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Genome analysis of intergeneric hybrids of apomictic and sexual Australian *Elymus* species with wheat, barley and rye: implication for the transfer of apomixis to cereals

J. Torabinejad [1] **and R. J. Mueller** [2]

[1] Department of Range Science, Utah State University, Logan, UT 84322-5230, USA
[2] Department of Biology, Utah State University, Logan, UT 84322-5305, USA

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Summary. Four hybrids were obtained between three Australian *Elymus* taxa and three cereal grains: wheat, rye, and barley. Mean meiotic metaphase-I configurations were 41.14 I, 0.42 rod II, 0.003 ring II, and 0.01 III for *E. scabrus* var 'plurinervis' × *Triticum aestivum* (1 hybrid plant), 22.27 I, 2.63 rod II, 0.06 ring II, and 0.12 III for *E. scabrus* var 'scabrus' × *Secale cereale* (4 hybrid plants), and 26.65 I, 0.66 rod II, 0.00 ring II, and 0.01 III for *E. scabrus* var 'plurinervis' × *Hordeum vulgare* (13 hybrid plants). The I genome of barley also paired very little in a B_{III} hybrid of apomictic *E. rectisetus* × *H. vulgare* (2 hybrid plants). Megasporogenesis in this B_{III} hybrid was at least facultatively apomeiotic, with the same sort of nuclear elongation, apomeiotic division, and dyad formation seen previously in *E. rectisetus* itself. All four hybrid combinations were sterile. While spike morphology in the *E. scabrus* × *T. aestivum* and *E. scabrus* × *H. vulgare* hybrids were intermediate to their parents, *E. scabrus* × *S. cereale* and *E. rectisetus* × *H. vulgare* looked like their maternal parents.

Key words: Apomixis – Wheat – Barley – Rye – Wide hybridization

Introduction

At least two and possibly four species of hexaploid wheatgrasses are endemic to southeastern and coastal southern Australia. One of them, *Elymus rectisetus* (Nees in Lehm.) A. Löve & Connor, contains numerous highly apomictic strains and is the only embryologically documented apomict in the Triticeae (Hair 1956; Crane and Carman 1987). As such, it is a potential donor of apomixis for stably seed-propagated hybrid cereals. Therefore, the genomic relationships of the Australian taxa to one another and to Northern Hemisphere Triticeae are of agronomic as well as biosystematic interest. Previous hybridization studies have indicated that the Australian *Elymus* are genomically isolated, with the greatest similarity to SSYY and SSHHYY *Elymus* species in southern and eastern Asia (Torabinejad et al. 1987, 1989). Previously published attempts to cross apomictic *E. rectisetus* to wheat and rye have failed (Zenkteler and Nitzsche 1984; Torabinejad et al. 1987), perhaps because of its low pollen fertility (at most 40% according to Löve and Connor 1982). Using in ovulo embryo culture, Ahmad and Comeau (1991) have recently obtained hybrids of *Triticum aestivum* (L.) emend. Thell with *E. scabrus* (R. Br.) Löve.

We have obtained hybrids of the sexual Australian species, *E. scabrus*, with barley (*Hordeum vulgare* L.), wheat (*T. aestivum*), and rye (*Secale cereale* L.). The two latter combinations involved *E. scabrus* var 'plurinervis', while the former involved *E. scabrus* var 'scabrus'. We have also obtained a B_{III} (addition) hybrid between *E. rectisetus* and barley. Here B_{II} and B_{III} hybrids refer to regular hybrids and hybrids resulting from the fertilization of an unreduced egg, respectively.

This article presents the meiotic analysis of these hybrids and the reproductive mode of the B_{III} hybrid.

Materials and methods

Accessions of *Elymus rectisetus* (PI 533090, 2n = 41), *E. scabrus* var 'scabrus' (PI 533218, 2n = 42), and *E. scabrus* var 'plurinervis' (PI 533193, 2n = 42) were crossed as seed parents at intervals from August, 1988, to May, 1991. The *E. rectisetus* accessions were pollinated with *Hordeum vulgare*; *E. scabrus* var 'scabrus' was pollinated with *Secale cereale*, and *E. scabrus* var 'plurinervis' was pollinated with *H. vulgare* and *Triticum aestivum*. All

Correspondence to: R. J. Mueller

spikes were hand emasculated before pollination, and each floret received one drop of 75 ppm gibberellic acid (GA_3) at 8 and 32 h after pollination. In some instances a drop of a 25 ppm 2,4 dichlorophenoxyacetic acid was used as a pretreatment in each floret. All the crosses were performed in a greenhouse at Logan, Utah.

At 18–20 days after pollination, enlarged caryopses were excised and surface sterilized 10 min in 10% commercial bleach (cal. 0.5% sodium hypochlorite). Embryos were removed aseptically and cultured on orchid agar (Difco), Murashige-Skoog (MS), or Shenck-Hildebrandt (SH) media. Actively growing plantlets were transferred to 1:1:1 peat-perlite-vermiculite, hardened off, and grown out in a temperature-controlled greenhouse with supplemental lighting and automatic watering and fertilization.

For somatic chromosome counts, root tips were treated in 0.05% colchicine and dimethylsulfoxide (9 drops/20 ml) on filter paper for 3.5–4.5 h at room temperature and then fixed in 2% aceto-orcein (Mujeeb-Kazi and Miranda 1985). For meiotic analysis, spikes were fixed in Carnoy's 6:3:1 fixative (95% ethanol, chloroform, acetic acid) with one drop of saturated $FeCl_3$ for a few hours and then, in some cases, stored at −20 °C. Anthers at metaphase I were squashed in 2% aceto-carmine. To assess pollen viability, pollen was mounted in I_2-KI; fully stained grains were considered viable. To determine the reproductive mode of the B_{III} hybrid, ovaries were cleared in 2:1 benzyl benzoate:dibutly phthalate (Crane and Carman 1987). Stretched megasporocyte nuclei and persistent megaspore dyads were considered to be apomeiotic.

Results

Somatic chromosome numbers in both varieties of *E. scabrus* were consistently 2n = 42. Meiosis was regular, with almost exclusively bivalent pairing and a high arm-binding frequency (c-value). In consequence, their pollen stainability exceeded 80%. In contrast, the *rectisetus* parent, accession 533090, had 2n = 41 (Fig. 1 a) and 39% stainable pollen. In other accessions of *E. rectisetus* there was great variation in chiasma and univalent frequency, but all of the apomictic accessions had low pollen fertility and occasionally high frequencies of 2n pollen, which is in accordance with Hair (1956). Accession 533090 was among the most pollen fertile of these apomicts. Nevertheless, its small anthers and low pollen fertility impeded hybridization, as Zenkteler and Nitzsche (1984) and Torabinejad et al. (1987) had noted for other accessions. Several twin embryos were observed in *E. rectisetus*, as had also been noted by Hair (1956). While polyembryony indicates apomixis in species with adventitious embryony, for example the *Panicum* system or sometimes the *Poa pratensis* system (Hanna and Bashaw 1987), polyembryony in *E. rectisetus* more likely resulted from an extra egg apparatus in embryo sacs arising from hemidyads or directly from binucleate embryo sacs (embryo sacs with a binucleate egg; Crane and Carman 1987), or from post-zygotic events unrelated to apomixis.

All of the hybrids were perennial and pollen sterile with indehiscent anthers, and no seed was set upon open pollination in the greenhouse. The *E. scabrus* var 'scabrus' × *S. cereale* and *E. scabrus* var 'plurinervis' × *T. aestivum* hybrids were as expected, euploid with 2n = 28 (Fig. 1 b) and 42, respectively. The seven *Secale*

Table 1. Metaphase-I chromosome associations of species and hybrids

Species or hybrids	Plant identification no.	2n	Genomes	Number of cells	MI association[b]							Mean arms associated
					I	oII	rII	Total II	III	oIV	rIV	
E. rectisetus[a]	2891-2	42	SSYYWW	101	0.15 0–4	19.74 12–21	1.12 0–7	20.86 19–21	0.03 0–1		0.01 0–1	40.70 31–42
E. scrabus var *plurinervis*[a]	2885-5	42	SSYYWW	67		19.90 17–21	1.10 0–4	21.00 21				40.90 38–42
E. scabrus var *scabrus*[a]	2887-5	42	SSYYWW	82		20.35 18–21	0.65 0–3	21.00 21				41.35 39–44
E. scabrus var *scabrus* × *S. cereale*	116	28	SYWR	94	22.27 15–28	0.06 0–1	2.63 0–5	2.69 0–5	0.12 0–2			2.99 0–7
E. scabrus var *plurinervis* × *T. aestivum*	118	42	SYWABD	300	41.14 35–42	0–1	0.42 0–3	0.42 0–3	0.01 0–1			0.43 0–4
E. scabrus var *plurinervis* × *H. vulgare*	130	28	SYWI	82	26.65 22–28		0.66 0–3	0.66 0–3	0.01 0–1			0.68 0–3
		27		18	25.22 23–27		0.89 0–2	0.89 0–2				0.89 0–2
	131	28	SYWI	50	26.60 22–28		0.70 0–3	0.70 0–3				0.70 0–3

[a] J. Torabinejad et al. (1987)

[b] I, Univalent; oII, ring bivalent; rII, rod bivalent; III, trivalent; oIV, ring quadrivalent rIV, rod quadrivalent

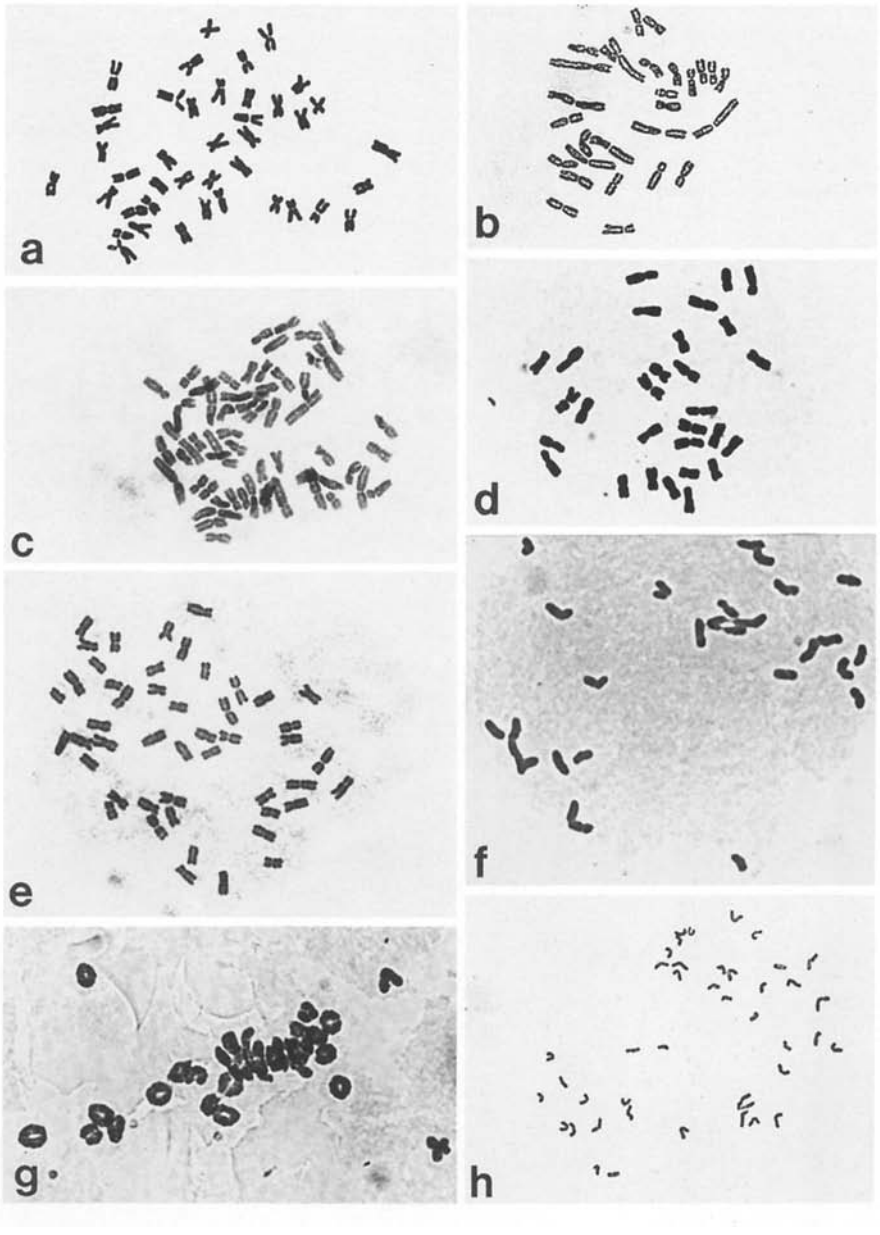

Fig. 1 a–h. Mitotic root-tip chromosomes and metaphase-I chromosome pairing in *E. rectisetus* and F_1 hybrids. **a** *E. rectisetus* (2n = 41), **b** *E. scabrus* var 'scabrus' × rye (2n = 28), **c** spontaneously doubled cell found in a root tip of *E. scabrus* var 'scabrus' × rye (2n = 56), **d** *E. scabrus* var 'plurinervis' × barley (2n = 29), **e** *E. rectisetus* × barley (2n = 48), **f** *E. scabrus* var 'plurinervis' × barley (1 trivalent), **g** spontaneously doubled cell from the same hybrid combination as in **f** (2 rods and 26 rings), **h** *E. scabrus* var 'plurinervis' × wheat (42 univalents)

(R-genome) chromosomes in the former hybrid were about twice the length of the *Elymus* chromosomes, and one root tip had spontaneously doubled to 2n = 56 (Fig. 1 c). Root-tip cells in 6 out of 10 plants of *E. scabrus* var 'plurinervis' × *H. vulgare* unexpectedly varied from 2n = 25 to 2n = 29 (Fig. 1 d), perhaps as a consequence of mitotic nondisjunction of chromatids; the other 4 plants were stable at 2n = 28. The 2 *E. rectisetus* × *H. vulgare* B_{III} hybrids had 2n = 48 (Fig. 1 e) and 2n = 47, presumably seven chromosomes from *H. vulgare* plus an unreduced or nearly unreduced complement from *E. rectisetus*. As expected for a strong apomict, interspecific pollination of *E. rectisetus* also produced numerous maternal offspring.

Chromosome stickiness precluded meiotic analysis of the B_{III} hybrid of *E. rectisetus* with barley; the best-spread cells had little association between *Elymus* and the larger barley chromosomes. All of the B_{II} hybrids had little chromosome association at meiotic metaphase I, although the hybrids with rye had more than those with wheat or barley (Table 1). Exemplary cells are depicted in Figs 1 f–h, and 2 a–c. In Fig. 1 f, from a hybrid of *E. scabrus* var 'plurinervis' × barley, a rare, somewhat heteromorphic trivalent appears, along with 25 univalents. The mean configurations for this hybrid included no ring bivalents and 0.01 trivalent, so there is no significant information on which to judge the pattern of rela-

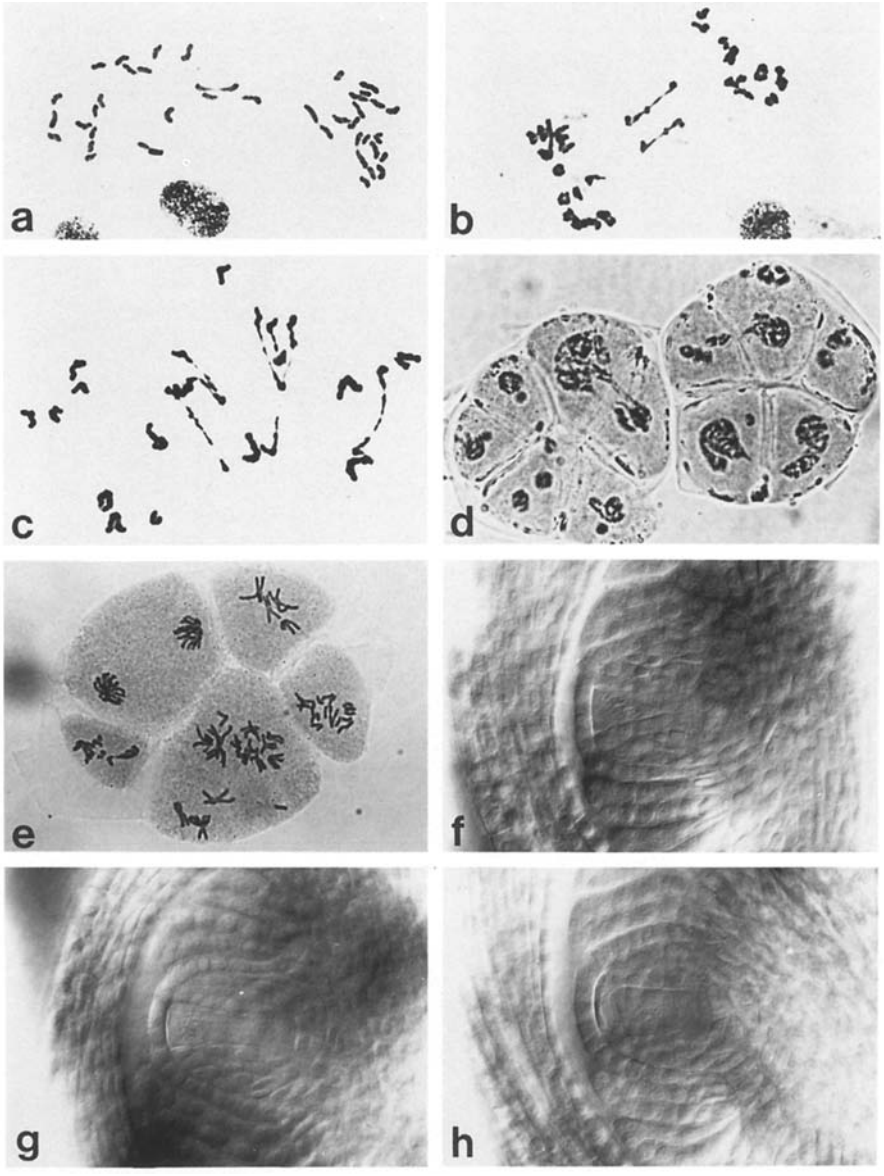

Fig. 2a–h. Meiotic associations or megasporogenesis stages in F_1 hybrids. **a** *E. scabrus* var 'plurinervis' × wheat (2 rod bivalents), **b** *E. scabrus* var 'scabrus' × rye (2 rod bivalents), **c** *E. scabrus* var 'scabrus' × rye (2 trivalents, 3 rod bivalents), **d** *E. scabrus* var 'plurinervis' × barley (interkinetic polyads), **e** *E. scabrus* var 'plurinervis' × wheat (metaphase II), **f–h** cleared ovules of *E. rectisetus* × barley seen with Nomarski DIC optics: **f** meiosis in ovule, **g** apomeiotic division, **h** stretch monad

tive genomic affinity. In Fig. 1 g a spontaneously doubled cell appears from the same hybrid combination, with approximately 28 II (two rods and 26 rings), which indicates an absence of genetically controlled asynapsis or desynapsis in the undoubled hybrid.

Many cells with 42 univalents were observed in the *E. scabrus* var 'plurinervis' hybrid with wheat (Fig. 1 h). Figure 2 a shows two somewhat heteromorphic rod bivalents in the same hybrid combination. Even though there are 50% more chromosomes, the MI association is even lower than in the hybrid with barley, and there is insufficient chiasmatic association on which to assess its pattern of genomic affinity. Pairing is substantially higher, though still low, in the hybrid of *E. scabrus* var 'scabrus' × rye (Fig. 2 b, c). The two definitely heteromorphic rod bivalents in Fig. 2 b indicate an association between rye (large) and *Elymus* (small) chromosomes. Up to two trivalents occur per cell (Fig. 2 c), and the 2:1 ratio of mean frequencies of trivalents to ring bivalents would conform to a completely random pairing of distantly related genomes in a triploid (Sybenga 1988). Nevertheless, the overall chiasma frequency is still too low to reliably distinguish genome relatedness.

Other meiotic abnormalities were observed as well. In the *E. scabrus* var 'scabrus' hybrid with rye, prophase I was sometimes abnormal, with unequal clumps of pachytene chromosomes isolated from one another within the same cell. In *E. scabrus* var 'plurinervis' × barley or

Table 2. Metaphase-I chromosome associations of hybrids and haploids

Hybrid or haploid	2n	Genomes	MI association[a]				Reference
			I	II	III	IV	
T. aestivum × *E. scabrus*	42	ABDSYW	32.83	4.27	0.20	0.02	Ahmad and Comeau (1991)
E. yezoensis × *T. aestivum*	35	ABDSY	33.54	0.73			Sharma and Gill (1983)
E. shandongensis × *T. aestivum*	35	ABDSY	34.49	0.25			Lu and von Bothmer (1989)
E. cylindricus × *T. aestivum*	42	ABDSHY	40.73	0.59	0.02		Yen and Liu (1987)
E. ciliaris × *T. aestivum*	35	ABDSY	26.18	4.25	0.11		Sharma and Gill (1983)
E. dahuricus × *T. aestivum*	42	ABDSHY	38.06	1.93	0.01		Yen and Liu (1987)
E. trachycaulus × *T. aestivum*	35	ABDSH	33.89	0.55			Sharma and Gill (1983)
E. canadensis × *T. aestivum*	35	ABDSH	34.85	0.07			Mujeeb-Kazi and Bernard (1985)
E. canadensis × *T. aestivum*	35	ABDSH	34.57	0.21	0.01		Yen and Liu (1987)
E. caninus × *T. aestivum*	35	ABDSH	33.87	0.51	0.04		Sharma and Baenziger (1986)
E. pseudonutans × *S. cereale*	21	SYR	15.51	2.42	0.18		Lu et al. (1990)
E. shandongensis × *S. cereale*	21	SYR	15.59	2.62	0.08		Lu et al. (1990)
E. semicostatus × *S. montanum*	21	SYR	19.63	0.65			Lu et al. (1990)
E. canadensis × *S. cereale*	21	SHR	19.97	0.53	0.01		Hang and Franckowiak (1984)
H. californicum × *S. anatolicum*	14	HR	13.65	0.18			Gupta and Fedak (1987)
H. bogdanii × *S. cereale* spp. *segetale*	14	SR	12.95	0.52	0.01		Gupta and Fedak (1987)
P. spicata × *S. montanum*	14	SR	12.93	0.52	0.01		Wang (1987)
P. inermis × *S. montanum*	14	SR	13.01	0.45	0.01		Wang (1987)
E. canadensis × *H. vulgare*	21	SHI	19.51	0.53	0.21	0.01	Mujeeb-Kazi and Rodriguez (1982)
H. bogdanii × *E. canadensis*	21	SHI^b-SHH^b	9.98	5.40	0.08		Dewey (1971)
E. patagonicus × *H. vulgare*	28	SHH_1H_2	19.63	2.63	0.80	0.14	Mujeeb-Kazi (1985)
E. semicostatus × *H. bogdanii*	21	SHY	20.00	0.50			Lu and von Bothmer (1990)
E. semicostatus × *H. roshevitzii*	21	SHY	19.96	0.52			Lu and von Bothmer (1990)
E. parviglumis × *H. bogdanii*	21	SHY	20.08	0.46			Lu and von Bothmer (1990)
E. pseudonutans haploid	14	SY	12.82	0.55	0.03		Lu et al. (1990)
E. shandongensis haploid	14	SY	12.59	0.68	0.01		Lu and von Bothmer (1989)
E. semicostatus haploid	14	SY	12.70	0.79	0.02		Lu et al. (1990)
E. dolichatherus haploid	14	SY	12.29	0.81			Lu (1992)
E. brevipes haploid	14	SY	13.48	0.21			Lu (1992)
E. canadensis haploid	14	SH	12.97	0.49			Torabinejad et al. (1987)
E. tsukushiensis haploid	21	SHY	20.61	0.18	0.004	0.002	Sakamoto (1964)

[a] I, Univalent; II, bivalent; III, trivalent; IV, quadrivalent

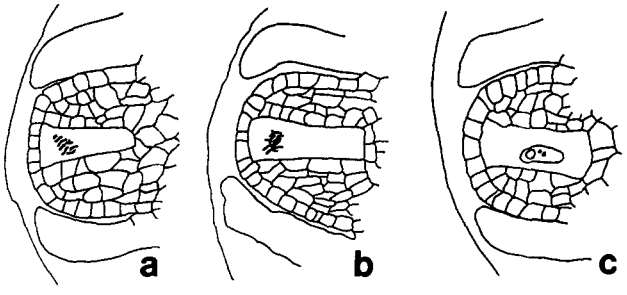

Fig. 3a–c. Drawings of cleared ovules in Fig. 2f–h, respectively

wheat, a multipolar anaphase I led to interkinetic polyads (Fig. 2d), in which the subsequent meiosis II was somewhat asynchronous (Fig. 2e).

Megasporogenesis in the B_{III} hybrid of barley to *E. rectisetus* was strongly apomeiotic, although meiotic metaphase I (MI) was also seen (Fig. 2f, 3a). The apomeiotic division resembled meiosis II, as seen from the metaphase in Fig. 2g and 3b, and was followed by dyad formation and development of the embryo sac from the chalazal dyad member. Tetrads of reduced megaspores were absent, even though the population of ovules was selected by appropriate same-floret pollen stages to find them. Before the apomeiotic division, the megasporocyte nucleus enlarged and elongated (Fig. 2h, 3c), as in apomictic *E. rectisetus* itself (Crane and Carman 1987).

Discussion

Various Northern Hemisphere SSHH, SSHHH'H', and SSYY *Elymus* species have been crossed with wheat and cultivated and wild ryes and barleys. Meiotic data from the literature are collected in Table 2 for some of these hybrids and for *Elymus* haploids. All of the haploids have low pairing, especially the haploid of hexaploid *E. tsukushiensis*. Perhaps because it has more genomes to regulate, it is adapted to even tighter genetic pairing

regulation than the tetraploids. A hybrid of *E. canadensis* with *H. vulgare* (Mujeeb-Kazi and Rodriguez 1982) had insignificantly more chiasmata per cell than the *E. canadensis* haploid (Torabinejad et al. 1987), indicating that there was little similarity between the *Elymus* H genome and the I genome of barley. Hybrids of *E. canadensis* with *H. bogdanii* (*Critesion bogdanii*) have much higher pairing, with up to seven bivalents per cell, indicating a much closer relationship between the *H. bogdanii* H genome and the H genome of *Elymus* (Dewey 1971). Hybrids of *E. patagonicus* (SSHHH'H') with *H. vulgare* had 2.63 total bivalents per cell (Mujeeb-Kazi 1985), which was attributed to autosyndesis of H genomes.

Hybrids of wheat with SSHH or SSH^vH^v *Elymus* species likewise have little mean pairing per cell: 0.55 bivalents with *E. trachycaulus* (Sharma and Gill 1983), 0.21 bivalents (Yen and Liu 1987) or 0.07 bivalents (Mujeeb-Kazi and Bernard 1985) with *E. canadensis*, and 0.51 bivalents with *E. caninus* (Sharma and Baenziger 1986). Wheat hybrids with SSYY *Elymus* were similarly non-pairing: 0.73 bivalents with *E. yezoensis* (Sharma and Gill 1983), 0.25 bivalents with *E. shandongensis* (Lu and von Bothmer 1989), 0.59 bivalents with *E. cylindricus* (Yen and Liu 1987), and 1.93 bivalents with the hexaploid *E. dahuricus* Yen and Liu (1987). In contrast, higher pairing has been observed in wheat hybrids with *E. scabrus* (Ahmad and Comeau 1991) and *E. ciliaris* (Sharma and Gill 1983). This may be due homeologous pairing of wheat genomes. The wheat hybrids with *E. canadensis* and *E. shandongensis* have even less pairing than their *Elymus* parents, suggesting that the *Ph1* system is fully operative and perhaps stronger than the native pairing regulation in *Elymus*.

Hybrids of rye with *Elymus* and *Hordeum* (*Critesion*) species usually have significantly greater pairing than that found in haploid *Elymus*, although the hybrid with *E. canadensis*, with 0.53 bivalents per cell (Hang and Franckowiak 1984), was an exception. Hybrid per-cell bivalent frequencies were 2.42 with *E. pseudonutans* and 2.62 with *E. shandongensis* (Lu et al. 1990) versus 2.63 with *E. scabrus* var 'scabrus' in the present study. This level of pairing is much higher than what is found in the available haploids of *Elymus* species. It also considerably exceeds that found in hybrids between *Secale* and diploid SS or HH species: 0.45–0.52 bivalents per cell with *Pseudoroegneria inermis* and *P. spicata* (Wang 1987). Only 15–30% of the total pairing in rye-*Critesion* hybrids is between the R and H genomes (Gupta and Fedak 1987), and only 7–8% of that in *Elymus*-rye hybrids involves the large rye chromosomes with the smaller chromosomes of *Elymus* (Lu et al. 1990). These lines of evidence indicate promotion of autosyndetic pairing by gene(s) on the rye genome; perhaps this promotion does not overcome the pairing regulator in *E. canadensis*, although it does partially overcome the *Ph1* system in wheat (Feldman 1968; Dvorak 1977; Cuadrado et al. 1991). A final alternative, that the third genome of *E. scabrus* is related to R, seems unlikely in that the pairing is increased almost identically in the aforementioned rye hybrids to tetraploid *Elymus*. Moreover, the third genome is found to be from *Australopyrum* species endemic to Australia (Torabinejad and Mueller in press).

The first step in a wide-hybrid breeding program is to obtain viable hybrids. Hormonal treatments pre- and post-anthesis with Giberellic acid (GA_3) and 2.4-D, followed by embryo rescue and culture on appropriate media, permit the production of more and more remote hybrids in the Triticeae. Dewey (1984) anticipated the low pairing observed in Australian *Elymus* hybrids to cereal Triticeae, and remarked, "even if the hybrids can be obtained, that may be the simplest aspect of the intended transfer of apomixis from *E. scabrus* (sic) to *Triticum*". Critical unresolved issues include female fertility of the hybrids, transmissivity and expression of apomixis in F_1 and backcross hybrids, and possible linkage of apomixis to agronomically undesirable dominant genes in *E. rectisetus*. Promising techniques include the development of addition and substitution lines and the use of ionizing radiation (Knott 1987) and molecular genetic engineering. There is also a chance that spontaneous translocations occur between the *Elymus* and cereal Triticeae chromosomes. Obviously, much work needs to be done, but the hybrids obtained in the present study are an encouraging sign that the transfer of apomixis to cereal Triticeae is possible.

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References

Ahmad F, Comeau A (1991) Production, morphology, and cytogenetics of *Triticum aestivum* (L.) Thell × *Elymus scabrus* (R. Br.) Löve intergeneric hybrids obtained by in ovulo embryo culture. Theor Appl Genet 81:833–839

Crane CF, Carman JG (1987) Mechanisms of apomixis in *Elymus rectisetus* from Eastern Australia and New Zealand. Am J Bot 74:477–496

Cuadrado C, Romero C, Lacadena JR (1991) Meiotic pairing control in wheat-rye hybrids. II. Effect of rye genome and rye B-chromosomes and interaction with the wheat genetic system. Genome 34:76–80

Dewey DR (1971) Synthetic hybrids of *Hordeum bogdanii* with *Elymus canadensis* and *Sitanion hystrix*. Am J Bot 58:902–908

Dewey DR (1984) The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. In: Gustafson JP (ed) Gene manipulation in plant improvement. Plenum Press, New York, p 209–279

Dvorak J (1977) Effect of rye on homoeologous chromosome pairing in wheat × rye hybrids. Can J Genet Cytol 19:549–556

Feldman M (1968) Regulation of somatic association and meiotic pairing in common wheat. In: Finlay KW and Sheperd KW (eds) Proc 3rd Int Wheat Genet Symp. Canberra Australia, pp 169–178

Gupta PK, Fedak G (1987) Preferential intragenomic chromosome pairing in two new diploid intergeneric hybrids between *Hordeum* and *Secale*. Genome 29:594–597

Hair JB (1956) Subsexual reproduction in *Agropyron*. Heredity 10:129–160

Hang A, Franckowiak JD (1984) Cytological analysis of an *Elymus canadensis* × *Secale cereale* hybrid. J Hered 75:235–236

Hanna WW, Bashaw EC (1987) Apomixis: its identification and use in plant breeding. Crop Sci 27:1136–1139

Knott DR (1987) Transferring alien genes to wheat. In: Heyne EG (ed) Wheat and wheat improvement. ASA Inc CSSA Inc SSSA Inc Publ, Madison, Wisconsin, USA, pp 462–471

Löve A, Connor HE (1982) Relationships and taxonomy of New Zealand wheatgrasses. N Z J Bot 20:169–186

Lu BR (1992) Dihaploids of *Elymus* from the interspecific crosses *E. dolichatherus* × *E. tribeticus* and *E. brevipes* × *E. panormitanus*. Theor Appl Genet 83:997–1002

Lu BR, Bothmer R von (1989) Cytological studies of a dihaploid and hybrid from intergeneric cross *Elymus shandogenesis* × *Triticum aestivum*. Hereditas 111:231–238

Lu BR, Bothmer R von (1990) Intergeneric hybridization between *Hordeum* and Asiatic *Elymus*. Hereditas 112:109–116

Lu BR, Salomon B, Bothmer R von (1990) Cytogenetic studies of progeny from the intergeneric crosses *Elymus* × *Hordeum* and *Elymus* × *Secale*. Genome 33:425–432

Mujeeb-Kazi A (1985) Cytogenetics of a *Hordeum vulgare* × *Elymus patagonicus* hybrid (n = 4x = 28). Theor Appl Genet 69:475–479

Mujeeb-Kazi A, Bernard M (1985) Cytogenetics of intergeneric *Elymus canadensis* × *Triticum aestivum* hybrids (n = 5x = 35, SHABD) and their backcross progenies with *T. aestivum*. Z Pflanzenzuecht 95:50–62

Mujeeb-Kazi A, Miranda JL (1985) Enhanced resolution of somatic chromosome constrictions as an aid to identifying intergeneric hybrids among some Triticeae. Cytologia 40:701–709

Mujeeb-Kazi A, Rodriguez R (1982) Cytogenetics of hybrids of *Elymus canadensis* × *Hordeum vulgare*. J Hered 73:77–79

Sakamoto S (1964) Cytogenetic studies in the tribe Triticeae. I. A polyhaploid plant of *Agropyrōn tsukushiensis* var 'transiens' (OHWI) found in a state of nature. Jpn J Genet 39:393–400

Sharma HC, Baenziger PS (1986) Production, morphology, and cytogenetic analysis of *Elymus caninus* (*Agropyron caninum*) × *Triticum aestivum* F_1 hybrids and backcross-1 derivatives. Theor Appl Genet 71:750–756

Sharma HC, Gill BS (1983) New hybrids between *Agropyron* and wheat. 2. Production, morphology and cytogenetic analysis of F_1 hybrids and backcross derivatives. Theor Appl Genet 66:111–121

Sybenga J (1988) Models for estimating preferential pairing and recombination in triploid hybrids. Genome 30:745–757

Torabinejad J, Mueller RJ, Genome constitution of the Australian hexaploid grass, *Elymus scabrus* (Poaceae: Triticeae). Genome (in press)

Torabinejad J, Carman JG, Crane CF (1987) Morphology and genome analyses of interspecific hybrids of *Elymus scabrus*. Genome 29:150–155

Torabinejad J, Carman JG, Crane CF (1989) Further studies on the genomic composition of Australian *Elymus* (Poaceae). Agron Abstr 1989:102

Wang RR-C (1987) Diploid perennial intergeneric hybrids in the tribe Triticeae. III. Hybrids among *Secale montanum*, *Pseudoroegneria spicata*, and *Agropyron mongolicum*. Genome 29:80–84

Yen Y, Liu D (1987) Production, morphology, and cytogenetics of intergeneric hybrids of *Elymus* L. species with *Triticum aestivum* L. and their backcross derivatives. Genome 29:689–694

Zenkteler M, Nitzsche W (1984) Wide hybridization experiments in cereals. Theor Appl Genet 68:311–315