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Absence of Qualitative Genes Controlling Interspecific Pairing in Rye B Chromosomes

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Summary. The meiotic behaviour of hybrids between *Secale cereale* carrying B chromosomes and *S. vavilovii* has been studied in order to estimate the effects of B chromosomes on hybrid meiotic pairing. The possible effect of Bs on the meiotic pairing of the offspring from backcrosses with *S. vavilovii* has been studied also. The results obtained clearly indicate that no detectable differences existed in chromosome pairing of hybrids with or without B chromosomes. The hypothetical existence of epistatic genes on *cereale* genome masking the effect of Bs has been rejected after the results obtained in backcrosses. Therefore, lack of qualitative genes controlling interspecific pairing on rye B chromosomes has been concluded. A quantitative effect of B chromosomes was detected only when they were in alien cytoplasm.

Key words: B-chromosomes - Cytoplasmatic-factor - Homoeology - *Secale* - Translocations

Introduction

The relation of B chromosomes with meiotic pairing of A chromosomes has been investigated on several occasions. Comparison of data obtained in different varieties, species or interspecific hybrids leads to the conclusion that B chromosome effect, if any, is very variable, with the results even being contradictory in some instances. Table 1 shows a summary of the references concerning rye and interspecific hybrids, where it can be clearly observed that the variation in A chromosome behaviour due to Bs depends on many factors: the species considered, the number of Bs, the genetic background, etc.

In this present work, the meiotic behaviour of the hybrids between *Secale cereale* carrying Bs and *Secale vavilovii* has been studied in order to estimate the effect of B chromosomes on hybrid meiotic pairing.

The possible effect of Bs on the meiotic pairing of the offspring from backcrosses with *S. vavilovii* has been studied too. It could be possible that epistatic genes, masking the B chromosome effect on homoeologous pairing, exist in *S. cereale;* thus, the backcross segregation should reveal this possibility.

The main reason for choosing *S. vavilovii* was that it is an autogamous species, while *S. cereale* is an allogamous one. This reproductive isolation may have led to a greater divergence between these species than between any other rye species. In addition, it has already been demonstrated (Jain 1960; Khush and Stebbins 1961) that *S. cereale* and *S. vavilovii* differ by three reciprocal translocations involving 6 chromosomes; therefore, the critical configuration of hybrids is one hexavalent plus four bivalents.

The chromosomes involved in these translocations have been identified by Heemert and Sybenga (1972) and by Sing and Röbbelen (1977).

The presence of multivalents in hybrids represented two different advantages. First, the higher variation of meiotic configurations; that is, a higher number of different situations where the possible effect of B chromosomes could be detected. Secondly viable gametes formed by hybrids are dependent on multivalent coorientation at Metaphase I, which increases the probability of the production of more *vavilovii* genome in backcrosses than that obtained by random segregation in the case of bivalent formation. For instance, the alternate coorientation of the hexavalent will lead to a segregation at Anaphase I of three *cereale* chromosomes to one pole and three *vavilovii* to the other pole. Backcrossing with *vavilovii*, two types of indivuduals will be obtained, half of them forming 1^{VI} + 4^{II} and half forming 7^{II}. In the latter, it will be cer-

Table 1. Effects of B chromosomes on A chromosome meiotic pairing

Authors	Material	Observed effect
Jones and Rees, 1967	*S. cereale*	Bs did not influence the mean chiasma frequency, but they increased the variance in zigzag depending on odd or even numbers of Bs.
Zecevic and Paunovic, 1969	*S. cereale*	B chromosomes had a great influence on A chiasma distribution.
Tsumoto and Sasaki, 1972	*S. cereale*	In one line, chiasma frequency increased when the number of Bs increased; in other line it decreased.
Evans and Macefield, 1972, 1973	*Lolium temulentum* x *L. perenne* hybrids	In hybrids without Bs, meiosis was regular. With Bs, chiasma frequency decreased drastically.
Evans and Macefield, 1974	*L. multiflorum* x *L. perenne* hybrids	B chromosomes reduced chiasma frequency and the number of bivalents by a small but significant amount.
Taylor and Evans, 1976	*L. rigidum* x *L. temulentum* hybrids	B chromosomes reduced chiasma frequency but homoeologous pairing can be modified quite substantially by the A chromosome genotype.
Bowman and Thomas, 1973	*L. perenne* x *Festuca arundinacea* hybrids	Bs reduced homoeologous pairing.
Dover and Riley 1972 a, b Vardi and Dover 1972	*Triticum aestivum* x *Aegilops mutica* and *T. aestivum* x *Ae. speltoides* hybrids	In 5B presence, no differences were observed in interspecific pairing in absence or presence of B chromosomes. In 5B absence, hybrids with Bs had low pairing and hybrids without Bs had high pairing.
Roothaan and Sybenga, 1976	*T. aestivum* x *S. cereale* hybrids	B chromosomes were entirely ineffective in compensating for the 5B effect in nulli 5B, 2 Bs types.

tain that at least 3 of the 7 pairs will be *vavilovii* already. Although there are many other possible meiotic configurations (adjacent coorientation, pentavalents, quadrivalents, etc.), they will not be considered because it can be supposed that, in only one backcross generation, more *cereale* chromosomes will be eliminated than would be eliminated after a regular meiosis without multivalents.

Material and Methods

Secale cereale of the line JNK carrying B chromosomes and *Secale vavilovii* have been used. The former was provided by Dr. H. Kishikawa (University of Saga, Japan) and the latter by Dr. Kuckuck (Hannover, BRD).

The crosses carried out are illustrated in Fig. 1. From the offspring obtained, all individuals with a chromosome constitution of 2n = 14 and 2n = 14 + 2B were studied.

Anthers were fixed in acetic-alcohol 1:3 and stained by the usual Feulgen method. The preparations were made permanent with Sandeural.

30 PMCs of each individual were observed. Special care was taken to consider only those slides in which

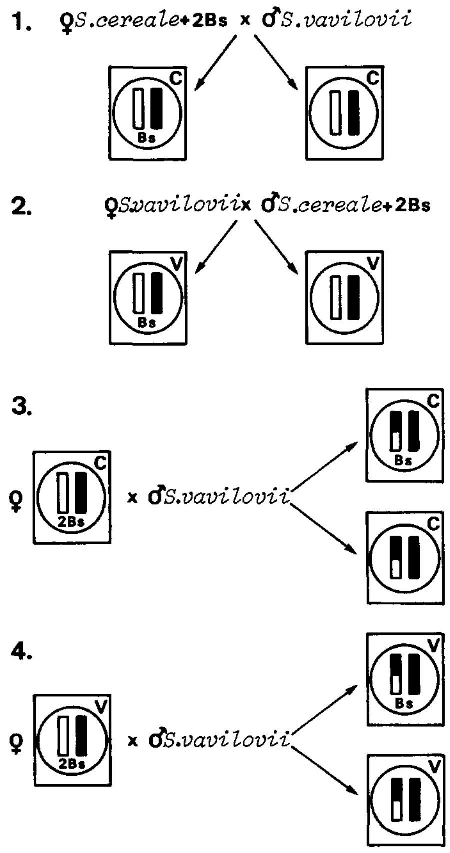

Fig. 1. Scheme showing the crosses carried out (white bar represents *cereale* genome; black bar represents *vavilovii* genome)

Table 2. Meiotic pairing at Metaphase I of hybrids *Secale cereale* + Bs × *Secale vavilovii* (30 cells of each plant were scored)

Plant	Cells with hexavalent pentavalent or 2 trivalents	Cells with quadrivalent or trivalent	Cells with bivalents	Mean chiasma frequency	Variance	Pairs of univalents	Number of B chromosomes	Cells with B bivalent	Female parent
1	13	14	3	12.56	0.45	0	2	28	*cereale*
2	17	9	4	12.33	0.82	1	2	26	*cereale*
3	9	16	5	12.06	0.66	0	2	26	*cereale*
4	4	15	11	11.80	1.03	5	2	27	*cereale*
5	8	12	10	12.23	0.65	0	0		*cereale*
6	12	10	8	12.06	0.56	2	0		*cereale*
7	13	12	5	12.00	0.53	0	0		*cereale*
8	7	13	10	12.43	0.78	2	2	13	*vavilovii*
9	4	6	20	12.10	1.82	6	2	7	*vavilovii*
10	11	16	3	12.10	0.69	1	2	23	*vavilovii*
11	1	15	14	11.36	1.30	5	2	6	*vavilovii*
12	7	13	10	11.53	0.65	1	0		*vavilovii*
13	6	15	9	11.26	0.79	4	0		*vavilovii*
14	2	11	17	11.23	1.04	3	0		*vavilovii*

cells at Metaphase I were not together with Anaphase I or other phases.

To count the number of chiasmata, 2 chiasmata were considered in ring bivalents, 1 in rod bivalents and 0 in the pairs of univalents; that is, one chiasma per each pair of bounded arms.

Results

I. Hybrids

In Table 2, the meiotic behaviour of hybrids is illustrated.

The hexavalents at Metaphase I were always chain shaped, which indicates the small size of one of the translocations.

The first evidence was the large homology between the two species, as demonstrated by the high pairing in all hybrids. This fact had been already observed by Khush (1962, 1963) and by Khush and Stebbins (1961).

It is known that the mean chiasma frequency is about 13.5 both in *S. cereale* and *S. vavilovii*. The chain multivalent in hybrids decreases 1 chiasma per cell in every case. In addition, when translocated chromosomes do not form multivalents, the translocated segments increase the formation of rod shaped bivalents. Besides they do not completely prevent the formation of ring bivalents (only in 0.1% of the PMCs, were 7 ring bivalents observed). In summary, in hybrids a decrease of at least one chiasma per cell was expected due only to the presence of translocations.

In Table 2 it can be easily observed that no differences existed between hybrids with or without B chromosomes and that meiotic pairing was very high in every case.

The average of mean chiasma frequencies of hybrids with B chromosomes was compared with that of hybrids without Bs, by a t test. The means did not differ significantly ($0.4 > P > 0.2$). The same comparison was made between hybrids on *cereale* cytoplasm and those on *vavilovii* cytoplasm (irrespective of the presence or absence of B chromosomes), when the t value was at the limit of significance ($0.10 > P > 0.05$). These results are shown in Table 3.

Other details of lesser interest have also been considered, namely:

- The possible influence of B chromosomes on multivalent formation (presence or absence of Bs in relation to higher or lower multivalent frequency). No differences could be detected.
- The possible relation between B chromosome pairing (B univalents or B bivalent formation) with a higher or lower A chromosome pairing. No relation was apparent.
- The possible influence of Bs on multivalent coorientation and segregation. No effect was observed, Ana-

Table 3. Comparison by a t test of different types of hybrids

Type of plants	Average mean	Variance	Level of significance
Hybrids with Bs	12.09	0.185	$0.40 > P > 0.20$
Hybrids without Bs	11.72	0.526	
Hybrids in *cereale* cytoplasm	12.15	0.018	$0.10 > P > 0.05$
Hybrids in *vavilovii* cytoplasm	11.71	0.335	

phase I segregation being 7-7 in 94.5 % of the cases. In some instances (15%) anaphasic bridges without fragments have been observed, both in hybrids with and without B chromosomes.

- The meiotic pairing of B chromosomes, which was typical according to Kishikawa (1965), although on *vavilovii* cytoplasm it was diminished.

II. Backcrosses

From backcrosses ♀ (♀ *S. vavilovii* × ♂ *S. cereale*) × ♂ *S. vavilovii*, 20 seeds were obtained, 12 of them having a chromosome constitution of $2n = 14$ and the remaining 8 having $2n = 14 + 2B$. From backcrosses ♀ (♀ *S. cereale* × ♂ *S. vavilovii*) × ♂ *S. vavilovii*, 31 seeds were obtained, 4 having $2n = 14$ and 27 having $2n = 14 + 2B$. Although not all of them grew to maturity, those considered in Tables 4 and 5 had.

In Tables 4 and 5, the meiotic behaviour of the offspring obtained from backcrosses with *S. vavilovii* is detailed.

In 9 plants out of the total of 32 descendants studied, no multivalent was observed, indicating that the 3 *cereale* chromosomes involved in translocations had been eliminated; therefore, these plants carried at least 3 *vavilovii* pairs. In 4 plants out of the remaing 23, no hexavalents but quadrivalents were formed, which implies that 2 of the translocated chromosomes had been lost.

Among individuals with *cereale* cytoplasm, no differences between plants with or without B chromosomes were observed, while among plants with *vavilovii* cytoplasm there were only 3 plants with a certain decrease in pairing, the 3 plants carrying Bs (35, 36 and 37 in Table 5).

Table 6 shows four different comparisons made among these individuals, namely:

- Plants with and without B chromosomes irrespective of the cytoplasm carried. They did not differ significantly ($0.20 > P > 0.10$);

Table 4. Meiotic pairing at Metaphase I of backcrosses in *cereale* cytoplasm: ♀ (♀ *S. cereale* + Bs × *S. vavilovii*) × ♂ *S. vavilovii* (30 cells of each individual were scored)

Plant	Cells with hexavalent pentavalent or 2 trivalents	Cells with quadrivalent or trivalent	Cells with bivalents	Mean Chiasma Frequency	Variance	Pairs of univalents	Number of B chromosomes	Cells with B bivalent
15	-	-	30	12.30	1.74	2	2	22
16	18	11	1	12.06	0.66	1	2	20
17	7	18	5	12.02	0.62	1	2	21
18	-	-	30	11.93	1.39	14	2	25
19	-	-	30	11.86	1.71	4	2	24
20	10	17	3	11.80	1.09	5	2	28
21	12	13	5	11.76	1.44	6	2	22
22	16	9	5	11.70	1.01	6	2	22
23	-	-	30	11.70	2.81	7	2	23
24	-	-	30	11.23	2.18	11	2	30
25	-	-	30	10.43	1.84	14	2	27
26	-	27	3	12.20	0.76	2	0	
27	14	13	3	11.96	0.96	2	0	
28	-	12	18	11.83	0.78	6	0	
29	18	11	1	11.76	0.86	2	0	

Table 5. Meiotic pairing at Metaphase I of backcrosses in *vavilovii* cytoplasm: ♀ (♀ *S. vavilovii* × ♂ *S. cereale* + Bs) × ♂ *S. vavilovii* (30 cells of each individual were scored)

Plant	Cells with hexavalent pentavalent or 2 trivalents	Cells with quadrivalent or trivalent	Cells with bivalents	Mean Chiasma Frequency	Variance	Pairs of univalents	Number of B chromosomes	Cell with B bivalent
30	13	17	-	12.30	0.34	2	2	28
31	7	13	10	12.13	0.51	5	2	18
32	17	10	3	11.59	0.98	2	2	24
33	-	21	9	10.80	1.89	9	2	14
34	12	9	9	10.46	2.71	17	2	12
35	9	12	9	9.73	1.20	9	2	13
36	-	4	26	9.50	3.18	25	2	7
37	-	3	27	8.23	5.78	42	2	22
38	-	-	30	12.93	2.10	0	0	
39	-	-	30	12.66	1.66	4	0	
40	8	15	7	11.80	0.74	4	0	
41	18	10	2	11.76	1.04	0	0	
42	-	-	30	11.46	1.45	7	0	
43	-	15	15	11.43	1.51	4	0	
44	12	16	2	11.00	1.20	4	0	
45	9	16	5	10.97	1.16	5	0	
46	12	16	2	10.70	1.54	6	0	

- Plants with *cereale* cytoplasm and plants with *vavilovii* cytoplasm, irrespective of the presence or absence of Bs. The t value was at the limit of significance (0.10 > P > 0.05);
- Plants with Bs in *cereale* cytoplasm and plants without Bs irrespective of the cytoplasm. They did not differ significantly (P > 0.50);
- Plants with Bs in *vavilovii* cytoplasm and plants without Bs, irrespective of the cytoplasm. They differed significantly (0.025 > P > 0.010).

Discussion

The species used in the present work, *Secale cereale* and *Secale vavilovii*, differ morphologically and in their reproductive mechanisms. *S. cereale* is an allogamous species carrying genetic systems of pollen-style incompatibility (Lundqvist 1956, 1958) while *S. vavilovii* is an autogamous one. However, hybrids showed a high degree of meiotic pairing with a decrease of mean chiasma frequency of about one chiasma per cell when compared with parental species. This diminution can be attributed only to reciprocal translocation heterozygosity. This indicates, in spite of the phenotypic divergences, a high degree of chromosome homology.

The results obtained clearly indicate that no detectable differences existed in chromosome pairing at Metaphase I of *S. cereale* × *S. vavilovii* hybrids with or without B chromosomes. In interspecific hybrids previously obtained by other authors (see Table 1) the

Table 6. Comparison by a t test of different types of backcrosses

Type of plants	Average mean	Variance	Level of significance
Backcrosses with Bs	11.24	1.129	0.20 > P > 0.10
Back. without Bs	11.73	0.325	
Backcrosses in *cereale* cytoplasm	11.77	0.170	0.10 > P > 0.05
Backcrosses in *vavilovii* cytoplasm	11.14	1.440	
Back. with Bs in *cereale* cytoplasm	11.71	0.186	P > 0.50
Back. without Bs	11.73	0.325	
Back. with Bs in *vavilovii* cytoplasm	10.59	1.780	0.025 > P > 0.10
Back. without Bs	11.73	0.325	

effect of B chromosomes on pairing was quite drastic, with the exception of rye-wheat hybrids obtained by Roothaan and Sybenga (1976). Therefore, two alternative hypotheses could be made to explain our results:

i.) Rye B chromosomes do not carry any gene (at least with qualitative effect) nor suppressor, nor promotor of homoeologous pairing, while it seems that they do in *Lolium* and *Aegilops* species.

ii.) Rye B chromosomes really carry this hypothetical gene or genes, but they would not be effective in the presence of rye A chromosomes; that is, *cereale* genome is epistatic on Bs, in the same way as in *Triticum* × *Aegilops* hybrids, in which B chromosome effect cannot be detected in the presence of 5B chromosome of *Triticum*, but it can in the absence of 5B (Vardi and Dover 1972; Dover and Riley, 1972a,b; Dover, 1974).

In order to eliminate one of these hypotheses, the *S. cereale* × *S. vavilovii* hybrids were backcrossed with *S. vavilovii*. If the second possibility were right, in the progeny (in which several *cereale* chromosomes would have been eliminated) one would be able to find plants in which the possible effect of B chromosomes would be manifested due to the segregation of those hypothetical epistatic genes.

From 32 plants obtained from backcrosses, 19 carried 2 Bs and in not one of them was a clear decrease in mean chiasma frequency observed. Nothing similar to segregation of a few loci could be established. There were no significant differences between plants with or without B chromosomes, although plants carrying Bs had a mean chiasma distribution displaced to low classes (Tables 4,5 and 6). Therefore, the second hypothesis can be rejected.

On several occasions it has been suggested that B chromosomes increase the variance of chiasma distribution (Jones and Rees 1967; Taylor and Evans 1976). This has been interpreted as being caused by interactions between Bs with different A genotypes. In connection with this fact, there are two matters to be considered from our results.

Firstly, the variance of mean chiasma distribution increases (Tables 4 and 5) but the distribution displacement is asymetrical because of the existence of a top for chiasma formation. Counting one chiasma for each pair of bounded arms at Metaphase I, no more than 14 chiasmata per cell can be counted in rye, or 13 due to translocation heterozygosity in this particular case. Therefore an increase of variance due to Bs can only be detected at low classes of the distribution; seeming then B chromosomes decrease meiotic pairing.

Secondly, from our results it seems that the increase of distribution variance is due to B chromosome interactions with *vavilovii* cytoplasm more than interactions with A chromosome genotpyes. In other words, in both the hybrids and backcrosses studied here, it can be assumed that cytoplasm has a greater effect than B chromosomes on homoeologous pairing (Tables 3 and 6). In addition, the interaction between Bs and *vavilovii* cytoplasm is apparent. The average mean of backcrosses carrying Bs in *cereale* cytoplasm (11.71) was almost identical to that of plants without Bs is any cytoplasm (11.73), while plants with Bs in *vavilovii* cytoplasm had an average mean (10.59) which differed from that of plants without Bs, with individuals ranging from 12.30 to 8.23 mean chiasma frequency.

All data of the present work are in agreement with the hypothesis that rye B chromosomes do not carry any qualitative gene controlling interspecific pairing. However, in backcrosses their quantitative effect was apparent when they were present in an alien cytoplasm. This does not necessarily mean that B chromosomes carry quantitative genes involved in pairing, because other non-genetic effects cannot be excluded.

In contradiction with this assumption, it would be possible that plants forming many univalents (34, 36 and 37 in Table 5) were those in which the hypothetical epistatic *cereale* gene or genes inhibiting B chromosome effect would have been eliminated. But this possibility can be rejected on two counts: first, not one plant with Bs in *cereale* cytoplasm existed with a low mean chiasma frequency; second, among plants with Bs in *vavilovii* cytoplasm, the variation of mean chiasma frequency was continuous, while if a qualitative gene were involved, another type of segregation would be found.

The question is then, how do B chromosomes and cytoplasm interact to decrease meiotic pairing? A possible coadaptation between B chromosomes and cytoplasm of the carrier species could be suggested but certainly with the data we have up to now, no hypothesis on the fine mechanisms involved can be made.

Our data together with that of Roothaan and Sybenga (1976) tend to reject the idea of any original relationship between B chromosomes and the genetic systems preventing homoeologous pairing in Triticineae, at least concerning rye B chromosomes.

Since the cytoplasm in interspecific pairing with B chromosomes seems to be very important, it would be worth stressing that further work on the matter should indicate the type of plant used as male or female parent. For instance, hybrids involving *Lolium* species as well as those involving *Triticum* and *Aegilops* (see Table 1) in which the effect of Bs has been revealed as drastic have been made (as far as we know) using as male parent the species carrying B chromosomes; thus, Bs on hybrids were in alien cytoplasm. What would occur with reciprocal crosses?

Finally, it is worth mentioning that the results obtained in this present work are indirect evidence for the process of preferential distribution of B chromosomes occurring normally in hybrids, both in *cereale* and *vavilovii* cytoplasm. That is, the offspring obtained from backcrosses was of a chromosome constitution of 14 or 14 + 2, but no plant of 14 + 1 was obtained. If non-disjunction and preferential distribution did not occur, no plant of 14 + 2, but all of 14 or 14 + 1, would be obtained. This might be an indication that this process was controlled by the B chromosome itself.

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Jahuar (1977) reports absence of influence of B chromosomes on mean chiasma frequency of *Lolium* and *Festuca* hybrids when Bs were contributed by the female parent. This result is in clear agreement with our conclusions. Jahuar, P.P., 3rd Int. Congr. SABRAO (1977).