Pl. Syst. Evol. 191: 199–211 (1994)

Plant Systematics and Evolution

Genomic relationships between species of the *Elymus semicostatus* group and *Elymus* sensu lato (*Poaceae*)

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Received October 10, 1993; in revised version February 17, 1994

Key words: *Poaceae, Triticeae, Elymus.* – Interspecific hybridization, chromosome pairing, genome analysis, relationships.

Abstract: Meiotic pairing behaviour in 19 interspecific *Elymus* hybrids is reported and discussed. The hybrids were made between four species belonging to the *E. semicostatus* group of sect. *Goulardia*, viz., *E. semicostatus, E. abolinii, E. fedtschenkoi*, and *E. panormitanus* (all 2n = 28), and *Elymus* species of seven different sections, viz., sect. *Clinelymiopsis*: *E. caucasicus* (2n = 28); sect. *Elymus*: *E. sibiricus* (2n = 28); sect. *Goulardia*: *E. caninus* (2n = 28), *E. trachycaulus* (2n = 28), and *E. tsukushiensis* (2n = 42); sect. *Hyalolepis*: *E. batalinii* (2n = 42); sect. *Hystrix*: *E. hystrix* (2n = 28); sect. *Macrolepis*: *E. canadensis* (2n = 28); and sect. *Turczaninovia*: *E. dahuricus* (2n = 42). Chromosomal pairing at meiotic metaphase I indicated that the species of the *E. semicostatus* group are genomically closer to the tetraploid *E. caucasicus* and the hexaploid species, regardless of sectional origin, than to the other tetraploid species of section *Goulardia*. Highest meiotic pairing was found in hybrids involving *E. caucasicus, E. tsukushiensis*, and *E. dahuricus*. The presence of pairing regulating genes in *E. abolinii* is suspected.

Studies of meiotic chromosomal behaviour in interspecific and intergeneric hybrids in the *Triticeae* have provided extensive information that can be used in comprehending evolutionary relationships (KIMBER 1983, DEWEY 1984, WANG 1989). However, the relationships indicated by meiotic data are not always consistent with the relationships suggested by morphological similarities. For example, *Hordeum* L. was divided into four sections based on morphology (BOTHMER & JACOBSEN 1985) and four genomic groups based on genome analysis (BOTHMER & al. 1986), but none of the genomic groups agreed with the morphological groups. In *Elymus* L., species of five different sections represented only two different genomic groups, and the morphological characters used for sectional delimitations showed no correlation with genomic content (SALOMON & LU 1992).

Regardless of whether the delimitation of the genus *Elymus* is based on morphology (TZVELEV 1976) or on genome constitution (DEWEY 1984), the genus comprises only polyploid species that all have a perennial or semiperennial growth habit. The majority of the approximately 150 species in the genus are tetraploids, about 30 are hexaploids, and only a few species are known to be octoploid (DEWEY 1984). The tetraploid species can be divided into two genomic groups (SALOMON

Table 1. Chromosome numbers, number of accessions, and native areas of the *Elymus* species used in the interspecific hybridizations. *Species in the *E. semicostatus* group

Section	Species, accession no.	2n	Genomes	General distribution, locality of collection
Anthosachne (STEUD.) TZVEL.	*E. enysii* (KIRK) LÖVE & CONNOR	28	SSHH	New Zealand,
	H 3153			New Zealand, Christchurch
Anthosachne	*E. scabrus* (R. BR.) LÖVE s.l.	42	SSYYWW	Australia and New Zealand
	H 3152			New Zealand, Lake Lyndon
Clinelymiopsis (NEVSKI) TZVEL.	*E. caucasicus* (KOCH.) TZVEL.	28	SSYY	The Caucasus
	H 3207			Armenia, Dilidjan
Dasystachyae LÖVE	*E. erianthus* PHILIPPI	42	unknown	Southern South America
	H 6428			Argentina, Mendoza, Punte del Inca
Elymus L.	*E. sibiricus* L.	28	SSHH	Central and North-East Asia
	H 3094			Russia, unspecified origin
	H 7729			China, Xinjiang, Tianshan, Houxia plateau
Elytrigia (DESV.) MELD.	*E. repens* (L.) GOULD	42	SSSSXX	Eurasia, and as weed in all temperate areas
	H 7880			China, Xinjiang, Tianshan, Balguntai
Goulardia (HUSNOT) TZVEL.	*E. abolinii* (DROB.) TZVEL.*	28	SSYY	Central Asia
	H 3208			Khirgizia, Terskei-Alatau, SW of Prshevalsk, Dzeto-Oghuz river
	H 3209			China, Xinjiang, Side canyon off the road to Tian lake, ENE of Urumqi
	H 3265			China, Xinjiang, Eastern shore of Tian Lake, ENE of Urumqi
	H 3266			China, Xinjiang, Side canyon off the road to Tian lake, ENE of Urumqi
	H 3306			Kazakstan, between Alma-Ata and Medeo
	H 3307			China, Xinjiang, near Tian Lake, ENE of Urumqi
Goulardia	*E. caninus* (L.) L.	28	SSHH	Europe and North-West and Central Asia
	H 3169			Sweden, Västmanland, Kungsör
	H 3369			Kazakhstan, 30 km SW of Alma-Ata
	H 7550			China, Xinjiang, Habahe, Teilike
	H 7589			China, Xinjiang, Tacheng, Abdula valley

Goulardia	*E. fedtschenkoi* TZVEL.*	28	SSYY	Central Asia
	H 4040			Pakistan, Gilgit, S side of Bathura glacier
	H 7535			China, Xinjiang, Habahe, Teilike
Goulardia	*E. panormitanus* (PARL.) TZVEL.*	28	SSYY	Eastern Mediterranean and SW Asia
	H 3279			Turkey, near Pulumur, Tunceli
	H 4152			Ukraine, southern Crimea
Goulardia	*E. semicostatus* (NEES ex STEUD.) MELD.*	28	SSYY	The Himalayas
	H 3286			Afghanistan, Kataghan
	H 3288			India, Mandi
	H 4002			Pakistan, Gilgit, between Gilgit and Hunza, Murtazabad
	H 4058			Pakistan, Gilgit, Nagar valley, Minapin
	H 4104			Pakistan, Hazara, below Shogran
	H 4109			Pakistan, Swat, between Kalam and Ushu
	H 4130			Pakistan, Swat, between Monkial and Bahrain
Goulardia	*E. trachycaulus* (LINK) GOULD & SHINN.	28	SSHH	NE Asia and North America
	H 4230			USA, Wyoming, Teton Co., Moose village
Goulardia	*E. tsukushiensis* HONDA	42	SSYYHH	Central and Eastern China and Japan
	H 3198			China, Sichuan, Yibin, Xinwen
	H 7083			China, Sichuan, Wenchuan
	H 7379b			China, Sichuan, Wenchuan
Hyalolepis (NEVSKI) LÖVE	*E. batalinii* (KRASN.) LÖVE	42	SSYYPP	The Himalayas and Central Asia
	H 7801			China, Xinjiang, Tianshan, Wensu, Tachlake
Hystrix (MOENCH) LÖVE	*E. hystrix* L.	28	SSHH	Eastern North America
	H 5495			Canada, unspecified origin
Macrolepis (NEVSKI) JAASKA	*E. canadensis* L.	28	SSHH	North America
	H 5429			USA, unspecified origin
Sitanion (RAFIN.) LÖVE	no species available			North America
Stenostachys (TURCZ.) LÖVE & CONNOR	no species available			New Zealand
Turczaninovia (NEVSKI) TZVEL.	*E. dahuricus* TURCZ. ex GRISEB.	42	SSYYHH	Central and eastern Asia
	H 4083			Pakistan, Gilgit, Babusar valley, S of Babusar village
	H 7283			China, Gansu, Wenxian, Nanping
	H 7597			China, Xinjiang, Urumqi, Yongfeng

& LU 1992). The first group has the SH genomes and a worldwide distribution, and the second group has the SY genomes and is principally confined to Eurasia (SALOMON 1994). Nine species of the latter group distributed in C and SW Asia constitute the *Elymus semicostatus* group, which is classified in section *Goulardia*. They are characterized by large and erect spikes, large glumes, and rounded paleas (SALOMON 1994).

The aim of the present study was to elucidate the genomic relationships between species of the *Elymus semicostatus* group and species of as many other groups and sections in *Elymus* s.l. as possible. Four species of the *E. semicostatus* group were selected, namely *E. semicostatus* (NEES ex STEUD.) MELD., *E. abolinii* (DROB.) TZVEL., *E. fedtschenkoi* TZVEL., and *E. panormitanus* (PARL.) TZVEL. Each species represented one of the four subgroups within the *E. semicostatus* group (see SALOMON 1994). The three first-mentioned species are indigenous to the C Asiatic mountain area. The fourth species is native to the eastern Mediterranean and SW Asia. A representative worldwide selection of *Elymus* species was made following the designation of LÖVE (1984), who divided the genus into eleven sections, namely *Elymus, Turczaninovia* (NEVSKI) TZVEL., *Macrolepis* (NEVSKI) JAASKA, *Goulardia* (HUSN.) TZVEL., *Hystrix* (MOENCH) LÖVE, *Sitanion* (RAFIN.) LÖVE, *Clinelymiopsis* (NEVSKI) TZVEL., *Anthosachne* (STEUD.) TZVEL., *Stenostachys* (TURCZ.) LÖVE & CONNOR., *Dasystachyae* LÖVE, and *Hyalolepis* (NEVSKI) LÖVE. In addition, a species of sect. *Elytrigia* (DESV.) MELD. was included in agreement with the classification of MELDERIS (1978, 1980). There are indications that the sectional delimitations of *Elymus* hitherto made do not accurately reflect the phylogenetic relationships of the genus (see SALOMON & LU 1992). However, since no alternative hypotheses exist of a worldwide infrageneric classification of the genus, LÖVE's (1984) delimitation was presently accepted as a basis for selection of material. The type species of each section were preferred for use in the crossing program.

Material and methods

Four species of the *E. semicostatus* group and 13 species representing 10 of the 12 sections of *Elymus* were used in the interspecific crosses. The chromosome numbers, number of accessions, and general distribution of the species are given in Table 1.

All species were grown and hybridized in a glasshouse. Florets were emasculated shortly before anthesis and stigmas immediately brushed with newly broken anthers from the paternal species. Methods of harvesting, embryo rescue, and treatment of plantlets have been described previously (BOTHMER & al. 1983). Voucher specimens of species and hybrids were collected and will be deposited in the herbarium of Lund University (LD). For estimating pollen fertility, 200 pollen grains per hybrid plant were checked after staining in cotton blue for a minimum of one hour. Only darkly stained and completely filled pollen grains were considered normally developed.

Spikes for cytological analyses were collected and fixed in Carnoy's fixative (6 : 3 : 1 – absolute ethanol : chloroform : acetic acid) for approximately 6 h and subsequently transferred to 70% ethanol for storage in a freezer (– 18 °C) until analysis. The spikes were then stained with alcoholic hydrochloric acid-carmine at 60 °C for 48 h (SNOW 1963) and squash preparations performed according to LU & BOTHMER (1989). The chromosomal pairing was analysed at meiotic metaphase I in pollen mother cells. Pairing categories were defined according to SALOMON (1993), i.e., the pairing is defined as low pairing when less than half of the chromosome arms are paired (0–< 14 chiasmata/cell) and as high pairing when half or more of the arms are paired (14–28 chiasmata/cell). Pairing within the high

pairing range in the lowest 25 percentage interval (14–< 17.5 chiasmata/cell) is classified as moderately high, whereas pairing within the highest 25 percentage interval (> 24.5 chiasmata/cell) is referred to as very high. Our estimates of best fitting model for chromosome associations were compared with those calculated by the WSSD (Weighted Sums of Squares of Differences) computer program (CHAPMAN & KIMBER 1992).

Results

Data on seed set and hybrid plants obtained are summarized in Table 2. Hybrids involving species of the *E. semicostatus* group were obtained with 11 of the 13 species of *Elymus* s.l. used in the crosses. Only the attempts to produce hybrids with *E. enysii* (KIRK) LÖVE & CONNOR (sect. *Anthosachne*) and *E. erianthus* PHILIPPI (sect. *Dasystachyae*) failed, though two attempts, respectively, were made. Twenty hybrid combinations were produced from crosses which average seed set was 41%. No obvious differences were observed between reciprocal crosses. The seed set ranged between 4% and 84%. The lowest seed set was found in *E. dahuricus* TURCZ. ex GRISEB. × *E. fedtschenkoi* and the highest in *E. caucasicus* (KOCH.) TZVEL. × *E. abolinii*.

In most hybrid combinations the excised embryos grew well on nutrient medium and developed into vigorous plants. However, in the combination *E. dahuricus* × *E.*

Table 2. Results of the interspecific hybridizations between species of the *E. semicostatus* group and species of other groups and sections of *Elymus* s.l. *Percent of pollinated flowers

Section	Hybrid combination	Crosses	Flowers	Seedset		Plants
				no.	%*	
Anthosachne	*E. enysii* × *E. semicostatus*	2	35	0	0	0
Anthosachne	*E. scabrus* × *E. semicostatus*	1	12	1	8	1
Clinelymiopsis	*E. caucasicus* × *E. semicostatus*	3	31	17	55	6
	× *E. abolinii*	3	45	38	84	23
	× *E. fedtschenkoi*	1	16	11	69	5
	× *E. panormitanus*	2	26	12	46	3
Dasystachyae	*E. erianthus* × *E. semicostatus*	2	39	0	0	0
Elymus	*E. sibiricus* × *E. semicostatus*	3	29	5	17	3
Elytrigia	*E. repens* × *E. semicostatus*	1	14	5	36	0
Goulardia	*E. caninus* × *E. semicostatus*	3	44	25	57	14
	× *E. panormitanus*	1	22	13	59	5
Goulardia	*E. trachycaulus* × *E. semicostatus*	2	30	4	13	4
Goulardia	*E. tsukushiensis* × *E. semicostatus*	1	20	5	25	4
	× *E. abolinii*	2	31	17	55	14
	× *E. fedtschenkoi*	1	22	5	23	4
	× *E. panormitanus*	1	25	8	32	8
Hyalolepis	*E. batalinii* × *E. semicostatus*	1	6	2	33	1
Hystrix	*E. hystrix* × *E. semicostatus*	2	29	10	34	4
Macrolepis	*E. canadensis* × *E. semicostatus*	1	18	4	22	4
Turczaninovia	*E. dahuricus* × *E. semicostatus*	2	52	22	42	11
	× *E. abolinii*	2	25	15	60	15
	× *E. fedtschenkoi*	1	26	1	4	0

fedtschenkoi the embryos failed to grow and in the only combination involving sect. *Elytrigia* [*E. repens* (L.) GOULD × *E. semicostatus*] the embryos produced roots but no shoots. The sole hybrid plant with sect. *Anthosachne* [*E. semicostatus* × *E. scabrus* (R. BR.) LÖVE] was vigorous but died before meiosis could be assessed.

Spike morphology of the hybrids was generally intermediate to their parental species. In all combinations the hybrids were sterile with non-dehiscent anthers. Pollen stainability was very low in all combinations with a maximum of 4.5% (*E. tsukushiensis* HONDA × *E. semicostatus*) and in most of the hybrids all pollen grains aborted.

All species used in the study behaved as strict alloploids, predominantly forming ring-bivalents and only rarely multivalents at meiotic metaphase I. A total of 19 hybrids involving seven sections were meiotically analysed (Table 3). All hybrids had the expected chromosome number, i.e., 2n = 28 and 2n = 35, respectively, dependent on parental combination. They were all characterized by a disturbed meiosis with univalents and multivalents.

Hybrids with sect. *Clinelymiopsis*. Nine hybrid families involving all four representatives of the *E. semicostatus* group were obtained but all hybrids with *E. fedtschenkoi* were weak and died before flowering, which precluded further analysis. The *E. panormitanus* × *E. caucasicus* hybrid was characterized by high pairing and the *E. caucasicus* × *E. semicostatus* hybrid by moderately high pairing at meiosis, whereas the *E. caucasicus* × *E. abolinii* hybrid was of a low pairing type. The chiasma frequencies were 18.84, 17.00, and 13.26 and the bivalent frequencies 10.01, 9.82, and 8.36, respectively, for the three hybrids.

Hybrids with sect. *Elymus*. Three hybrid families of *E. sibiricus* L. × *E. semicostatus* were produced, two of which were analysed. Chromosome pairing at metaphase I was low in both hybrids. The number of chiasmata per cell averaged 5.20 and 5.23 for the two hybrids. They had high frequencies of univalents, with means of about 19 per cell and the number of bivalents per cell was consequently low, ranging from 0 to 7.

Hybrids with sect. *Goulardia*. Three hybrid families of *E. semicostatus* with *E. caninus* (L.) L. and one hybrid family with *E. panormitanus* were obtained. One hybrid plant of each combination was analysed. The pairing was low in both hybrids averaging 4.96 and 4.90 chiasmata per cell, and 4.04 and 3.82 bivalents per cell, respectively, about 85% of which were rods. *Elymus trachycaulus* (LINK) GOULD & SHINN. was only hybridized with *E. semicostatus*. Pairing was analysed in one of the two hybrid families. The hybrid had low pairing with a mean of 8.03 chiasmata per cell. The frequency of bivalents was 5.43 per cell. The 5 hybrids with *E. tsukushiensis* were of two types meiotically. The *E. tsukushiensis* × *E. semicostatus* and *E. tsukushiensis* × *E. fedtschenkoi* hybrids showed high pairing at metaphase I with chiasma frequencies of 18.07 and 19.54, respectively, whereas the two *E. tsukushiensis* × *E. abolinii* hybrids only averaged 10.42 and 11.12 and the *E. tsukushiensis* × *E. panormitanus* hybrid 13.68 chiasmata per cell.

Hybrids with sect. *Hyalolepis*. The single hybrid combination obtained was *E. batalinii* (KRASN.) LÖVE × *E. semicostatus*. It was characterized by low pairing and the mean chiasma formation was 12.60 per cell. On average, 8.10 bivalents were observed at meiosis with a maximum of 11 bivalents per cell.

Hybrids with sect. *Hystrix*. The North American taxon *E. hystrix* L. was successfully hybridized with *E. semicostatus*. Pairing was low and averaged 10.86 chiasmata per cell and mean bivalent formation was 6.62 per cell, with a maximum of 9. About 60 percent of the bivalents were rings.

Hybrids with sect. *Macrolepis*. The *E. canadensis* L. × *E. semicostatus* hybrid had low pairing and a mean of 8.74 chiasmata per cell. The hybrid had a high frequency of univalents with a mean of 16.78 and 5.48 bivalents per cell, over half of which were rings.

Hybrids with sect. *Turczaninovia*. Two hybrid families of both *E. dahuricus* × *E. semicostatus* and *E. dahuricus* × *E. abolinii* were produced. One hybrid plant of the former and two of the latter combination were meiotically analysed. The hybrid with *E. semicostatus* was of high pairing type, averaging 20.79 chiasmata per cell, while the hybrids with *E. abolinii* had low to moderately high pairing, averaging only 10.71 and 14.02 chiasmata per cell.

Discussion

The accumulated knowledge obtained from the many interspecific and intergeneric hybridizations made with *Elymus* species has revealed a pattern of genomic relationships in the genus. The tetraploid species are of alloploid origin and can be divided into two groups based on different genomic constitutions. One group has the SH genomes and the other the SY genomes (SALOMON & LU 1992). The S genome is found at the diploid level in *Pseudoroegneria* (NEVSKI) LÖVE, the H genome originates from *Hordeum*, while the Y genome is from a still unknown ancestor (DEWEY 1984). In the present study, *E. sibiricus, E. caninus, E. trachycaulus, E. canadensis*, and *E. hystrix* are all presumed to belong to the SH genome group (DEWEY 1984), whereas the species of the *E. semicostatus* group and *E. caucasicus* are SY genome species (JENSEN & HATCH 1988, SALOMON & LU 1992, SALOMON 1993, LU & BOTHMER 1993). The hexaploids show a more complex pattern encompassing SYH, SYW, SYP, SSY, and SS"X" genome species, in which the P genome is from a diploid species of *Agropyron* GAERTNER s.str., W is from *Australopyrum* (TZVEL.) LÖVE, and "X" represents unidentified genomes (DEWEY 1984, JENSEN 1990 a, JENSEN & al. 1994, LU & al. 1994, TORABINEJAD & MUELLER 1993).

Among the tetraploid hybrid combinations, species of the *E. semicostatus* group showed low meiotic pairing at metaphase I in hybrids with species of all sections except *Clinelymiopsis* (*E. caucasicus*). From the meiotic data it is concluded that *E. caucasicus* shares basic genomes with species of the *E. semicostatus* group, although chromosome pairing in one of the hybrids better fitted a 2 : 1 : 1 model (see Table 3). The pairing in the *E. panormitanus* × *E. caucasicus* hybrid was even higher than that found in some hybrids among species within the *E. semicostatus* group (SALOMON 1993). Details on the relationships within the *E. semicostatus* group have previously been reported by SALOMON (1993, 1994). The meiotic data indicate that species of the *E. semicostatus* group have low genomic similarity with the species of the sections *Elymus* (*E. sibiricus*), *Macrolepis* (*E. canadensis*), and *Hystrix* (*E. hystrix*). The pairing observed in these hybrids supports the presumed genomic formula "SSYH", i.e., up to seven bivalents due to allosyndetic pairing between the two homoeologous S genomes, and confirms the data of DEWEY (1984). Although it fits the 2 : 1 : 1 model best, the *E. semicostatus* × *E. hystrix* hybrid

Table 3. Chromosome pairing at meiotic metaphase I in pollen mother cells of the interspecific *Elymus* hybrids, with estimation of best fitting model for chromosome associations using WSSD (Weighted Sums of Squares of Differences) by CHAPMAN & KIMBER (1992). Pairing values are means, with ranges in parentheses. *SALOMON & LU (1992); **LU & BOTHMER (1993)

Hybrid (♀ × ♂)	No.	2n	N	I	II			III	IV	V	VI	Chiasmata/ cell	WSSD
					total	rods	rings						
E. caucasicus (H 3207) × *E. semicostatus* (H 4104)	BB 7072*	28	49	5.94 (0–13)	9.82 (6–14)	4.46 (1–9)	5.36 (2–8)	0.35 (0–2)	0.31 (0–1)	0.02 (0–1)	0.02 (0–1)	17.00 (11–22)	2:2
E. caucasicus (H 3207) × *E. abolinii* (H 3266)	BB 7264**	28	50	10.01 (4–18)	8.36 (4–12)	4.43 (2–7)	3.93 (1–7)	0.40 (0–2)	0.02 (0–1)			13.26 (6–19)	2:1:1
E. panormitanus (H 4152) × *E. caucasicus* (H 3207)	BB 7219**	28	50	4.02 (0–10)	10.01 (6–14)	4.16 (2–8)	5.85 (2–10)	0.44 (0–2)	0.22 (0–1)	0.04 (0–1)	0.26 (0–1)	18.84 (12–24)	2:2
E. sibiricus (H 3094) × *E. semicostatus* (H 4104)	BB 6233*	28	40	19.18 (14–28)	3.98 (0–7)	3.33 (0–6)	0.65 (0–3)	0.22 (0–2)	0.05 (0–1)			5.23 (0–9)	2:1:1
E. sibricus (H 7729) × *E. semicostatus* (H 4002)	BB 7332	28	30	19.43 (14–26)	3.93 (0–7)	3.13 (0–7)	0.80 (0–2)	0.23 (0–2)				5.20 (1–9)	2:1:1
E. semicostatus (H 3288) × *E. caninus* (H 3169)	BB 7364*	28	50	19.30 (14–24)	4.04 (2–7)	3.54 (1–6)	0.50 (0–3)	0.18 (0–1)	0.02 (0–1)			4.96 (2–9)	2:1:1
E. panormitanus (H 3279) × *E. caninus* (H 3169)	BB 7394	28	50	19.82 (13–26)	3.82 (1–7)	3.14 (0–7)	0.68 (0–3)	0.18 (0–2)				4.90 (2–10)	2:1:1
E. trachycaulus (H 4230) × *E. semicostatus* (H 4058)	BB 7405	28	30	16.60 (12–22)	5.43 (3–7)	3.20 (1–5)	2.23 (0–5)	0.13 (0–1)	0.03 (0–1)			8.03 (3–12)	2:1:1
E. tsukushiensis (H 7083) × *E. semicostatus* (H 4109)	BB 6810	35	57	11.39 (5–20)	11.28 (6–15)	5.12 (2–8)	6.16 (3–11)	0.12 (0–1)	0.14 (0–1)			18.07 (12–23)	2:2:1
E. tsukushiensis (H 3198) × *E. abolinii* (H 3208)	BB 7196	35	50	17.46 (13–25)	8.66 (5–12)	7.16 (5–11)	1.50 (0–5)	0.06 (0–1)	0.02 (0–1)			10.42 (5–18)	2:2:1

E. tsukushiensis (H 7083) × *E. abolinii* (H 3306)	BB 7222	35	50	17.44 (11–23)	8.62 (5–12)	6.36 (4–10)	2.26 (0–9)	0.08 (0–1)	0.02 (0–1)	11.12 (6–21)	2 : 2 : 1
E. tsukushiensis (H 7083) × *E. fedtschenkoi* (H 4040)	BB 7234	35	50	10.70 (6–15)	11.86 (9–14)	4.52 (2–9)	7.34 (3–12)	0.14 (0–1)	0.04 (0–1)	19.54 (14–26)	2 : 2 : 1
E. tsukushiensis (H 7379b) × *E. panormitanus* (H 4152)	BB 7231	35	50	15.54 (9–23)	8.88 (5–12)	5.26 (1–10)	3.62 (0–8)	0.30 (0–2)	0.20 (0–1)	13.68 (9–20)	2 : 2 : 1
E. semicostatus (H 3286) × *E. batalinii* (H 7801)	BB 7411	35	30	17.03 (13–22)	8.10 (4–11)	4.83 (2–8)	3.27 (1–6)	0.37 (0–2)	0.17 (0–1)	12.60 (7–17)	2 : 1 : 1 : 1
E. semicostatus (H 4058) × *E. hystrix* (H 5495)	BB 7402	28	50	14.40 (10–20)	6.62 (4–9)	2.62 (0–6)	4.00 (1–7)	0.12 (0–2)		10.86 (6–15)	2 : 1 : 1
E. canadensis (H 5429) × *E. semicostatus* (H 4058)	BB 7403	28	50	16.78 (14–20)	5.48 (3–8)	2.44 (0–6)	3.04 (0–6)	0.10 (0–1)		8.74 (5–14)	2 : 1 : 1
E. dahuricus (H 7283) × *E. semicostatus* (H 4109)	BB 6803	35	40	9.21 (6–15)	12.13 (9–14)	4.72 (4–7)	7.41 (4–10)	0.31 (0–2)	0.15 (0–1)	20.79 (16–24)	2 : 2 : 1
E. dahuricus (H 4083) × *E. abolinii* (H 3209)	BB 7507a	35	50	13.74 (9–21)	9.68 (7–13)	6.66 (4–10)	3.02 (1–7)	0.50 (0–2)	0.10 (0–1)	14.02 (11–19)	2 : 2 : 1
E. dahuricus (H 4083) × *E. abolinii* (H 3307)	BB 7508c	35	50	17.86 (11–26)	8.22 (3–11)	6.21 (1–10)	2.01 (0–6)	0.22 (0–1)		10.71 (6–16)	2 : 2 : 1

showed higher than expected pairing in some cells (maximum 9 bivalents and 15 chiasmata) and implies participation of a third genome. This result is probably an effect of a low degree of homoeology between the Y genome from *E. semicostatus* and the two S genomes, and confirms results obtained by LU & BOTHMER (1989) and LU & al. (1990). Furthermore, all the hybrids with the genomic formula "SSYH" have a low proportion of trivalents. In the present investigation, the highest mean value, 0.23 trivalents per cell, was found in one of the *E. sibiricus* × *E. semicostatus* hybrids.

The section *Goulardia* is of special interest since the species of the *E. semicostatus* group are classified in this section, and *Goulardia* contains both tetraploid and hexaploid taxa. Hybrids among species of the *E. semicostatus* group and the two tetraploid SH genome species, *E. caninus* and *E. trachycaulus*, showed, as mentioned above, low meiotic pairing. The third species of section *Goulardia*, the hexaploid *E. tsukushiensis*, shared a higher genomic similarity with the *E. semicostatus* group than did the two tetraploid species. *Elymus tsukushiensis* and *E. dahuricus* (sect. *Turczaninovia*) have both been assumed to possess the SYH genomes (DEWEY 1984, LU & BOTHMER 1990). The pairing in our hybrids supports the conclusion that *E. tsukushiensis* and *E. dahuricus* have two genomes in common with *E. semicostatus* and *E. fedtschenkoi*. However, the pairing in the hybrids with *E. abolinii* is much lower than expected when compared with the other combinations. For example, the amount of pairing in *E. tsukushiensis* × *E. abolinii* is even lower than in *E. semicostatus* × *E. hystrix* ("SSYH"). Despite this anomaly, the pairing patterns best fit the 2 : 2 : 1 model, and the genomic formula should be "SSYYH". Unexpectedly low pairing in *E. abolinii* hybrids has also been reported by SALOMON & LU (1994). In the study, hybrids of *E. abolinii* with other SY genome species showed a wide range of pairing. Highest pairing was observed in a hybrid with *E. tibeticus* (MELD.) SINGH, which averaged 21 chiasmata per cell and the lowest pairing in a hybrid with *E. pendulinus* (NEVSKI) TZVEL., which averaged only 7 chiasmata per cell. Other species investigated did not show the same range in pairing ability as did *E. abolinii*. A plausible explanation would be that there are genes in *E. abolinii* which, at least in some hybrid combinations, suppress homoeologous pairing. *Elymus abolinii* should consequently be avoided as a genomic analyser species in future investigations.

The results from the hybrid with *E. batalinii* (sect. *Hyalolepis*) can be compared with the data given by JENSEN (1990 b), who reported means of 12.11 bivalents and 17.3 chiasmata in an *E. batalinii* × *E. abolinii* [as *E. dentatus* (HOOK f.) TZVEL. subsp. *ugamicus* (DROB.) TZVEL.] hybrid. Our hybrid had noticeably lower pairing averaging 8.10 bivalents and 12.60 chiasmata per cell, which is not high enough unambiguously to support the genomic formula "SSYYPP" for *E. batalinii*. Furthermore, the best fitting model is 2 : 1 : 1 according to the WSSD program, rather than the expected 2 : 2 : 1 (see Table 3). However, based on the data given by JENSEN (1990 b) and the morphological features of this species, we concur with their opinion that *E. batalinii* possesses the SYP genomes, but more hybrids should be studied, especially between *E. batalinii* and diploid *Agropyron* spp.

It was not possible to record meiosis in the hybrid with *E. scabrus* of sect. *Anthosachne*. Hence, no information can be given regarding genome relationships in this hybrid. Fortunately, meiotic data for similar hybrids were reported previously

by CARMAN & al. (1989), who recounted mean values of up to 11.72 bivalents and 17.80 chiasmata per cell in *E. scabrus* × *E. semicostatus* hybrids. Thus *E. scabrus* is also likely to contain the SY genomes together with an additional third genome that TORABINEJAD & MUELLER (1993) recently designated as W.

DEWEY (1984) did not place *E. repens* in *Elymus* but in the genus *Elytrigia* DESV. However, since it has many similar morphological features to *Elymus* species it was included in this study in agreement with MELDERIS (1980). To distinguish *Elytrigia* from *Elymus* a few morphological traits are considered important, namely presence of rhizomes, abscission layer below the glumes, long anthers, and self-incompatibility. However, rhizomes are also found in *E. macrourus* (TURCZ. ex STEUD.) TZVEL. and *E. dentatus* (HOOK. f.) TZVEL., and the anthers of *E. borianus* (MELD.) COPE are equal in length to those of *E. repens*. Furthermore, the predominantly cross-fertilizing and rhizomatous species *E. lanceolatus* (SCRIBN. & SMITH) GOULD is included in *Elymus* (BARKWORTH & DEWEY 1985), and other genera of the *Triticeae* also contain both self-fertilizing and cross-fertilizing species, for example, *Hordeum* (BOTHMER 1979). DEWEY (1984) concluded that *E. repens* has two homoeologous sets of the S genome and a third unknown genome, which he designated "X", and speculated that the "X" genome could possibly be related to either the J genome of *Thinopyrum* LÖVE or the H genome of *Hordeum*. The genomic formula would then be "SSS'S'JJ" or "SSS'S'HH". A closer relationship to *Thinopyrum* is indicated by some morphological characters and the extent of spontaneous hybridization (DEWEY 1984), whereas a closer relationship to *Hordeum* (or *Elymus*: SH genome species) might be postulated from meiotic pairing data (DEWEY 1984; M. ASSADI, unpubl.) and DNA studies (VERSHININ & al. 1994). Whatever may be the true phylogenetical relationships, there are no morphological, cytological, or molecular data available from which to conclude that *E. repens* is closely related to the species of *E. semicostatus* group or any other species containing the SY genomes.

It was not possible to obtain hybrids with *E. erianthus* of sect. *Dasystachyae* or with *E. enysii* of sect. *Anthosachne*. However, on a purely morphological basis these species are not likely to be genomically closely related to the *E. semicostatus* group, since they do not have the distinguishing characteristics of the palea typical of all SY genome species (SALOMON & LU 1992). It is even doubtful whether *E. erianthus* should be included in the genus *Elymus*. LÖVE & CONNOR (1982) reported *E. enysii* as having the SH genomes but this needs to be confirmed, since they also reported up to 14 bivalents in the hybrid with *E. longearistatus* subsp. *canaliculatus* (NEVSKI) TZVEL., an SY genome species (SALOMON & LU 1992).

In conclusion, from the data on genomic relationships presented in this study there are strong indications that the tetraploid species of the *E. semicostatus* group of sect. *Goulardia* are genomically closer to the hexaploid *Elymus* species (regardless which section they belong to) and the tetraploid *E. caucasicus* of sect. *Clinelymiopsis* rather than to the other tetraploid species of sect. *Goulardia*. Hence, there is no support for the sectional delimitations used by LÖVE (1984). However, the data also illustrate the vulnerability of genome analysis in phylogenetic studies, since the results are highly dependent on the presence or absence of pairing regulating genes similar to those (probably) responsible for the low pairing in certain *E. abolinii* hybrids.

Prof. R. VON BOTHMER, Dr S. FREDERIKSEN, Dr R. PICKERING, and Dr O. SEBERG made helpful comments on the manuscript.

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Accepted February 17, 1994 by F. EHRENDORFER