Chromosome pairing in tetraploid rye with monosomic-substitution wheat chromosomes

Barbara APOLINARSKA

Institute of Plant Genetics, Polish Academy of Sciences, Poznań, Poland

Abstract. In tetraploid rye with single-substitution wheat chromosomes – 1A, 2A, 5A, 6A, 7A, 3B, 5B, 7B – chromosome pairing was analysed at metaphase I in PMCs with the C-banding method. The frequency of univalents of chromosome 1A was considerably higher than that of the other four wheat chromosomes of genome A (6A, 5A, 7A and 2A). Among chromosomes of genome B, the lowest mean frequency of univalents was observed for chromosome 5B. In monosomic lines, wheat chromosomes 1A, 2A, 5A, 6A, 7A and 5B paired with rye homoeologues most often in rod bivalents and in chain quadrivalents (also including 3B). The 47% pairing of 5B-5R chromosomes indicate that the rye genomes block the suppressor Ph1 gene activity. In monosomic plants with chromosomes 5A, 2A, 6A, 7A and 5B, a low frequency of rye univalents was observed. It was also found that the wheat chromosomes influenced the pairing of rye genome chromosomes, as well as the frequency of ring and rod bivalents and trin- and quadrivalents. However, the highest number of terminal chiasmata per chromosome occurred in the presence of chromosomes 5A and 2A, and the lowest – in the presence of chromosomes 3B and 7B. In the presence of chromosome 5B, the highest frequency of bivalents was observed. The results of the present study show that the rye genome is closer related to the wheat genome A of than to genome B. The high pairing of wheat-rye chromosomes, which occurs in tetraploid rye with substitution wheat chromosomes, indicates that there is a high probability of incorporating wheat chromosome segments into rye chromosomes.

Key words: C-banding, chromosome pairing, monosomic wheat chromosome, substitution, tetraploid rye.

Introduction

Suppressor genes block homoeologous pairing between chromosomes of three wheat genomes as well as between wheat and rye chromosomes. The most impor-
tant suppressor gene *Ph1* has been localized on the long arm of chromosome 5B (RILEY, CHAPMAN 1958). The second gene, according to the strength of the influence on the suppression of homoeologous pairing, was localized by MELLO-SAMPAYO (1968, 1971a, 1971b) and DRISCOLL (1972) on the short arm of 3D chromosome and was identified by SEARS (1982) as gene *Ph2*. Suppressor genes, located on the short arms of the third homoeologous wheat chromosome group, were described also by MILLER et al. (1983).

The rye genomes have a promoting effect on the pairing of homoeologous chromosomes in wheat-rye hybrids (MILLER, RILEY 1972, RILEY et al. 1973, DWORAK 1977). MILLER and RILEY (1972) observed a dosage effect of rye genomes (*Secale cereale*) on homoeologous pairing in wheat. LELLEY (1976) indicated that increasing the dosage of rye genomes can break down the isolation barriers of homoeologous pairing, genetically controlled by the 5B (*Ph1*) system.

The aim of the present study was to examine the influence of rye genomes on homoeologous pairing of monosomic wheat chromosomes with rye chromosomes and to analyse the influence of individual wheat chromosomes on pairing of the rye chromosomes in tetraploid rye with substitution wheat chromosomes.

**Material and methods**

Material for the study included substitution tetraploid rye lines obtained from hybrids of tetraploid rye × tetraploid triticale with tetraploid rye (APOLINARSKA 1996a, 1996b). In BC₁-F₇ generation, plants with monosomic-substitution wheat chromosomes were selected for cytological analysis of chromosome configurations at metaphase I.

The anthers collected from the spikelets were fixed in ethanol and acetic acid mixture (3:1 v/v) and placed in the refrigerator until analysis. Then the anthers were transferred to 45% acetic acid for 1-3 hours and squashed. PMCs were stained with the C-banding method. Three rye plants with monosomic-substitution wheat chromosomes 2A, 5A, 7A, and 7B, two plants with chromosomes 1A and 3B, four plants with chromosome 5B and one plant with chromosome 6A were analysed. In each plant, chromosome pairing at metaphase I was investigated in 50 PMCs, i.e., in 150, 100, 200 and 50 cells, respectively. The number of terminal chiasmata per chromosome was calculated, assuming that ring bivalents have two terminal chiasmata, rod has one and univalents have none, while ring trivalents have three, chain and “frying pan” have two; ring and “8” quadrivalents have five; chain, cross and “OK” quadrivalents have three; while ring and chain pentavalents and hexavalents have five and four, and six and five terminal chiasmata, respectively.
Results and discussion

The frequency of univalents of four of the wheat chromosomes of genome A – 6A, 5A, 7A and 2A – was very low and its mean value per PMC ranged from 0 for 6A, to 0.04 for 2A. The frequency of 1A chromosome was considerably higher and amounted on average to 0.73 univalent per PMC. Among chromosomes of genome B, the lowest frequency of univalents, 0.53 per PMC, was recorded for chromosome 5B (Table 1).

Monosomic-substitution wheat chromosomes – 1A, 2A, 5A, 6A, 7A and 5B – pairing with rye homoeologues, usually formed open configurations: rod bivalents (Figure 1a, b), on average from 0.18 (1A) to 0.70 (6A) per PMC, and chain quadrivalents (Figure 2b) (chain quadrivalents were formed also with 3B), on average from 0.02 (3B) to 0.27 (2A) per PMC. Only rarely wheat chromosomes paired with rye homoeologues in ring bivalents (Figure 2a), on average from 0 (1A) to 0.13 (2A) per PMC. Five monosomic wheat chromosomes – 7A, 6A, 5B, 5A, 2A – occurred in ring quadrivalents with mean frequencies from 0.01 (7A) to 0.07 (2A). Monosomic chromosomes of the A genome and the monosomic 5B chromosome occurred in chain trivalents with mean frequencies from 0.01 (5A and 5B) to 0.09 (7A). Two monosomic chromosomes 1A and 2A occurred in ring trivalents, and one monosomic 5B chromosome in “frying pan” trivalent.

NARANJO and FERNANDEZ-RUEDA (1996) showed that in wheat-rye hybrids with genome constitution ABDR, in the presence of \( \text{Ph1b} \) allelic gene, wheat chromosomes 1A, 2A, 5A and 5B paired with rye homoeologues. However, those authors did not notice any pairing of wheat chromosomes 6A, 7A with rye homoeologues. In the present study, in monosomic-substitution tetraploid rye plants with 6A and 7A chromosomes, 100% pairing of chromosome 6A and 0.98% of chromosome 7A with rye homoeologues per PMC was observed. Exceptionally numerous translocations with the arms of 6A and 7A chromosomes in the progeny of plants with these monosomic chromosomes are the proof of pairing of chromosomes 6A and 7A (APOLINARSKA 1998). In the present study, in monosomic-substitution 4x rye plants, 1A-1R chromosomes paired with the lowest frequency (0.23) in comparison to the remaining chromosomes of the A genome. Chromosomes 5A-5R and 2A-2R paired with frequencies 0.99 and 0.96 per PMC, respectively. The homoeologous pairing 1A-1R and 5A-5R was observed also in wheat-rye hybrids (ABDR) with 5B and 3D deficiency (NARANJO et al. 1987), as well as 1AL-1RL in the hybrids with allelic genes \( \text{ph1b} \) and \( \text{ph2b} \) and with 5B deficiency (NARANJO et al. 1989).

The exceptionally high homoeologous wheat-rye pairing in the tetraploid rye with monosomic-substitution wheat chromosomes 1A, 2A, 5A, 6A, 7A, may indicate the presence of strong promoter allele(s) of homoeologous genomes A-R
Table 1. Pairing frequency (mean number per cell) in monosomic-substitution tetraploid rye

<table>
<thead>
<tr>
<th>Wheat chromosome</th>
<th>Wheat I</th>
<th>Rye</th>
<th>Wheat-rye chromosomes</th>
<th>Rye chromosomes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>II</td>
<td>III</td>
</tr>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>1A</td>
<td>0.73</td>
<td>1.27</td>
<td>0.18</td>
<td>0</td>
</tr>
<tr>
<td>2A</td>
<td>0.04</td>
<td>0.20</td>
<td>0.39</td>
<td>0.13</td>
</tr>
<tr>
<td>5A</td>
<td>0.01</td>
<td>0.07</td>
<td>0.65</td>
<td>0.11</td>
</tr>
<tr>
<td>6A</td>
<td>0</td>
<td>0.54</td>
<td>0.70</td>
<td>0.12</td>
</tr>
<tr>
<td>7A</td>
<td>0.02</td>
<td>0.58</td>
<td>0.58</td>
<td>0.07</td>
</tr>
<tr>
<td>3B</td>
<td>0.53</td>
<td>0.34</td>
<td>0.26</td>
<td>0.03</td>
</tr>
<tr>
<td>7B</td>
<td>0.99</td>
<td>1.41</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

*a* = rod, *b* = ring, *c* = frying pan

Table 2. Frequency (mean number per cell) of different multivalents in monosomic-substitution tetraploid rye

<table>
<thead>
<tr>
<th>Wheat chromosome</th>
<th>Trivalent</th>
<th>Quadrivalent</th>
<th>Pentavalent</th>
<th>Hexavalent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>chain</td>
<td>ring</td>
<td>frying-pan</td>
<td></td>
</tr>
<tr>
<td></td>
<td>chain</td>
<td>OK</td>
<td>cross</td>
<td>closed config.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1A</td>
<td>0.28</td>
<td>0.02</td>
<td>0.07</td>
<td>0.47</td>
</tr>
<tr>
<td>2A</td>
<td>0.09</td>
<td>0.02</td>
<td>0.02</td>
<td>0.37</td>
</tr>
<tr>
<td>5A</td>
<td>0.03</td>
<td>0.01</td>
<td>0.05</td>
<td>0.38</td>
</tr>
<tr>
<td>6A</td>
<td>0.34</td>
<td>0.04</td>
<td>0.20</td>
<td>0.52</td>
</tr>
<tr>
<td>7A</td>
<td>0.24</td>
<td>0.01</td>
<td>0.09</td>
<td>0.90</td>
</tr>
<tr>
<td>3B</td>
<td>0.50</td>
<td>0.01</td>
<td>0.15</td>
<td>1.16</td>
</tr>
<tr>
<td>5B</td>
<td>0.29</td>
<td>0.10</td>
<td>0.05</td>
<td>0.25</td>
</tr>
<tr>
<td>7B</td>
<td>0.39</td>
<td>0</td>
<td>0.05</td>
<td>1.34</td>
</tr>
</tbody>
</table>

*a* = rod, *b* = ring, *c* = frying pan
pairing in rye. The pairing of 5B-5R chromosomes was observed in 47% of analysed PMCs, which indicates that the rye genomes are blocking the activity of the \textit{Ph1} suppressor gene. Rye genomes break-down suppression of homoeologous pairing genetically controlled by 5BL. Analysis of homoeologous pairing of monosomic wheat chromosomes with rye suggests that the rye genomes in substitution plants of tetraploid rye are acting as promoters of homoeologous pairing between chromosomes of wheat genome A and rye, but considerably less intensive in the case of genome B. LELLEY (1976) suggested

Figure 1. Chromosome pairing at metaphase I in monosomic-substitution tetraploid rye. (a) Monosomic of wheat 7A pairing in rod bivalent, two rod bivalents, eleven ring bivalents. (b) Monosomic of wheat 5B pairing in rod bivalent, two rod bivalents, six ring bivalents, one ring trivalent, one “frying-pan” trivalent, one ring quadrivalent.
that in rye there is a system that suppresses the activity of the \textit{Ph} locus, consisting of more than two alleles which may act additively, may be located on different chromosomes and may differ in number in the same genotype. GUPTA and FEDAK (1986) stated the presence of a polygenic system in rye, controlling homoeologous chromosome pairing. Those authors suggested that varieties of rye may carry genes or gene systems with both major and minor effects. MILLER

Figure 2. Chromosome pairing at metaphase I in monosomic-substitution tetraploid rye. (a) Monosomic of wheat 7A pairing in ring bivalent, two rod bivalents, eleven ring bivalents. (b) Monosomic of wheat 5A pairing in chain quadrivalent, one rod bivalent, ten ring bivalents.
and Riley (1972) assumed that an increase in the rye dosage in wheat-rye combinations increases the probability of homoeologous pairing. The maximum probability of incorporating rye segments in wheat breeding programmes will arise when the wheat genome is in a low dosage and the rye genome is in a high dosage. On the basis of frequency of monosomic wheat chromosomes with rye homoeologous pairing, as well as numerous and differentiated wheat-rye translocations in 4x rye, observed by Apolinarska (1998), it may be concluded that the introducing of wheat chromosome fragments into the rye genome is the easiest when single wheat chromosomes are present, and the rye genome exists in high doses. It is probably because exceptionally strong alleles for homoeologous pairing exist in rye (Lelley 1976).

The influence of wheat chromosomes on frequency of rye univalents in tetraploid rye was observed in this study. The low frequency of rye univalents occurred in the presence of four monosomic chromosomes of genome A and one chromosome of genome B. The lowest frequency of univalents was observed in the presence of chromosome 5A, on average 0.07 per PMC and next in the increasing frequency: 2A (0.20); 5B (0.34); 6A (0.54); 7A (0.58). Three chromosomes – 1A, 3B and 7B – increased considerably the frequency of rye univalents: in the presence of chromosome 1A, the mean frequency of univalents amounted to 1.27, while for 3B and 7B, it reached 1.34 and 1.41 per PMC, respectively. The monosomic wheat chromosomes in rye genomes influenced chromosome pairing, as well as the frequency of ring and rod bivalents and tri- and quadrivalents. The activity of the diploidizing system of chromosomes 5B, shown by Riley and Chapmann (1958), was observed in the studied tetraploid rye. The highest frequency of bivalents occurred in the presence of 5B monosomic, on average 10.04 per PMC, from which 8.59 were ring bivalents. The next, according to their influence on frequency of ring bivalents, were chromosomes 5A and 2A. Chromosomes 3B and 7B essentially lowered the frequency of ring bivalents and closed quadrivalents: ring and “8”-shaped (Table 2).

The influence of eight different wheat monosomic chromosomes on chromosome pairing in tetraploid rye is particularly visible in the number of terminal chiasmata per chromosome. The highest numbers of terminal chiasmata were recorded in plants with monosomic chromosome 5A (1.90) and 2A (1.85), and the lowest in those with 3B (1.52) and 7B (1.43). These results indicate that chromosomes 5A and 2A have a positive influence on chromosome pairing in tetraploid rye. The results confirm earlier conclusions of Dworak (1976), Cuadrado et al. (1991) and Ceoloni et al. (1986), that short arms of both monosomic chromosomes 5A (Dworak 1976, Cuadrado et al. 1991) and 2A (Ceoloni et al. 1986) contain the promoter of homoeologous pairing. The promoting effect was also shown by chromosome 5BS (Riley, Chapman 1967, Dworak 1976, Cuadrado et al. 1991). Cuadrado et al. (1991) indicated that the promoter on 5BS is stronger than the 5AS promoter. The data presented in this paper suggest that from three chromosomes of genome B, chromosome 5B
has the strongest influence on the number of terminal chiasmata per chromosome, which is considerably lower than for chromosomes 5A and 2A. Slightly higher numbers of terminal chiasmata per chromosome were recorded also in plants with 7A monosomic substitution, but no information on promoter gene localized on this chromosome was found in the literature. On the other hand, DRISCOLL (1972) reports that no chromosome of the seventh group is able to influence the level of homoeologous pairing.

The results obtained for monosomic substitution with chromosome 1A differ considerably from those with remaining A chromosomes and are more similar to the results obtained for plants with B genome chromosomes: 3B and 7B. The plants with chromosome 1A have the lowest number of chiasmata per chromosome, in comparison to the remaining A chromosomes. Chromosome 1A appears with a high frequency as univalents, causing a considerable increase in the frequency of rye univalents and, simultaneously, of rod bivalents. On the basis of the obtained results it can be concluded that this chromosome influences considerably the lowering of chromosome pairing in 4x rye. Similarly, in 4x Secaloitricum APOLINARSKA (2003) observed the highest mean frequency of univalents and rod bivalents in plants with chromosome 1A. Probably in the analysed material chromosome 1A has a small translocation with chromosomes of the B genome, which has not been detected by differential staining and which could be the cause of the lower pairing level (ŁAPINSKI, SCHWARZACHER 1998). The lowering of pairing level may be caused by the gene localized on the 1A chromosome, whose action was observed on the tetraploid level: 4x rye and 4x Secaloitricum. Until now the meiotic instability in triticale was connected only with the short arm of 1B chromosome (DARVEY, LARTER 1973, THOMAS, KALTSIKES, after GUSTAFSON 1976).

The analysis of homoeologous wheat-rye chromosome pairing in monosomic-substitution 4x rye showed that the wheat A genome is closer related to rye genome R, than to the wheat B genome. The above conclusions do not confirm the opinion of NARANJO and FERNÁNDEZ-RIUDA (1996), as their results showed a closer relation of B-R genomes than of A-R and D-R genomes.

Conclusions

Rye genomes are acting as promoters of homoeologous pairing between chromosomes of wheat genome A and rye. Homoeologous pairing of 5B-5R chromosomes indicated that in the rye genomes there exists a system that suppresses the activity of the Ph1 gene. The diploidizing system of chromosome 5B is also active in tetraploid rye.

From the breeder’s point of view, the results of the present study are of special interest. The high frequency of wheat-rye chromosome pairing indicates that in-
corporating wheat segments into rye chromosomes in tetraploid rye with substitution wheat chromosomes is possible.

REFERENCES


