

Transfer of chromosomes of the A and B genomes of wheat to tetraploid rye

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Abstract. Tetraploid rye was crossed with different tetraploid triticale lines. The F₁ generation of tetraploid rye × tetraploid triticale hybrids was backcrossed with 4x rye. After backcrossing, all BC₁-F₁ plants were subjected to open pollination, whereas in the BC₁-F₂ generations only plants with wheat chromosomes in their karyotypes were open-pollinated. Substitution, addition and addition-substitution lines of wheat chromosomes in tetraploid rye were isolated from the F₂ and F₃ of BC₁. In 60 plants of BC₁-F₂, 59 chromosomes from the A genome and 9 from the B genome of wheat were recovered. The wheat chromosomes were monosomic except for five plants which were disomic, viz. 1A and 5A in two plants each, and a translocated 3AS/5AL in one plant. In 235 BC₁-F₃ plants, 174 wheat addition and substitution chromosomes were found, 143 from the A genome and 31 from the B genome. All wheat chromosomes except 3A from the A genome and four chromosomes from the B genome – 2B, 3B, 5B and 7B were recovered. The number of substitutions ranged from one to four per plant, only two plants having four. In the group of addition plants the number of added wheat chromosomes ranged from one to two, and in the case of addition-substitution plants – from two to four. Wheat chromosomes occurred in monosomic form, except 10 plants. Six substitution plants were disomic for 1A, 2A, 5A, 7A, 2B and 3B, respectively. One was disomic for 1A and 5A in two addition plants. Two addition-substitution plants were double disomic: 1A and 5A – in one, and 1A and 3B in the other. In the BC₁-F₃ generation, 23 different translocations were found, four of which occurred between wheat chromosomes and the remaining 19 – between wheat and rye chromosomes. Translocated chromosomes were monosomic, except four plants. Two of them were disomic for 3AS/4RL, one for 4AS/4RS and one for 7AS/7RS. The fertility of both addition and substitution plants ranged from 0 to 38.0 seeds/spike, regardless of the chromosome number, with a mean of 9.61 seeds/spike. Plants with 28 chromosomes showed significantly higher fertility than plants with 29 and more chromosomes, except addition plants with chromosomes 5A and 5B. The analysis of the influence of particular wheat chromosomes on plant fertility showed that both substitution

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and addition plants with chromosome 6A had the highest average fertility, while plants with chromosome 2B in substitution lines as well as plants with chromosome 2A in addition and addition-substitution lines had the lowest fertility.

Key words: addition, substitution, tetraploid rye, tetraploid triticale, translocation, wheat.

Introduction

Rye is one of the most important cereals in Europe. In Poland it is the main cereal crop on account of specific climate and soil conditions (WOLSKI 1994). Its strong root system is little susceptible to water deficiency (WOJCIESKA 1983). Besides, it shows low susceptibility to soil acidification. Rye chromosomes contain genes controlling aluminium tolerance (ANIOŁ, GUSTAFSON 1984) and have many genes conferring resistance to diseases (McINTOSH 1988). As compared to wheat, the nutritive and feeding value of rye, however, is significantly lower: rye grain contains antinutritive compounds inhibiting growth of young animals (RAKOWSKA 1994). To sum up, rye calls for improved quality to meet growing feed demands.

In plant breeding, agronomic, especially quality characteristics, are more and more often improved through alien gene transfer, chiefly from related species. An example may be numerous wheat varieties with incorporated rye chromatin. Rye genes were most frequently transferred into wheat via chromosome translocations (ZELLER, KOLLER 1981, FRIEBE et al. 1990, LUKASZEWSKI 1990). Translocation of the first homoeologous group chromosomes deserves special attention. The short arm of rye chromosome 1R with the genes Lr 26, Sr 31, Yr 9 and Pm 8 confers disease resistance in wheats (McINTOSH 1988). The important translocation 1BL.1RS, conferring resistance to leaf, stem and stripe rusts and powdery mildew in wheat (ZELLER 1973, MARAIS et al. 1994), also transfers high yield potential to this crop (RAJARAM et al. 1983). The combination of both advantageous traits has led to a widespread use of this translocation in breeding programmes (LUKASZEWSKI 1990, GUPTA, SHEPHERD 1992). The 1AL.1RS translocations, also important in breeding programmes, transfer genes responsible for green bug, stem rust and powdery mildew resistance from rye into wheat (SEBESTA, WOOD 1978). Disease resistance was successfully transferred from rye into wheat also through 4A/2R translocation (DRISCOLL, JENSEN 1964, DRISCOLL 1968) and 3A/3R (BARBER et al. 1968). The 2BS/2RL translocation carries a gene or gene complex that conditions antibiosis to Hessian fly larvae (FRIEBE et al. 1990), while 2AL.2RL translocation (SEARS 1972) markedly increases protein content in seeds (MAY, APPELS 1978).

The examples mentioned above show, that many valuable genes of rye were used in qualitative wheat breeding. Wheat, as a crop species characterized by the most profitable qualitative characters may and should be a source of genetic variation of rye. The first work in this field was done by SCHLEGEL (1982). He reported a transfer of genetic wheat material into diploid rye in the form of addition chromosomes. A few addition lines obtained later (SCHLEGEL, KYNAST 1986, 1988, BAUM 1991, MELZ et al. 1991) were characterized by a poor viability, low fertility and instability. As a final consequence of these factors, genetic material of wheat was usually eliminated from rye.

This paper presents an efficient method enabling introduction of genetic wheat material into tetraploid rye, as well as its maintenance and increase in subsequent generations as additions, substitutions and translocations.

Material and methods

Tetraploid rye derived from twin embryos received from S. SULINOWSKI (Institute of Plant Genetics, PAS, Poznań) was pollinated with a mixture of pollen grains of several of stabilized tetraploid triticales with different constitution of wheat chromosomes described previously by LUKASZEWSKI et al. (1984). In the wheat genome of tetraploid triticales, each A and B chromosome was represented. The F_1 generation of tetraploid rye \times tetraploid triticales hybrids was backcrossed to 4x rye (male parent). After backcrossing, all BC_1 - F_1 plants were subjected to open pollination, whereas in the BC_1 - F_2 generations only plants with wheat chromosomes in their karyotypes were open-pollinated. Tetraploid rye without wheat chromosomes was eliminated from further studies. Chromosome constitution was determined in 60 BC_1 - F_2 and 235 BC_1 - F_3 plants using the C-banding method described by LUKASZEWSKI and GUSTAFSON (1983). The C-banding patterns of wheat chromosomes were in agreement with the patterns described previously by LUKASZEWSKI and GUSTAFSON (1983), GILL et al. (1991), FRIEBE and GILL (1994).

Results and discussion

Among the F_2 and F_3 of backcross hybrids of tetraploid rye \times tetraploid triticales with 4x rye the following four groups of plants were distinguished at a tetraploid level: tetraploid rye with substituted wheat chromosomes (substitution lines), tetraploid rye with added wheat chromosomes (addition lines),

tetraploid rye with added and substituted wheat chromosomes (addition-substitution lines). The fourth group of plants was constituted by the maternal form – tetraploid rye.

Table 1. Frequency of rye plants with A and B wheat genome chromosomes in BC₁-F₂ and BC₁-F₃ (4x rye × 4x triticales) × 4x rye hybrids

Wheat chromosome	No. of rye plants with wheat chromosome in generation	
	BC ₁ -F ₂	BC ₁ -F ₃
1A	15	31
2A	1	14
3A	–	–
4A	8	4
5A	16	40
6A	4	3
7A	15	51
Sum	59	143
1B	–	–
2B	1	3
3B	3	10
4B	–	–
5B	–	9
6B	–	–
7B	5	9
Sum	9	31

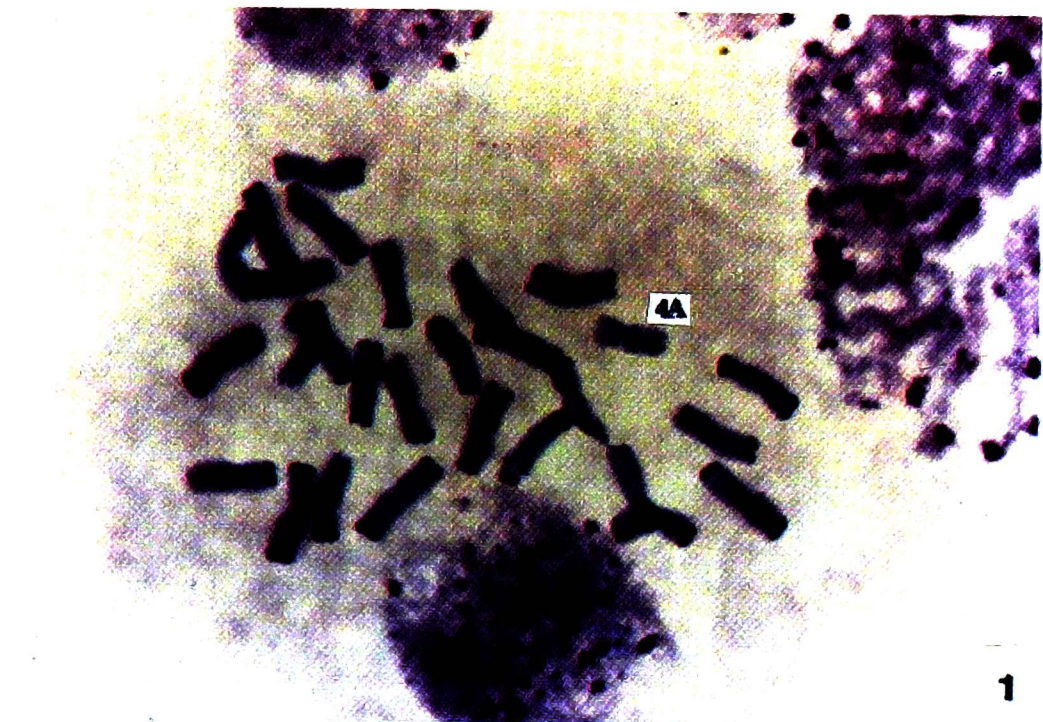
In 28-chromosome substitution hybrids of the BC₁-F₂ generation wheat chromosomes 1A, 4A, 5A, 6A and 7A from the A genome and chromosomes 2B, 3B and 7B from the B genome were found. Only two chromosomes – 1A and 5A – were disomics, chromosome 1A in one plant and chromosome 5A in two plants. The number of substitutions in substitution plants ranged from 1 to 3.

In the rye addition lines the chromosome number ranged from 29 to 31. All the chromosomes from the A genome were represented, except 3A, while only 3B and 7B from the B genome were present. In all addition lines, the chromosomes were monosomic except in two plants: one had a pair of chromosomes 5A, one a pair of translocated chromosomes 3AS/5AL.

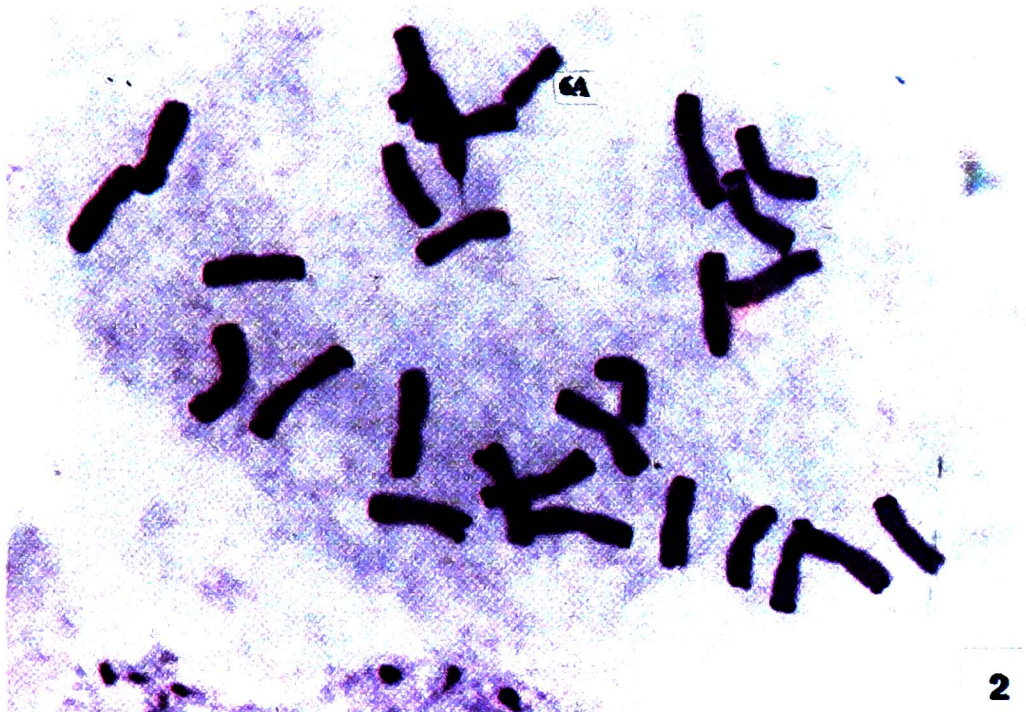
In 29-30-chromosome addition-substitution lines the chromosomes 1A, 4A, 5A, 7A and 7B were found.

In the F₂ of the backcross tetraploid rye × tetraploid triticales with 4x rye the majority of the added and substituted wheat chromosomes was from A genome and only 9 chromosomes were from B genome. All of the wheat chromosomes, except 3A, were from the A genome and only three chromosomes – 2B, 3B and 7B – from B genome (Table 1).

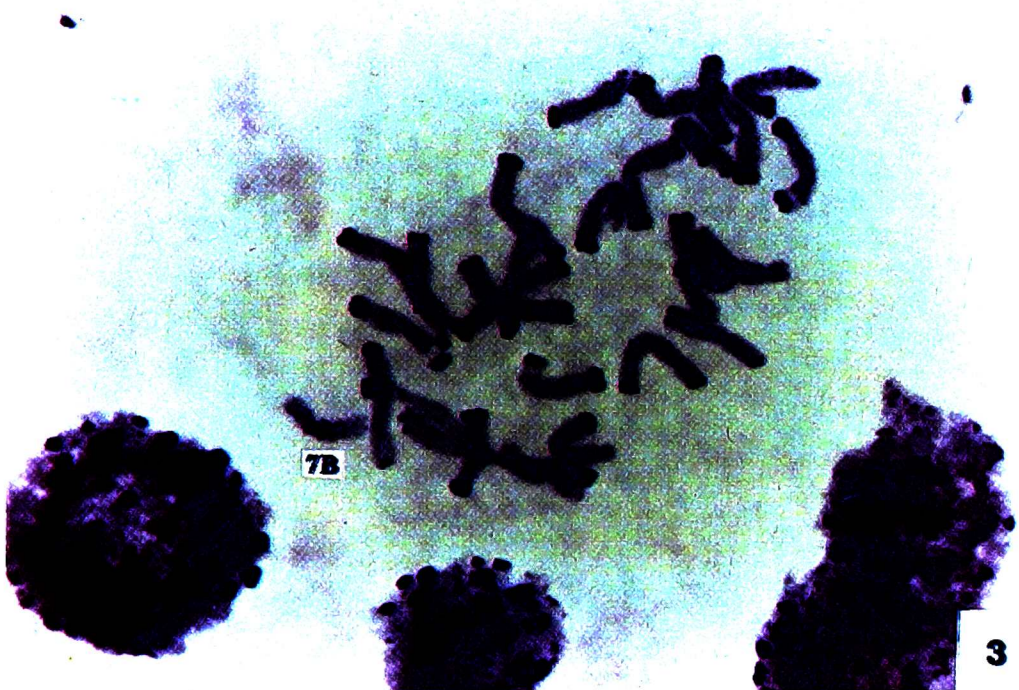
The chromosome number in the F₃ generation varied from 26 to 30. Only in three plants the chromosome number was different, approximating 21 and in two cases – 35 chromosomes. A single 21-chromosome plant had 14 rye chromosomes and 7 wheat chromosomes – 1A, 2A, 3B, 4B, 5B, 6A, 7B. Of two 35-chromosome plants one had 28 rye chromosomes and 7 wheat chromosomes, whereas the other had 21 rye chromosomes and 14 wheat chromosomes.



1

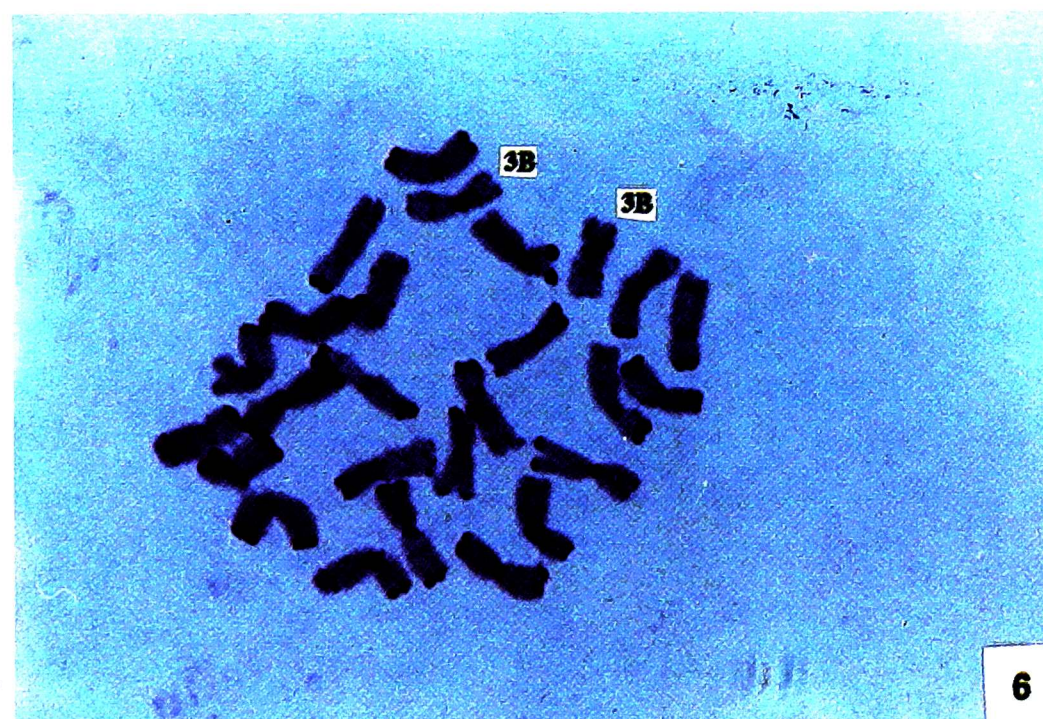
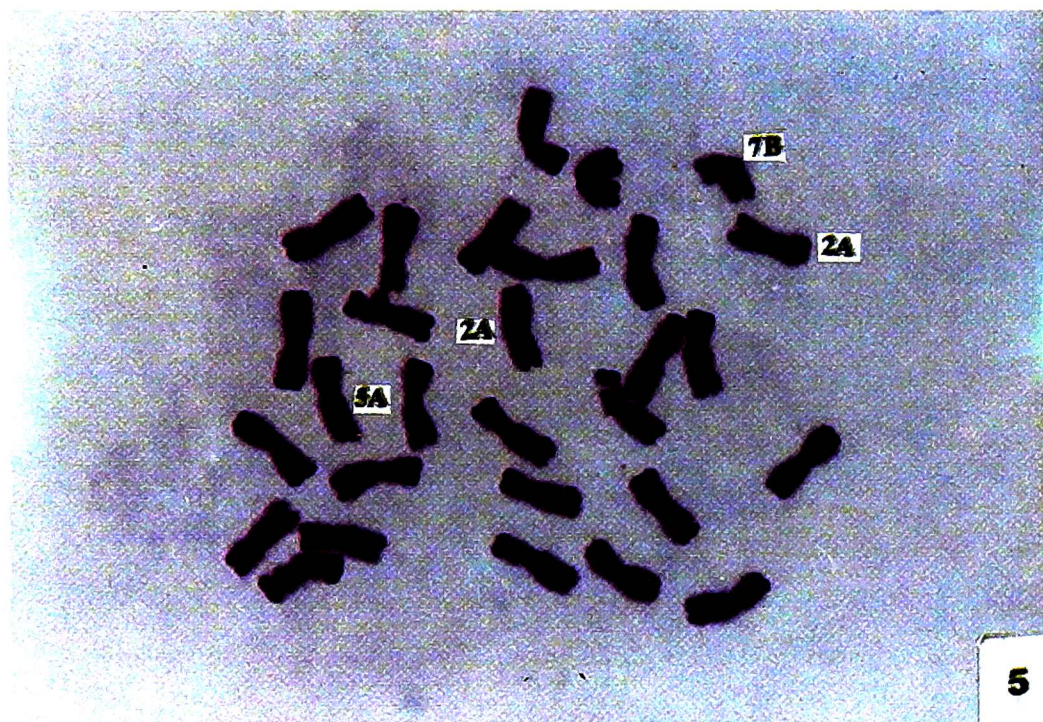
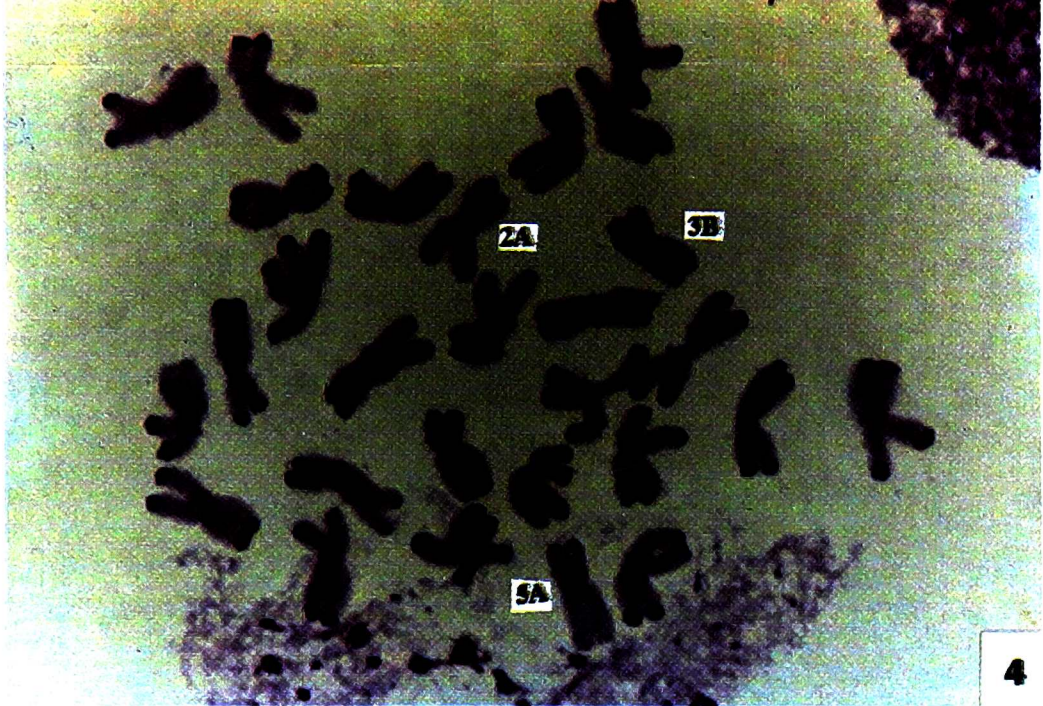


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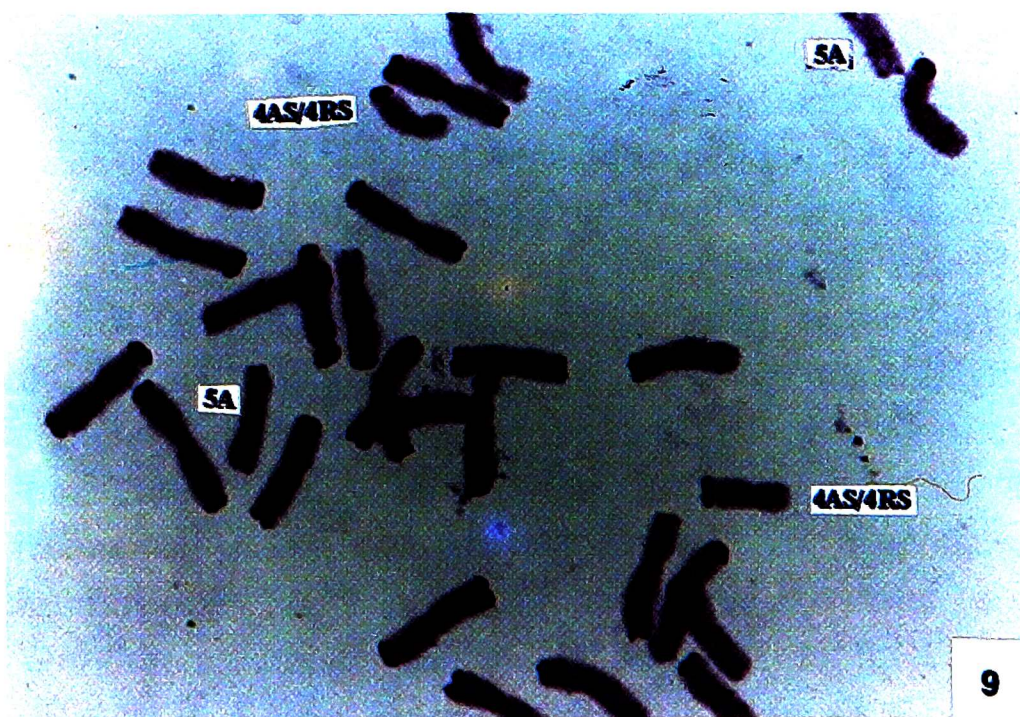
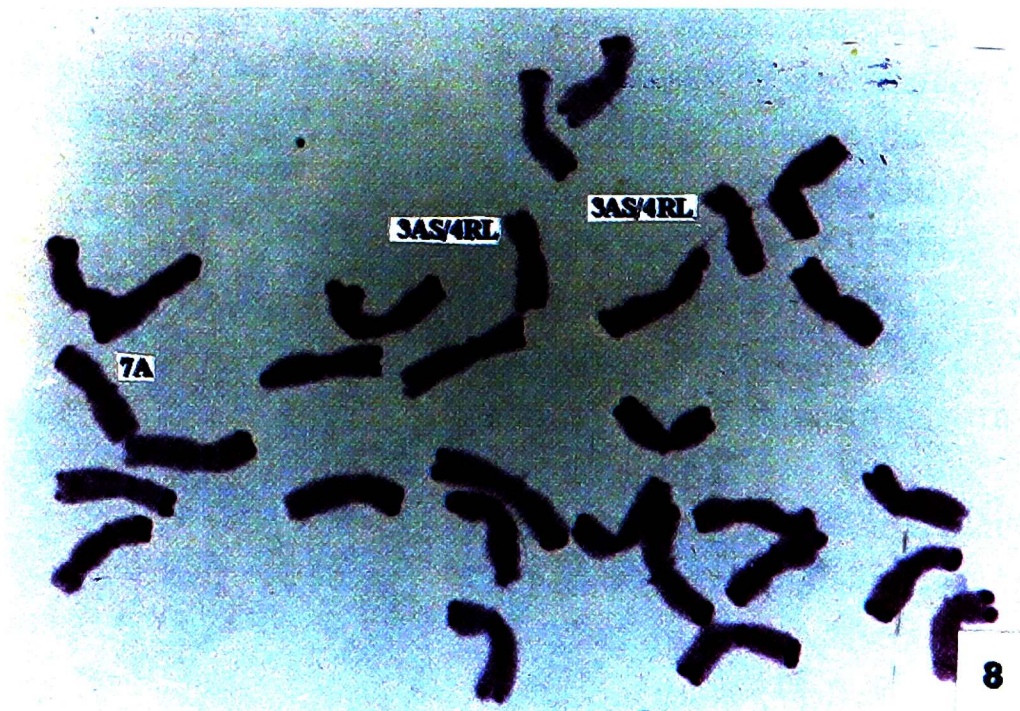


3

Figs. 1-3. Somatic metaphase of rye 4x – Giemsa C-banded chromosomes with one wheat chromosome (designated in the picture)



Figs. 4-6. Somatic metaphase of rye 4x Giemsa C-banded chromosomes with marked wheat chromosomes
 4 – three monosomics, 5 – two monosomics and one disomic, 6 – one disomic (designated in the picture)



Figs. 7-9. Somatic metaphase of rye 4x – Giemsa C-banded chromosomes with marked wheat chromosomes

7 – one translocation between wheat chromosomes, 8 – one monosomic and one disomic with translocation between wheat-rye chromosomes, 9 – one disomic and one disomic with translocation between wheat-rye chromosomes (designated in the picture)

Among the remaining plants the largest group was constituted by 27- and 28-chromosome substitution rye making up 61.2% of the analysed plants. The number of substitutions per plant ranged from one to four per plant, only two plants had four substitutions. (Figs. 1-5).

In the origin of the 21- and 35-chromosome plants different factors may be involved. All plants have tetraploid rye in their pedigree, which was obtained from twin embryos. It may be that predisposition to atypical plant production is dependent on the maternal form, the more so, as triticale with completely altered genome structure – ABRRRR has been obtained from the same cross

Table 2. Number of rye plants (BC_1 - F_3) with wheat chromosomes transferred through pollen of the (4x rye \times 4x triticale) \times 4x rye hybrids

Wheat chromosome	No. of rye plants
1A	10
2A	8
3A	–
4A	3
5A	21
6A	3
7A	24
3B	5
5B	9
7B	1

combination (APOLINARSKA, in press). One of the reason of obtaining plants with different chromosome constitutions and numbers may be disturbances in the second meiotic division during microspore formation (APOLINARSKA 1988) or meiotic restitution. At this stage of studies it is hard to establish unambiguously the reason of obtaining different chromosome combinations in 21- and 35-chromosome plants.

In the group of addition plants the number of wheat chromosomes ranged from 1 to 2, while in the case of addition-substitution plants – from 2 to 4. In the progeny of substitution and addition rye, wheat chromosomes were eliminated in 21.5% of the offspring. It was simultaneously found that the range of addition and substitution wheat chromosomes in the BC_1 - F_3 generation extended in com-

parison to that of the BC_1 - F_2 generation. This indicates that wheat chromosomes in addition and substitution lines of 4x rye are transmitted also from the paternal gametes. Chromosomes of the A genome are significantly more frequently transmitted through pollen than chromosomes of the B genome. The most frequently transmitted was chromosome 7A from the A genome and next chromosomes 5A, 1A, 2A, 6A and 4A in the order of decreasing frequency. Only three chromosomes 5B, 3B and 7B from the B genome were transmitted (Table 2). Transmission of additional wheat chromosome through pollen also took place in diploid addition rye. SCHLEGEL, KYNAST (1988)

found that the wheat chromosome 6B was transmitted through the pollen in 8.5% of the plants.

It was found that the examined 235 F₃ plants, the progeny of substitution, addition and addition-substitution tetraploid rye, had 174 wheat chromosomes, 143 of which were from the A genome and 31 – from the B genome. The most frequent A genome chromosome was 7A, followed by 5A, 1A, 2A, 4A and 6A in the order of decreasing frequency, whereas 3B was the most frequent from B genome. Two chromosomes 5B and 7B occurred with an equal frequency, and 2B only in three plants (Table 1). No wheat chromosomes 3A, 1B, 4B and 6B were observed, although they were present in tetraploid triticale.

In the first wheat-cytoplasmic addition lines of diploid rye obtained by SCHLEGEL (1982) from hybrids of tetraploid triticale with diploid rye there occurred six wheat chromosomes, three of which were from A genome (3A, 4A, 7A), two – from B genome (5B, 6B) and one was from D genome (2D) (SCHLEGEL, KYNAST 1986). THIELE et al. (1988) using LAP-isozyme system, found only 6B of the possible seven different available additions in rye-cytoplasmic rye-wheat addition line. BAUM (1991) through self-pollination of 21-chromosome hybrids of tetraploid triticale with diploid rye and through in vitro culture of hybrid embryos, after somatic propagation obtained monosomic and double monosomic rye-wheat addition lines – plants with one-, two- and four-wheat chromosome additions. Added chromosomes were wheat monosomics: four – 1A, 2A, 4A, 7A from A genome, and four – 3B, 4B, 5B, 6B from B genome (BAUM 1991). MELZ et al. (1991) obtained rye-wheat additions with seven wheat chromosomes – 1A, 2A, 3B, 4B, 5B, 6B, 7A and 4BL. Among wheat monosomics in all addition lines of diploid rye the most frequent was the chromosome 6B (SCHLEGEL, KYNAST 1986, THIELE et al. 1988, BAUM 1991, MELZ et al. 1991). However, the present study did not confirm this chromosome, although it was present in tetraploid triticale.

Wheat chromosomes in substitution and addition lines of 4x rye (BC₁-F₃) were monosomic except ten plants. A single disomic of the chromosomes 1A, 2A, 5A, 7A 2B and 3B (Fig. 6) occurred in six different substitution plants, whereas disomics of the chromosomes 1A and 5A occurred in the addition plants. In two 30-chromosome addition-substitution plants there occurred double disomics: 1A and 5A – in one and 1A and 3B – in another.

Chromosome translocations also occurred in the studied material. Three different translocations were found in eight BC₁-F₂ plants. Two translocations occurred between wheat chromosomes 3AS/5AL, 3AS/5BL, and one – between rye and wheat chromosome – 7AS/7RL. In the examined 235 substitution and addition BC₁-F₃ plants 23 different translocations were found : 22 of them

covered the whole chromosome arms, four occurred between wheat chromosomes (Fig. 7), while the remaining ones occurred between wheat and rye chromosomes (Table 3, Figs. 8-9). Translocations occurred between both homoeologous and nonhomologous chromosomes. It seems highly probable that most of the translocations described here resulted from misdivision of univalents of meiosis and subsequent random fusion of telocentric chromosomes

Table 3. Frequencies of translocations in the substitution and addition lines of BC₁-F₃ hybrids of tetraploid rye × tetraploid triticale with tetraploid rye

Translocation wheat/wheat	No. of plants	Translocation wheat/rye	No. of plants
3AS/5AL	6	1AS/RS	3
3AS/5BL	2	1AS/1RL	1
3BS/5AL	1	1AL/1RL	2
6AL/7AS	2	2AS/2RL	3
		2AS/4RL	1
		2AL/R	1
		3AS/4RL	4
		4AS/4RS	2
		4AL/4RS	2
		4AL/R	1
		5AS/4RL	1
		5AS/5RL	1
		5AS/R	3
		5AL/2RL	1
		5AL/5RS	1
		5AL/R	1
		5BL/4RL	1
		6B.6R	1
7AS/7RL	9		

(i.e. centric break fusion).

A similar type of translocation was obtained by LUKASZEWSKI and GUSTAFSON (1983) in populations of triticale-wheat hybrids. The influence of homoeologous and nonhomologous chromosome pairing on the formation of translocated chromosomes cannot be discounted. The lack of the chromosome 5B with the homoeologous pairing suppression gene (RILEY, CHAPMAN 1958) as well as an increase of rye genome dosages in relation to wheat (MILLER, RILEY 1972, RILEY et al. 1973, LELLEY 1975) and the fact that chromosome 5R is a suppressor of Ph wheat genes (BIELIG, DRISCOLL 1970, RILEY et al. 1973) may break down homoeologous pairing suppression in substitution

and addition lines of 4x rye and as a final effect – the occurrence of translocations between different chromosomes, including rye and wheat chromosomes. It seems that these factors will cause translocation increase in the next generations, what is indicated by a large difference in the number and diversity of translocations between BC₁-F₂ and BC₁-F₃ generations. Translocated chromosomes were monosomics, except four plants. Two of them were disomic for 3AS/5RL (Fig. 8), one for 4AS/4RS (Fig. 9) and one for 7AS/7RS.

Visible intercalary bands near the centromere in one plant gave some indications that there occurred a pair of chromosomes 6R translocated with the chromosome 6B. Chromosome 6R is a carrier of dominant gene (Anu) or genes conditioning antinutritive properties of rye (THIELE et al. 1989). In this connection, translocation of 6B.6R chromosomes is particularly interesting, since it can contribute to elimination of undesirable, antinutritive rye genes. Two types of translocations of the 6R rye chromosome with an amount of the 6B wheat chromosome were also obtained by SCHLEGEL and KYNAST (1986), but that was accomplished in 14-chromosome plants of rye, in the progeny of additions lines, premeiotic spikes of which were subjected to X-rays.

An equally interesting rye chromosome translocation was obtained by MELZ and THIELE (1990). Genetic wheat material consisting of small fragments of the chromosome 3B with two genes *Rpml* and *Got-B3* was introduced into the rye cv. Esto through a somatic, spontaneous translocation. Translocation of chromosome 3R was invisible in the chromosome morphology, and only the isozyme analysis indicated of the presence of wheat genes.

Plants of the F₂ backcross hybrids of tetraploid rye × tetraploid triticales with 4x rye, which were found to have substitution wheat chromosomes, showed considerably weaker growth in comparison with the maternal form and headed 1-2 months later. In the next generation, the substitution and addition plants of tetraploid rye did not deviate from 4x rye in the growth rate and heading date. It may be suggested that these plants have already incorporated genetically alien material in their chromosome constitutions. Fertility of both addition and substitution plants was very variable on account of the chromosome number and ranged from 0 to 38 seeds/spike with a mean of 9.61 seeds/spike. Fertility of addition lines of diploid rye obtained by BAUM (1991) and MELZ et al. (1991) was somewhat different. The monosomic additions of diploid rye (BAUM 1991, MELZ et al. 1991) also showed various degrees of fertility. Most of double monosomics (BAUM 1991), however, were sterile or not viable. Two plants with four additions of wheat chromosomes died at the seedling stage.

Wheat-cytoplasmic lines of diploid rye obtained by SCHLEGEL and KYNAST (1986) were characterized by weak growth and low fertility. The low fertility was slightly increased by subsequent backcrosses accompanied by a decrease in the number of wheat chromosomes.

When comparing the fertility of substitution plants with that of addition and addition-substitution plants, it was found that 28-chromosome plants show significantly higher fertility than plants with 29 and more chromosomes, except

plants with 5A and 5B chromosomes (Table 4). Chromosomes of the fifth homoeologous group of wheat apparently decrease the fertility of substitution tetraploid rye in plants, which were found to have three 5R chromosomes and one wheat chromosome in the fifth homoeologous group.

Chromosome pairing of rye is controlled polygenically (LELLEY 1975). Wheat chromosomes of the fifth group, particularly 5B chromosome with Ph gene (RILEY, CHAPMAN 1958), probably effected a decrease in the level of chromosome pairing in substitution plants. There probably occurred unival-

Table 4. Influence of wheat chromosomes on the fertility (seed no. per spike) of substitution and addition lines of tetraploid rye

Chromosome	Seed no. / spike	
	substitution lines $2n = 28$	addition lines $2n = 29$ and more
1A	11.74	8.09
2A	6.46	5.00
4A	18.33	13.50
5A	8.68	9.88
6A	22.00	17.67
7A	10.50	6.00
2B	4.53	—
3B	12.07	9.64
5B	5.30	11.38
7B	9.44	8.08

ents and as a final effect the fertility was decreased. SCHLEGEL et al. (1991) experimentally proved that the monotelodisomic 5B with the dominant Ph allele affected homoeologous chromosome pairing in the addition line of diploid rye, caused an increase in the number of univalents and simple bivalents and thus decreased the level of chromosome pairing (reduced chiasma frequency). In addition and addition-substitution plants the activity of additional 5A chromosome and especially that of 5B chromosome, is likely to be significantly limited by the action of four rye 5R chromosomes. As shown by RILEY et al. (1973), short arm of the rye chromosome 5R, namely, is a promotor of homoeologous chromosome pairing in a wheat background.

When analysing the influence of particular wheat chromosomes on plant fertility (Table 4) it was found that both substitution and addition plants with chromosome 6A have the highest average fertility, while plants with chromosome 2B in substitution lines as well as plants with chromosome 2A in addition and addition-substitution lines have the lowest fertility. It may be inferred that chromosome 6A interacts the best with rye gene and probably contributes the least to irregularities in meiotic divisions, due to which the fertility of plants with this chromosome is the best. According to PIECH and SUPRYN (1979) chromosome 6A is especially important, since it prevents seeds from losing their viability in wheat.

The obtained results indicate that crossing of tetraploid rye × tetraploid triticale to 4x rye is an effective method of extending variation of tetraploid rye. Genetic material of wheat has been transferred into rye genomes in the form of numerous substitutions, additions and translocations. Particularly interesting is the fact that the number of rye lines with wheat chromosomes increases from generation to generation with a simultaneous maintenance of plant fertility. In future investigations the influence of wheat chromosomes, especially chromosome 5B with the Ph gene, on chromosome pairing in meiosis of substitution and addition rye lines will be studied.

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