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Introduction of D-genome chromosomes from *Aegilops squarrosa* L. into tetraploid triticale (AB)(AB)RR (2n=28)

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Summary. Tetraploid triticale with the genome constitution (ABD) (ABD)RR (2n=4x=28) selected from the progenies of DDRR × (AB)(AB)RR hybrids (D(AB)RR) were karyotyped using C-banding. The aneuploidy frequency was 10.7% with 4.4% hypoploids and 6.3% hyperploids in the F_5. Among 67 plants having 28 chromosomes, 41.8% had a stabilized karyotype, while 58.2% were unstabilized with at least one homoeologous group segregating for A-, B- or D-genome chromosomes. The stabilized plants represented ten different karyotypes that contained one to five disome substitutions of D-genome chromosomes for A- or B-genome chromosomes. Two (BD) (BD)RR tetraploids had no A-genome chromosomes. The average number of D substitutions was 3.0 per line. Of the seven substitutions possible only one, 4D(4B), was not present. In the progeny of plants selected for fertility a selection pressure acted against wheat chromosomes 1B, 3B, 4D and 7D. The most favoured chromosome constitution of the (ABD) mixed genome was 1D, 2A, 3D, 4B, 5B, 6A and 7B. Plants of that karyotype but with a heterologous pair of chromosomes 5B and 5D had the best seed set. Evolutionary and breeding aspects of tetraploid triticale are discussed.

Key words: Aneuploidy – Genome stabilization – C-banding

Introduction

Tetraploid triticale (X *Triticosecale* Wittmack) ist the youngest wheat-rye hybrid relative to the hexaploid and octoploid triticale forms. The first three (AB) (AB)RR tetraploid triticale selected by Krolow (1973) had a mixture of A- and B-genome chromosomes of wheat (*Triticum turgidum* L.) and a complete rye (*S. cereale* L.) genome (Gustafson and Krolow 1978). The only, so far published, self-fertile primary tetraploid triticale with the rye genome of *S. cereale* is a hybrid *Aegilops squarrosa* L. × *S. cereale* L. with the genome constitution DDRR (Krolow and Lukaszewski 1986; Bernard and Bernard 1987).

A new approach was started to produce improved secondary (ABD) (ABD)RR tetraploids with D-genome chromosomes of *Ae. squarrosa* by crossing DDRR with (AB) (AB)RR tetraploid triticale. This is the first report on the study of the chromosomal stabilization process in (ABD) (ABD)RR tetraploid triticale with D-genome chromosomes of *Ae. squarrosa* selected for short straw, good seed characteristics and fertility.

Materials and methods

The DDRR tetraploid triticale (2n=28) is an *Aegilops squarrosa* var 'strangulata' (Japan) × *Secale cereale* amphiploid. The (AB) (AB)RR tetraploid triticale line P7/82 used in this study was the same as that described by Lukaszewski et al. (1984) and Hohmann (1985). The line had a mixture of A- and B-genome chromosomes: 1B, 2A, 3B, 4B, 5B, 6A and 7B from *Triticum turgidum* L. and a complete rye genome from *S. cereale* L.

To obtain (ABD) (ABD)RR tetraploid triticale the DDRR triticale was crossed as female to the (AB) (AB)RR triticale. The F_1 hybrids D(AB)RR and following generations were self-pollinated. Plants were selected for morphology, fertility and short straw.

The F_5 progenies were C-banded to determine their chromosome constitution. Only 28-chromosome plants were karyotyped. The chromosome identification was carried out by using the C-banding pattern published by Lukaszewski and Gustafson (1983) and corrected by Lukaszewski et al. (1987a). The nomen-

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Table 1. Variation of somatic chromosome number and aneuploid frequency in the progenies of (ABD)(ABD)RR tetraploid triticale selected from crosses between DDRR and (AB)(AB)RR tetraploid triticale

Triticale line/generation	Chromosome number (2n)							No. of plants	% aneuploids
	25	26	27	28	29	30	Mean		
(ABD)(ABD)R									
F_1	–	–	1	13	–	–	27.93	14	7.1
F_2	–	–	15	13[a]	4	5[a]	27.97	37	64.9
F_3	1	10	37	75	2	–	27.54	125	40.0
F_4	–	–	1	16	1	–	28.00	18	11.1
F_5	–	–	5	100	7	–	28.02	112	10.7
DDRR	–	–	4	90	5	1	28.03	100	10.0
(AB)(AB)RR	–	–	–	98	–	–	28.00	98	0.0

[a] One plant with two telocentric chromosomes

Table 2. Mean chromosome pairing at metaphase I in 28-chromosome plants of F_1 hybrids D(AB)RR, DDRR and (AB)(AB)RR tetraploid triticale

Triticale	No. of PMC	Univalents		Bivalents		Trivalents		Quadrivalents		Chiamata/	
		Mean	(Range)	Mean	(Range)	Mean	(Range)	Mean	(Range)	PMC	Bivalent
F_1 D(AB)RR	633	11.97	(2–22)	8.00	(3–13)	–		0.01	(0–1)	12.23	1.38
DDRR	612	2.02	(0–14)	12.88	(9–14)	0.036	(0–1)	0.028	(0–1)	18.94	1.46
(AB)(AB)RR	1,058	0.12	(0– 8)	13.94	(10–14)	0.001	(0–1)	–		26.88	1.92

clature of the wheat chromosomes follows that designated by the workshop of the Seventh International Wheat Genetic Symposium, Cambridge, 1988.

Results

The chromosome number of the F_1 D(AB)RR obtained by crosses between DDRR and (AB) (AB)RR tetraploid triticale ranged from 27 to 28 with the majority of plants having 28 chromosomes (Table 1). In F_2 the chromosome number ranged from 27 to 30 with 35.1% of the plants having 28 chromosomes. In the F_3 generation, derived from a progeny of fertile aneuploid plants with either 27 or 29 chromosomes, 60.0% of the plants had 28 chromosomes and 38.4% were hypoaneuploid. The tendency towards a lower chromosome number was evident. Additionally, 13 plants not listed had chromosome numbers between 14 and 21. All plants had a complete rye genome.

In F_5 the chromosome number varied from 27 to 29 with an aneuploidy frequency of 10.7%; this is comparable to the variation in chromosome number in the female DDRR triticale parent. Plants with telocentric chromosomes appeared in the F_2 only.

The meiotic analysis of the euploid F_1 hybrids with the genome constitution D(AB)RR and 28 chromosomes revealed on average 11.97 univalents and 8.00 bivalents at metaphase I (Table 2). Among 633 PMCs analysed one quadrivalent was observed. The maximum number of 13 bivalents indicated homoeologous pairing between the wheat chromosomes of the D genome and the (AB) mixed genome. At least 12 out of 14 wheat chromosomes had paired, and interchanges between homoeologous chromosomes were theoretically possible. Among the PMCs, 56.7% showed less than 14 univalents and had more than 7 bivalents, implying pairs of homoeologous wheat chromosomes. In subsequent generations the overall pairing of chromosomes increased, and the maximum of 14 bivalents per PMC appeared in the F_2.

Of 67 plants in the F_5 the chromosome constitution of only 28 plants (41.8%) had a stabilized (ABD) genome. Thirty-nine plants (58.2%) were unstabilized with at least one homoeologous group segregating for A- and D- or B- and D-genome chromosomes. The 28 stabilized (ABD) (ABD)RR tetraploids were assigned to ten different karyotypes (Table 3).

The number of D-genome chromosomes ranged from one pair ($A_2B_4D_1$) to five pairs ($A_0B_2D_5$). With the exception of the 4D(4B) substitution, all A- and B-genome chromosomes of the (AB) (AB)RR tetraploid triticale could be substituted by D-genome chromosomes of *Ae. squarrosa* L. at least once (Fig. 1). The most frequent (ABD) karyotype had two A-, three B- and two D-genome chromosomes ($A_2B_3D_2$): 1D, 2A, 3D, 4B, 5B, 6A and 7B. One (BD) (BD)RR tetraploid triticale line had

Table 3. Stabilized chromosome constitution in the homoeologous groups of the wheat genome of (ABD)(ABD)RR tetraploid triticale (F_5)

Homoeologous group							Type of (ABD) genome	No. of plants	Karyotype no.
1	2	3	4	5	6	7			
BB	AA	DD	BB	BB	AA	BB	$A_2B_4D_1$	1	1
DD	AA	DD	BB	BB	AA	BB	$A_2B_3D_2$	7	2
DD	DD	DD	BB	BB	AA	BB	$A_1B_3D_3$	6	3
DD	AA	DD	BB	DD	AA	BB	$A_2B_2D_3$	3	4
DD	AA	DD	BB	BB	DD	BB	$A_1B_3D_3$	2	5
BB	DD	BB	BB	DD	AA	DD	$A_1B_3D_3$	1	6
DD	DD	DD	BB	DD	AA	BB	$A_1B_2D_4$	2	7
DD	DD	DD	BB	BB	DD	BB	$A_0B_3D_4$	4	8
DD	AA	DD	BB	DD	DD	BB	$A_1B_2D_4$	1	9
DD	DD	DD	BB	DD	DD	BB	$A_0B_2D_5$	1	10
							Total	28	10
DD	DD	DD	DD	DD	DD	DD	$A_0B_0D_7$	1	
BB	AA	BB	BB	BB	AA	BB	$A_2B_5D_0$	1	

Table 4. Frequency (%) and mean number of homologous and heterologous chromosome pairs in stabilized and unstabilized (ABD)(ABD)RR tetraploids (F_5)

Homoeologous group	Stabilized triticale			Unstabilized triticale				
	Chromosome pairs (%)			Chromosome pairs (%)				
	AA	BB	DD	AA	BB	DD	AD	BD
1	–	7.1	92.9	–	2.6	97.4	–	0.0
2	50.0	–	50.0	38.5	–	17.9	43.6	–
3	–	3.6	96.4	–	2.6	89.7	–	7.7
4	–	100.0	0.0	–	100.0	0.0	–	0.0
5	–	71.4	28.6	–	30.8	20.5	–	48.7
6	71.4	–	28.6	64.1	–	10.3	25.6	–
7	–	96.4	3.6	–	97.4	2.6	–	0.0
Mean pairs	1.21	2.79	3.00	1.02	2.33	2.39	0.69	0.59

four pairs of D-genome chromosomes (1D, 2D, 3D and 6D) and three pairs of B-genome chromosomes (4B, 5B and 7B). Another (BD) (BD)RR line had five pairs of D-genome chromosomes, and only the less frequent chromosomes 4D and 7D were replaced by 4B and 7B.

The frequencies of individual disome D-genome chromosomes were different with respect to the seven homoeologous groups (Table 4). The order of decreasing frequency of D-genome chromosomes in stabilized lines was 3D (96.4%), 1D (92.9%), 2D (50.0%), 5D and 6D (28.6%), 7D (3.6%) and 4D (0.0%). Consequently, the only single substitution was the 3D(3B) substitution ($A_2B_4D_1$). There was a significant ($P<0.05$) selection pressure for chromosomes 1D, 3D, 4B and 7B and some selection pressure for chromosomes 5B and 6A. Therefore, the preferred karyotype was 1D, 2A or 2D, 3D, 4B, 5B or 5D, 6A or 6D and 7B. The 1D-3D and 4B-7B chromosome combination was observed very frequently.

Among the 39 lines with an unstabilized (ABD) genome a chromosomal segregation was found for A- and D or B- and D-genome chromosomes in the homoeologous groups 2, 3, 5 and 6. The most unstable group was homoeologous group 5, followed in order of increasing stability by groups 2, 6 and 3. The homoeologous groups 1, 4 and 7 had no detectable heterologous chromosome pairs of B- and D-genome chromosomes and were stabilized. On average, heterologous chromosome pairs of A- and D-genome chromosomes (0.69 pairs) wer more frequent than pairs of B- and D-genome chromosomes (0.56 pairs). Within unstabilized lines a selection of "new" stabilized chromosome constitutions was not possible. In stabilized lines the average number of homologous pairs of A-, B- and D-genome chromosomes was 1.21, 2.79 and 3.00, respectively.

In all stabilized (ABD) (ABD)RR tetraploids there was some variation in the banding pattern of A-, B- and

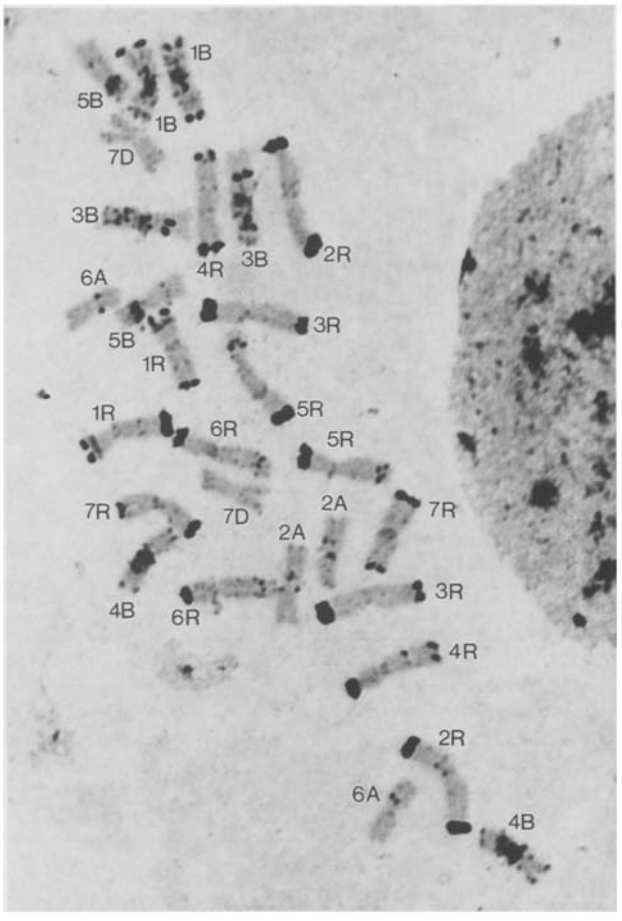

Fig. 1. C-banded mitotic chromosomes of (ABD)(ABD)RR tetraploid triticale with the chromosome constitution 1B, 2A, 3B, 4B, 5B, 6A and 7D present in F_4

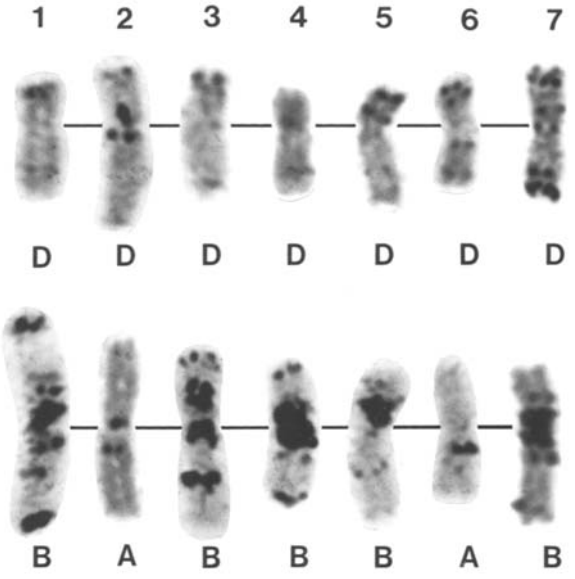

Fig. 2. C-banded wheat chromosomes present in F_1 D(AB)RR triticale (DDRR × (AB)(AB)RR)

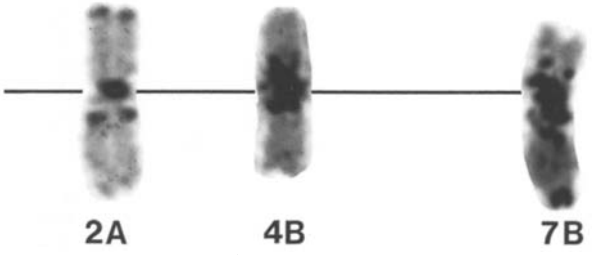

Fig. 3. Modified C-banded wheat chromosomes 2A, 4B and 7B present in (ABD)(ABD)RR tetraploid triticale

D-genome chromosomes in comparison to the banding pattern published by Lukaszewski and Gustafson (1983). The lack of the terminal band on the short arm of chromosome 5B was identified in the (AB (AB)RR line and in the F_1 D(AB)RR (Fig. 2). In addition, consistent differences in the C-banding pattern of wheat chromosomes 2A, 4B and 7B were observed in (ABD) (ABD)RR tetraploid triticale (Fig. 3).

An additional terminal band on the short arm of chromosome 2A was present in the karyotypes number 1, 2, 4, 5 and 9 (Table 3). The origin of this band is unclear at the moment. An additional terminal band on the long arm of chromosome 7B was identified in the karyotypes number 1, 2, 3, 4, 5, 8, 9 and 10. The lack of terminal bands on the long and short arm of chromosome 4B was found in one unstabilized line only. This unstabilized line may have a reciprocal translocation between terminal segments of either chromosome arms 4BL and 7BL or arms 4BS and 7BL. The rye genome was stable in all lines, but some variation was observed in the amount of heterochromatin present. The secondary constriction on chromosome 1R (or the satellite on chromosome arm 1RS) was observed only in the absence of both wheat satellited chromosomes 1B and 5D.

The plant morphology of (ABD) (ABD) triticales was intermediate between their parents except for spike length (Table 5). In general, the DDRR triticale used as female had a lasting influence on the morphology (Fig. 4a). The reduction in plant height of the (ABD) (ABD)RR tetraploids (110.4 cm) in comparison to DDRR (139.5 cm) and (AB) (AB)RR tetraploids (146.0 cm) was one of the favourable characteristics of the new forms. Furthermore, the (ABD) (ABD)RR tetraploids had good seed characteristics (Figure 4b).

The unstabilized lines had a slightly better seed set, with 0.72 seeds per spikelet, than the stabilized lines, with 0.64 seeds per spikelet. The plants of two karyotypes with heterogeneity in homoeologous group 5 (that is where chromosome 5B and 5D in group 5 is present) showed significant improved fertility (1.08 to 1.25 seeds per spikelet) over their comparable karyotypes with homogeneous chromosomes in group 5 (0.58 to 0.78 seeds per

Table 5. Spike morphology and fertility of the stabilized and unstabilized (ABD)(ABD)RR tetraploids (F_5)

Triticale	Plants *n*	Spike length (cm)			Spikelets/spike			Seeds/spike			Seeds/spikelet		
		Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
(ABD)(ABD)RR													
Stabilized	28	10.0	6	14	22.8	13	32	15.2	0	30	0.64	0.00	1.42
Unstabilized	39	10.5	7	14	25.0	16	36	17.6	0	39	0.72	0.00	1.63
DDRR	90	13.9	11	17	19.4	16	24	10.0	4	16	0.52	0.20	0.84
(AB)(AB)RR	89	15.1	8	19	38.1	28	45	55.1	23	82	1.45	0.61	1.95

spikelet). Heterogeneity in homoeologous group 2 had little or no decreasing influence on fertility, whereas plants only heterogeneous for chromosomes in group 6 clearly showed reduced seed set. Plants with chromosome pairs of 1B and 3D were sterile.

Discussion

In this study the existing intergenomic homoeology of tetraploid triticales offers a potential for creating new chromosomal and genetic variation by crossing DDRR to (AB) (AB)RR tetraploid triticale. The production of (ABD) (ABD)RR triticales from F_1 D(AB)RR hybrids provides a system for studying the evolution of new species comparable to the hybrid swarm of hexaploid triticale described by Gustafson (1976).

The aneuploidy frequency in the F_5 progeny of (ABD) (ABD)RR triticale with 10.7% aneuploids was comparable to the female DDRR tetraploid triticale parent with 10.0% aneuploids and with a small predominance of hyperploids. The conventional (AB) (AB)RR tetraploids showed, on average, the same distribution for hyperploids and hypoploids, but a lower aneuploidy frequency with 2.5% in the F_5 (Krolow 1974). Secondary (AB) (AB)RR tetraploids obtained by crossing two different (AB) (AB)RR lines had aneuploidy frequencies of 5.6% in the F_6 and 4.8% in the F_8 (Hohmann 1985). A larger sample of (AB) (AB)RR tetraploids was tested by Lukaszewski et al. (1987b, c) with 5.77% aneuploids in stabilized and 4.74% aneuploids in unstabilized lines.

The continuous process of genome stabilization in (ABD) (ABD)RR triticale was proven by 41.8% of the plants having 28 chromosomes and stabilized karyotypes in F_5. The average number of chromosome pairs of the A-genome (1.21 pairs), B-genome (2.79 pairs) and D-genome (3.00 pairs) was in good agreement with the assumption of a random distribution and a similar compensating ability of each chromosome.

The frequencies of individual wheat chromosomes or chromosome combinations present in the analysed materials could be a measure of selection pressure for or against those chromosomes or chromosome combinations. The most frequent chromosome constitution of (ABD) (ABD)RR tetraploids was 1D, 2A or 2D, 3D, 4B, 5B or 5D, 6A or 6D and 7B. On the other hand, while in conventional (AB) (AB)RR tetraploids there was no indication of a selection for a specific mixture of wheat chromosomes, the most probable combination was 1A, 2A, 3B, 4A, 5A or 5B, 6A or 6B and 7B (Lukaszewski et al. 1984). In the investigation of Lukaszewski et al. (1984) the chromosomes 1B, 2B, 4B and 7A did not form very successful combinations with the rye genome.

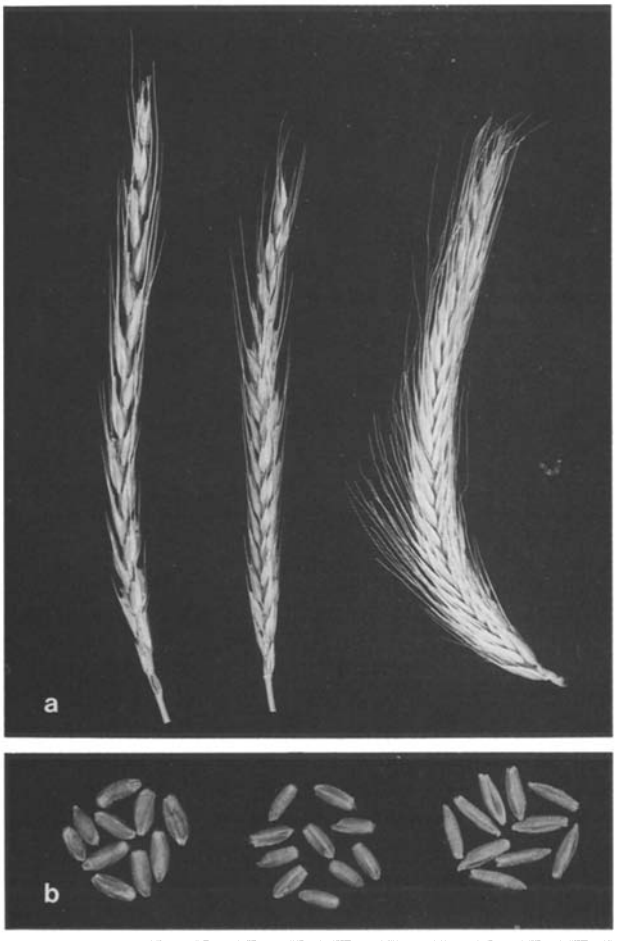

Fig. 4a, b. Spikes (**a**) and seeds (**b**) of tetraploid triticale DDRR (*left*), (ABD)(ABD)RR (*middle*) and (AB)(AB)RR (*right*)

The present results indicate that wheat chromosomes 1B and 3B can be frequently substituted by D-genome chromosomes. A single chromosome substitution disomic for 1D(1B) or a fertile disomic 3D(3B) substitution could not be detected in the F_5. Plants either with the chromosome combination 1D-3D (observed in F_4) or 1D-3D were self-sterile. The double chromosome substitution involving 1D(1B) and 3D(3B) occurred at a high frequency in the (ABD) (ABD)RR tetraploids analysed. The retention of the 1D(1B) component appears to have a favourable association to the prevalent 3D(3B) substitution. However, the 3D(3B) and the 1D(1B) substitutions are not necessarily associated with improved species fitness.

There was a high frequency of the 4B-7B chromosome combination. Modifications in the banding pattern of chromosome 7B indicated the presence of a translocation. Translocations between non-homoeologues tend to limit the spectrum of possible chromosome combinations in tetraploid triticale (Lukaszewski et al. 1984). The rye chromosomes 4R and 7R are translocated chromosomes and have a limited compensating ability to both the homoeologous groups 4 and 7 (Zeller and Koller 1981). The 4B-7B combination present in tetraploid triticales probably interacts much better with the rye genome. Apparently, there is a tendency for chromosomes from the same genome to be present not only in homoeologous groups 1 and 3 but also in homoeologous groups 4 and 7.

On the other hand, the presence of individual D-genome chromosomes depends on their compensating ability. Those D-genome chromosomes that compensate fully for their A- or B-genome chromosomes would be expected to segregate at random and lower compensation should reduce their frequency. Therefore, chromosomes 1D and 3D should have a high, and chromosomes 4D and 7D a low, compensating ability. The chromosomes 2D, 5D and 6D of *Ae. squarrosa* should have a good compensating ability in (ABD) (ABD)RR tetraploids. The heterologous chromosome pairs that were observed in homoeologous group 2 (2A and 2D), 5 (5B and 5D) and 6 (6A and 6D) indicated a slow process of stabilization and a slow selection pressure for or against A-, B- or D-genome chromosomes. In (AB) (AB)RR triticale there was a similar tendency with group 2 being the most unstable homoeologous group followed by group 6 and 5 (Lukaszewski et al. 1984).

With respect to the D-genome chromosomes of *T. aestivum* present in tetraploid triticale there are only preliminary results (Krolow et al. 1985; Krolow and Lukaszewski 1986). The incorporated D-genome chromosomes were present in homoeologous groups 1, 4 and 5 with the most frequent chromosome substitution being 5D(5A) or 5D(5B).

The segregation for chromosomes 5B and 5D in this study shows that there is no strong selection pressure for or against chromosomes 5B and 5D. Moreover, the high fertility of plants heterologous for chromosome 5B and 5D in homoeologous group 5 indicates that heterogeneity could be of an advantage and could help to maintain these chromosomes in a population. It is not clear, therefore, whether these observations are typical only of the (ABD) (ABD)RR tetraploids that were selected for fertility and analysed here, or if they can be generalized. The double aneuploid plants with one heterologous chromosome pair have a qualitatively larger genetic variation. These plants may have a better vitality in comparison to those with 14 pairs of homologous chromosomes during the process of genome stabilization in (ABD) (ABD)RR triticale. This confirms similar observations made in (AB) (AB)RR triticales where the plants with single heterologous chromosome pairs AB set on average twice as many seeds as the comparable homologous plants with chromosome pairs AA or BB (Lukaszewski et al. 1987c).

The *Ph* gene located on chromosome 5B is of little or no importance for meiotic stability in tetraploid triticale. It is the rye genome that had a predominant effect on overall chromosome pairing in tetraploid triticale (Lukaszewski et al. 1987b). The overall chromosome pairing in F_1 hybrids D(AB)RR implied the pairing of one homoeologous pair of wheat chromosomes. Homoeologous pairing of D-genome chromosomes with their homoeologues of the A- and B genome in triticale was assumed to be less than one (Bernard and Bernard 1985). In F_1 hybrids ABRR chromosome pairing showed a similar behaviour (Baum and Lelley 1988). Obviously, in both tetraploid F_1 hybrids D(AB)RR and ABRR, the 14 wheat chromosomes tend to pair frequently with their homoeologues.

In unstabilized tetraploid triticales, homoeologous wheat chromosomes generally paired at high frequencies, except for the 4A-4B pair (Lukaszewski et al. 1987c). Homoeologous pairing facilitates recombination between wheat chromosomes and an accumulation of translocations in a developing hybrid swarm of tetraploid triticale. In addition, homoeologous pairing impedes the selection of wheat chromosomes not recombined in both selfed and backcrossed F_1 hybrids.

In breeding tetraploid triticales the existing investigations demonstrated that heterozygotes with 28 chromosomes were favoured whenever the plants were selected for fertility. This may explain the high frequency of plants with heterologous chromosome pairs. To summarize, none of the conventional methods, neither the cytological selection of plants with 28 chromosomes or 14 bivalents in metaphase I nor the selection of plants with high fertility, will lead to improved tetraploid triticale lines in early generations.

The new synthesized and stabilized (ABD) (ABD)RR tetraploids have been useful for widening the chromosomal, genetic and cytoplasmic variation of tetraploid trit-

icale. They may be helpful for both the particular transfer and the enrichment of D-genome chromosomes to the hexaploid level by crossing them to octoploid triticale. Homoeologous pairing and recombination of D-genome chromosomes from *Ae. squarrosa* and *T. aestivum* can facilitate the transfer of segments from *Ae. squarrosa* to hexaploid triticale. The synthesized (BD) (BD)RR tetraploid triticale could help to produce hexaploids with the genome constitution of AA (BD) (BD)RR. Therefore, the induced tremendous variation of tetraploid triticale offers new possibilities for improving hexaploid triticale.

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