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No 5-B Compensation by Rye B-chromosomes

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Summary. Chinese Spring mono-5B wheat was crossed with rye plants, with and without B-chromosomes, to produce polyhaploids with and without 5B and with and without rye B-chromosomes. As expected, absence of 5B resulted in a strong increase of homoeologous pairing. It was accompanied by a decrease in chiasmata in the rye B-chromosomes. The rye B-chromosomes were entirely *ineffective* in compensating for the 5B effect in nulli 5B, 2 rye B types.

Introduction

The failure of pairing of homoeologous chromosomes in allopolyploids is conditioned by factors in the chromosomes themselves and also may be regulated by genetic systems operating on the genome as a whole. The latter systems have been extensively studied in wheat, where there appears to be a major regulating gene or gene complex located in the long arm of chromosome 5B (Ph = pairing homoeologues). In the presence of Ph homoeologous pairing is prevented. In its absence pairing and crossing-over are possible but do not reach the level of that between homologues. This is probably mainly caused by the basic, locally conditioned differentiation between the attraction systems of the chromosomes involved, somewhat modified by the action of genes other than Ph. In species which may have contributed the 5B chromosome to wheat or which may be related to it, the same allele is not encountered, although several other genes affecting homoeologous pairing are present, some overruling the Ph allele present in wheat. The accessory chromosomes (also called B-chromosomes and not to be confused with chromosomes of the B genome) of at least two such species *(Aegilops speltoides* and *Ae. mutica)* however, have been found to have an effect very similar to that of the Ph gene of wheat (Vardi and Dover 1972; Dover and Riley 1972; Dover 1974). In *Lolium* species hybrids (Evans and Macefield 1972, 1973) accessory B-chromosomes have been found to suppress homoeologous chromosome pairing. It is interesting, therefore, to study the effect on homoeologous pairing of B-chromosomes of some more species. Since rye B-chromosomes are known to affect chromosome behaviour in rye (Jones and Rees 1964), and since these chromosomes can readily be introduced into wheat, it was decided to find whether rye B-chromosomes affect homoeologous pairing in wheat, by analysing their capacity to compensate for the Ph gene.

Materials and Methods

Several sister mono-5B Chinese Spring wheat plants (obtained from the Department of Plant Breeding, originally from Sears) were crossed with rye, with and without B-chromosomes, of Transbaikal origin (Müntzing). The B-chromosomes had earlier been crossed into the rye material of this Department. Since plants with B-chromosomes practically entirely produce pollen with B-chromosomes, control plants without B's had to be derived from another source. In order to make the two types comparable, the B-chromosome plants were crossed and backcrossed with the inbred line serving as the control parent. All wheat components in the hybrids were entirely comparable except for the presence or absence of the 5B chromosome, as they were derived from the same parent.

Rye-wheat F_1 plants, with or without the wheat 5B chromosome and with or without rye B-chromosomes, were grown in the greenhouse in 1974/75 and fixations were made in acetic-alcohol 1:3. Permanent squash preparations were made with Euparal after aceto-carmine staining. The numbers of chiasmata per cell were determined and the frequencies of different configurations recorded in 50 MI cells per fixation. Since meiosis in these hybrids is not very regular and the transition between MI and AI is often unclear (nonsynchronised anaphase separation of different configurations, desynapsis without orientation, neocentric activity), the following criteria for MI were used: Maximal condensation of chromosomes, configurations well spread and chromatids unseparated. At anaphase the chromatids appear separately visible. Only cells without serious deviation (double number of chromosomes, lumps of heterochromatin, abnormal spindles, delayed chromosomes) were scored.

Results and Discussion

The main data on the frequency of chiasmata and configurations are condensed in Table 1. Although there is considerable variation within each group, it is clear that the rye B-chromosomes do not compensate for the

Table 1. Configuration and chiasma frequencies in wheat-rye hybrids with and without wheat 5B and with and without two rye B-chromosomes. Because of high degree of terminalization, only chiasmate associations given for the A chromosomes. 50 cells per entry. Brackets indicate that fixations of a single plant are involved

	A-chromosomes							B-chromosomes			
	bivalents		trivalents			quadr.		rods	rings	chiasmata	
hybrid	rods	rings	chains	stars	frying pans		association freq.			freq.	var.
				wheat 5B present; 2 rye B-chromosomes							
[CS4 × 74651-3	0.52	-	-	-	-	-	0.52	0.54	0.40	1.42	0.37
CS4 × 74651-3]	0.40	0.02	-	-	-	-	0.44	0.52	0.44	1.50	0.38
CS4 × 74651-3	0.62	0.10	-	-	-	-	0.82	0.52	0.44	1.62	0.49
CS2 × 74654-9	0.76	0.04	0.06	-	-	-	0.96	0.46	0.40	1.40	0.69
CS7 × 74654-9	0.24	0.02	-	-	-	-	0.28	0.44	0.32	1.18	0.93
[CS14 × 74654-9	0.34	0.06	-	-	-	-	0.46	0.56	0.40	1.46	0.25
CS14 × 74654-9]	0.62	0.02	0.02	-	-	-	0.70	0.54	0.38	1.30	0.43
average	0.50	0.04	0.01	-	-	-	0.60	0.51	0.40	1.41	
				wheat 5B absent; 2 rye B-chromosomes							
CS4 × 74651-3	3.20	1.40	0.84	0.20	0.10	0.02	8.14	0.64	0.28	1.20	0.33
[CS2 × 74654-9	2.92	0.46	0.14	0.04	-	-	4.16	0.92	0.04	1.00	0.08
CS2 × 74654-9	3.20	0.52	0.12	-	-	0.04	4.60	0.90	0.06	1.02	0.10
CS2 × 74654-9]	3.14	1.08	0.48	0.10	-	0.02	6.42	0.64	0.24	1.14	0.16
CS7 × 74654-9	3.08	0.34	0.38	0.02	0.02	-	4.58	0.68	0.20	1.04	0.32
CS7 × 74654-9	2.86	0.74	0.32	0.04	0.02	0.02	5.12	0.80	0.16	1.12	0.17
CS7 × 74654-9	3.34	1.00	0.54	0.14	0.04	-	6.64	0.66	0.28	1.22	0.29
CS14 × 74654-9	3.06	1.24	0.70	0.24	0.08	-	7.34	0.58	0.18	1.16	0.72
CS25 × 74654-9	3.02	1.34	0.64	0.12	0.10	0.06	7.48	0.78	0.14	1.08	0.24
average	3.09	0.90	0.46	0.10	0.04	0.02	6.05	0.73	0.18	1.11	
				wheat 5B present; no rye B-chromosomes							
[CS7 × 001	0.78	-	0.02	0.02	-	-	0.84	-	-	-	-
CS7 × 001]	1.04	0.08	0.02	-	-	-	1.24	-	-	-	-
CS2 × 029	0.54	0.02	-	0.02	-	-	0.60	-	-	-	-
average	0.79	0.03	0.01	0.01	-	-	0.89	-	-	-	-
				wheat 5B absent; no rye B-chromosomes							
CS7 × 001	3.08	0.28	0.56	0.22	0.02	0.10	5.32	-	-	-	-
[CS2 × 029	3.54	0.88	0.80	0.12	0.02	0.02	7.12	-	-	-	-
CS2 × 029]	3.16	0.82	0.82	0.18	0.12	0.04	6.98	-	-	-	-
CS2 × 029	3.04	0.74	0.34	0.22	0.04	0.04	5.62	-	-	-	-
average	3.21	0.68	0.63	0.19	0.05	0.05	6.26	-	-	-	-

absence of the 5B wheat chromosome. The number of plants without rye B-chromosomes is small but their behaviour fits entirely within the range of corresponding groups with B-chromosomes. Much of the variation observed may be due to variation within plants, as different fixations of the same plant may vary considerably.

The 5B wheat chromosome seems to have some effect on chiasma formation in the B-chromosome of rye: in the absence of 5B, the frequency of chiasmata in the B-chromosome bivalent is lower than in the presence of 5B, contrary to what is observed in the A-chromosomes. This is primarily a result of the failure of chiasma formation in the short arm and reduction from two to one chiasmata in the long arm. The number of B-chromosome univalents did not increase. The effect may be explained in two ways: 1. Presence of 5B reduces interference in the B-chromosome bivalent. 2. Pairing is incomplete for rye chromosomes in a wheat background and not affected by 5B: there is a constant level of univalence resulting from asynapsis. In paired B-chromosomes the chiasma frequency is reduced by the absence of the 5B chromosome, perhaps as a result of an increase among the wheat chromosomes. It should be noted that here in a wheat + rye background in the rye B-bivalent, in the presence of 5B, the chiasma frequency is considerably higher than in a rye background

Table 2. Average number of configurations per cell. A comparison of different sources

Material	cells	bivalents rods	rings	total	triv.	quadriv.
wheat haploids (Kimber; Riley, 1963)						
nulli 5B	100	4.55	0.65	5.20	0.53	0.02
euploid	400	0.89	0.005	0.90	0.008	-
wheat-rye hybrids (Riley, 1960)						
nulli 5B	200			3.36	0.88	0.08
euploid	300			0.48	-	-
wheat-rye hybrids (present report)						
nulli 5B + 2B	450	3.09	0.90	3.99	0.60	0.02
nulli 5B + 1B	100	3.30	1.04	4.34	0.86	0.01
nulli 5B	200	3.20	0.69	3.89	0.86	0.05
euploid + 2B	350	0.50	0.04	0.54	0.01	-
euploid + 1B	100	1.06	0.04	1.10	-	-
euploid	150	0.79	0.03	0.82	0.03	-

(Sybenga and de Vries 1972) or in a complete wheat background (Müntzing et al. 1969). Even in the absence of 5B the level is high. It is not inconceivable that these high levels result from the reduction of chiasmata in wheat, mediated by inter-chromosome effects. Another striking observation was the more random distribution of the chiasmata in the rye B-bivalents than in the wheat configurations, where the chiasmata were almost without exception terminally located. Further, mean and variance were about equal for the A chromosome associations in the presence of 5B, indicating random formation of chiasmata (Poisson distribution). The variances were lower than the means in the absence of 5B, suggesting a restriction on the formation of chiasmata. The regression between A and B chromosomes was considerable (0.243), but the correlation coefficient insignificant ($r = 0.41$) in the presence of 5B. Regression was small (0.043) but the correlation coefficient positive and significant ($r = +0.80$; $P = 0.01$) in the absence of 5B.

Two plants had one rye-B-chromosome in the presence of the complete wheat complement. The frequency of rod bivalents was quite high: 1.16 and 0.96 per cell respectively. There were 0.00 and 0.02 rings. Of two plants with one rye B-chromosome and no wheat 5B-chromosome, one had 3.54 rod bivalents and 1.68 rings, fitting well in the comparable group with two B's, to which the other plant was very similar in all respects. One plant lacking 5B had an iso-B-chromosome (long arm). The meiotic behaviour was similar to that of all nulli-5B-plants.

Table 2 compares the summarized data of Table 1 with those reported in the literature for comparable material without rye B-chromosomes.

Unlike the B-chromosomes of *Aegilops*, rye B-chromosomes do not induce spindle or other meiotic abnormalities in the hybrid with wheat.

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