GENETIC CONTROL OF MEIOTIC PAIRING IN RYE

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Received 27.vii.81

SUMMARY

Meiotic pairing in euploid rye-triticale hybrids (*ABRR*, $2n = 28$) is compared with that in three hypoaneuploid *ABRR* hybrids, two with $2n = 26$ chromosomes and one with $2n = 27$, also obtained from the cross triticale by rye. The results show that the application of hypoaneuploidy compensated by homoeologous chromosomes is useful in the study of genetic control of meiotic pairing in diploid species. The aneuploid with $2n = 27$ chromosomes was identified as mono-5R by C-banding; its meiotic pairing indicated that chromosome 5R of rye is a strong promoter of homologous rye pairing and is also able to influence non-homologous (probably homoeologous) wheat chromosome pairing. This result reinforces Feldman's (1968) view that the *Ph* locus of hexaploid wheat arose by mutation of a promoter gene.

1. INTRODUCTION

THE *A*, *B*, and *D* genomes of hexaploid wheat (*Triticum aestivum*, $2n = 6x = 42$) derive from three different but related diploid species ($2n = 2x = 14$) within the subtribe Triticinae (Kihara, 1919; Sax, 1922; McFadden and Sears, 1946; Riley, Unrau and Chapman, 1958; Feldman, 1978). The corresponding homoeologous chromosomes of the three different genomes are genetically closely related, as shown by their ability to compensate for each other in nullisomic-tetrasomic combinations (Sears, 1952). Consequently, loss of chromosome segments, as in ditelocentrics, or even whole chromosomes, as in monosomics and nullisomics, can be tolerated. This has allowed the detection of the genetic systems controlling meiotic pairing, located on chromosomes 5B (Okamoto, 1957; Sears and Okamoto, 1958; Riley and Chapman, 1958) and 3D (Mello-Sampayo, 1971).

The genetic control of meiosis in diploid species has been studied by the use of meiotic mutants (Baker *et al.*, 1976), but an analysis similar to that in hexaploid wheat has not been possible since nullisomics or monosomics are lethal. However, monosomy or nullisomy can be tolerated by diploid species when compensating homoeologous chromosomes are present. Such compensated aneuploids would allow a study of factors involved in genetic control of meiosis in diploids.

To test the effect of the missing chromosomes in hypoaneuploids on meiotic pairing, comparison is made between the pairing observed in euploid rye-triticale hybrids (*ABRR*, $2n = 28$) and that of three hypoaneuploid *ABRR* hybrids. Such hybrids, of course, may not be considered diploids *sensu strictu*, but almost all pairing involves two sets of rye chromosomes.

2. MATERIAL AND METHODS

Two aneuploid *ABRR* hybrids with $2n = 26$ chromosomes and five *ABRR* euploid hybrids with $2n = 28$ chromosomes, obtained from the cross hexaploid triticales (*AABRRR*; $2n = 6x = 42$) by *Secale cereale* (*RR*, $2n = 14$) and kindly supplied by Dr Lacadena, were analyzed. Three lines (1, 2, and 3) of *ABRR* euploid hybrids ($2n = 28$) and one aneuploid with $2n = 27$ (detected in line 2) were obtained from the following crosses:

Line 1, five plants; "Cachirulo" triticales (*AABRRR*, $2n = 6x = 42$) $\times$ *S. cereale* cv. "Ailés" ($2n = 14$).

Line 2, six plants; "Cachirulo" triticales $\times$ *S. cereale* cv. "JNK" without *B*-chromosomes ($2n = 14$).

Line 3, six plants; "Cachirulo" triticales $\times$ *S. cereale* cv. "JNK" with *B*-chromosomes ($2n = 14 + 2B$, and $2n = 14 + 4B$). All plants in this line carried two *B*-chromosomes ($2n = 28 + 2B$).

These lines were *C*-banded using the procedure of Giráldez *et al.* (1979).

3. RESULTS

(i) *Meiotic pairing*

The pairing data obtained in both euploid and aneuploid hybrids are presented in table 1. In the euploid hybrids some rye chromosomes failed to pair, and some wheat chromosomes were involved in homoeologous pairing; the latter can be inferred from the occurrence of PMCs with less

TABLE 1

Mean values of meiotic pairing in euploid and aneuploid ABRR hybrids both obtained from the cross hexaploid triticales (AABRRR) by Secale cereale (RR) and studied using the Feulgen technique

Pairing	Euploid <i>ABRR</i> hybrids ($2n = 28$)*	Aneuploid <i>ABRR</i> hybrids ($2n = 26$)	
		1042	1606
Bivalents	6.65 ± 0.14	5.08 ± 0.25	2.93 ± 0.30
Trivalents	0.17 ± 0.04	0.06 ± 0.05	0.02 ± 0.03
Quadrivalents	0.02 ± 0.01	—	0.01 ± 0.02
Bound arms	9.03 ± 0.20	6.65 ± 0.36	3.23 ± 0.35
PMCs with less than seven associations, %	37.83	85	100
PMCs with less than fourteen univalents, %	37.01	15	2
Total PMCs	489	100	100

* The number of PMCs analyzed per plant was respectively 100 in three cases and 91 and 98 in the other two.

than fourteen univalents and from the occurrence of trivalents and quadrivalents. We assumed that multivalent associations did not include rye-rye translocations, since if this was the case there would be a higher frequency of quadrivalents than trivalents, but this was not so.

Aneuploid hybrids show lower pairing levels than euploid hybrids. Assuming that the two missing chromosomes have no effect on the pairing

Plate I

FIG. 1.—Metaphases I of a mono-5R ABRR plant ($2n=27$) obtained from the cross “Cachirulo” triticale by *Secale cereale* cv. “JNK” without B-chromosomes and stained with C-banding. (a) 6 rye bivalents, 1 wheat bivalent (chromosomes are already at anaphase I), 12 wheat univalents and chromosome 5R as univalent (arrow) showing its secondary constriction and its subterminal C-band (this chromosome also shows a telomeric band on the short arm). (b) 1 rye bivalent and 25 univalents, centromere position (arrow) on the submetacentric chromosome 5R is indicated. Bar represents 10 μm .

of the remaining chromosomes, the following three alternatives could be expected: (1) If the two chromosomes lost were both from wheat (*A* or *B*) the expected pairing values would be very close to that of euploid hybrids; (2) if the missing chromosomes were one from rye and the other from wheat (*A* or *B*) the expected pairing values would be about six bivalents; (3) if two non-homologous rye chromosomes were lost there would be around five bivalents. The latter could be the case in aneuploid 1042 with a mean of 5.08 bivalents per cell. The possibility that two rye homologous chromosomes were lost is not considered, since, it assumes the formation of hypoaneuploid pollen grains. Aneuploid 1606 (2.93 bivalents per cell) differs greatly from any of the above predictions. This relatively low pairing suggests that one or both missing chromosomes in this aneuploid are required for a regular meiotic pairing of homologous rye chromosomes.

(ii) *C*-banding

The aneuploid with $2n = 27$ chromosomes detected in line 2 was shown to be monosomic for a submetacentric rye chromosome, which appeared unpaired at metaphase I. Therefore, any of the three submetacentric chromosomes 4R/7R, 5R or 6R of the rye complement could be involved in the monosomy. Two cytological markers, namely, a secondary constriction frequently observed (Bielig and Driscoll, 1970) and a thin subterminal heterochromatic band (Darvey and Gustafson, 1975; Giráldez *et al.*, 1979) both in the long arm (fig. 1) indicated that the unpaired submetacentric chromosome corresponded to 5R.

The pairing levels are clearly lower in the mono-5R plant than in euploid hybrids (table 2), especially those referring to bound arms per cell. The

TABLE 2

Mean values of meiotic pairing in three euploid ABRR lines ($2n = 28$) and one mono-5R ABRR plant ($2n = 27$) obtained from the cross hexaploid triticale (AABRRR) by Secale cereale (RR) and analyzed using C-banding. Line 3 carries 2 B-chromosomes of rye

Pairing	Euploid ABRR lines*			Aneuploid mono-5R
	1	2	3	
Rye bivalents	6.44 ± 0.06	6.49 ± 0.06	6.63 ± 0.04	4.07 ± 0.16
Rye bound arms	10.84 ± 0.15	10.28 ± 0.15	11.18 ± 0.12	5.20 ± 0.24
Wheat bivalents	2.06 ± 0.11	2.41 ± 0.09	2.25 ± 0.09	0.82 ± 0.10
Wheat bound arms	2.42 ± 0.14	2.90 ± 0.12	2.62 ± 0.11	0.90 ± 0.11
Wheat-rye associations (biv. + triv.)	0.11 ± 0.03	0.01 ± 0.01	0.02 ± 0.01	0.01 ± 0.01
Total PMCs	500	740	750	235

* In line 1 100 PMCs per plant were analyzed, in line 2 100 PMCs per plant in four and 90 and 250 in the other two plants, and in line 3 100 PMCs per plant in five plant and 250 in the other one.

mean values of bound arms decreased to 50 per cent for rye homologous pairing and to 65 per cent for homoeologous wheat pairing. Such data clearly indicate that the 5R chromosome is both a strong promoter of preferential homologous pairing, and also affects homoeologous pairing in these rye-triticale hybrids.

4. DISCUSSION

From the results it is evident that hypoaneuploidy may be tolerated when homoeologous chromosomes are also present to compensate for the deficiency. The localization of genetic factors controlling meiotic pairing in hybrids may be achieved using such chromosome combinations.

The three aneuploids probably originated in triticales, the female parent; the reasons for drawing this conclusion are (1) pairing failure, which mainly affects rye chromosomes, is frequent in triticales (Scoles and Kaltsikes, 1974); (2) compensation of the missing chromosomes by homoeologous chromosomes may be possible; (3) it is improbable that hypo-haploid gametes were formed in the pollen.

The differences observed between the mono-5R plant and euploid *ABRR* hybrids in meiotic pairing indicate that chromosome 5R is a strong promoter of rye homologous pairing. One dose of 5R apparently is not enough to meet all requirements, and its deficiency is not compensated by any of the wheat chromosomes present.

The results observed in aneuploid 1606 suggest that one (or two) chromosome(s) controlling preferential homologous rye pairing were lost. Although there are wheat chromosomes which carry factors promoting meiotic pairing (Sears, 1976), these were probably not lost; if rye promoter chromosomes were also present the expected pairing would be more than that observed. This is supported by the high level of rye pairing observed in plants (0-7)*A*(0-7)*BRR* carrying 6, 7, and 8 wheat chromosomes (Naranjo and Lacadena, 1980). Therefore, the chromosome(s) lost in aneuploid 1606 is probably a rye chromosome. We do not know whether there is any other rye chromosome besides 5R affecting rye meiotic pairing. However, on the basis of the most likely constitution of the 1042 aneuploid, as suggested by its meiotic pairing, it seems that some other rye chromosomes have no effect on pairing.

Chromosome 5R also promotes homoeologous pairing between wheat chromosomes as can be deduced from the decrease observed in the mono-5R plant. This activity may be included among the promotive effects of rye chromosomes on wheat homoeologous pairing (Miller and Riley, 1972; Riley, Chapman and Miller, 1973; Lelley, 1976; Dvorak, 1977; Bernard and Bernard, 1978; Jouve and Montalvo, 1978; Naranjo, Lacadena and Giráldez, 1979). Riley, Chapman and Miller (1973) suggest that the rye promotive effect is mediated by chromosome 5R and more specifically by its short arm, the suppressor activity detected in the long arm being lower in effectiveness. On the other hand, Lelley (1976) suggests that in the rye species *Secale cereale* and *S. montanum* the promoter system of homeologous pairing consists of more than two alleles and may be located on different chromosomes.

The euploid hybrids show lower total pairing levels (6.65 bivalents per cell) than the C-banded euploid hybrids (8.50, 8.90, and 8.88). Likewise, differences exist between the above values and those obtained by different authors. Lelley (1975) reported 5.77, 6.39, and 6.83 bivalents per cell respectively for three different *ABRR* genotypes; Bernard and Bernard, (1978) 7.9 bivalents per cell; Jouve and Montalvo, (1978) 6.7, 8.8 and 9.5 bivalents per cell respectively for three plants derived from the same cross. Soler *et al.* (1980) reported data showing differences affecting both

homologous and homoeologous pairing. Homologous pairing variation may be correlated with the presence or absence of rye telomeric heterochromatin (Merker, 1976; Naranjo and Lacadena, 1980).

It is also worth mentioning that the indiscriminate promotive activity of pairing (homologous and homoeologous) of chromosome 5R differs from that of the *Ph* locus of hexaploid wheats, which acts as a suppressor of homoeologous pairing (Okamoto, 1957; Sears and Okamoto, 1958; Riley and Chapman, 1958) and, therefore the genetic system located on chromosome 5R is essentially different from *Ph*. Three likely sources of *Ph* have been suggested (Dover and Riley, 1972): (1) it was already present in the diploid species from which the B genome was derived, (2) it appeared by transfer from an accessory chromosome to chromosome 5B, (3) it originated by mutation some time after the formation of the *AABB* polyploid. In relation to the first possibility, suppressors have been detected in diploids but none with a power similar to *Ph* (Sears, 1976). On the other hand, contradictory results concerning a possible suppressor activity of chromosome 5R have been reported by Bielig and Driscoll (1970) and Riley, Chapman and Miller (1973). Origin by mutation includes two possibilities: duplication or greater multiplication of the locus which contains a suppressor gene (Sears, 1976) and mutation of a promoter gene to *Ph* (Felman, 1968). Our results indicate that a promoter activity with similar intensity but different character to that of *Ph* is present in diploid rye and it is located on the same homoeologous group as *Ph*. On the assumption that other diploid species in the Triticinae are probable carriers of genetic systems like that of chromosome 5R, which control their meiotic pairing, the idea that mutation of a promoter gene may be the origin of *Ph* is realistic.

Acknowledgments.—We thank Dr Lacadena for supplying a sample of *ABRR* hybrids and Dr Rubio for his helpful comments.

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