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# New hybrids between *Agropyron* and wheat

## 2. Production, morphology and cytogenetic analysis of $F_1$ hybrids and backcross derivatives*

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**Summary.** Intergeneric hybrids of *Triticum aestivum* ($2n=42$,AABBDD) with *Agropyron ciliare* ($2n=28$,SSYY), *A. trachycaulum* ($2n=28$,SSHH), *A. yezoense* ($2n=28$,SSYY) and *A. scirpeum* ($2n=28$) are reported for the first time. $F_1$ hybrids of *T. aestivum* were also produced with *A. intermedium* ($2n=42,E_1E_1E_2E_2Z_1Z_1$) and *A. junceum* ($2n=14$,JuJu). All wheat-*Agropyron* hybrids were obtained by embryo rescue technique. Cultivars and reciprocal crosses differed for seed set, seed development and $F_1$ plant production. The $F_1$ hybrids were sterile. Attempts to obtain amphiploids were unsuccessful. However, backcross derivatives were obtained with wheat as the recurrent parent.

The level of chromosome pairing in *A. trachycaulum* × wheat, *A. yezoense* × wheat and wheat × *A. junceum* hybrids provided no evidence of homologous or homoeologous pairing. Mean pairing frequencies in *A. ciliare* × wheat, wheat × *A. scirpeum* and wheat × *A. intermedium* hybrids indicated homoeologous or autosyndetic pairing. *Ph* gene was more effective in regulating homoeologous pairing in *A. yezoense* × wheat hybrids than in *A. ciliare* × wheat hybrid. 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.

**Key words:** *Triticum aestivum* – *Agropyron* – Intergeneric hybrids – Embryo culture – Chromosome pairing

## Introduction

*Agropyron* is a large genus comprising about 150 species. Over 90% of the species are polyploid and genomes S, E, Ju, C, J, H, X and Y have been identified (Stebbins and Pun 1953; Stebbins 1956; Sakamoto and Muramatsu 1966; Sakamoto 1973; Dewey 1982). The diploid donors of the genomes were *A. spicatum* (Pursh) Scribn. & Smith (S), *A. elongatum* (Host) Beauv. (E), *A. junceum* (L.) Beauv. (Ju), *A. cristatum* (L.) Gaertn. (C), *Elymus junceus* Fisch. (J) and *Hordeum bogdanii* Wilensky (H). The origin of the genomes X and Y is unknown.

Few species in the *Agropyron* complex have been hybridized with bread wheat, *Triticum aestivum* L. (Sharma and Gill 1983): *A. elongatum* 2x (Jenkins 1958); *A. elongatum* 4x (Wakar 1935; Peto 1936; Dvorak 1981); *A. elongatum* 10x (Wakar 1935; Peto 1936; and many others); *A. intermedium* (Host) Beauv. (syn. *A. trichophorum, A. glaucum* and *A. amurense*) (Peto 1938; Smith 1943; and many others); *A. junceum* 2x (Alonso and Kimber 1980); *A. juneum* 6x (Rodriguez and Mujeeb 1981); *A. distichum* (Thumb.) Beauv. (Pienaar 1981); *A. podperae* (Dewey 1981) and *A. caespitosum* Koch (Dvorak 1981). Rodriguez and Mujeeb (1981) reported an $F_1$ hybrid of common wheat with *A. yezoense* Honda which was correctly identified later as *A. fibrosum* (Schrenk) Franch (A. Mujeeb-Kazi personal communication; Mujeeb-Kazi and Bernard 1982). Attempts to hybridize *A. ciliare* (Trin.) Franch, *A. trachycaulum* (Link) Malte and *A. yezoense* with wheat were unsuccessful (McFadden 1934; Veruschkine 1936; Johnson 1938; Smith 1942). However, only a limited genetic variability was utilized and embryo culture was not used. From our laboratory, we reported hybrids of common wheat with *A. ciliare* and *A. smithii* Rydb. (later correctly identified as *A. trachycaulum*, D. R. Dewey personal communication) (Sharma and Gill 1981 a). *A. scirpeum* Persl., *A. trachycaulum*, *A. junceum* 2x and *A. intermedium* (Sharma and Gill 1981 b), and *A. yezoense* (Sharma and Gill 1983).

Wheat × *Agropyron* intergeneric hybrids allow the detailed cytogenetic analysis of *Agropyron* genomes with the genome of wheat. The genetic relationships of diploid *A. elongatum* with

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wheat chromosomes have been studied extensively in wheat-*A. elongatum* addition and substitution lines (Dvorak 1979, 1980, 1981; Dvorak and Knott 1974). No other *Agropyron* genome has been analyzed in its entirety. *A. elongatum* chromosomes showed considerable induced homoeologous pairing with wheat chromosomes (Sears 1972). Several chromosomes transferred into wheat from polyploid species of *Agropyron, A. intermedium* and *A. elongatum* 10x also showed homoeology with specific wheat homoeologous groups (Knott 1964, 1968; Johnson 1966; Quin and Driscoll 1967; Larson and Atkinson 1970; The and Baker 1970; Weinhues 1971; Knott et al. 1977).

Several genes have been transferred to common wheat from *A. elongatum* and *A. intermedium.* About two dozen commercial cultivars now grown over large areas of the world derived their rust resistance along with other traits from *A. elongatum* and *A. intermedium* (Sharma and Gill 1983). Perhaps no alien genus has more impact on commercial wheat production than *Agropyron* and this provides an ample justification for the production of new wheat-*Agropyron* hybrids and addition and substitution lines, and for further research on the genetic relationships between wheat and *Agropyron* species. The objective of this paper is to report detailed observations on the production, morphology and cytology of hybrids and backcross derivatives of common wheat with *A. ciliare, A. trachycaulum, A. yezoense, A. scirpeum, A. junceum* and *A. intermedium.* Apart from cytogenetic analysis of *Agropyron* species genomes, our long-term purpose of this research is the production of germplasm resistant to wheat streak mosaic virus (WSMV) and barley yellow dwarf virus (BYDV).

## Materials and methods

*Agropyron* species used in hybridization, their genome symbols, chromosome numbers, geographic origin, and source of seed are given in Table 1. Accessions of these species used in the present study had excellent resistance to WSMV and/or BYDV. We also tried *A. caninum* (L.) Beauv., *A. caespitosum, A. leptourum* (Nevski) Grossh., *A. ferganense* Drob., *A. spicatum* and *A. libanoticum* Hack. but no hybrids with wheat were produced (Sharma and Gill 1983). For more detail about various *Agropyron* species, see Sharma and Gill 1982).

Reciprocal crosses were made between common wheat cultivars and various *Agropyron* species (Table 2) in the greenhouse. One to two top and bottom spikelets of the female parent were removed. The two lower florets of the remaining spikelets were retained, hand emasculated and pollinated. Hybrid seed development was monitored very closely and 10–14 days after pollination seeds were dissected and embryos were cultured on artificial medium (Murashige and Skoog 1962). The medium was supplemented with 0.4 mg/l thiamine-HCl, 100 mg/l i-inositol, 10 mg/l each L-arginine-HCl, glycine and L-tyrosine, 4% sucrose, and 0.8% Bactoagar. To grow some of these proembryos, it was necessary to supplement the medium with kinetin (1 mg/l). The germinated embryos, however, had to be transferred to a medium without kinetin for further growth. Plantlets were later transferred to soil. The hybrids were cloned and treated with 0.05% colchicine plus 1.5% DMSO. The original hybrids and some of the clones were backcrossed to wheat as the recurrent male parent.

Observations were made on morphology and fertility of $F_1$ hybrids and backcross derivatives. Chromosome counts were made by the method of Sharma (1982). For meiotic studies, spikes were fixed in 1:3 acetoalcohol and squashes were made in 1% acetocarmine. Up to 20 or more cells were scored in each case except when chromosome spread was poor. If more than one hybrid plant was obtained from a specific cross, values for chromosome pairing were averaged. Male fertility was estimated as the percentage of pollen stainable in IKI solution. Female fertility was obtained on the basis of percent seed set on selfing.

To evaluate the extent of homology between genomes, the observed chiasma frequency for each hybrid was used to calculate expected chromosome configurations and mean arm pairing frequency (c) (Driscoll et al. 1979; Espinasse and Kimber 1981). These analyses were kindly performed by Dr. G. Kimber, University of Missouri, Columbia.

## Results

### *$F_1$ Hybrids*

*Production.* The number of florets pollinated, number of hybrid seeds set, nature of embryo and endosperm development, and number of $F_1$ hybrid plants produced are given in Table 2. Up to 1–7 intergeneric

**Table 1.** Genome symbols, chromosome numbers, geographic origin, source of seed, supplier's accession number and K-State accession number of various *Agropyron* species hybridized with common wheat, *Triticum aestivum*

| *Agropyron* species | Genome symbol | Chromosome no. | Geographic origin | Source of seed | Supplier's acc. no. | K-State acc. no. |
|---|---|---|---|---|---|---|
| *A. ciliare* | SSYY | 28 | Asia | D. R. Dewey | CS-9-11:20 | TA2006 |
| *A. trachycaulum*[a] | SSHH | 28 | N. America | D. R. Dewey | EPC-122 | TA2052 |
| *A. trachycaulum* | SSHH | 28 | N. America | D. R. Dewey | B-63-47 | TA2015 |
| *A. yezoense* | SSYY | 28 | Asia | D. R. Dewey | PI-275776 | TA2017 |
| *A. scirpeum*[b] | – | 28 | Europe | G. Kimber | 77AJO1-5 | TA2204 |
| *A. junceum*[b] | JuJu | 14 | Europe-W. Asia | G. Kimber | AHO1 | TA2201 |
| *A. intermedium* | $E_1E_1E_2E_2Z_1Z_1$ | 42 | Europe-W. Asia | – | – | TA2059 |

[a] Received as *A. smithii*, correctly identified as *A. trachycaulum*

[b] Originally also from D. R. Dewey

**Table 2.** Number of florets pollinated, number of hybrid seeds set, nature of embryo and endosperm of 10 – 14 days old seed, and number of various *Triticum aestivum-Agropyron* hybrids produced by embryo culture. Reciprocal hybridization results are in parentheses

| Cross | | No. of florets pollinated | Hybrid seeds obtained | | Embryo[b] | Endosperm[b] | No. of $F_1$ hybrids raised |
|---|---|---|---|---|---|---|---|
| Wheat cv. × | *Agropyron* sp., Acc. no. | | No. | % | | | |
| CS | *A. ciliare*, TA2006 | 98 (32) | 0 (7) | 0.00 (21.9) | – (2 or 3) | – (C) | 0 (1) |
| Others[c] | *A. ciliare*, TA2006 | 116 (318) | 0 (56) | 0.00 (17.6) | – (3) | – (C) | 0 (0) |
| CS | *A. trachycaulum*[a], TA2052 | 154 (156) | 1 (9) | 0.6 (5.4) | 2 (2) | B (C) | 0 (1) |
| 'TAM105' | *A. trachycaulum*[a], TA2052 | 98 (112) | 2 (9) | 2.1 (8.0) | 2 (2) | B (C) | 0 (1) |
| Others[d] | *A. trachycaulum*[a], TA2052 | 363 (–) | 2 (–) | 0.5 (–) | 2 (–) | B (–) | 0 (–) |
| CS | *A. trachycaulum*, TA2015 | 178 (46) | 0 (4) | 0.0 (8.7) | – (2) | – (C) | 0 (4) |
| Others[e] | *A. trachycaulum*, TA2015 | 61 (303) | 0 (47) | 0.0 (15.5) | – (3) | – (B or C) | 0 (0) |
| CS | *A. yezoense*, TA2017 | 92 (79) | 0 (17) | 0.0 (21.5) | – (3) | – (C) | 0 (2) |
| 'Wichtia' | *A. yezoense*, TA2017 | – (80) | – (7) | – (8.8) | – (3) | – (C) | – (3) |
| 'Newton' | *A. yezoense*, TA2017 | 118 (68) | 0 (11) | 0.0 (16.2) | – (3) | – (C) | 0 (0) |
| CS | *A. scirpeum*, TA2204 | 144 (48) | 15 (5) | 10.4 (10.4) | 1 or 2 (0) | B (B) | 7 (0) |
| Others[f] | *A. scirpeum*, TA2204 | 50 (126) | 0 (8) | 0.0 (6.4) | – (0) | – (B) | 0 (0) |
| CS | *A. junceum*, TA2201 | 64 (64) | 6 (2) | 9.1 (3.0) | 1 (0 or 3) | A (B or C) | 1 (0) |
| Others[f] | *A. junceum*, TA2201 | 194 (32) | 2 (0) | 1.0 (0.0) | 0 (–) | C (–) | 0 (0) |
| CS | *A. intermedium*, TA2059 | 199 (24) | 5 (7) | 2.5 (29.2) | 1 or 2 (3) | A or B (B) | 2 (0) |
| 'Wichita' | *A. intermedium*, TA2059 | 24 (–) | 13 (–) | 54.2 (–) | 1 or 2 (–) | A or B (–) | 2 (–) |

[a] Incorrectly reported as *A. smithii* in Sharma and Gill (1981 a)

[b] *1* large with scutellum, *2* small with scutellum, *3* torpedo-shaped without scutellum, *0* no embryo; *A* starchy, *B* watery, *C* no endosperm

[c] 'Newton', 'TAM105', 'Vona'; [d] 'Newton', 'Turkey'; [e] 'Newton', 'TAM105', 'Sturdy', 'Turkey'; [f] 'Newton', 'TAM105', 'Wichita'

– Cross not attempted; *CS* 'Chinese Spring'

hybrid plants of common wheat with *A. ciliare, A. trachycaulum, A. yezoense, A. scirpeum, A. junceum* and *A. intermedium* were obtained.

Reciprocal crosses produced different results. In all cases except *A. junceum,* seed set was higher when wheat was the male parent (Table 2). Intergeneric hybrids with *A. ciliare, A. yezoense* and *A. trachycaulum* were produced only when wheat was the male parent. Seed development was also different in reciprocal crosses. For example, no embryo was observed in 10 days or older seeds in *A. scirpeum* × wheat cross whereas the reciprocal cross produced embryos with large to small scutellum. Similarly, *A. junceum* × wheat seeds had either no embryo or torpedo-shaped embryo without scutellum compared to large embryo with scutellum in a reciprocal cross. Endosperm in crosses with wheat as the female parent was starchy or watery. In reciprocal crosses, either there was no endosperm or there was watery endosperm (Table 2). It appears, therefore, that in wheat (♀) × *Agropyron* (♂) crosses prefertilization barriers were stronger, while in the reverse direction post-fertilization barriers were stronger.

Crossability differences among wheat cultivars were observed, crosses with cv. 'Chinese Spring' (CS) being the most successful in the production of intergeneric hybrids with *Agropyron* species (Table 2). Hybrid seed set was invariably higher with CS as the wheat parent compared to other wheat cultivars. In wheat-*A. trachycaulum* cross and wheat-*A. intermedium* cross, the seed set was lower with CS compared to 'TAM105' and 'Wichita', respectively, but the proportion of hybrid seeds resulting in hybrid plants was again higher with CS as the wheat parent. Crossability differences persisted even in $BC_1$ generation. Whereas *A. yezoense* × CS, *A. trachycaulum* × CS and CS × *A. intermedium* $F_1$ hybrids produced $BC_1$ seeds, *A. yezoense* × Wichita, *A. trachycaulum* × 'TAM105' and 'Wichita' × *A. intermedium* $F_1$ hybrids bore no $BC_1$ seed even after 486, 968 and 80 pollinations, respectively. Probably the same crossability genes ($Kr_1$, $Kr_2$) that regulate crossability of wheat with rye (Lein 1943), *H. bulbosum* L. (Falk and Kasha 1981) and other potential pollinators (Thomas et al. 1981), are operating in wheat-*Agropyron* crosses and wheat cultivars other than CS used in the present study do not seem to possess these crossability genes.

Seed set in wheat-*Agropyron* crosses was high considering the evolutionary distance between *Agropyron* and *Triticum.* Fertilization and seed set were not as serious a cause of reproductive isolation, at least in one direction of cross, as post-zygotic mechanisms. Development of most seeds ceased about 10 days after pollination. Dissected embryos from these were deformed and poorly developed, small-sized with small scutellum or torpedo-shaped with no scutellum. The majority of embryos did not develop in culture and eventually

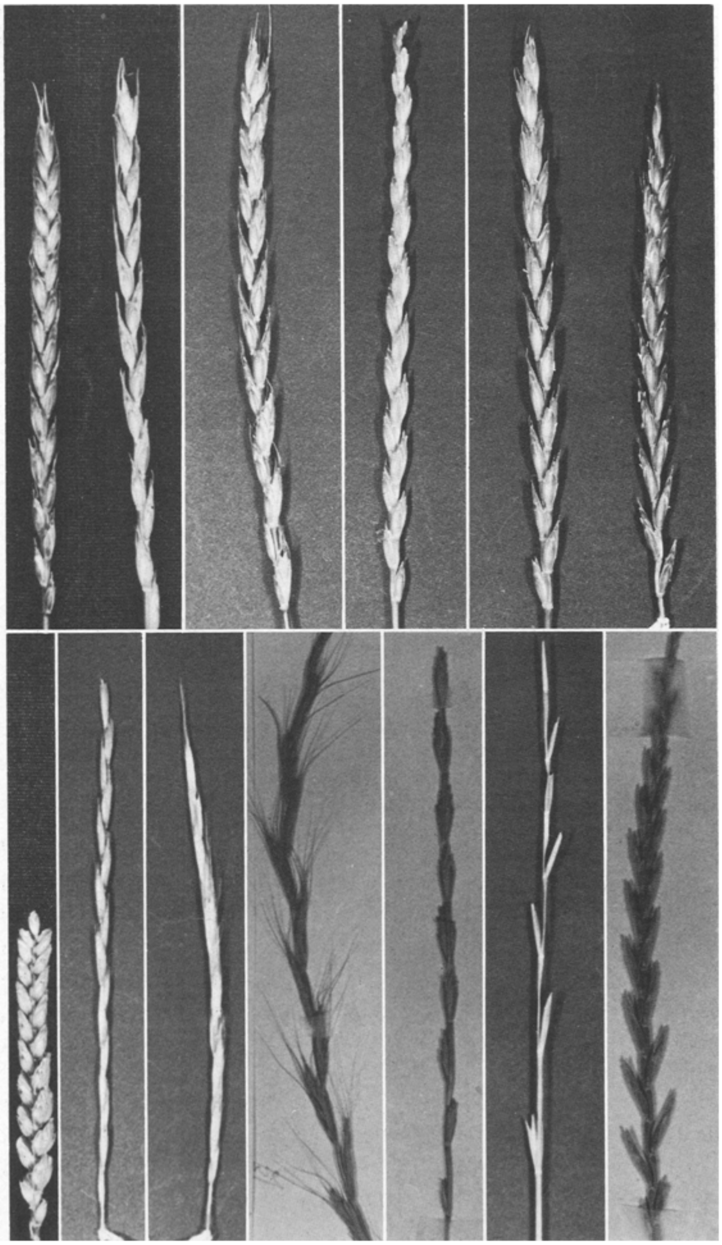

**Fig. 1.** Spikes of wheat-*Agropyron* $F_1$ hybrids and parents. Hybrid spikes are intermediate in morphology: *Top* (L–R), *A. trachycaulum* × *T. aestivum* cv. 'Chinese Spring', *A. ciliare* × *T. aestivum* cv. 'Chinese Spring', *A. yezoense* × *T. aestivum* cv. 'Chinese Spring', *T. aestivum* cv. 'Chinese Spring × *A. scirpeum, T. aestivum* cv. 'Chinese Spring' × *A. junceum, T. aestivum* cv. 'Chinese Spring' × *A. intermedium; Bottom* (L–R), *T. aestivum* cv. 'Chinese Spring', *A. trachycaulum, A. ciliare, A. yezoense, A. scirpeum, A. junceum, A. intermedium*

turned brown and died. Some produced a callus while others died after rudimentary coleoptile or root development. *A. yezoense* × wheat hybrid embryos germinated only when kinetin was used in the culture media. On the basis of success in producing hybrid plants in the present study (Table 2), it is suggested that with *A. ciliare*, *A. trachycaulum* and *A. yezoense*, wheat should be used as a male parent whereas with *A. scirpeum*, *A. junceum* and *A. intermedium*, wheat should be used as a female parent.

*Morphology.* The morphology of the $F_1$ hybrid plants, spikes and spikelets was intermediate (Fig. 1). All the hybrid plants were vigorous, tillered profusely, and were intermediate in number of florets/spike and intermediate to heterotic in plant height and spike length. Like the *Agropyron* parents, the hybrids tended to be perennial and expressed other characters of *Agropyron*. For example, *A. ciliare* × CS $F_1$ hybrid had white scales, *A. trachycaulum* × CS had purple stem base, the top leaves of CS × *A. scirpeum* were curled and all leaves had pubescence and white scales. *A. yezoense* × wheat hybrids had purple color at the base of tillers and leaves very broad, long and dark green. The $F_1$ hybrids, however, had the growth stage of spike for meiosis early and anther extrusion in early morning like wheat.

**Table 3.** Mean chromosome pairing in parents and hybrids of *Triticum aestivum* with several *Agropyron* species (ranges in parentheses)

| Parent/$F_1$ hybrid | Chro. no. | Genome | I | Rod II | Ring II | Total II | III | Xma | Mean arm pairing frequency (c) |
|---|---|---|---|---|---|---|---|---|---|
| *A. ciliare* | 28 | SSYY | 0.00<br>(0) | 1.22<br>(0 – 4) | 12.78<br>(10 – 14) | 14.00<br>(14) | 0.00<br>(0) | 26.78<br>(24 – 28) | – |
| *A. trachycaulum* | 28 | SSHH | 1.00<br>(0 – 2) | 0.94<br>(0 – 5) | 12.56<br>(9 – 14) | 13.50<br>(13 – 14) | 0.00<br>(0) | 26.06<br>(23 – 28) | – |
| *A. yezoense* | 28 | SSYY | 0.00<br>(–) | –<br>(–) | –<br>(–) | 14.00<br>(–) | 0.00<br>(–) | –<br>(–) | – |
| *A. scirpeum* | 28 | – | 0.14<br>(0 – 2) | 1.82<br>(0 – 5) | 12.05<br>(9 – 14) | 13.87<br>(12 – 14) | 0.04<br>(0 – 1) | 26.00<br>(23 – 28) | – |
| *A. junceum* | 14 | JuJu | 0.00<br>(0) | 0.91<br>(0 – 2) | 6.09<br>(5 – 7) | 7.00<br>(14) | 0.00<br>(0) | 13.09<br>(12 – 14) | – |
| *A. intermedium* | 42 | EEEEZZ | 0.00<br>(0) | 3.04<br>(1 – 5) | 17.96<br>(16 – 20) | 21.00<br>(21) | 0.00<br>(0) | 38.96<br>(37 – 41) | – |
| *T. aestivum* cv. CS[a] | 42 | AABBDD | 0.28<br>(0 – 2) | –<br>(–) | –<br>(–) | 20.86<br>(20 – 21) | 0.00<br>(0) | –<br>(–) | – |
| *A. ciliare* × CS | 35 | ABDSY | 26.18<br>(14 – 35) | 3.84<br>(0 – 9) | 0.41<br>(0 – 3) | 4.25<br>(0 – 9) | 0.11<br>(0 – 1) | 4.88<br>(0 – 11) | 0.174 |
| *A. trachycaulum* × CS[d] | 35 | ABDSH | 33.89<br>(24 – 35) | 0.44<br>(0 – 2) | 0.11<br>(0 – 1) | 0.55<br>(0 – 2) | 0.00<br>(0) | 0.66<br>(0 – 2) | 0.024 |
| *A. yezoense* × CS | 35 | ABDSY | 33.54<br>(32 – 35) | 0.73<br>(0 – 3) | 0.00<br>(0) | 0.73<br>(0 – 3) | 0.00<br>(0) | 0.73<br>(0 – 3) | 0.026 |
| CS × *A. scirpeum* | 35 | ABD?? | 38.40<br>(20 – 35) | 2.51<br>(0 – 6) | 0.67<br>(0 – 4) | 3.18<br>(0 – 6) | 0.08<br>(0 – 1) | 4.01<br>(0 – 11) | 0.143 |
| CS × *A. junceum* | 28 | ABDJu | 26.23<br>(22 – 28) | 0.83<br>(0 – 3) | 0.04<br>(0 – 1) | 0.87<br>(0 – 3) | 0.01<br>(0 – 1) | 0.93<br>(0 – 3) | 0.033 |
| CS × *A. intermedium*[b] | 42 | ABDEEZ | 27.80<br>(18 – 40) | 5.71<br>(1 – 10) | 0.66<br>(0 – 4) | 6.37<br>(1 – 12) | 0.42<br>(0 – 2) | 8.02<br>(1 – 16) | 0.191 |
| CS euhaploid | 21 | ABD | 20.76 | – | – | 0.24 | – | – | 0.019 – 0.081[c] |

[a] Cauderon (1966), [b] 0.05 (0 – 1) IV, [c] McGuire and Dvorak (1982), [d] Data based on 35-chromosome PMC's, *CS* 'Chinese Spring'

*Chromosome number and chromosome pairing relationships.* The somatic chromosome counts revealed that all the $F_1$ hybrids had the expected chromosome number (Table 3) except the *A. trachycaulum* (TA2052) × wheat hybrid in which the chromosome number varied from 26 to 42 in different cells.

The chromosome pairing in *Agropyron* species used was quite regular with mostly ring bivalents (Table 3). Only *A. trachycaulum* and *A. scirpeum* had up to two univalents.

The level of chromosome pairing in *A. trachycaulum* × wheat (0.55 II) (Fig. 2a), *A. yezoense* × wheat (0.73 II) (Fig. 2b) and wheat × *A. junceum* (0.87 II) (Fig. 2c) hybrids was too low to provide any evidence of homologous or homoeologous pairing. Pairing in these hybrids was only slightly higher than that in CS euhaploid (0.24 II) (Miller and Chapman 1976). Mean pairing frequencies in *A. ciliare* × wheat (4.25 II, 0.11 III) (Fig. 2d), wheat × *A. scirpeum* (3.18 II, 0.08 III) (Fig. 2e) and wheat × *A. intermedium* (6.37 II, mostly rods, 0.42 III, 0.05 IV) (Fig. 2f) hybrids were lower than expected homologous pairing frequencies and indicated homoeologous pairing (Table 3). The best fit for the *A. ciliare* × wheat pairing data was to the 2:2:1 model where two genomes are assumed to show more affinity (Espinasse and Kimber 1981). The models 3:1:1 and 4:1 which indicate random pairing were poor fits. For chromosome pairing data on CS × *A. scirpeum* $F_1$ hybrid, the fit to the 2:1:1:1 model was the best with the lowest sums of squares. Probably there is some residual homoeology between two of the genomes. There is no model available to deal with pairing analysis in wheat × *A. intermedium* hexaploid hybrids, but data do show homoeology between two genomes.

The mean arm pairing frequency, which provides a more valid comparison of the amount of chromosome pairing among plants of different ploidy levels, was not different in *A. trachycaulum* × wheat, *A. yezoense* × wheat and wheat × *A. junceum* $F_1$ hybrids than in

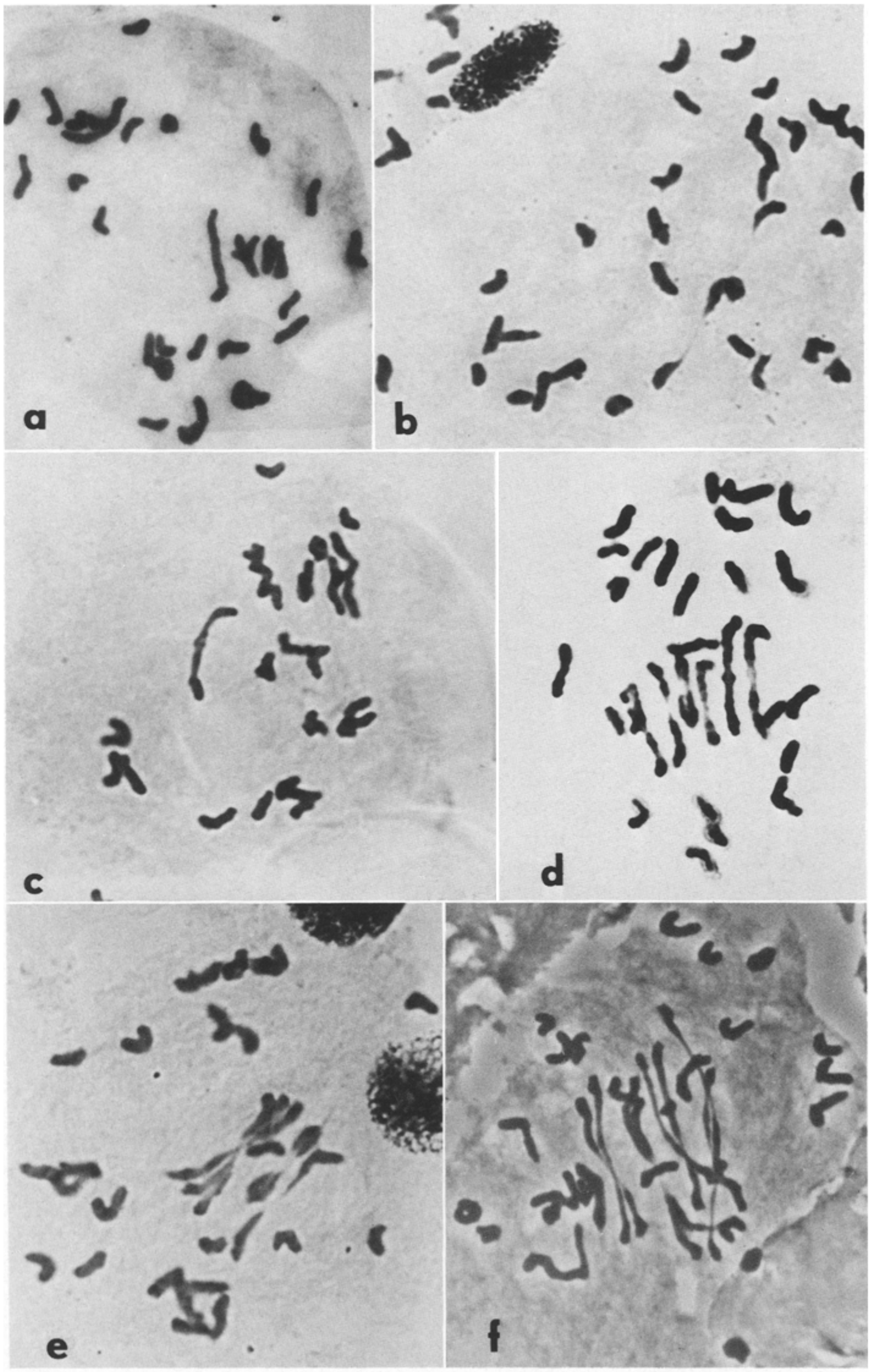

**Fig. 2a – f.** Chromosome pairing at Metaphase I in wheat-*Agropyron* $F_1$ hybrids: **a** *A. trachycaulum* × *T. aestivum* cv. 'Chinese Spring', 1 II (Rd), 33 I (1300×); **b** *A. yezoense* × *T. aestivum* cv. 'Chinese Spring', 1 II (Rd), 33 I (750×); **c** *T. aestivum* cv. 'Chinese Spring' × *A. junceum*, 1 II (Rd), 26 I (750×); **d** *A. ciliare* × *T. aestivum* cv. 'Chinese Spring', 6 II (5 Rd, 1 Rg), 23 I, (1300×); **e** *T. aestivum* cv. 'Chinese Spring' × *A. scirpeum*, 5 II (4 Rd, 1 RG), 25 I, (750×); **f** *T. aestivum* cv. 'Chinese Spring' × *A. intermedium*, 10 II (9 Rd, 1 Rg), 1 III, 19 I (1050×)

euhaploid of CS (Table 3). *A. trachycaulum, A. yezoense* and *A. junceum* genotypes used in this study, therefore, do not seem to affect homoeologous pairing in the hybrids. By similar comparison, it may be concluded that the genotypes of *A. ciliare, A. scirpeum* and *A. intermedium* used, promote homoeologous pairing in hybrids with wheat.

*Meiotic irregularities.* No meiotic irregularities were observed in *A. ciliare.* Meiotic irregularities were not examined in *A. yezoense. A. trachycaulum, A. scirpeum, A. junceum* and *A. intermedium* had 2.1, 6.2, 4.8 and 17.7% cells, respectively, with one-two inversion bridges at A-I.

Meiotic irregularities in $F_1$ hybrids included bridges and laggards at A-I and micronuclei at quartet stage (Table 4). Some triads, hexads, and secondary associations of two-three chromosomes were observed. In the first meiotic division, disjunction of sister chromatids leading to the formation of restitution nuclei was also observed in some cells. Chiasma frequency was negatively correlated with all three meiotic irregularities ($r = -0.61$ to $-0.82$). The positive correlations ($r = 0.75$ to 0.95) between inversion bridges, laggards and micronuclei suggested that all these irregularities were interrelated.

*Fertility.* The hybrids were male sterile (0.0–3.8% stainable pollen). *A. trachycaulum* (TA2015)×CS $F_1$ hybrids lacked stamens and pistil. Attempts to double the chromosome number of all the hybrids by colchicine treatment were unsuccessful. As noted earlier, *A. trachycaulum*×'TAM105', *A. yezoense*×'Wichita' and 'Wichita'×*A. intermedium* $F_1$ hybrids set no $BC_1$ seed with 'TAM105', 'Wichita' and 'Wichita', respectively, as the recurrent parent. In other hybrids, percent $BC_1$ seed set was lower (Table 5) than percent $F_1$ seed set (Table 2). However, a higher proportion of the $BC_1$ embryos resulted in plants as compared to $F_1$ hybrid embryos.

## *Backcross 1 derivatives*

The $BC_1$ seeds, when cultured 15–30 days after pollination, varied from normal seed, normal embryo, and normal endosperm to a little green seed, 'no' or

**Table 4.** Percent cells with mean-per-cell and range of bridges, laggards and micronuclei in hybrids of *T. aestivum* cv. 'Chinese Spring' (*CS*) with several *Agropyron* species

| $F_1$ hybrid | Bridges | | | Laggards | | | Micronuclei | | |
|---|---|---|---|---|---|---|---|---|---|
| | % cells | Mean/ cell | Range | % cells | Mean/ cell | Range | % cells | Mean/ cell | Range |
| *A. ciliare*×CS | – | – | – | 80.0 | 3.00 | 0–7 | 45.5 | 1.03 | 0–6 |
| *A. trachycaulum*×CS | 40.0 | 0.70 | 0–2 | 89.4 | 2.58 | 0–6 | 75.0 | 2.77 | 0–10 |
| *A. yezoense*×CS | – | – | – | 75.0 | 3.20 | 0–6 | 57.9 | 2.60 | 0–7 |
| CS×*A. scirpeum* | 55.5 | 0.55 | 0–1 | 60.0 | 2.40 | 0–7 | 58.7 | 1.20 | 0–5 |
| CS×*A. junceum* | – | – | – | 100.0 | 3.50 | 2–5 | – | – | – |
| CS×*A. intermedium* | 41.7 | 0.42 | 0–1 | 55.5 | 2.00 | 0–9 | 75.0 | 1.80 | 0–4 |

– Not recorded

**Table 5.** Production of $BC_1$ seed and $BC_1$ plants on various *Triticum aestivum* cv. 'Chinese Spring' (*CS*)-*Agropyron* $F_1$ hybrids

| $F_1$ hybrid | Recurrent wheat cultivar | No. of $BC_1$ seeds set | % $BC_1$ seed set | No. of $BC_1$ seeds dissected and embryos cultured | No. of $BC_1$ plants raised |
|---|---|---|---|---|---|
| *A. ciliare*×CS | CS | 8 | 2.02 | 7 | 3 |
| | 'Newton' | 1 | 0.72 | 1 | 1 |
| *A. trachycaulum*×CS | CS | 21 | 2.20 | 15 | 12 |
| *A. yezoense*×CS | CS | 7 | 3.73 | 6 | 6 |
| | 'Wichita' | 1 | 3.12 | 1 | 1 |
| CS×*A. scirpeum* | CS | 15 | 2.11 | 11 | 6 |
| CS×*A. junceum* | CS | 11 | 6.87 | 4 | 4 |
| CS×*A. intermedium* | CS | 7 | 2.71 | 6 | 4 |

**Table 6.** Chromosome association in some of the $BC_1$ derivatives of wheat-*Agropyron* hybrids (ranges in parentheses)

| $BC_1$ particulars | Plant no. | Chro. no. | I | Rod II | Ring II | Total II | III | Xma |
|---|---|---|---|---|---|---|---|---|
| (*c*×CS)×CS | 10 | 56 | 11.50<br>(7 – 16) | 7.50<br>(6 – 10) | 14.00<br>(10 – 17) | 21.50<br>(20 – 23) | 0.50<br>(0 – 1) | 36.50<br>(30 – 40) |
| (*c*×CS)×'Newton' | 2 | 54 | 19.01<br>(13 – 25) | 5.20<br>(2 – 14) | 10.60<br>(4 – 16) | 15.80<br>(10 – 19) | 1.13<br>(0 – 3) | 29.79<br>(24 – 37) |
| (*t*×CS)×CS | 1 | 56 | 15.06<br>(10 – 22) | –<br>(–) | –<br>(–) | 19.27<br>(17 – 22) | 0.80<br>(0 – 2) | –<br>(–) |
| | 2 | 51 | 20.00<br>(13 – 27) | –<br>(–) | –<br>(–) | 14.50<br>(12 – 19) | 0.67<br>(0 – 2) | –<br>(–) |
| (*y*×CS)×CS | 2 | 56 | 14.90<br>(10 – 18) | 3.80<br>(1 – 8) | 16.35<br>(11 – 20) | 20.15<br>(17 – 23) | 0.60<br>(0 – 2) | 37.70<br>(34 – 43) |
| | 3 | 53 | 13.00<br>(7 – 17) | 5.89<br>(3 – 9) | 13.45<br>(11 – 15) | 19.34<br>(15 – 23) | 0.44<br>(0 – 2) | 33.67<br>(31 – 38) |
| (*y*×CS)×'Wichita' | 1 | 52 | 13.33<br>(12 – 18) | 6.56<br>(4 – 10) | 12.78<br>(10 – 15) | 19.34<br>(17 – 20) | 0.00<br>(0) | 32.12<br>(28 – 35) |
| (CS×*s*)×CS | 6 | 45 | 8.33<br>(7 – 9) | 3.00<br>(3) | 15.33<br>(15 – 16) | 18.33<br>(18 – 19) | 0.00<br>(0) | 33.66<br>(33 – 35) |
| (CS×*j*)×CS | 9 | 49 | 6.60<br>(5 – 7) | 1.65<br>(0 – 4) | 19.55<br>(17 – 21) | 21.20<br>(21 – 22) | 0.00<br>(0) | 40.75<br>(38 – 43) |
| | 7 | 49 | 6.83<br>(5 – 8) | 2.50<br>(1 – 4) | 18.33<br>(16 – 20) | 20.83<br>(19 – 22) | 0.17<br>(0 – 1) | 39.50<br>(37 – 41) |
| (CS×*i*)×CS | 4 | 56 | 10.42<br>(7 – 16) | 5.50<br>(4 – 8) | 16.42<br>(12 – 20) | 21.92<br>(20 – 24) | 58<br>(0 – 2) | 39.50<br>(32 – 44) |
| | 5[a] | 49 | 9.25<br>(5 – 11) | 4.50<br>(2 – 8) | 14.75<br>(11 – 28) | 19.25<br>(16 – 22) | 0.25<br>(0 – 2) | 34.86<br>(31 – 38) |

[a] 0.12 (0 – 1) IV

*c A. ciliare, t A. trachycaulum, y A. yezoense, s A. scirpeum, j A. junceum, i A. intermedium*

*CS* 'Chinese Spring'

torpedo-shaped embryo and watery endosperm but most were normal. Many of the abnormal embryos did not germinate.

All the $BC_1$ plants were annual. $BC_1$ plants with CS as the recurrent parent needed no vernalization. There was reduction in plant height, tiller number, spike length, spikelets/spike, spikelet length and florets/spikelet in $BC_1$ plants compared to $F_1$ hybrids. Morphologically the $BC_1$ plants regressed toward wheat.

The chromosome number of the $BC_1$ derivatives of hybrids between wheat and *A. ciliare, A. trachycaulum, A. scirpeum, A. yezoense, A. junceum* and *A. intermedium* varied from 52–56, 48–57, 45–56, 52–58, 46–49 and 45–56, respectively. Usually, unreduced gametes functioned on the female side to produce $BC_1$ plants. Chromosome number in some $BC_1$ plants was higher than expected on the basis of unreduced gamete formation and was probably due to nondisjunction or inclusion of split univalents into the same gamete. The proportion of $BC_1$ plants resulting from unreduced gametes was higher in crosses of wheat with *A. yezoense* (71%), *A. junceum* (67%) and *A. trachycaulum* (75%) compared to those of wheat with *A. ciliare* (40%), and *A. scirpeum* (50%). The chromosome pairing was higher in the latter group than in the former group of hybrids (Table 3). It seems, therefore, that the higher pairing led to the formation of quartets and a greater proportion of reduced or partially reduced gametes while lack of pairing resulted in a higher frequency of meiotic nonreduction and unreduced gamete formation. An exception to this phenomenon was wheat×*A. intermedium* cross which had high pairing (Table 3) and high proportion of unreduced gamete formation (67%).

$BC_1$ plants which received unreduced chromosome complement from the $F_1$ hybrids had up to 21 II or more (Table 6). But the number of rod bivalents even in these hybrids was somewhat higher. $BC_1$ plants that received partially reduced chromosome complement from the female side and 21 chromosomes from the recurrent wheat parent had less than 21 II.

Male and female fertility and backcross seed set increased in $BC_1$ derivatives (Table 7) compared to $F_1$ hybrids (Table 5). The male and female fertility in wheat×*A. junceum* and wheat×*A. scirpeum* $BC_1$ derivatives increased more than in others (Table 7). Negative and significant correlation ($r = -0.45$) between

**Table 7.** Chromosome number, male and female fertility of BC$_1$ derivatives of wheat-*Agropyron* hybrids and BC$_2$ seed produced with *Triticum aestivum* 'Chinese Spring' (*CS*) as the recurrent parent

| Backcross | Chro. no. | Pollen stainability | Self seed set | | BC$_2$ seed set | |
|---|---|---|---|---|---|---|
| | | | % | No. | % | No. |
| (*A. ciliare* × CS) × CS | 52 – 56 | 44.3 – 48.0 | 0.0 – 3.7 | 0 – 2 | 11.1 – 50.0 | 1 – 13 |
| (*A. ciliare* × CS) × 'Newton' | 54 | 45.6 | 3.1 | 2 | 15.7 | 16 |
| (*A. trachycaulum* × CS) × CS | 48 – 57 | 3.9 – 19.1 | 0.0 – 0.7 | 0 – 1 | 0.0 – 26.3 | 0 – 10 |
| (*A. yezoense* × CS) × CS | 53 – 58 | 0.0 – 0.5 | 0.0 | 0 | 8.3 – 16.6 | 5 – 9 |
| (*A. yezoense* × CS × 'Wichita' | 52 | 0.0 | 0.0 | 0 | 14.7 | 8 |
| (CS × *A. scirpeum*) × CS | 45 – 56 | 25.0 – 77.0 | 77.8 – 98.2 | 56 – 106 | 45.0 – 69.5 | 9 – 34 |
| (CS × *A. junceum*) × CS | 46 – 49 | 60.3 – 74.1 | 51.0 – 97.5 | 54 – 184 | 58.4 – 92.3 | 14 – 23 |
| (CS × *A. intermedium*) × CS | 45 – 56 | 25.0 – 40.0 | 0.0 – 41.0 | 0 – 5 | 4.2 – 10.2 | 2 – 7 |

chromosome number in BC$_1$ derivatives and percent BC$_2$ seed set indicates that plants with lower chromosome number bore more BC$_2$ seed. Correlations of chromosome number with percent stainable pollen and percent self seed set were also negative ($r = -0.37$ in either case), although not significant. Percent pollen stainability was positively and significantly correlated with percent self seed set ($r = 0.74$).

The BC$_2$ seeds were harvested at maturity. The BC$_3$ plants raised from *A. ciliare* × wheat and *A. trachycaulum* × wheat hybrid derivatives had 43–46 chromosomes. By selfing 43 chromosome plants, some disomic addition lines have been isolated. These results beyond the BC$_1$ generation about all the hybrids and the effect of *Agropyron* cytoplasm will be described elsewhere.

## Discussion

Hybrids of *T. aestivum* with *A. junceum* and *A. intermedium* have been produced by other workers, but this is the first report of successful production of intergeneric hybrids of common wheat with *A. trachycaulum, A. ciliare, A. yezoense* and *A. scirpeum.* The wheat-*Agropyron* hybrids reported here were obtained by exploiting reciprocal cross differences, variability for crossability, seed set and seed development in conjunction with in vitro embryo rescue at early stages of seed development, using different formulations of media. Embryo culture facilitated the production of four new wheat-*Agropyron* hybrids previously thought to be noncrossable. These wheat-*Agropyron* hybrids encompass *Agropyron* genomes SS, HH, YY, the genomes of *A. scirpeum* being unknown. This is also the first report of the incorporation of S and Y genomes into wheat. The S genome is perhaps the most widespread genome in Triticeae (Dewey 1982). These crosses would lead to better understanding of evolutionary affinities of genomes S, H and Y.

*A. junceum* is diploid, whereas other species used are polyploid. The higher seed set with wheat as the male parent in all cases except *A. junceum* (Table 2) may have two implications. For any species of *Agropyron* above the diploid level, seed set may be easy with wheat as the male parent because *Agropyron* species are poor pollen producers under greenhouse conditions. At the diploid level, the buffering capacity is lacking to tolerate imbalance in embryo:endosperm chromosome ratio. Secondly, with *Agropyron* species as the female parents, a reverse cross with wheat as female will have to be made in order to reconstitute the wheat cytoplasm or to produce euplasmic addition lines.

Chromosome pairing data of wheat-*Agropyron* hybrids suggest that *Agropyron* genomes are different from each other as well as from wheat (Table 3) and that there are no homologous genomes shared between these *Agropyron* species and wheat. *A. trachycaulum* × wheat, *A. yezoense* × wheat and wheat × *A. junceum* crosses do not provide any evidence of homoeologous pairing. In *A. ciliare* × wheat, wheat × *A. scirpeum* and wheat × *A. intermedium* crosses, it is unclear which two genomes are involved in pairing. No evidence of this kind can be obtained from these hybrids. It is just as likely to be two of the wheat genomes as it is one of the *Agropyron* with one of wheat or the two *Agropyron* genomes. The chromosome pairing in CS haploid is only 0.24 II (Miller and Chapman 1976) and in *A. tsukushiense* (Honda) Ohwi haploid is 0.0 (Sakamoto 1964). Both genomes of *A. ciliare* are similar to two of the three genomes of *A. tsukushiense* (Sakamoto and Muramatsu 1966). Assuming that an *A. ciliare* haploid would behave like an *A. tsukushiense* haploid, pairing in the *A. ciliare* × wheat hybrid could be speculated between wheat and *Agropyron* chromosomes. However, this is unlikely because A, B, and D genomes are more closely related to one another than to S and Y. Furthermore, *Agropyron* chromosomes are longer than wheat chromosomes and most of the univalents were longer (Fig. 2d). Autosyndesis is, therefore, more likely the case.

*A. ciliare* and *A. yezoense* both have the same genomes. Hybrids between these two species exhibit, on the average, 11.29 II, 0.2 III, 0.36 IV (Sakamoto and Muramatsu 1966). However, pairing was significantly higher in the *A. ciliare* × CS hybrid than in the *A. yezoense* × CS hybrids (Table 3, Fig. 2b, d). The difference indicates genetic differentiation among parental *Agropyron* species. The *A. yezoense* genome may be acting as a weak suppressor while the *A. ciliare* genome acts as a strong suppressor of the *Ph* locus of wheat. The *Ph* locus regulating homoeologous pairing is more effective in suppressing homoeologous pairing in the wheat-*A. yezoense* hybrids but less effective in the wheat-*A. ciliare* hybrid, or *A. ciliare* may have a system which counteracts the *Ph* system of wheat. High pairing in wheat × *A. intermedium* hybrids may also be due probably to the suppression of *Ph* locus of wheat. *A. intermedium* is known to suppress the activity of genes controlling meiotic pairing (Gaul 1959) and thus promotes pairing in hybrids with *T. aestivum* (McGuire 1980).

The absence of homologous or homoeologous pairing in *A. trachycaulum* × wheat, *A. yezoense* × wheat and wheat × *A. junceum* hybrids is of concern if useful characteristics of *Agropyron* are to be incorporated into wheat. If pairing in these hybrids represents a random pairing of any one of the *Agropyron* chromosomes with corresponding homoeologues of the A, B or D genome of wheat, recombinants may still be obtained but by handling large populations. Using *Ph* mutant or nulli-5B of 'Chinese Spring' in the initial hybridization with such species may enhance the chance of genic exchange. It is assumed, however, that at least some of the homoeologous pairing would be intergeneric.

Reduced pairing in $BC_1$ plants may imply that there is probably not always preferential elimination of *Agropyron* chromosomes, rather some of the wheat chromosomes also may be eliminated from inclusion into gametes produced by the $F_1$ hybrids. Schulz-Schaeffer et al. (1973) observed that in $BC_1$ (*T. durum* Desf. × *A. intermedium*) × *A. intermedium*, the average number of bivalents was significantly lower than the expected values. The *Triticum* univalents which decreased from $BC_1$ to $BC_2$ apparently had an asynaptic effect on the normal pairing of *Agropyron* homologues. This is supported by the data of Person (1956) who reported partial asynapsis causing an excessive number of univalents in monosomic *T. aestivum*. Early desynapsis, in fact, was observed by us in some cells of $BC_1$ plants. *Agropyron* genomes may, therefore, be causing reduced pairing or asynapsis of wheat homologues. Reduced pairing in $BC_1$ plants where the recurrent wheat parent was a different cultivar may be due partially to reduced pairing between chromosomes of wheat cultivars (Dvorak and McGuire 1981).

All the *Agropyron* species except *A. junceum* that we have crossed with wheat are polyploid and contain two or more genomes each. Thus, recovery, identification and transfer of the individual genomes into wheat may not be possible. Analysis of $BC_2$ derivatives of *A. ciliare* × wheat and *A. trachycaulum* × wheat hybrids showed a high proportion of 49-chromosome plants. This may indicate genome segregation rather than random segregation of unpaired *Agropyron* chromosomes and may be used to isolate and identify single genome transfers of polyploid *Agropyron* species into wheat and to relate *Agropyron* addition lines to a particular *Agropyron* genome.

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