MOST OF THE HOMOEOLOGOUS PAIRING AT METAPHASE I IN WHEAT-RYE HYBRIDS IS NOT CHIASMATIC

JUAN ORELLANA

Departamento de Genética, Facultad de Biología, Universidad Complutense, 28040 Madrid, Spain

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ABSTRACT

The use of telomeric C-bands in wheat-rye hybrids has made it possible to distinguish three types of wheat-wheat ($1B^L$) and wheat-rye associations (*a*, end-to-end extremely distal; *b*, end-to-ed distal; and *c*, interstitial) between homoeologous chromosomes at different metaphase I stages (early, middle and late) and also to estimate the actual recombination frequencies for such associations at anaphase I. There was a decrease of the *a* and *b* association frequencies during the different metaphase I stages, whereas the *c* type remained without variation in all stages. A good fit between the frequencies of *c* associations at metaphase I and the number of recombinant chromosomes at anaphase I, assuming a maximum of one chiasma per bond, was found; however, there was no correspondence between metaphase I and anaphase I data when all associations ($a + b + c$) were considered. In addition, rye-rye homologous pairing was observed at metaphase I, but no evidence for rye-rye recombination was found at anaphase I. The results indicate that most of end-to-end (*a* and *b*) homoeologous and nonhomologous associations are actually nonchiasmatic and are a remnant of prophase pairing.

IT generally has been believed that the number of associations between chromosome arms at metaphase I is equivalent to chiasma formation frequency (earlier meiotic stages, such as diplotene, that might give more precise indications are unreliable in higher plants). This assumption has lead many cytogeneticists and breeders to accept the idea that homoeologous pairing frequency in interspecific hybrids is a good reflection of genetic transfer between two species. However, as it has been pointed out by JONES (1978), this equating is notoriously imprecise due to the highly condensed state of the bivalents at metaphase I. In addition, careful studies comparing metaphase I bound arms and anaphase I recombinant chromosomes for specific chromosomal markers detected by C-banding in rye have demonstrated that the number of bound arms at metaphase I is not equivalent to the actual number of chiasmata (crossing overs) formed at first meiotic prophase, because more than one chiasma per bond could be formed in some chromosomes (GIRALDEZ and ORELLANA 1979; ORELLANA and GIRALDEZ 1981). Moreover, in desynaptic plants there is clear evidence that some of the bonds appearing at metaphase I are

nonchiasmatic and are simply a remnant of prophase pairing (ORELLANA and GIRALDEZ 1983, 1984).

The meiotic behavior of wheat-rye hybrids has been analyzed extensively at meiosis (for a review, see CUADRADO and ROMERO 1984), and a polygenic control of rye chromosome pairing has been postulated (LELLEY 1976; DVOŘÁK 1977); however, no study has been made of the relationship between wheat-rye homoeologous pairing and wheat-rye recombination. This probably has been due to an inability to distinguish between wheat and rye chromosomes at meiosis by conventional staining methods. The high levels of homoeologous pairing reported in many cases and the low frequency of gene transfers obtained in most breeding programs seems to indicate, indirectly, that there is a great discrepancy between pairing and recombination in wheat-rye plants. This is true in spite of the fact that lines without chromosome *5B* or *ph* mutant plants are normally used for obtaining the hybrids (see KNOTT and DVOŘÁK 1976).

For measuring the relationship between the frequency of chromosome associations and the frequency of chiasmata (crossing over), a system of morphologically marked chromosomes is needed that will allow one to unambiguously distinguish rye chromosomes, wheat chromosomes and their recombinant forms. The rye genome has each chromosome marked in one or both arms with telomeric heterochromatin (see WEIMARCK 1975; GIRALDEZ, CERMEÑO and ORELLANA 1979), whereas none of the wheat chromosomes possess telomeric heterochromatin except for chromosome *1B* (which can be distinguished from the rye chromosomes). The use of C-banding allows a clear recognition of the telomeric heterochromatin. These experimental features have been utilized in this study to examine the frequency of wheat-rye associations and to compare these frequencies with the frequency at anaphase I of recombinant rye chromosomes that had exchanged a piece of rye chromatid for a piece of wheat chromatid. The aim of this work was to study the nature of the different morphologically distinguishable metaphase I associations and their relationships with the recombination processes in wheat-rye hybrid plants.

MATERIALS AND METHODS

Four types of wheat-rye hybrid plants obtained from the crosses between diploid rye cv. Merced (genome constitution *RR*) and three different lines of hexaploid wheat cv. Chinese Spring (genome constitution *AABBDD*) formed the material for this study. The wheat lines used were monosomic plants for chromosome *5B*, nullisomic for chromosome *5B* and tetrasomic for chromosome *5D* and *ph* mutant euploid plants. These lines were crossed as females with only one plant or rye (homozygous for telomeric C-bands in all chromosomes) as the male in order to obtain different wheat-rye genome combinations—namely, *ABDR*, *ABDR − 5B*, *ABDR − 5B + 5D*, *ABDR(ph)*—with the same rye genetic background.

For meiotic cells, anthers were fixed in acetic acid:ethanol (1:3) and were stored at 0–4° for 2 months. The fixed material was squashed and stained following the Giemsa C-banding technique described previously (GIRALDEZ, CERMEÑO and ORELLANA 1979).

In all wheat-rye hybrid plants obtained from the cross between the *ph* mutant and rye, the mean number of bound arms per cell for each type of pairing (wheat-wheat, wheat-rye and rye-rye) and the pairing of each identified bivalent arm at metaphase I were scored in anthers in which at least 50% of the meiocytes were in an earlier stage than metaphase I (early metaphase

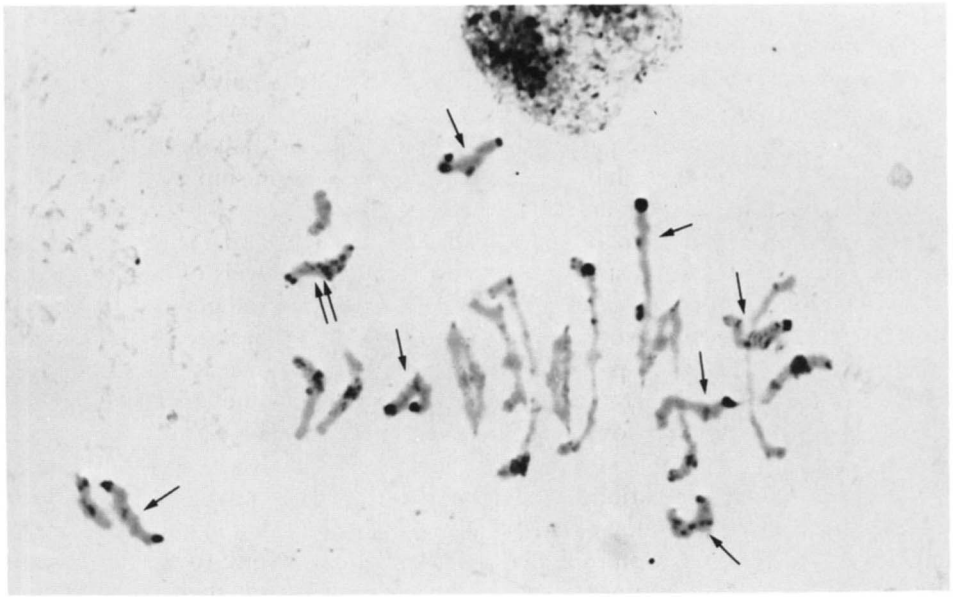

FIGURE 1.—C-banded metaphase I cell of a *ABDR(ph)* wheat-rye hybrid plant. Arrows indicate rye chromosomes. Double arrow indicates wheat chromosome *1B*.

I), in anthers in which all cells were at metaphase I (middle metaphase I) and in anthers in which at least 50% of the cells were in a later stage than metaphase I (late metaphase I). In the other wheat-rye hybrids it was only possible to score middle metaphase I.

In all cases the number of bound arms are equivalent to the minimum number of chiasmata that explain each meiotic configuration. The chromosome nomenclature used was the one proposed at the workshop on rye chromosomes nomenclature and homoeology relationships held at Wageningen, The Netherlands (SYBENGA 1982).

RESULTS

The C-banding technique makes it possible to distinguish rye and wheat chromosomes at meiosis, because C-bands are preferentially located in the telomeres of rye chromosomes, but are pericentric and scattered throughout the chromatids in wheat (Figure 1).

Using the C-bands as cytological markers, it is possible to estimate the frequencies of wheat-wheat or wheat-rye homoeologous (Figure 2) and rye-rye nonhomologous (Figure 3) associations in all metaphase I configurations of the different wheat-rye hybrid plants.

Table 1 shows the average of the different wheat-wheat, wheat-rye and rye-rye meiotic configurations observed in metaphase I. As mentioned above, in *ph* mutants the three metaphase I stages (early, middle and late) were separately scored. As expected, the absence of chromosome *5B* in *ABDR − 5B* and *ABDR − 5B + 5D* hybrids or the suppression of *Ph* activity in *ABDR(ph)* plants produces an increase of wheat-wheat and wheat-rye types of homoeologous pairing (see SEARS 1976).

Bound arms loss during metaphase I: As in the *ABD(ph)* hybrids, the mean

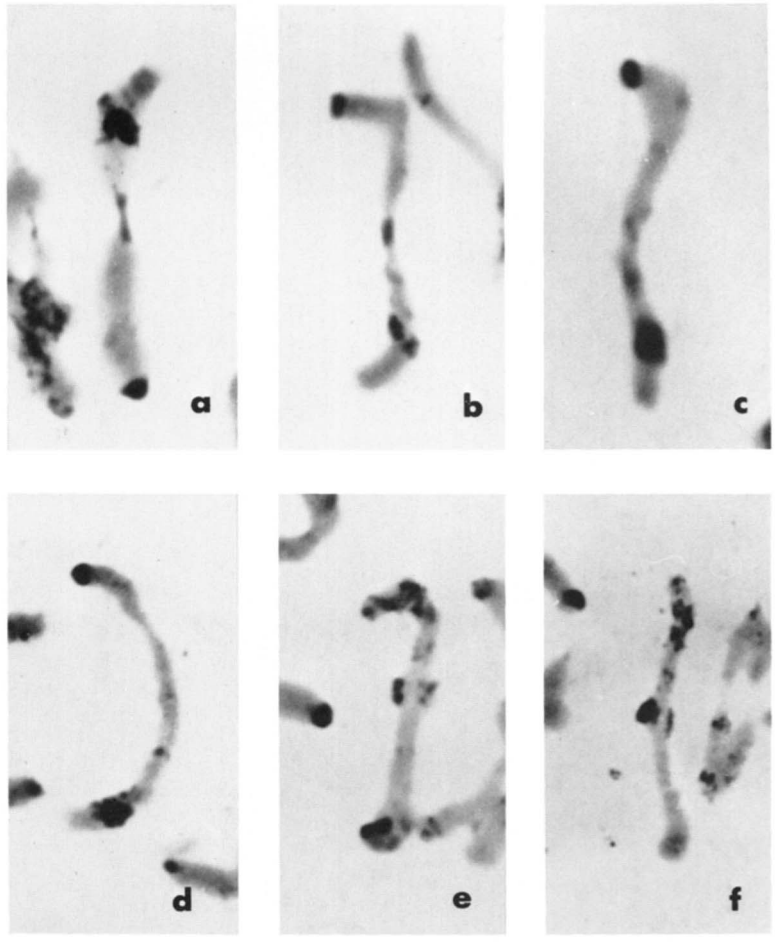

FIGURE 2.—Metaphase-I configurations formed between homoeologous chromosomes. *a* and *b*, End-to-end very distal euchromatic-heterochromatic wheat-rye associations (type *a*); *c* and *d*, end-to-end euchromatic-euchromatic wheat-rye associations (type *b*); *e*, interstitial $1B^L$-$1R^L$ association (type *c*); *f*, interstitial $1B^L$-wheat association (type *c*).

number of wheat-wheat and wheat-rye bound arms per cell was estimated at early, middle and late metaphase I stages; it could be observed (Table 1) that these types of homoeologous pairing decreased as metaphase I progressed. In all cases the differences were significant at the 1% level when paired *t* tests were performed; $t_5 = 27.0359$ for wheat-wheat and $t_5 = 79.1018$ for wheat-rye between early-middle; $t_5 = 13.6877$ for wheat-wheat and $t_5 = 54.9885$ for wheat-rye between middle-late and $t_5 = 32.4924$ for wheat-wheat and $t_5 = 46.3799$ for wheat-rye between early-late metaphase I stages. Rye-rye nonhomologous associations have not been considered in this analysis due to their low frequency.

The use of C-banding technique has allowed for the identification of both arms of the following chromosomes at different metaphase I stages: *1R* (sub-

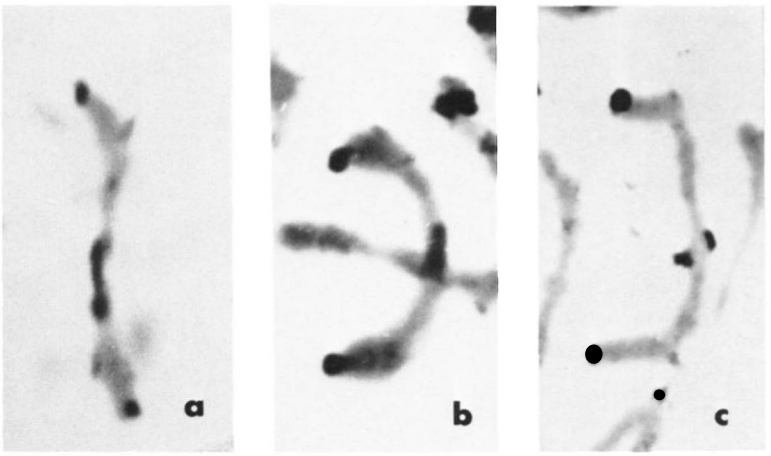

FIGURE 3.—Metaphase-I configurations showing nonhomologous pairing between rye chromosomes. *a*, End-to-end very extreme association (type *a*); *b*, end-to-end association (type *b*); *c*, interstitial association (type *c*).

metacentric with telomeric C-bands in both arms and the nucleolar organizer region in the short arm) (Figures 1 and 2e), *4R*, *5R* and *6R* (with C-bands only in the short arms) (Figure 2c and d) and *1B* (with disperse perirentric heterochromatin and a thin telomeric C-band in the long arm) (Figures 1, 2e and f, 4a and d). Chromosomes *2R*, *3R* and *7R* (metacentrics with C-bands in both arms) (Figure 2a and b) can be differentiated from wheat ones, but not from one another (see Figure 1); therefore, pairing frequencies of specific arms could not be ascertained, and the data for these three chromosomes were pooled.

Moreover, it has been possible to distinguish three types of bonds at metaphase I according to the wideness of the joined regions between the chromosomes associated; namely *a*, end-to-end extremely distal associations (these bonds have been considered in many cases as "debil" chiasmata) (see Figures 2a and b, 3a); *b*, end-to-end distal associations (see Figures 2c and d, 3b); and *c*, interstitial associations (see Figures 2e and f, 3c).

Table 2 shows the total *a*, *b* and *c* bound arm frequencies for the distinguishable chromosome arms in the different types of wheat-rye hybrids analyzed. It is worth noting that the probability of wheat-wheat and wheat-rye pairing is different for each specific chromosome arm, and in all cases this frequency is higher at early metaphase I than it is at the middle and late stages for bonds of types *a* and *b*, whereas the frequency of the type *c* is rather constant at the early and middle stages and somewhat lower at the late stage. These results indicate that in the *ABDR(ph)* plants there is a clear loss of bound arms during the different metaphase I stages (early, middle and late) for all bivalents identified.

The relationship between homoeologous pairing and anaphase I recombination: The absence of telomeric C-bands in wheat chromosomes (except in $1B^L$ chromosome arm) and their presence in most rye chromosome arms (see Figure 1)

TABLE 1

Average of the different wheat-wheat, wheat-rye and rye-rye meiotic configurations observed at metaphase I in all wheat-rye plants analyzed

Genome constitution	Meta-phase I stage	Type of pairing: Wheat-wheat IV	III	R	O	U	Bonds/cell[a]	Wheat-rye IV	III	R	O	U	Bonds/cell	Rye-rye O	Bonds/cell	No. of cells
ABDR	Middle		0.19	0.31	2.28	15.16	3.32		0.01		0.10	6.84	0.11	0.03	0.03	200
ABDR − 5B	Middle	0.003	1.39	1.72	2.28	7.14	9.08	0.03	0.07		0.48	6.31	0.57	0.06	0.06	200
ABDR − 5B + 5D	Middle	0.013	0.96	0.95	2.20	7.69	9.85	0.01	0.02		0.52	6.34	0.55	0.05	0.05	150
	Early	0.063	1.58	2.54	2.37	5.01	11.67	0.06	0.19	0.003	0.62	6.02	0.88	0.05	0.05	300
ABDR (ph)	Middle	0.040	1.23	2.02	2.58	7.16	9.76	0.05	0.11	0.003	0.42	6.36	0.42	0.03	0.03	300
	Late	0.006	0.76	1.83	2.97	8.73	8.41	0.01	0.04		0.25	6.70	0.29	0.003	0.003	300

Abbreviations: IV, Quadrivalents; III, trivalents; R, ring bivalents; O, open bivalents; and U, univalents.

[a] Only the associations between wheat chromosomes in wheat-rye quadrivalents or trivalents are included in this class.

allows one to estimate the amount of wheat-rye recombination at anaphase I. In this phase, two types of chromosomes can appear: (1) parental type—chromosomes in which both chromatids have the same C-heterochromatin constitution (Figure 4a) and (2) recombinant type—chromosomes in which each chromatid has a different C-heterochromatin constitution as a consequence of recombination (Figure 4b and d).

Eleven chromosome arms of rye and $1B^L$ of wheat could be analyzed at anaphase I. In Table 3 are shown the recombinant chromosome frequencies for these arms. The $4R^L$, $5R^L$ and $6R^L$ chromosome arms could not be studied at anaphase I due to the absence of telomeric C-bands in all of them.

Under the assumption of one chiasma per bond, one would expect a close correspondence between the frequencies of wheat-rye bound and unbound arms at metaphase I and the frequencies of recombinant (*Fr*) and parental (*Fp*) chromosomes at anaphase I.

When a comparison between the total ($a + b + c$) number of wheat-rye and $1B^L$-wheat associations at metaphase I and the number of wheat-rye and $1B^L$-wheat recombinant chromosomes at anaphase I was performed, an excess of anaphase I parental chromosome types was found (Table 4). However, when the comparisons were made only between bound arms of type *c* (assuming that *a* and *b* types are nonchiasmatic) and the number of recombinant chromosome type at anaphase I, there was a good fit in all cases (Table 5).

DISCUSSION

Homoeologous pairing: Usually, associations between two chromosome arms at metaphase I have been assumed to be a consequence of chiasma formation at first meiotic prophase. For this reason, in earlier studies on chromosome pairing of interspecific hybrids it was concluded that the number of bound arms at metaphase I, involving chromosomes of the two related species, must be a reflection of the number of chromosomal segments transferred between both species. However, this can only be tested if material with appropriate cytological markers are available. Such is the case with wheat-rye hybrid plants in which the telomeric C-bands of rye chromosomes can be used as markers, as has been done in this study.

If chromosome pairing at metaphase I was truly a reflection of crossing over, one would expect the results of this study to show a clear correspondence between the wheat-rye pairing frequency at metaphase I and the frequency of recombinant chromosomes at anaphase I, supposing a maximum of one chiasma per wheat-rye bond. However, there was a clear discrepancy, in all plants, between the total number of wheat-rye and $1B^L$-wheat homoeologous bound arms ($a + b + c$ types of bonds) at metaphase I and chromatid exchanges at first anaphase caused by an excess of anaphase I parental chromosome type (Table 4). These results can be explained if more than one chiasma per bond were formed or if some of the bonds were nonchiasmatic during metaphase I. If the first possibility were true, one would expect the appearance of rye chromosome arms without C-telomeric bands and wheat chromosome arms with telomeric C-bands of rye in both chromatids at anaphase I as a conse-

TABLE 2

Number of a, b *and* c *types of wheat-rye and* 1B*-wheat homoeologous associations observed at metaphase*

Genome constitution	MI stage	Chromo $1R^S$ a	b	c	$1R^L$ a	b	c	$4R^S$ a	b	c	$4R^L$ a	b	c	$5R^S$ a	b	c
ABDR	Middle					1					3	1				
ABDR − 5B	Middle				3	20	4			1	1	19	2			
ABDR − 5B + 5B	Middle					14	3		3	1		4	1		1	
ABDR (ph)	Early	2	3		12	19	4	7	8	2	12	19		2	3	
ABDR (ph)	Middle		1	1	3	13	5	2	8	2	5	14			2	
ABDR (ph)	Late				3	5	6	1	2	2	4	6	2			

quence of four-strand double crossing overs (complementary). These types of chromosomes have never been found in any hybrid, and consequently, it can be concluded that more than one chiasma per homoeologous bond did not occur. Nevertheless, there is a clear correspondence between metaphase I and anaphase I data when only bound arms of type *c* (with more interstitial localization) are considered (Table 5).

On the other hand, a bound arm loss from early until late metaphase I stages has been observed in *ABDR(ph)* hybrids (see Tables 1, 2 and 4), and that is a general feature either for wheat-wheat or wheat-rye homoeologous types of pairing. The bonds lost do not seem to be due to chiasma terminalization because univalents and rod bivalents showing evidence of recombination have not been observed at metaphase I.

The possibility to distinguish three types of pairing (*a*, *b* and *c*) that differ in the degree of association between two chromosome arms allows one to study the evolution of such associations during early, middle or late metaphase I stages in *ABDR(ph)* hybrids. As shown in Table 2, the frequencies of *a* and *b* types of pairing decreased as metaphase I progressed, whereas the number of *c* associations are very similar during all metaphase I stages.

The maintenance of *c* associations during metaphase I and their correspondence with the recombinant chromosomes at anaphase I indicate that such associations are really chiasmata. However, *a* and *b* ones are probably nonchiasmatic, and their dissociations result in the observed decrease in bound arms.

Most of *a* and *b* wheat-rye bonds at metaphase I are end-to-end associations involving heterochromatic and euchromatic ends (see Figure 2) due to the presence of prominent telomeric C-bands in eleven rye chromosome arms and to the absence of such bands in wheat chromosomes (except in $1B^L$ chromosome arm). If these associations were really chiasmata, then crossing over would have to occur between euchromatic and heterochromatic regions; however, it usually has been considered that chromosomal exchanges do not form within Giemsa C-banded regions (FOX, CARTER and HEWITT 1973; HULTÉN 1974; MARKS 1974; JOHN 1976; JONES 1978), and no evidence for chiasmata within C-heterochromatin has been obtained in studies analyzing crossing over

I (MI) in all hybrids analyzed

some arm

$5R^L$			$6R^S$			$6R^L$			$2R + 3R + 7R$			$1B^S$			$1B^L$		
a	b	c	a	b	c	a	b	c	*a*	*b*	*c*	a	b	c	a	b	c
3	1	1				1	2	1	3	4		2			7	5	
3	16	1				1	10	2	6	23	2	4	4		8	35	2
2	14	1					15		4	15	5	2	2		4	25	8
11	37	6	3	1		13	19	3	22	45	12	11	17		24	50	21
4	33	4	1	1	2	5	16	3	4	37	10	2	9		6	33	18
6	10	2				3	7	4	3	11	11	2	1		5	13	16

frequencies in rye cultivars heterozygous for certain blocks of C-heterochromatin (GIRALDEZ and ORELLANA 1979; ORELLANA and GIRALDEZ 1981).

Therefore the location of C-bands in many rye chromosome ends could lead to the exclusion of chiasmata formation at or near the chromosome ends. This fact gives further evidence suggesting that *a* and *b* associations may represent nonchiasmatic bonds as a remnant of prophase pairing. However, euchromatic-heterochromatic bonds of type *c* do not suffer such impediment, because they are located at rather interstitial sites and crossing over could be formed in euchromatic regions near the border of C-bands (see Figure 2e and f). This result is in agreement with those of JONES (1978) in *Secale* and LOIDL (1979) in *Allium*, both of whom demonstrated that meiotic crossing over can occur very close to C-banded heterochromatin. Probably many of euchromatic-euchromatic wheat-rye associations are nonchiasmatic also, but the impossibility of detecting recombination at anaphase I does not allow one to contrast metaphase and anaphase data.

Nonhomologous pairing: The C-banding procedure, however, has made it possible to detect a certain amount of rye-rye nonhomologous meiotic pairing at metaphase I (see Table 1, Figure 3). Rye-rye nonhomologous pairing seems to be a usual feature in wheat-rye hybrid plants (DHALIWALL, GILL and WAYNES 1977; SCHLEGEL and WERYSZKO 1979), although it occurs with low frequency.

In all polyhaploids analyzed in this work, only open bivalents have been found, the frequency of nonhomologous chromosome pairing being lower than it is in natural *S. cereale* haploids (MÜNTZING 1937; NORDESKIÖLD 1939; LEVAN 1942; HENEEN 1965; PUERTAS and GIRALDEZ 1979). As SCHLEGEL and WERYSZKO (1979) suggested, this may be explained, because in the haploid rye all meiotic pairing must occur between nonhomologous chromosomes, whereas in the wheat-rye hybrids a preferential homoeologous pairing takes place and decreases the relative frequency of rye-rye associations.

Most of rye-rye bonds are terminal associations (*a* and *b*) involving euchromatic or heterochromatic ends indiscriminately, and they disappear at the later stages of metaphase I (see Table 1); in addition, no rye-rye recombinant chromosome has been observed at anaphase I, therefore rye-rye nonhomologous associations could be considered nonchiasmatic.

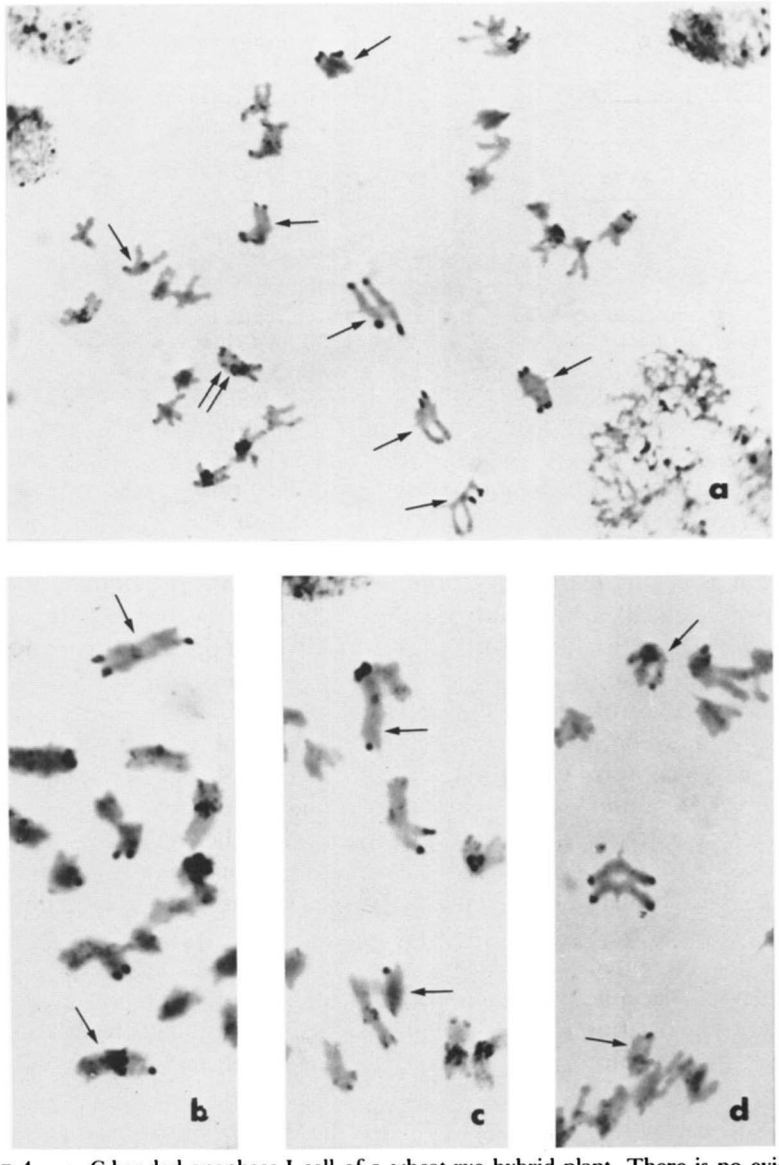

FIGURE 4.—*a*, C-banded anaphase-I cell of a wheat-rye hybrid plant. There is no evidence for wheat-wheat or wheat-rye recombination. Arrows indicate rye chromosomes. Double arrow indicates chromosome *1B*. *b* and *c*, Anaphase-I segregating chromosomes with evidence for wheat-rye recombination. Arrows indicate recombinant chromosomes. *d*, Anaphase-I segregating chromosomes with evidence for recombination between $1B^L$ and a wheat chromosome. Arrows indicate recombinant chromosomes.

Wheat-wheat nonhomologous pairing can also occur, but in this case the absence of cytological markers makes it impossible to study directly such hypothetical associations, if they exist. However, the meiotic configurations larger than trivalents, exclusively involving wheat chromosomes, could be taken as

TABLE 3

Frequencies of rye and 1B *recombinant chromosomes observed at anaphase I in all hybrids analyzed*

Genome constitution	Chromosome arm							No. of cells
	$1R^S$	$1R^L$	$4R^S$	$5R^S$	$6R^S$	$2R + 3R + 7R$	$1B^L$	
ABDR		*1*				*3*	*1*	*200*
ABDR − 5B		*3 (3)*				*8*	*7 (3)*	*200*
ABDR − 5B + 5D		*4 (3)*	*1*			*6*	*9 (3)*	*150*
ABDR (ph)		*4 (1)*	*2*		*1*	*9*	*21 (1)*	*300*

The numbers in brackets represent $1B^L - 1R^L$ recombinant chromosomes.

indirect evidence of nonhomologous pairing, since only three different homoeologous wheat genomes, *A*, *B* and *D*, are present in wheat-rye hybrids. In *ABDR(ph)* plants a certain frequency of quadrivalents was observed at early and middle metaphase I, but such observations are rare at the late stage (Table 1). These results could be explained not only in terms of nonhomologous pairing but also as a consequence of reciprocal translocations among wheat chromosomes. Thus, KOBREHEL and FEILLET (1975) and BENITO and PEREZ DE LA VEGA (1979), after studying the chromosomal location of peroxidase structural genes in wheat, have proposed the existence of reciprocal translocations involving the $7B^S$, $4B^L$ and $7A^S$ chromosome arms. In this work it is impossible to discern between both possibilities; probably the best way to solve this point would be to make a meiotic analysis of wheat-rye hybrids with telocentric chromosomes for homoeologous groups 4 and 7.

It seems that nonhomologous bonds are mainly located in terminal or subterminal regions (types *a* and *b* of this work), and they have been referred to as "anomalous" chiasmata (WHITE 1973), but, unfortunately, no study determining their chiasmatic or nonchiasmatic nature has been made previously in plants.

The results obtained in this work support rather well the existence of nonchiasmatic associations between wheat and rye chromosomes at metaphase I. This type of association is well known in nonchiasmatic organisms where chromosomes remain paired until anaphase I (see JOHN and LEWIS 1965; GALUBOVSKAYA 1979).

Rye can be considered a good source of potentially valuable genes to transfer into wheat, since the species of this genus cross rather easily with wheat and there is a comparatively high degree of wheat-rye homoeologous chromosome pairing (see CUADRADO and ROMERO 1984). However, recombination between wheat and rye chromosomes detected by breeding experiments is very low, even when *Ph* activity does not occur. In spite of this, there is considerable evidence indicating the close genetic relationship between wheat and rye, because rye chromosomes can compensate genetically for their wheat homoeologs (RILEY 1965). In addition, there are many DNA segments with very close comparable nucleotides sequences between wheat and rye species (FLAVELL, RIMPAU and SMITH 1977).

TABLE 4

Comparison between the total number of bound arms (a + b + c) *at metaphase I and the frequencies of recombinant chromosomes at anaphase I, assuming a maximum of one chiasma per bond*

		Wheat-rye					$1B^L$-wheat				
		Metaphase I		Anaphase I[a]			Metaphase I		Anaphase I		
Genome constitution	MI stage	*a + b + c*	Not bound	*Fr*	*Fp*	χ^2	*a + b + c*	Not bound	*Fr*	*Fp*	χ^2
ABDR	Middle	8	2192	4	2196	1.34	12	188	1	199	9.62**
ABDR − 5B	Middle	59	2141	11	2189	33.45**	45	155	4	196	39.10**
ABDR − 5B + 5D	Middle	46	1604	11	1639	21.87**	37	113	6	144	26.09**
ABDR (ph)	Early	145	3155	16	3284	105.94**	95	205	20	280	60.51**
ABDR (ph)	Middle	90	3210	16	3284	52.50**	57	243	20	280	20.40**
ABDR (ph)	Late	44	3256	16	3284	13.19**	34	266	20	280	3.99*

[a] *Fr* represents the recombinant and *Fp* represents the parental chromosomes, respectively.
*Significant at the level of 5%; **significant at the level of 1%.

TABLE 5

Comparison between the number of c *associations at metaphase I and the frequencies of recombinant chromosomes at anaphase I, assuming a maximum of one chiasma per bond*

		Wheat-rye					$1B^L$-wheat				
		Metaphase I		Anaphase I[a]			Metaphase I		Anaphase I		
Genome constitution	MI stage	*c*	Not bound + *a* + *b*	*Fr*	*Fp*	χ^2	*c*	Not bound + *a* + *b*	*Fr*	*Fp*	χ^2
ABDR	Middle		2200	4	2196			200	1	199	
ABDR − 5B	Middle	7	2193	11	2189	0.89	2	198	4	196	
ABDR − 5B + 5D	Middle	9	1641	11	1639	0.20	8	142	6	144	0.30
ABDR (ph)	Early	27	3273	16	3284	2.83	21	279	20	280	0.03
ABDR (ph)	Middle	27	3273	16	3284	2.83	18	282	20	280	0.11
ABDR (ph)	Late	27	3273	16	3284	2.83	16	284	20	280	0.47

[a] *Fr* represents the recombinant and *Fp* represents the parental chromosomes, respectively.

The existence of nonchiasmatic bonds between wheat and rye chromosomes reported in this study may largely explain the reduced gene transfer found between the chromosomes of both species, despite the high levels of homoeologous pairing observed. It is now clear that equating the frequencies of bound arms at metaphase I to chiasma frequencies leads to large errors in the estimation of crossing over frequency. These results should be taken into account by breeders who try to introduce genetic variability by inducing homoeologous pairing.

The appearance of nonchiasmatic bonds at metaphase I is a phenomenon associated with desynapsis (see CERMEÑO, ORELLANA and LACADENA 1984), and they could represent a suggestive mechanism to assure regular chromosome segregation at meiosis when chiasmata associations are reduced or even lacking. This mechanism may be related to the processes of chromosome pairing, and further studies concerning the synapsis initiation sites and the interaction between C-heterochromatin and synaptonemal complex and chiasma formation are required.

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