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# Production, morphology, and cytogenetic analysis of *Elymus caninus* (*Agropyron caninum*) × *Triticum aestivum* $F_1$ hybrids and backcross-1 derivatives

**H. C. Sharma and P. S. Baenziger**

Monsanto Company, 700 Chesterfield Village Parkway, Chesterfield, MO 63198, USA

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**Summary.** Intergeneric hybrids were produced between common wheat, *Triticum aestivum* (2n = 6x = 42, AABBDD) and wheatgrass, *Elymus caninus* (*Agropyron caninum*) (2n = 4x = 28, SSHH) – the first successful report of this cross. Reciprocal crosses and genotypes differed for percent seed set, seed development and $F_1$ hybrid plant production. With *E. caninus* as the pollen parent, there was no hybrid seed set. In the reciprocal cross, seed set was 23.1–25.4% depending upon wheat genotype used. Hybrid plants were produced only by rescuing embryos 12–13 days post pollination with cv 'Chinese Spring' as the wheat parent. Kinetin in the medium facilitated embryo germination but inhibited root development and seedling growth. The hybrids were vigorous, self sterile, and intermediate between parents. These had expected chromosome number (2n = 5x = 35, ABDSH), very little chromosome pairing (0.51 II, 0.04 III) and some secondary associations. The hybrids were successfully backcrossed with wheat. Chromosome number in the $BC_1$ derivatives varied 54–58 with 56 as the modal class. The $BC_1$ derivatives showed unusually high number of rod bivalents or reduced pairing of wheat homologues. These were sterile and $BC_2$ seed was produced using wheat pollen.

**Key words:** *Triticum aestivum* – *Agropyron caninum* – *Elymus caninus* – Intergeneric hybrids – Chromosome pairing

## Introduction

*Agropyron* complex (Cauderon 1966) encompassing *Agropyron, Elymus, Pseudoroegneria, Elytrigia, Thinopyrum, Pascopyrum, Psathrostachys* and *Leymus* (Dewey 1984) contains about 250 species and is one of the most important sources of alien variation for wheat breeding. *Agropyron elongatum* (*Thinopyrum elongata*) and *A. intermedium* (*Th. intermedia*) crossed with common wheat (*Triticum aestivum*, AABBDD) earlier provided useful disease resistance genes for wheat improvement (Sharma and Gill 1983 a).

In 1970's, advances in hybridization techniques and embryo culture were made and 21 more species were hybridized to common wheat: *A. junceum* (*Th. bessarabicum*), *A. distichum* (*Th. distichum*), *A. podperae* (*Th. podperae*), *A. scirpeum* (*Th. scirpea*), *A. caespitosum* (*Th. caespitosa*), *A. stipifolium* (*Pseudoroegneria stipifolia*), *A. geniculata* (*P. geniculata*), *A. repens* (*Elytrigia repens*), *A. pungens* (*El. pungens*), *A. fibrosum* (*Elymus fibrosa*), *A. trachycaulum* (*E. trachycaulus*), *A. yezoense* (*E. yezoensis*), *A. ciliare* (*E. ciliaris*), *E. dahuricus, E. canadensis, E. giganteus* (*Leymus giganteus*), *E. triticoides* (*L. triticoides*), *E. angustus* (*L. angustus*), *E. arenarius* (*L. arenarius*), *E. racemosus* (*L. racemosus*), *E. mollis* (*L. mollis*) (Tsitsin and Petrova 1976; Mujeeb and Bernard 1982; Mujeeb et al. 1983; Sharma and Gill 1983 a; Dewey 1984).

Whereas the benefits of the recently generated hybrids listed above are mainly in the future, the rest of the 200 species of the *Agropyron* complex have yet to be hybridized, the first and critical step to exploit the full potential of this gene pool. Furthermore, in order to use these alien species effectively their cytogenetic characteristics and biological relationships must be understood (Kimber 1984; Dewey 1984). Several new sources of genetic variation have been identified among different species of *Agropyron* complex for pathogen resistance (Knott and Dvorak 1976; Sharma et al. 1984), salt tolerance (Elzam and Epstein 1969; McGuire and Dvorak 1981; Gorham et al. 1984), alkalinity tolerance and large seeds (Dewey 1984), water stress (Shimshi et al. 1982), protein and lysine content (Lawrence et al. 1958) and gametocidal chromosomes/genes (Kibirige-Sebunya and Knott 1983).

Within *Agropyron* complex, according to genomically based nomenclature (Dewey 1984), *Elymus* contains approximately 150 species. These are polyploid species and contain combinations of S, H or Y genomes. The diploid donors of the genomes were *A. spicatum* (S) and *Hordeum bogdanii* (H). The origin of genome Y is unknown. In the past, attempts to cross *Triticum* with *Elymus* species particularly those of group *Roeg-*

*neria* (Nevski 1934; Cauderon 1966; Sakamoto 1973), including *E. caninus*, were unsuccessful either because of no seed set or early seed abortion (Peto 1930; McFadden 1934; Veruschkine 1936; Johnson 1938; Smith 1942; Matsumura 1942). Only in recent years have six of such crosses been reported and all required embryo culturing. Sharma and Gill (1983 b) produced hybrids of common wheat with *E. ciliaris* (SSYY), *E. yezoensis* (SSYY) and *E. trachycaulus* (SSHH). These hybrids led to an insight into *Elymus* – wheat genomic relationships. Mujeeb and Bernard (1982) reported hybrids of common wheat with *E. fibrosa* (SSYY), *E. canadensis* (SSHH) and *E. dahuricus* (SSHHYY?), and Muramatsu et al. (1983) obtained hybrids of common wheat with *E. tsukushiense* even though meiotic data have not yet been reported.

The purpose of this paper is to report the production, morphology and cytology of wheat – *E. caninus* $F_1$ hybrids and their backcross-1 ($BC_1$) derivatives.

## Materials and methods

Spring wheat line 'Chinese Spring' (CS), winter wheat line B393 (courtesy of HybriTech Seed Company) and *E. caninus* accession TA 2004 (courtesy of Dr. B. Gill) were used. *E. caninus* is a self-fertilizing, short lived perennial allotetraploid (2n=4x=28, SSHH) from Eurasia (Dewey 1980). Accession TA 2004 has excellent resistance to Barley yellow dwarf and wheat streak mosaic viruses (Sharma et al. 1984).

*E. caninus* seeds were surface sterilized in 10% chlorox for 5–10 min and germinated in Petri dishes on filter papers moistened with either water or 2,000 μM $GA_3$. Germination was 66% with $GA_3$ and only 40% with water. At the 1–2 leaf stage, seedlings were transplanted in 2½ inch pots. As the precise vernalization requirement of this grass was not known, seedlings were vernalized for 7–10 weeks. Several sets of wheat lines were grown periodically to synchronize flowering with *E. caninus*. After vernalization, seedlings were grown in 8 inch pots in a greenhouse at 21 °C day and 18 °C night temperature and 10 h photoperiod for tillering, and then at 25 °C day and 21 °C night temperature and 18 h photoperiod to initiate flowering. With 7–10 weeks vernalization, *E. caninus* tillered profusely and headed about 2 weeks later than wheat vernalized for 6 weeks and transplanted in the greenhouse along with *E. caninus*.

Crosses were made reciprocally and florets were pollinated twice during two days of post-emasculation. Hybrid seed development was monitored and 10–15 day-old seeds were dissected. Observations were made on seed, endosperm and embryo condition, and embryos, if found, were cultured. We used Murashige and Skoog (1962) media supplemented with 0.4 mg/l thiamine-HCl, 100 mg/l myo-inositol, 10 mg/l L-arginine, L-glycine and L-tryosine, 3% sucrose, 0.8% Bacto-agar, and with or without 1 mg/l kinetin. Embryos on the medium were incubated at 24 °C, 12 h photoperiod and high humidity. Some of the hybrid seeds were allowed to mature on the mother plants.

The $F_1$ hybrids and $BC_1$ plants were backcrossed to wheat as the recurrent male parent. Observations were made on morphology and fertility of the $F_1$ hybrids, $BC_1$ derivatives and the parents. Chromosome counts were made from root tips. For meiotic studies, spikes were fixed in 1 : 3 acetic acid: ethanol overnight, stored in 70% ethanol and squashed in 1% acetocarmine. Chromosome pairing data were pooled over the $F_1$ hybrids. To evaluate the extent of homology between genomes, the observed chiasma frequency was used to calculate expected chromosome configuration and mean arm pairing frequency (c) (Espinasse and Kimber 1981).

## Results

Reciprocal cross differences were apparent (Table 1). No seed was obtained from wheat × *E. caninus* cross even after making 710 pollinations. Seed set in the reciprocal cross varied from 23.1–25.4% depending upon wheat genotype used. In all, 95 *E. caninus* × CS and 125 *E. caninus* × B393 hybrid seeds were produced.

Eighty-eight *E. caninus* × B393 and 85 *E. caninus* × CS $F_1$ hybrid seeds were dissected 10–15 days post-pollination (Table 2). Seeds were green and shrivelling by day 10 but completely shrivelled and dry by day 15 (Fig. 1). Eleven-to 14-day old seeds were a mixture of greenish and drying seeds. There was no endosperm in dry seeds and only degenerate endosperm in greenish seeds. Invariably embryos were found in drying seeds and not in green seeds.

Embryo recovery was low. Out of 88 *E. caninus* × B393 seeds, only 3 (3.4%) had embryos. The embryos were very small torpedo shaped with little or no scutellum. Two of these were cultured but did not germinate. Among 85 *E. caninus* × CS seeds dissected, 9 (10.6%) had embryos. These embryos varied from torpedo shaped to almost normal heart shaped embryos. Four $F_1$ hybrid plants were raised by culturing these 9 embryos (44.4% success in embryo rescue). Success in embryo rescue was better with kinetin in the medium. Three of the 4 hybrid plants were obtained by culturing embryos on medium containing kinetin. One embryo germinated on the medium without hormone and was almost normal otherwise. Root development and seedling growth were very slow on the kinetin-containing medium and seedlings turned pale if not transferred about a week after germination of embryos to medium lacking kinetin.

Embryos at different stages of seed development showed differential response. It was from embryos from

**Table 1.** Number of pollinations made and number of wheat – *E. caninus* $F_1$ hybrid seeds set. CS and B393 are *Triticum aestivum* lines and TA2004 is an *E. caninus* accession

| Cross | | Florets pollinated | Seeds set | % Seed set |
|---|---|---|---|---|
| Female | Male | | | |
| CS | TA2004 | 326 | 0 | 0.0 |
| B393 | TA2004 | 384 | 0 | 0.0 |
| | | 710 | 0 | 0.0 |
| TA2004 | CS | 412 | 95 | 23.1 |
| TA2004 | B393 | 492 | 125 | 25.4 |
| | | 904 | 220 | 24.3 |

**Table 2.** Number of *E. caninus* × wheat $F_1$ hybrid seeds dissected at different stages, number of embryos found and cultured, and number of $F_1$ hybrid plants produced

| Cross | No. of seeds dissected | Age (days after pollination) | No. of embryos found | Embryo condition | No. of embryos cultured | Media | No. of hybrid plants obtained |
|---|---|---|---|---|---|---|---|
| *E. caninus* × B393 | 20 | 10 | 1 | Very small globular with a little scutellum | 1 | $Kin^+$ | 0 |
| | 20 | 11 | 1 | Small torpedo without visible scutellum | 1 | $Kin^+$ | 0 |
| | 11 | 13 | 0 | – | – | – | – |
| | 37 | 14 | 1 | Small torpedo without visible scutellum | 0 | – | – |
| Total | 88 | | 3 | | 2 | | 0 |
| *E. caninus* × CS | 1 | 11 | 1 | Small globular | 1 | $Kin^-$ | 0 |
| | 42 | 12 | 3 | Small but almost normal heart shaped with scutellum | 3 | $Kin^-$ | 1 |
| | | | 2 | Small with undifferentiated (deformed) scutellum | 1 | $Kin^-$ | 0 |
| | | | | | 1 | $Kin^+$ | 1 |
| | 38 | 13 | 3 | Small torpedo with very little scutellum | 3 | $Kin^+$ | 2 |
| | 4 | 15 | 0 | – | – | – | – |
| Total | 85 | | 9 | | 9 | | 4 |

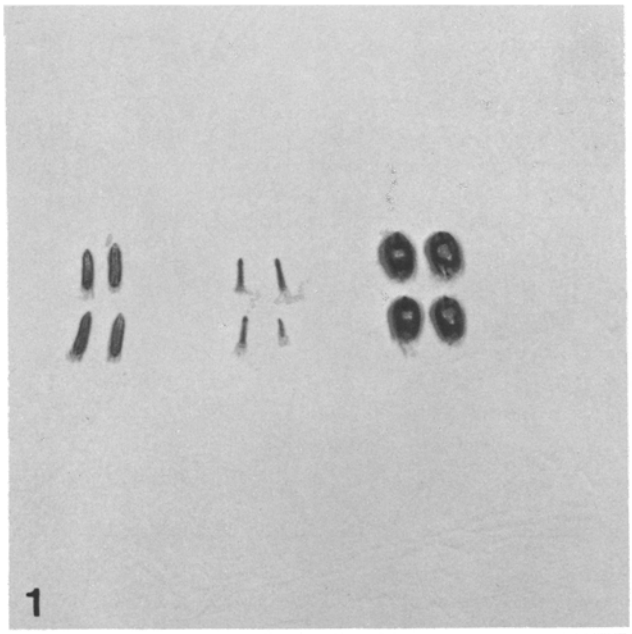
12–13-day old seeds that hybrid plants were obtained (Table 2). Embryos younger than 12 days did not grow and in 15-day old seeds, embryos had completely aborted. The $F_1$ hybrid seeds harvested at maturity were completely shrivelled and inviable.

The $F_1$ hybrids were intermediate between parents (Fig. 2), but heterotic for spikelet number/spike. The $F_1$ hybrids were uniform among themselves and self-sterile. Chlorotic leaf trait of *E. caninus* was expressed in the hybrids.

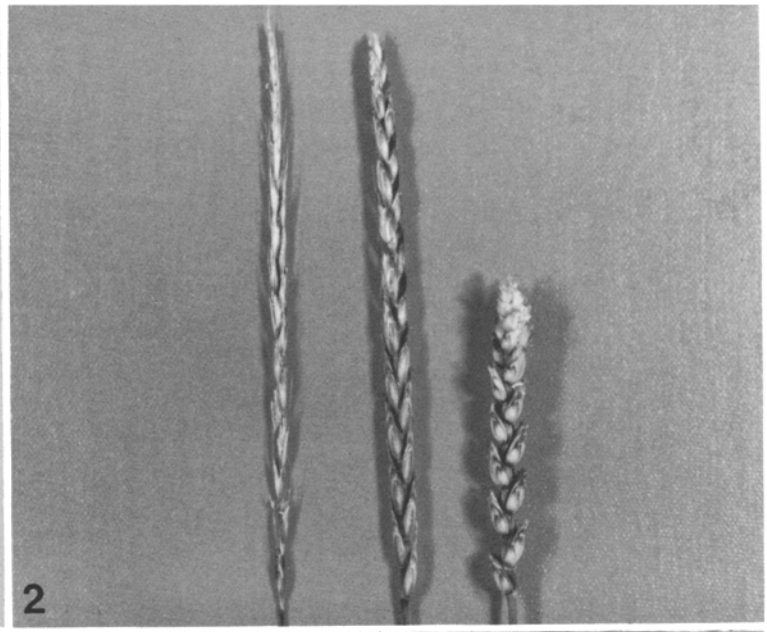
The $F_1$ hybrids had the expected chromosome number, $2n = 35$ (Fig. 3). The larger 14 chromosomes are probably of *Elymus*. Chromosome pairing in *E. caninus* and wheat was regular with mostly ring bivalents. In the $F_1$ hybrids, chromosome pairing averaged 0.51 II and 0.04 III (Fig. 4, Table 3) and mean arm pairing frequency was 0.022 per cell. Secondary association among chromosomes was observed in the $F_1$ hybrids (Fig. 5). In cells where there was no pairing at all (35 I), there was more secondary association. Out of 85 cells scored, 55 had secondary association (37 end-to-end, 5 side-by-side, 2 side-to-end, and 11 combinations of these). These associations between univalents may be due to corresponding genetic similarities, random association due to heterochromatic fusions or other forces (Soler et al. 1980). Mean number of laggards, micronuclei and bridges in the *E. caninus* × wheat hybrids was 3.4, 3.8 and 0.8 per cell, respectively. As a result of such meiotic irregularities, there appeared polyads of different kinds (triads 11%, pentads and nonads 10%) in addition to tetrads.

$BC_1$ seed set on the $F_1$ hybrids using CS and B393 pollen was lower (17.7%) than the $F_1$ seed set probably because only unreduced or almost unreduced gametes formed by rare restitution in the $F_1$ hybrids functioned. However, frequency of embryo recovery and embryo

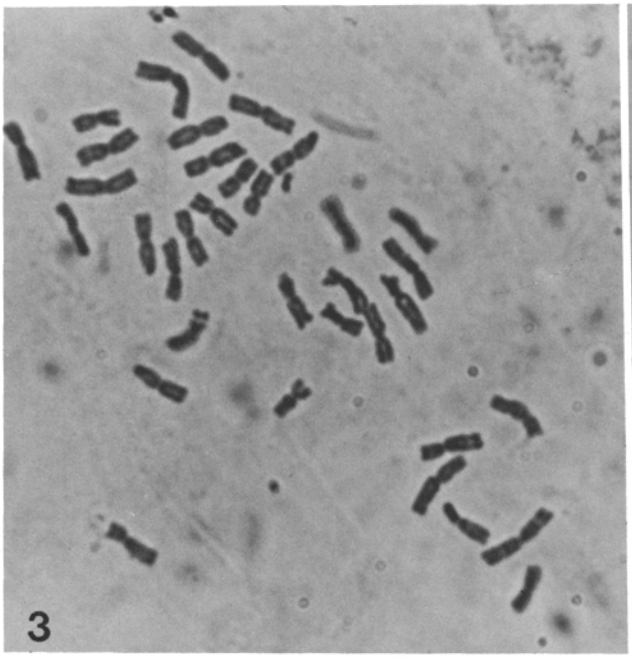
**Fig. 1.** Dorsal view of 12 day old seeds: *Left* = *E. caninus; middle* = *E. caninus* × wheat (CS) $F_1$ hybrid; *right* = CS. **Fig. 2.** Immature spikes, *left-right* = *E. caninus, E. caninus* × wheat (CS) $F_1$ hybrid, CS. **Fig. 3.** Somatic chromosome spread of *E. caninus* × wheat $F_1$ hybrid ($2n = 35$) (1,050×). **Fig. 4.** A pollen mother cell of *E. caninus* × wheat $F_1$ hybrid showing 1 rodII and 33I (unpaired) chromosomes (1,300×). **Fig. 5.** A pollen mother cell of *E. caninus* × wheat $F_1$ hybrid showing secondary association: 1 end-to-end (E–E), 1 side-by-side (S–S) and 1 chain of 3 (C-III) (850×). **Fig. 6.** A pollen mother cell in (*E. caninus* × CS) × B393 $BC_1$ derivative showing approximately 112 chromosomes (850×)



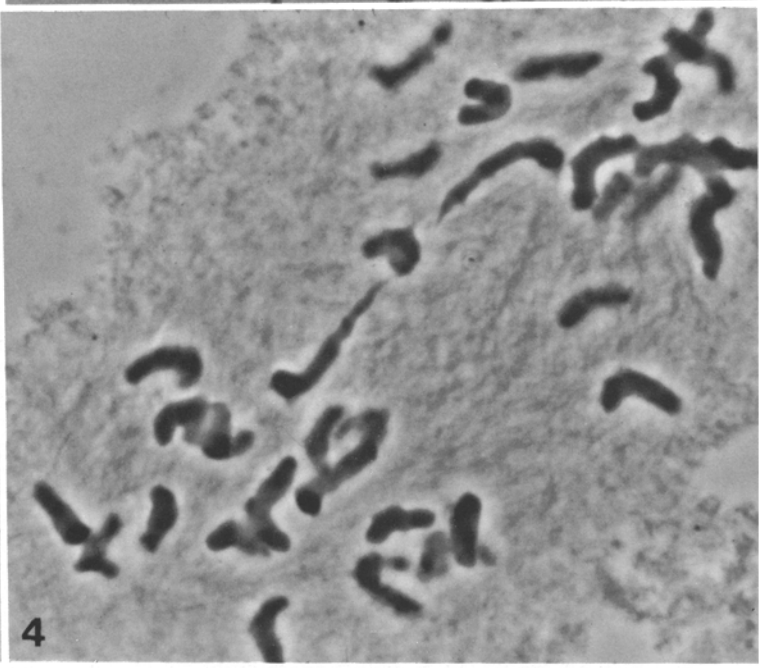
1



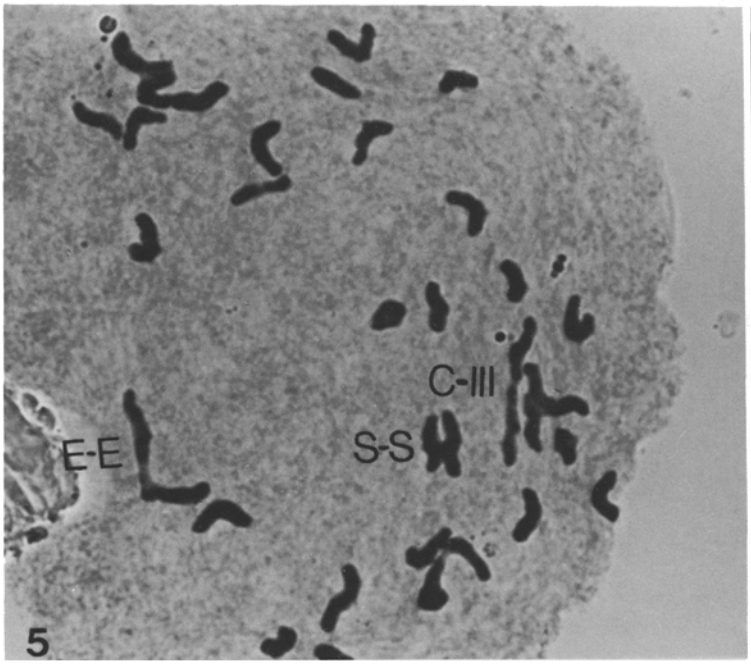
2



3



4




5

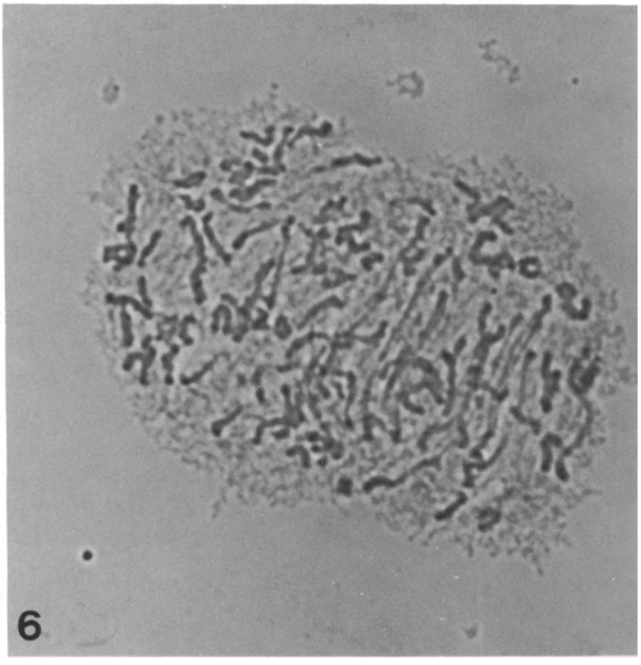


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**Table 3.** Mean chromosome pairing and range values (in parentheses) of parents and *E. caninus* × 'Chinese Spring' $F_1$ hybrid

| Material | Genome | Chromosome no. | No. of cells scored | Chromosome pairing | | | | | Xma | Mean arm pairing frequency (c) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | I | Rod II | Ring II | Total II | III | | |
| *E. caninus* | *SSHH* | 28 | 7 | 0.30 (0–2) | 1.14 (0–2) | 12.71 (12–14) | 13.85 (13–14) | 0 | 26.57 (25–28) | 0.949 |
| 'Chinese Spring' | *AABBDD* | 42 | 9 | 0.66 (0–4) | 1.33 (0–3) | 19.33 (18–21) | 20.67 (19–21) | 0 | 40.00 (37–42) | 0.952 |
| *E. caninus* × 'Chinese Spring' | *ABDSH* | 35 | 137 | 33.87 (29–35) | 0.49 (0–3) | 0.02 (0–1) | 0.51 (0–3) | 0.04 (0–1) | 0.61 (0–3) | 0.022 |
| 'Chinese Spring' euhaploid[a] | *ABD* | 21 | – | 20.76 | – | – | 0.24 | – | – | 0.019–0.081 |

[a] McGuire and Dvorak 1982

**Table 4.** Chromosome pairing, and fertility of backcross-1 plants having 2n = 56

| Particulars of $BC_1$ plant | No. of cells scored | Chromosome pairing | | | | | | Xma | Pollen stainability (%) | $BC_2$ recurrent parent | Seed set | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | I | Rod II | Ring II | Total II | III | IV | | | | % | No. |
| (*E. caninus* × CS) × B393-1 | 6 | 14.17 (10–16) | 5.00 (2–7) | 15.66 (13–18) | 20.67 (20–23) | 0.17 (0–1) | 0.00 0 | 36.67 (33–40) | 3.0 | B393 | 11.5 | 17 |
| × B393-2 | 15 | 16.27 (12–25) | 5.52 (3–9) | 13.80 (7–18) | 19.32 (14–22) | 0.27 (0–1) | 0.07 (0–1) | 33.87 (23–39) | 11.9 | B393 | 33.3 | 10 |
| (*E. caninus* × CS) × CS-1 | 11 | 14.45 (8–19) | 8.00 (5–12) | 12.10 (6–17) | 20.10 (17–24) | 0.45 (0–1) | 0.00 0 | 33.09 (26–40) | 27.9 | CS<br>B393 | 11.0<br>12.5 | 9<br>3 |
| × CS-3 | 31 | 17.96 (11–30) | 6.16 (1–11) | 12.23 (5–17) | 18.39 (13–22) | 0.42 (0–2) | 0.00 0 | 31.46 (18–38) | 8.8 | CS | 2.5 | 3 |
| × CS-6 | 21 | 25.74 (16–45) | 4.95 (1–8) | 9.71 (3–15) | 14.67 (4–20) | 0.24 (0–1) | 0.05 (0–1) | 25.00 (8–33) | 4.0 | * | * | * |

* Not backcrossed

rescue was much higher compared to $F_1$ hybrids and 21 $BC_1$ plants were raised by culturing 26 embryos 15–17 days post pollination. Among the $BC_1$ seeds harvested at maturity, 75% were viable but thin and grass-like.

Chromosome number of 16 $BC_1$ plants checked varied from 54 to 58, 50% of the plants having 2n = 56. Among $BC_1$ plants with 2n = 56, 3 (*E. caninus* × CS) × B393 plants were uniform but 5 (*E. caninus* × CS) × CS plants varied phenotypically: plant No. 1 unlike all others had no chlorotic leaves, lacked white scale on stems, had the highest pollen stainability (Table 4) and was resembling CS the most closely; plant No. 3 had most vigorous spikes and thickest tillers; and others had thin stems and appeared more like the $F_1$ hybrids. This variation may be due to heterozygosity of the *Elymus* parent.

$BC_1$ plants having 56 chromosomes showed reduced chromosome pairing or an unusually high number of rod bivalents resulting in a lower chiasma frequency (Table 4). In some of these plants, 2.5–6.2% pollen mother cells had approximately 112 chromosomes. Chromosome pairing in these cells was not recordable because of clumping but does not seem to be regular (Fig. 6). Stainable pollen among $BC_1$ plants varied from 2.0 to 27.9% and no seed developed on spikes left to self pollinate. The $BC_2$ seed set varied from 2.5 to 33.3% (Table 4).

## Discussion

By facilitating fertilization through the use of reciprocal crosses and genetic variation, and by isolating and rescuing hybrid embryos, we produced four *E. caninus* × *T. aestivum* hybrids – the first successful *E. caninus* × wheat cross. Production of this intergeneric hybrid is significant because *E. caninus* would be useful

for germplasm development by introgressing new genes into wheat (Sharma et al. 1984).

Failure to obtain hybrid seed with *E. caninus* as the male parent may be due to poor pollen production by this wheatgrass in greenhouse. The anthers were small and stainable pollen was only 43% compared to 87% or more in wheat. Reciprocal cross differences as observed in the present study also indicate that the parent with lower chromosome number may not always be the better male parent. It is also interesting that the percent hybrid seed set with B393 which is not known to possess crossability genes and with CS which possesses crossability genes is of the same order even though rate of embryo recovery was much lower in *E. caninus*× B393 cross and hybrid plants could be produced only with CS as the wheat parent. Whether the same crossability genes facilitate seed development or it is due to something else in CS is not known.

Since not the seed set, at least with *E. caninus* as the female parent, but early seed abortion was more serious a problem, the success rate can probably be improved by early embryo rescue. Higher rate of embryo rescue but inhibition of root development by kinetin in the medium indicate that kinetin may facilitate initial cell division and cell elongation but root primordia so initiated fail to elongate in the presence of kinetin. Cytokinins appear to affect seed germination (Khan 1975; Smith and Van Staden 1978). The level of cytokinins in wheat seed increased with an increase in endosperm material (Thomas and O'Toole 1978), and cytokinin activity in rice embryo increased rapidly and was higher in endosperm than in embryo during germination (Saha et al. 1984) which may suggest that there is a delicate balance of cytokinin between embryo and endosperm and the endosperm may supply cytokinins until the embryo is able to synthesize its own cytokinins. Because in *E. caninus*×wheat hybrid there was endosperm degeneration and embryo starvation, the embryo may have been deficient in cytokinins and cytokinin in the medium may have substituted for a viable endosperm as the cytokinin source during germination. Kinetin inhibits root elongation (Stenlid 1982) and leads to necrosis of the root primordia (Raghavan 1980). Such necrosis and poor root development in the present study probably led to poor seedling growth by starvation. Using lower concentrations of kinetin or replacing kinetin by natural or more labile cytokinins might be worth testing.

The level of chromosome pairing in *E. caninus*× wheat hybrids is too low to provide any evidence of homologous or homoeologous pairing. A low mean arm pairing frequency indicates that there is no homology between wheat and *E. caninus* chromosomes and that *E. caninus* is an allotetraploid. The mean arm pairing frequency in the hybrids was not different from euhaploid of CS (Table 3). *E. caninus* used in this study, therefore, does not affect homoeologous pairing in the hybrids. *E. trachycaulus*, a North American tetraploid species hybridized to wheat (Sharma and Gill 1983 b) also has the same genomic formula as does *E. caninus*. It appears that the $F_1$ hybrids of these two species with wheat behave very similarly. Negligible pairing in these hybrids indicates that (1) SH genomes differ from wheat as well as from each other, (2) there are no homologous genomes shared between wheat and these *Agropyron* species and (3) SH genomes are not suppressing *Ph* locus of wheat. As there is very little pairing (even that may be between wheat chromosomes), gene transfer by crossing over per se may have low probability. Thus, alien addition lines of *E. caninus* in wheat will have to be produced and other means of gene transfer, such as irradiation, promotion of nonhomologous chromosome pairing, or encouraging gene transfer in tissue culture, will be needed.

Reduced pairing and unusually high number of rod bivalents in the $BC_1$ derivatives may be interpreted to mean that large number of *Elymus* univalents hinder pairing in some way and affect normal pairing of wheat chromosomes. Such an effect has also been reported in (*T. durum*×*A. intermedium*)×*A. intermedium* $BC_1$ plants (Schulz-Schaeffer et al. 1973) and in (*E. trachycaulus*×wheat)×wheat $BC_1$ plants (Sharma and Gill 1983 b). Alien univalents may have asynaptic effect on the normal pairing of homologues (Person 1956; Sharma and Gill 1983 b) and early desynapsis was observed by these authors as well as in the present study.

The occurrence of pollen mother cells with about 112 chromosomes in some of the $BC_1$ plants indicates that the chromosome number in these cells has doubled. This may be due to a chance occurrence of genetic sectoring as observed by Mujeeb et al. (1976) in pentaploid wheat hybrid. In their case, restituted cells seen in root tip did not transgress to the gametic tissue. Such mixoploid situation must be there in the root tips of our $BC_1$ plants but apparently has been overlooked. The reduction in chromosome pairing in 16× cells is difficult to explain unless chromosome 3B is deficient in these cells.

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