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Translocations and Modifications of Chromosomes in Triticale × Wheat Hybrids*

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Summary. Several generations of four triticale × wheat populations were cytologically analyzed on a plant-by-plant basis using C-banding. Among 785 karyotyped plants, 195 wheat/rye and 64 rye/rye translocated chromosomes were found, as well as 15 rye chromosomes that were modified by deletion or amplification of telomeric heterochromatin. Most of the translocations involved complete chromosome arms; only a few involved smaller segments of chromosomes. Out of 39 identified wheat/rye translocations, 10 occurred between homoeologous and 29 between non-homoeologous chromosomes, five involved A-genome chromosomes, six B-genome chromosomes and the remaining 28 involved D-genome chromosomes. The study indicated that wheat/rye translocations can be produced in sufficient numbers to allow the use of this method for the introduction of alien variation into wheat research programs. Changes in the C-banding technique used are discussed in detail.

Key words: Wheat/rye translocations – C-banding

Introduction

Chromosome translocations between wheat (*Triticum aestivum* L. em. Thell.) and various other species are of interest in wheat breeding and cytogenetic research programs. Wild and cultivated relatives of wheat offer vast germplasm pools for various agronomic and quality characteristics and for resistance and tolerance to pests, diseases and adverse environmental conditions. Generally the transfer of desirable genes into a wheat background has not been an easy process and requires a large input of labor and resources with mixed results (Sears 1972). Amphiploids between wheat and alien species do not necessarily combine the best characteristics of the parents involved, and only triticale (× *Triticosecale* Wittmack), after a great deal of effort, is beginning to compete as a commercial cereal. Substitutions of alien chromosomes into wheat are generally thought to be of questionable value, because many undesirable characteristics can be transferred into wheat along with the desired genes. However, in recent years it has been demonstrated that a 1B/1R substitution (or a 1B/1R translocation) is present in many European and Brazilian wheats. The 1R chromosome or 1RS arm from rye gave resistance to mildew and yellow rust, and some tolerance to low pH soils (Metting et al. 1973; Zeller 1973; Blüthner and Mettin 1977; S. Rajaram, pers. comm.). Translocation of alien segments or arms seems to be the most promising, because half or more of the chromosome is wheat, and this has been used to transfer genes and chromosome segments from a variety of alien species (Sears 1956, 1967; Knott 1968; Wienhues 1966; Bakshi and Schlehuber 1959; Driscoll and Jensen 1965; Riley and Kimber 1966; Sharma and Knott 1966; Sebesta and Wood 1978; for list of wheat/rye translocations, see Zeller 1981). These transfers generally involved a great deal of cytological work, especially where small segments of an alien chromosome were being introduced, and this has slowed down the wider application of such techniques to research programs.

A previous study on the substitution and transmission of rye chromosomes through the eggs and pollen of triticale × wheat hybrids established that a large number of rye/rye and wheat/rye translocated chromosomes were formed (Lukaszewski et al. 1982 b). Because of the potential of these translocations to triticale and wheat research programs around the world, the populations were increased and re-analyzed in order to identify which wheat and rye chromosomes were involved and the frequency of occurrence.

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Materials and Methods

Triticale × Wheat Populations

Materials analyzed in the present study consisted of the same four triticale × wheat populations described previously (Lukaszewski et al. 1982b) in the following generations:

triticale Mo2355 × *T. aestivum* cv. 'Atlas 66'
triticale DC3 × *T. aestivum* cv. 'Kasper'
generations: F_2, F_3, BC_1 and BC_2 to wheat, and BC_1 to triticale
triticale 'Beagle' × *T. aestivum* cv. 'Alfa'
generations: F_2 and BC_1 to wheat
T. aestivum cv. 'INIA 66' × triticale 94-3
generations: F_3 and BC_1 to wheat.

All backcrosses to wheat were made using *T. aestivum* cv. 'Grana' as the male parent. Only those BC_1 plants that carried rye/rye or wheat/rye translocations (and possibly some normal rye chromosomes) were further backcrossed to wheat.

Half of the F_2 and all BC_1 and BC_2 generations were grown in the greenhouse in Columbia, Missouri; the other half of the F_2 were grown in the field in Poznan, Poland. The F_3 populations of Mo2355 × Atlas 66 and DC3 × Kasper consisted of two groups of plants: 1) derived from greenhouse-grown F_2 of known chromosome constitution, and 2) derived from field-grown F_2 of unknown chromosome constitution. Whenever the chromosome constitution of an F_2 or BC_1 was known, only newly arisen translocations in F_3 or BC_2 were included in the data presented. Only the INIA 66 × 94-3 F_2 and F_3 populations were subjected to selection pressure (for insensitivity to photoperiod) and therefore may not represent maximum variation possible in these populations. The remaining three populations were not subjected to any breeding selection pressure and the analyzed plants were a random sample (25 to 50%) of all plants in the populations.

Karyotypes of Wheat and Rye

A set of 40 ditelo-monotelosomic lines and a double ditelosomic line for chromosome 7D of Chinese Spring developed by E.R. Sears was kindly supplied by Dr. G. Kimber. Karyotypes were constructed from telocentrics which showed the maximum possible banding pattern for the respective arms of a given chromosome, and were matched to a complete chromosome from Chinese Spring (Fig. 1). The karyotypes of the complete chromosomes were selected on the basis of clarity of banding rather than size or arm ratio. Chromosome length, arm ratio and position of C bands on the ideograms (Fig. 1) represent the mean values from measurements of 10 telocentrics for each arm of each chromosome. Solid lines on these ideograms represent bands that were frequently observed, while dotted lines represent bands that were infrequently observed.

The rye karyotype (Fig. 1) is a karyotype of *S. cereale* cv. 'Dankowskie Zlote', which is the rye component of triticales DC3 and 94-3 used in this study. The chromosomes in Fig. 1 were from DC3, while arm ratios and chromosome length in the ideogram were taken from a previous study (Lukaszewski et al. 1982a).

C-banding Technique

The C-banding technique employed in this study was essentially the University of Manitoba technique (Bennett et al. 1977) with the following modifications: Cold water was used as a pretreatment (0–2 °C., 24 h). Aceto-orceine was replaced with 45% acetic acid. Hydrolysis time in 0.2 N HCl was reduced to 1 h. The three-step treatment in ethanol was replaced with a one-step absolute ethanol treatment for 1 h.

All translocations were identified primarily on the basis of their C-banding pattern and by arm length and ratio when necessary. All photographs were taken on high contrast Kodak film (No. 2415) with light-green and light-blue filters, using a Zeiss research microscope with planapochromatic 63 × lens.

Results

Karyotypes of Wheat and Rye

For all telocentric chromosomes, with the exception of those for 6A and 2D, a corresponding complete Chinese Spring chromosome could be identified by banding pattern, arm length and ratios. Chromosomes 1D and 6D had similar banding patterns, especially on the long arm, but could be distinguished by their arm ratios. Chromosome 7D had a distinctive banding pattern, but was not very consistent in showing all the bands. After the identification of 19 chromosomes, all preparations of Chinese Spring ditelo-monotelosomic lines for 6A and 2D were reanalyzed in order to establish which of the complete chromosomes were missing in those preparations. This led to positive identification of the two chromosomes in question. In addition, chromosome 6A as identified here was observed in tetraploid wheats and primary hexaploid triticales, while the 2D chromosome was not. It appeared that telo 6AL had lost part of the distal region, or, at least, the band distal to the centromere was not present. The short arm of chromosome 2D and telo 2DS were similar both in length and in banding pattern (Fig. 1); however, the long arm of the complete 2D was about half the length of the telocentric 2DL and the banding pattern was also different. The banding pattern indicated that the line labeled ditelo-monotelosomic 6AS 6AL might be 6AS 2DL, while the line labeled ditelo-monotelosomic 2DS 2DL might be 2DS 6AL (Fig. 1). However, no other data are available to support that indication.

Due to a distinctive banding pattern, 10 arms of the rye chromosomes were easy to identify (Fig. 1). The remaining 4 arms (2RS, 3RS, 4RS and 5RS) could be identified by their relative length in comparison to other rye chromosomes or arms present in the same cell. The C-banding pattern of the rye component of the triticale Beagle was the same as that of Dankowskie Zlote. The rye chromosomes of Mo2355 showed distinctive differences in that the amount of heterochromatin was about 30% lower than in other rye components, and the most visible reduction in band size was noted in both telomeres of chromosomes of 1R and 3R, and in the 7RS telomere. Chromosome 1R had an additional band adjacent to the telomeric band on 1RL, and chromosome 4R did not have the band present in Dankowskie Zlote located approximately

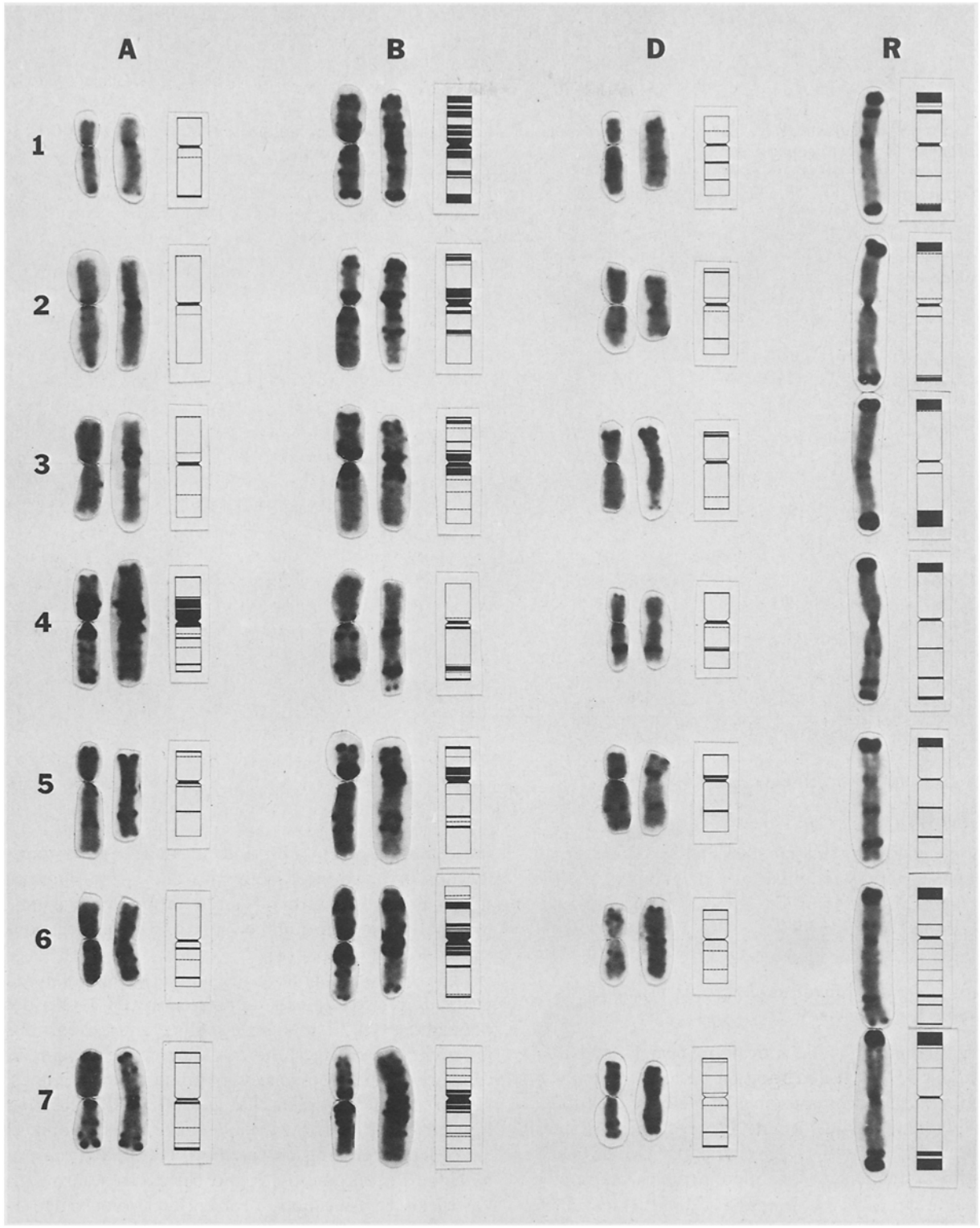

Fig. 1. C-banded karyotype of *T. aestivum* cv. Chinese Spring in columns *1, 2* and *3* and *S. cereale* cv. Dankowskie Zlote in column *4*. Wheat chromosomes on the left in each column are composed from two telocentrics. The middle column contains normal Chinese Spring chromosomes. Solid lines on ideograms represent frequently observed bands; dotted lines rarely observed bands. *A* = A-genome, *B* = B-genome, *D* = D-genome of Chinese Spring, and *R* = rye genome

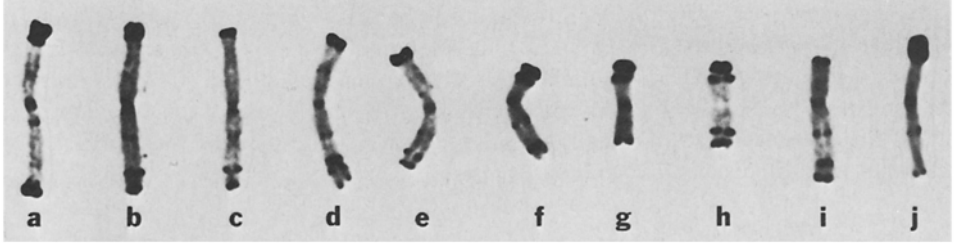

Fig. 2. Examples of rye/rye translocations in triticale × wheat hybrids. *a* 7RL/2RL; *b* 7RS/4RL; *c* 2RL/4RL; *d* 1RL/6RL; *e* 3RL/4RL; *f* 1RS/5RL; *g* 1RS/6RS (deletion of heterochromatin on 6RS); *h* 1RL/1/3 4RL; *i, j* modified 4R chromosomes: *i* deletion, *j* amplification of telomeric heterochromatin. Upper arms are listed first

Table 1. Frequencies of wheat/rye and rye/rye translocations and modifications of rye chromosomes in four triticale × wheat populations

Pedigree/generation	Number of analyzed plants	Number of wheat/rye translocations	Number of rye/rye translocations	Number of modified rye chromosomes
DC3 × Kasper				
F_2	31	7	4	0
F_3	84	23	10	0
F_3 [a]	75	65	18	6
BC_1 to wheat	87	26	6	1
BC_2 to wheat	176	25	6	0
BC_1 to triticale	58	3	2	1
Mo2355 × Atlas66				
F_2	16	2	3	1
F_3	48	20	12	1
F_3 [a]	31	2	0	1
BC_1 to wheat	58	3	0	1
BC_2 to wheat	16	0	0	0
BC_1 to triticale	39	4	1	0
INIA 66 × 94-3				
F_3 [a]	47	11	0	0
BC_1 to wheat	3	0	0	3
Beagle × Alfa				
F_2	2	0	1	0
BC_1 to wheat	14	4	2	0
Total	785	195	64	15

[a] From F_2 plants which were not cytologically anlyzed

4/5 of the length of the long arm (Fig. 2j). However, all the bands generally required for a diagnosis of specific arms were also present on these rye chromosomes (Darvey and Gustafson 1975).

Translocations and Modifications of Chromosomes Within the Rye Genome

Among 308 plants of the triticale × wheat F_2 and BC_1 generations to wheat and triticale, 52 telocentric chromosomes and 2 isochromosomes of rye were identified. This represented 5.2% of all the rye chromosomes present in the plants of those generations. Out of the 52 telocentrics, frequencies for different rye chromosomes involved were 7.7%, 11.5%, 15.4%, 23.1%, 11.4%, 3.8% and 26.9% for 1R through 7R, respectively. The two isochromosomes were for 5RL and 7RL. The frequencies and identities of the telocentric rye chromosomes observed in F_3 and BC_2 generations were not scored.

Among the total of 785 plants analyzed, 64 rye/rye translocations were found, of which 56 were clearly centric break-fusion types (Table 1; Fig. 2a–g). The remaining 8 translocations were noncentric break-fusion types; 7 involved the short arm of chromosome 1R and about ⅓ of the long arm of chromosome 4R distal to the centromere (Fig. 2h), and one unidentified translocation involved most likely 5RS and a small portion of an unidentified arm of a rye chromosome with a terminal band. The number of rye/rye translocations ranged from 0 to 3 per plant.

The differences both in the sample size of analyzed generations (511 plants analyzed in DC3 × Kasper populations vs. 16 in Beagle × Alfa), and genetic differences between lines, did not allow for a meaningful comparison of frequencies of these translocations. However, it did not seem that the rye/rye translocation frequencies varied in the different genetic backgrounds.

Differences were observed in the frequencies of both the rye chromosomes and chromosome arms involved in translocations (Table 2). Chromosome 4R was involved in 33 translocations (4RL being involved in 28 of those) while chromosome 3R was involved in only 7 translocations. As previously stated, this may be partly due to difficulty in the identification of 3RS. On the other hand, chromosome 6R, which exhibited highly diagnostic bands in both arms, was involved in only 13 translocations. It was likely that a substantial number (possibly as high as 30) of the translocations like 3RS/2RL, 2RS/3RL etc. was not reliably identified in the analyzed material because of the similarity of banding patterns.

Table 2. Arm combinations involved in rye/rye translocations from four triticale × wheat populations

		7R		6R		5R		4R		3R		2R	
		S	L	S	L	S	L	S	L	S	L	S	L
1R	S	–	1	1	1	3	1	–	8	–	–	–	1
	L	–	1	–	2	–	–	–	–	–	–	–	–
2R	S	–	–	–	–	2	1	–	–	–	–		
	L	1	–	–	1	1	1	–	4	–	–		
3R	S	–	–	–	–	–	1	–	–				
	L	–	–	1	1	1	2	–	1				
4R	S	1	1	–	–	2	1						
	L	2	9	–	–	2	2						
5R	S	–	–	4	–								
	L	–	–	1	–								
6R	S	–	–										
	L	–	1										

Among the 785 analyzed plants, 13 were found that had one rye chromosome modified by a deletion or amplification of a telomeric heterochromatin band, and one F_3 plant was disomic for amplification of the C-band on 4RS (Table 1; Fig. 2i, j). Deletions of heterochromatin were noted on chromosome arms 1RS, 1RL, 3RS, 4RS, 5RS and 6RS, while amplifications were seen on 1RL, 4RS and 5RS.

Translocations Between Wheat and Rye Chromosomes

In all the material analyzed (785 plants) 195 translocated wheat/rye chromosomes were found (Table 1). Each translocated chromosome was counted as one, regardless of the frequency with which it was found in analyzed populations. Moreover, eight F_3 plants derived from the F_2's that were not analyzed were disomic for one translocation and one was disomic for two translocations. Those ten disomic translocations were included as 20 in the above total which therefore appears inflated. Disomic condition in the F_3 indicates a single translocation occurrence in F_1 meiosis leading to segregation in F_3. However, inheritance in the F_3 of translocations identified in the analyzed F_2 in general did not indicate selection against translocated chromosomes; a chance for any translocation to become eliminated due to segregation was roughly equal to its chance to become disomic (ratio 1 : 2 : 1). Therefore, the total number of 195 translocations seemed to be correct, although it may not have included a full range of possible combinations. The number of translocations per plant ranged from 0 to 5. The average number of translocations per plant was the highest in the DC3 × Kasper populations (0.29) and the lowest in Mo2355 × Atlas 66 (0.15). The F_3 generation of DC3 × Kasper grown in the field had an average of 0.86 translocated chromosomes per plant and grown in the greenhouse 0.24 translocations per plant, while Mo2355 × Atlas 66 F_3 grown in the field had only 0.07 translocations per plant and 0.42 translocations per plant in the greenhouse.

Out of the 195 translocations observed, 188 were centric break-fusion types (Fig. 3a–g). Among the remaining seven, three appeared to have rye heterochromatin attached to the telomeres of chromosomes 4B (Fig. 3r), 1D and 5D, and two were translocations of the long arm of chromosome 1D and a small distal portion of an unidentified rye chromosome (Fig. 3s). In the remaining two cases, long, multicentromere chromosomes were formed: one with 2 centromeres where

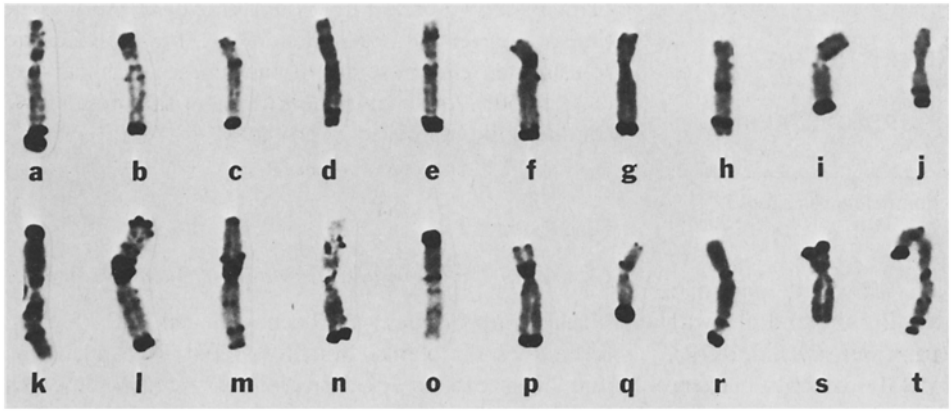

Fig. 3. Examples of wheat/rye translocations in triticale × wheat hybrids. *a* 7DS/7RL; *b* 2DS/2RL; *c* 1DS/1RL; *d* 5DL/4RL; *e* 4DL/7RS; *f* 5DS/2RL; *g* 3DS/2RL; *h* 4DS/5RL; *i* 7DS/4RS; *j* 7DS/1RS; *k* 2RS/2BL; *l* 4AL/2RL; *m* 7BL/4RL; *n* 5BL/3RS; *o* 6RS/5AL; *p* 5BS/3RL; *q* 3AS/6RS; *r* chromosome 4B with big telomeric band; *s* unidentified fragment of rye chromosome/1DL; *t* 4RS/unidentified wheat fragment/4RL-two centromere chromosome. Upper arms are listed first

Table 3. Frequencies of rye arms involved in wheat/rye translocations in four triticale × wheat populations

Pedigree and generation	1R		2R		3R		4R		5R		6R		7R		Σ
	S	L	S	L	S	L	S	L	S	L	S	L	S	L	
DC3 × Kasper															
F_2	1		2	2			1		1						7
F_3	2			5	1	1	2	1	1	6				3	22
F_3	8	10		14	3		3	8		5	5		4	5	65
BC_1 wheat	1	1	3	4	1		5	2	1	1	2		3	2	26
BC_2 wheat	2	2	1	3	1	2	2	1	1	4	2		1	2	24
BC_1 triticale											2			1	3
Mo2355 × Atlas 66															
F_2				1							1				2
F_3		1	1	3	1	5	1				1	1	1	3	18
F_3													1	1	2
BC_1 wheat					1				1						2
BC_1 triticale						2			1		1				4
INIA × 94-3															
F_3				8	1						1		1		11
Beagle × Alfa															
BC_1 wheat					1	1			1	1					4
Total arms	14	14	7	40	10	11	14	12	7	17	15	1	11	17	190
Total chromosomes	28		47		21		26		24		16		28		190

Table 4. A list of identified wheat/rye translocations

Rye chromosome	Chromosome arms involved
1R	1RS/1DS[a], 1RS/7DS, 1RL/1DS[a], 1RL/2DS, 1RL/3DS
2R	2RS/2BL[a], 2RL/4AL, 2RL/2DS[a], 2RL/3DS, 2RL/5DS, 2RL/5DL
3R	3RS/5BL, 3RL/5BS, 3RS/1DS
4R	4RS/1DS, 4RS/2DL, 4RS/3DL, 4RS/4DS[a], 4RS/7DS, 4RL/7BL, 4RL/4DS[a], 4RL/5DL
5R	5RS/5AS[a], 5RS/5DL[a], 5RL/1AS, 5RL/1DS, 5RL/1DL, 5RL/4DS
6R	6RS/3AS, 6RS/5AL, 6RS/1DS, 6RS/2DS, 6RS/6DS[a], 6RL/1BL
7R	7RS/4BL, 7RS/3DL, 7RS/4DL, 7RL/4DS, 7RL/7DS[a]

[a] Translocations occurring within homoelogous groups

the outside arms were 4RS and 4RL with part of a wheat chromosome in the center (Fig. 3 t) and one with 4 centromeres where the rye arms were 2RS and 2RL with an interstitial chain of wheat segments between them. Neither of those two chromosomes was transmitted to the next generation. Frequencies with which different rye chromosomes were involved in translocations with wheat chromosomes ranged from 16 for 6R to 47 for 2R, with 6RL being involved in only one translocation and 2RL in 40 translocations (Table 3).

Among 188 wheat-rye centric break-fusion translocations, 39 different ones were identified (Table 4). Out of those, five occurred between chromosomes of the A and R genomes, six between the B and R genomes (each of the 11 occurred once) and 28 between the D and R genomes (present in different numbers each). Only 10 translocations occurred between homoeologous chromosomes, while 29 were between non-homoeologous chromosomes.

The effect of the wheat/rye translocations on the plant phenotye or fertility is not known at the present time. The female transmission of the monocentric translocated chromosomes in backcrosses to wheat was close to 50%, and maintaining them in the monosomic condition did not pose any problems.

Discussion

C-banding Technique and Chromosome Identification

Marked improvement has been achieved in C-banding techniques for plants, from low reliability and a low rate of success in identification of rye chromosomes (Merker 1974; Bennett 1974; Darvey and Gustafson 1975) to the point where 10 out of 14 arms of rye chromosomes show a highly reliable diagnostic banding pattern allowing for easy identification

(Sybenga 1982). Similar progress has been made in the identification of wheat chromosomes. Compared to earlier studies (Gill and Kimber 1974; Hadlaczky and Pelea 1975; Gustafson and Krolow 1978; and Iordansky et al. 1978), the present technique allows for the identification of 19 out of 21 wheat chromosomes, with the remaining two (1D and 6D) showing similar banding patterns. Although the staining intensity can still vary both between different areas on a single preparation and between different preparations, it no longer presents an identification problem.

At present, the critical steps in the staining procedure for good results appear to be the alcohol treatment, a short time (1–2 days) in a dessicator, the buffer concentration, and the quality of the Leishman stain. Leishman stain from different companies as well as shipments from the same company vary to a certain degree, which can result in some minor variation in staining intensity.

With the present technique the phosphate buffer concentration (at pH 6.8) seems to be one of the most important factors in the procedure. Buffer concentrations of 0.2 M or higher yield C-band patterns that are similar to the patterns obtained with N-banding, where the major bands on nine wheat chromosomes (the B genome, 4A and 7A) allow for easy identification and the remaining chromosomes do not show bands consistent enough for reliable identification (Gerlach 1978; Jewell 1978). As with N-banding, the high buffer concentrations ($\geqq$0.2 M) do not stain rye chromosomes or stain poorly. However, the present C-banding technique seems to show a greater number of bands on the 9 wheat chromosomes vs. N-banding, in addition to bands on other chromosomes which could stem from the fact that it is milder and allows for an easier distinction of areas of different staining intensity. The results indicated that C-banding and N-banding stain the same chromosome regions. Similar conclusions were reached by Armstrong (1982). The N-banding technique employs a 1 M NaH_2PO_4 treatment at 94 °C, followed by staining in a 1/15 M phosphate buffer at pH 6.8 (Gerlach 1977). The buffer concentration used in the present study was in the range of 1.01–0.005 M, depending on the manufacturer of the buffer.

Other steps in the C-banding procedure did not seem to be as important. Minor variation in both the time and temperature regimes did not affect the final results. However, the speed with which chromosomes pick up the Leishman stain can vary from species to species. In wheat-rye hybrids the chromosomes of rye reach a satisfactory level of banding, both terminal and interstitial bands, much earlier than wheat chromosomes. However, rye chromosomes appear to have a wide margin of staining time before they overstain and get too dark, which allows time for the wheat chromosomes to properly stain. The *Haynaldia* chromosomes of a wheat-*Haynaldia* hybrid have a staining time span similar to rye, while the *Agropyron* chromosomes of a wheat-*Agropyron* hybrid appear to stain at the same speed as wheat (Lukaszewski, unpublished data).

Modifications of Rye Chromosomes

The term 'chromosome modifications' was first used to cover morphological changes of rye chromosomes in wheat background (Tarkowski and Stefanowska 1972), but recently it has been used in reference to changes in the amount of telomeric heterochromatin (Gustafson et al. 1980).

A positive effect of heterochromatin deletions on early endosperm development and kernel characteristics in triticale has been established (Gustafson and Bennett 1982; Bennett and Gustafson 1982). Rye chromosomes with reduced amount of telomeric heterochromatin are common in spring triticales (Pilch 1981), while in winter triticales such modifications were found to be rare (Lukaszewski and Apolinarska 1981 and unpublished data; Seal and Bennett 1981). The adaptive values of such modifications in triticale have been postulated (Seal and Bennett 1981). The results presented here established that modifications do occur in winter material, though with low frequency (0.2% of deletions, 0.07% of amplifications). The mechanisms and implications of such deletions and amplifications in the genus *Secale* and in triticale were discussed elsewhere (Gustafson et al. 1982).

Chromosome Translocations

In the present study an average of one wheat/rye translocation in every four plants grown was found. There was no indication that those translocations resulted from homoeologous pairing between chromosomes of wheat and rye. Formation of wheat/rye bivalents in meiosis is very low (Mettin et al. 1976; Schlegel et al. 1980). In mathematical models simulating chromosome pairing in hybrids, the rye genome was so remote from any of the wheat genomes that the A, B and D genomes of wheat appeared to be homologous (Kimber and Alonso 1981). Therefore, homoeologous pairing could not possibly account for the high frequency of translocations. Indeed, the frequency of translocations occurring within homoeologous groups was substantially lower than between homoeologous groups (Table 4). It seemed highly probable that most of the translocations described here resulted from misdivision of univalents at meiosis and subsequent random fusion of telocentric chromosomes (i.e. centric break-fusion). It was first shown by Sears (1972) that fusion of misdivision products could be practically utilized in inducing alien translocations; however, the frequencies which were in the order of 1 translocation per 400 plants, were still too low for wide use of the method. Sears' experiment involved only one chromosome of rye (5R) and one chromosome of wheat (6B). In the present study, all R- and D-genome chromosomes were present as uni-

valents in at least one generation and were thus given a chance to misdivide, resulting in a very high frequency of fusion.

It seems likely that in a highly disorganized meiosis where theoretically pairing was 14″ + 14′, a high rate of misdivision took place, yielding a high frequency of telocentric chromosomes and creating more favorable conditions for telocentric fusion. It could be expected, and was observed, that in earlier generations of triticale × wheat hybrids the frequency of translocations (or fusions) occurring within homoeologous groups was lower than in later generations (F_2 vs. F_3, BC_1 vs. BC_2). Assuming random fusion being responsible for most translocations occurring, the probability of homoeologous chromosome fusions would be a function of the number of univalents, and their tendency to misdivide and to fuse with other telocentrics. With the increasing stability of plants as generations advance, the number of univalents decreases and the proportion of univalents from the same group increases. This increases the chance for homoeologous chromosome arms to fuse, up to the point where two univalents from the same homoeologous group (one R and one D) after misdivision have a 50% chance to form a homoeologous translocation. That type of programmed translocation was demonstrated by Sears (1972).

Certainly, the frequency of translocations occurring by fusion of telocentric chromosomes would depend on the tendency of chromosomes to misdivide at meiosis and the ability of misdivision products to fuse with other telocentrics. At the present time there is no complete set of data on the frequency of misdivision of wheat univalents, but from the data given by Sears (1952), Morrison (1953), Sears (1973) and Morris et al. (1977) it is clear that the misdivision frequency varies for different chromosomes and for the same chromosome in different genetic backgrounds. The misdivision frequency of rye chromosomes in this study, as judged by the frequency of telocentrics and translocations, was not related to their size, even though the differences with which individual rye chromosomes were present as telocentrics or were involved in translocations were substantial. Indeed, chromosome 2R, which is the longest in the rye genome and has the highest DNA content (Lukaszewski et al. 1982 a), was the most frequent to misdivide. However, chromosome 6R, which is the third longest in the genome, showed the lowest frequency both as a telocentric and in translocations. Moreover, marked differences were observed in the frequency with which different chromosome arms were involved, both in rye/rye and wheat/rye translocations, 2RL being the most frequent of all, 6RL the least frequent. The results indicated that chromosomes and even chromosome arms showed different tendencies to fuse with other telocentrics. Chromosome 3R, which represented 15.4% of all rye telocentrics identified in F_2 and BC_1 generations, showed the lowest frequency of involvement in translocations, while on the other hand chromosome 2R showed a low frequency as a telocentric but a high frequency of involvement in translocations, which indicated its ease in fusion. In turn, chromosomes 4R and 7R both showed high frequency as telocentrics (telocentrics of those two chromosomes made up 50% of all telocentrics in F_2 and BC_1) and high frequency in translocations. It can be speculated that chromosome 6R had the lowest rate of misdivision, while chromosomes 4R and 7R had the highest; chromosomes 2R, 4R and 7R had a high rate of fusion, while 3R and 6R had a low rate of fusion.

Unfortunately, neither the frequency nor identity of wheat telocentrics was recorded in the analyzed material. However, it seemed that their frequency was not any lower than that of rye telosomes, and this was supported by the high frequency of wheat-rye translocations.

Out of the 188 centric break-fusion wheat/rye translocations, 11 involved A- and B-genome chromosomes, or 5.9% of all translocations. The occurrence of A/R and B/R translocations was hardly unexpected; it has been shown that in hexaploid triticale (AABBRR) wheat as well as rye chromosomes can contribute to univalency (Shigenaga and McGinnis 1971; Merker 1973). From data presented by Thomas and Kaltsikes (1976) it can be calculated that an average of 10.6% of univalents at the first meiotic division in seven triticale lines were wheat univalents, and this frequency ranged from 5.7% to 20.0% between lines. If A- or B-genome chromosomes were also present as univalents in this material, then they were likely to misdivide and become available for fusion with the misdivision products of other chromosomes.

Assuming that the fusions occurred at random, it can be speculated that the number of centric break-fusions within and between the D genome or A and B genomes must have also been high. Okamoto and Sears (1962) showed such translocations do take place and suggested that they were caused by pairing and crossing over. However, in view of the frequency of misdivision and fusion observed in the present study, it seems more likely that at least the non-homoeologous translocations in their study occurred by telocentric fusion.

From the detailed data on chromosome pairing in four hexaploid triticale × hexaploid wheat F_1 hybrids presented by Sanchez-Monge and Sanchez-Monge (1977) it can be calculated that the mean pairing failure for A- and B-genome chromosomes was 6.9%. This figure is close enough to the figure for the frequency of A/R and B/R translocations found here (5.9%) to indicate that there was no preferential fusion between misdivision products of D- and R-genome chromosomes. This also allowed speculation that the number of translocations within and/or between A- and B- and D-genome chromosomes might have been similar to the number of A/R and B/R translocations and the number of translocations within the D genome might have been close to the number of translocations within the rye genome.

It was more difficult to explain the mechanisms by which non-centric translocations occurred. Only five out of 195 wheat/rye translocations were of that type. Three of those possibly involved a transfer of rye heterochromatin to wheat chromosomes. It is not known whether transfers of that kind resulted from homoeologous pairing. On the other hand, in somatic cells heterochromatic threads between heterochromatin regions of wheat and rye chromosomes were observed both

here and in another study (Gustafson et al. 1982). Two of the non-centric wheat/rye and seven rye/rye translocations seemed to have one incomplete arm consisting of a terminal segment of a rye arm. A possible mechanism for this phenomenon would be the fusion of a chromosome fragment lacking a centromere with a telocentric having a complete centromere. Similar explanations may explain the chain chromosomes observed having multiple centromeres. However, the occurrence of chain chromosomes was so rare that pairing and chiasma formation cannot be excluded as possible causes.

The results presented to not allow for precise comparison of the effect of the genetic background on the univalent misdivision and subsequent fusion of telocentric chromosomes. No differences in the occurrence of rye telocentrics and rye/rye translocations between populations were noted. It seemed likely, though, that the frequency of misdivision of wheat chromosomes and fusion with ryes was higher in DC3 × Kasper hybrids. If that indication was correct, then the most likely candidate to blame was the wheat parent of the DC3 triticale, the Do1 line selected from a *T. persicum* × *T. dicoccoides* hybrid (Lapinski et al. 1980). Some of the cytological peculiarities of the line have been previously described (Apolinarska and Lukaszewski 1980). However, the results for all the four triticale × wheat populations indicate that the phenomenon was not limited to one particular line but could occur in a wide range of materials. Occurrence of similar wheat/rye and rye/rye translocations were reported by Merker (1979) in hybrids between lines of wheat with different numbers of rye chromosomes, while Rogalska (1980) reported on 6RS/1RL translocations in triticale.

The value, stability, and phenotypic effects of these translocations are not known at the present time. It is likely that a good proportion of them (especially those involving non-homoeologous chromosomes) will not be able to fully compensate for the missing arms of wheat chromosomes. The female transmission rate of some of the translocations was close to 50%, but it is usually the male transmission rate that is affected by incomplete compensation. On the other hand, because the homoeology of rye chromosomes 4R and 7R to wheat remains somewhat unclear, there is a chance that some of the translocations between wheat and rye chromosomes from groups 4 and 7 will compensate better than complete rye chromosomes (Zeller and Koller 1981).

The results presented indicated that mass production of wheat/rye translocations is possible, not only between the D-genome and rye chromosomes, but also between the A- and B-genome and rye chromosomes. High frequencies of telocentric fusion warrant application of this method of introducing alien variation into wheat in field-level research programs. Careful screening for desired characters (e.g. resistance to diseases, pests, aluminum tolerance) could facilitate stabilizing the translocations in lines without need for extensive cytological work. It also seems feasible to use the same method to introduce chromosome segments from other species to wheat.

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