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**Cytogenetics of Intergeneric
Elymus canadensis × *Triticum aestivum* Hybrids
($n=5x=35$, SHABD)
and their Backcross Progenies with *T. aestivum***

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With 2 figures and 6 tables

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Key words: *Triticum aestivum* — *Elymus canadensis* — intergeneric hybridization — chromosome pairing — backcross progeny — aneuploidy

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Conventional bread wheat *Triticum aestivum* L. ($2n=6x=42$, AABBDD) improvement depends upon the availability of appropriate germplasm. When variability is limited for specific characters, diverse genera can be utilized.

Several species of the *Elymus* genus possess a substantial range of genetic variation of practical potential for incorporation into *T. aestivum*, especially

for the much needed resistance to the pathogens *Fusarium graminearum* (scab) and *Helminthosporium sativum*. Intergeneric hybrids of *T. aestivum* and *Elymus* that have been produced thus far involve *T. aestivum* × *E. giganteus* (MUJEEB-KAZI and RODRIGUEZ 1980, 1981 b), *T. aestivum* × *E. mollis* (TSITSIN, pers. inform. via MERKER), and combinations with *E. angustus*, *E. agropyroides*, *E. cinereus*, *E. dahuricus*, and *E. triticoides* (MUJEEB-KAZI, unpubl.).

This paper reports on a new intergeneric hybrid combination, that of *E. canadensis* ($2n=4x=28$, SSHH) and *T. aestivum* ($2n=6x=42$, AABBDD). The cytogenetic emphasis is to establish genome relationships between the genera involved and thus to provide a measure of success in obtaining alien genetic transfers.

Materials and Methods

Elymus canadensis L. ($2n = 4x = 28$, SSHH) and *Triticum aestivum* L. var. 'Chinese Spring' ($2n = 6x = 42$, AABBDD) plants were grown in pots with a soil mix, and maintained under greenhouse conditions of 20°C/15°C, 14 h natural day light, and approximately 45 % to 50 % relative humidity.

E. canadensis spikes were pollinated with *T. aestivum* pollen on the second day after emasculation, i.e. before stigma receptivity was visible. A second pollination followed on the third day after emasculation. Eight hours after pollination, gibberellic acid (GA_3 , 75 ppm aqueous) was applied with a syringe to the floret cups. After 20 days of development, the embryos were excised and cultured for three weeks on a medium of TAIRA and LARTER (1978). After three weeks, embryos which differentiated into plantlets or increased in size were transferred to an MS medium (MURASHIGE and SKOOG 1962) for further development. The differentiated plantlets were transferred to peat pots and maintained in the growth chamber (20°C/15°C, 14 h day/10 h night, 70 % r.h.) until their final transfer to soil in pots, under greenhouse regimes described earlier.

Hybrids were initially identified on the basis of their somatic chromosome number of $n = 5x = 35$, and genomic constitution of SHABD, using the schedule developed by MUJEEB-KAZI and MIRANDA (1984). For confirmation spikes were fixed for meiotic analyses in 6 : 3 : 1 (ethanol : chloroform : acetic acid) for 48 hours, then transferred to 70 % ethanol and refrigerated until use. Anthers were stained in alcoholic-acid carmine for 48 hours, squashed in 45 % acetic acid and then observed for chromosome relationships at metaphase I.

The self-sterile F_1 hybrids were backcrossed with *T. aestivum* varieties 'Chinese Spring', 'Genaro 81' or 'Zaragoza 75' to obtain backcross I (BC_1) seed. The florets on the self-sterile F_1 spikes were clipped and pollinated on two consecutive days with *T. aestivum* pollen. Gibberellic acid (75 ppm aqueous) was applied with a syringe to the floret cups 8 hours after each pollination. BC_1 seeds were allowed to mature on the F_1 hybrid. BC_1 plants upon pollination with *T. aestivum* produced BC_2 seed. Spikes of BC_2 plants were allowed to self-pollinate to produce BC_2F_1 seed if they were self-fertile. Some BC_2 plants were emasculated and pollinated by *T. aestivum* to form BC_3 seed.

Results

Pollination of 86 florets (3 spikes) of *E. canadensis* by *T. aestivum* var. 'Chinese Spring' produced 3 seed, from which 3 embryos were excised. These differentiated to produce 3 plantlets that grew vigorously and were perennial. The morphology of the hybrid spikes reflected a cumulative genome effect of both genera (Fig. 1, Table 1).



Fig. 1 Representative photographs of: A) Spike of *Elymus canadensis* L. ($2n = 4x = 28$); dorsal and ventral views of B) F_1 spikes of *E. canadensis*/*T. aestivum* ($n = 5x = 35$) and C) *T. aestivum* L. var. 'Chinese Spring'

The *E. canadensis*/*T. aestivum* hybrids were somatically stable and possessed 35 chromosomes from the expected SHABD genomic combination (Fig. 2a). The 1B and 6B satellited *T. aestivum* chromosomes were consistently observed, but in none of the 50 cells analyzed did the satellite expression of the *E. canadensis* complement appear, which is consistent with the amphiplastic effects observed in several intergeneric hybrids. The mean meiotic chromosome associations in the hybrids were 34.85I 0.072II (rods) with a 0.072 mean chiasma frequency per cell (Fig. 2b).

Pollinating the self-sterile *E. canadensis*/*T. aestivum* F_1 hybrids with *T. aestivum* varieties produced BC_1 seed (Table 2). These were allowed to mature on the F_1 plant. BC_1 seed set ranged from 2.56 up to 5.58 per cent. The BC_1 seed were expected to possess 56 chromosomes due to the fertilization of an unreduced egg cell ($n = 5x = 35$, SHABD) by *T. aestivum* pollen ($n = 3x = 21$,

Tab. 1 Mean spike characteristics of *Elymus canadensis*, *E. canadensis*/*Triticum aestivum* var. Chinese Spring (n=5x=35), and *T. aestivum* var. Chinese Spring

	<i>E. canadensis</i> *	<i>E. canadensis</i> / <i>T. aestivum</i>	<i>T. aestivum</i> var. Chinese Spring
Spike:			
Length (cm)	20.14	8.10	8.30
Width (cm)	1.42	0.68	0.95
Rachis:			
Nodes/spike	31.4	12.75	27.00
Internode length (cm)	0.59	0.56	0.40
Spikelet:			
Length (cm)	X	1.30	1.00
Width (cm)	X	0.63	0.93
Spikelets/spike	62.8	12.75	26.44
Florets/spikelet	4.5	3.69	4.55
Glume:			
Body length (cm)	1.28	0.80	0.95
Awn length (cm)	1.48	0.18	0.05
Lemma:			
Body length (cm)	1.36	0.98	0.85
Awn length (cm)	3.08	0.37	0.05
Anther length (cm)	0.34	0.20	0.40

* From Dewey 1971

ABD). Deviations in chromosome number were from 52 to 61 chromosomes (Table 3), possibly because of meiotic aneuploidy on the maternal side. A BC₁ plant with 54 chromosomes, from the combination *E. canadensis*/*T. aestivum* var. 'Chinese Spring'/*T. aestivum* var. 'Zaragoza 75', possessed a mean meiotic chromosome association of 32.68I 3.13II (rings) 6.81II (rods), 0.48III, with a 14.02 chiasma frequency per cell. Two meiocytes expressed chromosome

Tab. 2 Backcross I seed set data from pollinating *Elymus canadensis*/*Triticum aestivum* by *T. aestivum* varieties 'Chinese spring', 'Genaro 81', and 'Zaragoza 75'

Maternal parent	<i>T. aestivum</i> varieties (male parent)	Number of spikes pollinated	Number of florets pollinated	Seed set	Percentage seed set
<i>E. canadensis</i> / <i>T. aestivum</i>	C. Spring	9	412	23	5.58
<i>E. canadensis</i> / <i>T. aestivum</i>	Genaro 81	9	402	12	2.99
<i>E. canadensis</i> / <i>T. aestivum</i>	Zaragoza 75	3	117	3	2.56

associations of 34I 5II (rings) 5II (rods), 28I 2II (rings) 8II (rods) 2III. Similar relationships were also observed for several other BC₁ plants that expressed chiasma frequencies ranging between 12.36 and 15.85 per cell.

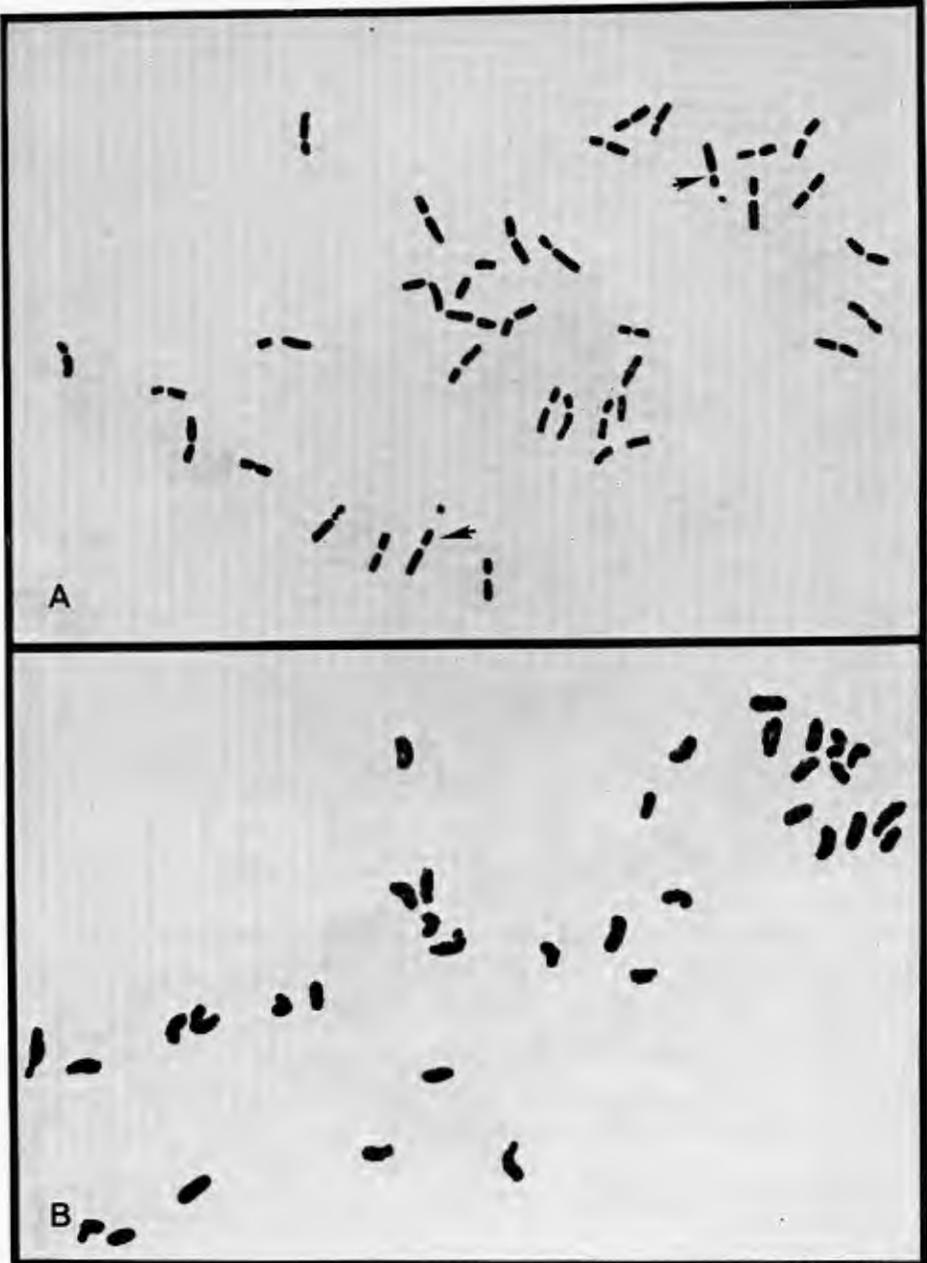


Fig. 2 A) Somatic cell of *Elymus canadensis*/*Triticum aestivum* F₁ hybrid with $n = 5x = 35$ chromosomes. The single satellited *T. aestivum* chromosomes 1B and 6B are arrowed. B) Metaphase I cell of *E. canadensis*/*T. aestivum* with 35 univalent chromosomes

Tab. 3 Backcross I seed germination and somatic cytological details of the *Elymus canadensis*/*Triticum aestivum* var. 'Chinese Spring'//*T. aestivum* variety combination

Backcross I combination ⁺	Seed planted	Seed germination	Somatic count	Number of plants
<i>E. canadensis</i> //2* <i>T. aestivum</i> ¹	20	12	55	1
			55 (2t*, 3d)	1
			56	1
			57	4
			57 (1t)	1
			57 (1d)	1
			58	1
			59	1
			61	1
<i>T. canadensis</i> //2* <i>T. aestivum</i> ²	9	8	52	2
			54 (1d)	1
			55 (1t)	1
			56	1
			58	2
			59	1
<i>E. canadensis</i> //2* <i>T. aestivum</i> ³	3	2	59	1

+ = BC₁ parent variety: 1 C. Spring 2 Genaro 81 3 Zaragoza 75

* = Telocentric and d = dicentric chromosomes

Backcross I plants set BC₂ seed when pollinated by *T. aestivum* varieties (Table 4). The somatic chromosome number of 108 BC₂ plants was from 42 to 56 in which telocentric and dicentric chromosomes were observed. The meiotic relationships of some BC₂ plants were typically asynaptic with a substantial range in chiasma frequency prevalent from total asynapsis (0.45 chiasma/cell), to intermediate pairing (19.34 chiasma/cell), to high pairing (37.40 chiasma/cell) (Table 5). The detailed meiotic associations of these plants is shown in Table 6. Backcross III seed were obtained from pollinating BC₂ plants with *T. aestivum* varieties. Of the BC₂ plants 13 were self-fertile. An additional nine BC₂ plants were also self-fertile, but BC₃ seed could not be obtained due to a scarcity of pollen. The BC₃ seed set ranged from 3.3 to 83.3 per cent.

E. canadensis has been "tentatively" identified as a source of resistance to stem rust and *Helminthosporium sativum* (G. BEKELE, pers. comm.). Field testing of the *E. canadensis*/*H. vulgare* hybrid clones (MUJEEB-KAZI and RODRIGUEZ 1982) substantiates the resistance observations, as checked against the control *H. vulgare* varieties. Neither *E. canadensis*/*T. aestivum* hybrid clones nor the BC progenies have yet been subjected to field testing, but they are now so programmed.

Discussion

E. canadensis L. is a widely distributed North American species. It is an allotetraploid (2n=4x=28) with two distinctly different genomes and a basic

Tab. 4 Backcross II combinations of *Elymus canadensis*/*Triticum aestivum* var. 'Chinese Spring'//*T. aestivum* backcross I plants with different varieties of *T. aestivum* with BC₂ cytological details

Backcross I parental combination	Chromosome number	Backcross II <i>T. aestivum</i> cultivar	Number of backcross II plants	Somatic counts of backcross II plants
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Zaragoza 75	54	Zaragoza 75	8	47, 49, 46, 52, 52, 52, 43/(t) 57
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Zaragoza 75	59	Zaragoza 75	4	57 (t), 50, 52, 48 (t)
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. C. Spring	57	Jupateco	4	48, 49, 47, 51
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. C. Spring	57	Nacozari	14	49, 49, 50, 56, 48, 50, 47, 40, 56, 49, 48, 50, 46, 53
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. C. Spring	55, 2t	C. Spring-Ciano (E)	8	50, 54, 47, 48, 54, 47, 49, 51
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. C. Spring	57, t	C. Spring-Ciano (E)	10	49, 50, 50, 45, 49, 50, 47, 53, 50, 46
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Genaro 81	52	Genaro 81	9	50, 48, 44, 50, 49, 45, 45, 50, 49
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Genaro 81	59	Genaro 81	10	48, 48, 50, 48, 47, 51, 48, 51, 56, 56
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Genaro 81	54	Genaro 81	17	51, 49, 48, 56, 49, 54, 52, 52, 43, 56, 46, 45, 55, 51, 52, 53, 50
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Genaro 81	54, d	Genaro 81	10	44, 50, 51, 45, 48t, 51, 46, 49, 42t, 47
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Genaro 81	58	Genaro 81	6	53, 47, 48, 53, 51, 51
<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i> cv. Genaro 81	55t	Genaro 81	8	50, 47, 50t, 51, 50, 48, 49, 48t
			Total: 108	Range: 42t to 56

(t) = telocentric

Tab. 5 Mean and standard derivations of the chiasma frequencies per pollen mother cell in F₁, some BC₁ and BC₂ plants of *Triticum aestivum*/*Elymus giganteus* and *E. canadensis*/*T. aestivum* combinations

Lab. Number	Intergeneric combination	Generation	Chromosome number	Mean chiasma frequency/cell
1002	<i>T. aestivum</i> / <i>E. giganteus</i>	F ₁	35	1.02±X
5121	<i>T. aestivum</i> / <i>E. giganteus</i> // <i>T. aestivum</i>	BC ₁	56	36.40±0.55
5124	<i>T. aestivum</i> / <i>E. giganteus</i> // <i>T. aestivum</i>	BC ₁	56	32.95±0.68
5126	<i>T. aestivum</i> / <i>E. giganteus</i> // <i>T. aestivum</i>	BC ₁	56	34.65±0.69
5129	<i>T. aestivum</i> / <i>E. giganteus</i> // <i>T. aestivum</i>	BC ₁	56	33.20±0.84
5132	<i>T. aestivum</i> / <i>E. giganteus</i> // <i>T. aestivum</i>	BC ₁	56	35.20±0.66
5135	<i>T. aestivum</i> / <i>E. giganteus</i> // <i>T. aestivum</i>	BC ₁	56	32.29±0.73
5139	<i>T. aestivum</i> / <i>E. giganteus</i> //2* <i>T. aestivum</i>	BC ₂	52	39.54±0.28
5141	<i>T. aestivum</i> / <i>E. giganteus</i> //2* <i>T. aestivum</i>	BC ₂	45	39.40±0.30
5142	<i>T. aestivum</i> / <i>E. giganteus</i> //2* <i>T. aestivum</i>	BC ₂	44	38.00±0.49
1024	<i>E. canadensis</i> / <i>T. aestivum</i>	F ₁	35	0.07±X
4115	<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i>	BC ₁	56	15.85±0.48
L-82	<i>E. canadensis</i> / <i>T. aestivum</i> // <i>T. aestivum</i>	BC ₁	54	14.04±X
7050	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	46	32.06±1.24
7051	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	52	29.12±0.78
7052	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	51	28.34±0.73
7062	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	48	0.45±X
7065	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	51	35.48±0.28
7110	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	50	37.40±0.54
7130	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	55	31.19±0.47
7136	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	50	35.40±0.85
7138	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	49	15.25±1.26
7143	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	42	33.81±0.48
7154	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	51	0.56±X
7297	<i>E. canadensis</i> / <i>T. aestivum</i> //2* <i>T. aestivum</i>	BC ₂	45	19.34±0.41

genome formula of SSHH. S is the genome of the *Agropyron tauri-libanoticum-spicatum* complex, and H is the genome derived from *Hordeum* (DEWEY 1971). The success of its hybridization with variety 'Chinese Spring' seemingly is attributed to the kr_1kr_1 , kr_2kr_2 , kr_3kr_3 crossability genes this variety possesses for its crossability with rye. The codominant spike phenotype (Fig. 1) observation was similar to the codominant phenotypic expression reported for the *T. aestivum*/*E. giganteus* F₁ (MUJEEB-KAZI and RODRIGUEZ 1981a). The spikes of the *E. canadensis*/*T. aestivum* hybrids no longer retained the maternal nodding characteristic and their phenotypic similarity was more akin to *T. aestivum*. Apparently in hybrids with *Triticum ssp.* when only one parent is a diploid (*H. vulgare*) complete phenotypic dominance occurs in the progeny that resembles the higher polyploid parent (KRUSE, pers. comm.). That this dominant phenotypic expression is independent of the crossing direction has been demonstrated with barley (*H. vulgare*) and wheat (*T. aestivum* or *T. turgidum*) hybrids (MUJEEB-KAZI and RODRIGUEZ 1980, 1983 a, b, 1984). We believe such hybrids have a lack of alien genetic expression and are questionable as to their utilization in practical agriculture. Hence, a codominant phenotypic selection at F₁ forms a sieve for hybrid progeny advance and is justified for this *E. canadensis*/*T. aestivum* combination.

Tab. 6 Mean meiotic chromosome associations of some backcross II plants from *Elymus canadensis*/*Triticum aestivum*//*T. aestivum*

Lab Number	Backcross II Combination	Somatic chromosome number	Number of cells	Mean chromosome associations					Chiasma frequency per cell
				I	II rings	II rods	III	IV	
7050	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Zaragoza 75	46	17	10.1	14.1	3.8	0.06	—	32.06
7051	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Zaragoza 75	52	43	16.4	11.2	6.7	—	—	29.12
7052	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Zaragoza 75	51	26	16.3	10.9	6.3	—	0.08	28.34
7062	<i>E. canadensis</i> /2* <i>T. aestivum</i> C. Spring/2/Jupateco	48	38	47.1	—	0.5	—	—	0.45
7065	<i>E. canadensis</i> /2* <i>T. aestivum</i> C. Spring/2/Jupateco	51	95	9.4	14.3	5.5	0.61	0.07	35.48
7110	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Genaro 81	50	20	8.7	16.7	3.4	0.04	—	37.40
7130	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Genaro 81	55	47	17.1	11.8	5.8	0.85	—	31.19
7136	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Genaro 81	50	15	8.4	14.4	5.8	—	—	35.40
7138	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Genaro 81	49	12	22.7	4.1	7.1	—	—	15.25
7143	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Genaro 81	42	16	3.9	14.5	3.8	0.05	—	33.80
7154	<i>E. canadensis</i> / <i>T. aestivum</i> var. C. Spring//2* Genaro 81	51	32	49.9	—	0.56	—	—	0.56

The meiotic associations in F_1 with a 0.072 chiasma frequency suggests no autosyndetic pairing among the SH genomes of *E. canadensis*, a lack of genome homology among *E. canadensis* and *T. aestivum* chromosomes, and maintenance of the diploidizing mechanism of the 5B locus of *T. aestivum*.

The meiotic cycle beyond metaphase I was similar to that of *T. aestivum*/*E. giganteus* F_1 (MUJEEB-KAZI and RODRIGUEZ 1981b), *H. vulgare*/*T. aestivum* F_1 (MUJEEB-KAZI and RODRIGUEZ 1984), and *H. vulgare*/*T. turgidum* (MUJEEB-KAZI and RODRIGUEZ 1983 a). It also resembled the development of *Aegilops heldreichii*/*T. durum* F_1 hybrids demonstrated by MANN and SASAKUMA (1977). These observations suggested that presence of restitution nuclei may occur quite frequently and facilitate production of BC_1 progeny. This progeny however was aneuploid (52 to 61 chromosomes, Table 3) with chiasma frequencies estimated between 12.36 and 15.85 per cell after meiotic analyses.

Since the F_1 hybrid did not indicate any intergenomic or autosyndetic pairing, the meiotic observations for the BC_1 plants were surprising. A considerably higher pairing frequency of bivalents was anticipated, but apparently the *T. aestivum* chromosomes did not pair normally. This may be due to (1.) the aneuploidy of several BC_1 plants, that (2.) may presumably be linked with the *E. canadensis* cytoplasmic and/or genetic composition. The aneuploid composition apparently is of maternal derivation where the egg cell instead of possessing $n=5x=35$ SHABD chromosomes may have built in duplications, deletions, etc., of critical chromosomes, that in general are randomly distributed over both parents, thereby altering the BC_1 meiotic relationships. Hence, it is possible that two BC_1 plants with an apparently normal (56) chromosome number may be aneuploid. This was not checked in the present study, but such chromosomal behaviour, contributing to variations in "reduced" egg cell composition has been observed for several other intergeneric hybrids (JEWELL and MUJEEB-KAZI 1982, MUJEEB-KAZI and BERNARD 1982, MUJEEB-KAZI and RODRIGUEZ 1982, 1983 a and b, RODRIGUEZ and MUJEEB-KAZI 1981). MUJEEB-KAZI and RODRIGUEZ (1981b) reported a typical nonhomologous meiotic trend for the *T. aestivum*/*E. giganteus* hybrid wherein an occasional open bivalent was present. Further, in the BC_1 plants of this hybrid with *T. aestivum*, meiotic relationships in the 56 chromosome plants were generally 21II 14I. In the present findings with the *E. canadensis* based BC_1 it is inferred that univalency in F_1 need not be positively correlated with organized meiosis in BC_1 . This may be a consequence of the aneuploid status of the egg cell, and we can additionally speculate as to whether the *E. canadensis* cytoplasm may be an influencing factor.

BC_1 seed setting for *E. canadensis*/*T. aestivum*//*T. aestivum* is consistent with similar observations for other hybrid combinations. In *H. vulgare*/*T. aestivum* hybrids, all BC progenies with *T. aestivum* were sterile when selfed after BC_2 or BC_3 and set seed only if backcrossed again to *T. aestivum* varieties (MUJEEB-KAZI, unpubl.). Pistilloidy was present in such backcrosses and was attributed to the *H. vulgare* cytoplasm (ISLAM et al. 1975, 1978). The cytoplasm problems were removed via the reciprocal cross combination of *T. aestivum*/*H. vulgare* and its backcross with *T. aestivum* (ISLAM

and SHEPHERD 1981, ISLAM et al. 1975, 1978, 1981). Relatively easy BC progeny advancement was also observed for the *T. aestivum*/*E. giganteus* combination (MUJEEB-KAZI and RODRIGUEZ 1981a, 1981b), in which the self-sterile F₁ hybrids set from 1 to 3 seed (if seed set occurred) when pollinated by different *T. aestivum* cultivars. BC₁ plants, though self-sterile, set BC₂ seed more frequently when pollinated by *T. aestivum* than did the F₁ spikes for BC₁ seed production. The BC₂ plants were partially self-fertile, set abundant BC₃ seed, and had fairly regular meiosis. It is speculated that the maternal *T. aestivum* cytoplasm may be a contributing factor to cytogenetic normalcy and BC₂ self-fertility for the *T. aestivum*/*E. giganteus* combination. The cytological meiotic variations of the restituted nuclei in the *E. canadensis*/*T. aestivum* hybrid as reflected in the aneuploid BC₁ progeny, have not been an obstacle to obtaining BC₂ plants and BC₂ F₁ progeny, (Table 4), even though the meiotic relationships of some BC₂ plants were typically asynaptic. The chiasma frequencies were 1.02 per cell for *T. aestivum*/*E. giganteus*, and 0.07 per cell for *E. canadensis*/*T. aestivum* (Table 5). In *T. aestivum*/*E. giganteus*/*T. aestivum* BC₁ plants (8x = 56), of the 42 wheat chromosomes a majority paired normally and the *Elymus* chromosomes were generally present as univalents. The chiasma range of 32.29 to 36.40 reflects upon the wheat pairing mentioned above (Table 5). In the BC₂, *T. aestivum*/*E. giganteus*//2* *T. aestivum* a high degree of normalcy was observed (chiasma range 38.0 and over). The cytogenetic normality of the BC progenies of *T. aestivum*/*E. giganteus* is in sharp contrast to the *E. canadensis*/*T. aestivum* BC₁ and BC₂ meiotic relationships (Table 6), wherein a substantial range in chiasma frequency is observed in BC₂ progenies.

We attributed the variation observed in *E. canadensis*/*T. aestivum* BC progenies to several as yet undetermined processes: (1.) aneuploidy in BC₁, (2.) *E. canadensis* cytoplasm, (3.) *E. canadensis* genetic influence, either as a direct expression or through an alteration of the *T. aestivum* complex, or (4.) nucleocytoplasmic interactions. We have not attempted the reciprocal *T. aestivum*/*E. canadensis* combination, but it will be of interest to determine and evaluate any cytological variations occurring in BC₁. The selective restoration of self-fertility in the BC₂ progeny is encouraging, for it portends the advancement of the *E. canadensis*/*T. aestivum*//2* *T. aestivum* combination for practical agricultural utility. The advancement of the BC₃ and BC₂ self-fertile progenies will soon be originated, with screening pressure for resistance to leaf and stem rust, scab and *Helminthosporium sativum*.

The complexities of alien genetic transfer are directly correlated with the difficulties inherent in hybridizing distant genera and the likelihood of their possessing unrelated genomic compositions. It is when the cytological variations in BC₁ progeny dominate in hybrid combinations (Table 3) that the investigator must establish a balance of methodology for achieving agricultural utility. However, after observing the nonhomologous genome trends of several hybrids involving species of *Agropyron*, *Elymus*, *Hordeum*, *T. aestivum* and *T. turgidum* (MUJEEB-KAZI and RODRIGUEZ 1980, 1981a, 1981b, 1982), exemplified here for the *E. canadensis*/*T. aestivum* hybrids, it now seems logical

to incorporate into distant hybridization the manipulative procedures that relate to the 5BL locus of *T. aestivum* or *T. turgidum* wherever possible. This may preferably be done at the initial cross, and for *T. aestivum* in a background other than 'Chinese Spring'. Application of mathematical inputs on F_1 meiotic analyses (KIMBER 1982) may additionally prove to be of advantage in determining the advance of a cross combination. These aspects shall presumably allow genetic recombinations to function more effectively than has so far been the case for several intergeneric hybrids.

Zusammenfassung

Zytogenetik der Hybriden von *Elymus canadensis* und *Triticum aestivum* ($n=5x=35$, SHABD) und ihrer Rückkreuzungsnachkommenschaften mit *T. aestivum*

Hybriden zwischen *Elymus canadensis* L. ($2n=4x=28$, SSHH) und *Triticum aestivum* L. 'Chinese Spring' ($2n=6x=42$, AABBDD) besitzen eine intermediäre planotypische Ausprägung zwischen den beiden Arten. Die Hybriden besaßen $n=5x=35$ somatische Chromosomen mit durchschnittlich 34,85 Univalenten in Metaphase I. Rückkreuzung mit 'Chinese Spring', 'Genaro 81' und 'Zaragoza 75' ergab 32 Samen, von denen 22 Pflanzen erhalten wurden. Wenige hatten die Chromosomenzahl 56, während die übrigen zwischen 54 und 61 Chromosomen besaßen. Die Chiasmafrequenz variierte zwischen 12,86 und 14,54. In der zweiten Rückkreuzung wurden 198 Pflanzen erhalten mit Chromosomenzahlen zwischen 42 bis 56 und 0,56 bis 35,47 Chiasmata je Zelle. Nach Selbstung waren diese Pflanzen entweder steril oder setzten einige Samen an. Alle Pflanzen ergaben Samen nach erneuter Rückkreuzung mit *T. aestivum*. Zytologisch stabile Genotypen mit erwünschten Eigenschaften sollen in das *T. aestivum*-Zuchtprogramm inkorporiert werden.

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