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Chromosomal identification and meiotic behavior of reciprocal translocations in a rye polymorphic population. Evolutionary implications

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Summary. The spontaneous interchange polymorphism of rye cultivar "Ailés" is composed, as can be deduced from the chromosomal identification of the interchanges analyzed, of several different reciprocal translocations in which the chromosomes of its haploid complement are involved with a similar frequency, except for chromosomes *4R* and *6R*. Several features of chromosome behavior at metaphase I, such as configuration and orientation of quadrivalents and frequency of chiasmata, were analyzed in structural heterozygotes for different interchanges. The two main factors affecting the orientation of quadrivalents at metaphase I proved to be the morphology of these chromosome associations at metaphase I and, in particular, the frequency of bound chromosome arms that they showed. A genotypic control of alternate orientation of quadrivalents independent of chiasmata frequency was not detected. In addition, the frequency of alternate orientation shows no relation to the fitness. Possible evolutionary implications of the results obtained are discussed.

Key words: Rye interchanges – Chromosomal identification – Meiotic behavior – Fitness

Introduction

In order to understand the evolutionary significance of the chromosomal polymorphisms for reciprocal translocations, it is necessary to achieve a deep knowledge of the cytogenetic characteristics of such rearrangements. This includes the morphology of the multivalent association appearing, the identification of the chromosomes involved, and the meiotic behavior of the structural heterozygotes, particularly at metaphase I.

It has been stated that one of the main factors which determines the fitness of the structural heterozygotes and, therefore, their probability of maintenance or elimination in the populations is the disjunctional segregation of the chromosomes forming a multivalent association during the first meiotic stages. When there is no alternate co-orientation for the centromeres inside the multivalent, gametes carrying duplications and deletions of chromosomal segments arise. These gametes are generally not viable and, consequently, the structural heterozygote will have a reduced fertility (see Rickards 1983 for a review).

It has been proposed that several factors play a role in the multivalent centromeric co-orientation phenomenon (Rickards 1983; Sybenga and Rickards 1987 for a review). Some of these factors are the structural characteristics of the standard chromosome complement (centromere position, the size and mechanical flexibility of the chromosomes, and the chiasma frequency and location), the structural characteristics of the translocated chromosomes, such as degree of symmetry of the multivalent cross during pachytene and diplotene and, finally, the genotypic control of co-orientation. However, the influence of such factors and their relevance are not well known, mainly due to the fact that in each case just one or a few of these factors are analyzed and the derived conclusions might not be in total agreement.

In a previous work (Candela et al. 1979) we have already described the chromosomal polymorphic rye cultivar "Ailés," which presents a constant frequency of about 15%–20% of plants heterozygous for a number of different reciprocal translocations. The frequency of heterozygosity for more than one interchange in a single individual is very low and no homozygotes for rearranged karyotypes were found. This suggests a high

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spontaneous chromosome mutation rate, which was estimated afterwards as 6.12×10^{-2} per plant and generation (Candela et al. 1982). The simultaneous analysis carried out comparing the fitness of the homozygous and heterozygous plants, which is higher for the former, supports the hypothesis that this chromosomal polymorphism could be maintained by a mutation-selection equilibrium (Candela et al. 1982).

In this work we have evaluated the types and frequencies of the different interchanges present in the original "Ailés" population and the meiotic behavior of the structural heterozygotes, in order to ascertain the possible evolutionary implications of this type of polymorphism.

Materials and methods

The samples analyzed for the chromosomal identification and meiotic behavior of heterozygous plants were obtained by two different breeding systems of the original population of cv "Ailés". The generation G_0 was open-pollinated and contains structural homozygotes for standard arrangement (SHm) and structural homozygotes (SHt). In addition, G_0SHt plants carrying different translocations were crossed with two or three different G_0SHm plants with the standard arrangement, in order to obtain progenies with different genetic backgrounds carrying the same interchange of the parental G_0SHt. These progenies were generically named sample G_1C.

All the interchanges used in this study had a spontaneous origin and all samples were grown under the same experimental conditions.

Plants were classified as SHm or SHt according to the metaphase I (MI) configurations (7II or 1IV + 5II, respectively) in the pollen mother cells (PMCs). The spikelets were collected at the appropriate stage and fixed in alcohol:acetic 3 to 1. Staining was with ammonium-ferric-sulphate and hematoxilin (Figueiras et al. 1983).

The identification of the translocated chromosomes was made in G_0SHt plants according to their C-banding patterns at metaphase I (Fig. 1 a–f). The chromosomes were classified following the nomenclature proposed by Sybenga (1983). This technique, described by Giráldez and Orellana (1979), was not successful for the identification of chromosomes *3R, 7R,* and sometimes *2R*. In those cases in which some of these chromosomes were involved in a given translocation (Fig. 1 g), their identification was carried out following the method described by Figueiras et al. (1985) and based on linkage analysis between the translocations and isozymic markers, whose chromosome location is known (Table 1). Despite using both methods for chromosomal identification, not all chromosomes involved in the analyzed interchanges of samples G_0 and G_1C could be identified (i.e., T 385 and T 399).

In order to analyze the cytogenetic characteristics and the meiotic behavior of the SHt for each group of plants studied, 25 PMCs at mid-MI per plant were analyzed when it was possible to classify most of the PMCs. The approximate morphology of multivalents was studied at early diplotene.

The number of chiasmata per cell has been estimated as the number of bound arms per cell (BA/cell). This value ranged from 11 to a maximum of 14. In sample G_1C, this parameter was scored separately in the quadrivalent and in the remaining five bivalents within each PMC.

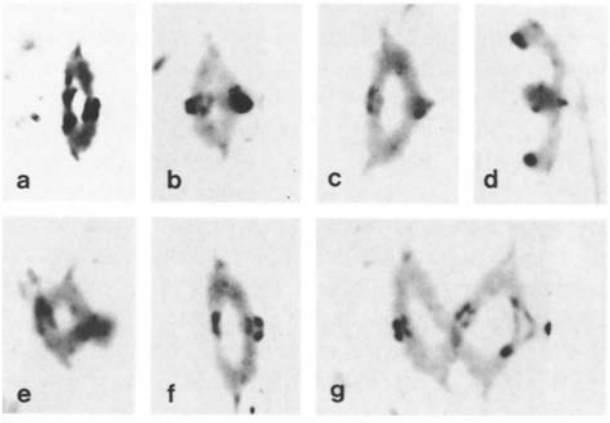

Fig. 1 a–g. C-banding pattern of rye chromosomes at metaphase I cells. Bivalents *1R* (**a**), *2R* (**b**), *4R* (**c**), *5R* (**d**), *6R* (**e**), and one undetermined (*3R* or *7R*) (**f**). Quadrivalent in which an unidentified chromosome and the chromosome *1R* are involved (**g**)

Table 1. Chromosomal location of isozyme structural genes in *Secale cereale* L. cv Imperial, cv King II, and cv Dakold

Enzymes	Genes	Chromosome or chromosome arm of genome R	References
Glucose phosphate isomerase-1 [a]	*Gpi-1*	*1p*	Hart (1979), Chojecki and Gale (1982)
6-Phosphogluconate dehydrogenase-2 [a]	*6-Pgd-2*	*1q*	Lawrence and Appels (1986)
Malate dehydrogenase-1 [a]	*Mdh-1*	*1*	Figueiras et al. (1985)
Leaf peroxidases	*Per-2,3*	*2p*	Salinas and Benito (1984b)
Esterase-2	*Est-2*	*3(q?)*	Barber et al. (1968), Bergman and Maan 1973)
Glutamate oxaloacetate transaminase-3 [a]	*Got-3*	*3(q?)*	Tang and Hart (1975)
Malate dehydrogenase-2b	*Mdh-2b*	*3(q?)*	Salinas and Benito (1985a)
Phosphoglucomutase-1	*Pgm-1*	*4p*	Salinas and Benito (1985b)
Alkaline phosphatase	*Alk-2,3*	*7p*	Salinas and Benito (1984a)

p – short arm; *q* – long arm; *p?* or *q?* – chromosome arm assigned by homoeology with hexaploid wheat
[a] Dimeric enzymes

Results

Chromosome identification of translocated chromosomes

Chromosome identification of interchanges was totally or partially carried out on 19 SHt of a total of 27 detected in sample G_0 (Table 2). At least 12 of these carried different interchanges, when the chromosomes or chromosome arms implicated in the translocations are taken into account. All chromosome pairs appeared to be involved in interchanges with similar frequencies, with the exception of chromosome pairs *4R* and *6R*, which appear implicated in seven and six translocations, respectively. Both chromosome pairs seem to be also involved in another two translocation events. We must stress that we have not been able to identify with certitude the *7R* chromosome due to inherent difficulties of the C-banding technique. In addition, the lack of adequate genetic constructions prevents us from probing with the available isozymatic markers. Nevertheless, this chromosome could be involved in some of the seven interchanges, most likely in those were its presence could not be detected.

In relation to the morphological characteristics of the quadrivalent association, Fig. 2 shows the three main types of diplotene crosses found: symmetric with translocated segments of medium and aproximately similar size (a), symmetric with small translocated segments (c), and asymmetric with translocated segments of different sizes resulting in a long and a small chromosome (e). Figure 2 also shows the adjacent quadrivalent configurations at MI (b, d, and f, respectively). In Table 2, the classification of the interchanges analyzed according to these three main morphological types of quadrivalents is also indicated. The degree of asymmetry was variable, reaching the highest values in some cases, i.e., the T 243, T 244, T 331, or T 344 interchanges. According to the morphology of the diplotene crosses, we can extend the minimal number of different translocations up to 15, since T 112 and T 344 would be different, also T 116 and T 135 and, similary, T 101 in relation to T 47 and T 331.

Table 2. Chromosome identification of interchanges in heterozygous plants from cv Ailés (sample G_0)

Pairs of chromosomes involved in the interchange	Interchanges
1R–3R	T 245[a]
1RL–4RL	T 92[a]
1R–6R	T 130
2R–6R	T 47[c]
2RL–4RS	T 23[b]
2RS–6RL	T 331[c]
3R–4R	T 62[a]
3R–6R	T 344[c]
3R?–7R?	T 116[b]
4RS–(3R or *7R)**	T 231[a]
4RS–5RL	T 146[b]
4RL–5RS	T 243[c], T 244[c]
4RL–5RL	T 59[c]
6R–(2R, 3R or *7R)**	T 101[b], T 112[a], T 237
*(2R, 3R, 7R)***	T 135[c]
*(3R, 4R, 7R)***	T 456[c]

S – short arm; *L* – long arm
* One of these chromosomes would be involved in the interchange
** Two of these chromosomes would be involved in the interchange
[a] Diplotene cross symmetric with translocated segments of medium and approximately similar size
[b] Diplotene cross symmetric with small translocated segments
[c] Diplotene cross asymmetric with translocated segments of different size; also, interchanges T 385 and T 399

Meiotic behavior of heterozygotes

The meiotic behavior of the SHt of samples G_0 and G_1C was very similar. Thus, the percentage of PMCs showing a quadrivalent is always very high ($\bar{X}=94.12\pm0.87$). The quadrivalents appear more frequently as rings ($\bar{X}=82.98\pm2.12$) than as chains. As a whole, alternate orientation is more frequent in chain ($\bar{X}=86.53\pm4.50$) than in ring ($\bar{X}=62.06\pm3.23$) quadrivalents, except in very few plants. Directed segregation of quadrivalents (more than 50% alternate orientation) seems to be a general trend in interchanges of this rye cultivar ($\bar{X}=66.18\pm3.14$), although extreme values for alternate orientation (such as 5% or 95%) have been found.

In most cases, the location of chiasmata in the quadrivalent is distal or subdistal. Intermediate chiasmata (not a chiasma in an interstitial segment but in the middle of the chromosome) were found in some ring and chain quadrivalents, with alternate or adjacent orientation of some interchanges (T 59, T 243, T 331, T 385, and T 399) that showed asymmetric crosses in diplotene (Fig. 2e–f).

Table 3 shows the results of meiotic behavior obtained for the same variables previously cited in analyzing the G_0SHt mother plants and their progenies obtained by crossing with different structural standard homozygotes. This behavior is clearly different among the translocations analyzed in this work; however, progenies from different crosses carrying the same translocation behave in a similar way. Consequently, data were pooled and only the mean values of crosses are shown.

On the other hand, correlations between mother plant values and the mean of each respective progeny were made in SHt crossing groups (G_1C) for all cytogenetic features of the quadrivalent analyzed (ring multivalents, quadrivalents with alternate orientation, alternate rings, and alternate chains). Positive correlations were only found for alternate ring quadrivalent ($r=0.89$, t 26

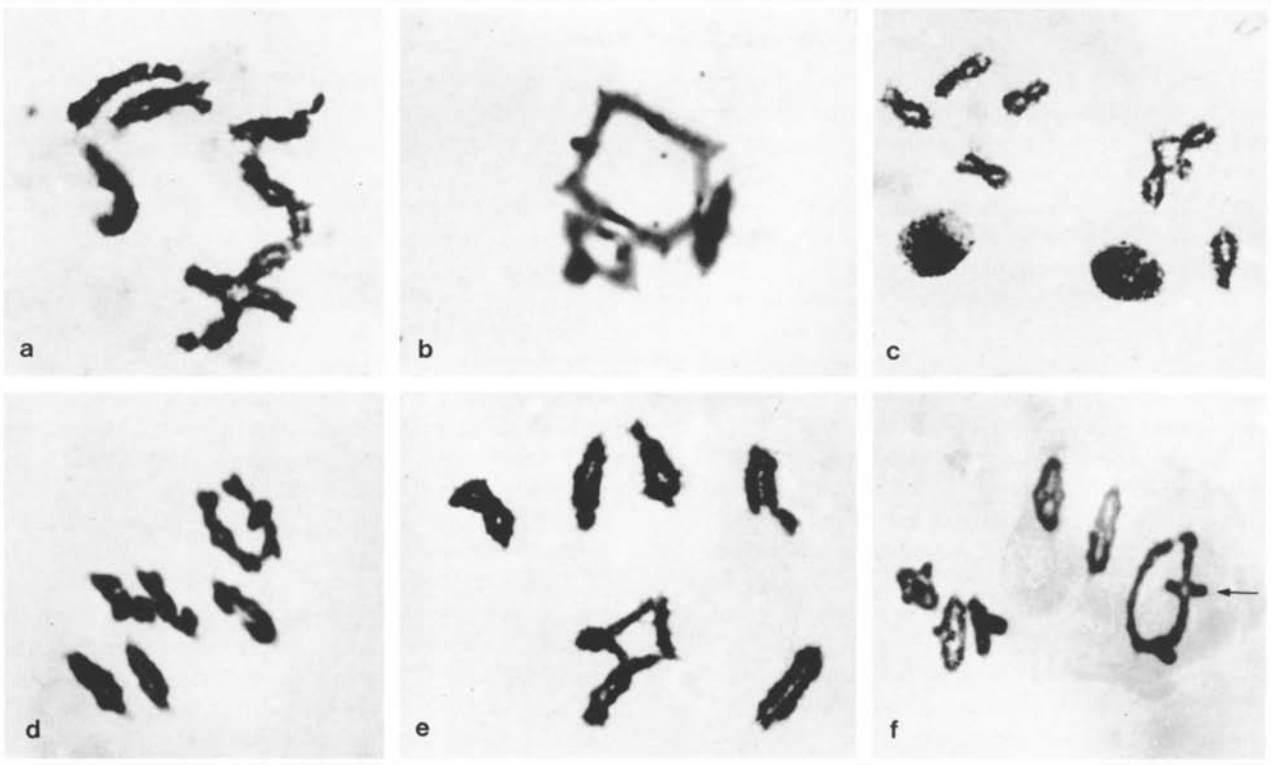

Fig. 2a–f. Types of quadrivalent associations at diplotene (**a**, **c**, and **e**) and their respective configurations at metaphase I (**b**, **d**, and **f**): symmetric with translocated segments of medium and approximately similar size (**a**, **b**); symmetric with small translocated segments (**c**, **d**); and asymmetric with translocated segments of different size (**e**, **f**). Intermediate chiasma observed in type "f" quadrivalent is indicated by *arrow*

Table 3. Meiotic behaviour at MI of SHt from G_1C sample and their respective G_1SHt mother plants

Interchange		No. of crosses analyzed	Total plants analyzed	PMcs with 1IV + 5II (%)	Ring quadrivalents (%)	Ring alternate quadrivalents (%)	Chain alternate quadrivalents (%)	Alternate quadrivalents (%)	BA/cel $\bar{X}$
T 399	(Mp)			40.00	90.00	0.00	50.00	5.00	12.04±0.20
	(Mo)	2	5	44.80±4.63	82.08±7.03	12.35±3.36	77.50±13.15	22.44±6.41	13.13±0.21
T 245	(Mp)			100.00	88.00	22.73	66.67	28.00	13.76±0.09
	(Mo)	2	17	97.88±0.70	65.69±6.46	49.36±4.44	86.31±3.13	59.71±4.29	13.41±0.10
T 385	(Mp)			94.00	91.49	34.88	100.00	40.42	13.66±0.07
	(Mo)	2	13	98.77±0.70	91.64±2.05	60.18±2.98	100.00±0.00	63.67±2.96	13.54±0.05
T 59	(Mp)			92.00	91.30	38.10	75.00	41.30	13.80±0.06
	(Mo)	3	21	96.19±0.75	84.86±3.09	44.29±2.82	85.43±3.87	49.77±3.25	13.50±0.07
T 243	(Mp)			96.00	100.00	54.17	–	54.17	13.64±0.10
	(Mo)	3	11	98.91±0.56	93.38±1.81	54.15±2.74	90.83±6.03	55.83±2.60	13.61±0.05
T 62	(Mp)			100.00	98.00	63.26	100.00	64.00	13.56±0.09
	(Mo)	3	20	99.00±0.49	85.89±2.96	64.47±3.06	90.97±3.31	67.90±3.05	13.43±0.06
T 116	(Mp)			100.00	98.00	65.31	100.00	67.34	13.88±0.05
	(Mo)	3	18	97.56±0.65	87.22±3.61	64.12±4.40	83.01±6.01	66.28±4.12	13.54±0.07
T 23	(Mp)			96.00	83.33	75.00	62.50	72.92	13.48±0.10
	(Mo)	2	11	98.73±0.78	92.59±1.54	63.24±3.94	100.00±0.00	65.97±3.84	13.65±0.06
T 112	(Mp)			96.00	93.75	75.56	66.67	75.00	13.18±0.10
	(Mo)	2	9	96.44±1.41	86.34±3.22	69.01±2.60	83.07±5.23	71.02±2.49	13.60±0.07
T 92	(Mp)			82.00	90.24	81.08	100.00	82.93	13.68±0.08
	(Mo)	2	19	95.37±1.11	85.28±3.09	69.96±2.13	94.91±2.42	73.15±1.90	13.49±0.06
T 344	(Mp)			96.00	79.17	84.21	100.00	87.50	13.44±0.13
	(Mo)	2	7	96.00±1.63	84.15±5.56	76.31±5.81	100.00±0.00	79.37±5.85	13.41±0.06
T 331	(Mp)			100.00	68.00	88.23	93.75	90.00	13.12±0.10
	(Mo)	2	9	97.60±1.60	76.43±6.72	80.47±6.61	100.00±0.00	86.16±4.69	13.32±0.05

(Mp) – mother plant; (Mo) – mean of the offspring

$df = 9.66$, $0.001 \gg p$) and alternate quadrivalent frequencies ($r = 0.88$, t 26 $df = 8.94$, $0.001 \gg p$). This could suggest that only these variables contain a significant genetic component in their variation although since each mother plant carries a different translocation, these positive correlations could also be a reflection of the influence of morphological features of individual interchanges.

Data showed in Table 3 indicate that the morphological differences (asymmetry and relative length of translocated segments) do not seem to produce clearly detectable effects on the meiotic behavior, particularly on MI orientation of quadrivalents.

Neither interchromosomal effects nor interchromosomal chiasma interference has been detected in the different translocations analyzed; i.e., SHm and SHt obtained by open-pollination present a similar frequency of BA per cell (13.49 ± 0.05 and 13.34 ± 0.06, respectively), indicating that the structural heterozygosity probably does not modify the chiasma frequency. Similarly, interchromosomal interference was tested within the same plants by analyzing the relative contribution of BA per chromosome in all chromosomes not involved in the interchange when the quadrivalent configuration is a ring or a chain. The results obtained indicate that the relative contribution of BA per chromosome pair in the bivalents to the BA per cell was not statistically different between PMCs showing chain (3 BA) or ring (4 BA) quadrivalents.

Relationship between quadrivalent orientation and fitness

For this purpose we have correlated the percentage of alternate orientation observed in the PMCs of the plants corresponding at the G_1C sample and their fitness, estimated as the number of seeds produced in each one of their offsprings. We have assumed that the frequency of the different types of quadrivalent orientation is sex independent, since in rye no sex differences between chiasma frequencies and distributions have been described (Davies and Jones 1974) and it is well known that both parameters are one of the main factors involved in the multivalent centromere co-orientation. No correlation between quadrivalent orientation and fitness have been found ($r = 0.45$, t 9 $df = 1.53$, $0.30 > p > 0.10$).

Discussion

The identification of the chromosomes involved in the interchanges analyzed indicates that the chromosomal polymorphism detected in the cv "Ailés" would consist of many different interchanges, the chromosomes of the haploid complement being involved at rather similar frequencies, with the exception of *4R* and *6R*. This result is in agreement with that obtained by Cermeño and Lacadena (1985) in translocations of rye induced by gamma-rays. These authors found that chromosomes *1R*, *4R*, and *5R* are more frequently involved in interchanges in the inbred line Pool and, similarly, this occurs in another inbred line (Riodeva) where the chromosomes most implicated in interchanges are *4R*, *5R* and *6R*. The proposed explanation was the large amount of heterochromatin present in these chromosomes in both lines with the exception of *4R*, although the influence of different genetic backgrounds could not be eliminated. In our case, the data obtained can neither be attributed to effects on the heterochromatic content, since chromosomes *4R* and *6R* of cv "Ailés" had a similar content in heterochromatin as the other ones (excepting *1R* and *5R*) (Fig. 1 a–f), nor can they be attributed to the differences in chromosome size.

It has also been stated that the non-random association of chromosomes in the nucleus can provide an explanation for the non-random nature of interchromosomal rearrangements (Coates and Smith 1984). If so, our data do not seem to support the concept of an ordered nucleus, because chromosomes *4R* and *6R* appear in translocations with any of the others at similar frequencies and, surprisingly, they never translocate between them. However, it is important to consider under this hypothesis the possible differential survival of all the different interchanges. In our case, so far we have no data for testing this suggestion; nevertheless, Cermeño and Lacadena (1985) indicate that the occurrence of any interchange more frequently than others would be due to a higher occurrence of such interchanges and not the differential elimination of them.

The meiotic behavior of the quadrivalents analyzed does not seem to be influenced either by the particular chromosomes involved in the interchange or by the morphology of diplotene crosses (Tables 2 and 3). It is likely that quadrivalent morphology at MI may have more influence on the final orientation; e.g., those interchanges, especially T 331 and T 344, showing asymmetric rings at MI (due to its inherent asymmetry or chiasma location) appeared to show higher alternate orientation frequency than symmetric ring quadrivalents, in agreement with some other studies reported by Rickards (1983).

However, the main factor that was shown to influence the orientation of quadrivalents at MI was the frequency of chiasmata of the quadrivalent since, in general, chain alternate quadrivalent frequencies are higher than ring ones (Table 3). This result is in agreement with those reported by Lewis and John (1963), Rees and Sun (1965) and Khoshoo and Mukherjee (1966) and it has been attributed, among other causes, to a theoretical higher flexibility of chains to adopt alternate orientations in comparison with that of rings. This hypothesis could also explain the absence of a positive correlation when the

number of alternate chain quadrivalents was analyzed between the progenies and their respective parentals. However, a positive correlation was detected when the frequency of ring alternate quadrivalents was analyzed, despite the similar mean of ring quadrivalents per cell that progenies and their mother plants showed. The different behavior of both types of configurations (ring and chain) suggests that the influence of structural factors (such as symmetry or asymmetry at MI) on ring and chain quadrivalents would be different, with rings being more intensely affected.

The existence of a direct genotypic control on quadrivalent orientation was not detected since, in general, the different progenies carrying a same interchange did not show significant differences on alternate orientation frequencies. This result would agree with that reported by Sun and Rees (1967) when *S. anatolicum* was crossed with six different species belonging to the same genus. In all progenies obtained, the quadrivalents behave in a similar way, although genotypic backgrounds are expected to be very different.

With regard to the existence of a directed segregation in the quadrivalents, Lawrence (1963) suggests that the population would have acquired a genetic system that increases the disjunctional frequency if the occurrence of spontaneously produced interchanges were a common phenomenon. An alternative hypothesis, also reported by Lawrence (1963), suggests an indirect genotypic control by means of genetically controlled factors, which were also of evolutionary significance in individuals having the standard karyotypic arrangement. The first hypothesis would be suitable in our case, since the chromosome mutation frequency is very high in cv "Ailés". The genetically controlled factors proposed by Lawrence (1963) should be fixed so as to explain the homogeneity found among the different progenies carrying a same interchange.

Everything mentioned above would agree with the fact that progenies carrying a same interchange showed similar behavior, while differences among progenies carrying different interchanges have been detected; that is, it may suggest that each interchange would have a basic specific disjunction pattern (Table 3).

We have not found a correlation between the frequency of alternate orientation and fitness. This may be due to the influence of the genotypic background of each heterozygote, especially on certain genic combinations (supergenes) which would have been preserved by the structural heterozygosity. Another explanation could be that some gametes arising from the adjacent orientations were viables, able to fecundate and to give viable individuals, as reported by Shalev and Ladizinsky (1976) in *Avena* and Menzel and Brown (1978) in *Gossypium*. Our data do not permit discarding any of these non-excluding hypothesis.

The data regarding chromosomal identification and fitness support the previous stated hypthesis as to the maintenance of chromosomal polymorphism in the cv "Ailés". Thus, this polymorphism may be due to a great number of different translocations with a lower fitness than that of the standard homozygous individuals, and to the level of polymorphism being kept constant by the replacement of some interchanges by other ones arising de novo. We must stress that, in fact, all the structural heterozygotes analyzed in this work do present a fitness value lower than that of their structural standard homozygous siblings (A. M. Figueiras, unpublished results). Nevertheless, other unpublished studies suggest that certain interchanges present a fitness value higher than the standard homozygous and, therefore, should not be eliminated from the population. Therefore, the evolution of cv "Ailés" could tend to the fixation in the hetero- or homozygous condition of these rearrangements, and elimination of the unfavorables.

The high frequency of different translocations detected in this cultivar, with chromosomes *4R* and *6R* more implicated in the interchanges, could suggest that they are related to a high transposon activity. This opens two possibilities: (i) the target sequences for the putative transposon insertions are evenly distributed in all the chromosomes, but those not affecting chromosomes *4R* and *6R* are deleterious in a majority of cases; (ii) the location of the targets is not random, being more frequent in chromosomes *4R* and *6R*. To date, we cannot discard any of these hypotheses, although some data obtained by one of the authors (Figueiras), in different crosses and concerning the isozymatic loci listed in Table 1, indicate a mutation genic frequency roughly of the same order as the estimated mutation chromosome frequency (10^{-2}), supporting the hypothesis of the existence of transposons in cv "Ailés".

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