Theor Appl Genet (1984) 69: 193–198



# The meiotic pairing of nine wheat chromosomes

E. Ferrer, J. M. González and N. Jouve
Department of Genetics, Faculty of Sciences, University of Alcalá de Henares, Madrid, Spain

Received April 10, 1984; Accepted May 4, 1984
Communicated by R. Riley

**Summary.** The meiotic identification of nine pairs of chromosomes at metaphase I of meiosis of *Triticum aestivum* (B genome, 4A and 7A) has been achieved using a Giemsa C-banding technique. As a result, the analysis of the pairing of each chromosome arm in disomic and monosomic intervarietal hybrids between 'Chinese Spring' and the Spanish cultivar 'Pané 247' could be carried out. Differences in the chiasmata frequencies per chromosome arm cannot be explained on the basis of relative arm lengths only. Possible effects of arm-to-arm heterochromatic differences on meiotic pairing are discussed.

**Key words:** C-banding – Heterochromatin – Meiosis – Common wheat – *Triticum aestivum*

## Introduction

Wheat telocentric chromosomes were first obtained by Sears in 'Chinese Spring' and have been used by Sallee and Kimber (1979) in a study of the pairing and chiasma frequencies of 41 of the 42 telocentrics. They suggested a relationship of these parameters to relative arm length, genomes and homoeologous groups. It was concluded that pairing and chiasma formation in the telocentrics could be a most reliable basis for predicting the behaviour of whole chromosomes. Dvorak and McGuire (1981) studied differences among homologous chromosomes of different cultivars of wheat and related species using telocentric lines.

The C-banding staining method permits chromosome characterization in accordance with the pattern of bands of individual chromosomes. Studies on individual chromosomes in karyotype analysis of hexaploid wheat using Giemsa techniques have been previously reported (Gill and Kimber 1974; Gerlach 1977; Zurabisvili et al. 1978; Jewell 1979; Seal 1982; Armstrong 1982; Van Niekerk and Pienaar 1983; Ferrer et al. 1984). However, very little Giemsa staining has been carried out on the meiotic chromosomes of wheat. This particular analysis has been performed on other species and hypotheses have been made on the effect of heterochromatic regions on pairing (review of Yamamoto 1979) and chiasma formation (review of John and Miklos 1979).

The present study was undertaken in order to investigate the meiotic behaviour of nine pairs of chromosomes of *Triticum aestivum* L. (4A, 7A and the seven of the B genome) in intervarietal hybrids. The effect of arm length and amount and/or distribution of heterochromatin on meiotic pairing well be taken into account.

## Material and methods

The following hybrids of common wheat (*Triticum aestivum* L.) formed the material for this study: $F_1$ 'Chinese Spring' × 'Pané 247' ('CS' × 'P-247') (2n = 42); $F_1$ mono$_i$ 'Chinese Spring' × 'Pané 247' (2n = 41), i = 1A, 5A, 7A, 2B, 3B, 5B and 7B.

Anthers for meiotic analysis were collected from sister plants that were grown in the greenhouse under optimal conditions until flowering. These were fixed in Carnoy's fixative (alcohol-acetic acid 3:1) and meiotic analysis were made using both Feulgen and C-banding staining methods. Giemsa staining was made according with a technique previously reported (Jouve et al. 1980).

## Results

The total number of ring bivalents, rod bivalents, univalents and open quadrivalents ('Chinese Spring'

and 'Pané 247' differed in a intervarietal translocation; Ferrer et al. 1984) were analyzed in metaphase I cells stained by the Feulgen method. The pairing level was measured as the total number of bound arms with respect to total number of paired chromosomes per cell, always taking into consideration the number of bound arms per cell as no. quadrivalents x 3 + no. ring bivalents x 2 + no. rod bivalents, and total number of paired chromosomes as the total number of chromosomes present in the cell minus the total number of univalents.

A mean value for this parameter was obtained per hybrid (Table 1). This figure permits comparison of hybrids with different chromosome numbers (2n = 42 or 2n = 41), and monosomics are thus comparatively equivalent to euploids with respect to meiotic pairing.

The probability of pairing of the euploid plant may represent the expected probability of euploid hybrids and corresponding values for monosomics have been compared with that by means of a Student's-*t*-test. If monosomic condition differences are the basis for the differences in pairing between hybrids, these should be grouped according to their particular tendencies. The results of the application of the Student's-*t*-test are given in Table 1. The hybrids were separated in two groups:

*Group 1*

Monosomic hybrids having no differences in pairing with respect to the euploid hybrid: mono 7A 'CS' × 'P-247', mono 2B 'CS' × 'P-247', mono 3B 'CS' × 'P-247' and mono 5B 'CS' × 'P-247'.

*Group 2*

Monosomic hybrids having significant differences in pairing at the 5% level with respect to the euploid hybrid: mono 1A 'CS' × 'P-247', mono 5A 'CS' × 'P-247' and mono 7B 'CS' × 'P-247'. The differences were attributable to the higher frequency of bound arms of this monosomic plants.

The C-banding method of staining meiotic chromosomes of PMCs from anthers of sister plants was applied to those chromosomes previously studied by the Feulgen method. The meiotic pairing of nine identifiable pairs was investigated. The heterochromatic characteristics of meiotic cells have been previously reported (Ferrer et al. 1984). An idiogram is shown in Fig. 1. Examination of the heterochromatic regions indicates that individual 4A and 7A chromosomes and seven of the B genome chromosomes have characteristic banding patterns, making it possible to identify them in meiotic configurations (Fig. 2). Frequencies of bound arms were calculated on the basis of the presence of one or more chiasmata per arm in paired chromosomes.

**Table 1.** Values of Student's-*t*-test obtained by comparing mean values of pairing in monosomic and disomic hybrids of common wheat

| Hybrid | Mean bound arms/paired chromosomes | No. of PMCs | *t*-values |
|---|---|---|---|
| 'CS' × 'P-247' | 0.9150 ± 0.040 | 112 | |
| m7A 'CS' × 'P-247' | 0.9244 ± 0.040 | 151 | 1.8800 |
| m2B 'CS' × 'P-247' | 0.9061 ± 0.043 | 100 | 1.5614 |
| m3B 'CS' × 'P-247' | 0.9155 ± 0.043 | 100 | 0.0877 |
| m5B 'CS' × 'P-247' | 0.9205 ± 0.044 | 100 | 0.9549 |
| m1A 'CS' × 'P-247' | 0.9285 ± 0.048 | 110 | 2.2288[a] |
| m5A 'CS' × 'P-247' | 0.9305 ± 0.045 | 100 | 2.6724[a] |
| m7B 'CS' × 'P-247' | 0.9330 ± 0.049 | 101 | 2.9508[a] |
| Group 1[b] | 0.9162 ± 0.007 | | |
| Group 2[b] | 0.9370 ± 0.003 | | |

[a] Significant to the 5% level
[b] See text

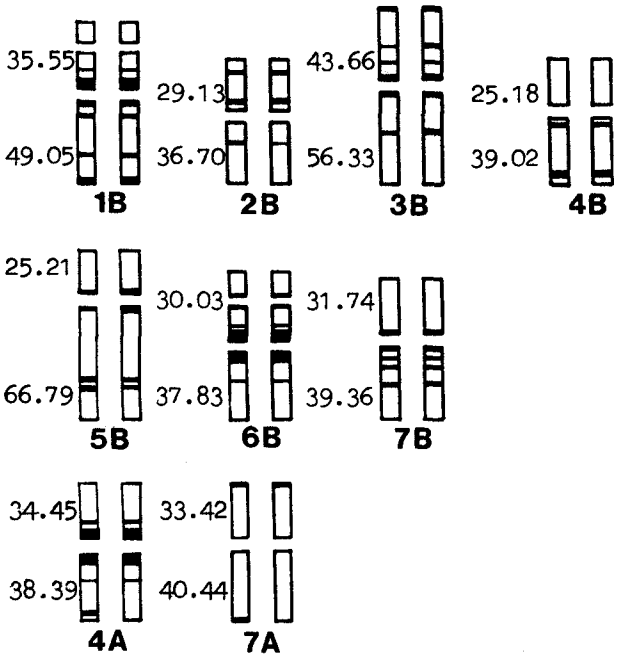


**Fig. 1.** Idiogram of the nine pairs of somatic chromosomes analyzed. The pattern of bands corresponds to that previously reported (Ferrer et al. 1984). Data on arm relative lengths are taken from Sallee and Kimber (1979). For each pair, *left* = 'Chinese Spring' and *right* = 'Pané 247'

The translocation that differenciates the karyotype of 'Chinese Spring' and 'Pané 247' involves the long arm of the 4A chromosome and an unidentified arm of the 2A chromosome. Open quadrivalents have been recorded as open bivalents bound by the short arm of the 4A chromosome.

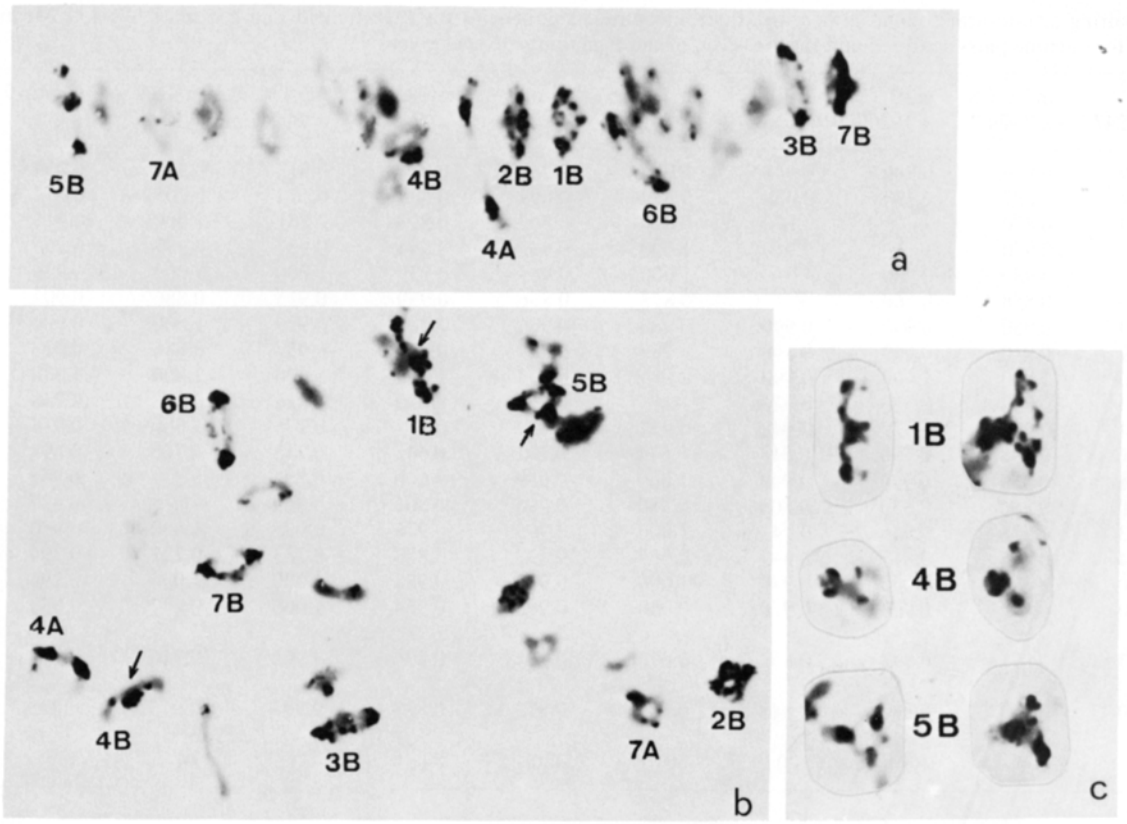


**Fig. 2a–c.** C-banding pattern in 'Chinese Spring' × 'Pané 247'. **a** Metaphase plate of euploid hybrid showing the nine pairs of identified chromosomes; **b** Metaphase plate of hybrid mono 1A 'CS' × 'P-247', *arrows* indicate interstitial chiasmata; **c** *1B, 4B* and *5B* bivalents showing interstitial chiasmata

Pairing arm frequencies are given in Table 2. The mean frequency of pairing for each arm was calculated from data of the same chromosome arm in different hybrids of the same group. These results are included in Table 2 and were lower than those estimated without arm identification from Feulgen staining observations (Table 1).

The Student's-*t*-test comparison of the mean values for all arms included in group 1 ($0.9162 \pm 0.007$), and corresponding values, having taken into consideration only the nine identified chromosomes ($0.881 \pm 0.017$), had a value of 4.2927. When the comparison was made with respect to data collected from the B genome chromosomes, the test had a value of 3.1314, which is significant, as in the preceding case.

A corresponding Student's-*t*-test applied to the chromosome arm of group 2 had values of 4.1077 and 3.5944, also significant.

The correlation coefficient estimated from mean frequencies of pairing per chromosome arm between both group 1 and group 2 hybrids had a value of $r = 0.9942$, and was positive and significant. The meiotic behaviour of same chromosome arms in different hybrids was not significant.

A correlation coefficient calculated from data on arm relative lengths (Sallee and Kimber 1979) and mean values of pairing of the same chromosome arm had the following values: group 1, $b = 0.00547$, significantly different from zero; group 2, $b = 0.00446$, not significantly different from zero. However, within group 1, chromosome arms with similar lengths showed significant differences in meiotic pairing intensity, and an effect of chromosome length on meiotic pairing intensity could not be discarded in the hybrids of group 2.

Data on $\chi^2$ of a contingency test, comparing the meiotic behaviour of different chromosome arms per group of hybrids, are given in Table 3. Groups of arms were made having in common no significant difference in the intensity of pairing.

From all the above mentioned results the following must be taken into consideration:

1) chromosome arms having differences in the amount and distribution of heterochromatin and similar lengths

**Table 2.** Mean pairing arm-to-arm (bound arms/paired chromosomes) frequencies for each hybrid and group of hybrids. Mean values of pairing for the nine pairs analyzed and for the seven of the B genome are also given

| | 'CS' × 'P-247' | m7A 'CS' × 'P-247' | m2B 'CS' × 'P-247' | m3B 'CS' × 'P-247' | m5B 'CS' × 'P-247' | Group 1 | m1A 'CS' × 'P-247' | m5A 'CS' × 'P-247' | m7B 'CS' × 'P-247' | Group 2 |
|---|---|---|---|---|---|---|---|---|---|---|
| $1B^L$ | 0.959 | 0.970 | 0.980 | 0.948 | 0.978 | 0.967 | 0.987 | 0.913 | 0.977 | 0.959 |
| $1B^S$ | 0.724 | 0.687 | 0.790 | 0.639 | 0.659 | 0.699 | 0.638 | 0.674 | 0.705 | 0.672 |
| $2B^L$ | 0.889 | 0.870 | – | 0.870 | 0.820 | 0.862 | 0.893 | 0.851 | 1.000 | 0.915 |
| $2B^S$ | 0.939 | 0.970 | – | 0.950 | 1.000 | 0.965 | 0.964 | 0.957 | 0.977 | 0.966 |
| $3B^L$ | 0.980 | 0.980 | 0.980 | – | 1.000 | 0.985 | 0.939 | 1.000 | 1.000 | 0.979 |
| $3B^S$ | 0.930 | 0.858 | 0.760 | – | 0.878 | 0.856 | 0.939 | 0.915 | 0.886 | 0.905 |
| $4B^L$ | 0.969 | 0.950 | 0.990 | 0.990 | 0.980 | 0.976 | 1.000 | 0.979 | 1.000 | 0.993 |
| $4B^S$ | 0.929 | 0.940 | 0.949 | 0.848 | 0.780 | 0.889 | 0.867 | 0.957 | 0.886 | 0.903 |
| $5B^L$ | 0.980 | 1.000 | 1.000 | 0.990 | – | 0.993 | 1.000 | 1.000 | 1.000 | 1.000 |
| $5B^S$ | 0.780 | 0.732 | 0.520 | 0.626 | – | 0.665 | 0.630 | 0.826 | 0.818 | 0.758 |
| $6B^L$ | 0.874 | 0.939 | 0.979 | 0.948 | 0.957 | 0.939 | 0.987 | 0.936 | 1.000 | 0.974 |
| $6B^S$ | 0.716 | 0.798 | 0.796 | 0.618 | 0.574 | 0.700 | 0.645 | 0.745 | 0.705 | 0.698 |
| $7B^L$ | 0.896 | 0.959 | 0.990 | 0.949 | 1.000 | 0.959 | 1.000 | 0.891 | – | 0.945 |
| $7B^S$ | 0.760 | 0.806 | 0.830 | 0.806 | 0.780 | 0.796 | 0.805 | 0.869 | – | 0.837 |
| $4A^L$ | 0.943 | 0.978 | 0.946 | 0.947 | 1.000 | 0.963 | 0.976 | 0.935 | 1.000 | 0.970 |
| $4A^S$ | 0.724 | 0.826 | 0.817 | 0.649 | 0.667 | 0.737 | 0.878 | 0.783 | 0.721 | 0.794 |
| $7A^L$ | 1.000 | – | 1.000 | 0.970 | 1.000 | 0.993 | 0.988 | 1.000 | 1.000 | 0.996 |
| $7A^S$ | 0.980 | – | 0.960 | 0.970 | 0.940 | 0.963 | 0.964 | 1.000 | 0.977 | 0.980 |
| Mean for 9 pairs | 0.887 | 0.891 | 0.893 | 0.857 | 0.876 | 0.881 | 0.894 | 0.902 | 0.916 | 0.904 |
| Mean for B genome | 0.880 | 0.889 | 0.880 | 0.848 | 0.867 | 0.873 | 0.878 | 0.894 | 0.913 | 0.895 |
| No. of PMCs | 100 | 100 | 100 | 100 | 50 | 450 | 84 | 47 | 44 | 175 |

**Table 3.** Distribution numbers of bound and unbound arm-to-arm results in each one of the group of hybrids analyzed. $\chi^2$ contingency test, comparing the observed distributions for group of arms showing similar behaviour, are also given

| Arm analyzed | Group 1 | | | Group 2 | | | Contingency $\chi^2$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | Bound arm | Unbound arm | Total | Bound arm | Unbound arm | Total | Arms which are compared | Group 1 | Group 2 |
| $1B^L$ | 426 | 24 | 450 | 167 | 8 | 175 | $5B^L$–$7A^L$–$3B^L$–$4B^L$ | 6.168 | –[a] |
| $2B^L$ | 303 | 47 | 350 | 159 | 16 | 175 | | d.f. = 3 | |
| $3B^L$ | 342 | 8 | 350 | 169 | 6 | 175 | $1B^L$–$7B^L$–$7A^S$–$2B^S$ | 3.738 | 4.698 |
| $4B^L$ | 435 | 15 | 450 | 173 | 2 | 175 | | d.f. = 3 | d.f. = 3 |
| $5B^L$ | 393 | 7 | 400 | 174 | 1 | 175 | $4A^L$–$6B^L$ | 1.710 | 0 |
| $6B^L$ | 409 | 41 | 450 | 166 | 9 | 175 | | d.f. = 1 | |
| $7B^L$ | 422 | 28 | 450 | 123 | 8 | 131 | $4B^S$–$3B^S$–$2B^L$ | 3.658 | 0.146 |
| $4A^L$ | 397 | 53 | 450 | 166 | 9 | 175 | | d.f. = 2 | d.f. = 2 |
| $7A^L$ | 347 | 3 | 350 | 174 | 1 | 175 | $4A^S$–$6B^S$–$1B^S$–$5B^S$ | 1.539 | 10.104[b] |
| $1B^S$ | 311 | 139 | 450 | 115 | 60 | 175 | | d.f. = 3 | d.f. = 3 |
| $2B^S$ | 335 | 15 | 350 | 169 | 6 | 175 | $6B^S$–$1B^S$–$5B^S$ | 1.544 | 2.186 |
| $3B^S$ | 297 | 53 | 350 | 160 | 15 | 175 | | d.f. = 2 | d.f. = 2 |
| $4B^S$ | 402 | 48 | 450 | 161 | 14 | 175 | $4A^S$–$7B^S$ | 11.536[c] | 0.104 |
| $5B^S$ | 263 | 137 | 400 | 127 | 48 | 175 | | d.f. = 1 | d.f. = 1 |
| $6B^S$ | 312 | 138 | 450 | 117 | 58 | 175 | | | |
| $7B^S$ | 353 | 97 | 450 | 106 | 25 | 131 | | | |
| $4A^S$ | 308 | 142 | 450 | 139 | 36 | 175 | | | |
| $7A^S$ | 338 | 12 | 350 | 171 | 4 | 175 | | | |

[a] Not calculated because of low frequency in unbound arm class
[b] Significant to the 5% level
[c] Significant to the 1% level

($4A^L$ and $4B^L$; $4A^S$ and $7A^S$; $7B^L$ and $4B^L$; $7B^L$ and $7A^L$) showed significant differences in meiotic pairing. This was higher for the lower banded arms than the others.

2) chromosome arms that exhibited subtelomeric bands ($4B^L$ and $2B^S$) showed a higher level of pairing with respect to the expected values obtained on the basis of their length only.

3) chromosome arms $4B^L$, $5B^L$ and $1B^L$ (Fig. 2b, 2c) showed a higher number of interstitial chiasmata than the others.

4) chromosome arms $6B^S$ and $1B^S$ are satellited (nucleolar organizers) and have in common the presence of large dark bands of heterochromatin. They showed a level of pairing lower than expected on the basis of their length only.

## Dicussion

The hybrid 'Chinese Spring' × 'Pané 247' showed a high level of stability (20.51 bivalents/PMC) with respect to 'Chinese Spring' parental (20.8 bivalents/PMC according with Sallee and Kimber 1979). The minor fall in meiotic pairing observed in the hybrid is in agreement with the general observation that hybrids between different lines of wheat are more irregular at meiosis.

Differences in meiotic stability of different monosomic $F_1$ hybrids have been previously reported (Morrison 1953; Person 1956; Khan 1962; Sasaki et al. 1963). The higher level of pairing presented by monosomics of group 2 (1A, 5A and 7B) than that of group 1 (7A, 2B, 3B and 5B) is associated with the decrease in frequency of multivalents. However, the high correlation coefficient between pairing value frequencies of the same chromosome arms in both group of hybrids indicate a particular strong relationship in its behaviour.

Differences in pairing intensity among wheat genomes have been observed in intervarietal hybrids of common wheat (Dvorak and McGuire 1981), in analysis of meiotic behaviour of telocentrics of 'Chinese Spring' (Sallee and Kimber 1979), and in the study of genome relationships in interspecific hybrids involving *T. aestivum* and species with homoeologous genomes (Chapman and Riley 1966; Feldman 1966; Dvorak 1976; Kimber and Hulse 1978; Hutchinson et al. 1982). Data demonstrated a decreased pairing intensity in chromosomes of B and closely related genomes (B′ of *T. timopheevi* and *T. zhukowskyi*).

Sallee and Kimber (1979) assumed that different pairing intensity showed by chromosomes of different genomes could be related with their differences in length. Thus, the mean number of chiasmata in 'Chinese Spring' per unit relative arm length was significant higher in the D genome chromosomes than in the chromsosomes of A and B genomes. Our results are in agreement with this hypothesis.

Dvorak and McGuire (1981) studied the factors that influence the variation in the pairing frequencies among genomes of *T. aestivum*. They suggested that the differentiation at the level of pairing could be related to the amount of DNA and heterochromatin present in chromosomes – heterochromatin having a detrimental effect on chromosome pairing at metaphase I. This could explain the differences in pairing found when a general comparison between the behaviour of A and B genomes is carried out. Moreover, the effect of heterochromatin is clearly observed from comparative results of homoeologous chromosomes of the groups 4 (4A and 4B) and 7 (7A and 7B). The degree of heterochromatin effects on meiotic pairing of chromosomes having similar length has been observed in other materials (Sybenga and de Vries 1972; Thomas and Kaltsikes 1976; Jouve et al. 1982; Naranjo and Lacadena 1982).

Our results on C-banding meiotic analysis of wheat permit us to suppose the existence of an overlapping effect of both arm length and amount and distribution of heterochromatin on pairing.

Interstitial and subtelomeric C-bands of heterochromatin could facilitate the maintainance of chiasmata (Santos and Giraldez 1978; Loidl 1979; Naranjo and Lacadena 1982). The increased pairing level that the arms $4B^L$ and $2B^S$ exhibit could be explained in terms of heterochromatin interfering in the terminalisation of chiasmata. This assumption is supported by the observation of an enhanced frequency of bound arms at metaphase I relative to length of $4B^L$ and $2B^S$. These chromosome arms, and also $5B^L$ (with interstitial heterochromatin) and $1B^L$ (telomeric heterochromatin), showed a great number of intercalary chiasmata (Fig. 2).

## References

Armstrong KC (1982) N-banding in *Triticum aestivum* following Feulgen Hydrolysis. Theor Appl Genet 61:337–339

Chapman V, Riley R (1966) The allocation of the chromosomes of *Triticum aestivum* to the A and B genomes and evidence on genome structure. Can J Genet Cytol 8:57–63

Dvorak J (1976) The relationship between the genome of *Triticum urartu* and the A and B genomes of *Triticum aestivum*. Can J Genet Cytol 18:371–377

Dvorak J, McGuire P (1981) Nonstructural chromosome differentiation among wheat cultivars, with special reference to differentiation of chromosomes in related species. Genetics 97:391–414

Feldman M (1966) Identification of unpaired chromosomes in $F_1$ hybrids involving *T. aestivum* and *T. timopheevi*. Can J Genet Cytol 8:144–151

Ferrer E, González JM, Jouve N (1984) Identification of C-banded chromosomes in meiosis of common wheat, *Triticum aestivum* L. Theor Appl Genet 67:257–261

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

Gill BS, Kimber G (1974) Giemsa C-banding and the evolution of wheat. Proc Natl Acad Sci USA 71:4086–4090

Hutchinson J, Miller TE, Jahier J, Shepherd KW (1982) Comparison of the chromosomes of *Triticum timopheevi* with related wheats using the techniques of C-banding and in situ hybridization. Theor Appl Genet 64:31–40

Jewell DC (1979) Chromosome banding in *Triticum aestivum* cv. 'Chinese Spring' and *Aegilops variabilis*. Chromosoma 71:129–134

John B, Miklos GLG (1979) Functional aspects of satellite DNA and heterochromatin. Int Rev Cytol 58:1–114

Jouve N, Diez N, Rodríguez M (1980) C-banding in 6x-Triticale × *Secale cereale* L. hybrids cytogenetics. Theor Appl Genet 57:75–79

Jouve N, Montalvo D, Soler C (1982) C-banding in cytogenetics of 6x-Triticale × *Triticum aestivum* L. hybrids. Z Pflanzenzücht 88:311–321

Khan SI (1962) Monosomes and their influence on meiosis in 'Holdfast'. Cytologia 27:386–397

Kimber G, Hulse MM (1979) The analysis of chromsome pairing in hybrids and the evolution of wheat. In: Ramanyjan S (ed) Proc 5th Int Wheat Genet Symp. Indian Soc Genet Plant Breed, New Delhi, pp 63–72

Loidl J (1979) C-band proximity of chiasmata and absence of terminalisation in *Allium flavum*. Chromosoma 73:45–51

Morrison JW (1953) Chromosome behaviour in wheat monosomics. Heredity 7:203–217

Naranjo T, Lacadena JR (1982) C-banding pattern and meiotic pairing in five rye chromosomes of hexaploid triticale. Theor Appl Genet 61:233–237

Niekerk HA van, Pienaar RV (1983) Morphology and linear C-band differentiation of *Triticum aestivum* L. em Thell v. *aestivum* cv. 'Chinese Spring' chromosomes. Cereal Res Commun 11:115–122

Person C (1956) Some aspects of monosomic wheat breeding. Can J Bot 34:60–70

Sallee PJ, Kimber G (1979) Analysis of the pairing of wheat telocentric chromosomes. In: Ramanujam S (ed) Proc 5th Int Wheat Genet Symp. Indian Soc Genet Plant Breed, New Delhi, pp 408–419

Santos JL, Giraldez R (1978) The effect of C-heterochromatin in chiasma terminalisation in *Chorthippus biguttulus* L. (*Acrididae, Orthoptera*). Chromosoma 70:59–66

Sasaki M, Morris R, Schmidt JW, Gill BS (1963) Metaphase I studies on $F_1$ monosomics from crosses between 'Chinese Spring' and Cheyenne common wheat varieties. Can J Genet Cytol 5:318–325

Seal AG (1982) C-banded wheat chromosomes in wheat and triticale. Theor Appl Genet 63:49–56

Sybenga J, Vries JM de (1972) Chromosome pairing and chiasma formation in polysomic B-chromosomes in rye, *Secale cereale*. Biol Zentralbl 91:181–192

Thomas JB, Kaltsikes PJ (1976) The genomic origin of the unpaired chromosomes in triticale. Can J Genet Cytol 18:687–700

Yamamoto M (1979) Cytologial studies of heterochromatin function in the *Drosophila melanogaster* male: autosomal meiotic pairing. Chromosoma 72:293–328

Zurabishvili TG, Iordansky AB, Badaev NS (1978) Linear differentiation of cereal chromosomes. 2. Polyploid wheats. Theor Appl Genet 51:201–210