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Recombination of R-D chromosome in pollen plants cultured from hybrid of 6x *Triticale* × common wheat

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Summary. Ninety-three pollen plants derived from the hybrid F_1 of $6x$ *Triticale* × common wheat were observed cytologically. The rye chromosomes presented in these plants were identified by Giemsa-banding. Pollen plants having chromosome constitution $2n=24$ in haploids and $2n=46$ in diploids were found to be predominant. The chromosome distributions of the R and D genome are different. R chromosomes distributed randomly and tended to full combination in offspring, but D chromosomes distributed non-randomly and tended to maintain intact.

Key words: *Triticale* – Pollen plants – C-banding – Chromosome recombination

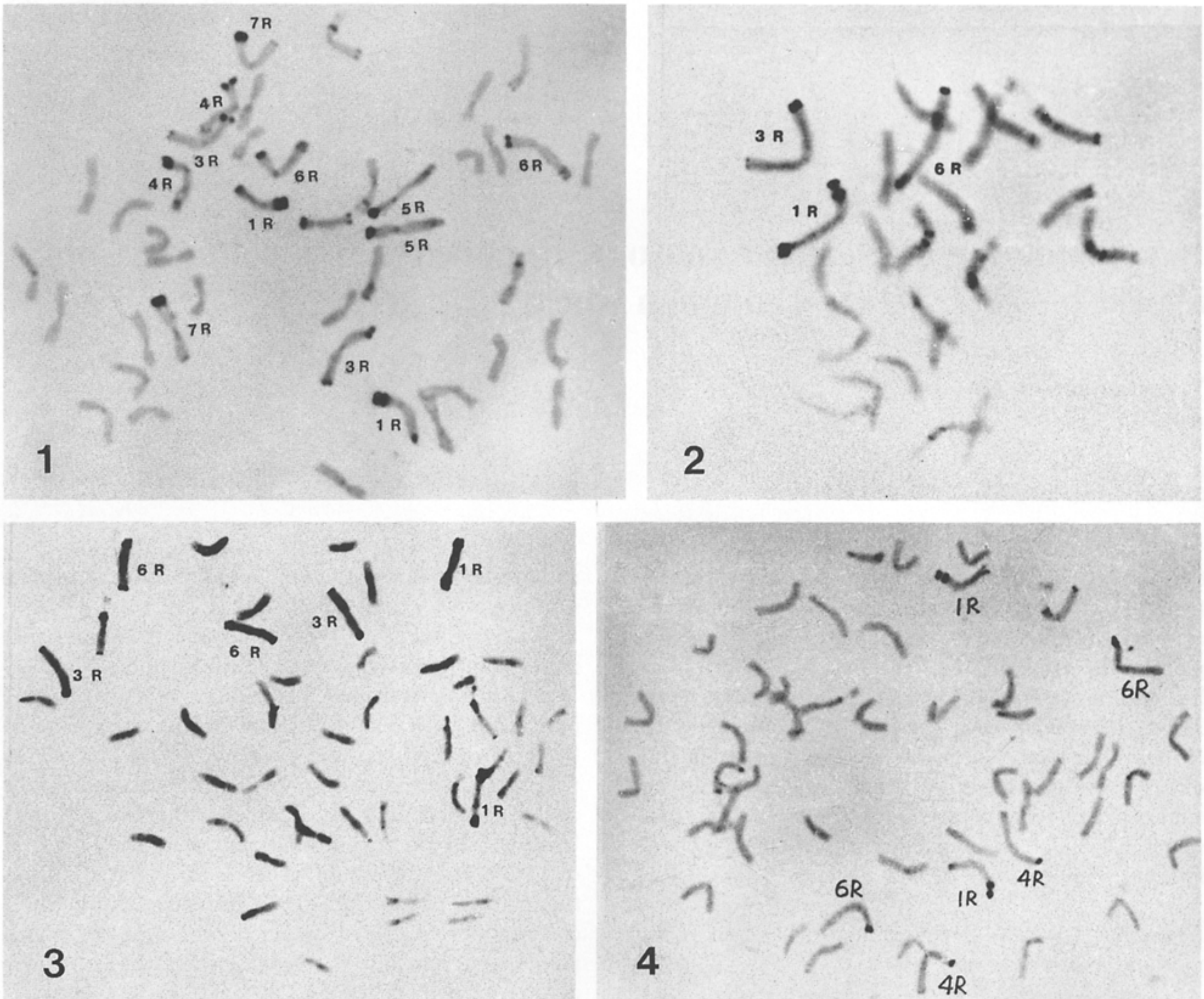
Introduction

The transfer of alien material to crop plants is an important method to increase genetic variability of different crop species. The cross of hexaploid *Triticale* × common wheat has encouraging potential in transferring useful genes from rye genome to wheat (Müntzing 1979; Gupta and Priyadarshan 1982). The F_1 hybrids of such a cross have the genomic constitution AABBDR and they will produce gametes with various compositions. Since the plants are predominantly self-pollinating, the ultimate result, after a few generations of selfing, would theoretically be a complete range of plants having a large number of mixtures of R and D chromosomes. Among the large number of possible combinations of R and D chromosomes, some may be desirable and can be used in a breeding program. However, such combinations are sometimes difficult to obtain because natural selection is also involved in the sexual process. It may be of interest to discover how the R and D chromosomes recombinate and to ascertain the pattern of rye chromosome transmission to progenies.

Many experiments have been conducted to look into these problems (Merker 1975; Gustafson and Zillingsky 1979; Lukaszewski and Apolinarska 1981), and some information was obtained. However, the materials used by these researchers were progenies of the hybrid between $6x$ *Triticale* and common wheat derived by the conventional method. Since anther culture has proven to be a fine tool for crop improvement, using the F_1 hybrid of $6x$ *Triticale* × common wheat as the material for anther culture, pollen plants with diversified chromosome constitutions might be obtained. The types of pollen plants were basically the same as the types of pollen chromosome constitutions formed by F_1 hybrid's meiosis (Hu 1983; Hu and Huang 1987). Using this knowledge, we can conveniently and directly investigate the problems mentioned above. The primary analysis of chromosome constitution of pollen plants derived from the hybrid of $6x$ *Triticale* × common wheat and $8x$ *Triticum-Agropyron* × common have been reported (Wang and Hu 1983, 1985; Miao et al. 1988). The aim of this paper is to investigate the combination of R and D chromosomes and to further search for the common pattern of rye chromosome transmission to offspring.

Materials and methods

The materials used in this study came from a cross between $6x$ *Triticale* cv Beagle and common wheat cv Orofen. The procedure of anther culture is the same as that of Wang and Hu (1983). For the observation of chromosome constitutions of root-tip cells, the aceto-carmin squash method was employed. The C-banding technique used in this study followed the method of Bennet and Smith (1975) and Bennet et al. (1977) with some modifications. The identification of rye chromosome is based on the C-banding pattern according to Sybenga (1983).



Figs. 1–4. 1 C-banded chromosomes of *Triticale* cv Beagle. **2** C-banded chromosomes of haploid ($2n=23$) and **3** and **4** diploid pollen plants ($2n=46$; $2n=48$)

Results

Based on 3,990 anthers of the F_1 obtained from $6x$ *Triticale* Beagle × common wheat Orofen cultured, 105 green pollen plants were obtained. The root-tip cells of 93 pollen plants, including 58 haploids and 35 diploids, were examined cytologically.

Chromosome number of pollen plants

The number of chromosomes of pollen plants ranged from 20–26 for haploids and 38–52 for diploids. There were more plants with chromosome constitutions $2n=24$ in haploids and $2n=46$ in diploids than any others.

Chromosome constitutions of pollen plants

The results of C-banding showed that maternal *Triticale* Beagle had only six pairs of rye chromosomes; it contained a whole set of R genome except 2R (Fig. 1).

The number of rye chromosome. Rye chromosome, ranging from 1–5 (pairs), were found in 90 pollen plants. The plants with three pairs of rye chromosomes were most often observed and the plants with six pairs of rye chromosomes were not observed (Figs. 2–4).

The number of wheat chromosome. The number of wheat chromosomes of pollen plants was from 17–22 (pairs), while 20 and 21 wheat chromosomes were frequently

Table 1. Chromosome number of pollen plants

No.	19	20	21	22	23	24	25	26	41	43	Mixo-	Total
	38	40	42	44	46	48	50	52			ploid	
Haploid		1	3	13	12	14	12	2				57
Diploid	1	1	3	4	6	4	1	1	1	1	12	35
Total	1	2	6	17	18	18	13	3	1	1	12	92
OF	0.011	0.022	0.065	0.183	0.194	0.194	0.140	0.032				
EF	0.110	0.154	0.173	0.154	0.110	0.062	0.024	0.006				

OF, observed frequency
EF, expected frequency
$\chi^2 = 170$
$P < 0.001$

Table 2. Number of rye chromosomes presented in pollen plants

No.	0	1	2	3	4	5
Haploid	1	2	9	24	17	5
Diploid	2	4	11	9	8	1
Total	3	6	20	33	25	6
OF	0.032	0.064	0.215	0.355	0.269	0.064
EF	0.016	0.065	0.161	0.313	0.161	0.065

OF, observed frequency
EF, expected frequency
$\chi^2 = 5.948$
$P > 0.05$

Table 3. The number of wheat chromosomes presented in pollen plants

No.	17	18	19	20	21	22
Haploid	2	3	7	23	17	6
Diploid	1	1	7	10	13	3
Total	3	4	14	33	30	9
OF	0.032	0.043	0.151	0.344	0.323	0.097
EF	0.219	0.273	0.219	0.110	0.031	0.004

OF, observed frequency
EF, expected frequency
$\chi^2 = 541$
$P < 0.001$

Table 4. Number of different rye chromosomes presented in pollen plants

Rye chromosome	1R	2R	3R	4R	5R	6R	7R
Single	35		32	25	24	41	20
Pair	20		14	15	10	19	6
Telosome	1		6		3		3
Total	56		52	40	37	60	29

found. This implies that all wheat chromosomes of D genome stayed intact (Table 3).

Transmission of rye chromosomes

Different rye chromosomes appeared differently in pollen plants. The most frequent of these were 6R, 1R, 3R; the second and the least frequent was 7R.

Statistical analysis

At meiosis, the typical chromosome pairing of the F_1 hybrid will be 14 bivalents + 14 univalents, where the bivalents are comprised of all the A and B chromosomes and the univalents represent 7R and 7D chromosomes. In a case of 14 univalents which are distributed at random into the gametes, the chromosome distribution can be demonstrated by the formula $(p+q)^n$, p and q representing the presence or absence of one chromosome respectively, and n being the number of the chromosomes analysed. As regards the distribution of R-D chromosome jointly and R chromosome, D chromosome separately, the n in the formula will be 14, 13 and 12, respectively. Comparing the chromosome distribution which we observed in pollen plants with that expected, one which came from the formula $(p+q)^n$, some interesting results were obtained. The χ^2 test indicated that the distribution of chromosomes which were involved in different genomes, e.g. R genome, D genome and R-D mixed genome were quite different. By considering D genome and R-D mixed genome, there was a significant deviation between the chromosome distribution observed and expected, but between R genome such deviation of chromosome distribution was not found (Figs. 5–7).

Discussion

Theoretically, 15 kinds of gametes in which the chromosome number ranged from 14–28 will be formed in the

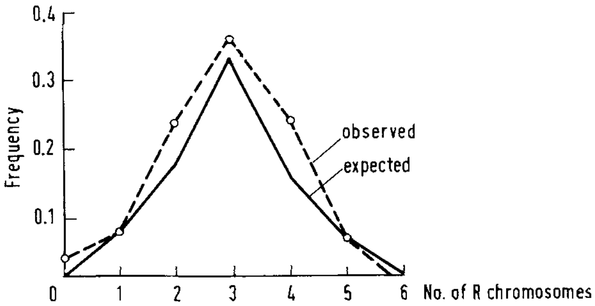


Fig. 5. The distribution of R chromosomes of pollen plants

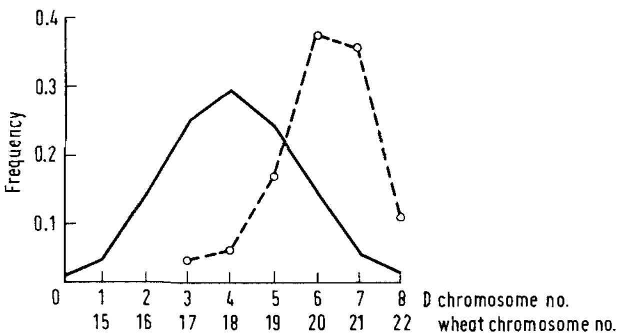


Fig. 6. The distribution of D chromosomes of pollen plants

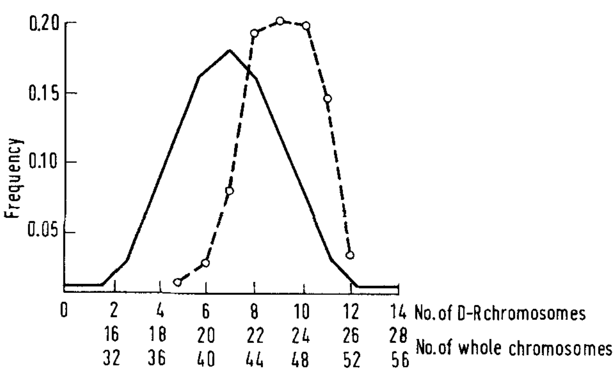


Fig. 7. The distribution of R-D chromosomes of pollen plants

hybrid of $6x$ *Triticale* × common wheat, because the R and D chromosomes remain univalents and are distributed at random into the gametes at meiosis. According to the distribution formula mentioned earlier, the gametes with 21 chromosomes should be predominant. This conclusion implies that among the population derived from anther culture, the plants with chromosome constitution $2n=21$ in haploid and $2n=42$ in diploid surely occur more frequently than others. However, the results we observed do not suggest such a conclusion. The predominant chromosome number of pollen plants was $2n=46$ or $2n=48$ rather than $2n=42$. Wang and Hu (1985) also found this phenomenon in their work.

It is of interest to note that in septuploid hybrids, the situation seems to be different. Miao et al. (1988) cytologically analysed pollen plants derived from F_1 of $8x$ *Triticum-Agropyron* (AABBDDEE) × $6x$ wheat (AABBDD). Eight kinds of gamete genotypes (ABDE 0–7) with chromosomes 21–28 were all found among 92 pollen plants which were examined cytologically. The statistical analysis by means of χ^2 test demonstrated that the distribution of various types having different number of chromosomes agreed with the expected one (Miao et al. 1988). Comparing the genomes AABBDDE and AABBDR, obvious differences in the part of heterologous chromosomes were observed. In the former, only the E genome was involved in the chromosome constitution, but the D and R genomes were involved in the latter. It is not difficult to imagine that the action controlled by the cooperation of two genomes is surely more complex than that controlled by only one genome. Although the distribution of R chromosomes is random, which is the same as E chromosome in $7x$ hybrid, the distribution of D chromosomes is not random. It is this non-random distribution of D chromosomes that caused the non-random distribution of total univalents of gametes. As a result of the cooperation of these two genomes, gametes having 23 or 24 chromosomes were produced predominantly. This is why the pollen plants with chromosome constitution of $2n=23/24$ in haploids and $2n=46/48$ in diploids were observed in the highest frequency. These pollen plants, whose chromosome constitution includes almost whole wheat chromosomes and different rye chromosomes as well, are difficult to obtain through conventional cross methods. They may play an important role in breeding practice and genetic research and will probably be a new species.

Both R and D genomes are monosomic dose in composition of the F_1 hybrid and have no homologous pairing at meiosis. But, just as we observed, they expressed different distribution. This result is difficult to explain mathematically by calculating random distribution. Analysing every genome of chromosome composition of hybrid, we noticed that the genetic background of R genome was very different from that of D genome. Just as A and B genome, D genome is also a part of chromosome constitution of common wheat, but R genome is only a distant relative genome. It is obviously that the homoeologous relationship between D, R and A, B genome are very different. Compared with the close relationship between D and A, B chromosomes, the relationship between R and A, B chromosomes seemed to be negligible (Kimber and Alonso 1981). The presence of this remote different relationship could be due to the different chromosome distribution of D and R genomes. However, in order to explain it clearly, further research is needed.

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