Theor Appl Genet (1985) 70:390–399

Meiotic pairing in hybrids between tetraploid Triticale and related species: new elements concerning the chromosome constitution of tetraploid Triticale

M. Bernard and S. Bernard

INRA, Station d'Amélioration des Plantes, F-63039 Clermont-Ferrand, France

Received December 12, 1984; Accepted January 23, 1985
Communicated by K. Tsunewaki

Summary. Two F5 strains of tetraploid triticale (2n = 4x = 28), obtained from 6x triticale × 2 rye progenies, were crossed with diploid and tetraploid rye, some durum and bread wheats, and various 8x and 6x triticale lines. Meiosis in the different hybrid combinations was studied. The results showed that the haploid complement of these triticales consists of seven chromosomes from rye and seven chromosomes from wheat. High frequencies of PMCs showing trivalents were observed in hybrids involving the reference genotypes of wheat and triticale. These findings proved that several chromosomes from the wheat component have chromosome segments coming from two parental wheat chromosomes. The origin of these heterogeneous chromosomes probably lies in homoeologous pairing occurring at meiosis in the 6x triticale × 2x rye hybrids from which 4x triticale lines were isolated. A comparison among different hybrids combinations indicated that the involvement of D-genome chromosomes in homoeologous pairing is quite limited. In contrast, meiotic patterns in 4x triticale × 2x rye hybrids showed a quite high pairing frequency between some R chromosomes and their A and B homoeologues.

Key words: Tetraploid triticale – Chromosome pairing – Interspecific hybridization – Genome re-arrangement – Genome affinity

Introduction

The development of polyploid forms is recognized as one of the pathways of plant evolution. It is generally accepted that polyploidization is related mainly to amphidiploïdization, that is, the adaptation of two different chromosome complements A and B to function as a new unit (AB).

This model has been reproduced experimentally and tested for quite a large number of polyploid species, some of which are of agronomic interest. However, it is likely that there are other models of polyploidization which do not result in the appearance of a new chromosome complement of which the chromosome number is equal to the sum of the parental chromosome numbers. This aspect has been discussed by several authors, notably by Vardi (1973).

The development of a 4x triticale species from crosses between 6x triticale and rye appears to be an example which will help in the understanding of biological events leading to a new genomic structure without any increase in ploidy. It is this aspect that seemed of interest in the studies of chromosome composition of the 4x triticales obtained in our laboratory since 1977.

According to their origin (Bernard and Bernard 1978) they may be expected to possess the 14 rye chromosomes (R genome) and 14 wheat chromosomes ("X" genome). These last chromosomes raise numerous questions: do they come from only one of the wheat genomes (A or B) or from both of them? Is each of the homoeologous groups represented? In this case, can any combination give rise to viable individuals? Various techniques, such as chromosome banding, enzyme electrophoresis, and meiotic analysis of hybrids, should be used to obtain answers to these questions.

Using C-banding techniques, Gustafson and Krolow (1978) tried to identify the chromosomes of homogeneous 4x triticale genotypes obtained by Krolow in 1975. At Clermont-Ferrand, we analysed the chromosome constitution of two F5 families of our 4x triticale, by both N-banding (in preparation) and by meiotic

analysis of F1 hybrids obtained from crosses with several reference genotypes. This paper presents the results of these analyses.

Materials and methods

The plants studied were F1 hybrids from crosses between:

- on the one hand, two F5 genotypes of 4x triticale, *X Triticosecale* Wittmack, 2n = 4x = 28, denoted T 4x1 and T 4x2, from a cross 'Clercal'[1] × self fertile rye 571, made at Clermont-Ferrand in 1974.
- on the other hand, the reference genotypes belonging to the following species:
- *Triticum aestivum* L., cultivar 'Talent' and two lines obtained in our station from the crosses: ('Mex. 9' × ('Mex. 50' × B 21'[2])) 22-1 and ('Champlein' × ('Jensen' × 'Washington')) 657.
- *Triticum turgidum* L., genotype no. 46 indicated by durum or DW, maintained in the wheat collection at the INRA Plant Breeding Station, Rennes.
- *Secale cereale* L., the population variety 'Beaulieu' (INRA Clermont-Ferrand), the self fertile line 595, both with 2n = 2x = 14 chromosomes; and two 4x populations: R 4x1 = no. 4210 (supplied by Dr. Guedes Pinto, Portugal) and R 4x2 = 2155 (received from Dr. Friedt, Federal Republic of Germany).
- *X Triticosecale* Wittmack, represented by the genotype T 206 (8x, obtained by Dr. Y. Cauderon from the cross FEC 28 × rye 51) and the genotype T 547 (6x, obtained at Clermont-Ferrand from the cross between T 206 and T 856, a hexaploid CIMMYT line received in 1971).

The crosses were made in order to obtain a series of hybrid combinations constituting most of the possible genome combinations so that step-by-step comparisons between more or less related hybrids were possible.

To reduce the probability of pre-existing important structural modifications which would impair the precision of observations, the 8x, 6x, and 4x triticale genotypes used were chosen as closely related as possible, having the same bread wheat parent.

The culture of immature embryos was necessary in order to obtain hybrid plants from the following crosses: 4x triticale × 2x rye; 4x triticale × 4x rye, and reciprocal; durum wheat × 4x triticale; bread wheat × 4x triticale.

The embryos which were formed were excised from developing caryopses 12–15 days after pollination and plated under sterile conditions on the R1 culture medium used in our laboratory (Bernard 1977). The plants which developed were transferred to pots, vernalized for 6–8 weeks at 5 °C ± 1 °C with a photoperiod of 16 h day/8 h night and then planted in soil in a greenhouse equiped with a cooling system (temperature not exceeding 27 °C).

The meiosis of F1 hybrids was analysed at the MI stage after dissection of anthers in a drop of ferric acetocarmine.

Results

Meiotic behaviour of 4x triticale

The results are presented in Table 1. Although their chromosome numbers were 28 or 28 + telosome, these plants did not show very regular chromosome behaviour. However, pairing of 14 bivalents was observed in several PMCs from most of the plants analysed. In addition, their progenies, following self-pollination, generally had 28 chromosomes.

(4x triticale × rye) hybrids

a 4x triticale × 2x rye. Seven hybrid plants with 2n = 21 were analysed, together with two plants having 2n = 20; 50 PMCs per plant were observed (Table 2). The mean numbers of couples of paired chromosome arms (here denoted as chiasmata) varied from 8.64 to 12.80 per plant. Analysis of variance confirmed that the population was heterogeneous (F = 54.3; DF = 8 and 441).

In comparison, the mean numbers of chiasmata observed in four heterozygous plants of 'Beaulieu' rye ranged between 13.01 and 13.88, whereas in four homozygous plants (line no. 595), they ranged from 11.26 to 12.14.

Of 350 PMCs analysed in euploid plants, 244 exhibited seven bivalents, which is in agreement with the expected structure XRR. However, the remaining 106 PMCs from five different plants showed more than 14 paired chromosomes (Table 3).

b (4x triticale × 4x rye) and reciprocal hybrids. There were 13 plants with this hybrid combination. Three had either 29 or 30 chromosomes. Of the ten others with 28 chromosomes, two could not be analysed. The results are given in Table 4.

An analysis of variance on the chiasmata number per PMC of the euploid plants indicated a highly significant variation among the plants (F = 48 for DF = 7 and 315). For 50 PMCs observed per plant, the l.s.d. was 0.72, while the extreme means differed by 5.08.

Two hyperploid plants with 29 and 30 chromosomes were included in the analysis. Although their chiasmata numbers were the highest among all others (15.36 and 14.76), they did not differ significantly from the hybrid (T 4x × R 4x) no 1. The plant with 28 + t showed a chiasmata number close to the overall mean (11.89).

Three plants, i.e., two (R 4x1 × T 4x1) plants and one (T 4x2 × R 4x2) plant were clearly more asynaptic than the others. The former two plants differed significantly from their reciprocals.

The mean number of trivalents also provided evidence for the heterogeneity of this population (from 2.44–4.36). The frequency distribution of trivalents in two groups of the hybrids, i.e., five strongly synaptic and three weakly synaptic ones, is presented in Fig. 1.

If these plants possess 21 rye chromosomes (X RRR), the seven groups of three homologues can in theory give meiotic configurations such as: (trivalent number + bivalent number) ≤ 7.

1 'Clercal': first hexaploid triticale cultivar released in France (INRA 1980)

Table 1. Meiotic chromosome configuration of the two 4x Triticale genotypes used in the crosses

Line		2n	No. of PMCs	Univalent		Bivalent		Trivalent		Mean chiasmata no.
				Mean	Range	Mean	Range	Mean	Range	
T 4x$_1$:	1	28	50	3.82	0–10	12.06	9–14	0–1	0.02	17.90
	2	28	20	1.20	0– 4	13.40	12–14	–	–	21.45
	3	28+t	50	6.32	1–13	11.34	7–14	–	–	15.94
	4	28+t	50	3.48	1– 7	12.76	10–14	–	–	20.0
T 4x$_2$:	1	28	26	2.77	0– 6	12.62	11–14	–	–	21.23
	2	28	50	2.44	1– 4	12.60	11–13	0–1	0.12	21.42

Table 2. Meiotic pairing of chromosomes at metaphase I in 4x Triticale × 2x rye hybrids

Hybrid		2n	Univalent		Bivalent		Trivalent		Quadrivalent		Mean chiasmata no.
			Mean	Range	Mean	Range	Mean	Range	Mean	Range	
T 4x$_1$ × 'Beaulieu':	1	21	7.96	6–13	5.74	4–7	0.52	0–1	–	–	8.64
	2	21	6.18	4–9	6.28	6–7	0.70	0–1	0.04	0–1	12.74
	3	21	7.01	5–9	7.00	6–8	–	–	–	–	12.64
T 4x$_2$ × R 595:	1	21	7.28	7–9	6.86	6–7	–	–	–	–	11.38
	2	21	6.98	5–9	6.92	6–8	0.06	0–1	–	–	12.80
	3	21	5.88	4–7	7.38	6–8	0.12	0–1	–	–	12.20
	4	21	6.44	5–9	7.28	6–8	–	–	–	–	10.58
	5	20	6.36	6–8	6.28	6–7	–	–	–	–	11.80
	6	20	6.48	6–8	6.76	6–7	–	–	–	–	11.58

Table 3. Number of PMCs showing x bivalents + y multivalents, in the F_1 plants, T 4x × R 2x with 21 chromosomes

y \ x	8	7	6	5	4
No trivalent	47	195	32	3	1
1 trivalent	–	3	54	12	1
1 quadrivalent	–	–	2	0	0

In fact, we recorded 45 cells, out of 323, showing more than seven paired figures. We could consider that this is an indication of homoeologous association, which is supported by the previous observations in the (T 4x × R 2x) hybrids. However, this observation does not indicate with certainty the existence of homoeologous pairing: actually, more than seven paired figures, including only rye chromosomes may be expected, if the R genomes differ between them by only one or two translocations.

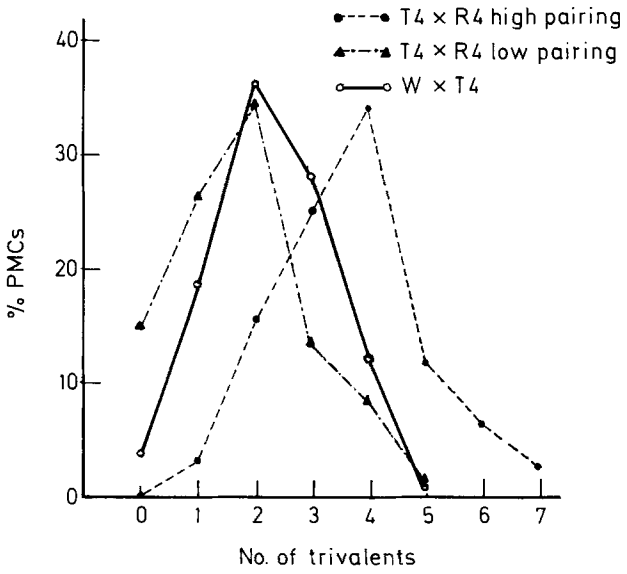

Fig. 1. Frequency distribution of trivalents in (T 4x × R 4x) and (wheat × T 4x) hybrids

Table 4. Meiotic chromosome pairing at metaphase I in T 4x × R 4x hybrids

Hybrid		2n	No. of PMCS	Univalent		Bivalent				Trivalent		Quadrivalent		Chiasmata no.[a]
				Mean	Range	Mean	Range	Rods	Rings	Mean	Range	Mean	Range	
T $4x_1$ × R $4x_1$	1	28	50	9.4	7–13	2.76	0–6	0.88	1.88	4.36	2–7	–	–	14.58
	2	28	44	10.9	8–14	3.70	0–8	1.93	1.77	3.23	0–6	–	–	12.27
	3	28	15	10.7	7–15	2.93	0–6	1.07	1.86	3.80	1–7	–	–	13.6
R $4x_1$ × T $4x_1$	1	28	50	13.06	8–18	4.48	2–8	3.42	1.06	1.94	0–5	0.04	0–1	9.92
	2	28	39	12.38	8–16	4.77	2–8	3.44	1.33	2.03	0–4	–	–	10.46
T $4x_2$ × R $4x_1$	1	28	25	10.64	9–13	3.76	2–6	1.24	2.52	3.28	0–5	–	–	13.6
	2	28	50	9.82	7–14	3.68	0–7	2.10	1.58	3.42	1–7	0.14	0–1	13.1
T $4x_2$ × R$4x_2$	1	28	50	13.76	10–18	4.88	3–7	3.38	1.50	1.44	0–3	0.04	0–1	9.4
T $4x_1$ × R $4x_1$	4	29	50	9.68	7–12	4.58	0–8	1.52	3.06	2.96	1–6	0.32	0–1	15.36
T $4x_2$ × R $4x_1$	3	28+f	50	12.56	9–17	4.10	1–6	2.2	1.90	2.72	0–5	0.02	0–1	11.94
	4	30	50	10.78	8–15	4.74	2–9	2.04	2.70	2.82	1–5	0.32	0–1	14.76
Mean of euploids				11.43		3.95				2.84		0.034		

[a] Chiasmata number of a closed trivalent is regarded as 3

Table 5. Meiotic chromosome pairing at MI of PMCs of bread wheat × T 4x hybrids

Hybrid		2n	No. of PMCS	Univalent		Bivalent				Trivalent		Quadrivalent		Mean chiasmata no.
				Mean	Range	Mean	Range	Rods	Rings	Mean	Range	Mean	Range	
BW 22 × T $4x_1$	1	35	50	18.62	14–33	4.18	3–7	1.80	2.38	2.62	0–4	0.04	0–1	11.94
	2	34+f	30	18.33	16–22	4.20	2–5	2.07	2.13	2.67	1–4	0.06	0–1	11.87
	3	34+f	50	18.30	16–23	3.96	2–6	2.14	1.82	2.82	0–4	0.08	0–1	11.74
	4	34+f	50	19.38	17–22	4.04	1–7	2.62	1.42	2.46	1–4	0.04	0–1	10.52
	5	34	30	19.73	16–24	3.03	1–6	2.06	0.97	2.60	0–5	0.10	0–1	9.52
	6	34	50	20.68	19–23	4.20	3–6	2.34	1.86	1.64	0–3	–	–	9.50
BW657 × T $4x_1$	1	34	50	18.80	15–22	2.96	1–6	2.68	0.28	2.96	1–4	0.10	0–1	9.32
BW 'Talent' × T $4x_2$	1	35	50	20.60	15–24	5.10	3–7	2.64	2.46	1.40	0–3	–	–	10.36

(4x triticale × wheat) hybrids

a T. turgidum no. 46 × 4x triticale. Two crosses each produced only one plant. The average meiotic chromosome configurations calculated from 50 PMCs are as follows:

12.08′ (8–16) + 4.24″ (3–6)* + 2.48‴ (1–4) and
13.38′ (10–15) + 5.30″ (2–6)* + 1.34‴ (0–2)

* constituted, respectively, by (1.28″ rod + 2.96″ ring) and (1.38″ rod + 3.92″ ring) and the mean chiasmata numbers are 12.26 and 11.94 (non significant difference).

b Bread wheat × 4x triticale. Eight plants resulting from three different crosses were studied (Table 5). Only two were euploid (2n = 35), three were subeuploid (34+ fragment) and three were aneuploid (34).

The analysis of variance on the mean chiasmata number calculated for five plants with 35 and 34+f indicated that this group was heterogeneous (F = 21.3; HS). The two plants with 2n = 35 differed significantly from each other. In contrast, the three plants with 2n = 34 were homogeneous and differed from the other plants.

Thus, in the two types of hybrids with durum and bread wheat, trivalents were present at quite a high frequency. Their maximum number varied from two to five, depending on the plants. Trivalent distribution in all the (durum × 4x triticale) and (bread wheat × 4x triticale) plants inclusively is presented in Fig. 1, in comparison with those obtained for both high and low-pairing 4x triticale × 4x rye hybrid types.

The frequencies of PMCs having different numbers of bivalents and trivalents, inclusively, were as follows:

Hybrids \ Figures	Total no. of bi- and trivalents					
	9	8	7	6	5	4
F1 (durum×T4x)	–	3	68	24	4	1
F1 (bread wheat×T4x)	1	22	137	61	9	–

The univalent distributions observed for the (DW×T4x) F1, the (BW×T4x) F1 with 2n=35 and the (BW×T4x) F1 with 2n=34 are presented in Fig. 2.

The presence of the D genome (seven chromosomes) caused in particular an increase in univalent number (+6.5 on average) and the formation of one or two quadrivalents in 3.8% of the PMCs.

4x triticale×6x or 8x triticale, and reciprocal

a (6x triticale×4x triticale). Ten plants from this cross were studied: seven euploids (2n=35), and three aneuploids (2n=33, 34 or 36 with an isochromosome). Their meiotic behaviour is presented in Table 6. The population of euploid plants was homogeneous for chiasmata number (x=22.06).

As for the hybrids with wheat, we observed a higher frequency of trivalents in the hybrids with T4x1 than in the hybrids with T4x2. The mean meiotic chromosome configuration of the seven euploids was: (6.32′+11.04″ +2.19‴+0.0004⁗).

In comparison with the mean meiotic chromosome configuration of (T4x×BW) hybrids, the mean number of univalents was reduced by 12.8, and the mean number of bivalents was increased by 6.75. These results agree quite well with those one might expect from the replacement of D genome by R genome in the present hybrid combinations.

b (8x triticale×4x triticale). Only three euploid plants (2n=42) were studied (Table 7). The few aneuploids obtained were not observed.

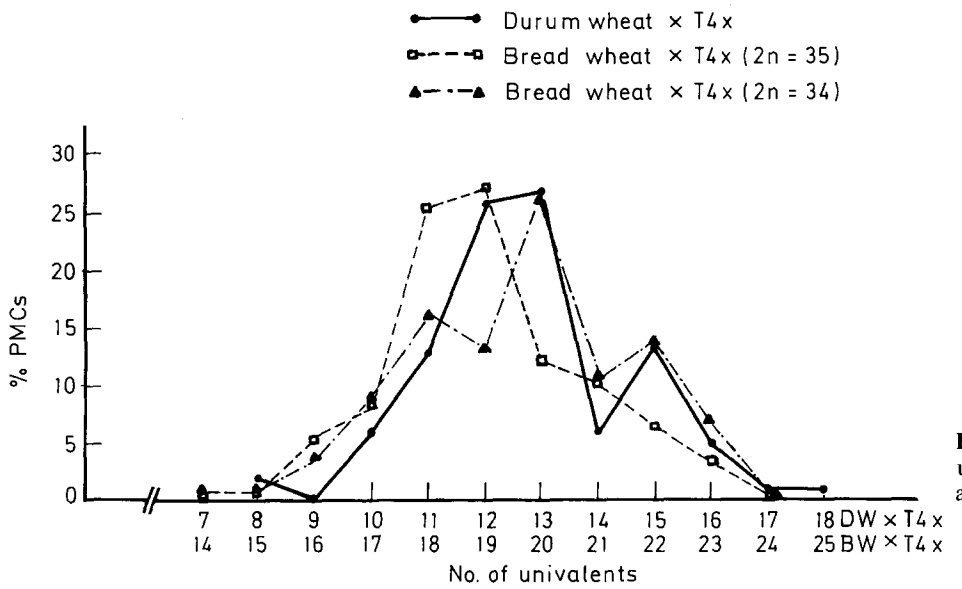

Fig. 2. Frequency distribution of univalents at MI in (BW×R 4x) and (DW×T4x) hybrids

Table 6. Meiotic chromosome pairing at MI of T6x×T4x hybrids

Hybrid		2n	No. of PMCs	Univalent		Bivalent		Trivalent		Quadrivalent	
				Mean	Range	Mean	Range	Mean	Range	Mean	Range
T6x×T4x$_1$	1	35	50	5.90	4–13	10.44	8–12	2.74	2–4	–	–
	2	35	50	5.66	3–10	10.80	8–14	2.58	0–4	–	–
	3	35	17	6.59	5–11	10.94	8–12	2.18	2–3	–	–
	4	35	27	6.19	5– 9	11.70	9–13	1.70	1–3	0.07	0–1
	5	36	41	6.44	4– 9	10.54	8–13	2.83	1–4	–	–
T6x×T4x$_2$	1	35	11	8.82	7–13	11.73	9–14	0.91	0–2		
	2	35	11	8.73	7–10	11.64	10–14	1.00	0–2		
	3	35	21	6.28	4–12	11.57	9–14	1.86	0–4		
	4	33	50	10.52	7–18	9.18	6–12	1.32	0–3	0.04	0–1
	5	34	50	8.50	6–13	10.68	8–12	1.38	0–2	–	–

Table 7. Meiotic chromosome pairing at MI of PMCs of T 8x×T 4x hybrids

Hybrid		2n	No. of PMCs	Univalent		Bivalent		Trivalent		Quadrivalent	
				Mean	Range	Mean	Range	Mean	Range	Mean	Range
T 206×T $4x_1$	1	42	50	12.24	7–13	11.28	8–15	2.32	1–4	0.06	0–1
T 206×T $4x_2$	1	42	10	12.9	8–20	12.1	8–15	1.5	0–3	0.10	0–1
	2	42	50	12.96	10–20	11.52	9–15	1.84	0–3	0.12	0–1

The average chromosome configuration observed was:

$12.42' + 11.39'' + 3.16''' + 0.09''''$.

In comparison with the preceding combination from which the present one differed by the addition of a D genome, the mean numbers of univalents and bivalents increased by 6.3 and 0.35, respectively. Compared to the (BW×T 4x) hybrids, the present hybrids, which differed from them by the addition of an R genome, had 7.09 more bivalents and 6.7 fewer univalents.

Discussion

4x triticale×2x rye

From the data on meiotic pairing, these 4x triticale appear to have a set of seven rye chromosome pairs (R) and seven wheat chromosome pairs coming from the A and B genomes. This last chromosome set will be denoted (AB).

However, an interesting result emerging from the study of this hybrid combination is the high frequency (30%) of PCMs showing fewer than seven univalents. Several hypotheses may explain this: trisomy of some R chromosome arms; homoeologous pairing between (AB)- and R-genome chromosomes; autosyndetic pairing between the chromosomes of the (AB)-genome. The first hypothesis assumes partial autotetraploidy of 4x triticale. However, no quadrivalents were observed at meiosis in this species. The second hypothesis, (AB)-R pairing, accounts for the occurrence of trivalents, but cannot explain the appearance of an extra bivalent. Thus, the autosyndetic pairing between (AB)-genome chromosomes is also likely to be involved.

D-genome participation in homoeologous pairing

The participation of the D-genome chromosomes in homoeologous pairing can be demonstrated by the following two comparisons:

(T 8x×T 4x) hybrid vs (T 6x×T 4x) hybrid
(BW×T 4x) hybrid vs (DW×T 4x) hybrid.

The mean univalent numbers of (T 8x×T 4x) hybrids and (T 6x×T 4x) hybrids were 12.42 and 6.32, respectively, the difference being 6.10. Similarly, the mean numbers of univalents of (BW×T 4x) hybrids and (DW×T 4x) hybrids were 19.11 and 12.73, respectively, the difference being 6.38. Both differences were very similar.

The mean number of D chromosomes participating to the homoeologous pairing is assumed to be less than one. A further indication is also given by comparing the proportions of PMCs exhibiting more than seven paired figures in (AB) A B R and (AB) A B D R combinations. These proportions are, respectively, 3 out of 100 PMCs, and 23 out of 230 (non significant difference). In both cases, the frequencies of quadrivalents are very low. We can therefore argue that D chromosomes are scarcely involved in homoeologous pairing. Even though this participation is not assessed with accuracy, the present results suggest quite a weak affinity between D- and A- or B-genome chromosomes. Furthermore, under our conditions, the influence of the D genome on the genetic control of pairing appears also very limited.

From the above considerations, we can assume that chromosome pairing observed in (AB) R R R hybrids, and in hybrids between bread or durum wheat with 4x triticale, mainly involves the 21 R chromosomes and the 21 (AB) A B chromosomes, respectively.

It is worth comparing the meiotic pairing behaviour of those two sets of 21 chromosomes, the former, a true triploid, being considered as a check. This comparison will be made using the model for meiotic pairing in triploid hybrids proposed by Alonso and Kimber (1981).

Analysis of triploid-like structures: tentative adjustment to the model for meiotic analysis of triploids proposed by Alonso and Kimber (1981)

For any given triploid structure (M, N, O) the model presented by Alonso and Kimber is based on the definition of two parameters:

c = the mean frequency with which two related chromosome arms pair, that is the mean number of "connections" per triplet of chromosome arms; x = the

relative affinity of the two most closely related genomes (for example: M-N); y=(1-x), represents the relative affinity between the third genome and the two others.

This model is based upon at least four assumptions which involve simplifications that we will not discuss further here (Espinasse 1982).

According to these parameters, Alonso and Kimber (1981) established the relations between them, permitting calculation of the frequencies of univalents, rod and ring bivalents, and trivalents. Reciprocally, from the numbers of the different meiotic figures observed, c and x can be calculated. The parameter x mainly influences the balance between trivalents and ring bivalents and the parameter c determines the frequency of rod bivalents.

a T 4x × R 4x. The values of c, calculated for eight euploid plants (2n=28) vary from 0.67 to 0.96. According to the values thus obtained, the values of x are very close to 0.5 for all the (T 4x1 × R 4x1) plants and their reciprocals, and for a (T 4x2 × R 4x1) plant (no. 2). One can thus conclude that for these six plants the three R genomes are equidistant (concerning the probability of pairing). In contrast, for the (T 4x2 × R 4x1) plant no. 1, and the (T 4x2 × R 4x2) plant, for which c varies from 0.92 to 0.67, the frequencies of ring bivalents are similar to those of trivalents: x near to 0.76 accounts for the behaviour observed. Thus, for these two plants, there appears to be a deviation from the equiprobability of pairing: the three R genomes are not equivalent. This behaviour, if it does not result from a sampling error, may reflect a tendency towards the diploidization of autotriploid or autotetraploid structures.

So it can be noted that even if there is, theoretically, equidistance between the three genomes involved, behaviour patterns which suggest a situation of type 2:1 rather than 3:0 may be observed. Sample size (number of PMCs observed) and environmental conditions may obviously influence results. However, a small number of translocations between triplet groups may lead to such a situation. Of course, in our case, the origin of the chromosomes having undergone any kind of "differentiation" cannot be specified.

b T 4x × wheat. The structure of the triploid component is also revealed by hybridization between T 4x and wheat species or other forms of triticale. In order not to complicate the analysis unnecessarily, only the (T 4x × wheat) euploid hybrids will be considered here, that is: two plants with 28 chromosomes involving durum wheat, two with 35 chromosomes involving bread wheat. In these hybrids, pairing involves for the most part the A and B genomes of wheat and the (AB)-genome of 4x triticale, of wheat origin, without notable interference from the other constituents (that is, R and D, being each represented by seven univalents). Using this hypothesis, the following four behavioural patterns are expected:

in T 4x1 × DW: $5.08' + 1.28''d + 2.96''a + 2.48'''$ with a maximum of 4'''
in T 4x2 × DW: $6.38' + 1.38''d + 3.92''a + 1.34'''$ with a maximum of 2'''
in T 4x1 × BW: $4.62' + 1.80''d + 2.38''a + 2.62'''$ with a maximum of 4'''
in T 4x2 × BW: $6.60' + 2.64''d + 2.46''a + 1.40'''$ with a maximum of 3'''.

In order to assess the values of parameters c and x, one can either determine the average behaviour for the 4 plants, or consider separately the hybrids involving T 4x1 and those involving T 4x2.

In the latter case, the hybrids with T 4x2 show:

$c = 0.795$ and $x \simeq 0.9$ which gives an average theoretical behaviour of

$6.15' + 2.18''d + 3.07''a + 1.41'''$

compared with an observed behaviour of

$6.49' + 2.01''d + 3.199''a + 1.37'''$

which appears a satisfactory approximation. For the hybrids made with T 4x1:

$c = 0.85$ and $x \simeq 0.8$

which corresponds to an average theoretical behaviour of

$4.78' + 1.78''d + 2.52''a + 2.52'''$

for an average observed behaviour of

$4.85' + 1.54''d + 2.67''a + 2.56'''$.

In the present case, the biological significance of the parameter x (measure of relative affinity between the 2 most closely related genomes) is not evident at all. If the corresponding theoretical genomic groups are denoted as M, N and O, situated at the apexes of an isoceles triangle, the problem is to determine how they are superimposed on the genomes A, B and (AB) associated in these hybrids. If N is one of the two original genomes (for example A), M, showing a relative affinity x=0.8 or 0.9 with N, cannot be B, for this would suppose a very close affinity; it must therefore be (AB). This genome (AB) is thus close to only one of its ancestor genomes, this latter and (AB) having a relative affinity of 0.2 with the third (Fig. 3 a).

Another possibility exists, closer to the results of Gustafson and Krolow (1978), i.e. (AB) is a mixture of chromosomes of A and B origin. The correspondance

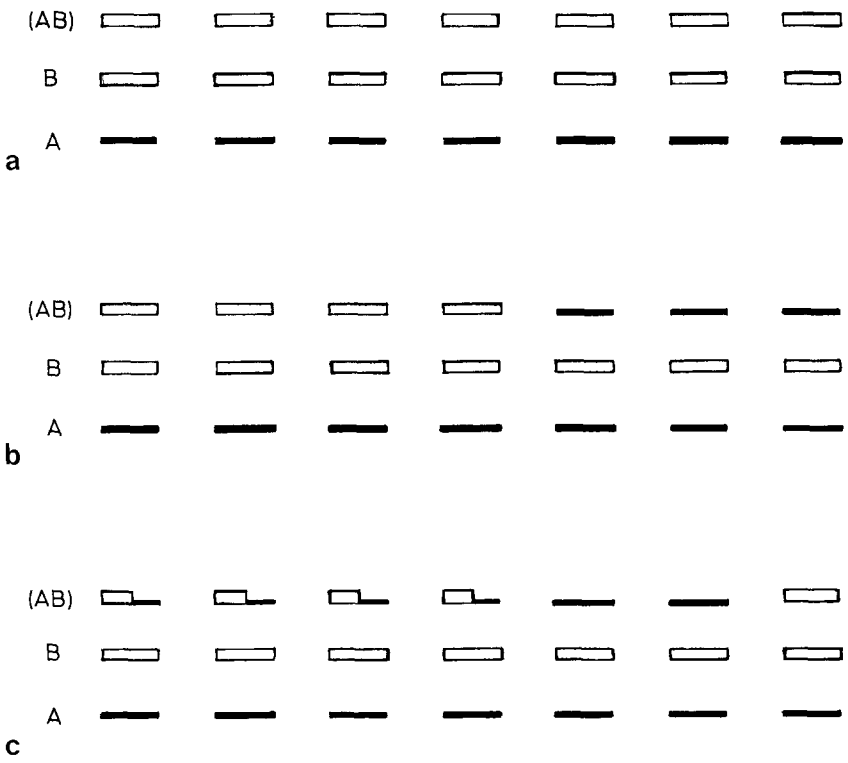

Fig. 3. Different possible structures of the wheat chromosome component present in 4x Triticale

with the theoretical model (M, N, O) is the following (Fig. 3 b).

M = mixogenome (AB)
N = A and B chromosomes "ancestors of (AB)"
O = A and B chromosomes "non ancestors of (AB)"

In the two cases described above, it could be concluded that the relative affinity y between A and B is about 0.2, whereas the relative affinity x of A with itself (or B with itself) is only 0.8. These values appear quite surprising. For example, in AA B or AAG hybrids studied by Barnhill (1977) and Alonso (not published, quoted by Alonso and Kimber (1981)), the relative affinity of A with itself is close to 1, the relative affinity of A with B and/or G close to 0: in the cases, the pairing is restricted to true homologous partners. Clearly, the proposed model for the relationships between A, B and AB does not fit with these results.

A quite different model can also be proposed (Fig. 3 c). This model, which requires the existence of a mixed heterogeneous structure, leads, other factors remaining constant, to an unchanged frequency of rod bivalents and to the frequencies of univalents, ring bivalents and trivalents which are given in Table 8. It suggests, for values of x close to 1 and of y close to 0 (that is, with homologous pairing favoured in comparison with homoeologous pairing) that trivalents, ring and rod bivalents may all appear at a high frequency. For example, for $c=0.85$ (consistent with our observations) and $x=0.9$ (strong affinity between strict homologues), for $k=4$ "heterologous" triplets, one will obtain an average behaviour of:

$1.74' + 1.02''d + 0.45''a + 2.44'''$

to which the behaviour of the remaining triplets (type 2 : 1) must be added

either:
for $c=0.85$ and $x=0.9$: $2.45' + 0.77''d + 1.49''a + 0.68'''$

or:
for $c=0.85$ and $x=1$: $3.15' + 0.77''d + 3.17''a$ (no trivalents).

The mean total pairing is thus:

$4.19' + 1.79''d + 1.94''a + 3.12'''$ or
$4.89' + 1.79''d + 2.62''a + 2.44'''$.

These values are also quite close to the average behaviour observed for the hybrids involving T 4x1.

The variations observed between hybrids can then be explained by variations of c and x, and also by variations in the number of heterogeneous chromosomes making up the mixogenome (AB). For example, for the same values of c and x as given above, the expected number of trivalents with two heterogeneous chromosomes is 1.22 and with three heterogeneous chromosomes, it is 1.83.

Table 8. Modified theoretical frequencies of meiotic figures for a heterogenous (AB A B type) triplet (c, x and y: parameters defined by Alonso and Kimber 1981)

Association (A)	A=0	A=1	A=2	
Probability: P (A)	$(1-c)^2$	2c (1−c)	c^2	
Meiotic configuration: K	3 I	1IId+1 I	1 IIa+1 I	1 III
No. of meiotic figures in (K): n				
I	3	1	1	0
II d	0	1	0	0
II a	0	0	1	0
III	0	0	0	1
Probability of the meiotic configuration K: D=	1	1	$\frac{2xy+y^2}{(x+2y)^2}$	$\frac{x^2+2xy+3y^2}{(x+2y)^2}$
Theoretical frequency of the meiotic figures n×P (A)×D				
I	$3(1-c)^2$	2c (1−c)	$c^2\frac{2xy+y^2}{(x+2y)^2}$	–
IIa	–	–	$c^2\frac{2xy+y^2}{(x+2y)^2}$	–
III	–	–	–	$c^2\frac{x^2+2xy+3y^2}{(x+2y)}$

The frequency of rod bivalents is unchanged [2c (1−c)]

This model is also of interest in that it permits ring bivalents/trivalents ratios of less than 0.5 to be taken into account: this is not possible with Kimber's original model for which this minimum value is obtained for x=0.5 (equal affinity of genomes). It also provides an explanation for the reduced number of ring bivalents in the plants with 34 chromosomes: it only requires, in one of the (7-k) triplets of type A-A-B (association 2:1), the absence of one of the 2 homologous chromosomes. If, on the contrary, the chromosome absent is the "non-homologous" chromosome, the number of univalents is reduced. Finally, if the chromosome absent belongs to one of the k heterogeneous triplets, the mean numbers of trivalents and ring bivalents will decrease.

This model, considering that the genome (AB) is made up of k heterogeneous chromosomes and (7-k) homogeneous chromosomes should lead to the sum "maximum number of trivalents + maximum number of ring bivalents" being rarely greater than seven in any plant. This was true for five BW×T 4x hybrid plants. For three others of the same type, and one DW×T 4x plants, this quantity was eight (with extreme numbers of ring bivalents only observed in one, two or three PMCs of 50). It was nine (a maximum of 5 bivalents was observed in two PMCs and four trivalents in eight PMCs) in the hybrid (DW×T 4x1).

These values can be explained either by the existence of heterogeneous chromosomes carrying translocations which involve only part of an arm, or by sufficiently high y values: y=0.1 is sufficient for a ring bivalent to replace a trivalent in a heterogeneous triplet in 1/7 of the PMCs.

Conclusion

Concerning the identity of the (AB) genome in 4x triticale, two hypotheses can explain the behaviour of hybrids in which this genome is present: model 2:1 (A-A-B type), and the model with a mixogenome composed of a number of heterogeneous chromosomes.

The first would require the existence of quite a strong relative affinity (y) between homoeologous partners – especially if we consider that two homologous partners are present – and this has not so far been reported in identical conditions.

The second model, while supposing that x and y have values close to 1 and 0, respectively, makes possible an explanation of the appearance of trivalents at a high frequency. It has in addition the advantage of explaining the results obtained by Gustafson and Krolow (1978) on their material, that is differences observed between chromosome banding patterns for ancestor chromosomes and those making up 4x triticale.

One question which remains to be answered is that of the origin of heterogeneous chromosomes. Miller and Riley (1972) and Bernard and Saigne (1977) reported observations of homoeologous pairing A-B at a high frequency in (T 6x×R 2x)

F1 plants: some PMCs in hybrids showed up to 13 bivalents and two univalents. It seems likely that this pairing favoured recombination between A- and B-genome chromosomes and thereby the emergence of heterogeneous chromosomes in some progenies, particularly in the 4x triticale obtained. We are currently testing this hypothesis by N-banding techniques (Gerlach 1977) which enables B-genome chromosomes to be readily distinguished from the A-genome chromosomes.

It may be asked whether the appearance of normally viable and fertile T 4x containing parts of the A and B genomes is linked with the existence of these chromosomes. The small number of T 4x genotypes studied so far makes it difficult to reply to this question.

The emergence of 4x triticale from T 6x × R 2x crosses is an interesting case of evolutionary phenomenon, that could well occur under natural conditions. In addition, it constitutes a model for study of the development of a new genomic entity from two ancestor genomes. It is clear that if such events leading to a mixogenome occur under natural conditions, the identification of the ancestor genomes will not be easy. It is possible that genome B had this type of origin, for its affinity with genome A appears quite considerable and its diploid ancestor has not been identified so far.

Acknowledgements. We gratefully acknowledge Mrs. Bernadette Saigne for the excellent technical assistance and Dr. Felicity Vear for her help with the English.

References

Alonso LC, Kimber G (1981) The analysis of meiosis in hybrids. 2. Triploid hybrids. Can J Genet Cytol 23: 221–234

Barnhill GL (1982) The evolutionary relationship of tetraploid wheat. MS Thesis, University of Missouri, Columbia MO, USA

Bernard M, Bernard S (1978) Methods of gene transfer from bread wheat and rye to hexaploid triticale. In: Sanchez-Monge E, Garcia-Olmedo F (eds) Interspecific hybridization in plant breeding. Proc 8th Eucarpia Congr, Madrid, Spain, pp 181–189

Bernard M, Saigne B (1977) Etude cytogénétique de F1 et F2 (Triticale hexaploïde × Seigle): mise en évidence d'une inhibition du système diploïdisant du blé tendre. Ann Amelior Plant 27:737–748

Bernard S (1977) Etude de quelques facteurs contribuant à la réussite de l'androgénèse par culture d'anthères in vitro chez le triticale hexaploïde. Ann Amelior Plant 27:639–655

Espinasse A (1982) Présentation rapide de la méthode d'analyse de la méiose développée par G. Kimber et collaborateurs. Agronomie 2:267–272

Gerlach WL (1977) N-banded karyotypes of wheat species. Chromosoma 62:49–56

Gustafson PJ, Krolow KD (1978) A tentative identification of chromosomes present in tetraploid triticale based on heterochromatic banding patterns. Can J Genet Cytol 20: 199–204

Miller TE, Riley R (1972) Meiotic chromosome pairing in wheat-rye combinations. Genet Iber 24:241–250

Vardi A (1973) Introgression between different ploidy levels. In: Sears ER, Sears LMS (eds) Proc 4th Int Wheat Genet Symp. Columbia Mo, USA, pp 131–141