

Dihaploids of *Elymus* from the interspecific crosses *E. dolichatherus* × *E. tibeticus* and *E. brevipes* × *E. panormitanus*

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Summary. Dihaploids ($n=2x=14$, SY) of two *Elymus* species, i.e., *E. dolichatherus* (Keng) Löve ($2n=4x=28$, SSYY) and *E. brevipes* (Keng) Löve ($2n=4x=28$, SSYY), were obtained from the interspecific hybrid combinations *E. dolichatherus* (♀) × *E. tibeticus* (Meld.) G. Singh (♂) and *E. brevipes* (♀) × *E. panormitanus* (Parl.) Tzvelev (♂). The dihaploids were probably formed through selective elimination of male parental chromosomes in early embryo development. Meiotic chromosome behavior was studied in *E. dolichatherus*, *E. brevipes*, and their dihaploids. The two parental *Elymus* species had regular meioses with predominantly ring bivalent formation. A low frequency of homoeologous chromosome pairing was observed, with an average of 0.81 bivalents and 0.03 trivalents in the dihaploid of *E. dolichatherus*, and 0.26 bivalents in the dihaploid of *E. brevipes*. Up to two chromatid bridges accompanied by small fragments were present at anaphase I of the *E. dolichatherus* dihaploid. It is concluded from this study that: (i) both *E. dolichatherus* and *E. brevipes* are allotetraploid species; (ii) a low affinity exists between the “S” and “Y” genomes of the two *Elymus* species.

Key words: *Elymus* species – Dihaploid – Interspecific crosses – Chromosome pairing – Genome

Introduction

Intergeneric and interspecific hybridizations in *Triticeae* Dumort. (Poaceae) have played an important role, not only in the utilization of wild germ plasms to improve cereal crops like wheat, barley, and rye (Riley and Chapman 1968; Sears 1983), but also in the investigation of phylogenetic relationships of the tribe (Dewey 1984;

Löve 1984). The detailed study of chromosome behavior in meioses of the species hybrids can provide valuable information about the genomic structure and relationships of different species and genera (Kimber 1983; von Bothmer et al. 1986; Lu and von Bothmer 1990 a, b). Particular cytogenetic events can also occur, such as the production of euploids as a result of elimination of one parental set of chromosomes following intergeneric and interspecific crosses, e.g., *Hordeum vulgare* × *H. bulbosum* (Kao and Kasha 1969; Kasha and Kao 1970), *H. bulbosum* × *Triticum aestivum* (Barclay 1975), *H. vulgare* × *Psathyrostachys fragilis* (von Bothmer et al. 1984), and *Elymus shandongensis* × *T. aestivum* (Lu and von Bothmer 1989).

Chromosome elimination has been reported in many combinations in *Triticeae* (Barclay 1975; Fedak 1977; Shigenobu and Sakamoto 1977; Surahmanyam 1977, 1978, 1979; von Bothmer et al. 1983, 1984, Wang 1987; Lu and von Bothmer 1989; Lu et al. 1990). Most of the haploid plants have been analyzed to assess homologous segments within a genome or homocologous affinity between genomes (Sadasivaiah and Kasha 1971; Subrahmanyam 1978; Neijzing 1982, 1985; Torabinejad et al. 1987; von Bothmer and Subrahmanyam 1988; Lu and von Bothmer 1989; Lu et al. 1990). These analyses have also led to a better understanding of the auto- or allo-ploid nature of some species, particularly in the genera *Hordeum* and *Aegilops* (Shigenobu and Sakamoto 1977; Subrahmanyam 1977; Wang 1988).

The present paper describes the production of two new dihaploids from the interspecific crosses *E. dolichatherus* × *E. tibeticus* and *E. brevipes* × *E. panormitanus*, in which all the *Elymus* species contain the “SY” genomes, as well as the analysis of chromosome behavior in meioses of *E. dolichatherus*, *E. brevipes*, and the dihaploids in order to evaluate the nature of polyploidy of the

Table 1. The origins of the *Elymus* species used in intergeneric hybridizations

Species	Accession no.	2n=	Locality and Collectors
<i>E. dolichatherus</i>	H 8024	28	China, Sichuan, Zhaojue; CS ^a
<i>E. tibeticus</i>	H 7709	28	China, Xinjiang, Tian Shan; CS ^a
<i>E. brevipes</i>	H 8235	28	China, Tibet, Yangbajing; CS ^a
<i>E. panormitanus</i>	H 3279	28	Turkey ^b

^a CS=Chinese and Scandinavian joint collecting mission

^b Seeds from Dr. D. R. Dewey, PI-206402

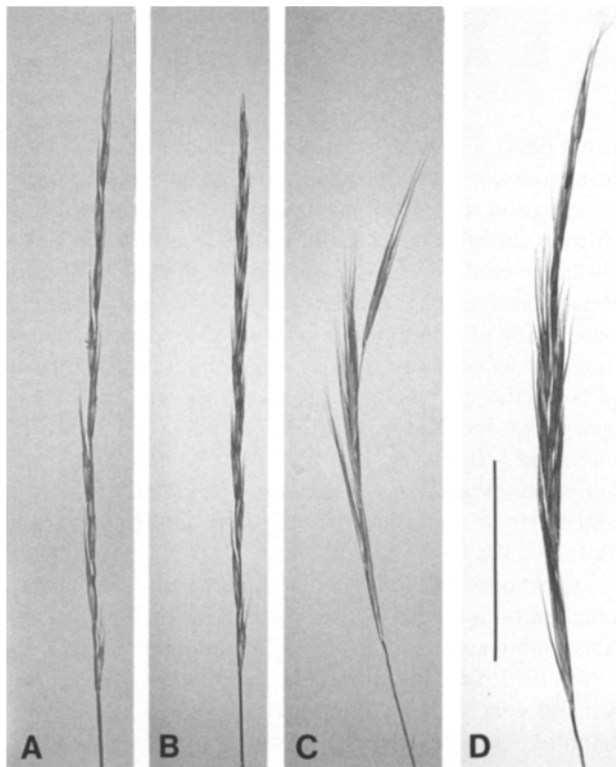


Fig. 1 A–D. Spike morphology of **A** *Elymus dolichatherus*; **B** the dihaploid of *E. dolichatherus*; **C** the dihaploid of *E. brevipes*; **D** *E. brevipes*. Bar=5 cm

two *Elymus* species, and the homoeologous affinity between the “S” and “Y” genomes.

Materials and methods

Four tetraploid *Elymus* species ($2n=4x=28$) were involved in the crosses to produce dihaploids. *E. dolichatherus* (Keng) Löve, *E. brevipes* (Keng) Löve, and *E. tibeticus* (Meld.) G. Singh (syn. *Roegneria stricta* Keng) are all Chinese endemic species distributed in western mountainous areas (Kuo 1987), whereas *E. panormitanus* (Parl.) Tzvelev occurs in Western and Central Asia (Tzvelev 1976). Origins of the species used in the study are listed in Table 1.

The method for cultivation of plants, crossing procedure, embryo culture technique, and growth conditions were according to von Bothmer et al. (1983). The chromosome number was determined in root-tip cells of adult plants, and meiotic pairing was analyzed in pollen mother cells (PMCs). The procedures of fixation and staining of cytological materials, mitotic, and meiotic preparations were as described previously (Lu and von Bothmer 1990 a).

Results

Crosses and development of the dihaploids

The combination *E. dolichatherus* (♀) × *E. tibeticus* (♂) produced five seeds from 16 pollinated florets (seed set 31.3%). All of the seeds possessed embryos that germinated on nutrient medium and developed into adult plants. Four of the plants were vegetatively vigorous and morphologically intermediate between their parental species. They were consequently proved to be true hybrids with chromosome number $2n=4x=28$ (details of the hybrids will be reported separately). One of the plants grew rather weakly and resembled the maternal parent in all aspects (Fig. 1 A, B), and contained 14 chromosomes in root-tip cells. It was thus a dihaploid of *E. dolichatherus*. From the combination *E. brevipes* (♀) × *E. panormitanus* (♂), three seeds out of 14 pollinated florets were obtained (seed set 21.4%). Three embryos were excised and germinated on the medium, and eventually only a single adult plant was produced. This plant was identical to the female parent (Fig. 1 C, D), developed

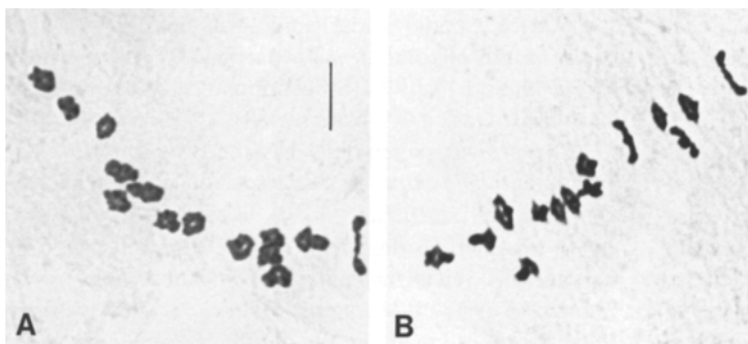


Fig. 2 A, B. Meiotic configurations at metaphase I of **A** *E. dolichatherus* and **B** *E. brevipes*. Bar=10 μm

Table 2. Meiotic pairing at metaphase I in *Elymus dolichatherus*, *E. brevipes* and the polyhaploids (r=range)

Parents and dihaploids	Chromosome number	Genomes	No. of cells observed	Chromosome configuration					Chiasmata/cell
				I	II			III	
					Total	rings	rods		
Parents									
<i>E. dolichatherus</i>	28	SSYY	50	0.12 r (0-2)	13.94 (13-14)	13.52 (12-14)	0.42 (0-2)	-	27.48 (26-28)
<i>E. brevipes</i>	28	SSYY	50	0.28 r (0-2)	13.86 (13-14)	12.94 (11-14)	0.92 (0-9)	-	26.81 (25-28)
Polyhaploids									
<i>E. dolichatherus</i>	14	SY	100	12.29 r (6-14)	0.81 (0-4)	0.01 (0-1)	0.80 (0-4)	0.03 (0-1)	0.86 (0-4)
<i>E. brevipes</i>	14	SY	50	13.48 r (19.21)	0.26 (0-3)	-	0.26 (0-3)	-	0.26 (0-3)
<i>E. pseudonutans</i> ^a	14	SY	33	12.82 r (9-14)	0.55 (0-2)	-	0.55 (0-2)	0.03 (0-1)	0.61 (0-2)
<i>E. shandongensis</i> ^a	14	SY	114	12.59 r (6-14)	0.68 (0-4)	0.03 (0-1)	0.65 (0-4)	0.01 (0-1)	0.73 (0-4)
<i>E. semicostatus</i> ^a	14	SY	117	12.70 r (8-14)	0.79 (0-3)	0.03 (0-1)	0.76 (0-3)	0.02 (0-1)	0.85 (0-4)
<i>E. canadensis</i> ^b	14	SH	500	12.97 r (8-14)	0.49 (0-3)	0.002 (0-1)	0.49 (0-3)	0.01 (0-1)	0.53 (0-3)
<i>E. caninus</i> × <i>Secale cereale</i> ^c	21	SHR	77	20.74 r (17-21)	0.10 (0-3)	-	-	-	0.10 (0-3)
<i>E. tsukushiensis</i> ^a	21	SHY	442	20.61 r (15-21)	0.18 (0-3)	-	-	0.004 (0-1)	0.20 (0-3)
<i>E. semicostatus</i> × <i>H. bogdanii</i> ^e	21	SHY	50	20.00 r (19-21)	0.50 (0-2)	-	0.05 (0-2)	-	0.50 (0-2)
<i>E. semicostatus</i> × <i>H. roshevitzii</i> ^e	21	SHY	50	19.96 r (17-21)	0.52 (0-2)	-	0.52 (0-2)	-	0.52 (0-2)
<i>E. parviglumis</i> × <i>H. bogdanii</i> ^e	21	SHY	50	20.08 r (17-21)	0.46 (0-2)	0.44 (0-2)	0.02 (0-1)	-	0.48 (0-3)

^a Lu et al. (1990)^b Torabinejad et al. (1987)^c Lu and von Bothmer (1991), only including *Elymus-Elymus* chromosome pairing^d Sakamoto (1964), no indication of rod and ring bivalents; IV=0.002^e Lu and von Bothmer (1990 a)

rather weakly, and possessed $n=2x=14$ in root-tip cells. It was a dihaploid of *E. brevipes*. The two dihaploid plants had non-dihescent anthers and were completely seed sterile.

Cytology of *E. dolichatherus*, *E. brevipes*, and the dihaploids

E. dolichatherus and *E. brevipes* both had invariably $2n=28$ in root tips and PMCs. Meiosis of the two *Elymus* species was regular, with averages of 26.81 and 27.48 chiasmata per cell at metaphase I (Table 2, Fig. 2A, B).

The two dihaploids invariably had $n=2x=14$ in all the PMCs. The chromosomes occurred mostly as univalents at metaphase I of the plants (Table 2, Fig. 3A-E). There was no sign of metakinesis or the organization of

a normal spindle. The univalents, therefore, were lying scattered about in the cells. The dihaploid of *E. dolichatherus* formed an average of 0.81 (up to 3), predominantly rod, bivalents and 0.03 chain trivalents per cell (Fig. 3C-E), in addition to a low frequency (0-3) of loose secondary associations at metaphase I. Up to two chromatid bridges accompanied by one to two small fragments at anaphase I were observed in some cells of this dihaploid (Fig. 3F), whereas the dihaploid of *E. brevipes* presented an average of 0.26, only rod, bivalents per cell at metaphase I (Fig. 3A, B). Lagging chromosomes were commonly found at anaphase I and II in both dihaploids. At the tetrad stage, varying numbers of diads, triads, and monads were present. Micronuclei were often observed at this stage.

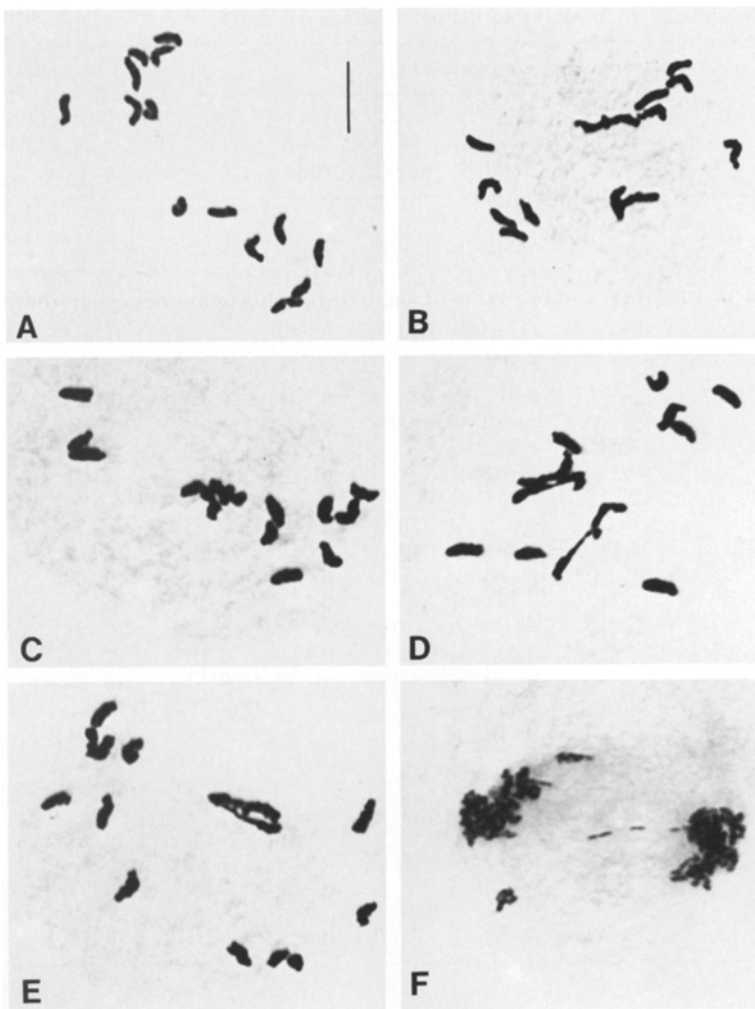


Fig. 3 A–E. Meiotic configurations at metaphase I in the dihaploids of **A, B** *E. brevipes* and **C–E** *E. dolichatherus*. **A** 14 univalents; **B** 12 univalents and one bivalent; **C** ten univalents and two bivalents; **D** eight univalents and three bivalents; **E** 11 univalents and one trivalent. **F** Anaphase I of *E. dolichatherus*, showing lagging chromosomes in addition to a bridge. Bar = 10 μ m

Discussion

Two haploid plants with $n = 2x = 14$ both in root-tip cells and PMCs were derived from the interspecific hybrid combinations, i.e., *E. dolichatherus* \times *E. tibeticus* and *E. brevipes* \times *E. panormitanus*. The four *Elymus* species are morphologically distinct. Therefore, judging by their particular morphological features, in which none of the characteristics of *E. tibeticus* or *E. panormitanus* were exhibited, the two plants were obvious dihaploids of the female parents, i.e., *E. dolichatherus* and *E. brevipes*, respectively. The formation of the dihaploids was most likely a result of selective elimination of the chromosomes of the male parental *Elymus* species from the hybrids, even though there might be an alternative explanation in which the production of the dihaploids was due to parthenogenetic development.

The production of euhaploids following wide hybridizations either by selective elimination of one

parental set of chromosomes or through the other pathways has been widely reported in many combinations in the tribe Triticeae. The most well-known example is the combination *H. vulgare* \times *H. bulbosum*, in which chromosomes of *H. bulbosum* were eliminated (Kasha and Kao 1970). This combination is known to be used as a breeding method for production of doubled haploids (Kasha and Reinbergs 1981). Interspecific or intergeneric hybridizations have so far led to the production of monohaploids or polyploids of many Triticeae species, for example, of *T. aestivum* ($n = 21$, genomes ABD; Barclay 1975; von Bothmer and Claesseeon 1990), *Hordeum* species ($n = 7, 14, 21, I, H$; Subrahmanyam 1977, 1978, 1979; von Bothmer et al. 1984; von Bothmer and Subrahmanyam 1988), *Agropyron mongolicum* ($n = 7, P$; Wang 1987), *Secale cereale* ($n = 7, R$; Neijzing 1982), *Aegilops* species ($n = 7, 14, 21$; Riley and Chapman 1957; Chapman and Miller 1977; Shigenobu and Sakamoto 1977), and *Elymus* species ($n = 14, SY, SH$; Torabinejad

et al. 1987; Lu and von Bothmer 1989; Lu et al. 1990). Most of the euploids were meiotically analyzed for the assessment of homologous segments within a genome in the monhaploids, or homoeologous affinities between genomes in the polyhaploids. Sadasivaiah and Kasha (1971) observed rather high association of non-homologous chromosomes at pre-meiosis stages in the haploid of *Hordeum vulgare* ($n=7$, I), but only a low frequency of rod bivalents at metaphase. They concluded that very little chromosome duplications existed in the haploid set of barley. Neijzing (1982, 1985) studied Giemsa-banded metaphase chromosomes in haploid *Secale cereale* ($n=7$, R), and found several sets of homologous segments in the rye genome. Further cytogenetic investigations on polyhaploids have led to a better understanding of the ploidy nature of species in *Hordeum* (von Bothmer and Subrahmanyam 1988; Wang 1988), *Aegilops* (Shigenobu and Sakamoto 1977), and homoeologous relationships between different genomes in *Elymus* (Lu and von Bothmer 1989; Lu et al. 1990). By comparing meiotic pairing in polyhaploids and intergeneric hybrids involving the same *Elymus* species, Lu et al. (1990) and Lu and von Bothmer (1991) found out that the "R" genome of *S. cereale* could promote chromosome associations between different genomes of *Elymus*, which is similar to the results in the hybrids of rye with wheat (Dvorak 1977) and with *Hordeum* species (Gupta and Fedak 1985, 1987; Petersen 1991).

The perennial genus *Elymus*, containing only polyploid species, is the largest genus in the tribe Triticeae. Genomic relationships have been largely investigated between species within the genus and, particularly, to the other genera in the tribe. Consequently, four basic genomes, namely, "S," "H," "Y," and "P" genomes in different combinations, have so far been identified as the genomic constitution of the genus. The genomes are supposedly derived from different origins (Dewey 1971, 1974, 1984; Jensen 1990, 1991). However, investigations of the relationships between these genomes are still limited. Sakamoto (1964) reported a low frequency of homoeologous chromosome pairing, with ca. 0.2 chiasmata per cell between the different genomes in a spontaneous trihaploid of *E. tsukushiensis* ($n=3x=21$, SHY). Lu and von Bothmer (1990a) synthesized three intergeneric hybrids ($n=3x=21$) containing the "SHY" genomes from the combination *E. semicostatus* (SSYY) \times *H. bogdanii* (HH), *E. semicostatus* \times *H. roshevitzii* (HH), and *E. parviglumis* (SSYY) \times *H. bogdanii*. The homoeologous chromosome pairing in these SHY genome hybrids was similar to that of the trihaploid reported by Sakamoto (1964), although with somewhat higher chiasma frequency (ca. 0.5/cell on average). Torabinejad et al. (1987) obtained a dihaploid of *E. canadensis* L. ($n=14$, SH) through interspecific cross with *E. scabrus* ($2n=6x=42$), where very low affinity between the "S" and "H"

genomes was also estimated, with ca. 0.5 chiasmata per cell. Recently, dihaploids of three *Elymus* species containing the "SY" genomes were produced from the hybrid combinations, namely, *E. shandongensis* (SSYY) \times *Triticum aestivum*, *E. pseudonutans* (SSYY) \times *H. vulgare* ssp. *spontaneum*, and *E. semicostatus* \times *H. bulbosum*, probably through elimination of male parental chromosomes. A low affinity between the "S" and "Y" genomes and non-homologous chromosomes of the same genomes was reported, with ca. 0.6–0.9 chiasmata per cell in these studies (Lu and von Bothmer 1989; Lu et al. 1990).

The two parental species *E. dolichatherus* and *E. brevipes* both contain the SY genomes, because their hybrids with *E. caninus* ($2n=4x=28$, SSHH) formed less than 7.5 chiasmata, whereas the hybrids with *E. semicostatus* had about 19–22 chiasmata per cell (B. R. Lu in preparation). In this study, meiotic pairing in *E. dolichatherus* and *E. brevipes* was characterized by the predominant bivalent and no multivalent formation, which suggests an allotetraploid nature of the two species. Predominant univalent formation in meiosis of the two dihaploids supported the conclusion. The dihaploid of *E. dolichatherus* formed an average of 0.81 (maximum of 4) chiasmata per cell, whereas the dihaploid of *E. brevipes* had 0.26 (maximum of 3) chiasmata, which indicates that the "SY" genomes have a low degree of affinity, similar to our previous reports (Lu and von Bothmer 1989; Lu et al. 1990). The formation of multivalents in the dihaploid of *E. dolichatherus* suggests the pairing between the non-homologous chromosomes, which could be due to duplicated segments within a same genome, as demonstrated in monohaploids of *H. vulgare* (Sadasivaiah and Kasha 1971) and *S. cereale* (Neijzing 1985).

In a previously reported hybrid *E. caninus* \times *S. cereale* ($n=21$, SHR), homoeologous chromosome pairing between the "SH" genomes was observed with ca. 0.1 chiasmata per cell, because the pairing between different genomes could be identified by the conspicuous differences in the chromosome size (Lu and von Bothmer 1991). The homoeologous pairing between the "S" and "Y" genomes in the dihaploids of *E. brevipes* and *E. dolichatherus* was 0.26 and 0.86 chiasmata per cell, respectively. A comparison of the homoeologous pairing in all the polyhaploids listed in Table 2 shows that the affinity between the "SY" or "SH" or "SHY" genomes apparently varies in the different *Elymus* species.

A low frequency of chromatid bridges and fragments (up to two per cell) was observed at anaphase I in the dihaploid of *E. dolichatherus*. This could result from crossing-over in paired homoeologous segments, which were in reverse order on the chromosomes, or be due to breakage and rejoining of the synapsed chromatids in the U-type manner, as described by Jones and Brumpton (1971).

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