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NEW HYBRIDS BETWEEN *AGROPYRON* AND WHEAT. III. BACKCROSS DERIVATIVES, EFFECT OF *AGROPYRON* CYTOPLASM, AND PRODUCTION OF ADDITION LINES[1]

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SUMMARY

Agropyron ciliare (2n=28, SSYY) (♀) × *Triticum aestivum* cv. Chinese Spring and *A. trachycaulum* (2n=28, SSHH) (♀) × Chinese Spring hybrids and their BC_1 derivatives reported earlier were advanced to BC_3 stage. Chromosome number in BC_2 derivatives varied from 43–57 with modal class as 49 chromosomes while the BC_3 derivatives had 42–49, mostly 43–46 chromosomes. The proportion of 2n=44 plants was higher in selfed progenies of 2n=44, 45, 46 BC_3 and BC_2 plants than in the progenies of 2n=43 BC_3 plants. However, the proportion of disomic additions was higher in the progenies of monosomic additions than in those of double monosomic additions and no disomic additions were recovered on selfing 45- and 46-chromosome plants. Some double monosomic and monosomic additions on selfing produced monotelosomic additions. Unfavorable nuclear-cytoplasmic interactions were evident and led to seed shrivelling, embryo abortion, failure of seed or cultured embryos to germinate, seedling death, plant weakness and sterility in the backcross derivatives. The alloplasmic additions and the telosomic additions isolated are probably for the critical *Agropyron* chromosome(s) only.

INTRODUCTION

The genus *Agropyron* contains about 100 species but only a small number, *A. intermedium*, *A. elongatum*, *A. junceum*, *A. distichum*, *A. caespitosum*, *A. podperae*, and *A. fibrosum*, have been successfully hybridized with common wheat (Sharma and Gill 1983a). We started our wheat-*Agropyron* hybridization program in 1980 and described new intergeneric hybrids of *Triticum aestivum* cv. Chinese Spring (CS) with *A. ciliare* (2n=28, SSYY), *A. trachycaulum* (2n=28, SSHH), *A. yezoense* (2n=28, SSYY) and *A. scirpeum* (2n=28, $E^SE^SE^{Sc}E^{Sc}$) (Sharma and Gill 1981, 1983b). *A. trachycaulum* × wheat and *A. yezoense* × wheat hybrids provided no evidence of homologous or homoeologous pairing, whereas *A. ciliare* × wheat and wheat × *A. scirpeum* hybrids showed homoeologous or autosyndetic pairing. BC_1 derivatives with wheat as the recurrent parent were obtained and described (Sharma and Gill 1983b).

The purpose of this paper is to describe the subsequent backcross derivatives of *A. trachycaulum* × wheat and *A. ciliare* × wheat hybrids, the effect of *Agropyron* cytoplasm on

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hybrid derivatives, and to report some alloplasmic addition lines. The research is aimed at the cytogenetic analysis of *Agropyron* species genomes and the production of germplasm resistant to wheat streak mosaic virus (WSMV) and barley yellow dwarf virus (BYDV).

MATERIALS AND METHODS

A. trachycaulum (accession TA2052), a North American tetraploid, and *A. ciliare* (accession TA2006), an Asiatic tetraploid, were hybridized with *T. aestivum* cv. Chinese Spring (CS). The *Agropyron* seed came from Dr. D. R. Dewey, USDA, Utah State University, Logan. Accession TA2006 was found to be resistant to WSMV and BYDV. Accession TA2052 was tested only for WSMV and found resistant.

We attempted reciprocal crosses but hybrids were obtained only with *Agropyron* as the female parent. Attempts to produce amphiploids were unsuccessful. Backcross derivatives were produced with wheat as the recurrent parent. The F_1 hybrids, BC_1 derivatives and a random sample of BC_2 and BC_3 seeds were raised by embryo culture on medium previously described by Sharma and Gill (1983b). Ten to 12 day-old embryos were cultured to obtain the F_1 hybrids and 15–20 day-old embryos were cultured to obtain backcross hybrids. Most of the BC_2 and BC_3 derivatives and all of their selfed progenies were raised from mature seed. Observations were recorded on morphology, plant vigor, fertility, chromosome number, chromosome pairing, seed shrivelling, and seed germination. For meiotic studies, 20 or more cells were scored except when chromosome spread was poor.

RESULTS

Of the 9 BC_1 seeds set on *A. ciliare* × CS F_1 hybrid, 2 had no embryo and little or no endosperm. Four of 6 embryos cultured grew into plants and the single seed left on the mother plant matured as shrivelled and inviable. Five of the 37 BC_2 seeds were dissected. One was shrivelled and dry with no embryo, 3 had green seed coats and watery endosperm, and 1 was a normal seed. Only the normal seed and a green coated seed produced plants. Of the 32 seeds harvested at maturity, 12 were shrivelled and only 2 germinated; of 19 plump seeds sown 15 germinated, 1 died as a seedling, and 1 grew as a weak, sterile plant. Thus 15 plants from mature seed and 2 from embryo culture were healthy and from these, 224 BC_3 seeds were obtained. When 17 of these seeds were dissected, 3 had no embryo, 9 embryos produced callus only, and 2 grew into weak, sterile plants. Of the remaining 207 seeds harvested at maturity, 58 were plump, 149 were shrivelled and 50 of the latter appeared inviable. Randomly selected 9 plump and 20 shrivelled BC_3 seeds were grown. All the 9 plump seeds germinated although 1 produced a weak, sterile plant. Out of the shrivelled seed sample, 1 did not germinate, 6 died as seedlings, 9 did not reach flowering and the remaining 4 grew into weak, sterile plants. Thus 11 BC_3 plants, 3 from embryo culture and 8 from plump seeds were normal looking.

Of the 21 BC_1 seeds set on *A. trachycaulum* × CS F_1 hybrid, 16 were dissected. One seed had watery endosperm and deformed embryo while the remaining 15 had starchy endosperm and normal to somewhat deformed embryos. Of the 16 embryos cultured, 3 did not germinate, 1 died as a seedling, and 12 plants were obtained. The 5 seeds that

matured on the mother plant were shrivelled and inviable. Of the 51 BC_2 seeds set, 5 were dissected and the embryos cultured, but only 3 embryos germinated. Of the remaining 46 seeds harvested at maturity, 24 were shrivelled and only 6 of these germinated while 3 died as seedlings. Of the 22 plump seeds, 3 did not germinate, and 14 died as seedlings. Thus 11 BC_2 normal growing plants, 3 by embryo culture, 3 from shrivelled seed, and 5 from plump seed were raised. In all, 234 BC_3 seeds were set of which 17 were dissected with exactly the same results as with 17 *A. ciliare* × CS BC_3 seeds. Of the remaining 217 seeds, 44 were plump, 173 were shrivelled, and 45 of the latter apparently were inviable. A sample of 6 plump and 14 shrivelled BC_3 seeds was sown. Of the 6 plump seeds, 1 failed to germinate but the other 5 produced healthy plants. Of the 14 shrivelled seeds, 9 failed to germinate, 1 died as seedling, 1 produced a weak, sterile plant and 3 produced relatively normal plants. Thus 11 BC_3 plants, 3 from embryo culture, 5 from plump seeds and 3 from shrivelled seed appeared normal looking.

The chromosome number in *A. ciliare* × CS and *A. trachycaulum* × CS BC_1 derivatives varied from 52–56 and 48–57, respectively, and in BC_2 derivatives from 43–57 and 43–54, respectively. Chromosome pairing data of BC_1 derivatives indicated that either some of the wheat chromosomes were eliminated or *Agropyron* chromosomes caused reduced pairing of wheat homologues (Sharma and Gill 1983b). The chromosome pairing in BC_2 plants increased over BC_1 plants. In some cases, however, pairing was still lower than expected (Table 1). Male and female fertility increased and plant vigor decreased (Table 2).

The *A. ciliare* × CS BC_3 derivatives had 42–49 chromosomes, all but 4 having 43–46 chromosomes. The *A. trachycaulum* × CS BC_3 derivatives had 43–49 chromosomes, all except 1 having 43–46 chromosomes. The normal BC_3 derivatives resembled CS in appearance, had relatively normal meiosis (Table 3, Fig. 1) and good fertility (Table 2). Plant height, tiller number and spike length decreased (Table 2). BC_3 plants with 44 and 43 chromosomes were presumably double monosomic and monosomic additions, respectively. The alien chromosomes were identified to be median or submedian (Table 3, Fig. 1).

Table 1. Mean chromosome pairing in some of the BC_2 derivatives of *A. ciliare* (c) × *T. aestivum* and *A. trachycaulum* (t) × *T. aestivum* hybrids.

BC_2 particulars	Chro. No.	Chromosome pairing						Xma
		I	Rod II	Ring II	Total II	III	IV	
c_{3-1}	48	5.60	3.33	17.27	20.60	0.40	0.00	38.67
c_{8-5}	47	5.81	3.71	16.62	20.58	0.08	0.07	37.57
c_{2-1}	49	8.80	6.20	13.34	19.54	0.20	0.13	33.67
-5	43	4.59	3.36	15.15	18.51	0.41	0.04	34.60
-7	46	4.19	5.00	15.56	20.56	0.07	0.12	36.62
-9	45	6.62	3.44	15.38	18.82	0.25	0.00	34.70
t_{2-1}	45	3.00	1.50	19.25	20.75	0.07	0.07	39.35
-2	49	6.86	10.43	10.00	20.43	0.43	0.00	31.29
-3	44	4.32	4.27	15.16	19.43	0.27	0.00	35.13
t_{8-2}	54	13.32	3.37	16.55	19.92	0.21	0.05	37.04
t_{12-1}	46	2.50	4.00	17.00	21.00	0.50	0.00	39.00

Table 2. Average values for chromosome member, plant height, tiller number, spike length, pollen stainability (P.S.), self and backcross seed set in wheat-*Agropyron* hybrids and their parents.

Cross	Generation	No. of plants	Chro. No.	Pl. Ht. (cm)	Tiller No.	Spike length (cm)	P. S. (%)	Self seed set (%)	Backcross seed set (%)
c×CS	Parents: c	3	28.0	87.0	15.0	25.0	70.0	91.7	21.9
	CS	3	42.0	84.0	12.0	7.2	81.3	93.3	—
	F_1	1	35.0	87.0	15.0	16.0	0.0	0.0	1.5
	BC_1	4	54.5	76.0	8.8	9.5	46.0	1.7	24.1
	BC_2	17	47.1	73.6	6.6	7.0	51.3	10.3	41.1
		19†	47.7	71.3	6.4	6.8	48.4	9.7	—
	BC_3	11	45.1	82.0	6.2	6.4	71.4	52.5	74.5*
		15†	44.5	67.1	4.9	5.4	51.0	38.5	—
t×CS	Parents: t	2	28.0	87.0	15.0	16.0	88.2	85.0	5.4
	F_1	1	35.0	75.0	16.0	17.0	0.0	0.0	2.2
	BC_1	12	54.4	73.2	5.9	7.8	9.3	0.1	7.8
	BC_2	11	46.6	69.6	5.7	5.7	42.6	9.0	33.2
	BC_3	11	44.7	83.2	5.6	6.2	64.8	35.1	61.5**
		12†	44.5	78.7	5.3	5.8	58.9	32.2	—

c=*A. ciliare*, t=*A. trachycaulum*, CS=Chinese Spring

*, ** based on 3 and 2 plants, respectively, others not backcrossed

† weak plants also included

Table 3. Mean chromosome pairing in some BC_3 derivatives of *A. ciliare* (c)×wheat and *A. trachycaulum* (t)×wheat hybrids.

BC_3 particulars	Chro. No.	I	II	Rg II	Total II	III	IV	Xma	Morphology of extra Chromosome(s)
c_{3-1-2}	46	3.20	2.45	18.65	21.10	0.20	0.00	40.15	one median*, one submedian*
c_{3-1-4}	44	2.24	2.29	18.59	20.83	0.00	0.00	39.47	Both submedian
c_{3-2-1}	44	2.80	2.00	18.60	20.60	0.00	0.00	39.20	—
$c_{2-8-P-2}$	45	3.86	3.00	17.57	20.57	0.00	0.00	38.14	—
$c_{2-10-P-4}$	44	2.00	1.19	19.81	21.00	0.00	0.00	40.81	one median, one submedian
t_{2-1-2}	44	2.00	1.43	19.57	21.00	0.00	0.00	40.57	Longer=submedian, Shorter=median
t_{2-1-3}	43	1.50	2.87	17.38	20.25	0.00	0.25	38.38	Median
t_{2-1-4}	43	1.09	2.00	18.96	20.96	0.00	0.00	39.92	Submedian
$t_{2-2-P-2}$	43	1.00	0.71	20.29	21.00	0.00	0.00	41.29	—

* In a 44 chromosome progeny plant

BC_3 plants were selfed to isolate alloplasmic addition lines. Shrivelled BC_2F_2 and BC_3F_2 seed had poor germination, high seedling mortality and produced several weak plants (Table 4). Germination of shrivelled seed was much slower than that of the plump seed. The average time difference between shrivelled and plump seed for harvesting root tips for mitosis varied from 12.0 to 45.2 hr in different progenies. Some shrivelled seeds had few, short roots and low mitotic index.

Table 4. Germination and chromosome constitution of the progenies of BC_2 and BC_3 derivatives of *A. ciliare* (c) × wheat hybrid and of the progenies of BC_3 derivatives of *A. trachycaulum* (t) × wheat hybrid.

BC_2 or BC_3 parent	Chro. No.	Self seed			Died as seedling or weak plants	No. of plants whose chro. no. determined	Frequency of plants with Chro. No.							
		Plump(P)/ Shrivelled(S)	Sown	Germinated			41	42	43	44	45	46	42+t′	43+t′
*C_{2-9}	45	P	15	15	0	15	1	3	6	3	1	1	0	0
		S	15	13	2	9	0	3	1	3	2	0	0	0
C_{3-1-2}	46	P	10	10	1	10	0	1	4	4	1	0	0	0
		S	10	10	10	8	1	2	2	1	2	0	0	0
C_{3-1-4}	44	P	10	10	0	9	0	0	5	3	0	0	1	0
		S	10	10	9	10	0	7	2	0	0	0	1	0
C_{3-2-1}	44	P	1	1	0	1	0	0	1	0	0	0	0	0
		S	5	5	2	4	0	1	1	2	0	0	0	0
t_{2-1-2}	44	P	5	5	0	4	0	0	0	3	0	0	0	1
		S	10	9	9	7	0	5	1	0	0	0	1	0
t_{2-1-3}	43	P	16	15	2	14	0	2	0	0	0	0	12	0
		S	13	12	12	11	2	9	0	0	0	0	0	0
t_{2-1-4}	43	P	15	15	0	13	0	0	6	4	0	0	3	0
		S	5	5	0	5	0	4	0	0	0	0	0	1

* BC_2, all others BC_3

The proportion of 41- and 42-chromosome plants was consistently much higher in shrivelled seed lots than in plump seed lots in BC_2F_2 and BC_3F_2 populations (Table 4). The 41-chromosome plants were lethal or weak and sterile. The 42-chromosome plants that came from shrivelled seed lots died as seedlings, did not reach flowering, or grew into weak and sterile plants (Fig. 2). From plump seed lots, 6 plants had 42 chromosomes. Two of these were weak and sterile and could be misclassifications of shrivelled seeds as plump seeds. The remaining 4 plants, 1 from *A. trachycaulum* × CS cross and 3 from *A. ciliare* × CS cross, grew normally and had some fertility (stainable pollen = 69.1–92.4%, self seed set = 23.6–71.4%). Two of the 3 plants studied showed a quadrivalent in some cells and 0–2 univalents, and the third showed 3–6 univalents (average = 5.0 I). These plants presumably resulted from chromosome substitution.

The proportion of 44 chromosome plants was highest in the progenies of 45- and 46-chromosome plants (26.2%), next in the progenies of 44-chromosome plants (22.9%) and lowest in the progenies of 43-chromosome plants (9.3%) (Table 4). However, chromosome pairing data revealed that all the 44-chromosome plants, except one, in the progenies of 46-, 45-, and 44-chromosome plants, had 1.55 to 2.40 univalents (Table 5). These, therefore, were double monosomic additions rather than disomic additions. This is further supported by the fact that the morphology of the two univalents was different and whenever 22 pairs occurred, one of the pairs was heteromorphic. On the other hand, meiosis was studied in two of the four 44-chromosome plants obtained by selfing monosomic additions and both appeared to be disomic additions (Table 5).

No monotelosomic additions (21″+t′) were recovered on selfing 45- or 46-chromosome plants (Table 4). Only two of the 24 BC_3F_2 seeds of *A. ciliare* × wheat cross and one of the 11 BC_3F_2 seeds of *A. trachycaulum* × wheat cross resulting from selfing 44-chromosome BC_3

Table 5. Mean chromosome pairing in 44 chromosome plants resulting on selfing one 45 chromosome BC_2 plant, one 46 chromosome, one 44 chromosome BC_3 plant of *A. ciliare* (c) × *T. aestivum* cross and one 43 chromosome BC_3 plant of *A. trachycaulum* (t) × *T. aestivum* cross.

BC_2 or BC_3 parent	Chro. No.	Plant No. of 44 chromosome plants*	Meiosis in 44 chromosome plants						Morphology of 2 univalents
			I	Rod II	Ring II	Total II	III	IV	
C_{2-9}	45	P-6	2.34	1.83	19.00	20.83	0.00		M, SM
C_{3-1-2}	46	P-1	1.88	1.62	19.26	20.88	0.12	0.00	M, SM
		P-3	1.55	1.85	18.90	20.75	0.25	0.05	M, SM
		P-4	2.40	2.00	18.20	20.20	0.40	0.00	M, SM
C_{3-1-4}	44	P-2	1.87	1.73	19.09	20.82	0.09	0.00	SM, SM
		P-7	0.67	2.69	19.00	21.67	0.00	0.00	SM, SM
t_{2-1-4}	43	P-14	0.23	1.56	20.27	21.83	0.00	0.03	SM, SM
		P-15	0.10	1.00	20.95	21.95	0.00	0.00	SM, SM

M=median, SM=Submedian

* All from plump seed

Table 6. Plant vigor and fertility of 42, 43, 44 and 42+t′ chromosome plants in the progenies of BC_3 plants of *A. ciliare* (c) × wheat cross and *A. trachycaulum* (t) × wheat cross. Ranges are given in brackets.

Progeny	Chro. No.	No. of plants in the progeny	Plant ht. (cm)	Tiller no.	Spike (cm)	Stainable pollen (%)	Self seed (%)
$C_{3-1-4}\otimes$	42	7	36.7 (35- 38)	5.2 (4- 8)	2.7 (2.5-4.0)	0.0 (0)	0.0 (0)
	43	7	76.7 (35- 88)	6.7 (5- 8)	5.1 (2.0-7.5)	86.1 (47.7-95.6)	53.1 (0.0-95.0)
	44	3	82.7 (81- 85)	8.0 (7-10)	5.8 (5.5-6.0)	78.6 (83.1-90.6)	87.8 (80.0-92.8)
	42+t′	1	84.0	9.0	6.5	79.1	85.3
$t_{2-1-3}\otimes$	42	11	38.7 (22- 83)	3.3 (2- 4)	2.8 (2.0-6.5)	11.5 (0.0-69.1)	3.9 (0.0-23.6)
	42+t′	12	91.7 (31-105)	5.8 (4- 7)	6.4 (2.5-7.0)	81.1 (62.0-90.2)	43.9 (32.6-61.9)
$t_{2-1-4}\otimes$	42	4	30.0 (25- 33)	5.0 (3- 6)	2.25 (2.0-2.5)	0.0 (0)	0.0 (0)
	43	6	102.8 (98-105)	6.0 (5- 7)	6.60 (6-7)	71.8 (56.6-86.7)	62.2 (30.0-98.7)
	44	4	94.2 (92- 99)	6.5 (5- 7)	6.0 (5.5-6.5)	77.0 (65.6-87.2)	25.0 (16.2-34.6)
	42+t′	3	103.0 (93-111)	5.3 (4- 7)	7.2 (7.0-7.5)	90.0 (88.2-93.3)	54.2 (28.6-79.2)

plants were monotelosomic additions. However, the proportion of monotelosomic additions was high (34.9%) in the progenies of 43-chromosome-BC_3 plants (Table 4).

The plant vigor and fertility data showed that the plants with monotelosomic additions had a definite advantage, especially when compared to 42-chromosome alloplasmic lines (Table 6, Fig. 2). Two monotelosomic additions, one from each *A. ciliare* × CS cross and

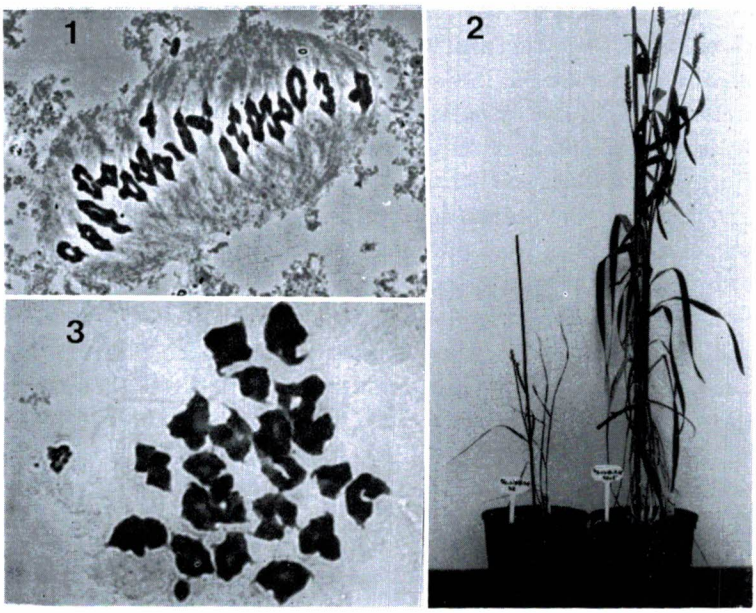

Fig. 1. A double monosomic addition *A. trachycaulum* × wheat BC_3 derivative, 21 II, 2 I; the larger univalent is submedian and the smaller univalent is median (1000×).

Fig. 2. Adult plants in the progeny of a monosomic addition of *A. trachycaulum* × wheat BC_3: left, a 42 chromosome-weak plant from a shrivelled seed; right, a monotelosomic addition (21″+t′) from a plump seed.

Fig. 3. Chromosome pairing in *A. trachycaulum* monotelosomic addition (21″+t′) (1400×).

A. trachycaulum × CS cross came from shrivelled seed and were weak and sterile. These were either misclassifications or had a non-critical telocentric chromosome.

The chromosome pairing in the monotelosomic additions varied from 0.00–0.12 I, 0.58–1.33 Rod II, and 19.67–20.36 Ring II (Fig. 3). The telochromosome was observed consistently in all the cells and never paired with any other chromosome. No micronuclei were observed at the quartet stage in monotelosomic additions. Thus, the telochromosome was included into gametes very stably.

DISCUSSION

Embryo and endosperm abortion, inability of cultured embryos to germinate, occurrence of shrivelled, inviable seed with no, slow or poor germination, lethal seedlings and weak and sterile plants in *A. ciliare* × wheat and *A. trachycaulum* × wheat backcrosses may well result from deleterious *Agropyron* cytoplasm, as both these hybrids have *Agropyron* as the female parent. Nuclear-cytoplasm interaction was further evident from increasingly reduced vigor reflected by reduced plant height, tiller number, and spike length as backcrossing continued (Table 2). In backcross generations, the *Agropyron* chromosomes were gradually eliminated, as evidenced by decreased chromosome number and increased chromosome pairing (Tables 1, 3) which led to more severe cytoplasmic effects. Probably

only those seeds and plants that had some critical *Agropyron* chromosome(s) to offset the harmful effect of *Agropyron* cytoplasm were healthy. A preferential transmission of an *Aegilops sharonensis* chromosome has been observed by Maan (1975) in *Aegilops* × *Triticum* crosses. The effect of *Agropyron* cytoplasm on wheat nucleus is not known except that SB lines of wheat with *A. trichophorum* or *A. glaucum* cytoplasm had good to slightly weak growth and good fertility, and with *A. intermedium* cytoplasm, weak growth and low fertility (Ivan Panayotov, pers. comm.). No normal spikes from weak 42-chromosome BC_3F_2 plants were available for meiosis, but these were presumably alloplasmic lines with the wheat nucleus in *Agropyron* cytoplasm. The genome of wheat is thus incompatible with the cytoplasm of *A. ciliare* and *A. trachycaulum*. One 49-chromosome BC_2 derivative of *A. trachycaulum* × wheat cross and one of *A. ciliare* × wheat cross that died or were weak probably had the chromosomes of the diploid *Agropyron* species that participated as the male parent in the evolution of these tetraploid *Agropyron* species. Those with less than 49 but more than 42 chromosomes may have chromosomes of the same genome or non-critical chromosomes from the female genome species, which could not compensate for the negative effect of *Agropyron* cytoplasm.

Because of deleterious cytoplasmic effects, we may obtain alloplasmic addition lines for only the critical *Agropyron* chromosome(s). Reverse crosses between wheat (♀) and backcross derivatives to isolate euplasmic addition lines have been attempted. Furthermore, if there is low or nontransmission of *Agropyron* chromosomes through pollen, addition lines for all the chromosomes may not be obtained. Sears (1956) obtained only 1.3% disomics from selfing monosomic addition of an *Aegilops umbellulata* chromosome to hexaploid wheat. In wheat-barley crosses, Islam *et al.* (1978) found that the transmission of barley chromosomes was very low. Mochizuki (1963) recovered no disomic addition line from an *A. elongatum* monosomic addition line to tetraploid wheat.

The lower frequency of disomic addition lines from double monosomic additions contrasts with the findings of Islam *et al.* (1978) who found double monosomic additions to be a better source than monosomic additions for the isolation of disomic addition lines of barley into wheat. Similarly, Cauderon (1966) obtained 13% disomics in the progeny of a selfed double monosomic addition of *A. intermedium* chromosome to wheat. However, Evans and Jenkins (1960) failed to isolate any disomic additions of rye chromosomes from the double monosomic additions.

The higher proportion of 44-chromosome plants in the selfed progenies of 44 to 46-chromosome backcross derivatives than in the progenies of 43-chromosome derivatives may result from reduced competition with normal 21-chromosome gametes in higher chromosome plants. The lower frequency or lack of recovery of disomic additions on selfing backcross derivatives having more than 43 chromosomes suggests a lower frequency of gametes carrying the same extra chromosome. Conversely, the gametes produced by the 43-chromosome plants carrying the extra chromosome would always carry the same alien chromosome. A low frequency of disomic addition lines (8.2%) in the progenies of 43-chromosome BC_3 plants (Table 4) could be due to low transmission of the extra chromosome through the male gamete.

The meiotic analysis shows that we have isolated at least two disomic additions from

A. trachycaulum and one from *A. ciliare* (Table 5). Recovery of alloplasmic disomic additions is interesting since Islam *et al.* (1978) failed to recover any alloplasmic addition lines from barley-wheat crosses. Also, their monosomic additions were sterile, exhibiting pistilloidy, while many of ours were normal and fertile. The difference may reflect on the evolutionary distances of barley and wheatgrass from wheat.

It is unclear to which genome the critical chromosome(s) and telocentrics belong. If they happen to be the same in both *A. ciliare* × wheat and *A. trachycaulum* × wheat hybrid derivatives, this will provide evidence for the hypothesis that the same diploid *Agropyron* species, hence an S genome species, has been the donor of cytoplasm to both *A. ciliare* and *A. trachycaulum*.

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