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Karyotype stabilization in intergeneric hybrids of the subtribe Triticinae

1. The effects of genome structure *

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Summary. The C-banded data obtained from Triticinae hybrids are studied with reference to the stabilization of their karyotypes. The types of hybrids distinguished according to genome structure are type I with minimally one diploid genome and type II with a haploid set only. Comparative analysis demonstrates that type I differs from II in karyotype stabilization. The chromosomes from various haploid genomes are combined into new genomes in type I; type II is represented only by amphiploids with the complete set of the chromosomes from all the genomes. The meiotic behaviour of the haploid genome chromosomes were found to have a modifying effect on karyotype stabilization: type II becomes I when homoeologous pairing level is high and when it is associated with the reductional division of univalents.

Key words: Intergeneric hybrids – Homoeologous pairing – C-banding – Karyotype evolution – Triticinae – Triticale

Introduction

Since Kattermann there has been much progress in the substitution hexaploid wheat (*Triticum aestivum* L. 2n = 42) of chromosomes of diploid rye (*Secale cereale* L. 2n = 14) (see Friebe 1976, and also O'Mara 1947; Sears and Okamoto 1958; Gupta 1971). Based on the C-banding patterns, it has been shown thàt some synthesized hexaploids are R-D (Merker 1975; Gustafson et al. 1980) while others are A-B substitution lines (Gustafson and Krolow 1978). In addition to having the practical purpose of developing new forms of Triticale, researchers placed emphasis on the problem of karyotype evolution in polyploid cereals. One approach to this problem was by analyzing karyotype stabilization in polyploid hybrids differing in genome structure.

Materials and methods

Karyotype stabilization was studied in plants through the F_1–F_4 generations (Table 1). The modified C-technique was used for this purpose (Khvostova and Shchapova 1974; Shchapova 1977).

Results and discussion

We determined that the karyotype of Triticale I-315820 has 12 rye + 30 wheat chromosomes, while that of the wheat varieties have no rye chromosomes. The majority of the 6x AABBDR F_2 plants possess 40–45 chromosomes. No plants with less that 39 or more than 49 chromosomes are encountered. Although this range is small (39–49), there is a large variation in the number of wheat + rye chromosomes (Table 2). The total number of chromosomes of the D + R genome type varies from 12–21 in these hybrids, being 14 in the majority. In all, 48 gamete types are identified among 84 plants examined. The variation in chromosome number is very similar in types D and R. The AABBDR × AABBDD F_2BC_1 plants were used for counting the chromosomes in the viable gametes. Eight types of gametes are identified (Table 3). Those gametes in which the total number of chromosomes of D and R types is 5–12 (with the predominance of the class with 7–9 chromosomes) are viable.

* The paper is dedicated to the memory of Professor V. V. Khvostova

Table 1. A characterization of hybrids in the subtribe Triticinae Trin. ex Griseb

Hybrid type	Cross	Genome of the F_1	No. of genomes	
			Diploid	Haploid
I[a]	Triticale I-315820 × *Secale cereale* L. var. 'Onohoiskaya'	ABRR	1	2
	Triticale I-315820 × *Triticum aestivum* L. var. 'Saratovskaya 29' and Hybrid 21	AABBDR	2	2
II[b]	*Triticum aestivum* L. var. 'Saratovskaya 29' and 'Ulianovskaya' × *Secale cereale* L. var. 'Onohoiskaya'	ABDR	–	4
	Triticum aestivum L. var. 'Saratovskaya 29' × *Agropyron glaucum* Desf. (Roem) et Schult.	ABDXYZ	–	6

[a] Type I has a diploid genome
[b] Type II has no diploid genome

Table 2. Frequency of hybrids having differing, numbers of rye and wheat chromosomes in the F_2 generation. F_2's were obtained from crosses between Triticale I-315820 and *Triticum aestivum* L. var. 'Saratovskaya 29'

No. of wheat chromosomes from D genome	No. of rye chromosomes											Total
	2	3	4	5	6	7	8	9	10	11	12	
3							1		1		2	4
4						1	3		2		1	7
5												–
6					1	1	4	2	1		5	14
7			1	1	1	2	2	1	1		1	10
8			2	1	2	3				2		10
9				2		4	2				2	10
10	1		4			2	1					8
11				1	3	1			2			7
12	2	2		2		2		1				9
13				1	1		2					4
14					1							1
Total	3	2	7	8	9	16	15	4	7	2	11	

Table 3. Chromosome sets in the viable gametes of the F_1 wheat-rye hybrids differing in the number of diploid + haploid genomes

Genome type	AABBDR			ABDR		
	Rye	Wheat	Total	Rye	Wheat	Total
1	4	15	19	5	17	22
2	5	15	20	7	16	23
3	5	16	21	6	17	23
4	5	17	22	6	18	24
5	4	18	22	7	18	25
6	5	18	23	7	20	27
7	6	18	24	6	21	27
8	6	20	26			
Variation range	4–6	15–20	19–26	5–7	16–21	22–27

Most of the AABBDR F_4 plants have 42 chromosomes. These plants show large variations in the number of set of rye chromosomes (Table 4). Thus, each of the 6 chromosomes of the D type was able to compensate for the missing homoeologous rye chromosome and, as a result, various R-D substitution lines arose. A backcross of the F_1 wheat-rye hybrid to the female parent (wheat) gave rise mainly to substitution lines with a single pair of rye chromosomes (Table 5). Forms with an eliminated 2R but with an almost always retained 1R, frequently occur among hexaploid Triticale selected for agronomically valuable characters (Merker 1975; Rogalska 1977; Gustafson et al. 1980). Among the Triticale plants not selected for these characters, there was no preferential occurrence of 1R and 2R chromosomes (Table 6).

The ABRR hybrids are sterile. The results of a karyological analysis of the ABRR×RR hybrids indicate that only those zygotes are viable which have 21–22 chromosomes (14 rye and 7–8 wheat). However, according to Gustafson and Krolow (1978), tetraploid Triticale with an A-B substitution appear occasionally among the progeny of the ABRR hybrids.

It may be concluded that karyotype evolution of type I hybrids with a diploid genome tended to decrease ploidy level of the haploid genomes and to combine genomes by means of intergenome chromosome substitution.

The ABDR and ABDXYZ hybrids are mainly sterile. However, there were some plants among the ABDR which set seeds after self-pollination. The seeds were sown, and plants were grown in the greenhouse where cross pollination was excluded. Two plants were chosen for analysis, one of which was found to have 54 chromosomes (42 wheat and 14 rye). There was a high incidence of sterility in progenies from the 49-chro-

Table 4. Variation in the karyotypes of the AABBDR F_4 and AABBDR×AABBDD F_4 BC_1

Type	No. of rye chromosomes	No. of lines		
		Total	F_4	F_4BC_1
1	0	34	5	29
2	1R	5	3	2
3	2R	6	1	5
4	3R	1	1	–
5	5R	3	2	1
6	6R	1	–	1
7	7R	9	3	6
8	1R+3R	4	3	1
9	1R+5R	1	–	1
10	1R+6R	3	1	2
11	1R+7R	1	–	1
12	2R+7R	2	2	–
13	5R+7R	4	3	1
14	6R+7R	2	2	–
15	1R+2R+6R	1	1	–
16	1R+3R+5R	1	1	–
17	1R+5R+6R	1	1	–
18	1R+5R+7R	1	1	–
19	1R+6R+7R	1	1	–
20	2R+5R+6R	1	1	–
21	2R+5R+7R	1	1	–
22	2R+6R+7R	1	1	–
23	3R+6R+7R	4	2	2
24	5R+6R+7R	2	2	–
25	1R+3R+5R+7R	1	1	–
26	2R+3R+5R+7R	2	1	1
27	2R+5R+6R+7R	2	2	–
28	1R+2R+3R+6R+7R	1	–	1
29	1R+3R+5R+6R+7R	4	4	–
30	2R+3R+5R+6R+7R	1	1	–
31	1R+2R+3R+5R+6R+7R	8	8	–

Table 5. Occurrence frequency of each rye chromosome in the AABBDR F_4 and AABBDR×AABBDD F_4BC_1 plants with an incomplete set of rye chromosomes

Hybrids	No. of families analysed	Rye chromosome					
		1R	2R	3R	5R	6R	7R
F_4	42	17	10	14	21	19	27
F_4BC_1	25	8	7	5	4	6	12
Total	67	25	17	19	25	25	39

Table 6. Variations in the number of chromosomes with terminally located bands from the *Agropyron* genome of the ABDXYZ×AABBDD F_4BC_1

No. of chromosomes without terminally located bands	No. of chromosomes with terminally located bands													Total no.
	0	1	2	3	4	5	6	7	8	9	10	11	12	
0									1					1
1														0
2		1	1		1	2		1	1	1	1			9
3														0
4		1			1	1								3
5			1	1			1	1						4
6			2		2	1	3		1				1	10
7	1			2		1	2			1	2			9
8					4		5		4					13
9			2	1	2		1	1						7
10				1	11	3	1				1			17
11		2	2	6				1						11
12			3										1	4
13		2	5	2	3			1						13
14			1	1		2								4
15			2					1						3
Total no.	1	6	19	14	24	10	13	6	7	2	4	0	2	

mosome plant to the F_5. In the F_6 we identified a plant with 28 wheat and 14 rye chromosomes; it was found to have chromosomes from all three genomes of common wheat. Karyological data from the ABDR×AABBDD hybrids indicate that only gametes with the almost complete set of chromosomes from all four genomes are viable (Table 3). The total number of chromosomes with viable gametes is 22–27; of these, 16–21 are wheat and 5–7 are rye chromosomes. Twenty-five seeds from seven different types of gametes were analysed (Table 3).

The sterility of the ABDXYZ is much higher than that of the ABDR hybrids. Six seeds only were obtained from 300 pollinated spikes. The remaining four plants have 61–63 chromosomes. The total number of chromosomes in these hybrids is also close to that in the complete set of the haploid genome of the F_1 hybrid. The viable gametes of type II hybrids (Table 5) were found to contain the almost complete set of chromosomes from the original hybrid with an aneuploid level of ± 1 chromosome per genome. Haploidy for some chromosomes in the viable hybrids of type II makes it possible, by back-crossing them to one of the parents, to obtain forms with reconstructed genomes. This reconstruction was achieved through substitution of chromosomes from one genome for another.

Analysis of the ABDR×AABBDD hybrids indicates that the frequency of occurrence of wheat-rye substituted forms in the F_4 hybrids is high. This supports and extends our previous observations (Shchapova and Kravtsova 1982). It should be emphasized that wheat chromosomes from various genomes are substituted by rye chromosomes so the forms obtained are hexaploid with R-ABD substitution (Fig. 1). The substitutions expected would be D-ABR in ABDR×AABBRR and R-D in ABDR×AABB crosses.

Analysis of the ABDXYZ×AABBDD hybrids demonstrated that their chromosome number is 45–66 with a predominance of the class with 56 chromosomes. The C-banded pattern of the original form of *Agropyron glaucum* shows 10 pairs of chromosomes with terminally located bands (Fig. 2). One of the chromosome sets from the F_4BC_1 plants consists of chromosomes from different *Agropyron* genomes. The karyotypes of these plants differ in the number of chromosomes with or without terminally located bands. There are five different types of chromosome associations in the combined *Agropyron* genome among the 56 chromosome hybrids; however, no plant with the chromosomes from the *Agropyron* genome have terminal bands and, vice versa, there is not a single C-banded pattern showing all the seven chromosomes without terminal bands (Table 6). This indicated that one group of *Agropyron* homoeologues has a telomeric band in all three chromosome pairs, another has none. As to the remaining five groups, four have each two chromosome pairs with telomeric bands and one just a single pair.

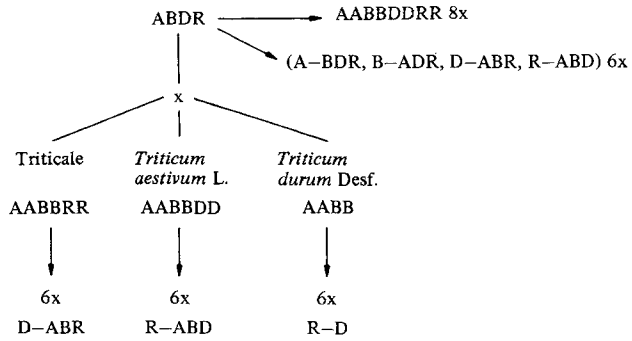

Fig. 1. A scheme for the intergenome chromosome substitutions possible in progenies from a self-pollinated wheat-rye hybrid, *ABDR* F_1, and from crosses of *ABDR* to Triticale (*AABBRR*) and wheat (*AABBDD* and *AABB*)

The stabilization of the ABDXYZ×AABBDD hybrids has, as its ultimate consequence, the emergence of an octoploid form with 42 wheat chromosomes and a set of *Agropyron* chromosomes from XYZ. In cereals, polyploid intergeneric hybrids with diploid genomes differ from those with haploid sets with respect to a fundamental feature – karyotype stabilization.

The observed difference between these hybrids in ploidy level could not be entirely attributed to selection favouring euploid gametes. It appeared rather that the meiotic behaviour of univalents determines whether chromosomes number will be reduced or remain unaltered in the gametes. Concerning meiotic chromosome behaviour in intergeneric hybrids, it is known that the homoeologous chromosomes of haploid sets can pair (Riley 1960; Sears 1977; Pohler and Kistner 1977; Feldman 1966; Schlegel and Weryszko 1979) and that univalents can divide equationally or reductionally (Naranjo and Lacadena 1982). It is also known that the level of homoeologous pairing in intergeneric hybrids is related to the interaction of genes controlling meiosis, genome dosage and genotypic environment (Sears and Okamoto 1958; Riley and Chapman 1958; Mello-Sampayo 1971; Driscoll 1972; Kempanna and Riley 1962; Wall et al. 1971; Lelley 1975; Lelley and Larter 1980; Schlegel and Weryszko 1979; Naranjo and Palla 1982; Naranjo 1982; Shkutina and Khvostova, 1971; Budashkina 1977; Leontjev and Budashkina 1980).

The ABDR plants differ in the number of homoeologous bivalents (Table 7). At meiosis, one division only took place in H100: univalent chromosomes are seen scattered in the cells. At the next stage, the daughter chromatids of the univalents start to move to the opposite poles. Because this movement is asynchronous, dyads with different chromosome numbers frequently arise. However, chromatids are distributed regularly in some cells. Two sequential divisions are observed in the cells of plants obtained from the same cross as H100. The irregularities at AII and consequent number of abnormal tetrads with micronuclei are related to the division pattern of univalents.

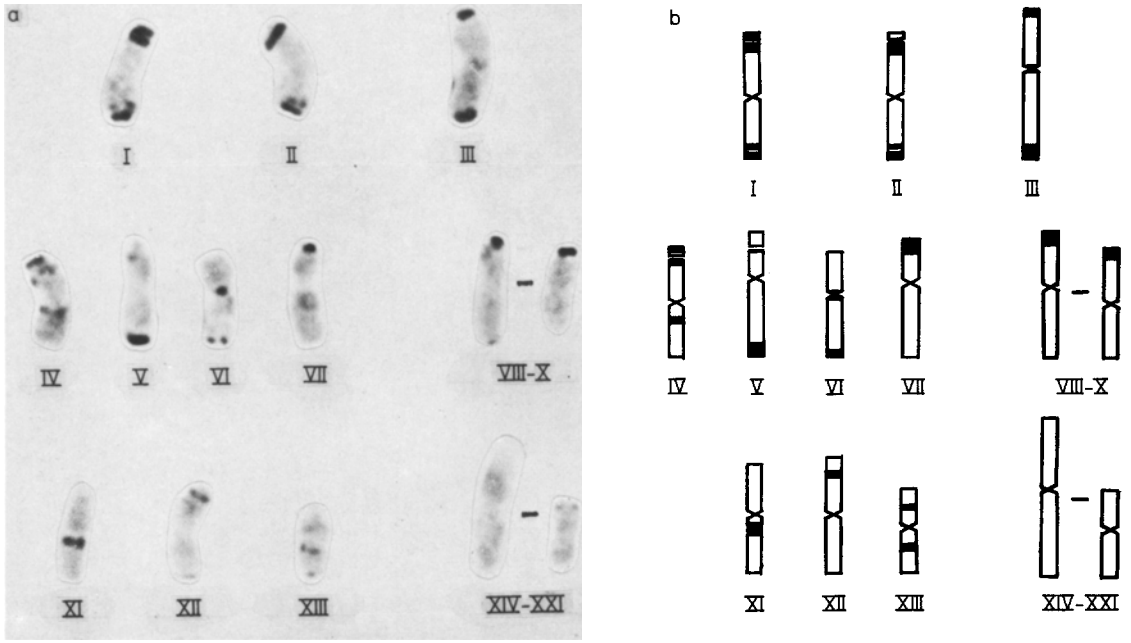

Fig. 2 a, b. The ideogrammatic representation of the haploid complement *Agropyron glaucum* $n=21$. Thick C-bands are located terminally in the long + short arms of chromosomes *I* and *III*, in one of the arms of chromosomes *IV–X*. Intercalary bands only are seen in chromosomes *IX–XIII*. Chromosomes *I–VIII, XI–XIII* (of these *II, IV* and *V* satellite) show individual banding patterns

Table 7. A characterization of the meiotic patterns in the ABDR hybrids

Hybrids	No. examined at MI	No. of cells with bivalents	Tetrads	
			Total no. examined	No. with micronuclei
Triticum aestivum L. var. 'Ulianovskaya' × *Secale cereale* L. var. 'Short-stemmed'				
217	100	12	366	50.82
219	100	–	250	65.60
228	100	6	150	95.33
236	100	1	332	55.42
248	100	11	76	97.37
127	100	8	341	91.21
Triticum aestivum L. var. 'Ulianovskaya' × *Secale cereale* L. var. 'Buryatskaya'				
111	100	10	204	63.64
267	100	2	75	93.33
100	100	–	–	–

Indeed, the ABDR hybrids differ in the number of tetrads with micronuclei (Table 7). It was very difficult to count the number of chromosomes dividing equationally or reductionally in these hybrids ($4x=28$). The number of tetrads with micronuclei allowed us to make predictions about the division patterns of univalents. H228 and H248 had the largest number of tetrads with micronuclei and, therefore, we expected that their univalents in most cells would divide equationally.

Naranjo and Lacadena (1982) has convincingly explained the differences in the number of equationally and reductionally dividing chromosomes in A and B genomes by the effect of the genotypic environment of rye genome. The differences we observed between the ABDR hybrids can be explained in the same way. In fact, homoeologous chromosomes showed a low pairing level (0.01–0.012 bivalents per cell) in these hybrids, but it did not affect ploidy levels of the gametes. However, the levels of chromosome pairing can be higher, two bivalents per cell (see for comparison Schlegel and Weryszko 1979, Table 1).

The ABDR F_1 hybrids differ considerably in the number of cells with bivalents and in the division patterns of the ABDR F_1 hybrids. To illustrate, H100 and H219 have no bivalents; in AI, all univalents segregate as a result of a single equational division in H100, but of both divisions, equational + reductional, in H219. The equational division of univalents and the regular passage of chromatids to the opposite poles give rise to dyads with an almost complete set from all genomes. In a related previous study, the level of homoeologous pairing was observed to be low (0.004 wheat-rye bivalents per cell) in the AABBDR plants with most of the univalents dividing reductionally.

The meiotic data for the ABDXYZ hybrids indicate that plants from this cross combination differ in the number of bivalents per cell (Table 8). The level of homoeologous pairing is very high, 9.60 bivalents per

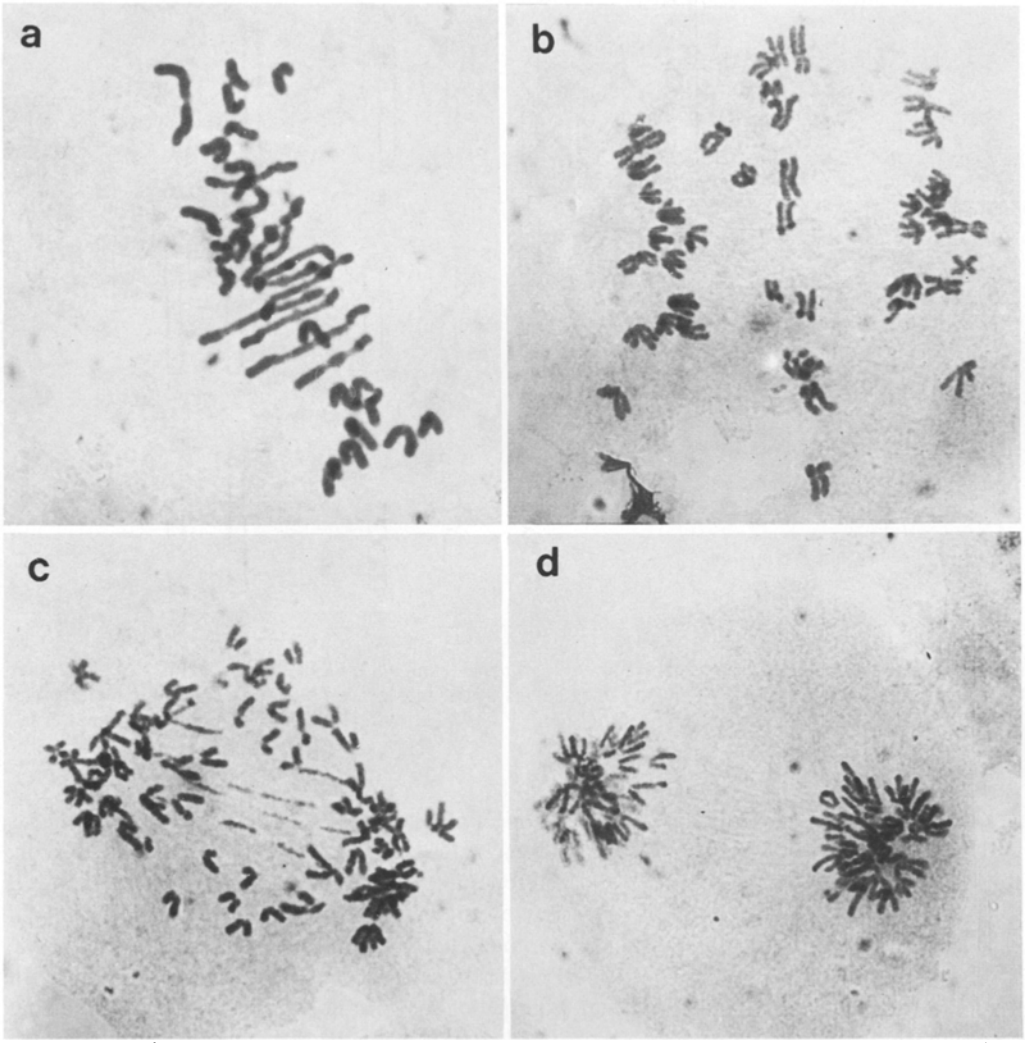

Fig. 3 a–d. Meiosis in a wheat – *Agropyron* hybrid F_1 (*ABDXYZ*, 6x = 42). **a** metaphase I; **b, c** anaphase segregation in univalents; **d** telophase

Table 8. Meiotic chromosome pairing in the ABDXYZ hybrids

Hybrids	No. of cells examined	Bivalents	
		No. cell M±m	Variation range
1	57	8.56±0.15	6–10
2	84	9.40±0.21	3–15
3	54	5.93±0.20	0– 9
4	53	7.11±0.59	0–15
5	50	6.94±0.18	5–10
6	50	10.16±0.28	6–13
7	50	6.70±0.18	4– 9
8	52	11.10±0.21	7–15
9	83	7.40±0.28	0–11
10	51	8.75±0.28	0–13
11	60	6.62±0.21	3–10
12	75	10.01±0.14	5–14
13	30	9.06±0.41	5–11
14	34	11.82±0.41	7–16
15	51	12.18±0.20	7–14
Total	835	8.82±0.52	0–16

cell (Fig. 3). In these hybrids, the majority of univalents divides equationally. As a result of equational division and regular segregation of chromatids to the opposite poles, dyads arise with the almost complete set from all six genomes.

There are reports indicating that the levels of wheat-rye meiotic pairing are high when the effects of genome dosage, genotypic environment and the interaction of genes controlling meiosis combine favourably. The genetics of the division of univalents has not been studied. Is there any relation between the level of homoeologous pairing and the regular division pattern of univalents as well as their misdivision? And is there any relation between the behaviour of univalents and the levels of ploidy in the viable gametes of the intergeneric hybrids of the first generations? If there are such relationships, how, then, is the behaviour of chromosomes in the haploid genome affected by the ploidy of the viable gametes of the F_1 hybrids, and how is

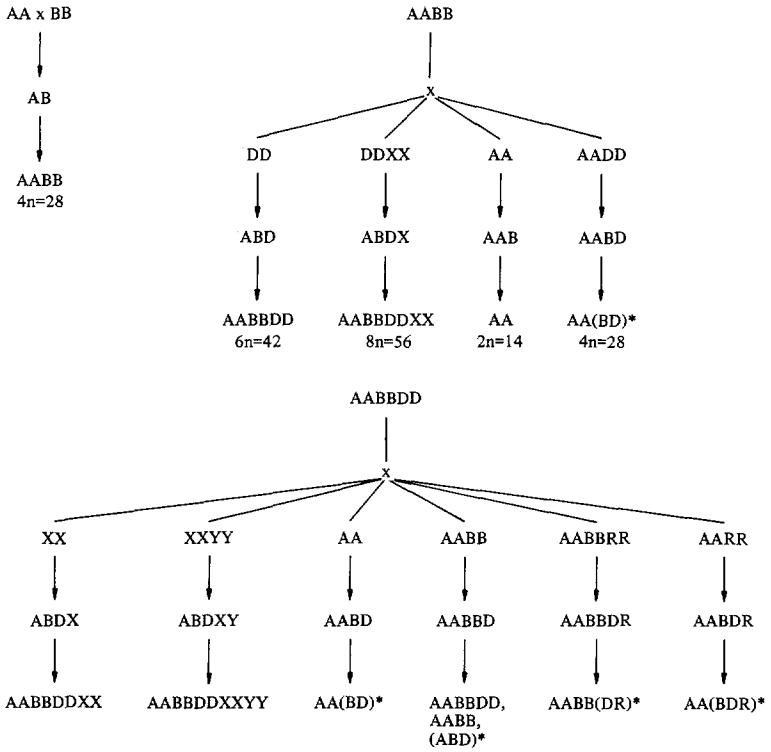

Fig. 4. A scheme for the possible pathways of karyotype stabilization in intergeneric hybrids obtained from different cross combinations

karyotype stabilization attained through successive generations?

Intergeneric hybrids with at least one diploid set of chromosomes (type I) differ from those with haploid sets only (type II) in the process of karyotype stabilization. The viable gametes of type I hybrids have a reduced number of haploid genome chromosomes, and these combine into diverse genomes offering opportunities for evolutionary improvement. Almost all the viable gametes of type II hybrids have complete sets from all the genomes. When self-pollinated, they give rise to primary amphiploids. Combinations of chromosomes giving rise to novel genomes are rare. Exceptional are instances when the gametes happen to be aneuploids for chromosomes from various homoeologous groups.

We interpret the results of our analysis of the behaviour of haploid genome chromosomes as being due to the interplay of different genomes, i.e., due to intergenomic effects. Thus viewed, increase in the level of homoeologous pairing in association with the reductional division of univalents would promote regular disjunction of chromosomes in the AII of meiosis and thereby reduce their number. The probability of gametes occurring with an balanced chromosome set during meiotic division of this kind would then be higher than in the case when there is predominantly equational separation and homoeologous pairing level is high. In type II hybrids, gametes with balanced chromosome sets may arise in either situation, viz., when the majority of univalents divide equationally in the absence of homoeologous bivalents and also when the majority of univalents divide reductionally at a high level of homoeologous pairing. One of the major factors determining karyotype stabilization in intergeneric hybrids appears to be the genome structure of the initial parents.

The data we have obtained may be expressed in terms of evolution. A scheme is suggested in which the contribution of genome structure to karyotype stabilization comes into the picture (Fig. 4). According to this scheme crosses between diploids produce amphiploids only. When tetraploid and hexaploid species are involved, there arise, along with primary amphiploids, forms with reconstructed genomes. The involvement of hexaploids is most consequential in giving newly associated genomes: this might have conceivably been how natural selection was at work, modelling, making multiplex, tinkering, discarding, perpetually changing and culminating in the creation of polyploids through the greatest diversity of karyotypes.

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