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TRITICALE

Proceedings of an international symposium
El Batan, Mexico, 1-3 October 1973

Editors: Reginald MacIntyre/Marilyn Campbell



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Preliminary Report on the Cytogenetics of Tetraploid \times Diploid Wheat Crosses¹

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Abstract Selections of *Triticum durum* and *T. persicum* were crossed to *T. monococcum*. Twenty-six seeds were obtained from the backcross of the F_1 plants to *T. monococcum*. Chromosome counts of 20 plants showed that 16 had 6 bivalents plus 9 univalents, or 7 bivalents plus 6-8 univalents. Each of the remaining four plants had 14 pairs of chromosomes. Because the F_1 plants failed to produce seeds without pollination, we believe a form of apomixis, pseudogamy, was involved in the origin of the four tetraploid plants. These four plants are self-fertile and exhibit characteristics of both parents. They will be used to expedite the transfer of desirable genes from *T. monococcum* into tetraploid and hexaploid wheats.

Sixteen of the 20 plants apparently resulted from the fertilization of eggs carrying 13 or 14 univalents. Apparently eggs carrying less chromosomes than 13 univalents were not fertilized or the young embryos aborted. Regardless of the cause, failure to obtain seeds carrying less than 20 chromosomes suggests it will be difficult if not impossible to develop a line carrying the A genome substituted into the cytoplasm of tetraploid wheats.

Résumé Des sélections de *Triticum durum* et de *T. persicum* ont fait l'objet de croisements avec *T. monococcum*. Le comptage des chromosomes de 20 plants a révélé que 16 d'entre eux comportaient 6 bivalents et 9 monovalents, ou 7 bivalents et 6-8 monovalents. Chacun des quatre plants restants comportait 14 paires de chromosomes. Etant donné que les plants F_1 n'ont pu produire de grains sans pollinisation, nous estimons qu'une forme d'apomixie, de pseudogamie, est intervenue à l'origine des quatre plants tétraploïdes. Ces quatre plants sont autogames et possèdent les caractères de leurs deux parents. On les utilisera pour activer le transfert des gènes désirables de *T. monococcum* aux blés tétraploïdes et hexaploïdes.

Il semble que 16 des 20 plants soient issus de la fécondation de noyaux comportant 13 ou 14 monovalents. Il semblerait que les noyaux comportant moins de 13 mono-

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valents ne soient pas fécondés ou que le jeune embryon avorte. Quelle qu'en soit la cause, le fait que l'on n'ait pu obtenir de grains comportant moins de 20 chromosomes laisse à penser qu'il est difficile, sinon impossible, de créer une lignée introduisant le génome A substitué dans le cytoplasme des blés tétraploïdes.

MANY selections of diploid wheat, *Triticum boeoticum* and *T. monococcum*, are resistant to one or more of the diseases that infect tetraploid and hexaploid wheats. Attempts to transfer resistance from diploid into tetraploid and hexaploid wheats have been seriously hampered by both female and male sterility of F_1 hybrids (Szalai and Belea 1962). All of the systems proposed to circumvent the sterility problem are complex and only a few seeds are produced each generation. Consequently, the probability that the desired genetic recombinants will be recovered in the advanced generations is very small.

Kihara et al. (1956) reported seed could be obtained from crosses of *T. persicum* \times *Aegilops squarrosa* as a result of union of unreduced gametes. Metzger and Silbaugh (unpublished data) obtained seeds from a cross of *T. durum*, selection D6644 \times *Secale cereale*, cult Antelope, which apparently resulted from the union of unreduced gametes.

Mann and Lucken (1970) reported cytoplasmic male sterility results when the AB or ABD genomes are substituted into cytoplasm of diploid wheats. Possible effects of tetraploid or hexaploid cytoplasm on the A genome have not been determined.

The objectives of the investigations covered in part by this preliminary report are: (a) to determine if the restitution process, followed by union of unreduced gametes, can be used to move genes from diploid into tetraploid wheats; (b) to determine if the A genome can be substituted into the cytoplasm of tetraploid wheats; and (c) to check for cytoplasmic-genome interactions.

Materials and Methods

Crosses were made between four diploid and four tetraploid species (Table 1). Two of the diploid lines (P.I. 167556 and W491-3) are resistant to all known races of common bunt, *Tilletia caries* and *T. foetida*. Selections W49-23 and 55B2.150 are susceptible. Saragolla, *T. durum*, is susceptible to bunt and it crosses readily with diploid wheats. *T. persicum* var. *stramineum* (hereafter designated T. per-5) is susceptible to bunt, crosses readily with diploid wheats, and, in crosses with *Ae. squarrosa*, seeds are produced by union of unreduced gametes (Kihara et al. 1956; Metzger and Silbaugh, unpublished data).

TABLE 1. Total number of tetraploid \times diploid F_1 plants produced, number used as female parents in backcrosses to diploid wheats, and number of backcross seeds obtained.

Tetraploid (female)	\times	Diploid (male)	No. F_1 plants		F_1 flowers pollinated by:			
			Total	Used in crosses	W49-23		55B2.10	
					Florets	Seeds	Florets	Seeds
Saragolla	\times	W49-1-3	38	5	3400	1		
"	\times	P.I. 167556	76	10	3700	0	1500	0
"	\times	W49-23	5	2	600	0		
"	\times	55B2.150	1	1	500	0		
<i>T. persicum</i> var. <i>stramineum</i>	\times	P.I. 167556	22	5	1500	4		
"	\times	P.I. 167556	22	5	800	0	400	0
NB69864	\times	W49-23	27	8	2400	10		
D6644	\times	P.I. 167556	21	6	1600	3	1800	7
"	\times	55B2.150	1	1	400	0		

Selection NB69864, *T. durum*, is a semi-dwarf winter type that crosses readily with diploid wheats. Its reaction to bunt is unknown. D6644, *T. durum*, crosses easily with diploid wheats and some selections of *Secale cereale* (Metzger and Silbaugh, unpublished data). We have failed in our attempts to cross D6644 with *Ae. squarrosa*.

The crosses and number of F_1 plants grown are listed in Table 1. The tetraploid parent was used as the female in each cross. Five to seven spikes on each of 32 F_1 plants were pollinated with pollen from diploid lines (Table 2). Twenty-four seeds were harvested from an estimated 10,000 pollinations. These

seeds were sown and the plants were again crossed to diploid wheats (Table 2).

Pollen mother cells (PMC's) were collected from F_1 plants and from 21 of the 25 backcross plants. Chromosome numbers were determined for representative F_1 plants of each cross and for 20 of the 25 backcross plants.

Results and Discussion

An analysis of chromosome numbers of the F_1 plants representing all five crosses revealed six pairs of chromosomes, seven univa-

TABLE 2. Chromosome numbers of backcross F_1 plants of (tetraploid \times diploid) $F_1 \times$ diploid wheats and number of seeds produced by florets pollinated by diploid wheats and selfed or open-pollinated flowers.

Plant no.	Backcross F_1 (Tetraploid \times diploid) $F_1 \times$ diploid		Chromosome no.	BC $F_1 \times$ diploid		BC F_1 selfed or open-pollinated		
				Florets pollinated	Seeds	Florets	Seeds	% set
G73- 2374	(Saragolla \times W49-1-3) F_1	\times W49-23		322	22	280	0	
2370	(T. per-5 \times P.I. 167556) F_1	\times W49-23	6" + (2') + 6'	96	1	1068	0	
2371	"	"	7" + 7'	372	1	729	0	
2372	"	"	6" + 9'	958	0	332	0	
2373	"	"	7" + 6'	186	0	204	0	
2351	(NB69864 \times W49-23) F_1	\times W49-23		52	0	468	0	
2352	"	"	7" + 8'	306	0	464	0	
2353	"	"	7" + 8'	192	0	564	0	
2354	"	"	"	312	1	364	0	
2355	"	"	7" + 7'	326	0	118	0	
2356	"	"	7" + 6' to 8'	380	0	330	0	
2357	"	"	7" + 8'	202	0	316	0	
2358	"	"	6" + 9'	318	1	642	0	
2359	"	"	7" + 8'	316	0	320	0	
2376	"	"	7" + 8'	444	0	460	0	
2361	(D6644 \times P.I. 167556) F_1	\times W49-23		126	0	334	0	
2362	"	"	7" + 8'	118	0	186	0	
2363	"	"	7" + 7'	296	2	238	0	
2364	(D6644 \times P.I. 167556) F_1	\times 55B2.10	14"	40	1	652	247	38
2365	"	"	14"	48	6	737	680	93
2366	"	"	14"			530	523	99
2368	"	"	14"			518	502	97
2360	"	"	"			328	0	
2367	"	"	6" + 9'	62	1	356	0	
2369	"	"	7" + 8'	188	0	272	0	

lents plus two univalents that frequently were attached by a thin thread of chromatin. Since the tetraploid and diploid parents have the A genome in common, we believe the six pairs plus the two univalents that were frequently associated represented the A genome chromosomes. Because one pair of the A chromosomes did not pair regularly, those two univalents were free to move to either pole at Anaphase I somewhat independently. Without exception the F_1 plants used in this study were vigorous and completely male sterile (Table 1). Information obtained from crosses of the F_1 plants with diploid lines (hereafter called backcrosses) follows.

(Saragolla \times W49-1-3) $F_1 \times$ W49-23

Although an estimated 3400 F_1 florets were pollinated with pollen from diploid plants, only one seed was set. The backcross plant grown from this seed was completely male sterile (Table 2). When it was crossed again to diploid wheats, 22 seeds were produced from 322 hand-pollinated florets. No seeds were produced by the 280 florets that were allowed to self- or open-pollinate. Sporocytes collected from this backcross plant, and analyzed much later, were found to have already undergone meiosis. Numerous micronuclei were observed in most of the immature pollen grains, which suggested the plant was an aneuploid carrying one or more univalents. We believe this plant resulted from the fertilization of an egg carrying the AB genomes with a male gamete carrying the A genome of the diploid parent. Phenotypically, the backcross plant was similar to the F_1 , which was used as the female.

(T. per-5 \times P.I. 167556) $F_1 \times$ W49-23

Four seeds were obtained from an estimated 1500 F_1 flowers pollinated with pollen of diploid wheat. Phenotypically, three of the four plants grown from these seeds were similar to the F_1 plants. These plants had chromosome counts of $7'' + 7'$, $6'' + 9'$, and $7'' + 6'$, respectively (Table 2). The fourth backcross plant, G73-2370, exhibited many characteristics of diploid wheat, *T. monococcum*, yet it had six pairs of chromosomes plus

eight univalents. Two of the univalents were infrequently joined by a thread of chromatin, which suggested they belong to the A genome. If true, the F_1 egg that was fertilized to give rise to this plant was apparently short one of the B chromosomes.

These four backcross plants were crossed again to diploid lines. Two seeds were obtained from 1612 pollinations (Table 2). All of the 2340 flowers that were allowed to self- or open-pollinate failed to set seed.

(D6644 \times P.I. 167556) $F_1 \times$ W49-23

Ten backcross seeds were harvested from an estimated 2400 F_1 florets pollinated with pollen of diploid wheats. The 10 plants grown from these seeds were phenotypically similar to the original F_1 plants. Chromosome numbers were determined for 8 of the 10 plants (Table 2). Five of the eight plants had seven pairs of chromosomes plus eight univalents. This suggests eggs carrying 15 univalents were fertilized by 7x male gametes. Because trisomics were not observed in the metaphase I plates, we assumed the extra univalent represented the chromosome from the A genome of NB69864 that paired infrequently in the F_1 plants. Apparently the eggs carried both chromosomes of that pair, one contributed by W49-23 and one by NB69864.

Chromosome numbers of the remaining three backcross plants were $7'' + 7'$ (G73-2355), $7'' + 6'$ to $8'$ (G73-2356), and $6'' + 9'$ (G73-2358) (Table 2). The A genome chromosome of the tetraploid parent that failed to pair in F_1 plants was apparently omitted from the egg fertilized to produce plant G73-2355.

An attempt was made to again backcross all 10 F_1 plants to diploid wheats. Two seeds were obtained from 2848 pollinations. This suggests the frequency of restituted female gametes or gametes, or both, carrying the A genome alone is very low. Flowers allowed to self or outcross failed to set seed.

(D6644 \times P.I. 167556) $F_1 \times$ W49-23

Three seeds were harvested from an estimated 1630 hand-pollinated flowers (Table 2). Chromosome numbers for two of the

three plants are also listed in Table 2. Phenotypically all three plants were similar to the original F_1 plant. Plants G73-2362 and G73-2363 were crossed again to diploid wheats. Two seeds were obtained from 540 florets. This again suggests restitution occurred infrequently in the backcross plants.

(D6644 \times P.I. 167556) $F_1 \times$ 55B2. 10

Phenotypically, the seven backcross plants, obtained from an estimated 1800 pollinations, fell into two classes: self-fertile and self plus cross-sterile. Four of the plants had 14 pairs of chromosomes and were self-fertile (Table 2). Seed set under bags ranged from 38% on plant G73-2364 to 99% on plant G73-2366. The origin of these four tetraploid plants is not clear. The F_1 plants were male sterile and failed to produce seeds when allowed to self-pollinate. It appears, therefore, that pollination was necessary for the formation of germinable backcross seeds. We suspect the unreduced egg cells were not fertilized but the male gamete united with the fusion nucleus to give rise to the endosperm. Apomicts of this type are not uncommon. Such pseudogamous species occupy an intermediate position between normally sexual species and typical apomicts, in which pollination is unnecessary (Muntzing 1967). In order for eggs carrying 14 pairs of chromosomes (AB genomes) to be produced, one must assume the first meiotic division was completed and that restitution occurred at telophase I. This would account for the loss of seven nonhomologous chromosomes of the A genome. Crossing over between homologous A genome chromosomes and the inclusion of one or more chromosomes of the diploid parent in eggs carrying 14 chromosomes would allow genes to be transferred from the diploid parent into the new apomictically produced tetraploids.

Backcross plant G73-2367 had six pairs of chromosomes plus nine univalents. One seed was obtained from the pollination of 62 florets with *T. monococcum* pollen. Seven pairs of chromosomes plus eight univalents were observed in PMC's of plant G73-2369. The chromosome number was not determined

for plant G73-2360. Because it was both self- and cross-sterile and phenotypically approached the F_1 , we believe it had either $7'' + 7'$ or $7'' + 8'$.

The recovery of tetraploids among the backcross plants of (D6644 \times P.I. 167556) $F_1 \times$ 55B2.10 indicates genes can be transferred from diploid lines of *T. monococcum* into tetraploid wheats as a result of either pseudogamy or the union of unreduced gametes. Because no seeds were produced by florets allowed to self-pollinate, the union of unreduced gametes appears unlikely. Seeds were set following pollination, which suggests unreduced eggs gave rise to embryos and the endosperms resulted from the union of the male gamete with the fusion nucleus.

Sixteen of the 20 plants checked cytologically resulted from the pollination of eggs carrying 13–15 univalents with pollen from the diploid parent. Apparently eggs carrying the A genome along were nonfunctional. This suggests it will be extremely difficult if not impossible to substitute the A genome of diploid wheats into tetraploid cytoplasm. We propose to continue backcrossing plants carrying $7'' + 7'$ to *T. monococcum*. After backcrossing for several generations, the A genome of these plants will be in the main of *T. monococcum* origin. Eggs carrying the A genome from these plants may be functional.

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