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A self-fertile trigeneric hybrid, *Triticum aestivum* × *Agropyron michnoi* × *Secale cereale*

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Abstract. Trigeneric hybrids between the (*Triticum aestivum* × *Agropyron michnoi*) F_1 (CM, $2n = 5x = 35$; ABDPP) and two winter rye (*Secale cereale* L., $2n = 2x = 14$; RR) cultivars, 'Wugong 774' and 'AR-132', were synthesized. Such trigeneric hybrids could be used to transfer resistance genes for powdery mildew from rye to CM and subsequently to common wheat and to identify (1) the effects of the P genome of *Agropyron* on the self-fertility of the hybrids and (2) the differences in genetic background between rye cultivars with marked differences in pollinating habit. The trigeneric hybrids varied widely in morphology and showed a high level of resistance to such diseases as barley yellow dwarf virus (BYDV), stripe rust, leaf rust, stem rust, and powdery mildew. Selfed and many backcross derivatives were obtained from the trigeneric hybrids. The results indicated that rye cvs 'Wugong 774' and 'AR132' arose from different gene pools and that the P genome of *Agropyron* carries gene(s) responsible for chromosome segregation, leading to functional gamete formation and self-fertility of the hybrids. The F_2 and BC_1 plants could be obtained in two ways – fusion of the unreduced gametes and the assumed apomixis of unreduced female gametes in the trigeneric hybrid plant II-4 – which indicates that this trigeneric hybrid may be a special genetic stock. Chromosome pairing in the trigeneric hybrids and ways of producing wheat/rye and wheat/*Agropyron* translocations are discussed.

Key words: Trigeneric hybrids – Self-fertility – Gene pool – Chromosome segregation – F_2 and BC_1 derivatives

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Introduction

Agropyron species have been found to possess traits that are potentially valuable for the improvement of wheat; these include tolerance to drought, low temperature and salinity, and resistance to diseases (Dong et al. 1992). Intergeneric hybrids have been synthesized in attempts to transfer these desirable traits into bread wheat (*Triticum aestivum* L., $2n = 6x = 42$; AABBDD) (Chen et al. 1989, 1990, 1992; Li and Dong 1990, 1991; Limin and Fowler 1990; Ahmad and Comeau 1991; Jauhar 1992). Meiotic studies of these intergeneric hybrids have shown that the P genome of *Agropyron* contains the *Ph* suppressor gene(s) (Chen et al. 1989, 1992; Li and Dong 1990; Ahmad and Comeau 1991) but that the activity of the *Ph* suppressor gene(s) varies among hybrids (Ahmad and Comeau 1991; Jauhar 1992), leading some investigators to believe that homoeology between the P genome and wheat genomes may exist (Li and Dong 1990; Limin and Fowler 1990; Jauhar 1992). If the latter is true, the homoeologous pairing of chromosomes of the P genome with wheat chromosomes should be sufficient to facilitate the transfer of desirable genes of *Agropyron* into wheat.

Although backcross derivatives were difficult to obtain from the hybrids of wheat × *Agropyron* (average seed set below 2%) (Chen et al. 1990, 1992; Ahmad and Comeau 1991), our hybrids produced seeds easily by backcrossing F_1 plants to common wheat (seed sets above 15%), and all F_1 hybrids were partially self-fertile (Li and Dong 1990, 1991). In the regenerated plants derived from immature inflorescences of these hybrids, selfed seed sets could reach 3% or higher (Li et al. 1992; Li and Dong 1993). The reasons for the higher fertility of these hybrids are complex (Li and

Dong 1990, 1993a). In addition, the irregular disjunction of chromosomes at anaphase I and the formation of unequally sized and odd-num-bered cells at quartet in those intergeneric hybrids indicated that the P genome might carry gene(s) responsible for regular chromosome disjunction and, thereby, increased vital gamete formation and fertility (Li et al. 1992).

The hybrids between *T. aestivum* cv 'Chinese Spring' (CS) and *A. michnoi* ($2n = 4x = 28$; PPPP), their F_2, and BC_1 derivatives, whether they were grown in the greenhouse or in the field, exhibited a high level of resistance to barley yellow dwarf virus (BYDV), stripe rust, leaf rust, and stem·rust. However, they were susceptible to wheat powdery mildew and had a poor tolerance to cold even though they contained the P genome of *A. michnoi*, a species which is very tolerant to cold. An attempt to produce variations in wheat powdery mildew resistance and cold tolerance from regenerated plants derived from callus induced from immature inflorescences of the hybrids was not successful (unpublished).

Rye (*Secale cereale* L., $2n = 2x = 14$; RR) is an important source of wheat powdery mildew resistance and is also extremely winter hardy (Heun and Friebe 1990; Izdebski 1992). An elaborate cytogenetic analysis has shown that homoeology between rye chromosomes and wheat exists (Naranjo and Fernandez-Rueda 1991). Therefore, it is possible to transfer genes for powdery mildew resistance and cold tolerance first from rye to intergeneric hybrids and then further to wheat through hybridization of the CS × *A. michnoi* hybrids containing the *Ph* suppressor genes with rye cultivars.

Two winter rye cultivars, 'Wugong 774' and 'AR132', both immune to powdery mildew but different in pollinating habits, were selected as male parents for crossing with the regenerated plants of CS × *A. michnoi* intergeneric hybrids in an attempt to: (1) transfer resistance genes for powdery mildew from rye to the intergeneric hybrids and further to wheat; (2) identify the effects of the P genome on self-fertility in hybrids; and (3) compare differences in genetic background between rye cultivars.

This paper presents data on the morphology, cytology, and fertility of *Triticum aestivum* × *Agropyron michnoi* × *Secale cereale* trigeneric hybrids and their F_2 and BC_1 progenies.

Materials and methods

The production and a cytogenetic study of the intergeneric hybrids between *Triticum aestivum* cv 'Chinese Spring' (CS) and *Agropyron michnoi* have been described previously (Li and Dong 1991). Plants regenerated from calli induced from immature inflorescences of a CS × *A. michnoi* hybrid and the morphological and genetic variation have also been described in detail by Li and Dong (1993b).

In the summer of 1990, the regenerated plants (CM) ($2n = 5x = 35$; ABDPP) of a CS × *A. michnoi* hybrid were used as female parent in a cross with two winter rye cultivars,'Wugong 774' and 'AR132', in the field. 'Wugong 774' is a cross-pollinated local variety from Wugong, Shaanxi Province, China. Through continuous selection for self-fertility for 6 years, 'AR132', with a self seed set above 80%, was obtained from rye cv 'Kustro', which was introduced from the CIMMYT, Mexico by the Institute of Crop Breeding and Cultivation, Chinese Academy of Agricultural Sciences, China. Spikes of CM were emasculated before pollination. One-half of the spikes of the same plant of CM used as female parent were pollinated by 'Wugong 774' and the other half by 'AR132', so that differences in genetic background between rye cultivars could be compared. The methods used in this experiment, such as pollination, immature embryo rescue, mitotic and meiotic studies have been described in detail by Li and Dong (1990, 1991).

All of the plantlets of the trigeneric hybrids were transplanted into the field at the end of September. The spikes of the trigeneric hybrids were emasculated before being pollinated by common wheat cultivars such as 'Han 38', 'Xiaoyan 6', and '914127' or rye cv 'Jingai 1' as recurrent parents. To investigate the self-fertility of trigeneric hybrids, spikes headed out before June were bagged for self-pollination, but those that emerged after June were open-pollinated since at this time wheat and rye had been harvested.

Results

Production

The number of seeds obtained, embryos excised, and plantlets of trigeneric CM × rye hybrid produced in the field are given in Table 1. Trigeneric hybrids between CM and rye were obtained easily. However, there was a marked difference in crossability measured by seed set when different rye cultivars were used as the male parent.

Table 1. Production of trigeneric hybrids between (*T. aestivum* cv 'Chinese Spring' × *A. michnoi*) F_1 (CM) and *Secale cereale*

Hybrid combination	Number of pollinated florets	Seeds		Embryos		Plantlets	
		Number	%	Number	%	Number	%
CM × *S. cereale* cv Wugong 774	286	15	5.3	12	4.2	9	3.1
CM × *S. cereale* cv AR132	277	63	22.7	53	19.1	48	17.3
Total	563	78	13.8	65	11.5	57	10.1

With 'Wugong 774' as the male parent, 15 seeds (5.3%) were obtained, whereas the pollination of CM by 'AR132' yielded 63 hybrid seeds (22.7%). Most of the hybrid seeds were shrivelled, and in all cases the endosperm was poorly developed or sometimes absent altogether. After the embryos had been rescued, 9 and 48 trigeneric hybrid plantlets were obtained from the crosses of CM with 'Wugong 774' and 'AR132', respectively.

Morphology

By the following spring, 12 of the 48 plants obtained from the cross of CM × 'AR132' had died as a result of a lack of winter hardiness; the remaining 36 plants also exhibited a certain degree of cold injury. The 9 plants obtained from the cross of CM × 'Wugong 774' developed well through the winter, indicating that those plants had a high level of cold tolerance.

Morphological variation was very narrow among hybrid plants obtained from both hybrid combinations. The leaves of the hybrid seedlings were wide and long, resembling those of common wheat. Heading began in May and lasted 2–3 months, a character of *A. michnoi.* Plant height ranged from 57 to 124 cm. Spike morphology varied widely, showing some phenotypes that could not be found in their parents. Additional spikelets in some of the rachis nodes in the middle parts of ears, a character found in a few CM plants, were observed in a few trigeneric hybrids. The awns of the spikes of the CM plants and rye cultivars differed in length, as did those of the trigeneric hybrids involving these parents. Hairy neck, a character inherited from rye, was present in 60% of the trigeneric hybrids. In general, the trigeneric hybrids were substantially more wheat than rye and *A. michnoi* parents with regard to plant morphology. Typical spikes of the trigeneric hybrids are shown in Fig. 1a, b. Morphological characteristics of the trigeneric hybrids are shown in Table 2.

With respect to disease resistance, the trigeneric hybrids, like their parent CM, exhibited a high level of resistance to diseases such as BYDV, stripe rust, leaf rust, and stem rust. However, the trigeneric hybrids differed from their parent CM for wheat powdery mildew reactions and showed an absolute resistance to all of the powdery mildew isolates tested.

Cytology

The parental CM lines were investigated by somatic chromosome counts and all showed 2n = 35. The parental rye cultivars, 'Wugong 774' and 'AR132', had 14 somatic chromosomes and no B chromosomes. An examination of the root tips from all of the trigeneric hybrid plants revealed that the chromosome number varied from 20 to 27. In the hybrids of CM × 'Wugong 774' (Combination I), the number of somatic chromosomes varied from 20 to 23 although most of the hybrids had 23. The number of somatic chromosomes in the hybrids of CM × 'AR132' (Combination II) varied from 25 to 27, with most of the hybrids having 26.

From the frequency distribution of chromosome number in these trigeneric hybrids, 5 and 10 plants, respectively, from the two crosses were analyzed for meiotic behavior. Chromosome pairing and range values in pollen mother cells (PMCs) in these trigeneric hybrids are given in Table 3, and some representative

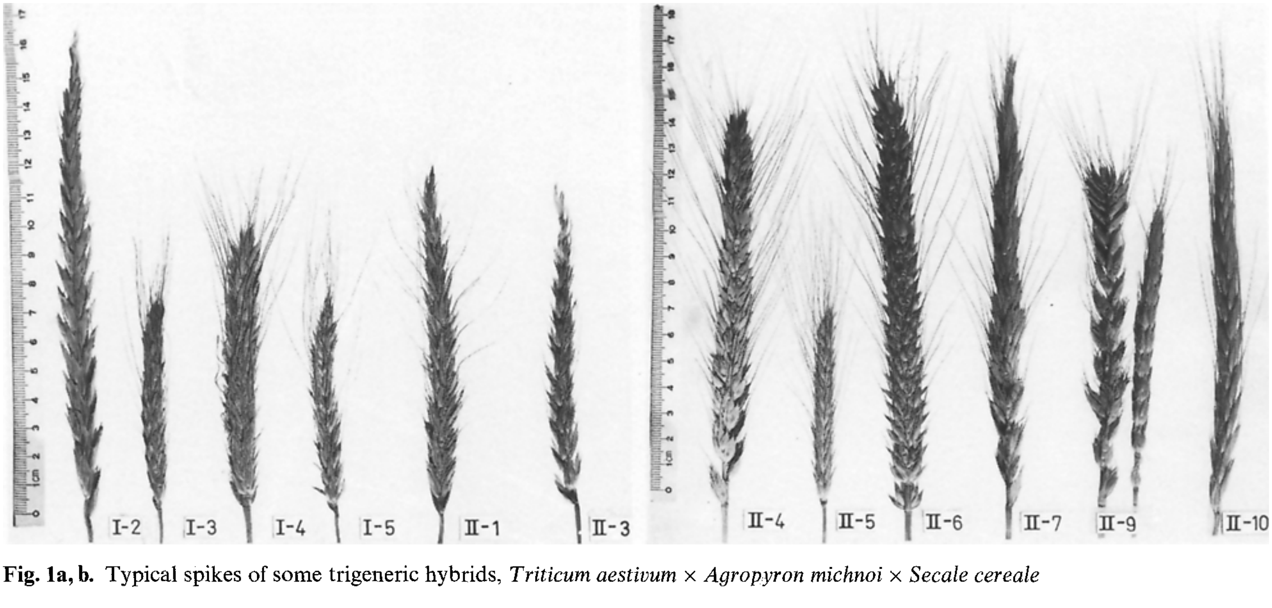


Fig. 1a, b. Typical spikes of some trigeneric hybrids, *Triticum aestivum* × *Agropyron michnoi* × *Secale cereale*

Table 2. Morphological characteristics of trigeneric hybrids between (*T. aestivum* cv 'Chinese Spring' × *A. michnoi*) F_1 (CM) and *Secale cereale*

Hybrid combination	Plant number	Chromosome number	Plant height (cm)	Spike length (cm)	Hairy neck[b]	Number of spikelets per spike	Awn (cm)
CM × Wugong 774	I-1	21	100	14.0	–	24	2.0
	I-2	22	109	17.0	+	34	2.0
	I-3	23	51	8.0	+	25	5.5
	I-4	23	94	8.0	+	26	10.0
	I-5	23	113	9.0	+	28	6.5
CM × AR132	II-1	25	98	11.5	–	22	6.0
	II-4	25	67	8.0	–	18	2.7
	II-3	26	75	12.0	–	22	5.5
	II-4	26	89	15.0	+	28	8.0
	II-5	26	85	9.0	+	27	7.0
	II-6	26	90	16.5	+	34	6.0
	II-7[a]	26	95	17.0	–	30	4.3
	II-8	26	90	16.0	+	34	5.0
	II-9[a]	27	77	12.5	–	27	4.5
	II-10	27	108	15.0	–	26	5.7

[a] These plants had additional spikelets in some rachis nodes in the middle parts of spikes

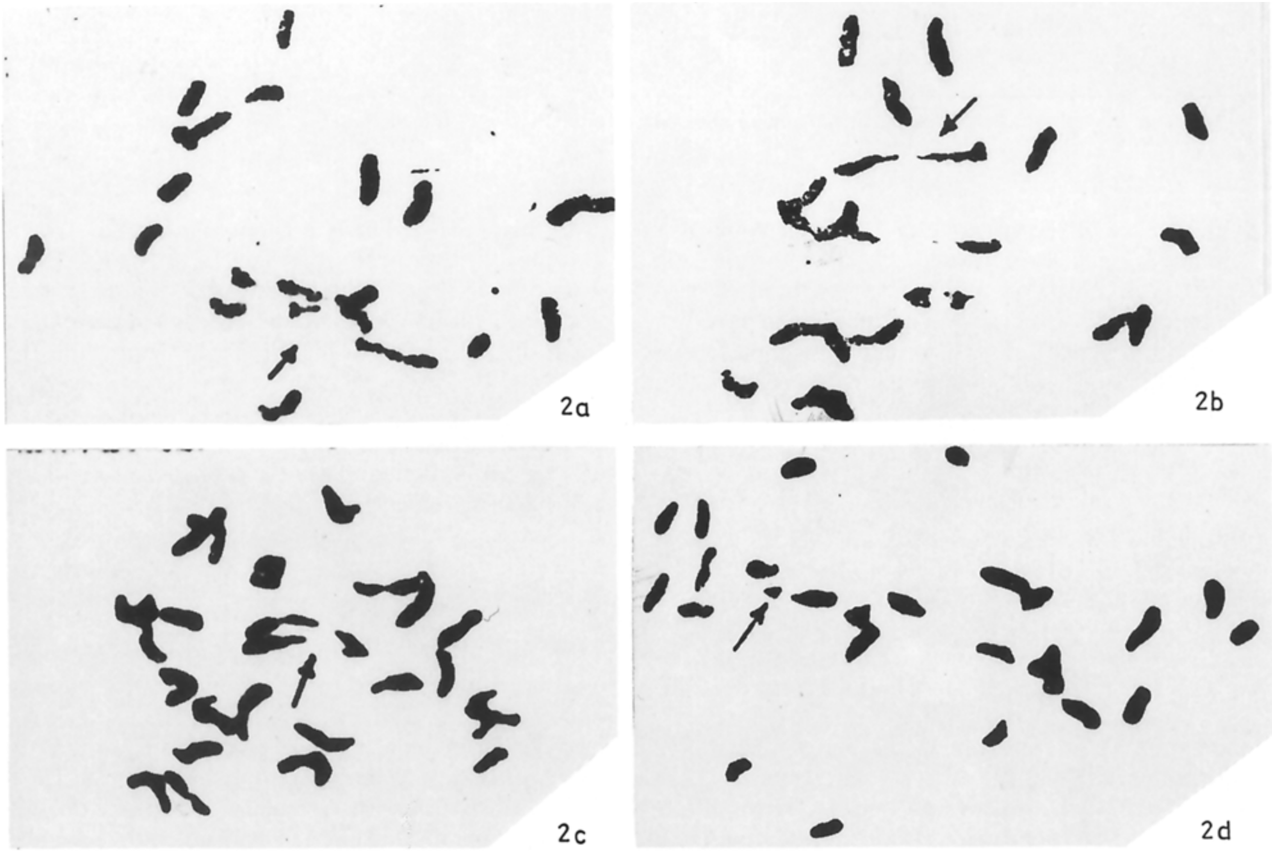
[b] +, Plant had a hairy neck; –, plant did not have a hairy neck

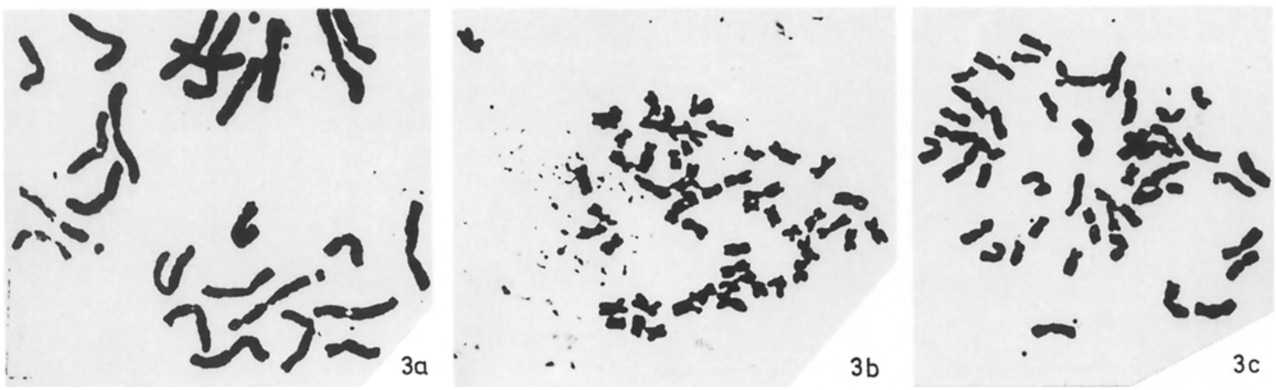
Table 3. Mean chromosome pairing and range values (in brackets) in trigeneric hybrids between (*T. aestivum* cv 'Chinese Spring' × *A. michnoi*) F_1 (CM) and *S. cereale*

Plant number	Chromosome number	Number of cells scored	Mean chromosome pairing per cell							
			I	Rod II	Ring II	Total II	III	IV	V	VI
CM	35	125	5.24	3.13	7.14	10.27	1.12	0.75	0.26	0.17
			(3–11)	(0–6)	(5–14)	(6–16)	(0–2)	(0–2)	(0–2)	(0–1)
Wugong 774	14	57	0.04	0.70	6.28	6.98				
			(0–2)	(0–3)	(4–7)	(6–7)				
AR132	14	32	0.02	1.52	5.47	6.99				
			(0–2)	(0–3)	(4–7)	(6–7)				
I-1	21	85	17.14	1.75	0.12	1.87	0.04			
			(11–21)	(0–5)	(0–1)	(0–5)	(0–1)			
I-2	22	80	19.31	1.11	0.10	1.21	0.09			
			(14–22)	(0–4)	(0–1)	(0–4)	(0–1)			
I-3	23	115	18.67	1.73	0.24	1.97	0.13			
			(16–23)	(0–3)	(0–1)	(0–3)	(0–1)			
I-4	23	158	20.32	1.05	0.17	1.12	0.08			
			(15–23)	(0–4)	(0–1)	(0–4)	(0–1)			
I-5	23	107	18.16	1.62	0.45	2.07	0.05			
			(13–23)	(0–4)	(0–2)	(0–5)	(0–1)			
II-1	25	50	24.98	0.01		0.01				
			(24–25)	(0–1)		(0–1)				
II-2	25	50	24.92	0.04		0.04				
			(24–25)	(0–1)		(0–1)				
II-3	26	50	25.76	0.12		0.12				
			(24–26)	(0–1)		(0–1)				
II-4	26	50	26							
II-5	26	50	25.68	0.16		0.16				
			(24–26)	(0–1)		(0–1)				
II-6	26	45	21.53	1.82	0.22	2.04	0.13			
			(18–26)	(0–4)	(0–2)	(0–5)	(0–1)			
II-7	26	50	25.92	0.04		0.04				
			(25–26)	(0–1)		(0–1)				
II-8	26	50	25.84	0.08		0.08				
			(24–26)	(0–1)		(0–1)				
II-9	27	50	26.88	0.06		0.06				
			(25–27)	(0–1)		(0–1)				
II-10	27	50	27							

PMCs are shown in Fig. 2a–d. Mean bivalent (rod and ring) frequencies varied from 1.12 to 2.07 per cell in plants from combination I and from 0 to 2.04 in plants from combination II. Pairing frequencies, including bivalents and trivalents, were much higher in combination I than those in combination II except for plant II-6. In general, the major proportion of the chromosome complement remained unpaired in all of the trigeneric hybrids. Nevertheless, some of the rod bivalents were clearly heteromorphic and often separated precociously.

Other chromosome irregularities were also noted in the meiocytes of the trigeneric hybrids, particularly





Figs. 2 and 3. **2** Cytological characteristics in pollen mother cells of trigeneric hybrids, *Triticum aestivum* × *Agropyron michnoi* × *Secale cereale*. **a** I-4, 15 I + 3 rod II. Note heteromorphic rod bivalent and precocious separation (*arrow*); **b** I-3, 17 I + 2 rod II + 1 ring II. Note heteromorphic rod bivalent (*arrow*); **c** II-6, 23 I + 1 III; **d** II-6, 25 I + 1 fragment (*arrow*), showing fragment present in some cells at meiosis. **3** Root-tip cells in the F_2 and BC_1 plants produced from the selfed and backcross seeds harvested from the same hybrid, plant II-4 ($2n = 26$). **a, b** F_2 plants, $2n = 26$ and $2n = 52$, respectively, showing unreduced gametes and apomixis occurred in the plant II-4; **c** BC_1 plant, $2n = 47$, showing that this plant has all 26 chromosomes of plant II-4 plus 21 wheat chromosomes

Table 4. Seed set upon selfing and backcrosses for trigeneric hybrids between (*T. aestivum* cv 'Chinese Spring' x *A. michnoi*) F_1 (CM) and *S. cereale*

Hybrid combination	Number of chromosomes in female parent	Number of pollinated florets	Seed		Plump (P)/ shrivelled (S)	Number of germinated seeds
			Number	%		
I-4 selfed	23	378	1	0.3	P	0
I-5 selfed	23	436	4	0.9	P and S	0
II-3 selfed	26	408	2	0.5	P	0
II-4 selfed	26	348	5	1.4	P and S	2
II-5 selfed	26	412	2	0.5	P	1
I-3 x 914127	23	146	4[a]	2.7	S	
II-4 x Xiaoyan 6	26	84	4	4.8	P	1

[a] The immature embryos from those seeds were cultured on MS medium for callus induction and plant regeneration

in the spikes of the small tillers. These irregularities included lagging chromosomes, dividing univalents at anaphase I, chromosome bridges, chromatid fragments, and the formation of unreduced gametes by two ways. The mechanism of unreduced gamete formation in this study will be reported in detail in another paper.

Fertility

Although spikes of the trigeneric hybrids were repollinated and treated with 75 ppm GA_3 the next day, only 8 seeds were obtained from all of the combination of backcrosses of common wheat I-3 x '914127' and II-4 x 'Xiaoyan 6' with seed set of 2.7% and 4.8%, respectively. No backcross seed was obtained from over 400 florets pollinated by rye cv 'Jingai 1'. The 4 backcross seeds from II-4 x 'Xiaoyan 6' reached maturity and were plump, whereas the other 4 backcross seeds from I-3 x '914127' failed to develop, with 1 of them drying out 16 days after pollination. Dissection revealed that while the embryos were well differentiated in these seeds, the endosperm had not developed.

No seed was obtained from the bagged spikes, but 14 plump seeds were obtained from the open-pollinated spikes involving 5 plants. The highest seed set was 1.4%, and considerable variation was noted for seed size and morphology. The seed set of trigeneric hybrids selfed and backcrossed with common wheat and rye are given in Table 4.

F_2 and BC_1 derivatives

All selfed and backcross seeds except for the 4 backcross seeds from I-3 x '914127' were germinated on moist filter paper at room temperature. Most of the seeds did not germinate and only 1 backcross and 3 selfed seeds produced plants (Table 4).

Among the germinated seeds, 2 selfed seeds and 1 backcross seed with common wheat were from the same plant, II-4. These 2 F_2 plants had 26 and 52 chromosomes, respectively (Fig. 3a–b). The BC_1 plant was $2n = 47$ (Fig. 3c), indicating that this BC_1 plant contained all 26 chromosomes of its female parent, plant II-4. The other F_2 plant obtained from plant II-5 had $2n = 49$.

Two of the 4 immature embryos from I-3 x '914127' formed compact calli on MS medium. As a result, 1 and 32 regenerated plants were obtained from these 2 embryo calli, respectively.

Discussion

With the advances in hybridization techniques and embryo culture, many trigeneric hybrids in *Triticeae* have been produced by crossing the intergeneric hybrids or amphiploid with other species (Cabrera and Martin 1992; Li et al. 1993), by crossing barley (*Hordeum vulgare* L.) with triticale (x *Triticosecale* Wittmack) (Balyan and Fedak 1989), or by crossing triticale with other amphiploids involving wheat (Fernandez-Escobar and Martin 1989). Trigeneric combinations in this tribe are of particular interest when studying genetic relationships among different genomes present in the same cytoplasmic background. The production of trigeneric hybrids also provides a possibility to introduce alien genes into cultivated species when selfed or backcross seeds can be obtained.

In the study reported here, a new trigeneric combination involving *Triticum*, *Agropyron*, and *Secale* was produced in which the genetic effect of both rye cultivars could be compared in the same background. The results are very similar to those reported earlier (Li et al. 1993) and suggest that both of the rye cultivars, 'Wugong 774' and 'AR132', may come from entirely different gene pools. 'Wugong 774' is a cross-pollinated local variety with genetic diversity; 'AR132' is an improved variety with a high frequency of selfing (above 80%) and relatively stable.

Although some bivalents, including ring bivalents and few trivalents, were observed in all of the plants from combination I and in plant II-6 from combination II, the major proportion of the chromosome complement were unpaired in all of the trigeneric hybrids of CM with 'Wugong 774' and 'AR132'. The expected distribution of chromosomes in the trigeneric hybrids between CM and rye would include 7 from the P genome, 7 from the R genome, and the remaining 6–13 chromosomes from the A, B, and D genomes at random. However, not all of the trigeneric hybrids contained a complete P genome since it has been shown that there is a certain degree of divergence between two P genomes in the tetraploid species of *Agropyron* (Li and Dong 1991; Ahmad and Comeau 1991; Jauhar 1992) and homoeology may exist between the P and the wheat genomes (Li and Dong 1990; Limin and Fowler 1990; Jauhar 1992). Therefore, the expected chromosome pairing frequency should be higher than the value observed in the trigeneric hybrids. Other factors also may promote a higher pairing frequency than the value observed in the trigeneric hybrids. Wang (1987) found that chromosomes between the P genome and the R genome exhibited 0.51 II + 0.03 III + 0.004 IV at metaphase I. A higher chromosome pairing frequency (4.92 II + 1.80 III + 0.04 IV) was present in hybrids between CS carrying the *Ph* suppressor gene and rye (Dhaliwal et al. 1977). In addition, the female parent, CM plants, of the trigeneric hybrids has also been found to have a high frequency of multivalents (1.12 III + 0.75 IV + 0.26 V + 0.17 VI) (Li and Dong 1993b). However, the P genome of *Agropyron* may carry an asynaptic or desynaptic gene (Limin and Fowler 1990) in addition to the *Ph* suppressor gene(s) (Chen et al. 1989, 1992; Li and Dong 1990; Ahmad and Comeau 1991). Similarly, rye is known to have a polygenetic system that controls the extent of pairing between homoeologous chromosomes of wheat (Dvorak 1977). Thus, a satisfactory explanation of precisely why chromosome pairing occurred in the trigeneric hybrids is difficult.

On the other hand, low chromosome pairing may lead to the formation of unreduced gametes in the trigeneric hybrids. Wagenaar (1968), Maan and Sasakuma (1977), and Islam and Shepherd (1980), all working with intergeneric hybrids within *Triticeae*, concluded that unreduced gametes almost exclusively arise from spore mother cells showing the highest degree of desynapsis. Similarly, the self-fertile trigeneric hybrids of *T. aestivum* × *A. desertorum* × *S. cereale* also exhibited very little chromosome pairing (Li et al. 1993).

Among the F_2 and BC_1 plants produced from plant II-4, the 2 F_2 plants were $2n = 26$ and $2n = 52$, which is identical to and double that of their parent, respectively, indicating that the selfed seeds may be obtained from this trigeneric hybrid in different ways. Whether or not these ways are determined by genetic factors will be clarified by further studying the F_2 plant having $2n = 26$. The F_2 plant with 52 chromosomes resembles an amphiploid, and the BC_1 plant with all 26 chromosomes of plant II-4 plus 21 wheat chromosomes may be important for transferring the expected genes from *A. michnoi* and rye into common wheat. Lukaszewski and Gustafson (1983) showed that many wheat/rye translocations could be produced by crossing triticale (6x) with common wheat. Thus, the production of wheat/rye and wheat/*Agropyron* translocations is possible through the backcrossing of these plants to common wheat. So far, many selfed and backcross derivatives have been obtained from these F_2 and BC_1 plants.

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