CHROMOSOME PAIRING AND SYNAPTONEMAL COMPLEX FORMATION IN HEXAPLOID WHEAT, NULLISOMIC FOR CHROMOSOME 5B

by

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Chromosome pairing and synaptonemal complex formation have been analyzed at the ultrastructural level in spread microsporocyte nuclei of allohexaploid wheat, nullisomic for chromosome 5B. Two plants were investigated, one was selected among the progeny of selfed monosomic 5B wheat and the other was obtained by anther culture of wheat monosomic for 5B. The absence of chromosome 5B in the two plants was confirmed by N-banding of root tip complements and at metaphase I several of the cells contained multivalents. The ultrastructural analysis of 18 spread nuclei ranging in stage from the beginning of zygotene to early diplotene revealed an arrest of chromosome pairing and synaptonemal complex formation in this genotype when on the average 35-40% of the complement had synapsed. At zygotene there were several exchanges of pairing partners, the number of lateral components in multiple associations exceeding that observed in euploid wheat by a factor of two to three. Many of the pairing partner exchanges were close to the telomeres. As crossing over between homoeologues can occur in nullisomic 5B wheat it is apparent that nullisomy for chromosome 5B has a dual effect on meiosis, namely to reduce the stringency of synapsis and to permit crossing over between chromosomes of partial homology.

1. INTRODUCTION

In the absence of chromosome 5B, crossing over and chiasma formation can occur between the homoeologues of allohexaploid wheat (5, 6, 7). RILEY (5) thus reported that in nullisomic 5B wheat there were at metaphase I a mean of 1.41 univalents, 17.22 bivalents, 0.47 trivalents, 0.59 quadrivalents, 0.02 pentavalents and 0.05 hexavalents. That these multivalents had arisen by crossing over between homoeologous chromosomes was subsequently shown by RILEY and KEMPANA (7), who, by crossing plants nullisomic for 5B with euhexaploid wheat, obtained plants that were heterozygous for translocations. The chromosomes involved in the transloca-

tions were identified by test crosses to lines in which one specific chromosome was monosomic and it was shown that the translocations had formed between homoeologous chromosomes, indicating crossing over between homoeologues in the nullisomic 5B wheat.

The present paper is a part of a series, attempting at the ultrastructural level to investigate the effect of different dosages of chromosome 5B on synapsis and chiasma formation (1, 2, 3, 9, 10, 11). In this study the results of the analysis of plants nullisomic for chromosome 5B are reported. The significance of the combined results of these ultrastructural investigations for understanding the regulation of the disomic inheri-

Figure 1. Figure 1 is a photograph of an N-banded root tip metaphase complement of a wheat plant nullisomic for chromosome 5B. A photograph of an N-banded chromosome 5B is included for comparison (insert). (Bar = 5 μ m)

tance of wheat is discussed in a separate paper (4).

2. MATERIALS AND METHODS

Allohexaploid wheat plants nullisomic for chromosome 5B were obtained from two different sources of material, namely from the

progeny of *T. aestivum* cv. Chinese Spring wheat monosomic for chromosome 5B and from pollen plants derived from anther culture of Chinese Spring wheat monosomic for chromosome 5B. The nullisomic 5B chromosome doubled pollen plants (6x-2) were kindly provided by M.Sc. XINGZHI WANG, Department of

Figure 2. Three phase contrast photographs of orcein stained metaphase I complements from nullisomic 5B wheat. Figure 2a shows a metaphase with 20 bivalents and no multivalents, Figure 2b presents a metaphase I with four univalents (arrows) lying outside the metaphase plane and in Figure 2c is shown a metaphase containing at least one multivalent (kinetochores of the multivalent are denoted by arrows). The kinetochores of another presumptive multivalent are denoted by asterisks. In the middle of the metaphase plate several ring bivalents appear to be interlocked. (Bar = 10 μ m)

Physiology, Carlsberg Laboratory and the monosomic 5B material by Dr. TERRY MILLER, Plant Breeding Institute, Cambridge.

About two hundred plants derived from seeds of plants monosomic for chromosome 5B were grown in a heated glass house at 20 °C. Two plants which displayed the phenotypic characteristic of nullisomy for chromosome 5B, i.e. narrow leaves and a somewhat less vigorous growth than the plants monosomic for chromosome 5B or euploid wheat (8), were selected and transferred to a growth cabinet at 20 °C day temperature and 15 °C night temperature with a light regime of 16 hours light and 8 hours darkness.

The production of pollen plants by cultivation of anthers from wheat monosomic for chromosome 5B was performed as described by WANG (9). Two plants were obtained which had narrow leaves and a chromosome number of 40. These were transferred to growth cabinets and grown under the temperature and light regime described above.

The genomic constitution of all plants selected in the present study was analyzed by light microscopy using orcein squashing and/or N-banding of the chromosome complements of root tips and metaphase I complements as previously described (2). The procedures for electron microscopy are described elsewhere (1).

3. RESULTS

3.1. Light microscopy

About one percent of the plants obtained by selfing allohexaploid wheat, monosomic for chromosome 5B, lacks both copies of chromosome 5B (8). The low frequency is attributed to a strong selection against aneuploid pollen on the male side, while on the female side, 75% of the egg cells lacks chromosome 5B due to preferential segregation (8). In the two plants selected for their morphological characteristics, the 2n chromosome number was 40. N-banding

of the root tip complements revealed, however, that only one of the plants, the one with the narrower leaves of the two, was nullisomic for chromosome 5B (Figure 1) while the other plant was monosomic for 5B, having presumably lost one of the other chromosomes. A similar result was obtained for two 40-chromosome pollen plants, obtained by cultivation of anthers from monosomic 5B wheat. Only one of these was nullisomic for chromosome 5B, while the other was monosomic for 5B.

Squashing and orcein staining of cells at metaphase I revealed multivalents in the nullisomic 5B plants, but substantial variations in the chromosome configurations were observed between the cells. In some cells, 20 bivalents were recognized (Figure 2a), others contained bivalents and a few univalents (Figure 2b) while multivalents were observed in other cells (Figure 2c). Several cells revealed very complex configurations with multiple interlockings and several multivalents. These were generally not interpretable and a scoring for the different types of chromosome configurations was not possible. In 39 metaphases, selected for a low complexity, there were a mean frequency of 0.49 univalents, 2.95 rod bivalents, 15.87 ring bivalents, 0.28 trivalents, 0.18 quadrivalents and 0.05 hexavalents, the mean chiasma frequency being 36. The frequency of multivalents is somewhat lower than that reported by RILEY (5) who found a mean of 0.47 trivalents, 0.59 quadrivalents, 0.02 pentavalents and 0.05 hexavalents in nullisomic 5B wheat. RILEY and CHAPMAN (6) also noted that some cells appeared to have several multivalents and the observed frequencies of multivalents in this as well as in the present study may thus be somewhat underestimated. In addition, some of the bivalent structures may result from chiasma formation between two similar sized homoeologues.

The population of microsporocytes appeared to be considerably less synchronous in anthers of

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Figure 3. A montage of micrographs of an early zygotene nucleus (EZ8, 13% pairing) from nullisomic 5B wheat. Most telomeres and paired segments are located within a limited part of the spread nucleus (asterisks). An idiogram of the traced complement of this nucleus is shown in Figure 4. (Bar = 10 µm)

Table I. Degree of pairing, lateral component (LC) length of one complement ($1/2$ LC length) and the number of lateral components or lateral component fragments involved in multiple associations in three early-mid zygotene (E-MZ) nuclei of wheat microsporocytes nullisomic for chromosome 5B. The number of multiple associations in parenthesis are switch back associations of type II (see section 3.2.2 for explanation). s.d., standard deviation. Data for euploid wheat (2) are included for comparison.

Nucleus number	% pairing	$1/2$ LC length μm	Number of LC's in multiple associations
EZ8	13	2632	23 (10)
E-MZ4	22	2718	27 (4)
E-MZ5	26	2724	24 (14)
Mean	20	2691	25 (6)
Euploid wheat			
Mean $\pm$ s.d.	39 ± 7	1984 ± 342	8 ± 4 (6 ± 3)

Figure 4. An idiogram of the traced complement of an early zygotene nucleus (EZ8, 13% pairing, see Figure 3) of nullisomic 5B wheat. The idiogram includes all synaptonemal complexes of the nucleus as well as the unpaired lateral components extending from the synapsed segments. Fragments of lateral components not associated with other lateral components or synaptonemal complexes are not included in the idiogram (518 μm of lateral component). Lateral components or lateral component fragments involved in multiple associations are shown first and are denoted by capital letters while bivalents or bivalent segments are numbered and arranged after decreasing length. The actual lengths of the synaptonemal complexes and the lateral components are represented by vertical lines. Breaks in lateral components are indicated by crosses.

nullisomic 5B wheat than in euploid wheat (1) or wheat monosomic for chromosome 5B (2). In addition, other developmental differences were apparent, as microsporocytes at early meiotic prophase in nullisomic 5B wheat often possessed the thick wall characteristic of late meiotic prophase in euploid wheat, indicating differences in the synchrony of development of the cell wall and the nucleus between the two genotypes.

3.2. Electron microscopy

3.2.1. General aspects

Tracings of the entire complement of lateral components are only possible in some of the spread nuclei, since breakage and intertwining of lateral components are too extensive in many nuclei to permit a detailed analysis. This is in particular a problem at early zygotene, while tracings are somewhat easier at later stages when more of the complement is paired with synaptonemal complexes. Hence in this, as well as in the other studies of spread wheat nuclei, tracings at the earlier stage are confined to synaptonemal complexes and as much as possible of the unpaired lateral components until the continuity of these is lost either due to breakage or overlap/intertwining. This implies that the number of multiple associations detected

should be regarded as a minimum, but since the traceable portion of the complement at the same stages appears to be roughly the same in the different genotypes, a comparison between the frequencies of lateral components in multiple associations recorded in the investigated genotypes is justified. Synapsis appeared to proceed in the same way in the two plants analyzed, and the data have accordingly been pooled.

3.2.2. Early-mid zygotene

Nuclei assigned to the early-mid zygotene stage were distinguished from nuclei at the mid-late zygotene stage by the presence of a distinct bouquet. In euploid and monosomic 5B wheat, 50% synapsis can also be regarded as a distinguishing characteristic between the two stages, but as pairing and synaptonemal complex formation are arrested at a relatively early stage of synapsis in the nullisomic 5B material, the two stages are primarily distinguished by the appearance of the bouquet.

Chromosome pairing and synaptonemal complex formation are initiated by the congression of the telomeres within a limited area of the nucleus (Figure 3), probably representing a part of the nuclear envelope. Three nuclei (13, 22 and 26% synapsis) were analyzed in detail, their mean degree of synapsis being 20%. Several

Table II. Degree of pairing, lateral component (LC) length of one complement ($1/2$ LC length) and the number of lateral components or lateral component fragments involved in multiple associations in five mid to late zygotene (M-LZ) nuclei of wheat microsporocytes nullisomic for chromosome 5B. The number of multiple associations in parenthesis are switch back associations of type II (see section 3.2.2 for explanation). s.d., standard deviation. Data for euploid wheat (1) are included for comparison.

Nucleus number	% pairing	$1/2$ LC length μm	Number of LC's in multiple associations
MZ7	33	2522	16 (0)
MZ9	43	1822	12 (8)
M-LZ1	42	2261	31 (10)
LZ12	47	1972	20 (7)
LZ2	50	2881	8 (8)
Mean $\pm$ s.d.	43 ± 6	2292 ± 425	17 ± 9 (7 ± 4)
Euploid wheat			
Mid zygotene	62 ± 7	2040 ± 254	5 ± 6 (3 ± 3)
Late zygotene	93 ± 1	1806 ± 160	5 ± 5 (0)

Figure 6. A micrograph showing two exchanges of pairing partners close to the telomeres in a mid zygotene nucleus (MZ7, 33% pairing) of nullisomic 5B wheat. The entire spread nucleus is illustrated in Figure 5. The individual lateral components are denoted by capital letters. In the regions marked by asterisks the lateral components marked A to D and F to H exchange pairing partners. The arrow denotes a segment where lateral component E folds back and pairs with itself forming a circular structure. (Bar = 1 μ m)

changes of pairing partners occur in nullisomic 5B wheat at this stage (Table I, Figure 4) and there were in the three nuclei approximately the same number of lateral components or lateral component fragments involved in multiple associations, the mean number being 25. A classification into different types has not been attempted except associations referred to in the

tables and in the text as associations of type II. These involve two partially paired bivalents or a bivalent and a univalent which exchange pairing partners over a short region, typically 0.5-1.0 μ m, whereafter the lateral components switch back to their original partners (e.g. the multiple associations in nucleus LZ2, Figure 9).

A comparison with data for euploid wheat

Figure 5. A montage of micrographs of a mid zygotene nucleus (MZ7, 33% pairing) from nullisomic 5B wheat. Pairing partner exchanges are shown in the enlargement in Figure 6. (Bar = 10 μ m)

Figure 7. A tracing of the synaptonemal complex complement of a mid to late zygotene nucleus (M-LZ1, 42% pairing). The four tracings include all synaptonemal complexes of the nucleus as well as the unpaired lateral components extending from the synapsed regions. Fragments of lateral components are not included in the tracings (320 μ m of lateral components). An idiogram of the complement of this nucleus is shown in Figure 8. For explanation of symbols see legend to Figure 4.

Figure 8. An idiogram of the traced complement of a mid to late zygotene nucleus (M-LZ1, 42% pairing) of nullisomic 5B wheat. A tracing of the complement presented in the idiogram is shown in Figure 7. For explanation of symbols see legend to Figure 4.

nuclei at early-mid zygotene reveals that the number of lateral components involved in multiple associations exceeds that observed in euploid wheat by a factor of three (25 lateral components versus 8, Table I). Furthermore, while nearly all associations in euploid wheat are of type II (six out of eight lateral components), the multiple associations are more complex and involve more lateral components in the nullisomic 5B genotype. It should be noted that while the comparison between these two sets of data is justified on the basis of the morphological characteristics of the cells (distinct bouquet), the difference in the degree of pairing (39% in the euploid versus 20% in the nullisomic) makes the comparison less straight forward. However, as described in the following section similar differences in the frequency of lateral components in

multiple associations are encountered when comparing euploid and nullisomic 5B nuclei displaying the same amount of synapsis.

Two additional characteristics distinguish the nullisomic 5B nuclei from euploid nuclei at the early-mid zygotene stage. The bouquet configuration appears to be more open in nullisomic 5B nuclei than in euploid wheat, and secondly single pairing partner exchanges close to the telomeres are observed regularly in the former material (e.g. lateral components B, C, D and E in Figure 4) but never in the latter. Intermediate characteristics between nullisomic 5B and euploid wheat are encountered for early-mid zygotene nuclei of monosomic 5B wheat (2), which also possess a more loose bouquet configuration than euploid nuclei at the same stage of pairing. Furthermore, a single example of a

distal exchange of pairing partners was found in one of the spread monosomic 5B nuclei.

Apart from these differences the kinetics of synaptonemal complex formation appear to be the same in the euploid, monosomic 5B and nullisomic 5B genotypes with respect to initiation of synapsis primarily from the telomeres and the frequent initiation interstitially as well as the distances between the sites along the chromosome where synaptonemal complexes have formed.

3.2.3. Mid to late zygotene

Five spread nuclei analyzed in detail were assigned to the mid to late zygotene stage, the

mean degree of synapsis amounting to 43% with a range from 33% to 50% (Table II). Nuclei at this stage still reveal some aggregation of the telomeres, but less pronounced than at the preceding stages. The morphology of a spread mid-late zygotene nucleus is illustrated in Figure 5, tracings of a nucleus are shown in Figure 7 and an idiogram of the traced complement in Figure 8.

A mean number of 17 lateral components or lateral component fragments are involved in multiple associations at this stage, the range being from 8 to 31 (Table II). On the average 9 of the lateral components were in type II switch back associations, but among the individual nuclei the frequency of type II associations

Figure 9. Idiograms of multiple associations observed in two late zygotene nuclei (LZ2 and LZ12) and a pachytene nucleus (P6) of nullisomic 5B wheat. For explanation of symbols see legend to Figure 4.

Table III. Degree of pairing, lateral component (LC) length of one complement ($1/2$ LC length) and the number of lateral components or lateral component fragments involved in multiple associations in four pachytene (P) nuclei of wheat microsporocytes nullisomic for chromosome 5B. The number of multiple associations in parenthesis are switch back associations of type II (see section 3.2.2 for explanation). s.d., standard deviation. Data for euploid wheat (1) are included for comparison.

Nucleus number	% pairing	$1/2$ LC length μm	Number of LC's in multiple associations
P3	35	1876	22 (14)
P11	36	1558	20 (7)
P10	37	1660	9 (0)
P6	61	1595	18 (3)
Mean $\pm$ s.d.	42 ± 13	1672 ± 142	17 ± 6 (6 ± 6)
Euploid wheat Pachytene	97 ± 7	1474 ± 220	0.6 (0.3)

varied considerably. In nucleus LZ2 with 50% synapsis, all multiple associations were of type II (Figure 9), in nucleus M-LZ1 (42% synapsis) only a third of the lateral components were in multiple associations of type II, while in nucleus MZ7 type II associations were not found. Exchanges of pairing partners close to the telomeres are frequent also at this stage (e.g. lateral components A to E and E to H in Figure 6 and lateral components M to P in Figure 8). In nucleus MZ7, three examples of distal pairing partner exchanges were found; in nucleus MZ9, one case; in nucleus M-LZ1, one case; in nucleus LZ12 (Figure 9), two cases of which one involved a double exchange of pairing partner and in nucleus LZ2, no cases.

In addition, there were a number of associations where several lateral components are involved (e.g. the associations of lateral components I to S in Figure 8). Associations of two lateral components where one or both lateral components have folded back and formed a synaptonemal complex with itself are also counted as multiple associations, (e.g. lateral components Ø and Å in Figure 8), as the extensive foldback pairing probably indicates a

lack of homology between the two lateral components. At the mid-late zygotene stage the number of lateral components in multiple associations in nullisomic 5B is more than threefold higher than at mid and late zygotene in euploid wheat (Table II). A more than twofold difference is observed when comparing nuclei from the two genotypes displaying the same extent of synapsis. At 42% synapsis there is in nullisomic 5B wheat a mean number of 17 lateral components in multiple associations, while at early to mid zygotene in euploid wheat at 39% synapsis there is a mean number of 8 lateral components in multiple associations.

3.2.4. Pachytene

In euploid wheat and monosomic 5B wheat, the pachytene stage can be distinguished from the late zygotene stage by the absence of a bouquet, a change in morphology of the spread nuclei from circular to irregularly elongated and a shortening of the complement length to about two-thirds of that found at late zygotene. A stage with similar morphological characteristics can be recognized in nullisomic 5B wheat (see Figure

Figure 10. A montage of micrographs of a pachytene nucleus (P3, 35% pairing) of nullisomic 5B wheat. Note the irregular outline of the nucleus characteristic of the pachytene stage. An enlargement of a pairing partner exchange is shown in Figure 11. (Bar = 10 μm)

Table IV. Degree of pairing, lateral component (LC) length of one complement ($1/2$ LC length) and the number of synaptonemal complex (SC) segments retained in 6 nuclei at the pachytene to diplotene transition (PD) of wheat microsporocytes nullisomic for chromosome 5B. s.d., standard deviation. ND, not determined.

Nucleus number	% pairing	$1/2$ LC length μm	Number of SC segments
PD1	31	1824	74
PD2	47	1453	75
PD3	27	1569	57
PD4	28	1745	67
PD5	24	1817	62
PD6	62	1926	ND
Mean $\pm$ s.d.	37 ± 14	1722 ± 177	67 ± 8

Figure 11. A micrograph of a region of pairing partner exchange close to the telomeres in a pachytene nucleus (P3) of nullisomic 5B wheat. The lateral components shifting pairing partners are denoted by capital letters. Centromere-like structures, which occasionally are seen in the spreads are marked by arrows. The entire pachytene nucleus is shown in Figure 10. (Bar = 1 μm)

10 for survey micrographs), and the data in Tables II and III illustrate that a shortening of the complement in the nullisomic 5B nuclei from a mean of 2292 μm at mid-late zygotene to 1672 μm at pachytene has taken place. In contrast to the situation in monosomic 5B and euploid wheat, where synapsis is almost complete, the mean degree of synapsis at pachytene in nullisomic 5B wheat is only 42%, showing that synaptonemal complex formation is arrested at a relatively early stage in this genotype.

The number of lateral components in multiple associations (mean of 17 per nucleus) is at this stage identical to that found at mid-late zygotene. Also the number of lateral components in associations of type II is nearly the same (means of 7 and 6 at two stages) and in most pachytene nuclei distal pairing partner exchanges are found (Figures 9, 11). In euploid wheat, however, nearly all multiple associations have disappeared at this stage (Table III).

3.2.5. Pachytene-diplotene transition and early diplotene

The pachytene to diplotene transition is marked by the initiation of synaptonemal complex and unpaired lateral component degradation. Nuclei with a pachytene morphology but showing clear signs of lateral component degra-

Figure 12. A montage of micrographs of an early diplotene nucleus (ED2) of nullisomic 5B wheat. (Bar = 10 μm)

Figure 13. A micrograph illustrating a pairing partner exchange in a spread nucleus of nullisomic 5B wheat at the pachytene-diplotene transition. The region of pairing partner shift is marked by an arrow. At the top of the micrograph the unpaired telomeres of two lateral components (asterisk) appear to perform some alignment with the telomeres of two synaptonemal complexes. (Bar = 1 μ m)

dation are assigned to this stage while nuclei with distinct fragmentation of synaptonemal complexes and unpaired lateral components are referred to as early diplotene nuclei (Figure 12). At the transition stage there was a mean of 67 synaptonemal complex segments per nucleus and a mean of 80 segments at early diplotene

(Tables IV and V). The mean degree of synapsis at the pachytene to diplotene transition was 37% (range from 24% to 62%) and 33% (range from 19% to 66%) at early diplotene, the mean lateral component length of the three genomes being 1722 μ m at both stages.

Multiple associations of lateral components

Table V. Degree of pairing, lateral component (LC) length of one complement ($1/2$ LC length) and the number of synaptonemal complex (SC) segments retained in 7 early diplotene (ED) nuclei of wheat microsporocytes nullisomic for chromosome 5B. s.d., standard deviation.

Nucleus number	% pairing	$1/2$ LC length μm	Number of SC segments
ED1	36	1836	125
ED2	22	1953	78
ED3	35	1706	79
ED4	32	2264	66
ED5	18	1217	52
ED6	66	1322	78
ED7	19	1756	80
Mean $\pm$ s.d.	33 ± 17	1722 ± 360	80 ± 22

are often observed at the pachytene to diplotene transition (Figure 13) and at early diplotene, but a quantitative analysis has not been attempted due to the frequent fragmentation of the lateral components.

4. DISCUSSION

The following conclusions may be drawn from the present study:

1) In the absence of chromosome 5B in hexaploid wheat synapsis is arrested at an early stage. On the average only about 35-40% of the complement is paired with a synaptonemal complex (pachytene: mean of 42%, pachytene to diplotene transition: mean of 37%, and early diplotene: mean of 33%). In contrast, synapsis is almost complete in euploid wheat or wheat monosomic for chromosome 5B. As deduced from studies of isochromosomes (3) the arrest in synaptonemal complex formation in nullisomic 5B wheat, results primarily from a lack of the short arms of chromosome 5B.

2) In nullisomic 5B wheat there is throughout zygotene two to three times more lateral components in multiple associations as in euploid wheat. While almost all multiple associations are eliminated prior to pachytene in euploid wheat, the multiple associations are maintained throughout pachytene into diplotene in nullisomic 5B wheat. Several of the pairing partner exchanges are close to the telomeres, while this type of pairing partner exchange is not seen in euploid wheat.

3) In spread nuclei of nullisomic 5B wheat the bouquet configuration is more open and appears to resolve at an earlier stage than seen in spread nuclei of euploid wheat.

As crossing over between homoeologues can occur in the absence of chromosome 5B it can be concluded that nullisomy for chromosome 5B has the dual effect of lowering the stringency of synapsis as well as permitting crossing over between the homoeologues. A summary and discussion of the results obtained from this analysis as well as a general discussion of the effect of chromosome 5B are given in a separate paper (4).

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