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PAIRING COMPETITION BETWEEN IDENTICAL AND HOMOLOGOUS CHROMOSOMES IN AUTOTETRAPLOID RYE. I. SUBMETACENTRIC CHROMOSOMES

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ABSTRACT

Meiotic pairing preferences between identical and homologous but not identical chromosomes were analyzed in ten induced tetraploid/diploid chimaeral rye plants (*Secale cereale*) heterozygous for telomeric heerochromatin C-bands in both arms of chromosome *1R*. These plants were the progeny of two crosses between only one plant of cv. Petkus, used as male, and two plants of the inbred lines E and R, respectively. Different pairing preferences for chromosome *1R* were found: (1) between plants, (2) between chromosome arms within the same plant and (3) between bivalents and multivalents within the same plant. The possible influence in the preferences of several factors such as differences in C-heterochromatin content in the chromosomes analyzed, specific genetic control and independence in pairing behavior between both arms and partner exchange is discussed.

MOST theoretical models concerning chromosome pairing in autotetraploids assume that the four chromosomes of each set are paired at random (absence of pairing preferences) at pachytene (JOHN and HENDERSON 1962; SYBENGA 1975; JACKSON and HAUBER 1982). This assumption has probably been made because of the impossibility of distinguishing among specific chromosome arms at meiosis by conventional stain techniques.

The application of C-banding techniques to chromosomes of rye has revealed the existence of wide variation in the presence or absence of telomeric C-bands in most of the members of the complement (WEIMARCK 1975; GIRALDEZ, CERMEÑO and ORELLANA 1979). This fact allows us to obtain plants in which the identification of specific chromosome arms at meiosis is possible.

Pairing preferences can be analyzed in autotetraploids if at least one of the four homologous chromosomes shows a different C-banding pattern. If a diploid plant in which a given homologous chromosome pair is heterozygous for telomeric C-bands in both arms is polyploidized by colchicine treatment, diploid/tetraploid chimeras are produced. In the tetraploid cells, each set of four chromosomes is formed by two pairs of identical chromosomes; *i.e.*, each chromosome is accompanied by one identical and two homologous, but not necessarily identical, chromosomes. Then, identical and homologous pairing frequencies can be accurately estimated for the marked chromosome arms, be-

cause identical pairing takes place between chromosome arms whose C-banding patterns differ.

Pairing preferences in autotetraploid plants of rye were studied by SANTOS, ORELLANA and GIRALDEZ (1983). In that case, only the long and the short arms of chromosomes *1R* and *2R*, respectively, were marked with telomeric C-bands, and, consequently, information about pairing preferences in the other arms of these chromosomes was not available because their type of pairing in multivalent configurations could not be ascertained.

In the present study we analyzed the different pairing preferences found for both arms of chromosome *1R* in bivalent and multivalent configurations in induced tetraploid/diploid chimaeral rye plants.

MATERIALS AND METHODS

Rye plants of two F_1's (F_1 PetE and F_1 PetR) obtained in crosses between a single plant of diploid rye cv. Petkus, as female, and two plants of the inbred lines E and R formed the material for this study. The plant of Petkus was homozygous for the presence of telomeric C-bands in both arms of chromosome *1R*, whereas such C-bands were absent in this chromosome from the inbred lines E and R (GIRALDEZ, CERMEÑO and ORELLANA 1979). Hence all F_1 plants were heterozygous for C-bands in both arms of chromosome *1R*.

At the three-leaf stage, 20 seedlings per F_1 were treated with colchicine, using the technique described by THOMAS and PICKERING (1979). Ten of the treated plantlets turned out to be tetraploid/diploid chimeras: four of F_1 PetE and six of F_1 PetR.

Anthers of the emerging spikes were stained in 2% acetic orcein and squashed in 1% acetic orcein to determine their diploid or tetraploid chromosome constitution. Spikes that turned out to be tetraploid were fixed in 1:3 acetic ethanol and were stored at 4° for several months. The fixed material was squashed following the Giemsa C-banding technique described previously (GIRALDEZ, CERMEÑO and ORELLANA 1979).

RESULTS

All F_1 diploid rye plants obtained from the crosses between the plant cv. Petkus and the inbred lines E and R were heterozygous for telomeric C-heterochromatin in both arms of chromosome *1R* (Figure 1). In the tetraploid cells obtained by colchicine treatment of these plants were two identical chromosomes *1R* with telomeric C-bands (derived from Petkus) and two other identical ones in which the telomeric heterochromatin was absent (derived from E or R). This C-banding pattern and the special stain characteristics of the nucleolar organizer region located in the $1R^S$ chromosomes arm made it possible to identify all metaphase I configurations (bivalents and multivalents).

Table 1 shows the bound arm frequencies (minimum number of chiasmata necessary to explain the different configurations) for the short and the long arms of chromosome *1R* in bivalents and multivalents. Between-plant variation was observed for both arms, although the variation in the short arms, especially in bivalents, was most accentuated. The appearance of $1R^L$ mean values higher than two in multivalents can be explained by the existence of meiotic configurations in which four $1R^L$ arms are paired in the same chromosome region and, consequently, at least three chiasmata have occurred.

Identical and homologous pairing between chromosome arms $1R^L$ and $1R^S$

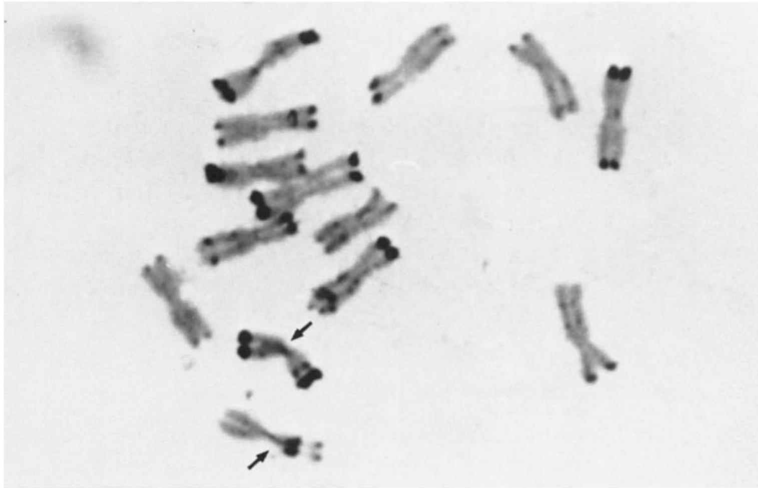

FIGURE 1.—C-banded somatic metaphase cell of the plant PetR12. Arrows indicate *1R* chromosomes.

TABLE 1

Bound arm frequencies at metaphase I (minimum number of chiasmata to explain each meiotic configuration) for $1R^S$ *and* $1R^L$ *chromosome arms in bivalents and multivalents*

Plant	Bivalents			Multivalents			Total bonds
	1R^S	*1R*^{L}	No. of cells	*1R*^{S}	*1R*^{L}	No. of cells	
PetE5	25 (0.45)	111 (1.98)	56	79 (1.20)	138 (2.09)	66	353
PetE12	30 (0.77)	75 (1.92)	39	24 (0.89)	67 (2.48)	27	196
PetE15	32 (0.62)	80 (1.51)	52	43 (1.16)	83 (2.24)	37	238
PetE16	87 (0.67)	242 (1.86)	130	90 (1.12)	164 (2.05)	80	583
PetR4	206 (0.84)	456 (1.86)	245	148 (1.28)	240 (2.07)	116	1050
PetR9	98 (0.69)	257 (1.81)	142	86 (1.09)	166 (2.10)	79	607
PetR11	22 (0.49)	82 (1.82)	45	13 (1.08)	25 (2.08)	12	142
PetR12	53 (1.06)	95 (1.90)	50	60 (1.09)	112 (2.04)	55	320
PetR14	53 (0.79)	122 (1.82)	67	46 (0.81)	141 (2.47)	57	362
PetR20	183 (0.63)	544 (1.88)	289	186 (1.00)	409 (2.20)	186	1322

The numbers in parentheses represent the bound arm mean per cell.

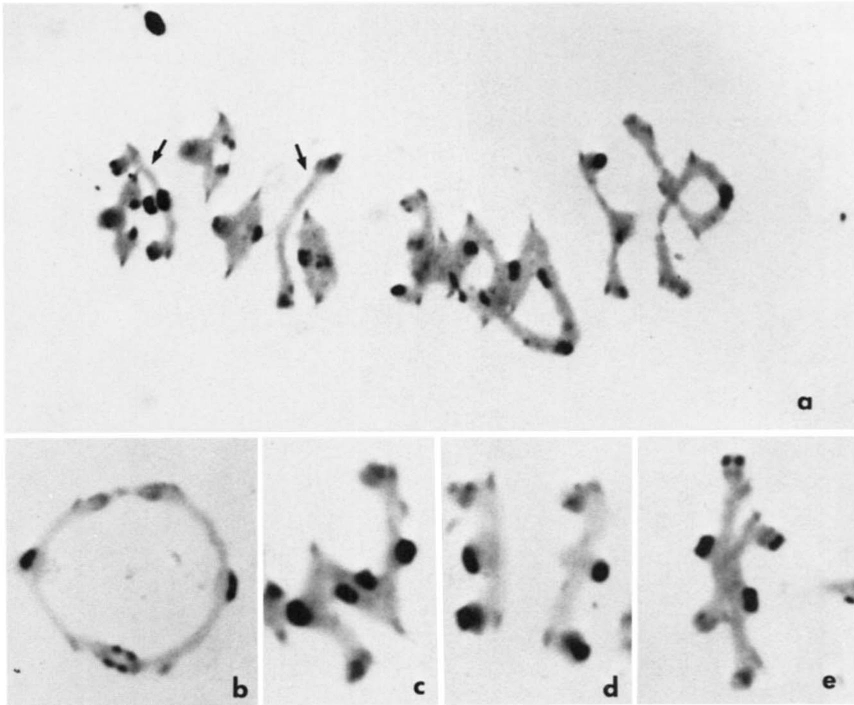

FIGURE 2.—Different meiotic configurations observed for *1R* chromosomes in tetraploid meiocytes of rye. a, The two open bivalents (arrows) are formed by the pairing of identical long arms; b, ring quadrivalent showing homologous pairing in the long arms and identical pairing in the short ones; c, chain quadrivalent showing homologous pairing in the long arms and identical pairing between the short arms with telomeric C-bands; d, the two open bivalents are formed by the pairing of homologous long arms; and e, quadrivalent showing undetermined pairing in the long arms.

could be distinguished in all meiotic configurations (Figure 2a–d), except in those in which three or four chromosome arms were paired in the same region (undetermined pairing; Figure 2e). Table 2 shows the frequencies of cells with at least one identical or homologous bound arm for $1R^S$ and $1R^L$ in bivalents and multivalents. Under the assumption that synapsis (and crossing over) between the four partners for each arm was random, a 2:1 ratio of homologous *vs.* identical pairing is expected. In the autotetraploid plants analyzed here, different pairing preferences among plants were found: $\chi^2(1R^S) = 46.69$; d.f. $= 9$; $P < 0.001$ and $\chi^2(1R^L) = 66.79$; d.f. $= 9$; $P < 0.001$ in bivalents and $\chi^2(1R^S) = 44.82$; d.f. $= 9$; $P < 0.001$ and $\chi^2(1R^L) = 76.22$; d.f. $= 7$; $P < 0.001$ in multivalents. Differences between bivalents and multivalents within the same plant have also been observed in both arms of chromosome *1R* (for summary, see Table 3). The influence of environmental factors in these results can be excluded because several anthers (5–10) of the same plant showed the same type of preferences, although they were collected from different spikes at different times.

In cells that show identical pairing preferences, a further analysis has been

TABLE 2

Numbers of cells with at least one identical or homologous bond at metaphase I for $1R^S$ *and* $1R^L$ *chromosome arms in bivalents and multivalents*

	Bivalents						Multivalents							
	Short			Long			Short				Long			
Plant	I	H	X^2	I	H	X^2	I	H	U	X^2	I	H	U	X^2
PetE5	7 (7.33)	15 (14.67)	0.02	11 (18.67)	45 (37.33)	4.73*	54 (21.33)	10 (42.67)		75.05**	(19.33)	58 (38.67)	8	28.99**
PetE12	9 (7.67)	14 (15.33)	0.35	18 (13)	21 (26)	2.88	7 (6.33)	12 (12.67)	2	0.11	1 (3.67)	10 (7.33)	16	
PetE15	18 (8.67)	8 (17.33)	15.06**	24 (17)	27 (34)	4.32*	12 (8)	12 (16)	7	3.00	4 (7)	17 (14)	16	1.93
PetE16	24 (21)	39 (42)	0.64	45 (43.33)	85 (86.67)	0.10	32 (21.67)	33 (43.33)	4	7.39**	12 (21)	51 (42)	17	5.79*
PetR4	99 (55.33)	67 (110.67)	51.70**	132 (81.67)	113 (163.33)	46.53**	39 (30.33)	52 (60.67)	20	3.72	35 (31)	58 (62)	23	0.77
PetR9	32 (26.67)	48 (53.33)	1.60	47 (47.33)	95 (94.67)	0.0035	31 (21.33)	33 (42.67)	6	6.58*	13 (18.33)	42 (36.67)	24	2.32
PetR11	9 (5.67)	8 (11.33)	2.93	23 (15)	22 (30)	6.40*	6 (3.33)	4 (6.67)			(2.67)	8 (5.33)	4	
PetR12	21 (13)	18 (26)	7.38**	25 (16.67)	25 (33.33)	6.24*	28 (14.67)	16 (29.33)	6	18.17**	7 (11.67)	28 (23.33)	20	2.80
PetR14	25 (14.33)	18 (28.67)	11.92**	41 (21.67)	24 (43.33)	25.87**	18 (13)	21 (26)	1	2.88	13 (7.67)	10 (15.33)	34	5.56*
PetR20	112 (50.67)	40 (101.33)	111.35**	174 (96.33)	115 (192.67)	94.00**	53 (46)	85 (92)	11	1.60	65 (38.67)	51 (77.33)	69	26.89**

The expected numbers are in parentheses. I, Identical pairing; H, homologous pairing; U, undetermined pairing.
* Significant at the level of 5%; ** significant at the level of 1%.

TABLE 3

Pairing preferences (identical, homologous or random) for $1R^S$ *and* $1R^L$ *chromosome arms in bivalents and multivalents*

	Bivalents		Multivalents	
Plant	Short	Long	Short	Long
PetE5	Random	Homologous	Identical	Homologous
PetE12	Random	Random	Random	
PetE15	Identical	Identical	Random	Random
PetE16	Random	Random	Identical	Homologous
PetR4	Identical	Identical	Random	Random
PetR9	Random	Random	Identical	Random
PetR11	Random	Identical		
PetR12	Identical	Identical	Identical	Random
PetR14	Identical	Identical	Random	Identical
PetR20	Identical	Identical	Random	Identical

made because two types of pairing involving either euchromatic (*eu-eu*) or heterochromatic (*het-het*) chromosome arms can be distinguished. Assuming the same probability of these types of identical pairing, a ratio of 1:1 *eu-eu* vs. *het-het* associations is expected. The results of this comparison are shown in Table 4. A significant deviation of this ratio due to an excess of *het-het* identical associations has been found in the $1R^S$ chromosome arm of plants PetE5, PetR4 and PetR12.

DISCUSSION

The results shown in Table 2 indicate the existence on pairing preferences for chromosome *1R*: (1) between plants, (2) between the two chromosome arms within the same plant and (3) between bivalents and multivalents within the same plant.

Pairing preferences observed at metaphase I could be due to preferences in initiation of synapsis and/or chiasma formation at first meiotic prophase. Similarities or differences between chromosomes in efficiency or activity for pairing and/or for chiasma formation might lead to random or identical pairing, respectively, at metaphase I. However, the homologous pairing preferences found [see for instance the plant F_1PR1 (SANTOS, ORELLANA and GIRALDEZ 1983) and the plant PetE5 in this work] cannot be explained by this assumption. Moreover, in plants with identical pairing preferences for a specific chromosome arm, we should expect significant deviations of the ratio 1:1 between *eu-eu* and *het-het* identical associations. A good fit to this ratio is observed in all plants in which $1R^L$ chromosome arm shows identical pairing (see Table 4). The few deviations observed for $1R^S$ will be discussed later. Therefore, pairing preferences appear not to depend mainly on differences in efficiency or activity between chromosomes, but rather on the affinities of the four chromosomes to pair.

The excess of identical over homologous preferences (17:3, see Table 3)

TABLE 4

Numbers of the two different types of identical chromosome pairing involving heterochromatic (het-het) *or euchromatic* (eu-eu) *chromosome arms in bivalents and multivalents*

Plant	Chromosome arm											
	1R short						*1R* long					
	Bivalents			Multivalents			Bivalents			Multivalents		
	eu-eu	*het-het*	X^2	*eu-eu*	*het-het*	X^2	*eu-eu*	*het-het*	X^2	*eu-eu*	*het-het*	X^2
PetE5	3 (3.5)	4		16 (33.5)	51	18.28**	10 (10.5)	11	0.05			
PetE12	6 (7.0)	8	0.29	2 (4.0)	6		18 (18.0)	18	0.00	1 (1.0)	1	
PetE15	9 (12.0)	15	1.50	4 (6.0)	8	1.33	14 (18.0)	22	1.78	4 (4.0)	4	
PetE16	15 (15.5)	16	0.03	18 (19.0)	20	0.11	42 (41.0)	40	0.05	10 (11.0)	12	0.18
PetR4	45 (58.0)	71	5.83*	17 (23.0)	29	3.13	111 (120.0)	129	1.35	25 (29.5)	34	1.37
PetR9	21 (19.0)	17	0.42	17 (18.0)	19	0.11	36 (40.0)	44	0.80	13 (10.5)	8	1.19
PetR11	5 (5.5)	6	0.09	4 (4.0)	4		21 (20.5)	20	0.02			
PetR12	11 (14.0)	17	1.29	5 (15.0)	25	13.33**	25 (25.0)	25	0.00	7 (7.0)	7	0.00
PetR14	18 (15.0)	12	1.20	9 (10.0)	11	0.20	36 (38.0)	40	0.21	10 (11.5)	13	0.39
PetR20	75 (67.5)	60	1.67	35 (34.0)	33	0.06	167 (162.0)	157	0.31	62 (62.5)	63	0.01

The figures in parentheses are the expected numbers under a ratio of 1:1 between *eu-eu* and *het-het* identical associations.
* Significant at the level of 5%, ** significant at the level of 1%.

might be interpreted as a reflection of the close proximity of identical chromosomes with respect to the homologous ones after chromosome doubling. However, homologous pairing preferences found in some plants could not be easily explained by this hypothesis. Moreover, due to the time in which the colchicine treatment was performed, the cell(s) in which polyploidy arose underwent many mitosis events before the resulting cells entered meiosis, making improbable the possibility that high proximity between identical chromosomes was maintained during these processes.

In a previous paper (SANTOS, ORELLANA and GIRALDEZ 1983), it was pointed out that different pairing affinities might be due to the existence of genotypic or cryptic structural differences between chromosomes. Likewise, the variation in pairing preferences found for chromosome *1R* in this work may be due to slight differences of this chromosome in different F_1 plants. The source of such differences must be the plant of cv. Petkus used to obtain the two F_1's (PetE and PetR). Since Petkus is an open-pollinated variety, one can expect the existence of different chromosome *1R* combinations (genotypic or structural), not detected by the C-banding technique, produced by the recombination process in the parental plant. Such variations would not be expected in the inbred lines E and R after 21 and 24 generations of inbreeding, respectively.

The most obvious structural difference among the four chromosomes *1R* analyzed here is the presence in two of them of conspicuous telomeric heterochromatic C-bands in both arms. The presence of C-heterochromatin around the telomeres has been used to explain pairing failures between rye and wheat chromosomes and between homologous rye chromosomes in triticales (for review see GUPTA and PRIYADARSHAN 1982) and in diploid rye (NARANJO and LACADENA 1980). THOMAS and KALTSIKES (1974) proposed that the effect of C-heterochromatin could arise from an overlap between the processes of DNA replication and meiotic prophase pairing. The telomeres, where pairing is supposed to start, may not be able to pair until DNA replication is finished. Therefore, differences in C-heterochromatin content between the four *1R* chromosomes might lead to different pairing probabilities and, consequently, to the different pairing preferences observed at metaphase I.

If the basic pairing pattern in rye were at random, a pairing reduction in the chromosomes with telomeric C-bands would determine the appearance of homologous pairing preferences at metaphase I. By contrast, if the basic preferred pattern were identical, homologous or random pairing could be observed at that stage depending on the different degree to which this pairing reduction was expressed. In both cases, a deviation of the 1:1 ratio of *eu-eu/het-het* identical pairing, due to a decrease of *het-het* associations, would be expected. No deviation is observed in most of the plants analyzed (see Table 4); this indicates that telomeric C-bands do not play an important role in the pairing preferences found and that, probably, there is no fixed pairing pattern in the plants of autotetraploid rye.

The excess of identical heterochromatic pairing observed in $1R^S$ chromosome arm of plants PetE5, PetR4 and PetR12 could be explained if some of

these associations are of nonchiasmate nature. They might be considered as a mechanism to assure regular chromosome segregation when chiasmata are reduced or even lacking (KING and JOHN 1980; CERMEÑO, ORELLANA and LACADENA 1984). A similar situation can occur in autotetraploids where chiasma formation tends to be reduced when it is compared with the diploid level (SYBENGA 1975).

Another possibility to explain pairing preferences may be the existence of a genetic control. In our case, the segregation of pairing gene(s)—not necessarily located in chromosome *1R*—in the plant cv. Petkus may be responsible for the pairing preferences found, although the different pairing preferences observed in both arms of chromosome *1R* within most of plants (see Tables 2 and 3) indicates that, if this control exists, it must be specific for each arm.

Genes affecting chiasma formation in specific individual chromosomes have been reported in desynaptic plants of *Hypochoeris radicata* (PARKER 1975) and *Crepis capillaris* (TEASE and JONES 1976). Unfortunately, in our system we cannot directly discern between preferences for chiasma formation and pairing preferences, because only metaphase I cells are available to analysis. However, when the mean of bound arms per cell (see Table 1) is plotted against identical pairing preferences per bond for the same chromosome arm in bivalents as well as multivalents, no correlation has been found (bivalents: $1R^S$, $b = 0.1656$; d.f. = 8; $0.90 > P > 0.80$; $1R^L$, $b = -0.1955$; d.f. = 8; $0.90 > P > 0.80$; multivalents: $1R^S$, $b = 0.1526$; d.f. = 8; $0.90 > P > 0.80$; $1R^L$, $b = -0.0286$; d.f. = 8; $P > 0.90$). A similar result is obtained when the homologous pairing preferences per bond are performed.

The different pairing preferences observed for the same chromosome arm in bivalents and multivalents within the same plant require further comments. We have calculated pairing preferences as deviations of the ratio of 2:1 homologous *vs.* identical pairing. This fact implies that we are assuming the following premises:

1. The four chromosome arms (for instance $1R^L$) have the same probability of pairing. The deviations from randomness have been discussed above.
2. Both arms of metacentric or submetacentric chromosomes are independent to pair and the pairing process is simultaneous in the four chromosomes of each set.
3. A ratio of 2:1 homologous *vs.* identical pairing is expected in all meiotic configurations.

In rye, pairing is often initiated from telomeric regions, but also occurs at several sites along the chromosomes (ABIRACHED-DARMENCY, ZICKLER and CAUDERON 1983). These authors have indicated that about six sites exist in the short arms and 13 sites in the long arms of chromosome *1R*. This fact might lead to differences in the timing of pairing initiation or in the rates at which pairing proceeds. These differences would be favorable to the long arms and, consequently, their pairing preferences might influence those of the short ones. For instance, if the long arms start to pair earlier and they show a total preference for identical pairing, the short arms are obliged to show identical pairing in bivalent configurations. Under these circumstances, a ratio of 1:0

identical *vs.* homologous pairing for the short arms is expected, whereas in ring and chain quadrivalents this ratio should be 0:1. In contrast, if long chromosome arms show a total preference for homologous pairing, we should expect ratios of 0:1 and 1:1 identical *vs.* homologous pairing for short arms in bivalents and ring or chain quadrivalents, respectively. This situation is more complex when the other multivalent configurations are considered, although the identical pairing frequency in short arms will always be lower than the homologous one, independent of the total pairing preferences in the long arms. Therefore, different ratios between homologous and identical pairing that are an apparent contradiction of the third premise may be expected in different meiotic configurations.

Obviously, these extreme situations are difficult to find in autotetraploids and, moreover, it is feasible to think of the existence of pairing preferences for the short arms. For example, identical pairing exhibited by the short arms in multivalents in plant PetE5 can only be explained if these arms have their own preferences. Therefore, mutual influences between both arms of metacentric or submetacentric chromosomes may prevent an accurate quantification of pairing preferences in these chromosome types, and the mere use of a theoretical ratio of 2:1 homologous *vs.* identical pairing may lead to artificial results, because in each plant the actual ratio is probably different. This might explain, in part, the different pairing preferences found between bivalents and multivalents within the same plant. Another explanation, that does not exclude the latter, can be related to a differential chiasma formation in both configurations.

Pairing configurations in autotetraploids with metacentric chromosomes have usually been calculated under the following premises (for review see SYBENGA 1975): (1) two independent points of pairing initiation, one in each end, per chromosome; (2) absence of pairing preferences; (3) same probabilities of chiasma formation in all meiotic configurations; and (4) free partner exchange between the two points where pairing starts in each chromosome. Then, a ratio of 2/3 multivalents (*IV* and *III*):1/3 bivalents is expected in organisms with pronounced distal chiasma localization. When the pairing is initiated at more than two sites and interstitial chiasmata occur, partner exchange can be more frequent and, consequently, the probability of multivalents to form is higher.

Rye usually has been considered as a clear example of distal chiasma localization (for review, see JONES 1978). However, recent studies have reported an appreciable frequency of interstitial chiasmata (ORELLANA and GIRALDEZ 1981; NARANJO and ORELLANA 1984). The observed frequencies of undetermined configurations involving three or four chromosome *1R* arms are in agreement with those results (Table 2). Moreover, it has been observed in diploid rye that the formation of the central element in each bivalent is initiated at telomere regions, as well as at several (7–18) interstitial sites (ABIRACHED-DARMENCY, ZICKLER and CAUDERON 1983). Both findings would lead to an expected multivalent frequency higher than 0.667, but we have observed much lower values (Table 1). An excess of bivalents in autotetraploid rye has

been explained by a tendency of four chromosomes to form bivalents at pachytene (TIMMIS and REES 1971; NARANJO and ORELLANA 1984). One of the possible explanations proposed by the latter authors is the existence of preferential pairing between two specific chromosomes. If it were true, we should expect the same pairing preferences in bivalents and multivalents, but this is not observed (Tables 2 and 3), because there is a major tendency for identical pairing in bivalents.

On the other hand, there are indications that partner exchange decreases chiasma frequency around the point where it occurs, the short arms being more affected (see SYBENGA 1975). Thus, partner exchange may be responsible, in part, for some increase of the metaphase I frequency of bivalents that would be derived from multivalent pairing at pachytene. In summary, the excess of bivalents at metaphase I may be due not only to pairing preferences but also to the reduction of chiasma formation in the short arms produced by partner exchanges. Nevertheless, further studies at earlier meiotic stages are necessary to elucidate this question.

In addition, the excess of identical pairing in bivalents might indicate that the decrease in chiasma formation would be higher when the short arms are homologously paired. For example, in pachytene quadrivalents in which long arms show identical pairing, the short arms are obliged to pair homologously. In this situation, failures in chiasma formation in the short arms would lead to an increase of open bivalents at metaphase I, with identical pairing for the long arms. However, pachytene quadrivalents in which the long arms are homologously paired allow identical or homologous pairing in the short arms and, thus, the increase of bivalents is expected to be lower. In an extreme situation, one would be able to find for the same chromosome arm identical pairing preferences in bivalents and homologous ones in multivalents (Plant PetR11).

Pairing preferences observed at metaphase I in organisms with metacentric or submetacentric chromosomes are the final result of several phenomena that have taken place at earlier meiotic stages, *i.e.*, establishment of points of initiation of pairing, synaptonemal complex progression in both arms, partner exchange and chiasma formation. The correction of synaptonemal complex (see RASMUSSEN and HOLM 1980) and the temporal interactions between synaptonemal complex and crossing over may add more difficulties to the analysis of this phenomenon. The more likely explanation is the existence of structural differences along the chromosomes: chromosomal condensation, particular associations between DNA and proteins or between DNA and synaptonemal complex that might lead to affinity differences responsible for the different types of pairing preferences observed at metaphase I.

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LITERATURE CITED

ABIRACHED-DARMENCY, M., D. ZICKLER and Y. CAUDERON, 1983 Synaptonemal complex and recombination nodules in rye (*Secale cereale*). Chromosoma (Berl.) **88:** 299–306.

CERMEÑO, M. C., J. ORELLANA and J. R. LACADENA, 1984 Evidence of non-chiasmate bonds at metaphase I in inbred rye. Can. J. Genet. Cytol. **26:** 409–414.

GIRALDEZ, R., M. C. CERMEÑO and J. ORELLANA, 1979 Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye. Z. Pflanzenzuchtg. **83:** 40–48.

GUPTA, P. K. and P. M. PRIYADARSHAN, 1982 Triticale: present status and future prospects. Adv. Genet. **21:** 255–345.

JACKSON, R. C. and P. HAUBER, 1982 Autotriploid and autotetraploid cytogenetic analyses: correction coefficients for proposed binomial models. Am. J. Bot. **69:** 646–648.

JOHN, B. and S. A. HENDERSON, 1962 Asynapsis and polyploidy in *Schistocerca paranensis*. Chromosoma (Berl.) **13:** 111–147.

JONES, G. H., 1978 Giemsa C-banding of rye meiotic chromosomes and the nature of terminal chiasmata. Chromosoma (Berl.) **66:** 45–57.

KING, M. and B. JOHN, 1980 Regularities and restrictions governing C-band variation in acridoid grasshoppers. Chromosoma (Berl.) **76:** 123–150.

NARANJO, T. and J. R. LACADENA, 1980 Interaction between wheat chromosomes and rye telomeric heterochromatin on meiotic pairing of chromosome *1R* of rye in wheat-rye derivates. Chromosoma (Berl.) **81:** 249–261.

NARANJO, T. and J. ORELLANA, 1984 Meiotic behaviour of chromosomes *1R*, *2R* and *5R* in autotetraploid rye. Chromosoma (Berl.) **89:** 143–150.

ORELLANA, J. and R. GIRALDEZ, 1981 Metaphase I bound arms and crossing over frequency in rye. I. Open pollinated varieties. Chromosoma (Berl.) **84:** 439–449.

PARKER, J. S., 1975 Chromosome specific control of chiasma formation. Chromosoma (Berl.) **49:** 391–406.

RASMUSSEN, S. W. and P. B. HOLM, 1980 Mechanics of meiosis. Hereditas **93:** 187–216.

SANTO, J. L., J. ORELLANA and R. GIRALDEZ, 1983 Pairing competition between identical and homologous chromosomes in rye and grasshoppers. Genetics **104:** 677–684.

SYBENGA, J., 1975 Meiotic configurations. In: *Monograph on Theoretical and Applied Genetics*, Vol. 1. Springer-Verlag, New York.

TEASE, C. and G. H. JONES, 1976 Chromosome-specific control of chiasma formation in *Crepis capillaris*. Chromosoma (Berl.) **57:** 33–49.

THOMAS, J. B. and P. J. KALTSIKES, 1974 A possible effect of heterochromatin on chromosome pairing. Proc. Natl. Acad. Sci. USA **71:** 2787–2790.

THOMAS, H. M. and R. A. PICKERING, 1979 Barley × rye crosses: the morphology and cytology of the hybrids and the amphiploids. Z. Pflanzenzuchtg. **82:** 193–200.

TIMMIS, J. N. and H. REES, 1971 A pairing restriction at pachytene upon multivalent formation in autotetraploids. Heredity **26:** 269–275.

WEIMARCK, A., 1975 Heterochromatin polymorphism in rye karyotype as detected by the Giemsa C-banding technique. Hereditas **79:** 293–300.

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