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Cytogenetic studies of the intergeneric hybrids between *Secale cereale* and *Elymus caninus, E. brevipes*, and *E. tsukushiensis* (Triticeae: Poaceae)

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Summary. Integeneric hybridizations were carried out between *Secale cereale* L. ($2n = 14$, RR) and three *Elymus* species, namely, *E. caninus* (L.) L. ($2n = 28$, SSHH), *E. brevipes* (Keng) Löve ($2n = 28$, SSYY) and *E. tsukushiensis* Honda ($2n = 42$, SSHHYY). Chromosome pairing was studied at metaphase I in the parental species and the hybrids. Meiotic configurations of the hybrids were $20.74\,\mathrm{I} + 0.14\,\mathrm{II}$ for *E. caninus* × *S. cereale* (SHR), $16.35\,\mathrm{I} + 2.17\,\mathrm{II} + 0.09\,\mathrm{III}$ for *E. brevipes* × *S. cereale* (SYR) and $25.84\,\mathrm{I} + 1.10\,\mathrm{II} + 0.02\,\mathrm{III}$ for *E. tsukushiensis* × *S. cereale* (SHYR), in addition to some secondary associations in the different hybrids. It is concluded from the study that (1) a certain, different homoeologous relationship exists among "S", "H" and "Y" genomes in the investigated *Elymus* species; (2) low homoeology is present between genomes of *Elymus* (S or H or Y) and rye (R); (3) the *Secale* genome affects homoeologous chromosome pairing between different genomes in *E. brevipes* and *E. tsukushiensis*.

Key words: Intergeneric hybrid – *Secale* – *Elymus* – Meiotic pairing – Genome

Introduction

Many intergeneric and interspecific hybrids have been produced in the tribe *Triticeae* Dumort. of the grass family (Stebbins et al. 1964; Bowden 1964; Jacobsen and Bothmer 1981; Dewey 1982, 1984; Sharma and Gill 1983; von Bothmer et al. 1983; Wang 1989). Those hybrids involving cereal grain species such as *Triticum aestivum* L., *Hordeum vulgare* L. and *Secale cereale* L. have been used for the introgression of desirable agronomic traits such as high protein quality and disease resistance from their relatives (Riley and Chapman 1968; Dvorak 1977b; Feldman 1983; Sears 1983). Genomic relationships between many of the species, and between different genera, have also been clarified after cytogenetic investigations of the hybrids (Dewey 1982, 1984; Kimber 1983; von Bothmer et al. 1986, 1987; Wang 1989), and a classification system based on genomic constitutions has been established in the tribe (Dewey 1984; Löve 1984). These studies have also elucidated specific cytogenetic events, such as the genetic control of homoeologous chromosome pairing: for example, the *Ph* (pairing homoeologous) gene system in *T. aestivum* (Sears and Okamoto 1958) and the genotype of *Aegilops speltoides*, which influences the homoeologous synapsis of wheat genomes (Riley and Chapman 1964).

Intergeneric hybrids involving the *Secale* species provide particularly favourable materials for judging whether auto- or allosyndesis occurs, since the *Secale* chromosomes are considerably larger than those of other genera in the Triticeae and can therefore be easily recognized at meiosis (Stebbins and Pun 1953; Gupta and Fedak 1985, 1987; Lu et al. 1990a). Hybridizations of *Secale* species have been reported with species of about ten genera in Triticeae (Crasniuk 1935; Stebbins and Pun 1953; Dvorak 1977a; Hutchinson et al. 1980; Gupta and Fedak 1985, 1987; Wang 1987a, 1988; Lu et al. 1990a). Investigations on autosyndesis in meioses of hybrids of *Secale* with, for example, *Triticum*, *Hordeum* and *Elymus* L. has revealed that the *Secale* genome (or genotypes) can promote the pairing of the homoeologous chromosomes (Dvorak 1977a; Fedak and Gupta 1985, 1987; Lu et al. 1990a).

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This paper reports the meiotic pairing of artificial hybrids of diploid *S. cereale* with three *Elymus* species representing the three different genomic constitutions, i.e. SH, SY and SHY, in the genus. Affinities among the three genomes in *Elymus* as well as their homoeology with the *Secale* genome (R) and the different effects of the *Secale* genome on homoeologous pairing regulation are discussed.

Materials and methods

E. caninus (L.) is a well-studied Eurasian species (2n = 28) containing SH genomes (Dewey 1974). *E. brevipes* (Keng) Löve is an endemic Chinese species (2n = 28) having the SY genomes (Keng and Chen 1963; Lu and Bothmer in preparation), whereas *E. tsukushiensis* Honda (Syn. *R. kamoji* Ohwi), a hexaploid East Asian species, contains the SHY genomes (Lu et al. 1988; Lu and von Bothmer 1990). The *Elymus* species came from our seed collections in China, and *S. cereale* was a Polish cultivar cv 'Chodan'. The species used in the study and their localities are listed in Table 1.

In the crossing attempts, *Elymus* species were used as female parents and *S. cereale* as the male parent. The procedures of hybridization, fixation and staining of the cytological materials and mitotic and meiotic preparation were as described previously (Lu et al. 1990a). Meiotic preparations were made permanent following the method of Lu and von Bothmer (1990).

For estimation of pollen fertility, pollen grains of hybrids were examined after staining in cotton blue for approximately 1 h.

Results

Crosses, development and fertility of the hybrids

All three combinations produced adult hybrid plants; the data on seed set, embryo yield and plant establishment through embryo rescue are presented in Table 2. The seed sets were generally high in the three combinations (39%–63%), but yields of embryos (19%–37%) and survival of the hybrid plants (3%–9%) were rather low (Table 2). All the hybrids were perennial and morphologically resembled both parents in some characters; for example hairy, narrow glumes and hairy lemma keels derived from *S. cereale* and long lemma awns from *Elymus* species. *E. caninus* × *S. cereale* and *E. brevipes* × *S. cereale* were vegetatively vigorous, being taller than the maternal parents. Chromosome numbers of the two combinations were invariably 2n = 3x = 21 in root tip cells. The hybrid plants of *E. tsukushiensis* × *S. cereale* were yellowish and no taller than 20 cm, and they only produced a few tiny spikes. The chromosome numbers in root tip cells were stable (2n = 4x = 28). The spikes of all of the hybrids had about two to three florets per spikelet with indehiscent anthers and less than 1% pollen stainability. No seeds were observed in any of the hybrids.

Table 1. The origins of *Secale cereale* and the *Elymus* species used for crosses

Species	Accession no.	2n	Origin
Secale cereale	HR 10857	14	cv 'Chodan', Poland
Elymus caninus	H 7550	28	Habahe, Xinjiang Province, China
E. brevipes	H 8147	28	Naidong, Tibet, China
E. tsukushiensis	H 3198	42	Yaan, Sichuan Province, China

Meiosis in the parents and hybrids

1. *Parents.* Only bivalents were found in the pollen mother cells (PMCs) of diploid *S. cereale* at metaphase I; there was an average of 13.4 chiasmata per cell. Meioses of the three *Elymus* species were regular with predominant ring bivalent formation and, except for *E. tsukushiensis*, no multivalents (Table 3).

2. *Triploid hybrids.* The triploid hybrids and stable chromosome numbers (2n = 21) in the PMCs, and the meioses were extremely irregular, but slightly different in the two combinations. Chromosomes of *E. caninus* × *S. cereale* were extremely condensed at metaphase I. Most of the cells at diakinesis and metaphase I contained 21 univalents (Fig. 1A, E); hence, a very low frequency of bivalents (approximately 0.14 per cell), mainly rods, was formed (Table 4, Fig. 1B–D). *E. brevipes* × *S. cereale* had predominantly univalent formation, with a few bivalents (approximately 2.17 per cell) plus a low number of trivalents (Table 4, Fig. 2). A few loose end-to-end or side-by side associations occasionally occurred in the two combinations (Figs. 1, 2). The chiasma frequency of

Table 2. Results of intergeneric crosses between *Secale cereale* and the *Elymus* species

Combinations	Cross no.	No. of florets pollinated	Seed set		Embryos		Plants	
			No.	%	No.	%[a]	No.	%[a]
E. caninus × *S. cereale*	BB7115	44	17	38.6	11	25.0	2	2.9
E. brevipes × *S. cereale*	BB7084	46	21	45.7	8	19.5	1	2.2
E. tsukushiensis × *S. cereale*	BB7094	64	40	62.5	24	37.5	5	9.4

[a] As percentage of pollinated florets

Table 3. Chromosome pairing at metaphase I in the parental species, and some di- and tri-haploids of *Elymus*

Parents and haploids	2n	Genomes	No. of cells observed	Chromosome configuration						Chiasmata/ cell
				I	II			III	IV	
					Total	Rings	Rods			
Parents										
S. cereale	14	RR	50	–	7.00 (7)	6.42 (5–7)	0.58 (0–2)	–	–	13.42 (12–14)
E. caninus	28	SSHH	50	0.04 (0–2)	13.98 (13–14)	13.30 (10–14)	0.68 (0–4)	–	–	27.32 (24–28)
E. brevipes	28	SSYY	50	0.28 (0–2)	13.86 (13–14)	12.94 (11–14)	0.92 (0–3)			26.81 (25–28)
E. tsukushiensis	42	SSHHYY	50	0.46 (0–4)	20.16 (18–21)	18.44 (15–21)	1.72 (0–5)	0.04 (0–1)	0.02 (0–1)	39.60 (36–42)
Haploids										
E. pseudonutans[a]	14	SY	33	12.82 (9–14)	0.55 (0–2)	–	0.55 (0–2)	0.03 (0–1)	–	0.61 (0–2)
E. shandongensis[a]	14	SY	114	12.59 (6–14)	0.68 (0–4)	0.03 (0–1)	0.65 (0–4)	0.01 (0–1)	–	0.73 (0–4)
E. semicostatus[a]	14	SY	117	12.70 (8–14)	0.79 (0–3)	0.03 (0–1)	0.76 (0–3)	0.02 (0–1)	–	0.85 (0–4)
E. canadensis[b]	14	SH	500	12.97 (8–14)	0.49 (0–3)	0.002 (0–1)	0.49 (0–3)	0.01 (0–1)	–	0.53 (0–3)
E. tsukushiensis[c]	21	SHY	442	20.61 (15–21)	0.18 (0–3)			0.004 (0–1)	0.002 (0–1)	0.20 (0–3)

[a] Lu et al. (1990a)

[b] Torabinejad et al. (1987)

[c] Sakamoto (1964), no indication of rod and ring bivalents

Table 4. Chromosome associations at metaphase I in the triploid and tetraploid *Elymus* × *Secale* hybrids

Hybrids	Chromosome number	No. of cells observed	I	II				III	Sedondary associations	Chiasmata/ cell
				E-E	E-R	R-R[d]	Total[e]			
E. caninus × *S. cereale* (BB 7115)	21	77	20.74 (17–21)	0.10 (0–3)	0.01 (0–2)	0.03 (0–1)	0.14 (0–3)	–	0.16 (0–2)	0.16 (0–7)
E. brevipes × *S. cereale* (BB 7084)	21	81	16.35 (10–21)	1.92 (0–5)	0.21 (0–2)	0.04 (0–1)	2.17 (0–5)	0.09 (0–1)	0.66 (0–3)	2.23 (0–5)
E. tsukushiensis × *S. cereale* (BB 7094)[a]	28	84	25.84 (15–21)	0.96 (0–5)	0.04 (0–1)	0.10 (0–1)	1.10 (0–5)	0.02 (0–1)	0.30 (0–3)	1.14 (0–5)
E. pseudonutans × *S. cereale*[b] (BB 6998-2)[c]	21	104	14.64 (9–21)	2.56 (0–6)	0.20 (0–2)	0.06 (0–1)	2.82 (0–6)	0.20 (0–2)	0.85 (0–4)	3.38 (0–7)
(BB 7021-1)	21	100	16.38 (11–21)	1.81 (0–5)	0.14 (0–2)	0.07 (0–2)	2.02 (0–6)	0.16 (0–1)	0.85 (0–4)	2.36 (0–6)
E. shandongensis × *S. cereale*[b] (BB 6993-2)	21	121	15.59 (10–21)	2.38 (0–6)	0.21 (0–2)	0.03 (0–1)	2.62 (0–6)	0.08 (0–1)	0.86 (0–3)	3.62 (0–8)
E. semicostatus × *S. montanum*[b] (HH 2488)	21	63	19.63 (15–21)	0.51 (0–3)	0.11 (0–1)	0.03 (0–1)	0.65 (0–3)	–	0.30 (0–3)	0.75 (0–3)

[a] Cells with more than 28 chromosomes are not included in the calculations

[b] From Lu et al. (1990a)

[c] Quadrivalents = 0.01 (0–1)

[d] *E–E*, *Elymus-Elymus* bivalents; *E-R*, *Elymus-Secale* bivalents; *R-R*, *Secale-Secale* bivalents

[e] Including both rod and ring bivalents

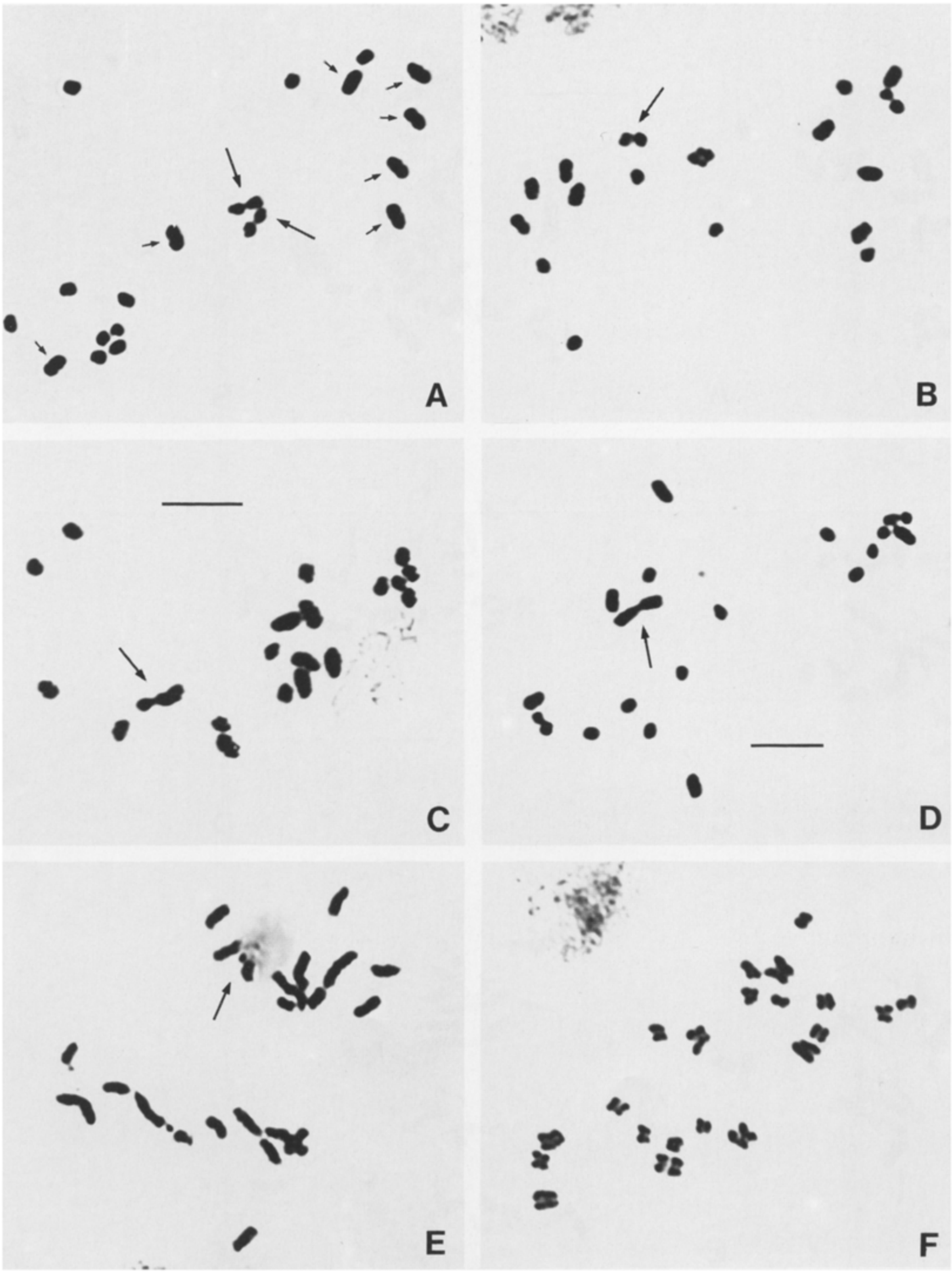

Fig. 1 A–F. Meiotic configurations in *E. caninus* × *S. cereale*. **A–D** Metaphase I. **A** 21 univalents, two end-to-end secondary associations (*arrows*); the rye chromosomes are indicated by *small arrows*. **B** 19 univalents and 1 E-E ring bivalent; an end-to-end secondary association is indicated by an *arrow*. **C** 19 univalents and 1 E-R bivalent (*arrow*). **D** 19 univalents and 1 R-R bivalent (*arrow*). **E** Diakinesis, showing 21 univalents; two chromosomes are attached to a nucleolus. **F** Anaphase I, showing unequal chromosome segregation. *Bar* = 10 μm

E. caninus × *S. cereale* (0.16 per cell) was distinctly lower than that of *E. brevipes* × *S. cereale* (2.23 per cell). Since the chromosomes of the two parents could be distinguished by the conspicuous differences in their sizes, the chromosome pairing in the hybrids could be classified as small homomorphic *Elymus-Elymus* (E-E) bivalents, larger homomorphic *Secale-Secale* (R-R) bivalents and heteromorphic *Elymus-Secale* (E-R) bivalents (Table 4, Figs. 1, 2). In *E. caninus* × *S. cereale* about 74% bivalents were E-E associations, 9% E-R and 18% R-R associa-

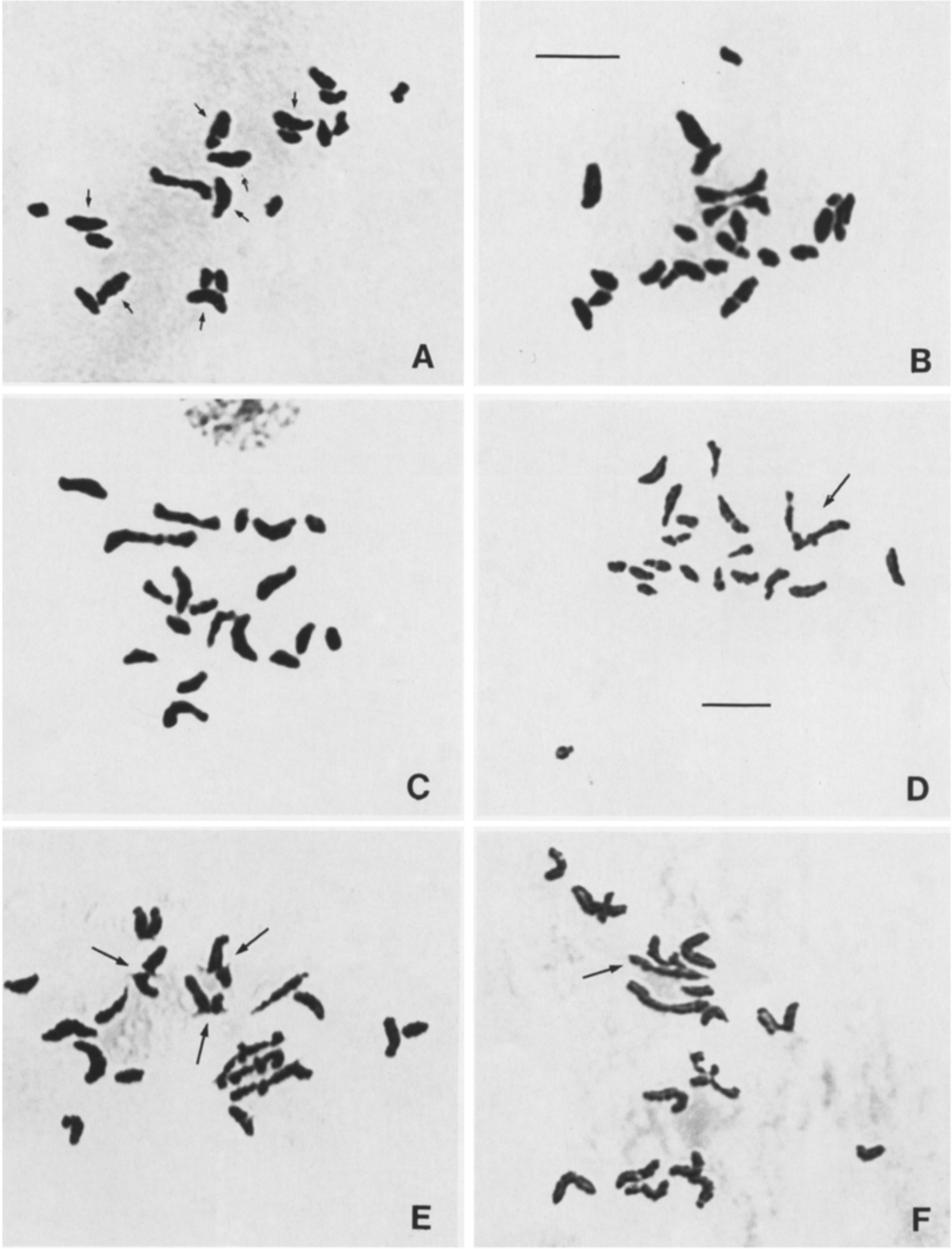

Fig. 2A–F. Meiotic configurations at metaphase I in *E. brevipes* × *S. cereale*. **A** 19 univalents and 1 E-E bivalent; the rye chromosomes are indicated by *small arrows*. **B** 17 univalents and 2 E-E bivalents. **C** 17 univalents, and 1 E-E and 1 E-R bivalent. **D** 18 univalents and 1 E-E-R trivalent (*arrow*). **E** 13 univalents and 3 E-E, 1 E-R bivalents; misdivisional univalents are indicated by *arrows*. **F** 14 univalents, 1 E-E and 1 E-R bivalent, and 1 E-E-E trivalent (*arrow*). *Bar* = 10 μm

tions, whereas *E. brevipes* × *S. cereale* hybrids had approximately 89% E-E, 9% E-R and 2% R-R bivalents. Trivalents were found as either E-E-E homomorphic (Fig. 2F) or R-E-E heteromorphic (Fig. 2D) associations.

3. *Tetraploid hybrids.* The hybrid *E. tsukushiensis* × *S. cereale* had 28 chromosomes in most of the PMCs (Fig. 3), but a few cells contained 29–31 chromosomes (Fig. 3C, D). Only cells with 28 chromosomes were meiotically analysed (Table 4). As in the triploid combinations, uni-

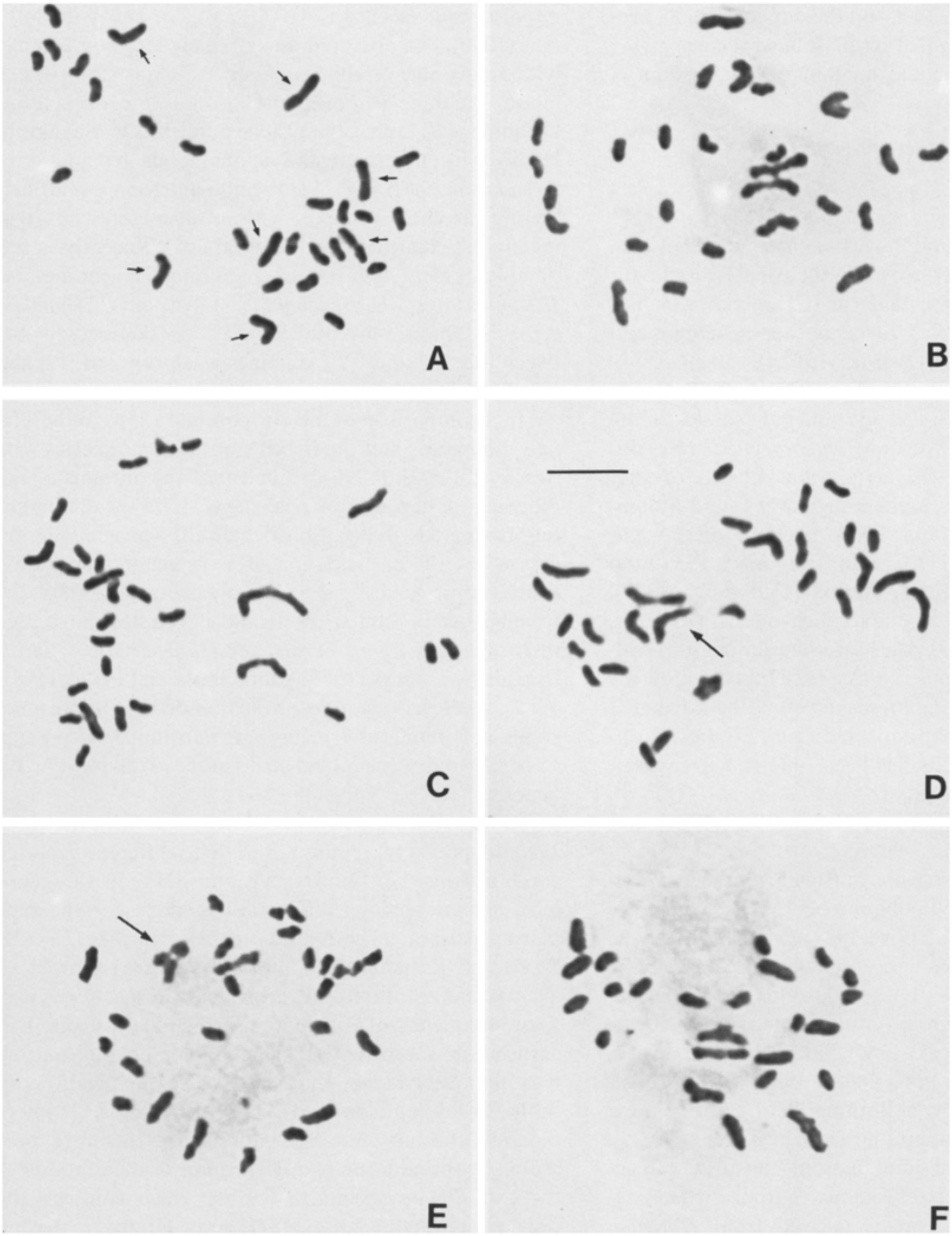

Fig. 3A–F. Meiotic configurations at metaphase I in *E. tsukushiensis* × *S. cereale*. **A** 28 univalents; the rye chromosomes are indicated by *small arrows*. **B** 24 univalents and 2 E-E bivalents. **C** 25 univalents, and 1 E-E and 1 R-R bivalent. **D** 23 univalents, and 2 E-E and 1 E-R (*arrow*) bivalents. **E** 25 univalents and 1 E-E-E trivalent (*arrow*). **F** 20 univalents and 4 E-E bivalents. *Bar* = 10 μm

valent formation predominated, but an average of 1.1 bivalents per cell, mostly E-E (approximately 88%) and a few E-R (3%) and R-R (8%) associations, were also observed in addition to some end-to-end or side-by-side associations. Low frequencies of trivalents were recorded, most commonly as E-E-E (Fig. 3 E) homomorphic and E-E-R (Fig. 3 D) heteromorphic associations.

4. *Other meiotic irregularities.* Meiosis beyond metaphase I was complicated by irregularities in all the hybrids.

Chromosomes remained scattered in unoriented groups in anaphase I cells (Fig. 1 F), and the duplication of chromosomes was accompanied by plasmic cleavages giving rise to one to several unequal daughter cells at the quartet stage.

Discussion

Intergeneric hybridizations have been attempted between *Secale* and several other genera in the tribe Triticeae; for example with *Agropyron* Gaertn. (Crasniuk 1935; Favorsky 1935; Wang 1987 a), *Elytrigia* Desv. (Stebbins and Pun 1953), *Triticum* (Dvorak 1977 a), *Aegilops* L. (Hutchinson et al. 1980), *Hordeum* (Fedak 1977; Gupta and Fedak 1985, 1987), *Psathyrostachys* Nevski (Wang 1987 b), *Thinopyrum* Löve and *Pseudoroegneria* (Nevski) Löve (Wang 1988) and *Elymus* (Lu et al. 1990 a). In early investigations some researchers regularly found a number of bivalents in the hybrids between *Secale* and *Agropyron cristatum* (L.) Gaertn. (Favorsky 1935) and *Elytrigia intermedia* (Host) Nevski (Ljubimova 1937), which they believed to be due to allosyndesis. However, Stebbins and Pun (1953), after careful examination, realized that the chromosome pairing which occured in the hybrids of *S. cereale* × *E. intermedia* could be attributed to autosyndesis of the chromosomes from *Elytrigia*. Confirmation of these results has been obtained from combinations of *Secale* with *Triticum aestivum* (Dvorak 1977 a), *Hordeum* (Gupta and Fedak 1985, 1987) and *Elymus* species (Lu et al. 1990 a).

Elymus is the largest genus in tribe Triticeae and contains approximately 150 polypoid perennials around the world (see Dewey 1984; Löve 1984). Many cytogenetic investigations have been carried out on the interspecific and intergeneric hybrids both within this genus and between species of *Elymus* and other related genera (Bowden 1964; Stebbins et al. 1964; Sakamoto and Muramatsu 1966; Sakamoto 1982; Dewey 1982, 1984; Lu et al. 1988, 1990 b; Lu and von Bothmer 1990). From these investigations it is apparent that three basic genomes, i.e. S, H and Y, in different combinations constitute the genus. The S genome probably emanates from *Pseudoroegneria*, and the H genome is derived from *Hordeum* (Dewey 1974, 1984), but the origin of the Y genome is still unknown. A basic genome P which came from *Agropyron* has been recently identified in some hexaploids of the genus (Jensen 1990). The affinities among the three basic genomes S, H and Y have not been sufficiently studied. A meiotic analysis of one artificial dihaploid of *E. canadensis* L. (n = 14, SH) showed a very low affinity between the S and H genomes (Table 3) (Torabinejad et al. 1987). After investigating SHY genome hybrids from crosses of *H. bogdanii* Wilensky (HH) and *H. roshevitzii* Bowden (HH) with *E. semicostatus* (Nees ex Steud.), Melderis (SSYY) and *E. parviglume* (Keng) Löve (SSYY), Lu and von Bothmer (1990) also observed an extremely low homoeology with an average of approximately 0.5 chiasmata per cell among the three genomes. The chromosome associations are somewhat higher than those published by Sakamoto (1964) who investigated a spontaneous trihaploid of *E. tsukushiensis* (n = 21, SHY) and reported a low affinity among the three genomes with an average of approximately 0.2 chiasmata per cell (Table 3). Recently, a few dihaploids of *Elymus* species containing SY genomes, i.e. *E. semicostatus*, *E. pseudonutans* Löve and *E. shandongensis* Salomon, were studied and a low homoeology between the "S" and "Y" genomes was proposed (Lu and von Bothmer 1989; Lu et al. 1990 a).

In a comparison of meiotic configurations in the *Elymus* dihaploids and the hybrids of the same species with *Secale*, Lu et al. (1990 a) found that the amount of homoeologous chromosome pairing (E-E) in the dihaploids (approximately 0.5–0.8 bivalents/cell) was generally increased by the participation of a rye genome in the hybrids (approximately 1.8–2.6 bivalents plus 0.08–0.2 trivalents/cell). Similar results have been deomonstrated in *Triticum aestivum* × *Secale*, and *Hordeum* spp. × *Secale* hybrids by Dvorak (1977 a) and Gupta and Fedak (1985, 1987), where associations of the homoeologous chromosomes in haploids of *Triticum aestivum* and *Hordeum* spp. were obviously promoted in hybrids involving the rye genome.

In this study the hybrids of *S. cereale* with the three *Elymus* species representing the three different genomic combinations, i.e. the SH, SY and SHY, in the genus have shown obvious differences in their chromosome pairing patterns. The hybrids with *E. brevipes* (2n = 21, SYR) and *E. tsukushiensis* (2n = 28, SHYR) showed an average of 1.92 and 0.96 E-E bivalents, respectively, plus a low frequency of trivalents in which at least one E-E association was involved. The homoeologous pairing was obviously higher than the average associations of both SY dihaploids and SHY trihaploids. Homoeologous chromosome associations are therefore promoted by the addition of a rye genome to the genomes of the two *Elymus* species, a finding which confirms the previous report by Lu et al. (1990 a). However, the hybrid *E. caninus* (2n = 21, SHR) had an even lower meiotic pairing (approximately 0.1 E-E bivalents) than the previously reported SH-dihaploid of *E. canadensis* (approximately 0.53 chiasmata per cell; Torabinejad et al. 1987). This indicates that chromosome associations were not affected by the rye genome in the combination *E. caninus* × *S. cereale*, and is in contrast with the previous report (Lu et al. 1990 a) and the two other *Secale-Elymus* hybrids in this study. The differences in meiotic configurations in the present study may be a result of a greater affinity between the SY genomes than that between the

SH genomes in the species studied, or that a certain genes(s) exists in *E. caninus* that inhibits the function of the rye genome regulating homoeologous pairing.

The *Elymus-Secale* (E-R) heteromorphic chromosome associations involved in both bivalents and trivalents were occasionally observed in the meioses of *Elymus* spp. × *S. cereale*. Thus, there is a low degree of homoeology between the genomes of R in *Secale* and the S, H or Y in *Elymus*, and this result confirms previous reports on the intergeneric hybrids between *Secale* and, for example, *Hordeum* (Gupta and Fedak 1985, 1987), *Elytrigia* (Stebbins and Pun 1953), *Pseudoroegneria* (Wang 1987a) and *Elymus* (Lu et al. 1990a).

A low frequency of *Secale-Secale* (R-R) associations, indicating non-homologous pairing between rye chromosomes, was found in the three hybrids. This state had been observed previously in hybrids of *Secale* with *E. shandongensis*, *E. pseudonutans* and *E. semicostatus* (Lu et al. 1990a), and supports the explanation of the results by Neijzing (1982, 1985). In a study of Giemsa-banded metaphase chromosomes in haploid rye, he found that several sets of homologous segments existed in the rye genome.

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