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CHROMOSOMA


# Metaphase I Bound Arms and Crossing Over Frequency in Rye

## I. Open Pollinated Varieties

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**Abstract.** Using a Giemsa C-banding procedure it has been possible to identify at meiosis three chromosome pairs of a local Spanish rye cultivar. Two of these chromosomes (3 and 5) were heterozygous for an interstitial C-band in the long arm and the other (chromosome 7) was heterozygous for a telomeric C-band, also in the long arm. From the frequency of being bound at metaphase I and the frequency of recombined chromatids at anaphase I in the arms considered, estimates of actual chiasma frequencies have been derived. The results have been compared with those obtained in a F1 between two inbred lines. It is concluded that: (i) Although the frequency of bound arms analyzed was similar in all cases, the chiasma frequency was higher in the cultivar than in the F1 plants. Cultivar plants showed a variation in chiasma frequency for the bivalent arms studied which was correlated with the frequency of bound arms per cell, indicating that the estimation for chiasma frequency by means of bound arm frequency has an error that increases with increasing number of bound arms per cell. (ii) Evidence of chiasma terminalization has not been found. (iii) It is suggested that the different rye chromosomes have different chiasma localization patterns, which, in turn, are related with the chiasma frequency.

### Introduction

In most instances, rye is a material in which only an association between bivalent arms can be observed at meiosis and then, chiasma frequency is often simply considered equivalent to the frequency of associated (bound) arms at metaphase I. However, a bound arm merely indicates that at least one chiasma has been formed, the actual number of chiasmata remaining undetermined.

In a previous paper (Giraldez and Orellana, 1979) a procedure was described for estimating chiasma frequency in specific chromosome arms of rye marked by Giemsa C-banding in meiosis. A hybrid between two inbred lines differing in respect to terminal C-heterochromatin in two chromosome arms was used. From the frequency of being bound at metaphase I and the frequency of recombi-

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nation at anaphase I and metaphase II in the arms considered, estimates of actual chiasma frequencies were derived. The results indicated that a maximum of one chiasma was produced in the short arm of chromosome 3 whereas in the long arm of chromosome 7 (SAT) two chiasmata could be formed with a low frequency (6.2%). Thus, the number of metaphase I bound arms and the chiasma frequency were not very different.

However, the results obtained in hybrids between inbred lines cannot be extended to open pollinated cultivars, since the appearance of univalents in these hybrids indicates that their chiasma frequency must be lower than that of cultivars, or their chiasma distribution pattern different.

In this study we have analyzed the chiasma frequencies of specific chromosome arms of an open pollinated variety of rye. Some of these chromosome arms were heterozygotes for an interstitial C-heterochromatic band and results on chiasma localization and terminalization were also obtained.

## Material and Methods

Plants of a rye cultivar taken from La Raña, Logrosán (Cáceres, Spain) as well as the offspring of some of these plants (Table 1), formed the material for this study. Fl plants of the cross between the two inbred lines P and M earlier studied by Giraldez et al. (1979) were used as a control.

**Table 1.** Origin of the plants studied and C-heterochromatin constitution of the long arms of chromosomes 3 (interstitial C-band), 5 (interstitial C-band) and 7 (telomeric C-band). In all cases the homozygous individuals had not such prominent C-heterochromatin bands in the corresponding regions

| Plant | Origin | C-heterochromatin constitution of chromosome arm | | |
|---|---|---|---|---|
| | | 3 long | 5 long | 7 long |
| R[a]12 | Cultivar | Het[a] | Hom[a] | Hom[a] |
| R[a]13 | Cultivar | Het[a] | Hom[a] | Hom[a] |
| R[a]18 | Cultivar | Het[a] | Hom[a] | Hom[a] |
| R[a]25 | Cultivar | Hom[a] | Hom[a] | Het[a] |
| R[a]35 | Cultivar | Hom[a] | Het[a] | Het[a] |
| R[a]47 | Cultivar | Het[a] | Hom[a] | Het[a] |
| R[a]301 | ♀ R[a]35 × ♂ R[a]18 | Het[a] | Hom[a] | Het[a] |
| R[a]302 | ♀ R[a]35 × ♂ R[a]18 | Het[a] | Hom[a] | Het[a] |
| R[a]311[b] | ♀ R[a]35 × ♂ R[a]18 | Het[a] | Het[a] | Hom[a] |
| R[a]400 | ♀ R[a]35 × ♂ R[a]25 | Hom[a] | Het[a] | Hom[a] |
| R[a]401 | ♀ R[a]35 × ♂ R[a]25 | Hom[a] | Het[a] | Hom[a] |
| R[a]402 | ♀ R[a]35 × ♂ R[a]25 | Hom[a] | Het[a] | Het[a] |
| R[a]407 | ♀ R[a]35 × ♂ R[a]25 | Hom[a] | Het[a] | Het[a] |
| R[a]408 | ♀ R[a]35 × ♂ R[a]25 | Hom[a] | Het[a] | Hom[a] |
| R[a]409 | ♀ R[a]35 × ♂ R[a]25 | Hom[a] | Het[a] | Hom[a] |
| Fl Plants | ♀ P × ♂ M | Hom[a] | Hom[a] | Het[a] |

[a] Het = heterozygote, Hom = homozygote

[b] This plant was also heterozygous for a telomeric prominent C-band in the short arm of chromosome 3

In order to obtain mitotic metaphase cells, seeds were germinated on wetted filter paper in Petri dishes at 20 °C. When primary roots were 1 cm long they were excised and immersed in tap water at 0 °C for 24 h to shorten the chromosomes. Subsequently the tips were fixed in acetic alcohol 1:3. For meiotic cells, anthers were fixed in acetic alcohol 1:3. Both root tips and anthers were maintained in the fixative during one to four months at 3–4 °C.

The fixed material was squashed and stained following the Giemsa C-banding technique described previously (Giraldez and Orellana, 1979).

The chromosome nomenclature used was that of Giraldez et al. (1979).

## Results

Using the C-banding technique, in some rye inbred lines and in their hybrids it is possible to identify the homologous chromosomes at mitosis as well as some specific bivalents at meiosis. Figures 1a and 2a show a mitotic metaphase cell and a metaphse I cell respectively, of the cross between the inbred lines P and M.

Most rye cultivars present a variability for their chromosome C-banding pattern which hampers this identification. Only chromosome 7(SAT), due to the special characteristics of the banding pattern of the nucleolar organizer region, can be accurately recognized at meiosis. However, in the cultivar from La Raña it is possible to identify some more bivalents due to the presence of specific markers. In addition to the variability for telomeric heterochromatin, this cultivar presents a polymorphism for prominent interstitial heterochromatic bands in the long arms of chromosomes 3 and 5. The interstitial band of chromosome 3 is located in the middle of the arm (Fig. 1b) and that of chromosome 5 is located subterminally (Fig. 2b–h). Table 1 indicates that C-heterochromatin constitution for the long arms of chromosomes 3, 5 and 7 in the plants analyzed. These three chromosomes were identified at metaphase I and anaphase I in

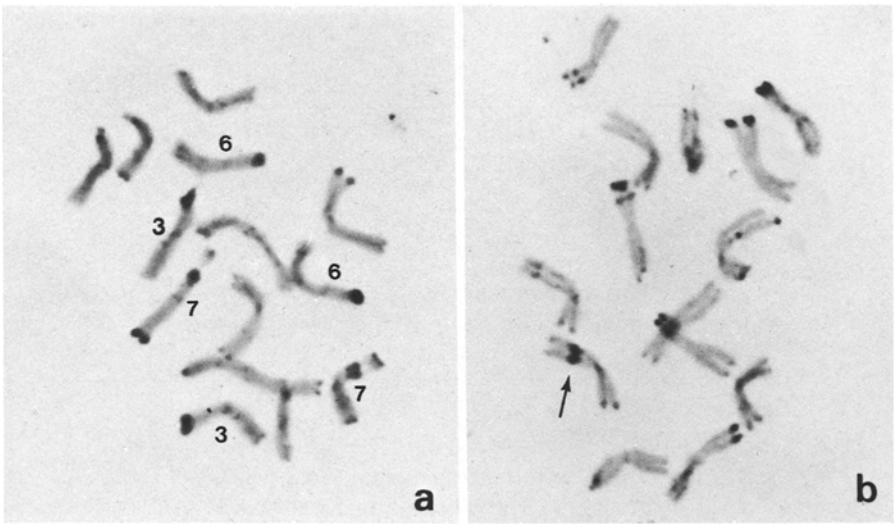


**Fig. 1a and b.** Mitotic metaphase plates of F1 between inbred lines P and M (**a**), and cultivar plant (**b**) heterozygote for interstitial C-band in the long arm of chromosome 3 (*arrow*)

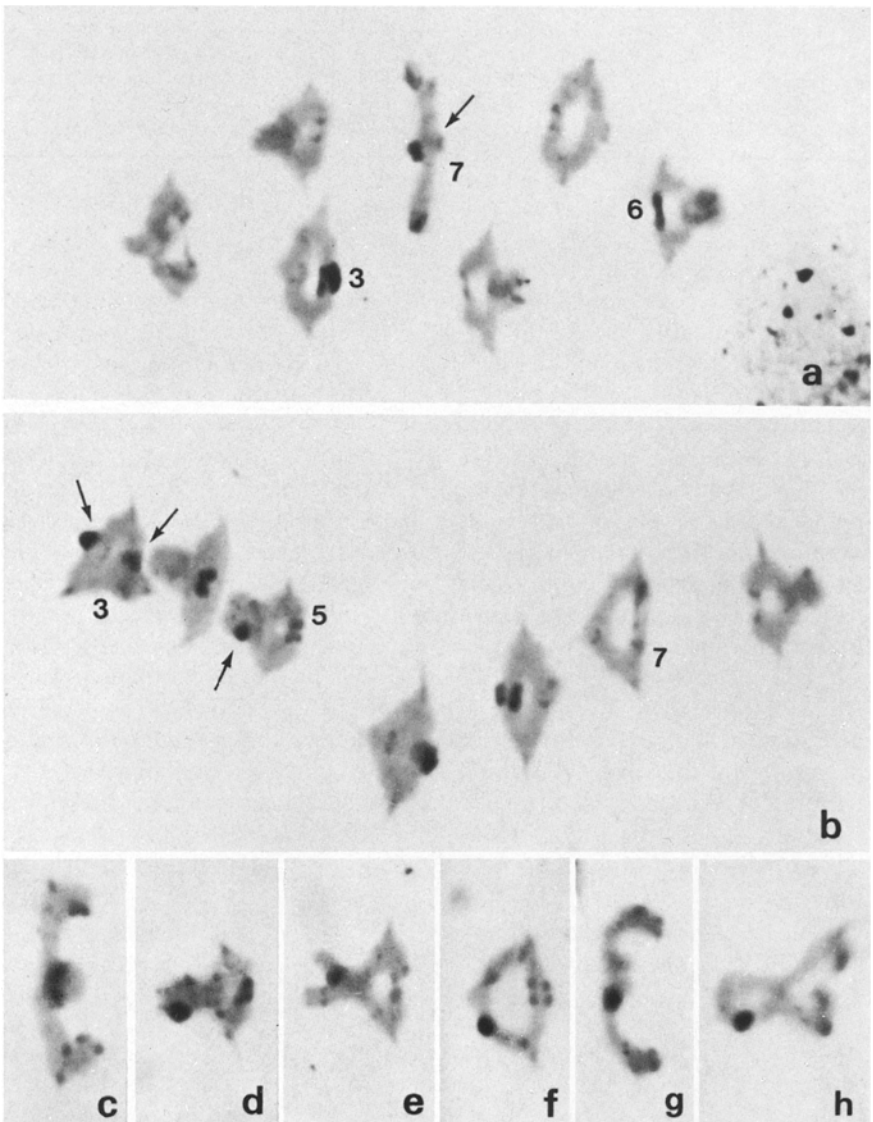


**Fig. 2. a** Metaphase I cell of Fl P × M. Arrow shows long arm of bivalent 7 (SAT). **b** Metaphase I cell of plant $R^a311$. Arrows show C-heterochromatic bands in chromosome 3 and 5 for which this plant is heterozygote. **c–h** The different configurations of bivalent 5 heterozygous for the interstitial C-band

the plants heterozygous for their C-banding pattern. Figure 2a–b shows C-banded metaphase I cells in which these bivalents can be distinguished.

Two types of chromosomes 3, 5 and 7 can appear at anaphase I: (i) Parental type: Both chromatids have the same heterochromatin constitution, showing no evidence of recombination. (ii) Recombinant type: each chromatid has a

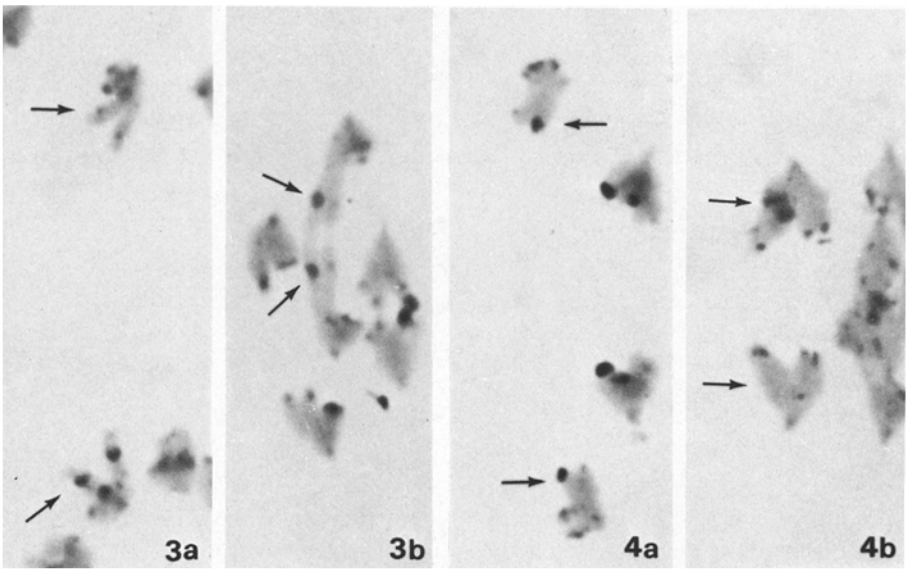


**Fig. 3a and b.** Anaphase I segregating chromosomes of a plant heterozygous for interstitial C-band in long arm of chromosome 5. **a** Parental type. **b** Recombinant type

**Fig. 4. a** Anaphase I segregating chromosomes of $F_1$ plant (recombinant type). **b** Anaphase I segregating chromosomes of plant heterozygous for interstitial band in long arm of chromosome 3 (parental type)

different heterochromatin constitution, showing evidence of recombination. Some examples of these anaphase I chromosome types are shown in Figs. 3 and 4.

If a bound arm corresponds to only one chiasma, the frequency of recombinant chromosomes in anaphase I must equal the frequency of bonds at metaphase I for a specific arm. However, an excess of anaphase I parental type chromosomes can appear if more than one chiasma is formed. Assuming that a maximum of two chiasmata were formed between the centromere and the heterochromatic band for which the two chromosomes are heterozygous, the two types of anaphase I chromosomes would appear depending on the number and positions of chiasmata as shown in Figure 5.

Now, if there is no chromatid interference, the frequencies of recombinant (Fr) and parental (Fp) anaphase I chromosomes would be:

$$Fr = f_1 + 1/2\, f_2, \qquad Fp = f_0 + 1/2\, f_2.$$

In which $f_0$, $f_1$ and $f_2$ are the frequencies of 0, 1 and 2 chiasmata, respectively. As $f_0$ can be estimated from the metaphase I observations, the frequencies of 1 and 2 chiasmata can be deduced.

If more than two chiasmata are considered, the frequency of anaphase I recombinant chromosomes would be (Mather, 1935):

$$Fr = f_1 + 1/2\, f_2 + 3/4\, f_3 + \ldots + 2/3[1 - (-1/2)^n]\, f_n$$

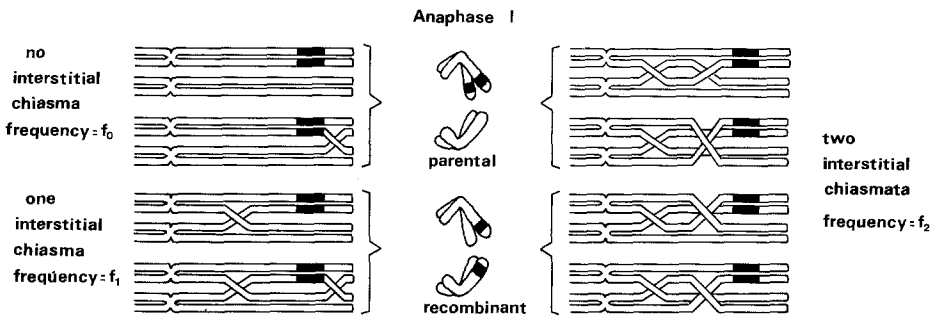


**Fig. 5.** The appearance of anaphase I parental and recombinant type chromosomes depending on number and positions of chiasmata between C-band and centromere in bivalents heterozygous for this band

*Bivalent 3*

All plants except $R^a$ 311 were homozygous for the banding pattern of the short arm. In this plant the fit between the frequency of association at metaphase I (96% in 100 cells) and the frequency of recombinant type chromosomes at anaphase I (95% in 100 cells) shows that double crossing over must have been rare or even absent.

In individuals heterozygous for the interstitial band, the long arm was bound distally (Fig. 2b) in all cases (700 cells), which corresponds with 100% parental type chromosomes at anaphase I (700 cells).

*Bivalent 5*

This bivalent could be identified in the plants of the cultivar heterozygous for the interstitial heterochromatic band located in the long arm.

At metaphase I several types of bivalents were found according to the chromosomal segments bound. Figure 2c–h show the different possibilities. In the long arm, bonds could be produced interstitially (between the C-band and the centromere), distally (between the C-band and the telomere) or both. Although in a few cases (about five per cent of the cells) the three possibilities could be distinguished (Fig. 2e–h), in most cases in which an interstitial bond was formed the appearance of the distal bivalent end was ambiguous and the possibility of a distal bond could not be ascertained (Fig. 2b–d). Then, four bivalent types were considered at metaphase I (Open bivalents in which the short arm was bound were not observed): Ring bivalents with at least an interstitial bond in the long arm (RI), rings with a distal bond in the long arm (RD), open bivalents with at least an interstitial bond in the long arm (OI) and open bivalents with the long arm bound distally (OD). Table 2 shows the frequency of the different metaphase I bivalents as well as the frequencies of anaphase I recombinant and parental chromosome types in the plants analyzed.

In most plants, no statistical tests could be made in order to determine the significance of the differences between the frequencies of metaphase I bonds

**Table 2.** Frequencies of different metaphase I configurations (RI, ring bivalents with at least an interstitial bond in the long arm; RD, rings with a distal bond in the long arm; OI, open bivalents with at least an interstitial bond in the long arm; OD, open bivalents with the long arm bound distally) and anaphase I chromosome types (parental, Fp and recombinant, Fr) for chromosome 5. The frequencies of 0 ($f_0$), 1 ($f_1$) and 2 ($f_2$) chiasmata as well as the genetic length (L) of the interstitial segment analyzed are also included. No univalents appeared at metaphse I. 100 cells per phase per plant were observed

| Plant | Metaphase I | | | | | | | Ana-phase I | | Chiasma frequencies | | | Genetic length (L) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bivalent 5 | | | | Rest of bivalents (pooled) | | Bound arms | | | | | | |
| | RI | OI | RD | OD | R | O | | Fr | Fp | $f_0$ | $f_1$ | $f_2$ | |
| R[a]35 | 83 | 16 | 1 | – | 592 | 8 | 13.76 | 97 | 3 | 0.01 | 0.95 | 0.04 | 51.5 |
| R[a]311 | 100 | – | – | – | 573 | 27 | 13.73 | 86 | 14 | – | 0.72 | 0.28 | 64.0 |
| R[a]400 | 80 | 16 | 4 | – | 588 | 12 | 13.72 | 95 | 5 | 0.04 | 0.94 | 0.02 | 49.0 |
| R[a]401 | 91 | 7 | 2 | – | 577 | 23 | 13.70 | 90 | 10 | 0.02 | 0.82 | 0.16 | 57.0 |
| R[a]402 | 72 | 11 | 16 | 1 | 561 | 39 | 13.49 | 86 | 14 | 0.17 | 0.83 | – | 41.5 |
| R[a]407 | 100 | – | – | – | 597 | 3 | 13.97 | 85 | 15 | – | 0.70 | 0.30 | 65.0 |
| R[a]408 | 82 | 16 | 2 | – | 593 | 7 | 13.77 | 94 | 6 | 0.02 | 0.90 | 0.08 | 53.0 |
| R[a]409 | 96 | 4 | – | – | 592 | 8 | 13.88 | 88 | 12 | – | 0.76 | 0.24 | 62.0 |

and anaphase I recombinant chromosomes. Nevertheless, assuming that between the centromere and the interstitial band a maximum of two chiasmata were formed, the frequencies $f_0$, $f_1$ and $f_2$ of 0, 1 and 2 chiasmata respectively, in this interstitial chromosome segment were deduced as:

$$f_0 = RD + OD, \quad f_2 = (Fp - f_0) \times 2, \quad f_1 = 1 - f_0 - f_2.$$

These values are also included in Table 2.

Of course, the estimates of $f_1$ and $f_2$ are very indirect and their error is great, especially for these plants in which the frequencies of parental and recombinant anaphase I chromosome types are not very different from the ones expected under the assumption of one chiasma per bond. In fact, in plant R[a]402 there was an insignificant excess of recombinant type chromosomes ($\chi^2 = 0.344$) and a meaningless negative value of $f_2$ resulted that was considered as 0.

The coincidence of heterozygosity for an interstitial C-band and the occurence of proximal chiasmata that is produced in this bivalent makes it a suitable material for the analysis of chiasma terminalization. But no evidence of such terminalization was found in this bivalent.

*Bivalent 7 (SAT)*

This bivalent was identified in all plants analyzed. Table 3 shows the number of metaphase I ring bivalents (R), open bivalents in which the long arm was bound (Ol), open bivalents in which the short arm was bound (Os) and univalent pairs (U), as well as the frequencies of parental (Fp) and recombinant (Fr) anaphase I chromosomes in the heterozygous plants for a telomeric C-hetero-

**Table 3.** Frequencies of the different metaphase I configurations (R, ring bivalents; Ol, open bivalents with the long arm bound; Os, open bivalents with the short arm bound; U, univalent pairs) and anaphase I chromosome types (parental, Fp and recombinant, Fr) for chromosome 7. The frequencies of 0 ($f_0$), 1 ($f_1$) and 2 ($f_2$) chiasmata as well as the genetic length (L) of the long arm are also included. 100 cells per phase per plant were observed

| | Plant | Metaphase I | | | | | | | | Ana-phase I | | Chiasma frequencies | | | Genetic length (L) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Bivalent 7 | | | | Rest of bivalents (pooled) | | | Bound arms per cell | | | | | | |
| | | R | Ol | Os | U | R | O | U | | Fr | Fp | $f_0$ | $f_1$ | $f_2$ | |
| F1 plants | PM3 | 41 | 59 | – | – | 461 | 136 | 3 | 11.99 | 90 | 10 | – | 0.80 | 0.20 | 60.0 |
| | PM5 | 47 | 53 | – | – | 491 | 107 | 2 | 12.36 | 93 | 7 | – | 0.86 | 0.14 | 57.0 |
| | PM6 | 25 | 75 | – | – | 494 | 106 | – | 12.19 | 89 | 11 | – | 0.78 | 0.22 | 61.0 |
| | PM7 | 55 | 44 | – | 1 | 467 | 130 | 3 | 12.18 | 94 | 6 | 0.01 | 0.89 | 0.10 | 54.5 |
| | PM8 | 60 | 40 | – | – | 480 | 120 | – | 12.40 | 90 | 10 | – | 0.80 | 0.20 | 60.0 |
| | Total | 228 | 271 | – | 1 | 2,393 | 599 | 8 | 12.22 | 456 | 44 | 0.002 | 0.826 | 0.172 | 58.5 |
| Cultivar plants | R[a]25 | 80 | 20 | – | – | 552 | 48 | – | 13.32 | 81 | 19 | – | 0.62 | 0.38 | 69.0 |
| | R[a]35 | 98 | 2 | – | – | 578 | 22 | – | 13.76 | 78 | 22 | – | 0.56 | 0.44 | 72.0 |
| | R[a]47 | 88 | 11 | 1 | – | 517 | 83 | – | 13.05 | 89 | 11 | 0.01 | 0.79 | 0.20 | 59.5 |
| | R[a]301 | 81 | 19 | – | – | 550 | 50 | – | 13.31 | 84 | 16 | – | 0.68 | 0.32 | 66.0 |
| | R[a]302 | 72 | 28 | – | – | 573 | 27 | – | 13.45 | 90 | 10 | – | 0.80 | 0.20 | 60.0 |
| | R[a]402 | 74 | 26 | – | – | 575 | 25 | – | 13.49 | 87 | 13 | – | 0.74 | 0.26 | 63.0 |
| | R[a]407 | 100 | – | – | – | 597 | 3 | – | 13.97 | 79 | 21 | – | 0.58 | 0.42 | 71.0 |
| | Total | 593 | 106 | 1 | – | 3,942 | 258 | – | 13.47 | 588 | 112 | 0.002 | 0.681 | 0.317 | 65.78 |

Contingency $\chi^2$ test for differences between the frequencies of anaphase I recombinant and parental chromosomes in the F1 and the cultivar plants: $\chi^2 = 13.3687$, $0.001 \geqq p$

chromatic band in the long arm. Although no statistical tests could be made, the excess of anaphase I parental type chromosomes under the assumption of only one chiasma per bond is probably significant in all cases. In Table 3 there are also included the frequencies $f_0$, $f_1$ and $f_2$ of 0, 1 and 2 chiasmata respectively in the long arm of this chromosome.

The frequency of parental type chromosomes at anaphase I (and, as a result, the chiasma frequency) in the plants of the cultivar is significantly higher than that in the F1.

## Discussion

### *I. Chiasma Frequency*

Giraldez and Orellana (1979) found a highly significant deviation of the distribution of chiasmata in specific bivalent arms of rye from a Poisson series. This was taken as evidence of within arm chiasma interference (Haldane, 1931). Such a comparison was not possible in most plants studied since the bivalent

arms considered were bound in every cell ($f_0=0$) and a theoretical distribution could not be calculated. However, in the few cases in which such analysis was possible, the differences between the expected and observed parental and recombinant anaphase I chromosomes were highly significant.

Under the assumption that, as a result of chiasma interference, a maximum of two chiasmata are formed in the chromosomal regions analyzed, the genetic length for these regions can be estimated from:

$$L=50(f_1+2f_2).$$

There is also the possibility of more than two chiasmata being formed. However, in absence of chromatid interference, lower values of $f_1$ would not account for the high frequency of anaphase I recombinant chromosomes found. Then, in this case the genetic length would be only slightly higher.

The values of genetic length obtained (Tables 2 and 3) are much lower than the ones calculated from the frequency of association in metaphase I using mapping functions in which an average chiasma interference is taken into account. Again, these estimates are not possible in the plants in which the bivalents segments considered are bound in every cell ($f_0=0$). With Kosambi's function (See Sybenga, 1975) the genetic lengths of the interstitial segment of chromosome 5 are: for plant $R^a35$, $L=133$; for $R^a400$, $L=97$; for $R^a401$, $L=115$; for $R^a402$, $L=59$; for $R^a408$, $L=115$. These differences may have two reasons: (i) The level of chiasma interference is much higher in this material than the average for which Kosambi's function is valid. (ii) There is chromatid interference involving an increase in disparate combinations and decrease of reciprocal and complementary combinations. This would, result in increased frequencies of recombinant type chromosomes at anaphase I and thus, an underestimate of $f_2$ and L ($Fp=1-Fr=f_0+1/2\ f_2$). However, this type of chromatid interference would be the contrary to the one occasionally found cytologically (Sybenga, 1975).

It is worth mentioning that the genetic length calculated in chromosome 5 corresponds to the segment between the interstitial C-band and the centromere, the length of the whole long arm being higher due to the presence of distal chiasmata.

The comparison between the frequencies of anaphase I recombinant and parental types for chromosome arm 7 long in the cultivar and the F1 plants (Table 3) indicates that the cultivar plants have a significantly higher chiasma frequency. The between plants variation is also higher in the cultivar. This between plants variation is especially clear in chromosome 5 (Table 2) in which the frequency of double chiasmata in the interstitial segment can vary from 0 to 30%. These estimates, however have a large error.

Figure 6 shows the chiasma frequency in the chromosomal segments considered plotted against the number of bound arms per cell at metaphase I in the F1 and in the cultivar plants. The regression coefficients of chiasma frequency in the long arm of chromosome 7 on mean bound arms per cell are $b=-0.037$ ($t=0.19$; $0.9>p>0.8$) for the F1 plants and $b=0.236$ ($t=2.22$; $0.1>p>0.05$) for the cultivar plants. The regression coefficient of chiasma frequency in the interstitial segment of chromosome 5 on mean bound arms per cell is $b=0.962$

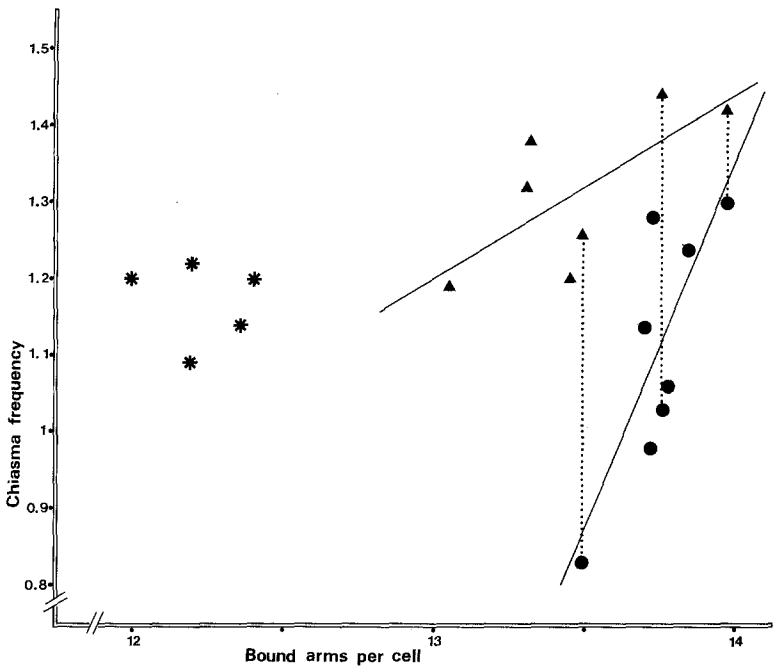


**Fig. 6.** Chiasma frequency in the chromosome segments analyzed plotted against mean number of bound arms per cell. * Long arm of chromosome 7 of F1. ▲ Long arm of chromosome 7 of cultivar. ● Interstitial segment in long arm of chromosome 5, in cultivar. Bivalents belonging to same plant joined by dotted line

($t = 3.23$; $0.02 > p > 0.01$). Then, the values considered are not correlated in the F1 plants, whereas in the cultivar plants the regression coefficient for chromosome 5 is significantly different from 0 and that of chromosome 7 is at the limit of significance.

From the results concerning the number of ring and open bivalents studied, it can be concluded that the variation in bound arm frequency is a reflection of the variation in bonds of the short bivalent arms. The analysis of chiasma frequency in the short arm of bivalent 3 suggest that short arms of rye have a chiasma frequency not very different from that with which they are bound. Then, the error introduced by equating the chiasma frequency per cell to the bound arm frequency is mostly due to the long bivalent arms.

Three double heterozygous plants ($R^a35$, $R^a402$ and $R^a407$) for the bivalents 5 and 7 have been studied (Table 1). The two bivalents of each plant are joined by a dotted line in Figure 6. The parallel tendency shown by these bivalents suggest that all chromosomes can be involved in the variation of chiasma frequency in the same direction.

Now, if each long bivalent arm has a chiasma frequency higher than that estimated by the number of bonds, the correlations found indicate that, although the bound arm frequency can be an estimate of the chiasma frequency, the error of this estimation increases with increasing number of bound arms per cell.

*II. Chiasma Localization*

Although there are some cases in which a highly abnormal and asymetrical distribution of chiasma between bivalents has been reported (Rees, 1955; Jones and Rees, 1964; Jones, 1967), rye is a material in which at metaphase I chiasmata are apparently localized distally in most bivalent arms. The nature of these terminal chiasmata have been discussed by Jones (1978), indicating that they could appear in some cases to result from stretching on the metaphase I spindle.

The two bivalent arms having an interstitial C-heterochromatic band which have been analyzed in this study show a different chiasma localization pattern.

For the long arm of bivalent 3 the metaphase I and anaphase I results (Figs. 2b, 4b) indicate that chiasmata are distally (i.e., between the C-band and the telomere) located. However, in the long arm of bivalent 5 (Figs. 2b–h, 3a–b; Table 2) two chiasmata are formed between the C-band and the centromere in several cases. Although the band in chromosome 5 is more distally located, when a interstitial double crossing over is produced the existence of chiasma interference would induce the most proximal chiasma to be placed at a short distance from the centromere.

On the other hand, corresponding with the results of Giraldez and Lacadena (1978), the correlation between the frequencies of interstitial chiasmata (i.e., between the C-band and the centromere) in chromosome 5 and the bound arms per cell frequency (Fig. 6), suggests that there is a variation in chiasma localization that is related to chiasma frequency: as chiasma frequency increases, chiasma positions tend to be more proximal.

## References

Giraldez, R., Cermeño, M.C., Orellana, J.: Comparison of C-banding pattern in the chromosomes of inbred lines and open pollinated varieties of rye. Z. Pflanzenzüchtg. *83*, 40–48 (1979)

Giraldez, R., Lacadena, J.R.: Relationships between frequency, localization and errors in chiasma formation in desynaptic rye. Chromosoma (Berl.) *66*, 193–204 (1978)

Giraldez, R., Orellana, J.: Metaphase I bonds, crossing over frequency, and genetic length of specific chromosome arms of rye. Chromosoma (Berl.) *72*, 377–385 (1979)

Haldane, J.B.S.: The cytological basis of genetical interference. Cytologia (Tokyo) **3**, 54–65 (1931)

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

Jones, G.H., Rees, H.: Genotypic control of chromosome behaviour in rye. VIII. The distribution of chiasmata within pollen mother cells. Heredity **19**, 719–730 (1964)

Mather, K.: Reductional and equational separation of the chromosomes in bivalents and multivalents. J. Genet. **30**, 53–78 (1935)

Rees, H.: Genotypic control of chromosome behaviour in rye. I. Inbred lines. Heredity **9**, 93–116 (1955)

Sybenga, J.: Meiotic configurations. Monogr. on theor. appl. Genetics, vol. 1. Berlin-Heidelberg-New York: Springer 1975

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