Interactions between wheat, rye and *Aegilops ventricosa* chromosomes on homologous and homoeologous pairing

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Different wheat-rye, *Ae. ventricosa*-rye and wheat-*ventricosa*-rye genome combinations were analysed at meiosis. In all cases it was possible to estimate the frequencies of the different types of homologous and homoeologous pairing, by using a C-banding technique. Rye homologous pairing decreased in the presence of wheat and *Ae. ventricosa* genomes with respect to that observed in diploid rye. However, the frequencies of all types of homoeologous pairing were very constant in all hybrids analysed and independent of the number of genomes which were present in the hybrids.

INTRODUCTION

The mutual influence between wheat and rye genomes on meiotic pairing has been reported in many wheat-rye combinations (see Naranjo *et al.*, 1979). Wheat chromosomes seem to produce a decrease of homologous pairing between rye chromosomes (Lacadena, 1967; Lelley, 1976), whereas the homoeologous pairing between wheat chromosomes increases when the dosage of rye genomes increases (Miller and Riley, 1972; Naranjo *et al.*, 1979).

Although most of these types of studies have been usually limited to wheat and rye chromosomes, there is some evidence for assuming similar interactions between *Aegilops* and rye chromosomes. Thus, in *Ae. ventricosa*-*Secale cereale* amphiploid plants it has been reported that a decrease of meiotic pairing either for rye and *Aegilops* chromosomes occurs with respect to that observed in their parental species (Cermeño *et al.*, 1985).

The aim of this work was to analyse the mode in which *Aegilops ventricosa*, rye and wheat genomes interact in different combinations.

MATERIAL AND METHODS

The materials used for this work were as follows:

Five plants of diploid rye *Secale cereale* (genome constitution RR) cv. La Raña, taken

from Logrosan, Cáceres (Spain) (Orellana and Giraldez, 1981).

Five plants of the synthetic amphiploid *Aegilops ventricosa*-*Secale cereale* (genome constitution DDUUnRR) kindly supplied by Dr F. Dosba, Plant Breeding Stn., Res. Center of Rennes, INRA (France). The designation of M^v genome of *Ae. ventricosa* has been changed for Un according to the new nomenclature proposed by Kimber *et al.* (1983).

Five plants of the first backcross obtained from the crosses between the amphiploid *Ae. ventricosa*-*S. cereale* and diploid rye cv. Dakold (genome constitution DUnRR).

Four triticales × rye hybrid plants (genome constitution ABRR) obtained from the crosses between hexaploid triticales cv. Cachirulo (genome constitution AABBRR) and diploid rye (RR), line E (Orellana and Giraldez, 1984).

Two trigeneric hybrid plants (genome constitution ABDUnRR) obtained from the crosses between hexaploid triticales cv. Cachirulo and *Ae. ventricosa*-*S. cereale* amphiploid plants.

In order to obtain meiotic cells, anthers were fixed in acetic ethanol 1:3 and stored following the Giemsa C-banding technique described previously (Giraldez *et al.*, 1979).

RESULTS

The C-banding technique makes it possible to distinguish the rye genome from the *Aegilops*

ventricosa as well as the wheat genomes in all hybrids analysed since rye shows telomeric C-blocks in most of its chromosomes whereas *Ae. ventricosa* and wheat possess intercalary and dispersed C-heterochromatin in some of their chromosomes (figs. 1-2). In addition, in *Ae. ventricosa* two chromosome groups may be differentiated according to their C-banding pattern, i.e., 16 chromosomes with prominent C-heterochromatin located at centromeric and pericentromeric regions and 12 almost entirely euchromatic (fig. 1). These differences could represent the Un (M^v in previous works) and D genomes, respectively, although obviously, at least one of the heterochromatic chromosomes should belong to the D genome. In previous work (Cermeno *et al.*, 1985) this chromosome could be distinguished from those of the Un genome in *Ae. ventricosa* and *Ae. ventricosa*-*S. cereale* amphiploid plants due to

the high degree of meiotic regularity observed for *Ae. ventricosa* chromosomes. By contrast, in this work only the two groups mentioned above can be accurately distinguished since the heterochromatic chromosome of the D genome is not identifiable when it is involved in bivalents in which homoeologous pairing takes place.

Similarly, in *Triticum turgidum*, which is used for making hexaploid triticales, two groups can be distinguished: 14 chromosomes without prominent C-heterochromatin and the other 14 with scattered and dispersed C-heterochromatin (fig. 2). These two groups represent the A and B genomes, respectively (see Gill and Kimber, 1974).

These different C-banding patterns has allowed us to estimate the frequencies of homologous and homoeologous pairing at meiosis in all the hybrids analysed.

Figure 1 Meiosis in DUnRR hybrid plants. (a) C-banded metaphase I cell (arrows indicate rye bivalents and univalents). (b) Homoeologous pairing between euchromatic and heterochromatic (eu-het) chromosomes of *Ae. ventricosa*. (c) Three bivalents formed by: one chromosome of rye and one euchromatic chromosome (R-eu) of *Ae. ventricosa* (open triangle), two heterochromatic chromosomes (het-het) of *Ae. ventricosa* (black triangle) and euchromatic and heterochromatic (eu-het) chromosomes of *Ae. ventricosa* (double triangle). (d) V-shaped trivalent formed by *Ae. ventricosa* chromosomes (het-eu-het). (e) V-shaped rye-ventricosa trivalent (R-R-het).

Figure 2 Meiosis in ABDUnRR hybrid plants. (a) C-banded metaphase I cell (arrows indicate rye bivalents and univalents). (b) A bivalent formed by one chromosome of rye and one heterochromatic chromosome (R-het). (c) Homoeologous pairing between two euchromatic (eu-eu) chromosomes. (d) A bivalent formed between one heterochromatic and one euchromatic (het-eu) homoeologous chromosomes. (e) V-shaped trivalent formed between *ventricosa* and wheat chromosomes.

(i) Homologous pairing

Although in the diploid rye there was a high degree of meiotic regularity, in all amphiploid and hybrid plants in the present study it was possible to detect a considerable degree of irregularities affecting rye chromosomes, leading to a decrease of rye homologous pairing.

The frequencies of univalents and open bivalents increased in the hybrid plants but they did not follow a fixed pattern since except for ABRR hybrids, a between plants heterogeneity within each genome constitution was found (table 1).

As it has been pointed out by Cermeño *et al.* (1985) the mere hybridisation and chromosome

doubling between *Ae. ventricosa* and *S. cereale* produces a decrease of homologous pairing in the genomes of both parental species in the amphiploid. However, in the present study it is worth mentioning that rye homologous pairing was always lower in *Ae. ventricosa*-rye combinations than in triticale-rye hybrids (table 1).

(ii) Homoeologous pairing

In hexaploid triticale as well as in the amphiploid *Ae. ventricosa*-*S. cereale* there are certain meiotic irregularities but meiotic pairing always occurs between homologous chromosomes (see Gupta and Priyadarshan, 1982; Cermeño *et al.*, 1985).

Table 1 Frequencies of the different rye-rye meiotic configurations (R, ring bivalents; O, open bivalents; U, univalents) observed at metaphase I in all plants analysed. The comparisons between the mean number of bound arms per cell in each type of plants is also included

Plant	Genome constitution																					
	RR				DDUnUnRR				DUnRR				ABRR				ABDUnRR					
	R	O	U	$\bar{x}$	R	O	U	$\bar{x}$	R	O	U	$\bar{x}$	R	O	U	$\bar{x}$	R	O	U	$\bar{x}$		
1	676	24	—	13.76	125	177	96	8.54	110	346	476	5.68	227	89	63	10.86	185	524	658	5.97		
2	673	27	—	13.73	104	194	104	8.04	77	132	156	6.98	201	114	62	10.32	101	328	531	5.31		
3	672	28	—	13.72	65	247	76	7.54	202	311	369	7.54	203	112	64	10.36						
4	670	30	—	13.70	70	221	118	7.22	65	169	212	6.14	213	104	57	10.60						
5	649	51	—	13.49	74	223	106	7.42	50	81	74	7.17										
Total	3340	160	—	13.68	438	1062	500	7.75	504	1039	1287	6.70	844	419	246	10.53	286	852	1189	5.64		
	$X^{2*} = 15.3911$				$X^{2*} = 49.3019$				$X^{2*} = 47.7375$				$X^{2*} = 5.9194$				$X^{2*} = 7.9734$					
	d.f. = 4				d.f. = 8				d.f. = 8				d.f. = 6				d.f. = 2					
	0.01 > p > 0.001				p < 0.001				p < 0.001				0.50 > p > 0.30				0.05 > p > 0.01					
$t(\text{RR-DDUnUnRR}) = 24.4966$;					d.f. = 8;				$p < 0.001$				$t(\text{DDUnUnRR-ABRR}) = 10.6920$;				d.f. = 7;				$p < 0.001$	
$t(\text{RR-DUnRR}) = 20.0661$;					d.f. = 8;				$p < 0.001$				$t(\text{DDUnUnRR-ABDUnRR}) = 5.1690$;				d.f. = 5;				$0.01 > p > 0.001$	
$t(\text{RR-ABRR}) = 26.50$;					d.f. = 7;				$p < 0.001$				$t(\text{DUnRR-ABRR}) = 10.6226$;				d.f. = 7;				$p < 0.001$	
$t(\text{RR-ABDUnRR}) = 23.9313$;					d.f. = 5;				$p < 0.001$				$t(\text{DUnRR-ABDUnRR}) = 2.21495$;				d.f. = 5;				$0.1 > p > 0.05$	
$t(\text{DDUnUnRR-DUnRR}) = 2.5117$;					d.f. = 8;				$0.05 > p > 0.01$				$t(\text{ABRR-ABDUnRR}) = 14.008$;				d.f. = 7;				$p < 0.001$	

A maximum of only one bivalent per cell between heterochromatic chromosomes was found. Moreover, no bivalent between euchromatic chromosomes was observed. These results indicate that the two groups of chromosomes (with C-heterochromatin and without C-heterochromatin) actually represent the Un and D genomes, respectively, and that non-homologous or non-homoeologous associations do not exist in our material.

As is shown in table 2 the frequency of homoeologous pairing between the heterochromatic chromosome pair was similar to that of the remaining six homoeologous pairs.

Now, if these six pairs of homoeologous have the same probability for pairing and if meiotic pairing is at random, the distribution of paired arms per cell should follow the binomial series. However, the observed and expected were very different when the comparison was performed (table 3). These results seem to indicate that the probabilities for pairing could be different for each homoeologous group.

On the other hand, if homoeologous pairing between rye and *ventricosa* occurs in DUnRR hybrids, trivalents and quadrivalents are expected (see table 2) (fig. 1e). Nevertheless trivalents involving only *ventricosa* chromosomes could not be explained simply by homoeologous pairing. In our material a maximum number of one trivalent per cell involving *ventricosa* chromosomes was found. This was always formed by two heterochromatic and one euchromatic chromosomes. The trivalents were always V-shaped, the euchromatic chromosome being located at the vertex of the V configuration (fig. 1d). This persistent disposition leads to the assumption of the existence of an interchange (translocation) between the D and Un genomes. Similar systems of differentiation among

Table 3 Comparison between the number of homoeologous associations per cell involving heterochromatic and euchromatic (het-eu) *ventricosa* chromosomes observed at metaphase I and the expected on the basis of a binomial distribution

	No. bound arms per cell						6 or more
	0	1	2	3	4	5	
Obs.	4	39	132	114	20	4	1
Exp.	17.78	57.68	85.76	77.27	47.00	20.33	8.17

$$\chi^2 = 94.00; \text{ d.f.} = 5; p < 0.001$$

related genomes have been reported from isozyme studies in *Triticum* (Kobrehel and Feillet, 1975; Benito and Perez de la Vega, 1979; Salinas and Benito, 1984), *Agropyron* (Kobrehel, 1977) and *Hordeum* (Benito *et al.*, 1985).

Table 4 shows the wheat-wheat and wheat-rye homoeologous pairing frequencies in the ABRR hybrids studied. The levels of homoeologous pairing were not very different between wheat-wheat and *ventricosa-ventricosa* or between wheat-rye and *ventricosa*-rye in the DUnRR and ABRR hybrids (see table 6).

In the trigeneric hybrid ABDUnRR, several types of homoeologous pairing could be also identified at metaphase I: homoeologous associations formed between rye and wheat or rye and *ventricosa* heterochromatic (R-het) (fig. 2b) or euchromatic (R-eu) (fig. 2e) chromosomes; and homoeologous pairing involved only wheat or *ventricosa* heterochromatic (het-het), euchromatic (eu-eu) (fig. 2c) or chromosomes with different heterochromatin constitution (het-eu) (fig. 2d). In these hybrids it was impossible to discern if the pairing observed was due to wheat or to *ventricosa* chromosomes because the C-banding patterns of A and B genomes were very similar to those of D and Un genomes, respectively.

Table 4 Frequencies of the different meiotic configurations (R, ring bivalents; O, open bivalents and trivalents) formed between homoeologous chromosomes in ABRR hybrids (taken from Orellana and Giraldez, 1984)

Plant	Bivalents				Trivalents wheat-rye*	Homoeologous associations/cell		No. cells
	wheat-rye		wheat-wheat			wheat-rye	wheat-wheat	
	R	O	R	O				
ABRR ₁	—	3	21	115	1	0.08	3.61	50
ABRR ₂	—	3	21	104	3	0.12	2.98	50
ABRR ₃	—	1	14	105	3	0.08	2.72	50
ABRR ₄	—	5	26	110	2	0.14	3.28	50
Total	—	12	82	434	9	0.105	3.15	200

* All trivalents observed were V-shaped trivalents

Table 5 shows the frequencies of the different meiotic configurations observed in these hybrids as well as the total frequencies of the types of homoeologous pairing mentioned above.

In the hybrids ABDUnRR the possibilities for establishing homoeologous pairing are, in principle, higher than in DUnRR or ABRR hybrids, because the first possesses two additional genomes, however no clear increase of any type of pairing was observed (see table 6).

DISCUSSION

Homologous pairing

In all amphiploids and hybrids studied here, rye-rye homologous pairing decreased in respect to that observed in diploid rye. This seemed to be due to the presence of the *Aegilops* and wheat genomes. The effect seemed to be higher when rye and *Aegilops* chromosomes were combined (table 1).

It has been reported that wheat chromosomes produce a decrease in homologous pairing between rye chromosomes (Lacadena, 1967; Lelley, 1976). Our results are in agreement with this assumption. However the reduction of the dosage of wheat and *Aegilops* genomes in wheat-rye and *ventricosa*-rye combinations does not seem to increase the probability of homologous pairing between rye chromosomes in disagreement with Miller and Riley (1972). At least in the first backcross hybrids ABRR and DUnRR the dosage of wheat and *ventricosa*

genomes have been reduced with respect to the parental amphiploids (AABBRR, DDUnUnRR), and however the rye-rye homologous pairing is lower than in those amphiploids (table 1) (see Naranjo and Lacadena, 1982; Cermeño *et al.*, 1985).

Thomas and Kaltsikes (1974; 1976) and Roupakias and Kaltsikes (1977) concluded that the presence of telomeric C-heterochromatin on rye chromosomes could be responsible for the rye meiotic irregularities observed in triticale and wheat-rye combinations, since heterochromatin is late replicating and therefore DNA replication of C-heterochromatin could interfere with meiotic prophase pairing. Nevertheless, this cannot explain our results because if the only cause of the decrease of the rye homologous pairing was the presence of telomeric C-blocks in the rye chromosomes, we would expect the same behaviour in the amphiploids as in the hybrids, and in the *Ae. ventricosa*-rye as in the wheat-rye hybrids. However the results are very different (table 1) in spite of the fact that the C-banding patterns for the rye chromosomes are very similar in all the amphiploids and hybrids.

Genetical differences between the rye cultivars used for obtaining the hybrids might explain different levels of rye homologous pairing detected. However if this is so, the rye system seems to be only operative in the wheat-rye and *Ae. ventricosa*-rye hybrids since intraspecific rye hybrids generally show similar levels of pairing (see Orellana *et al.*, 1984).

Table 5 Frequencies of the different meiotic configurations (R, ring bivalents; O, open bivalents and multivalents) formed between homoeologous chromosomes in ABDUnRR hybrids

Plant	Bivalents										Trivalents*						
	R-het		R-eu		het-eu		het-het		eu-eu								
	R	O	R	O	R	O	R	O	R	O	R-R-eu	R-R-het	R-eu-het	R-het-eu	het-eu-het	het-het-eu	het-eu-eu
ABDUnRR ₁	—	6	—	10	9	215	4	92	2	53	1	1	2	—	8	1	4
ABDUnRR ₂	—	6	—	2	3	92	1	43	1	22	—	1	—	1	1	—	2
Total	—	12	—	12	12	307	5	135	3	75	1	2	2	1	9	1	6

	Quadrivalents†		Homoeologous associations per cell					No. cell
	R-R-eu-eu		R-het	R-eu	het-eu	het-het	eu-eu	
ABDUnRR ₁	1		0.05	0.09	1.71	0.67	0.41	150
ABDUnRR ₂	—		0.08	0.02	1.03	0.45	0.26	100
Total	1		0.065	0.06	1.37	0.56	0.34	250

* All trivalents were V-shaped

† All quadrivalents were chain quadrivalents

(R): rye genome

(het): heterochromatic chromosome

(eu): euchromatic chromosome

Table 6 Homoeologous pairing frequencies per cell in all hybrids analysed. The comparisons of the total homoeologous pairing frequencies among the three type of hybrid plants are also included

Plant	Type of hybrid plant								
	DUnRR			ABRR			ABDUnRR		
	r-v	v-v	Total	r-w	w-w	Total	(r-w) + (r-v)	(v-v) + (w-w) + (v-w)	Total
1	0.10	2.75	2.85	0.08	3.61	3.68	0.14	2.79	2.93
2	—	3.17	3.17	0.12	2.98	3.10	0.10	1.74	1.84
3	0.03	2.52	2.53	0.08	2.72	2.80			
4	0.08	2.88	2.96	0.14	3.28	3.42			
5	—	2.62	2.62						
Total	0.042	2.79	2.83	0.105	3.15	3.25	0.12	2.26	2.385
$t(\text{DUnRR-ABRR}) = 2.1518$; d.f. = 7; $0.10 > p > 0.05$ $t(\text{DUnRR-ABDUnRR}) = 1.1153$; d.f. = 5; $0.40 > p > 0.30$ $t(\text{ABRR-ABDUnRR}) = 2.0951$; d.f. = 4; $0.20 > p > 0.10$									

(r) rye chromosome

(v) *ventricosa* chromosome

(w) wheat chromosome

Probably the mere combination of rye and any other alien genome can produce genetic interactions responsible for the decrease of rye homologous pairing. These types of interactions also occurs for wheat and *Aegilops* chromosomes. Thus, the addition of any rye or *Ae. umbellulata* chromosome to wheat produces a decrease of wheat-wheat homologous pairing (Orellana *et al.*, 1984; Cuñado, in preparation).

Homoeologous chromosome pairing

As described above, rye chromosomes show different levels of homologous pairing in each type of plants. However the total amount of homoeologous pairing is very similar in all hybrids (table 6). The similarities can also be observed for each specific type of homoeologous pairing formed between rye, *ventricosa* and wheat chromosomes (see tables 2, 4 and 5). The lack of relationship between homologous and homoeologous pairing might indicate the existence of a certain degree of independence among the genomes in relation to pairing.

In general, genetic control of meiosis is operative on the whole complement (see Riley and Law, 1965; Gale and Rees, 1970; Baker *et al.*, 1976) but there are a few exceptions. Thus, chromosome-specific controls of chiasma formation have been reported in desynaptic mutants of *Hipchoeris radicata* (Parker, 1975) and *Crepis capillaris* (Tease and Jones, 1976) and recently a case of genome-specific control has been found by Orellana *et al.* (1985) in meiotic mutants of the amphiploid *Ae. ventricosa*-*S. cereale*. In this case, irregular meiotic

behaviour was only limited to the *Aegilops ventricosa* chromosomes, which showed a high degree of asynapsis, whereas the rye chromosomes showed a normal behaviour. Similar results have been obtained in asynaptic individuals of *Locusta migratoria* and *Schistocerca gregaria* (Rees, 1957; John and Naylor, 1961) when the irregularities were limited to the longest and the shortest chromosomes of the complement, respectively.

It is reasonable to assume the existence of a general control which acts on the whole complement, but besides this control a genome-specific control on homoeologous pairing can occur. Although speculative, one can imagine that the homoeologous pairing control is essentially different from the homologous one, and therefore homoeologous pairing might be affected by factors which do not act on homologous pairing.

In the hybrids DUnRR and ABRR the values of *ventricosa*-*ventricosa* and wheat-wheat homoeologous pairing are similar. Therefore in the hybrid ABDUnRR double homoeologous pairing would be expected if the *ventricosa*-*ventricosa* and wheat-wheat types are independent. Obviously, *ventricosa* and wheat chromosomes can pair with each other as is demonstrated by the presence of euchromatic-euchromatic associations (fig. 2c) (pairing between A and D genomes) but even so, higher values of homoeologous pairing are expected than in the DUnRR or ABRR hybrids. However, similar or even slightly lower values were observed, although there was no significant deviation. This can only be explained by the existence of a control of a maximum level of homoeologous pairing.

It has been reported that in wheat-rye combinations, homoeologous pairing between wheat chromosomes increases with increasing the dosage of the rye genomes (Miller and Riley, 1972; Naranjo *et al.*, 1979). This behaviour has been explained in terms of an inhibition of the effect of a single dose of the Ph locus of chromosome 5B by two or more doses of chromosome 5R (Jouve *et al.*, 1980), however Miller and Riley (1972) concluded that the promotion of homoeologous chromosome pairing by the rye genotypes might reside in the activities of the complete genome and not necessarily in the homoeologous group 5 chromosome.

More recent studies have demonstrated that chromosome 5R affects wheat homologous pairing in wheat-rye addition lines but it is also true that any other rye addition produces a decrease of homologous pairing, though in this case the effect is lower (Orellana *et al.*, 1984). Moreover it seems clear that rye genomes may modulate the wheat homologous and homoeologous pairing in wheat-rye combinations and probably also in *ventricosa*-rye combinations, but the mode in which this control acts is unknown and further studies combining genomes in different doses are required.

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