Misdivision of Homoeologous Group 5 Univalent Chromosomes in Hexaploid Wheat

II. Univalents derived from American and European cultivars¹

R. Morris, T. Taira², J. W. Schmidt and M. Sasaki

University of Nebraska, Lincoln, U.S.A.
and Tottori University, Tottori, Japan

Received July 5, 1975

In the first paper of a cooperative study by scientists in Japan and the United States, Makino *et al.* (1976) presented information on misdivisions of wheat chromosomes 5A, 5B and 5D derived from ten Japanese cultivars. The monosomic state of each chromosome was obtained by crossing each cultivar to the Chinese Spring group 5 monosomics. The average misdivision frequencies for the ten cultivars were 15.3 % for 5A, 10.5 % for 5B, and 8.4 % for 5D, with a range of 3.1 % to 19.6 %. The chromosome differences and the chromosome-cultivar interactions were statistically significant, indicating that misdivision frequency was influenced by the specific chromosome and the genotypic background.

A preliminary report of misdivision frequencies in the homoeologous group 5 monosomes (univalent state at meiosis) derived from American and European wheat cultivars was published by Morris *et al.* (1971). A more complete and comprehensive presentation is given in this paper.

Materials and methods

The 22 wheat cultivars from which the group 5 chromosomes were obtained in the monosomic state are listed in Table 1. They represented different geographical regions of the United States, South America, and Europe. The American cultivars also included different kernel types (hard and soft), kernel colors (red and white), and growth habits (spring and winter).

In 1966 and 1967, crosses were made in the greenhouse at Lincoln, Nebraska, between each cultivar and Chinese Spring monosomics for 5A, 5B, and 5D, which had been developed by Dr. E. R. Sears, USDA, University of Missouri. An attempt was made to get at least two crosses for each chromosome type from each cultivar.

In 1968, seeds of F₁ progenies from 134 crosses were germinated on blotters

¹ Contribution from the Department of Agronomy, University of Nebraska-Lincoln, Lincoln, Nebraska 68583. Published as Paper Number 3747, Journal Series, Nebraska Agricultural Experiment Station. The research reported was conducted under Project No. 12-34, and was supported in part by Grant No. GF-281 from the National Science Foundation.

² Present address: Plant Science Department, University of Manitoba, Winnipeg, Canada.

Table 1. Wheat cultivars used in homoeologous group 5 chromosome study

Name	Type	Geographical origin
American (U.S.)		
Brevor	Soft white winter	Washington (state)
Burt	Hard white winter	Washington (state)
Ceres	Hard red spring	North Dakota
Elgin	Soft white winter (club)	Idaho-Oregon
Lemhi	Soft white spring	Idaho
Nebred	Hard red winter	Nebraska
Omaha	Hard red winter	Nebraska
Omar	Soft white winter (club)	Washington (state)
Rushmore	Hard red spring	South Dakota
Seneca	Soft red winter	Ohio
South American:		
Rafaela	Hard red spring	Argentina
European:		
Baragan 12	Soft red winter	Roumania
Candeal	Soft red indeterminate	Spain
Cappelle Desprez	Soft red winter	France
Fertodi 293	Soft red winter	Hungary
Harrach	Soft red winter	Austria
Heine VII	Soft red winter	Germany
Magdalena	Soft red winter	France
Nr 301	Soft red winter	Bulgaria
Ring	Soft red spring	Sweden
San Pastore	Soft red indeterminate	Italy
Skorospelka 3	Soft red winter	USSR

in petri dishes. Wrinkled seeds were selected to increase the chances of getting monosomic plants (Morris *et al.* 1970). Root tips were taken from each germinated seed, and the seedlings were held at 2–4°C until chromosome counts were made. The root tips were pretreated with a .002M 8-hydroxyquinoline solution at 13–16°C for 4 to 5 hours and the Feulgen reaction was used to stain the chromosomes.

In most cases, at least two monosomic seedlings per cross were transplanted to pots of soil in the greenhouse. During the spring of 1968, microsporocyte samples were taken from each plant, usually on two different dates, in an attempt to obtain dividing meiotic cells of good quality. The samples were stored in Carnoy's fixative at –10 to –15°C. Acetocarmine squash slides were prepared and made permanent using venetian turpentine mounting medium.

The anaphase I cells with a lagging monosome were observed to obtain quantitative data on three types of centromere behavior: normal division, misdivision involving one chromatid, and misdivision involving both chromatids. Information also was obtained on the poleward distribution pattern of the chromatids of the univalent, whether normally divided or misdivided. Where possible, 125 cells were scored for each plant. Each cultivar and each chromosome type i.e. 5A, 5B, or 5D, included four monosomic plants from two different crosses.

Analyses of variance were performed on both the original data and on arc sin transformations, in order to test the differences in misdivision rates among the three chromosomes within and between cultivar groups. Duncan's multiple range test was applied to various combinations of data. The cultivars Baragan 12, Brevor, Cappelle Desprez and Heine VII were omitted from statistical tests because of insufficient data.

Results

The frequencies of cells with misdivisions in Chinese Spring and F_1 plants with a group 5 monosome are given in Table 2. Each figure is based on over 400 cells with the following exceptions: Chinese Spring 5D (386), Brevor 5D (375), Baragan 5A, 5B and 5D (250 each), Cappelle Desprez 5A (375) and 5D (no data), and Heine VII 5B (375).

Table 2. Percentages of anaphase I cells with misdivision in group 5 monosomes of Chinese Spring and of F_1 plants from crosses between Chinese Spring monosomics and each of 22 cultivars

Cultivar	Chromosome and no. of chromatids misdivided								
	5A			5B			5D		
	One	Two	Total	One	Two	Total	One	Two	Total
Chinese Spring	25.8	15.6	41.4	12.6	2.5	15.1	6.2	0.5	6.7
Crosses/Amer. cultivars:									
Brevor	11.7	8.5	20.2	11.4	2.7	14.1	7.7	0.0	7.7
Burt	11.8	6.0	17.8	18.4	6.2	24.5	10.8	1.0	11.8
Ceres	11.4	3.0	14.4	8.7	3.3	12.0	10.2	1.7	11.9
Elgin	9.2	6.8	16.0	8.6	14.0	22.6	5.0	1.3	6.3
Lemhi	14.0	8.1	22.1	8.3	3.6	11.9	6.7	2.7	9.4
Nebred	7.6	4.0	11.6	13.8	2.0	15.8	8.2	0.8	9.0
Omaha	7.6	3.8	11.4	3.6	2.3	5.9	2.1	0.2	2.3
Omar	7.7	16.0	23.7	12.2	8.8	21.0	5.2	2.0	7.2
Rushmore	7.0	1.2	8.2	8.1	1.8	9.9	5.4	0.4	5.8
Seneca	13.8	12.5	26.3	9.0	27.1	36.1	14.5	5.2	19.7
Crosses/Eur. and S. Amer. cultivars:									
Baragan	4.8	1.6	6.4	4.0	2.4	6.4	5.6	0.0	5.6
Candeal	8.4	0.6	9.0	4.8	1.8	6.6	6.8	1.0	7.8
Cappelle Desprez	5.1	1.6	6.7	4.6	2.4	7.0	—	—	—
Fertodi 293	4.6	4.4	9.0	11.4	10.6	22.0	7.2	0.0	7.2
Harrach	8.8	4.2	13.0	11.4	4.6	16.0	7.2	0.4	7.6
Heine VII	6.0	2.4	8.4	5.1	1.6	6.7	4.2	0.0	4.2
Magdalena	5.8	2.7	8.5	2.6	1.1	3.7	1.2	0.0	1.2
Nr 301	8.2	4.8	13.0	12.2	9.2	21.4	11.4	1.8	13.2
Rafaella	1.7	0.6	2.3	2.8	0.4	3.3	1.7	0.2	1.9
Ring	5.8	2.1	7.9	4.7	0.2	4.9	5.7	1.0	6.7
San Pastore	5.5	2.7	8.2	4.5	1.0	5.5	2.9	0.9	3.8
Skorospelka	4.5	1.8	6.3	4.5	2.4	6.9	3.0	0.2	3.2

The data for Chinese Spring are averages for monosomic plants grown in the greenhouse in 1967 and 1970. They were not grown in the same year as the F1 progenies (1968). Chromosome 5A of Chinese Spring had the highest misdivision rate of any group 5 chromosome or cultivar source, but the rates for 5B and 5D were comparable to those of monosomes from some other cultivars.

In general, the misdivision frequency was higher for one chromatid than for both chromatids of the group 5 monosomes. The most striking exception was the American cultivar Seneca, where the misdivision rate of 5B was three times higher for both chromatids than for one chromatid. The South American cultivar Rafaela had the lowest misdivision rates for chromosomes 5A and 5B, which were only slightly higher than 5D. Since Rafaela behaved more like the European cultivars than the American cultivars in misdivision rates, it was included with the former group.

Analyses of variance using arc sin transformations were performed separately for the American group and the European group. Within each group, there were

Table 3. Analysis of variance using arc sin transformations for total misdivision rates in group 5 monosomes from American and European cultivar groups

Source	d.f.	MS
Total	215	
Cultivar groups	1	1811.64*
Cultivars/cultivar groups	16	255.51**
Chromosomes	2	628.35**
Cultivar groups $\times$ chromosomes	2	54.95
Cultivars/cultivar groups $\times$ chromosomes	32	37.93**
Plants/cultivars/cultivar groups	54	4.72
Error	108	3.74

* Significant at 5% level.

** Significant at 1% level.

significant differences at the 1% level among cultivars, chromosomes, misdivision types (one versus two chromatids), and the interaction of cultivars by chromosomes by misdivision types.

An analysis of variance for both the American and European groups, based on the total misdivision frequency for each chromosome, is given in Table 3. The tests of significance were based on the assumption that plants and cultivars were considered to be random effects. Differences in misdivision rates between the two cultivar groups were significant at the 5% level. Significant differences at the 1% level were found for chromosomes, cultivars within each group, and the interaction cultivars/cultivar groups by chromosomes. Similar results were obtained when the analyses were performed separately for misdivisions involving one chromatid versus both chromatids.

Duncan's multiple range test was applied to rank 18 of the cultivars for total misdivision rates in the group 5 chromosomes (Table 4). The American cultivar Seneca had a significantly higher misdivision frequency than all the others, which fell into five overlapping groups. Seven of the nine American cultivars were in-

cluded in the top two groups, but only three of the nine European cultivars.

A similar distribution pattern was obtained when Duncan's test was applied to misdivision involving both chromatids of a monosome (not shown). Seneca had a higher misdivision rate than any other cultivar except Omar, and the other cultivars were included in four overlapping groups. However, for misdivision involving one chromatid, there were eight overlapping groups with five to ten cultivars in each group.

In Table 5, the misdivision data are presented for each chromosome as means of cultivar groups. The misdivision frequencies affecting one or both chromatids of a univalent are shown separately in addition to the total misdivision rate. By means of Duncan's test, significantly higher misdivision rates were found for one

Table 4. Comparison of 18 cultivars in American and European groups for total misdivision frequency of all group 5 monosomes

Cultivar	Anaphase I cells (%) with misdivisions ^a			
Seneca	27.4	a		
Burt	18.0	b		
Omar	17.5	b		
Nr 301	15.9	b		
Elgin	15.1	b	c	
Lemhi	14.5	b	c	
Ceres	12.8	b	c	
Fertodi 293	12.7	b	c	d
Harrach	12.2	b	c	d
Nebred	12.1	b	c	d
Rushmore	8.0	c	d	e
Candael	7.8	c	d	e
Omaha	7.0		d	e f
Ring	6.5		d	e f
San Pastore	5.8			e f
Skorospelka 3	5.5			e f
Magdalena	4.5			e f
Rafaela	2.5			f

^a Numbers followed by the same letter are not significantly different at the .05 level of probability using Duncan's multiple range test applied to arc sin transformations of the data.

chromatid than for two chromatids. This applied to each chromosome within each cultivar group (note vertical arrows). The differences between 5A and 5B were not statistically significant in any of the comparisons. For comparisons between 5A and 5D or 5B and 5D within each cultivar group, the differences were significant for misdivision involving both chromatids but not for misdivision involving one chromatid. However, total misdivision rates in each cultivar group differed significantly, with 5D having the lower rate in each comparison. There also was a significant difference between cultivar groups in total misdivisions for each chromosome, with the rates for the American group almost twice as high as those for the European group.

The orientation patterns of normally divided and misdivided chromatids with

Table 5. Percentages of anaphase I cells with misdivision in one or both chromatids of group 5 monosomes from different cultivar groups. Figures connected by arrows are significantly different at 5% level with Duncan's test (using arc sin transformations of the data)

Cultivar group and misdivision type	Chromosome and mean per cent cells with misdivisions		
	5A	5B	5D
American group (9):			
One chromatid	9.9	10.1	7.5
Both chromatids	6.8	7.7	1.7
European group (9):			
One chromatid	5.9	6.5	5.1
Both chromatids	2.7	3.4	0.6
Total misdivisions:			
American group	16.7	17.7	9.3
European group	8.6	9.9	5.8

No misdivision (A)	54.6-94.6	0.0-5.0	0.4-11.4	0.6-10.2			
Misdivision in one chromatid (B)	0.3-5.6	0.0-4.4	0.0-0.2	0.0-1.4	0.4-7.8	0.0-1.4	
Misdivision in both chromatids (C)	0.0-0.4	0.0-0.7	0.0-21.0	0.0-0.6	0.0-0.7	0.0-0.7	0.0-1.9
	0.0-0.4	0.0-0.4	0.0-0.2	0.0-0.4	0.0-0.2	0.0-2.1	0.0-1.5

Fig. 1. Diagrams of orientation patterns at anaphase I of normally divided and misdivided chromatids of group 5 monosomes from 22 cultivars. Numbers in each cell represent the range (%) for each orientation type. See text for explanations.

respect to the poles of anaphase I cells are shown in Figs. 1 and 2. The range in frequency for the three chromosomes and 22 cultivars is given below each orientation type in Fig. 1. The ranges for the American and European cultivar groups were combined because they were similar in most cases.

The four categories under A refer to cases where the univalent divided normally.

Fig. 2. Photographs of some orientation patterns at anaphase I of normally divided and misdivided chromatids of group 5 monosomes. The letters and numbers on the photographs correspond to those on the diagrams of Fig. 1. The configurations in A4 and C4 are in the lower half of the cell, and in C5 in the upper half.

In most of these cases sister chromatids were directed to opposite poles (A1). However, there were some instances in which sister chromatids went to the same pole (A3 and A4), or in which one chromatid appeared to be stationary on the metaphase plate (A2), as though its centromere function had been impaired.

Misdivision in one of the two sister chromatids of a univalent gave two telochromosomes and a normal chromatid (B1 through 6). In these situations, the centromere must have first divided parallel to the chromosome thread to separate sister chromatids, then the centromere of one chromatid divided transversely. The telochromosomes went to opposite poles (B5) or to the same pole (B1, B3 and B6) with about the same frequency. In some cells (B2 and B4), one of the telochromosomes lay on the plate with no polar orientations. This behavior suggested that the centromere misdivided so that most or all of it went with one arm. In B1, B3, and B6 the misdivision event probably occurred after the chromatid started moving towards the pole, whereas in B2, B4, and B5 it likely took place while the chromatid was still on the metaphase plate.

Misdivision in both chromatids resulted in two isochromosomes (C3 and C14), two telochromosomes and an isochromosome (C4, C5, C7, C8, C9), or in four telochromosomes (C1, C2, C6, C10 through C13, C15, C16). Cells containing two isochromosomes resulted from one misdivision event. The isochromosomes usually separated to opposite poles (C3), but they were occasionally observed going to the same pole (C14). Each isochromosome must have received enough centromere material to move poleward. When one isochromosome and two telochromosomes were observed in the same cell, they could have resulted from a transverse split in the centromere region, followed by a linear split in the centromere material attached to one pair of arms. Or, where the telochromosomes remained on the plate (C5), the transverse split may have occurred to one side of the centromere, which went with the isochromosome. The manner in which four telochromosomes arose was suggested by their orientations at anaphase I. The configurations in C6, C10, C11, C12, and C13 most likely resulted from a misdivision event to give two isochromosomes, followed by linear separation of the chromatids in each isochromosome. Those in C1, C2, and C15 probably came from linear separation of sister chromatids in a univalent, followed by misdivision in each chromatid. Those in C16 could have arisen by either sequence of events. Each of the events which resulted in four telochromosomes occurred with a low frequency, at most representing less than 2% of the cells.

The distributions of the chromatids of group 5 univalents or their misdivision products to the poles also are shown in Fig. 1. Bipolar distributions occurred in A1, B1, B2, B5, C1, C2, C3, C4, C7, C8, C10, C12, C15, and C16; unipolar distributions in A3, A4, B6, C13, and C14. In A2, B3, B4, C5, C6, C9, and C11, one or more arms have gone to one pole, but part of the univalent has remained on the cell plate. These cells were not included in either the bipolar or unipolar distributions.

The frequencies of anaphase I cells with unipolar distributions ranged from 2.5–21.4% for American cultivars and from 5.4–22.0% for European cultivars (Table 6). Chromosomes 5A and 5B in each cultivar group had similar frequencies

of unipolar distributions, which were somewhat higher than those of 5D. For all three chromosomes, over 90% of the cells with unipolar distributions contained group 5 univalents which had not undergone any misdivision events.

Table 6. Frequencies of anaphase I cells with unipolar distributions of group 5 monosomes or misdivision products from American and European cultivars

Cultivar group and chromosome	Per cent unipolar distribution				Range
	No misdivision	Misdivision in one chromatid	Misdivision in both chromatids	Total	
American group (10)					
5A	10.8	0.3	0.3	11.4	5.4-16.8
5B	10.5	0.4	0.4	11.3	4.7-21.4
5D	7.5	0.2	0.1	7.8	2.5-12.1
Total	9.6	0.3	0.3	10.2	2.5-21.4
European group (12)					
5A	12.8	0.2	0.1	13.1	8.5-20.8
5B	11.7	0.2	0.1	12.0	7.1-22.0
5D	9.6	0.2	0.1	9.9	5.4-19.2
Total	11.4	0.2	0.1	11.7	5.4-22.0

Discussion

In our cooperative Japan-U.S. studies, we have determined misdivision rates of homoeologous group 5 chromosomes from three geographical groups of wheat cultivars. The data for the Japanese group were collected by Makino *et al.* (1976), whereas the American and European groups were used in the present study. In all cases the group 5 chromosomes were tested as univalents (monosomes) in F1 plants from crosses between each cultivar and Chinese Spring monosomics, which were used as female parents. The cytoplasm and one homologue of each chromosome pair came from Chinese Spring. The cultivars of each geographical group contributed a group 5 chromosome and the other homologue of the paired chromosomes. Any genetic effects on misdivision rates may be due to genes in a group 5 monosome, or to genes in one or more chromosome pairs. In the latter case, there may be differential interactions between genes from Chinese Spring and those from the American, European, or Japanese cultivars. There also may be differential interactions between the cytoplasm of Chinese Spring, which was present in all F1 plants, and the genomes of the different cultivar groups.

It has been suggested by B. C. Jenkins (personal communication) that misdivision events may be affected by the kind of environment in which the F1 progenies were grown compared to the native environment of the cultivars contributing the group 5 chromosomes. In order to determine if environment has an effect, the monosomes from each cultivar should be tested both in their native environment and in at least one other type of environment. None of the monosomes in our studies were tested in precisely this way. The only ones tested in two environments were Chinese Spring monosomics 5B and 5D, which were grown in the field

at Tottori, Japan and in the greenhouse at Lincoln, Nebraska. The misdivision rates for 5B were 9.3% at Tottori versus 15.1% at Lincoln. The rates for 5D were considerably lower than those for 5B at both locations, but the rate at Lincoln (6.7%) was slightly higher than the rate at Tottori (5.1%).

Some of the Chinese Spring monosomics have been tested in different years in the same location. For monosomic 5A, Sears (1952) obtained misdivision rates of 36.0% in 1945 and 43.5% in 1949 at Columbia, Missouri, and we obtained rates of 33.7% in 1967 and 43.5% in 1970 at Lincoln, Nebraska. We also tested monosomics for 5B and 5D in the same two years, but for each chromosome the difference between years was less than 1%. Steinitz-Sears (1966, 1973) found a difference of 4.3% between two years for misdivision rates of monosomic 3B, with a mean of 23.3%. These comparisons show that chromosome 5A of Chinese Spring had more variation in misdivision rate between years than the other chromosomes, but it also had a consistently higher rate.

The three cultivar groups used in our two studies were each tested in only one environment. The progenies for the Japanese group were field-grown at Tottori, Japan. Progenies for the American and European groups, which represented a

Table 7. Frequencies of anaphase I cells with misdivisions in group 5 monosomes from three wheat cultivar groups

Cultivar group	Chromosome and mean per cent cells with misdivisions (range in parentheses)		
	5A	5B	5D
American	16.7 (8.2-26.3)	17.7 (5.9-36.1)	9.3 (2.3-19.7)
European	8.6 (2.3-13.0)	9.9 (3.3-22.0)	5.8 (1.2-13.2)
Japanese	15.3 (9.5-19.6)	11.1 (3.1-14.5)	8.8 (3.8-16.5)

wide range of climatic conditions, were grown in a plastic greenhouse at Lincoln, Nebraska. The Japanese cultivars were grown under conditions closest to their native environment, so they might be expected to have lower misdivision rates than the other two groups. However, the European group had the lowest average misdivision rate for each chromosome (Table 7). The misdivision rates for 5A and 5D were almost as high in the Japanese group as in the American group. Within the American group, differences occurred between cultivars of similar type or geographical origin, such as Ceres and Rushmore, or Nebred and Omaha (Table 2). Thus, it appears that the genetic constitution of the group 5 monosomes and/or the chromosome background had an important influence on misdivision events.

Further support for genetic control of misdivision events is provided by information on the misdivision rate of Chinese Spring 5A. Unfortunately, Makino *et al.* (1976) were not able to obtain misdivision data for Chinese Spring monosomic 5A plants because their line was telosomic. We obtained an average frequency of 41.4% for two years under greenhouse conditions (Table 2). This is within the range of the frequencies obtained in two years by Sears (1952). These rates were much higher than those for 5A from any of the 32 cultivars used in our cooperative studies. Sears also found that, when 5A from each of three spring

cultivars was substituted into Chinese Spring, the misdivision rates were lower than Chinese Spring 5A in its own background. The high misdivision rate appears to be an inherent property of Chinese Spring 5A. However, it would be worthwhile to test this chromosome in cultivar backgrounds other than Chinese Spring, and also in different environments.

Joshi *et al.* (1970) determined the frequencies of telochromosomes and isochromosomes in progenies of the monosomic sets of Chinese Spring and Pb.C591. They found that most of the misdivision products were derived from monosomics for chromosomes 1B, 2D, 4B, and 4D. They concluded that these chromosomes carry genes controlling the integrity of the centromere, and that their monosomic state promotes misdivision. They also found that the frequencies of transmitted misdivision products were higher in progenies of crosses between either of the two monosomic sets and other cultivars than in the progenies of the monosomic sets. In this respect, their results differed from those for the group 5 chromosomes of our studies, in which misdivision frequencies were consistently higher for Chinese Spring monosomic 5A than for 5A in any of the F1 hybrids. Also, Chinese Spring monosomics 5B and 5D had higher misdivision rates than some of the F1 hybrids. However, our observations were made on cells in which the misdivision events had occurred, whereas Joshi *et al.* were dealing with the transmission of the misdivision products.

The ranges in misdivision frequency (Table 7) indicate the variable behavior of each group 5 chromosome from different sources. There was more variation among monosomes from different American cultivars than from different European or Japanese cultivars. However, the ranges overlapped both among chromosomes and cultivar groups. Sears (1952) obtained a range of 13.7–23.6% for 5A of Hope, Thatcher, and Red Egyptian substituted separately as monosomes into Chinese Spring. This range is similar to, but narrower than, the range we obtained for the American group. Sears (1973) found that misdivision rates varied from 14.6 to 26.9% for chromosome 3B from Hope, Thatcher, Red Egyptian, and Timstein when substituted separately as monosomes into Chinese Spring. In these two studies, the highest rates were obtained when 3B and 5A were derived from Red Egyptian. Chromosome 5A from Thatcher had a higher rate than 5A from Hope, whereas 3B from Hope had a higher rate than 3B from Thatcher. These comparisons indicate that there is considerable variation in misdivision rate for the same chromosome from different cultivars, but that different chromosomes from the same cultivar may not have the same relative rate.

Misdivisions affecting one chromatid of a group 5 univalent were, on the average, more frequent than misdivisions affecting both chromatids in each cultivar group (Table 8). The ratio of one-chromatid to two-chromatid misdivisions was about 2:1 in the American and European groups, and 5:1 in the Japanese group. This indicates that most misdivisions occurred after the linear division of the centromeres into two parts.

All ten cultivars of the Japanese group were consistent in having higher frequencies of misdivisions involving one chromatid than both chromatids (Makino and Sasaki, unpublished data). Most of the cultivars in the American and European

groups conformed to this behavior pattern, but there were a few exceptions (Table 2). The most notable one was the American cultivar Seneca, which had three times as many misdivisions involving both chromatids of chromosome 5B, and an almost

Table 8. Comparisons of misdivisions affecting one versus both chromatids of group 5 monosomes in three cultivar groups

Cultivar group	Average per cent anaphase I cells with misdivisions involving	
	One chromatid	Both chromatids
American	8.3	4.9
European	5.9	2.2
Japanese	9.7	1.9

equal number of the two types of misdivision events for 5A. A higher misdivision rate involving both chromatids also occurred for 5A from Omar and 5B from Elgin. The only deviation in the European group was for chromosomes 5A and 5B from the cultivar Fertodi 293, which had approximately equal misdivision frequencies affecting one and two chromatids. In all these exceptional cases, the behavior was consistent among the four plants tested for each cultivar. The result was an increase in the frequency of cells with two isochromosomes at opposite poles (Type C3 in Fig. 1). It is possible that some inherent structure of the chromosomes from these cultivars promotes misdivision before the sister chromatids separate.

Unipolar distributions of the group 5 monosomes or their derivatives at meiotic anaphase I resulted from non-disjunction of sister chromatids. The frequencies of unipolar distributions for the three cultivar groups are given in Table 9. For each

Table 9. Frequencies (%) of anaphase I cells with unipolar distributions of group 5 monosomes from three cultivar groups

Cultivar group and number	Chromosome			
	5A	5B	5D	Combined
American (10)	11.4	11.3	7.8	10.2
European (12)	13.1	12.0	9.9	11.7
Japanese (10)	31.7	34.7	18.1	28.3

group, the numbers of cells with unipolar distributions for 5A and 5B were similar and higher than for 5D. Makino *et al.* (1976) related this behavior to chromosome length in the Japanese group, with the longer chromosomes, 5A and 5B, having more unipolar distributions than 5D. The same trend is evident for the other two cultivar groups.

The American and European groups were similar in frequencies of unipolar distributions either for individual chromosomes or for the combined chromosomes. The Japanese group had a much higher frequency of unipolar distributions than either of the other two groups. This is due in a minor way to a difference in the collection of data among the cultivar groups. For the Japanese group, Makino

et al. (1976) included, in the unipolar classification, cells which had a group 5 monosome or derivatives at one pole and one or two arms on the plate. We omitted these cells for the American and European groups because we thought that they did not fit either distribution. In any case, the frequency of these cells was less than 4% for all three chromosomes of the Japanese group, which means that unipolar distributions were still much higher in this group.

It is of interest to see whether misdivision events influenced how the products were distributed to the poles (Table 10). In cells with no misdivisions, the ratio of bipolar to unipolar distributions was between 7 and 8:1 for the American and European groups, but only 2.6:1 for the Japanese group. When misdivisions involved one chromatid, the ratio of bipolar to unipolar distributions was 2:1 for the Japanese group, but more than 25:1 for the American and European groups. For misdivisions involving both chromatids, the ratio of bipolar to unipolar distributions was 17:1 for the American group, 20:1 for the European group, and 4:1 for

Table 10. Frequencies (%) of anaphase I cells with misdivisions involving one or both chromatids of group 5 monosomes from three cultivar groups in relation to polar distributions

Cultivar group and type of distribution	No misdivisions	Misdivisions		
		One chromatid	Both chromatids	Total
American (10)				
Bipolar	75.8	8.8	5.0	13.8
Unipolar	9.8	0.3	0.3	0.6
European (12)				
Bipolar	80.7	5.3	2.0	7.3
Unipolar	11.6	0.2	0.1	0.3
Japanese (10)				
Bipolar	63.9	6.2	1.5	7.7
Unipolar	24.5	3.4	0.4	3.8

the Japanese group. These results indicate that the chromatids of monosomes from the Japanese group went to the same pole more frequently than those from the American or European groups whether or not misdivision events had occurred. In the latter two groups, bipolar distributions were much more frequent after misdivision events had occurred than in their absence. Thus, there seems to be a basic difference between the Japanese group and the other two groups in the poleward movement of the group 5 monosomes during meiosis.

Telochromosomes and isochromosomes, which are the products of misdivision events, have significant applications in wheat cytogenetic studies. Therefore, it is worthwhile trying to find a specific genetic or environmental condition, or a treatment, which would consistently increase the frequency of misdivisions in monosomes when such events are desired. Comparisons of the results from our cooperative studies and those reported by others suggest that variations in misdivision frequency depend on the specific chromosome which is in a monosomic condition, the

genetic background in which it occurs, and possibly the environmental conditions under which the plants are grown. However, telochromosomes and isochromosomes are usually desired for all the chromosomes of cultivars which already have the monosomic set. Environmental conditions from a geographical standpoint are usually confined to the research institution where the work is carried on. For these reasons it would be more satisfactory to find a specific treatment which would induce misdivision events apart from any of these other conditions. Presumably this treatment needs to be applied at the time of meiosis in monosomic plants, when the univalent is in a vulnerable state. Some treatments which might be applied include irradiation (suggested by Darlington 1939), temperature shocks, or certain types of chemicals.

So far, only a few of the 21 chromosomes of hexaploid wheat have been tested for misdivision rates by observations of the meiotic cells in which misdivisions occurred. This type of information should be extended to all the chromosomes. A number of monosomic sets and chromosome substitution sets involving different cultivar backgrounds are available for such studies. It would involve extensive cytological observations to obtain data for all the chromosomes at one station. However, the work could be subdivided among graduate students for thesis problems, and among trained technicians. Comparisons could be made within and between homoeologous groups. A thorough investigation such as this could provide significant information concerning the normal and abnormal behavior of the centromeres of wheat chromosomes.

Summary

Misdivision rates of wheat chromosomes 5A, 5B and 5D were determined at meiotic anaphase I in F1 monosomic plants from crosses between the group 5 monosomics of Chinese Spring and ten American (U.S.), one South American, and eleven European cultivars. The misdivision rate was usually higher for one chromatid than for both chromatids of each group 5 univalent, but in 5B from the cultivar Seneca, misdivisions involving both chromatids were three times higher than those involving one chromatid. Significant differences in misdivision rates occurred between the European (including the South American cultivar) and American groups, and also among cultivars and chromosomes within each group. 5A and 5B had similar misdivision rates, which were generally higher than those for 5D. 5A of Chinese Spring in its own background had the highest misdivision rate of any group 5 chromosome or cultivar source. The European and American groups had similar ratios of bipolar versus unipolar distributions of normally divided or misdivided chromatids. The behavior of group 5 chromosomes was compared in these two groups and in a Japanese group reported in a companion paper. Misdivision rates seemed to be affected by the specific chromosome, the genetic background in which it occurred, and possibly environmental conditions.

Acknowledgment

Appreciation is expressed to the National Science Foundation for providing a grant for this cooperative study between Japanese and U.S. scientists. The following people assisted in making root-tip chromosome identifications of F1 plants: Mesdames Alma Chmelka-Lybyer, Lucile Schmidt, and Marjorie Sire. Dr. W. M. Schutz was consultant for the statistical analyses.

Literature cited

- Darlington, C. D. 1939. Misdivision and the genetics of the centromere. *J. Genetics* **37**: 341-364.
- Joshi, B. C., Sawhney, R. N., Singh, D. and Kumar, S. 1970. Genetic control of bipolar segregation of homologous chromosomes and integrity of the centromere in *Triticum*. *Caryologia* **23**: 359-362.
- Makino, T., Sasaki, M. and Morris, R. 1977. Misdivision of homoeologous group 5 univalent chromosomes in hexaploid wheat I. Univalents derived from Japanese cultivars. *Cytologia* **42**: 73-83.
- Morris, R., Schmidt, J. W. and Johnson, V. A. 1970. Advantages of seed selection in wheat aneuploid studies. *Euphytica* **19**: 194-198.
- , Taira, T. and Schmidt, J. W. 1971. Misdivision of homoeologous group 5 chromosomes from American and European wheat cultivars. *Seiken Zihô* No. **22**: 33-37.
- Sears, E. R. 1952. Misdivision of univalents in common wheat. *Chromosoma* **4**: 535-550.
- Sears, Lott M. S. 1973. Misdivision of five different 3B monosomes in Chinese Spring wheat. *Proc. Fourth Intern. Wheat Genetics Symp.*, Columbia, Mo., p. 739-743.
- Steinitz-Sears, L. M. 1966. Somatic instability of telocentric chromosomes in wheat and the nature of the centromere. *Genetics* **54**: 241-248.
-