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Gamete composition and chromosome variation in pollen-derived plants from octoploid *triticale* × common wheat hybrids

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Summary. Anther culture of secondary octoploid *triticale* (AABBDDRR) and F_1 hybrids (AABBDDR) of octoploid *triticale* × common wheat crosses was carried out, and 96 pollen-derived plants were developed and studied cytologically. In addition to the 8 types of pollen-derived plants with the theoretically predicted chromosome number, plants with the chromosome constitutions of $2n = 38$, 43, 45, 47, 74, and mixoploids were obtained. The haploids and the diploids had different distributions. The frequencies of plants with one and two (pairs of) rye chromosomes were extremely high, and anther culture may be an expeditious route for creating alien addition lines of distant hybrid F_1s. Chromosome aberrations, including deletions, inversions, translocations, as well as isochromosomes and ring chromosomes, were observed in some plants. Abnormal meioses, such as chromosome non-disjunction, were also found. The reasons for the chromosome aberrations are discussed.

Key words: Pollen-derived plants – C-banding – *Triticeae* – Chromosome aberrations – Chromosome non-disjunction

Introduction

In the *Triticeae* alien genomes are rich and useful sources of genes for crop improvement. Consequently, efforts have been made to transfer hardiness, and disease and insect resistance genes from the wild, related species to the cultivated species, and several disease and insect resistance genes have already been transferred to wheat (Sears 1956; Zeller 1973; Asiedu et al. 1990; Friebe et al. 1990). In particular, rye, *Secale cereale* L., is an important source of disease and pest resistance genes for the improvement of cultivated wheat (Riley and Macer 1966; Zeller and Hsam 1983).

Anther culture has many uses in genetic studies and plant breeding in that by means of this technique various types of recombinant gametes can be fully expressed at the plant level and new types of recombinant plants which are difficult to obtain by conventional methods can be created (Hu and Huang 1987). In combination with distant hybridization the anther culture technique has proved to be a unique and expeditious route for the introduction of alien genes or chromosomes into wheat cultivars (Wang and Hu 1985; Miao et al. 1988; Tao and Hu 1989).

In the paper presented here we describe a cytological survey of pollen-derived plants regenerated from the distant hybrid between octoploid *triticale* and common wheat and present evidence that all possible gametic types of the F_1 are fully represented at the pollen plant level. We also analyse the reasons for chromosome variation in pollen-derived plants and discuss the possibility of obtaining alien disomic addition lines directly by culturing the anthers of F_1 hybrids.

Materials and methods

Three lines of secondary octoploid *triticale*, AH1001F_5, AH1095F_4, and Xinmai No. 14, were crossed to common wheat cv 'Kedong 58'. The anthers of the three F_1 hybrids and Xinmai No. 14 were then cultured in vitro.

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Anther culture

Anthers at the late uninucleate stage were inoculated onto induction media, Potato-II medium (Chuang et al. 1978) and W_{14} medium (Ouyang JW et al. 1989). Induced calli were transferred onto 190-2 medium (Zhuang et al. 1984) for plant regeneration.

Investigations of somatic cells

Chromosomes of pollen-derived plants were examined at mitosis using squashed preparations of root tips. Actively growing root tips were excised and pretreated in ice-water for 24 h, fixed in 3:1 acetic-alcohol at room temperature for 1 day, then stored at 4 °C until examination. For staining, root tips were put into 1% aceto-carmine solution, heated slightly, and then squashed with 45% acetic acid.

C-banding

The C-banding technique used in this study followed the method of Wang and Hu (1985) and Tao and Hu (1989) with some modifications. Identification of the rye chromosomes is based on the C-banding pattern according to Sybenga (1983).

Investigation of chromosomes in pollen mother cells (PMC)

Young spikes at the appropriate stage were excised and fixed in 3:1 acetic-alcohol for 12 h. The anthers were then removed and squashed in 1% aceto-carmine solution for examination of meiotic chromosomes.

Results

Chromosome constitutions of the pollen plants

Pollen plants derived from 2n = 49 triticale hybrids. The three F_1 heptaploid hybrids differed greatly in frequencies of induction and regeneration from anther culture. Out of a total of 3305 anthers that were cultured, 938 calli were induced and 313 green plantlets produced. Subsequently, 88 of the green pollen-derived plants were cytologically examined. About 50% of the pollen-derived plants had doubled their chromosome numbers spontaneously.

Among the 88 pollen-derived plants, more than 13 groups of plants with various chromosome numbers were obtained. Pollen-derived plants with a chromosome constitution of 2n = 38, 43, 45, 47, and 74 and mixoploids were found, in addition to the 8 expected types. Pollen plants with a chromosome constitution of 2n = 23(46) were the most frequent, followed by n = 24 in the haploids and 2n = 44 in the diploids (Table 1).

Pollen plants derived from octoploid triticale. Octoploid *triticale* is not very stable and multivalents can be found in PMCs. Among the 8 pollen plants regenerated from Xinmai No. 14, 5 were aneuploid with chromosome numbers of 2n = 25 (2 plants) and 2n = 27 (3 plants); the rest were mixoploids. No pollen plants with 28 (or 56) chromosomes were obtained.

Chromosome variation in the pollen plants

In addition to a variation in chromosome number in the pollen-derived plants, such as 2n = 29, 38, 43, 45, 47, and 74, a variation in chromosome structure, including telocentrics, acrocentrics and dicentric chromosomes, isochromosomes, an inversion chromosome, a ring chromosome, and chromosome fragments, was also observed (Table 2). Unusual chromosome constitutions were found in many of the plants. For example, the usual chromosome number of plant B151 was 2n = 38. In one cell, a dicentric chromosome was found (Fig. 1a) and in another a chromosome fragment; however, most of the cells possessed neither of these, and C-banding of the mitotic chromosomes revealed the presence of two rye chromosomes, 1R and 3R. In the PMCs there were 10–14 bivalents (usually appearing to be ring bivalents) and 10–18 univalents. Plant VS47 had 44 chromosomes with a pair of 1R chromosomes, but contained a wheat telochromosome and a wheat deletion chromosome.

Most of the pollen-derived plants had an identical chromosome constitution within any 1 plant. Some

Table 1. Chromosome numbers of the pollen-derived plants regenerated from the F_1 hybrids

Number	21	22	23	24	25	26	27	28	38					Mixoploid	
	42	44	46	48	50	52	54	56		43	45	47	74		Total
Haploid	1	4	10	10	7	3		1	3					2	41
Diploid	3	7	14	5	3	2	1			1	4	4	1	2	47
Total	4	11	24	15	10	5	1	1	3	1	4	4	1	4	88
OF	.045	.125	.273	.170	.114	.057	.011	.011							
EF	.008	.055	.164	.273	.273	.164	.055	.008							

OF, Observed frequency; EF, expected frequency (based on binomial expectations)
$\chi^2 = 66.33$; $P < 0.005$

Table 2. Pollen-derived plants with chromosome structural variation

Number of chromosomes	24	25	29[b]	38	44	45	46	47	48	52
Number of plants	2	2	1	1	2	2	1	3	1	1
Aberration[a]	t, a	t	i	d	t, a	t, 1BL$^-$	t	t, r, inv	t, a	t

[a] a, Acrocentric chromosome; d, dicentric chromosome; i, isochromosome; r, ring chromosome; t, telocentric chromosome; inv, inversion chromosome; 1BL$^-$, 1B long arm deletion

[b] Derived from a 8x *triticale*, all others were derived from 7x hybrids

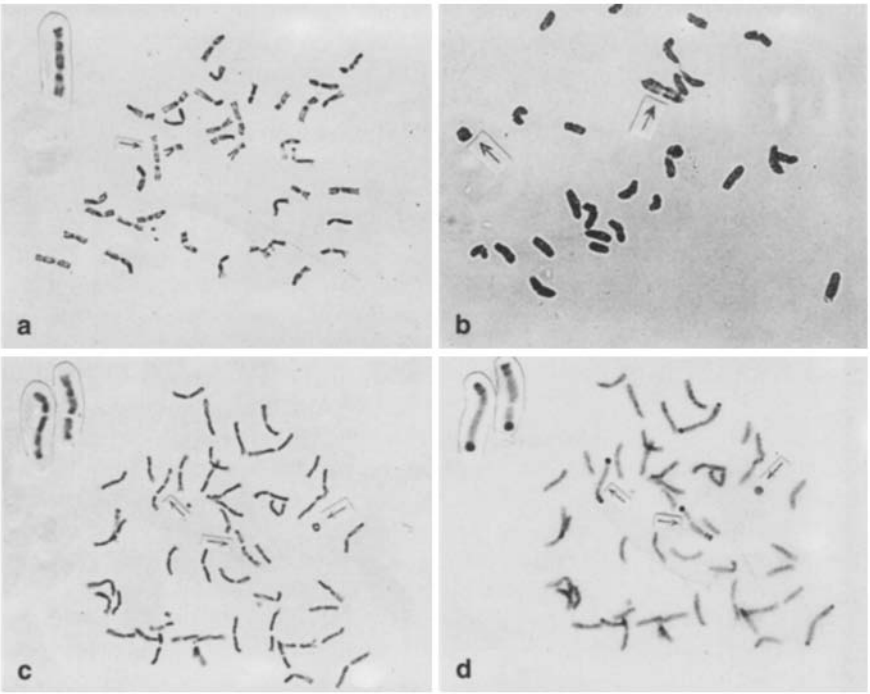

Fig. 1. a A root-tip cell of pollen-derived plant B151, 2n = 38, with a dicentric chromosome indicated by an *arrow*. **b** A pollen mother cell (PMC) of B115, 2n = 29, with a spherical univalent indicated by the *arrow* on the left and a ring bivalent indicated by the *arrow* on the right. **c** A root-tip cell of pollen-derived plant B150, 2n = 47 + r. **d** The same cell as **c** after Giemsa C-banding treatment. It contains a ring chromosome and a pericentric inversion for chromosome 1R. The *arrows from left to right* indicate the normal 1R chromosome, the inversion 1R chromosome, and a ring chromosome respectively

plants, however, were mosaics. Pollen plant B115, derived from the 8x *triticale*, for example, was a mosaic with two main kinds of chromosome constitutions in the root tips: 2n = 28(40%) and 2n = 29(60%), both possessing an evident isochromosome 1BS.1BS and one normal 6B. In the PMCs of B115, the percentages of the two kinds of cells, 2n = 28 and 2n = 29, were 54% and 46%, respectively. Of the PMCs with 28 chromosomes 35% had chromosome fragments while only 5% of the PMCs with 29 chromosomes had chromosome fragments. This difference in the ratio of n = 29 and n = 28 in somatic cells and PMCs demonstrates the tendency towards chromosome reduction. A spherical univalent and a ring bivalent were found in the PMCs (Fig. 1b) of pollen plant B115 that were rarely observed in other haploid pollen plants.

Pollen plant B150, which was derived from a heptaploid hybrid, was another mosaic. Of the 50 cells analysed cytologically, cells with 47 chromosomes were the most frequent (50%). Approximately 14% of the cells had 48 chromosomes, and about 25% had the constitution of 2n = 47 + a ring chromosome. A chromosome inversion was observed in some cells. Giemsa C-banding demonstrated that the cells of B150 possess two pairs of rye chromosomes, 1R and 3R. Comparing two photographs of 1 cell taken before and after Giemsa C-banding, we found a pericentric inversion in one of the two 1R chromosomes: it has two strong heterochromatin bands in the long arm and one strong band in the short arm. The other 1R was normal, with two heterochromatin bands in the short arm and one in the long arm (Fig. 1c, d). All of the cells with a ring chromosome in which 1R was identified by Giemsa C-banding had a 1R pericentric inversion. However, no 1R pericentric inversion was found in cells with 48 chromosomes.

Pollen plants B91 and B92, regenerated from different calli induced from the same donor plant, generally had a chromosome constitution of 2n = 47 (about 70%). Both had a pair of 6R chromosomes and

Table 3. The number of rye chromosomes in 20 pollen-derived plants

Chromosome numbers	23	24	38	42	43	44	46	47
No. of plants	2	1	1	1	1	6	5	3
No. of rye chromosomes	2	3	2	0	2	2	4	4
No. rye chromosome pairs	0	0	0	0	1	1	2	2

a pair of unidentified rye telochromosomes. However, segregation occurred in the H_2 progenies, and some of the progenies exhibited resistance to powdery mildew.

Abnormal meiosis was also found in some pollen plants. For example, plant VS118 was a diploid mixoploid in whose PMCs non-disjunction was found. At anaphase I of meiosis, two homologous bivalents were seen to move towards the same pole, while the others had separated, and the daughter chromatids of each homologous chromosome had moved towards their respective poles.

The number of rye chromosomes in the pollen plants

Twenty pollen plants derived from 7x *triticale* hybrids were examined with the Giemsa C-banding technique, and the results are listed in Table 3. Rye chromosomes existed as pairs in the diploids but were unpaired in the haploids. Generally when the chromosome numbers exceeded 21 (in haploids) or 42 (in diploids) the pollen plants contained a rye complement. This suggests that the plants with 21(42) to 28(56) chromosomes have zero to seven (pairs of) rye chromosome additions.

Discussion

We have used the anther culture technique to regenerate green pollen plants from both 8x *triticale* and 7x hybrids between octoploid *triticale* and hexaploid common wheat. Various gametic types were present in these pollen-derived plants, and chromosomal changes were also obtained.

Chromosomal composition of the pollen-derived plant

The hexaploid, genome constitution AABBDR, was employed in anther culture by Wang and Hu (1985) and Tao and Hu (1989). Wang and Hu (1985) obtained a variety of chromosome complements. The predominant chromosome number of the pollen-derived plants was $2n = 23(46)$ and $2n = 24(48)$ rather than $2n = 42$. Similar results were obtained by Tao and Hu (1989). To make a more thorough investigation, these workers distinguished rye chromosomes using C-banding and discovered that the chromosome distributions of R and D chromosomes were different: R chromosomes were distributed randomly, but D genome chromosomes were distributed non-randomly and tended to be maintained as a whole genome. Miao et al. (1988) cytologically analysed pollen plants derived from the F_1 of 8x *Tritirigia* (AABBDDEE) × wheat (AABBDD). All eight types of pollen-derived plants with the theoretically predicted chromosome numbers based on binomial probabilities were obtained, and statistical analysis by means of χ^2 tests demonstrated that the E genome chromosomes were distributed randomly (Miao et al. 1988).

In our study of pollen plants derived from a 7x hybrid, genome constitution AABBDDR, various gametic types were obtained. However, the rye chromosome distribution, if we use the statistical method used by the former authors, does not appear to be at random ($P < 0.005$), which is somewhat different from the conclusions drawn by Miao et al. (1988) and Tao and Hu (1989) (Table 1). We assume that all plants with an even number of chromosomes (in the diploid state) have completely homologous pairing. Almost all even numbered diploid plants came directly from doubled haploid plants without any variation in chromosome number, although variations in chromosome number did occur at low frequencies in pollen-derived plants, which usually then formed odd numbered plants in diploid. These even numbered plants ought to have only bivalents and not multiple univalents, and the results listed in Table 3 shows no exceptions.

A statistical analysis of the pollen-derived plants within each level of ploidy shows that the distributions of haploids and diploids were quite different. χ^2 tests demonstrated that the rye chromosomes distributed randomly in the haploids ($P > 0.05$) but not in the diploids ($P < 0.005$) (Table 4).

When the data obtained from Wang and Hu (1985), Miao et al. (1988), and Tao and Hu (1989) are analysed it is apparent that all the results suggest that the E or R chromosomes are distributed randomly in haploids but that the chromosome number tends to be diminished in diploids. Because the number of diploids in their studies was low, it is possible that the deviations of the diploids are not evident. In our study, however, the ratio of diploids is higher (about 53%), and the deviation is reasonably clear. It is the deviation caused by the diploids that makes the whole distribution of the pollen plants shift.

The results obtained by Zhong and Zhang (1987) correspond with the above explanation. They analysed a population of diploids in both F_2 (195 plants) and B_1F_1 (695 plants) generations of a 8x *Trititrigia*

Table 4. Observed and expected distributions of pollen-derived plants

Haploids									
Number	21	22	23	24	25	26	27	28	Total
ON	1	4	10	10	7	3	0	1	36
EN	0.3	2.0	5.9	9.8	9.8	5.9	2.0	0.3	36
$\chi^2 = 12.34$ $P > 0.05$									
Diploids									
Number	42	44	46	48	50	52	54	56	Total
ON	3	7	14	5	3	2	1	0	35
EN	0.3	1.9	5.7	9.6	9.6	5.7	1.9	0.3	35
$\chi^2 = 59.95$ $P < 0.005$									

ON, Observed number; EN, expected number

(AABBDDEE) × 6x common wheat (AABBDD) cross and found that both of the two observed distributions shifted towards the lower end, which contrasted expectations. They believed that the main factor causing the reduction in chromosome number was the loss of laggard univalents at meiosis. However, this can only be one of the factors for it cannot explain why the distributions of chromosome number are different between haploid pollen plants and diploid pollen plants. Chromosome compensation is possibly the predominant influence in the chromosome numbers of the plants.

Comparing the results here with those of Zhong and Zhang (1987), we get many varied genotypes from a smaller population (88 plants) within a shorter time by using anther culture. Moreover, most of the pollen plants are relatively stable without segregation and we can analyse the gametic types of a F_1 hybrid directly at the plant level. The frequency of pollen plants with 22 or 44 chromosomes, derived from F_1 heptaploid hybrids, is so high that we can obtain sufficient disomic alien addition lines directly by anther culture.

Chromosome variation in the pollen-derived plants

Types of aberration in plants. Chromosome variation is known to occur naturally in both wheat and *triticale*, and chromosomal variation has also been observed in hybrid offspring. Translocations and deletions have been found in the progenies and 6x *triticale* × wheat (May and Appels 1982; Lukaszewski and Gustafson 1983; Merker 1984). Plenty of reports have demonstrated that genetic variation occurs from in vitro culture (reviewed by Larkin 1986; Jordon 1990; Hu 1990). Armstrong et al. (1983), Lapitan et al. (1984), and Brettell et al. (1986) reported deletions during tissue culture of *triticale*. Armstrong et al. (1983) and Lapitan et al. (1984) also found wheat/rye translocations in regenerated plants. Lapitan et al. (1988) reported the duplication of repeated DNA sequences. Isochromosomes were also found by Karp and Maddock (1984) and Davies et al. (1986) in wheat tissue culture. Although inversions have seldom been reported in regenerated plants. Ahloowalia (1982) suggested that inversions do occur in regenerated wheat plants based on his observation of bridges and fragments at meiosis anaphase I.

The anther culture technique is not only a means of producing haploid and homozygotes but is also a good way of creating gametoclonal variation (Hu and Huang 1987). Variations such as telosomic and dicentric chromosomes, isochromosomes, and deletion and breakages were found by anther culture (Hu et al. 1982, 1983; De Buyser et al. 1985; Charmet et al. 1986). In our experiment of culturing anthers of 8x *triticale* and 7x *triticale* × wheat hybrids, nearly 20% of the pollen-derived plants possessed some kind of chromosome variation (including inversion), and it is clear that chromosome variability occurs very readily in pollen-derived plants.

Origins of variation. De Buyser et al. (1985) suggested that the chromosomal abnormalities found in DH plants originate in the anthers of donor plants or during the process of anther culture. Our study suggests that there are two periods that chromosome variation in the pollen plant may occur: before anther culture and/or during anther culture.

Before anther culture. Chromosome variation may already exist in the parent plants. Nakamura and Keller (1982) and Suarez et al. (1988) demonstrated the instability of secondary hexaploid *triticale* and wheat where abnormal meiosis may change the gametic chromosome number and induce structure change. Anther culture allows these abnormal gametes to be present at the whole plant level. Misdivisions produce isochromosomes, for example B115, and chromosome non-disjunction makes the gametic chromosome number either increase or decrease. The loss of laggard univalents may also reduce the gametic chromosome number. If we suppose that bivalent non-disjunction exists in the meiosis of the donor plant, we can successfully explain why some pollen-derived plants possess an abnormal number of chromosomes such as 29, 38, or even 74.

During anther culture. If no chromosomal variation occurs during culture, then the chromosome number of spontaneously doubled diploids must be even and all chromosomes (including aberrant chromosomes) should appear in pairs. Therefore, odd-numbered diploids, such as $2n = 41$, 43, 45, and 47, and those which have unpaired aberrations must have had their chromosome number and structure changed during culture. B150 is a good example of this and its chromosome inversion can only occur during culture. VS26 possesses 45 chromosomes with a $1BL^-$. It is interesting that $1BL^-$ and $6BL^-$ are repeatedly obtained from anther culture (Hu et al. 1982).

Wang and Hu (1985), Miao et al. (1988) and Tao and Hu (1989) have all observed abnormal chromosome constitution such as $2n = 41$, $2n = 43$ as well as chromosome structure variations in pollen plants, although they did not discuss the reason for the chromosome variation.

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