	21	46	0.32±0.11	0.56±0.05
	Total%		0.73	21.82	66.55		
Wheat-rye		*Homoeologous arms paired*					*PMCs with* 1^{II} *or* 1^{III}
		1RLH-1AL	1RLh-1AL	1RSh-1AS	1RLH-1BL	1RLh-1BL	
Trivalents	ABRR9	1	2	1	2		1
Bivalents	ABRR9		5		1	1	
Trivalents	ABRR14		1			1	1
Bivalents	ABRR14		4			2	
Trivalents	ABRR15		1				2
Bivalents	ABRR15	1	4			3	1
	Total%	0.71	6.07	0.36	1.07	2.5	0.30[b]

[a] PMCs without wheat-rye associations
[b] Wheat-rye association percentage per homoeologous group

lowest pairing level since the other rye chromosomes were not distinguished individually.

Chromosomes 1A and 1B when paired formed an OL bivalent in most cases. An OS bivalent was found in only two PMCs. Plant ABRR15 had the highest frequency of wheat-wheat homoeologous pairing in both group 1 and the remaining groups. The increase was strongest in the latter. In the other two plants the average frequency of bound arms per homoeologous chromosome pair showed similar values in both sets of chromosomes.

Wheat-rye pairing was observed in rod bivalents and in chain trivalents made up of two chromosomes of rye and one of wheat in alternate orientation. Both types of association consisted, in most cases, of chromosomes of group 1. They were observed in 10.71% of the PMCs. The average association frequency for each of the remaining groups was 0.30%. Chromosomes 1R and 1A or 1B were associated by their long arms except in one cell where 1R and 1A showed the short arm bound. Associations 1A–1R and 1B–1R presented different frequencies (7.14% and 3.57% respectively). The 1RL arm taking part was preferentially the one lacking telomeric heterochromatin.

(0–7)A(0–7)BRR Plants

Prior to analyzing the pairing behaviour of these plants, their chromosome constitution had to be well defined since some chromosomes carry translocations arising by recombination between homoeologous chromosomes (wheat-wheat or wheat-rye) in the parental ABRR plants. C-banding did not provide any direct evidence of wheat-rye translocations though non-specifically C-banded (chromosome 1At) or unmarked segments (chromosome 1Bt) could have been involved. This possibility has been rejected for chromosomes belonging to groups 2–7 because of low wheat-rye association frequency in the ABRR hybrids. Since none of chromosomes 1A, 1B, 1At and 1Bt carry the prominent telomeric band LH of chromosome 1RSHLH from "Cachirulo" triticale which is present in the parental ABRR and in case any of them carry a rye segment because of wheat-rye recombination, this segment would derive from the long arm of the other 1R chromosome. This fact implies that together with the wheat/rye chromosome the whole chromosome 1RSHLH from "Cachirulo", or an 1R chromosome carrying its long arm (LH), would be transferred to the offspring, (0–7)A(0–7)BRR, as can be deduced from Fig. 1f. Plants of this composition were: 2E11-1, 2E10, 2E6-1 and 2E16-2. Plant 2E15-1 carries chromosome 1B, plant 2E2 chromosome 1At, which has a terminal segment of the 1BL arm translocated. Plant 2E1 has chromosome 1Bt with a terminal segment of the 1AL.

Whether the long arm of chromosome 1A of plant 2E11-1 includes an unmarked rye segment or not may be concluded from pairing data of the ABRR hybrids under the assumption that it derives from a plant of 1RSHLH/1RShLh constitution in which pairing occurred with similar frequencies in macrosporogenesis and microsporogenesis, and one chiasma was produced in one bound armpair. In the first case plant 2E11-1 would derive from an egg cell with a translocated chromatid 1A/1R and a rye-rye recombinant chromatid 1RShLH but without chromatid 1B. This gamete can only be formed from megaspores containing the trivalent 1A(S)L-1RLhSh-1RSH(LH), unpaired arms in brackets, and chromosome 1B as univalent (1.43%). Because of the alternate orientation in the trivalent centromeres of chromosomes 1A and 1RSHLH move to the same pole at anaphase I. Then these chromosomes carry a recombinant chromatid (1A/1R and 1RShLH respectively) and a parental chromatid. Thus gametes with chromatids 1A/1R and 1RShLH appear with probability 1/8. As 1/2 of these gametes do not carry any chromatid 1B their frequency is $1/8 \times 1/2 \times 1.43\% = 0.09\%$.

If chromosome 1A does not include a rye segment plant 2E11-1 would derive from an egg cell carrying a parental chromatid 1A and a recombinant chromatid 1RShLH but without chromatid 1B, which arise from three different types of megaspores. Its frequency can be calculated as follows:

i) Megaspores where homologous chromosomes 1RSHLH and 1RShLh form a bivalent (70.91%). Assuming there is no chromatid interference in ring 1R bivalents gametes have a probability of 1/4 of carrying recombinant chromatid 1RShLH. As 1/4 of these gametes also include parental chromatid 1A but not 1B, regardless of the fact that chromosomes 1A and 1B were paired or not, their frequency is $1/4 \times 1/4 \times 70.91\% = 4.33\%$.

ii) Megaspores with the trivalent 1B(S)L-1RLHSH-1RSh(Lh), unpaired arms in brackets, and chromosome 1A as univalent (0.71%). Chromosome 1RSHLH is involved in two chiasmata. When both affect the same chromatid a double recombinant chromatid (1RSh/1BL) is formed; when each one affects a different chromatid two recombinant chromatids (1RShLH and 1RSH/1BL) are obtained. Assuming there is no chromatid interference both events have the same probability 1/2. Because of the alternate orientation in the trivalent gametes with chromatid 1RShLH but without chromatid 1B appear in frequency $1/2 \times 1/4$. As 1/2 of these gametes also include a parental chromatid 1A their frequency in this case is $1/4 \times 1/2 \times 1/2 \times 0.71\% = 0.04\%$.

iii) Megaspores containing the trivalent 1A(S)L-1RLhSh-1RSH(LH), unpaired arms in brackets, and

Table 2. Frequencies of rye-rye and wheat-rye pairing types at metaphase I for homoeologous group 1 as well as for groups 2 – 7 in seven (O-7)A(O-7)BRR plants

Plant and C-banding of chromosome pair 1R	Rye-rye pairing[a]				1W[b]	PMCs	Wheat-rye pairing									
	1RS %	1RL %	Mean of bound arms per chromosome pair				Homoeologous arms paired for group 1								Groups 2 – 7		
			1R	2R – 7R			1RLH – 1WL III	II	1RLh – 1WL III	II	1RSh – 1WS III	II	Total %	III	II	%[c]
2E15-1 ShLh/ ShLh	61.17	99.30	1.61±0.06	1.77±0.02	1B	400								17		0.71
2E2 SHLh/ ShLh	15.51	95.79	1.11±0.03	1.60±0.02	1At	400					3		0.75	1	1	0.08
2E1 SHLh/ ShLh	23.49	95.97	1.19±0.06	1.79±0.02	1Bt	300								1	1	0.11
2E11-1 ShLH/ ShLh	80.16	78.51	1.59±0.07	1.84±0.02	1A	400	2		57	6			16.25	14	1	0.63
2E10 ShLH/ ShLh	68.87	78.99	1.48±0.08	1.95±0.01	1B	400			19	23	1		10.75	15		0.63
2E6-1 SHLH/ ShLh	41.17	85.66	1.27±0.08	1.70±0.03	1Bt	300			6	13			6.33	11	3	0.78
2E16-2 SHLH/ Sh'LH	54.08	97.71	1.52±0.05	1.87±0.01	1Bt[d]	400	2	4					1.50	3		0.19

[a] Data correspond to PMCs without wheat-rye pairing and have been taken from Naranjo and Lacadena (1980)
[b] 1W = wheat chromosome of group 1 present in each plant
[c] Wheat-rye association percentage per homoeologous group
[d] This chromosome was present in both 2n = 20 and 2n = 19 ears

chromosome 1B as univalent (1.43%). The gametic frequency is $1/8 \times 1/2 \times 1.43 = 0.09\%$ (see above).

Thus the probability of chromosome 1A carrying an unmarked rye segment is:

$$\frac{0.09}{4.43 + 0.04 + 0.09 + 0.09} = 0.02$$

with the parental constitution as assumed.

By the same token, chromosome 1B of plant 2E10 does not have a rye segment, which is supported by the fact that the 1RL arm with a telomeric band similar to the one of 1BL shows up with a rather low frequency in rye cv. "Ailés" (Naranjo and Lacadena 1980). Plants 2E6-1 and 2E16-2 carry chromosome 1Bt. The probabilities of the translocation coming from rye or wheat (calculated as for chromosome 1A) are 0.10 and 0.90 respectively, which suggests that this translocation probably carries a terminal segment of the 1AL arm in both plants.

The seven plants analyzed can be classified into two groups; plants having a parental chromosome 1A or 1B, and plants with a translocated chromosome 1At or 1Bt. These groups show similar frequencies (3 and 4 respectively, Table 2). This segregation, however, does not fit that expected from the pairing of the ABRR hybrids. In fact, plants with one parental chromosome (1A or 1B) are expected with a frequency $1/2 \times 89.10\% + 1/4 \times 3.21\% + 1/8 \times 7.50\% = 46.29\%$ (89.10, 3.21 and 7.50 are the percentages of megaspores without group 1 wheat-rye association, with 1A–1R–1R or 1B–1R–1R trivalents, and with 1A–1R or 1B–1R bivalents; 1/2, 1/4 and 1/8 are the respective probabilities of obtaining gametes carrying one parental 1A or 1B chromatid from such megaspores). Plants having a translocated chromosome (1At or 1Bt) are expected with a frequency of $1/2 \times 21.82\% = 10.91\%$ (21.82% being the frequency of megaspores with an OL 1A–1B bivalent, and 1/2 the probability of gametes carrying a 1At or 1Bt recombinant chromatid). The rest (42.80%) corresponds to plants with the remaining group 1 chromosome constitutions (1A/1R, 1B/1R, 1A plus 1B etc.). The lack of adjustment might be due to different viability

of gametes produced by ABRR hybrids as fertility in the backcross ABRR×RR was very low (0.82%). The most balanced gametes are probably those carrying seven non-homoeologous wheat chromosomes, which should mainly be formed from megaspores showing a high number of wheat bivalents and, as a consequence, they transferred to the offspring parental or translocated wheat chromosomes with similar frequencies. This possibility is supported by the wheat chromosome constitution of these plants. Five plants had seven wheat chromosomes which were probably non-homoeologous because they seldom paired (mean values of wheat bivalents: 0.000 in plants 2E15-1 and 2E1; 0.002 in plant 2E2; 0.023 in plant 2E11-1; 0.026 in plant 2E6-1 respectively). In plant 2E10 with 8 wheat chromosomes one homoeologous pair had to be present but no more, as deduced from wheat-wheat pairing (0.076 bivalents per cell). Plant 2E16-2 was a mosaic 2n=20/2n=19 (6 wheat chromosomes in one ear and five in another one) and showed the highest mean value of wheat bivalents (0.235) mainly due to pairing between two specific (homoeologous) chromosomes which were present in the two ears analyzed. In all plants wheat bivalents never contained group 1 chromosomes.

Homologous rye pairing has been studied by Naranjo and Lacadena (1980) and their results are summarized in Table 2 together with those of wheat-rye paring. In all plants, wheat-rye pairing was observed in both rod bivalents and in chain trivalents made up of two rye chromosomes and one wheat chromosome showing alternate orientation. In plants 2E11-1, 2E10 and 2E6-1, which showed the highest frequencies of homologous pairing failure in the 1RL arm, wheat-rye pairing presented similar characteristics as observed in ABRR plants. This occurred, i.e., especially between the long arms of homoeologous chromosomes of group 1, arm 1RLh being more often involved than 1RLH, and 1AL–1RL associations (plant 2E11-1) also being more common than the 1BL–1RL ones (plant 2E10). In contrast, the frequencies of 1AL–1RL or 1BL–1RL pairing were much lower (turning to zero in three cases), in the remaining plants where homologous pairing failure in the 1RL arm was infrequent. There is a significant positive correlation between RR pairing failure and RA or RB pairing in the long arm of group 1 chromosomes ($r=0.95$, $p<0.01$), but this is not so for the short arm of these chromosomes in which wheat-rye associations occurred seldom even though homologous pairing failure reached rather high levels in some plants (2E2 and 2E1). In the remaining groups their correlation coeficient did not differ significantly from 0 ($r=-0.25$, $p>0.10$) thus suggesting that some chromosome arms or whole chromosomes behave like the short arm of group 1 chromosomes.

Discussion

Wheat-rye pairing is relatively low for homoeologous groups 2 to 7 in both ABRR and (0–7)A(0–7)BRR plants, with a maximum of 0.78%. In group 1 it seldom involves the short arm. For the long arm, it is closely and positively correlated with the failure of homologous pairing (Table 2) and reaches higher values than in the remaining groups with a maximum of 16.25%. In spite of the fact that the average number of bound arms was lower in pair 1R than in the remaining rye chromosome pairs, wheat-rye pairing variation between groups probably does not result from overall variation in homologous pairing failure because this is much smaller. Moreover, homologous paring failure and wheat-rye pairing were not correlated in the groups 2–7. This difference can be caused by greater affinity between wheat and rye chromosomes of group 1, or it could be related to the fact that these chromosomes have nucleoli which tend to fuse early in meiosis. These, however, occur in the short arms.

Chromsome 5B is an strong suppressor of homoeologous pairing and its presence or absence could influence wheat-rye pairing in (0–7)A(0–7)BRR plants. However, variation in the number of wheat-rye associations involving the long arm of group 1 chromosomes in these plants (0–16.25%, Table 2) should be basically determined by a different mechanism: homologous pairing failure in the 1RL arm. This is based on three main facts: a) Homologous pairing failure and wheat-rye pairing are correlated. b) In wheat-rye derivatives carrying wheat chromosomes in haploid dosage, the 5B suppressor effect is reduced by a promoter effect of rye. In fact, in ABRR plants where chromosome 5B is present, 1AL–1RL and 1BL–1RL associations were observed in 10.71% of PMCs. c) If chromosome 5B would cause the variation between plants, the remaining groups would also be affected. This was not so, as plants 2E15-1 and 2E10 differ in the number of their 1BL–1RL associations, (0 and 10.75% respectively), although they match in respect to wheat-rye associations for the remaining groups (0.71% and 0.63% respectively).

Two more factors (presence or absence of prominent telomeric heterochromatin in rye 1RL arm; number (one or two) of wheat homoeologous chromosomes of group 1) seem to influence wheat-rye pairing in the long arm of the chromosomes of group 1. The first is evident since wheat chromosomes pair preferentially with chromosome 1R which lacks telomeric heterochromatin in its long arm (Tables 1, 2). Telomeric heterochromatin, at least in heterozygous condition, has also been shown to interact with homologous pairing of chromosome pair 1R in (0–7)A(0–7)BRR plants (Naranjo and Lacadena 1980). It caused a reduction in chiasma frequency, but whether heterochromatin interfered with pairing or crossing-over could not be concluded. Desynaptic effects of heterochromatin have been detected and discussed earlier (Thomas and Kaltsikes 1976; Merker 1976; Naranjo

and Lacadena 1982). Yet, its possible interference with pairing which was suggested by Thomas and Kaltsikes (1974) has not been confirmed. Now, when telomèric heterochromatin is present in only one of the two 1RL arms, pairing between them may fail while pairing between the unmarked 1RL arm and any of its homoeologous 1AL or 1BL arms occurs; it seems reasonable to conclude that heterochromatin in heterozygous condition produces asynapsis affecting both homologous and homoelogous wheat-rye pairing. Perhaps the different contribution of chromosomes 1A and 1B to the wheat-rye pairing may be also due to the telomeric heterochromatin in the long arm of chromosome 1B.

Wheat-rye pairing levels for the long arm of group 1 chromosomes are higher in plants 2E11-1 and 2E10 with only one wheat chromosome of group 1 than in ABRR plants with two (Tables 1, 2) in spite of the fact that 1RL–1RL pairing failure in PMCs without wheat-rye pairing was higher in the last ones (32.65% in ABRR plants; 21.49% and 21.01% in plants 2E11-1 and 2E10 respectively). Decrease of wheat-rye pairing in ABRR plants is probably a result of competition between homoeologous chromosomes for pairing, 1AL–1BL association hindering 1AL–1RL or 1BL–1RL associations. The lack of competition may be the reason that wheat-rye pairing in the remaining groups is also higher in (0–7)A(0–7)BRR plants. Plant 2E6-1 differs from plants 2E11-1 and 2E10 in the wheat-rye pairing of group 1 (Table 2). This may be due to the translocation in chromosome 1Bt as well as a higher 1RL–1RL pairing.

Taking into account that rye chromosomes induce homoeologous pairing and chromosome 5B acts by suppressing it, Miller and Riley (1972) suggested that the maximum promotion of homoeologous pairing will possibly occur in 5B-deficient wheat-rye hybrids of the type *T. aestivum* × *S. cereale* 4×. Such a statement seemed likely at first. In fact plants with genome constitutions ABRR and ABRRR (Naranjo et al. 1979) showed higher wheat-rye pairing levels than plants having an ABDR constitution (Mettin et al. 1976; Schlegel 1977). Nevertheless, in view of my results this suggestion is unfounded because irrespective of the C-banding pattern of rye chromosomes, in nulli-5B ABDRR hybrids there are two sets of rye chromosomes which should pair up, by which wheat-rye pairing will partially be obstructed. Combinations with one or three genomes are probably more suitable.

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