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Meiosis and fertility of F_1 hybrids between hexaploid bread wheat and decaploid tall wheatgrass (*Thinopyrum ponticum*)

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Abstract As the first step in the transfer of barely yellow dwarf virus resistance and salt tolerance from decaploid tall wheatgrass (*Thinopyrum ponticum*) into hexaploid bread wheat (*Triticum aestivum* L.), octoploid intergeneric hybrids (2n = 8x = 56) were synthesized by crossing the tall wheatgrass cultivar 'Alkar' with wheat cvs. 'Fukuhokomugi' ('Fuko') and 'Chinese Spring'. ('Fuko' × 'Alkar') F_1 hybrids were studied in detail. The F_1 hybrids were perennial and generally resembled the male wheatgrass parent with regard to morphological features and gliadin profile. Most hybrids were euploid with 56 chromosomes and showed high chromosome pairing. On an average, in 6 hybrids 83.6% of the complement showed chiasmatic association, some between wheat and wheatgrass chromosomes. Such a high homoeologous pairing would be obtained if *Ph1*, the major homoeologous pairing suppressor in wheat, was somehow inactivated. Some of the 'Fuko' × 'Alkar' hybrids had high pollen fertility (18.5–42.0% with a mean of 31.5%) and high seed fertility (3–29 seeds wtih a mean of 12.3 seeds per spike), offering excellent opportunities for their direct backcrossing onto the wheat parent.

Key words *Triticum aestivum* L. · Homoeologous pairing · Barley yellow dwarf virus (BYDV) resistance · Intergeneric hybrids · Alien gene transfer

Introduction

Several studies have demonstrated that wide hybridization can effectively contribute to genetic enrichment of common wheat, *Triticum aestivum* L. (2n = 6x = 42; AABBDD) (Sharma and Gill 1983; Brar and Khush 1986; Jauhar 1993a; Jiang et al. 1994). The wheatgrass genus *Thinopyrum* Á. Löve is a rich source of genes for wheat improvement, although it remains largely untapped. Tall wheatgrass, *Thinopyrum ponticum* (Podp.) Barkworth and D. R. Dewey [= *Agropyron elongatum* ssp. *ruthenicum* Beldie; *Elytrigia pontica* (Podp.) Holb.; *Lophopyrum ponticum* (Podp.) Löve] (2n = 10x = 70) is a particularly valuable source of genes for resistance to barley yellow dwarf virus (BYDV) (Sharma et al. 1989) and for both leaf and stem rusts. It is the source of the leaf-rust resistance gene, *Lr24*, and stem-rust resistance gene, *Sr26*, to several wheat cultivars (Cox 1991; McIntosh 1991). Tall wheatgrass is also one of the most salt-tolerant grasses in the tribe Triticeae (Shannon 1978). To transfer these desirable traits into wheat, several workers have crossed tall wheatgrass with both durum and bread wheats (Armstrong 1936; Cugnac and Simonet 1953; Knott 1961; Sharma and Knott 1966; Dvořák 1976; Bai and Knott 1993 and references therein). However, these intergeneric hybrids were sterile; the lack of or low levels of chromosome pairing further minimized the chances of intergeneric gene transfers.

Octoploid hybrids (2n = 8x = 56) were synthesized by crossing the tall wheatgrass cultivar 'Alkar' with wheat cvs. 'Fukuhokomugi' ('Fuko') and 'Chinese Spring' (CS) as female parents (Jauhar 1991). Fuko proved to be highly crossable and produced several vigorous, perennial hybrids. The F_1 hybrids between 'Fuko' and 'Alkar' generally showed high chromosome pairing and were partially pollen- and seed-fertile and were, therefore, highly desirable for gene introgression from tall wheatgrass into wheat and vice versa. This report describes the gross morphological and reproductive features, and gliadin electrophoretic patterns of some of the promising ('Fuko' × 'Alkar') F_1 hybrids, and discusses the prospects of transferring desirable genes from *Th. ponticum* into common wheat.

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Materials and methods

Two highly crossable spring wheat cultivars, 'Fukuhokomugi' ('Fuko') and 'Chinese Spring' (CS), were crossed with the superior tall

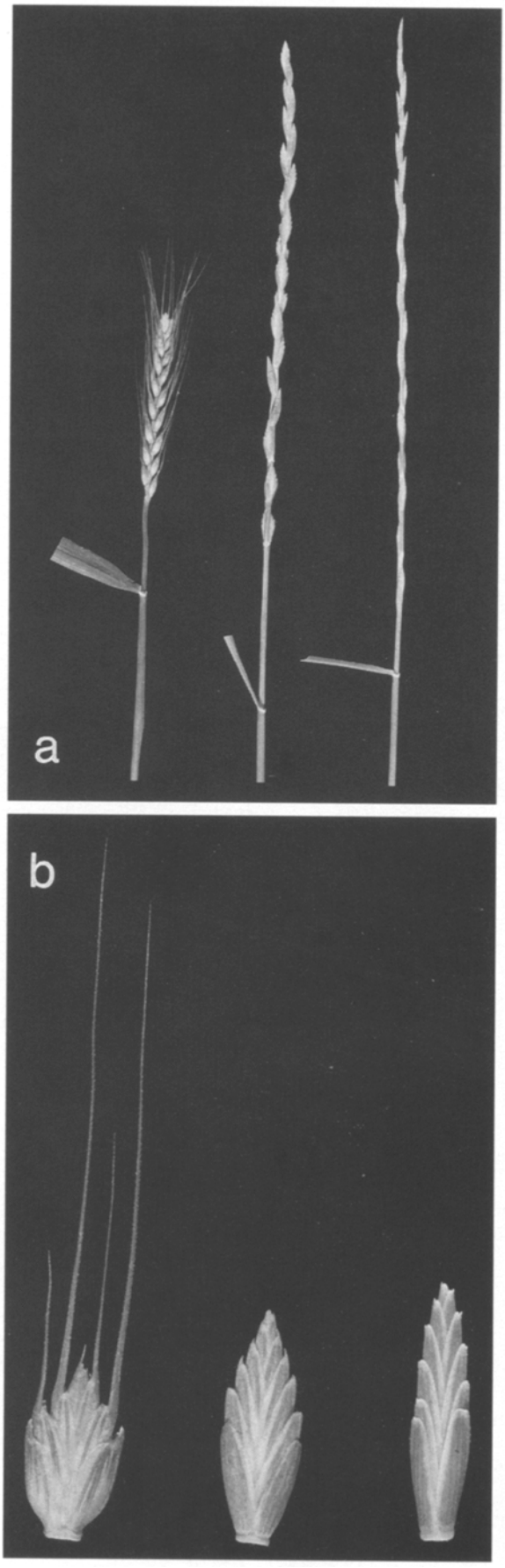


Fig. 1 **a** Spike morphology of the female wheat parent 'Fukuhokomugi' (*left*), intergeneric hybrid (*center*), and the male parent, decaploid tall wheatgrass cv. 'Alkar' (*right*). Note intermediate morphology of the hybrid spike, but awns of wheat are completely suppressed. **b** Spikelets of 'Fuko' (*left*), intergeneric hybrid (*center*), and 'Alkar' (*right*). Note complete suppression of awns in the hybrid

wheatgrass cultivar 'Alkar', using wheat as the female parent. The wheat spikes were emasculated and pollinated with 'Alkar' pollen. About 14 days after pollination, the developing embryos were cultured on orchid agar (Difco) medium supplemented with sucrose at 8 gm/l, and several hybrids were obtained. Some hybrid caryopses were allowed to ripen on the wheat parents and, thus, several viable hybrids were also obtained without embryo culture.

Hybrids were easily identified at the seedling stage by their grass-like morphology. Their hybrid nature was confirmed by somatic chromosome counts using the techniques described earlier (Jauhar 1993b). Cytologically confirmed hybrids were grown in the greenhouse, and some were transferred to the field at Evans Farm in Logan, Utah. The hybrids grew much better in the field than in the greenhouse. Pollen and seed fertility were therefore studied in the field-grown hybrids. Seed set was studied in 16 promising 'Fuko' × 'Alkar' hybrids.

For the meiotic study, spikes from the field-grown plants were fixed in freshly prepared Carnoy's fluid to which a few drops of aqueous ferric chloride had been added (Jauhar 1993b). The spikes were stored in the fixative at about 1°C until analyzed meiotically. Ring and rod configurations were scored at metaphase I (MI). Pollen fertility was estimated as the percentage of stainable pollen after staining for about 1 h with 1% cotton blue in lactophenol. Seed set on the open-pollinated F_1 hybrids was determined on an individual spike basis.

Seed of the parental species and open-pollinated F_1 hybrids was available for electrophoretic characterization of the seed gliadins (prolamins). Therefore, species-specifc gliadin markers and their expression in the hybrids were studied by gel electrophoresis. Native seed gliadins (alcohol-soluble prolamins from the seed gluten) were extracted by the method of Konarev et al. (1981). Twenty-five-microliter aliquots of the extracts were loaded into the wells of 180-mm × 120-mm × 1.5-mm vertical polyacrylamide slab gels (buffer pH = 3.2) and separated for 5.5 h at 30 mA per gel in an LKB Model 2001 Vertical Electrophoresis System. The gels were then simultaneously stained and fixed in 0.07% Coomassie Blue G250, 7% ethanol, and 12% trichloroacetic acid. Electrophoretograms of the hybrid seed were compared with those of the parents.

Results

Common bread wheat crosses easily with tall wheatgrass. Although bread wheat is a genomic allohexaploid, tall wheatgrass may not be an allodecaploid. Eighty-five intergeneric hybrids of both CS and 'Fuko' with 'Alkar' were obtained. However, some select 'Fuko' × 'Alkar' hybrids with 2n = 56 chromosomes were studied with regard to their morphological characteristics (Fig. 1a,b), gliadin profile (Fig. 2), chromosome pairing and pollen fertility (Tables 1 and 2), and seed fertility (Table 3). Four aneuploid hybrids with 2n = 54, 55, or 57 chromosomes and two 11-ploid hybrids with 2n = 77 chromosomes were also studied. Meiotic analysis was done only on 6 octoploid hybrids (Table 1), and the same hybrids were studied for their pollen fertility (Table 2).

All of the hybrids were perennial in growth habit; most of them were vigorous and tillered profusely. Morphologically, they generally resembled the male 'Alkar'

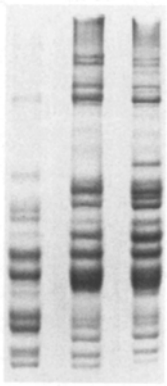


Fig. 2 Electrophoretogram comparing profiles of native gliadin proteins extracted from seeds of 'Fuko' (*left*), intergeneric hybrid (*center*), and 'Alkar' (*right*). Note similarity of intergeneric hybrid with the male parent 'Alkar'

larger than those of either parent. Such heterosis for spikelet size was evident in most hybrids.

Like most of the morphological features, the gliadin characteristics of the wild parent dominated in the hybrids. On the whole, the gliadin profile of the hybrids was similar to that of the 'Alkar' parent. The fast-moving, prominent band and several other bands of 'Alkar' were fully expressed in the hybrids (Fig. 2). Several slow-moving major and minor bands of 'Alkar' were also dominant.

The majority of F_1 hybrids had 56 somatic chromosomes (Fig. 3a), although aneuploid numbers were also found. Of the 40 hybrids studied, 26 had 2n = 56; 5, 2n = 57 (Fig. 3b); 3, 2n = 55; 3, 2n = 54; 2, 2n = 77

Table 1 Chromosome pairing in octoploid F_1 hybrids (2n = 8x = 56) between the hexaploid common wheat cultivar 'Fukuhokomugi' and the decaploid tall wheatgrass cultivar 'Alkar'

Hybrid	Number of cells scored	Mean and range of chromosome configurations at metaphase I												Chiasma frequency per cell	Percent complement paired
		VI	V	IV			III			II			I		
				Ring	Chain	Total	Frying pan	Chain	Total	Ring	Rod	Total			
1	50	0.04 (0–1)	0.02 (0–1)	0.04 (0–1)	1.04 (0–3)	1.08 (0–3)	0.16 (0–1)	2.88 (0–5)	3.04 (0–5)	10.52 (6–14)	6.32 (2–11)	16.84 (12–23)	8.52 (4–14)	37.16 (32–43)	84.75
2	50	0.08 (0–1)	–	0.06 (0–1)	1.00 (0–2)	1.06 (0–3)	0.20 (0–1)	1.96 (0–4)	2.16 (0–4)	12.24 (7–16)	5.60 (4–10)	17.84 (12–24)	9.16 (4–15)	38.24 (30–44)	83.71
3	50	0.04 (0–1)	0.04 (0–1)	0.04 (0–1)	1.20 (0–3)	1.24 (0–3)	0.10 (0–1)	1.80 (0–3)	1.90 (0–4)	11.60 (6–14)	7.20 (4–11)	18.80 (12–24)	7.30 (4–12)	38.52 (30–45)	86.96
4	100	0.08 (0–1)	0.04 (0–1)	0.04 (0–1)	1.04 (0–3)	1.08 (0–3)	0.16 (0–1)	2.04 (0–4)	2.20 (0–4)	11.20 (7–15)	6.40 (4–10)	17.60 (13–23)	9.28 (4–14)	37.20 (28–42)	83.60
5	50	–	–	0.10 (0–1)	1.12 (0–2)	1.22 (0–3)	0.10 (0–1)	1.60 (0–2)	1.70 (0–3)	12.60 (6–15)	5.60 (4–10)	18.20 (12–24)	9.82 (6–14)	38.06 (30–45)	82.82
6	50	–	0.02 (0–1)	0.12 (0–2)	0.80 (0–2)	0.92 (0–2)	0.10 (0–1)	1.20 (0–2)	1.30 (0–2)	12.40 (6–14)	6.10 (4–11)	18.50 (10–24)	11.30 (6–14)	34.40 (25–44)	79.78
Overall mean of six hybrids		0.05	0.02	0.06	1.03	1.09	0.14	1.93	2.07	11.68	6.23	17.91	9.24	37.25	83.60

Table 2 Pollen fertility[a] of octoploid F_1 hybrids (2n = 8x = 56) between hexaploid common wheat cultivar 'Fukuhokomugi' and decaploid tall wheatgrass cultivar 'Alkar'

Hybrid	Percentage of stainable pollen
1	38.4
2	32.0
3	18.5
4	24.6
5	42.0
6	33.2
Overall mean	31.5

[a] Based on pollen stainability

parent. They produced large, thick spikes with spikelet density intermediate between the two parents (Fig. 1a),but the awns of the wheat parent were completely suppressed (Fig. 1b). Individual spikelets were

Table 3 Seed set on some F_1 selected hybrids between hexaploid common wheat cultivar 'Fukuhokomugi' and decaploid tall wheatgrass cultivar 'Alkar'

Hybrid	Chromosome number 2n	Mean and range of seeds per spike (Mean of 10 spikes)
1	56	11.6 (3–27)
2	56	15.0 (7–29)
3	56	12.6 (6–17)
4	56	9.0 (5–20)
5	56	13.5 (7–24)
6	56	12.0 (5–20)
7	56	16.8 (8–25)
8	56	11.5 (6–19)
9	56	10.0 (5–16)
10	56	11.0 (4–16)
11	55	12.4 (4–18)
12	54	10.6 (5–17)
13	57	13.8 (6–17)
14	57	11.0 (4–18)
15	77	5.2 (0–9)
16	77	6.0 (3–11)

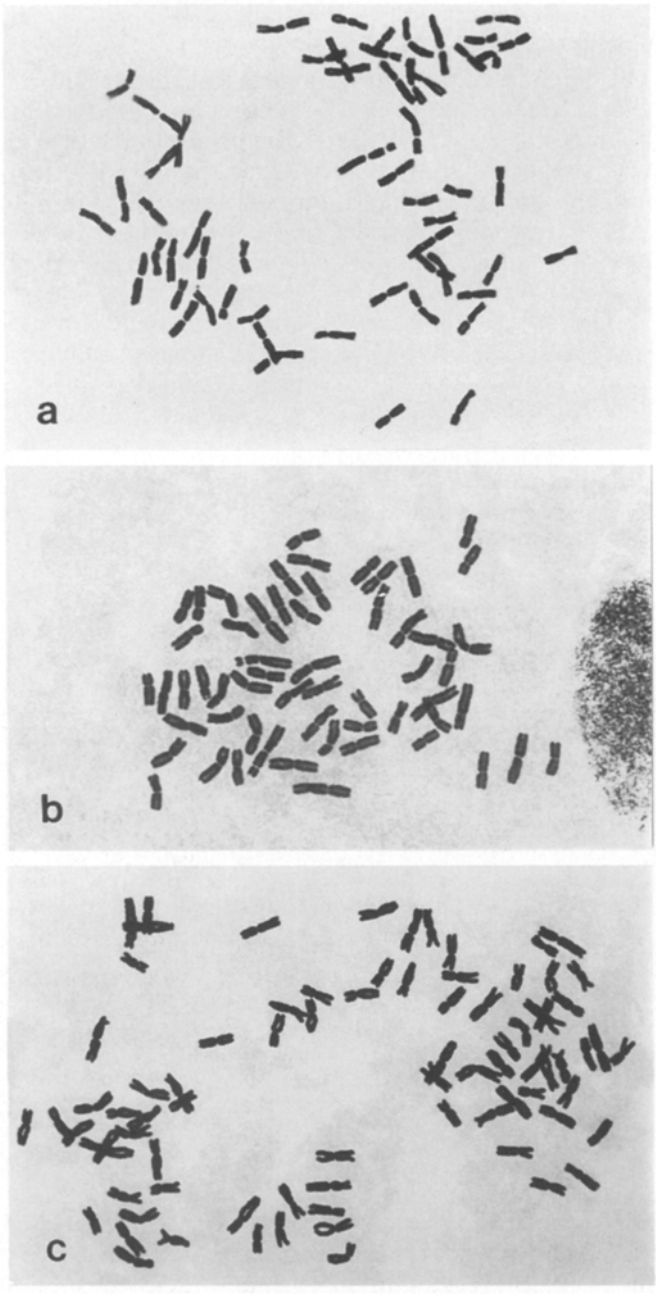


Fig. 3 Somatic chromosomes of ('Fuko' × 'Alkar') intergeneric hybrids. **a** 2n = 56, **b** 2n = 57, **c** 2n = 77

(Fig. 3c); and 1 had 2n = 78 chromosomes. All of the hybrids analyzed showed a remarkably high degree of pairing, characterized mostly by bivalent formation, although multivalents and univalents were also formed (Fig. 4a,b). A large proportion of the bivalents were rings. Heteromorphic bivalents and multivalents were formed. Univalents of different sizes were also observed (Fig. 4a,b). Meiotic configurations of 6 euploid (2n = 8x = 56) hybrids are listed in Table 1. On an average, 83.6% of the complement associated as bivalents or multivalents.

Despite the formation of multivalents, disjunctional stages were generally regular (Fig. 4c), and chromosomal elimination, as reflected in the formation of micronuclei, was low (Fig. 4d) and hence resulted in appreciable pollen fertility in the F_1 hybrids. Pollen stainability ranged from 18.5% to 42.0%, with a mean of 31.5% (Table 2). The female fertility of the F_1 euploid hybrids was unexpectedly high; most spikes contained some seed. Seed set per spike in 16 selected ('Fuko' × 'Alkar') hybrids ranged from 3 to 29 seeds, with a mean of 12.3 seeds per spike in the euploid hybrids (Table 3). Seed set in the 4 aneuploid hybrids studied was comparable to that in the euploids. However, seed fertility of the two 77-chromosome hybrids was about one-half that of the octoploid hybrids. Some of the shriveled seeds obtained from the F_1 hybrids did not germinate, but seed viability on the whole was about 80%.

The hybrid seeds with husk were larger than those of either parent (Fig. 5a). They were difficult to dehusk, but certainly not as difficult as those of the wild parent. Figure 5b shows the dehusked seeds of the F_1 hybrids (center) along with those of *Thinopyrum* and 'Fuko' wheat. Clearly, the hybrid seed had considerable resemblance to the wheat seed, but was somewhat elongated like the wheatgrass seed.

Discussion

Generally, intergeneric F_1 hybrids show poor chromosome pairing and consequently are highly sterile, which poses serious limitations on transferring genes across the generic boundaries. Thus, the hybrids of *Th. ponticum* with both durum and bread wheats synthesized by earlier workers were highly sterile (Bai and Knott 1993). Low levels of pairing have been observed in common wheat × *Th. ponticum* hybrids. Although Knott (1961) indicated the possibility of pairing between wheat and *Agropyron* (*Thinopyrum*) chromosomes, it was observed that no such pairing occurs in the presence of *Ph1* (Dvořák and Knott 1974). Kasaeva (1973) observed a high level of pairing in durum wheat × *Th. ponticum* hybrids. This was attributed to autosyndesis within the *Thinopyrum* complement, suggesting a close relationship among the five genomes of the decaploid wheatgrass.

The octoploid F_1 hybrids between hexaploid wheat and decaploid tall wheatgrass reported in the present study showed high chromosome pairing, with 83.6% of the complement paired. Although some of the meiotic associations obviously resulted from autosyndetic pairing within the 5x complement of *Thinopyrum*, and some from autosyndesis within the 3x complement of wheat, at least some of the pairing could have involved chromosomes of both the parental species. The formation of heteromorphic bivalents and multivalents was an indication of intergenomic pairing. Although autosyndesis can certainly result in heteromorphic configurations, the formation of as few as four univalents

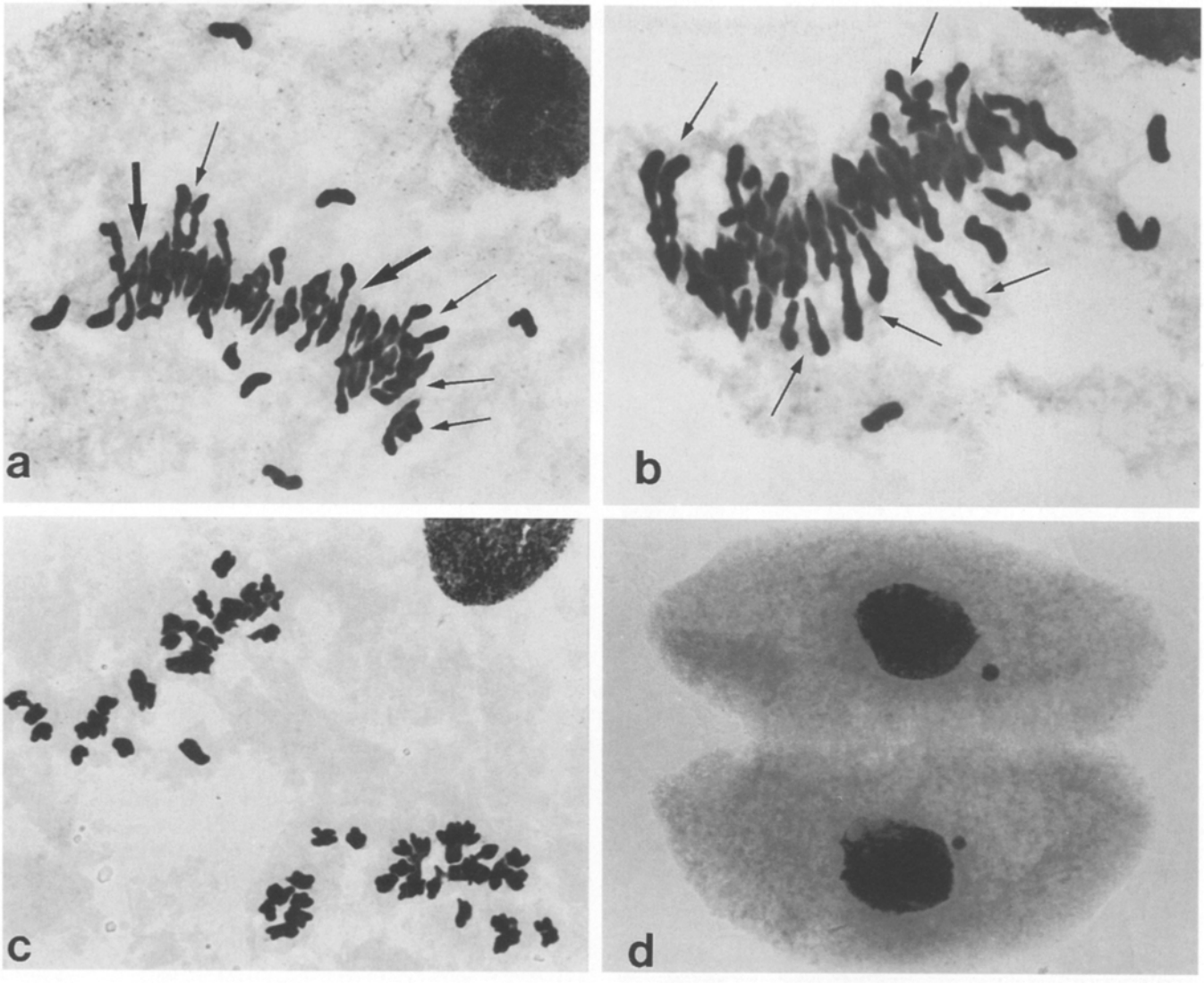
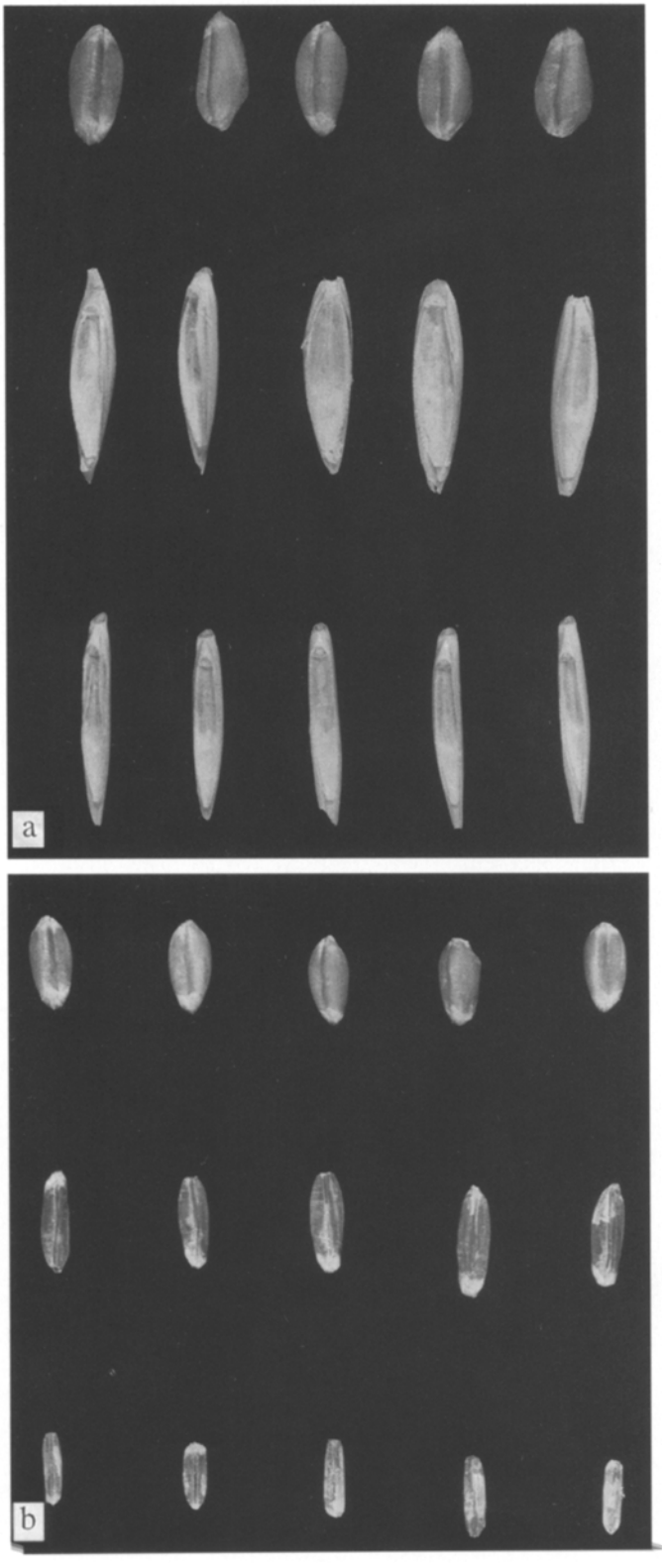


Fig. 4a–d Meiotic stages in the octoploid intergeneric hybrids (2n = 56). Note the high degree of homoeologous pairing, as evidenced by multivalent formation and heteromorphy of meiotic configurations. **a** Metaphase I with $2_{IV} + 4_{III} + 15_{II} + 6_{I}$; note preponderance of ring bivalents. Quadrivalents are marked with *thick arrows* and trivalents with *thin arrows*, **b** metaphase I with $5_{III} + 18_{II} + 5_{I}$; trivalents are marked with *thin arrows*, **c** anaphase I showing regular 28:28 disjunction, **d** relatively regular telophase I followed by cytokinesis. Note one micronucleus in each of the daughter cells

(Table 1) would indicate pairing between the chromosomes of the two parents. Such a high homoeologous pairing would be possible if *Ph1*, the principal homoeologous pairing suppressor in wheat, was inactivated. It is likely that the *Thinopyrum* genotype or perhaps the interaction between the two parental genotypes in the hybrids rendered *Ph1* inactive, thereby permitting substantial intergenomic pairing. Autosyndetic pairing within the *Thinopyrum* complement is fully expected to occur; however, autosyndesis within the wheat complement would occur only if *Ph1* is disabled. Large univalents were still observed (Fig. 4b), which most probably belonged to the wheat parent. Certain genotypes of alien species are known to inactivate the *Ph1* pairing regulator of wheat (Sears 1976; Jauhar 1992) and the pairing regulators of other allohexaploid species (Jauhar 1975, 1993b and references therein).

Knott (1961) and Sharma and Knott (1966) transferred the stem-rust resistance gene, *Sr26*, and leaf-rust resistance gene, *Lr19*, respecitvely, to wheat by irradiation treatments. Perhaps a more preferred method of inducing alien gene transfer would be by inducing pairing between the chromosomes of wheat and those of the alien gene donor. Various means of promoting such pairing that have heen tried by different workers include the use of chromosome 5B-deficient or *Ph1*- deficient stocks, and the use of alien genotypes that interfere with *Ph1* (see Jauhar 1993a, for references). Recently, *Ph1*-inhibiting genes, Ph^{I}, that promote homoeologous pairing, have been transferred from *Aegilops speltoides* L. into wheat (Chen et al. 1994). In the present study, however, no such manipulation was necessary because

Fig. 5a Seeds of the female parent 'Fuko' (*top row*), intergeneric hybrid (*middle row*), and the male parent 'Alkar' (*bottom row*); seeds of the hybrid and 'Alkar' have husks. Note the large size of the seeds of the hybrid, **b** seeds of 'Fuko' (*top row*), dehusked seeds of intergeneric F_1 hybrid (*center row*), and dehusked seeds of 'Alkar' (*bottom row*)



the male genotype seemed to bring about the desired homoeologous pairing. Such genotypes may be effective in accelerating alien gene transfer into wheat.

Despite high homoeologous pairing in the octoploid hybrids, they were partially pollen- and seed-fertile. Seed set was obtained on most F_1 hybrids. This is in sharp contrast to previous reports on wide hybrids (Brar and Khush 1986). Since the previous workers did not obtain fertility in the wheat × *Thinopyrum* hybrids, the fertility in the present hybrids may be attributed, at least partly, to the genotypes used. It is generally believed that irregular disjunction of mulitvalents that results in irregular distribution of chromosomes at anaphase I causes sterility. However, the disjunctional stages in the present hybrids were fairly regular, and chromosome erosion, as reflected in micronucleus formation, was low. Whether genetic regulation played a role in normal disjunction of multivalents is difficult to determine. Aneuploid gametes were also formed, but they were seemingly functional and produced viable hybrids. These included the 54-, 55-, and 57- chromosome hybrids.

Although the number of aneuploid hybrids available was limited, it appeared that seed set on them was comparable to that in euploids. By virtue of genetic buffering caused by a high level of polyploidy, deficiencies of 1 or more chromosomes seem to be tolerated. However, in view of the limited data no definite inferences on the effect of aneuploidy on seed set can be drawn. Unreduced female gametes of wheat functioned and, after fusion with normal male gametes, gave rise to 77-chromosome hybrids. However, the full (42-chromosome) complement of wheat did not seem to confer any more fertility on these two 77-chromosome hybrids than that of the 56-chromosome hybrids. It would appear, therefore, that to improve seed set in the ('Fuko' × 'Alkar') hybrid derivatives the chromosomal contribution of the wild parent must be reduced by successive backcrossing onto wheat.

Several features of the wild parent dominated in the hybrids: awnlessness, husks tightly adhering to the seed, and gliadin protein profile. This may be attributed to the much higher chromosomal contribution (five genomes) from the male *Thinopyrum* parent compared to only three genomes from the wheat parent. However, the level of seed fertility observed in the F_1 hybrids offers exciting possibilities for their direct backcrossing with the wheat parent and thereby restoring most of the wheat chromosome complement. In view of the high pairing in the F_1 hybrids, it may be possible to incorporate some of the desirable chromatin from the wheatgrass parent into the reconstituted wheat genome.

The perennial nature of the hybrids makes them particularly amenable to cytogenetic manipulations. The synthesis of reasonably fertile germplasm, incorporating three genomes of common wheat and five of the allied genus *Thinopyrum*, is the first important step in the introgression of alien genes into wheat. These hy-

brids could also help produce desirable forage hybrids with superior traits (e.g., leaf succulence) of wheat.

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