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Morphological and cytological characteristics of some wheat × barley hybrids

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Abstract As initial step in the transfer of dwarf bunt resistance from barley into wheat, the two cereal crops were hybridized. Using the wheat cultivars 'Fukuhokomugi' and 'Chinese Spring' (AABBDD genomes) as female parents and barley cultivar 'Luther' (II genome) as male, we synthesized 9 euploid hybrids ($2n = 4x = 28$; ABDI genomes). The hybrids were vigorous, but highly sterile. Meiotic analyses of seven hybrids showed considerable variation in chromosome pairing. Of the hybrids involving 'Fukuhokomugi' 3 had high pairing with a mean of 5.08–6.72 chiasmata per cell, while others had 2.16–3.52 chiasmata per cell. As many as 12 bivalents in some pollen mother cells would suggest at least some pairing between wheat and barley chromosomes. This level of homoeologous pairing, coupled with some, albeit low, female fertility of the F_1 hybrids, could offer an opportunity for intergeneric gene transfers from barley into wheat and vice versa.

Key words Bread wheat · Barley · Intergeneric hybrid · Homoeologous chromosome pairing · Gene transfer

Introduction

Bread wheat (*Triticum aestivum* L., $2n = 6x = 42$; AABBDD genomes) and barley (*Hordeum vulgare* L., $2n = 2x = 14$; II genome) are two of the most important cereal crops in the world. Dwarf bunt, a fungal disease produced by *Tilletia controversa* Kühn, causes smutting of the developing caryopses and dwarfing of the wheat plant, which can cause a serious reduction in grain yield and quality. Whereas bread wheat lacks bunt-resistant germplasm, some winter barley cultivars such as 'Luther', 'Boyer', and 'Mal' have some resistance to the pathogen. Thus, cultivated barley is a potential source of desirable genes for wheat improvement. However, very few wheat × barley hybrids with wheat cytoplasm have been produced (Fedak 1992). As a first step in the intergeneric gene transfer process, the two cereals were hybridized, using two select, crossable genotypes of spring wheat ('Fukuhokomugi' and 'Chinese Spring') as female parents and 'Luther' barley as male. If resistance genes can be transferred to these cultivars, these genes could then be transferred to other cultivars of winter and spring wheat.

Of the 9 euploid hybrids ($2n = 4x = 28$; ABDI genomes) with wheat cytoplasm, 7 were studied with respect to chromosome pairing and chiasma formation. A preliminary report on 2 of the hybrids has been published earlier (Jauhar 1991a). In this article, details of meiotic analyses of 7 hybrids are described and the breeding implications of homoeologous pairing are discussed.

Materials and methods

Two spring wheat cultivars, 'Chinese Spring' (CS) and 'Fukuhokomugi' (Fk)[1] were crossed with the winter barley cultivar 'Luther', using wheat as the female parent. The wheat florets were manually emasculated and treated with a 1:1 mixture of 2,4-D (25 mg per liter) and GA_3 (75 mg per liter) aqueous solution, 1 day before and 1 day after pollination with barley pollen. Both pre- and post-pollination treatments were applied by spraying individual florets with the growth regulator solution. In some cases pollinations were repeated, but hormonal treatment was applied only once as described above. The developing embryos were excised 10–17 days after pollination and cultured on Orchid Agar (Difco) medium.

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[1] In my earlier publications, I have, for the sake of convenience, abbreviated 'Fukuhokomugi' (which in Japanese means "wheat with rich ears") to 'Fuko', which I now understand means "misfortune" in Japanese. As a result of this enlightenment from Professor Tsunewaki, I have abbreviated 'Fukuhokomugi' as 'Fk' in this article; F and k stand for "Fukuho" and "komugi" (= wheat), respectively.

Hybrids were identified at the seedling stage, based on somatic chromosome counts from root tips using the technique described earlier (Jauhar 1991b). For meiotic analyses, spikes halfway in the flag leaf sheaths were excised and fixed in freshly prepared Carnoy's fluid. Chromosome configurations were scored at metaphase I (MI), and mean chiasma frequencies were calculated from 50 pollen mother cells (PMCs); in one hybrid, only 25 PMCs could be studied.

Pollen fertility was estimated as percentage stainable with 1% cotton blue in lactophenol.

Results

From about 1650 'Fukuhokomugi' florets pollinated with 'Luther' pollen, 19 embryos were rescued, which produced 13 plantlets; of these, 9 survived until maturity and 7 were euploid. On the other hand, some 1480 'Chinese Spring' florets were pollinated, from which 7 embryos were rescued and only 4 plantlets derived; of these, only 3 survived until maturity and 2 were euploid. Thus, 'Fukuhokomugi' proved to be more crossable than 'Chinese Spring', and 7 of the 9 euploid hybrids ($2n = 4x = 28$; ABDI genomes) obtained had this cultivar as the female parent. The morphological and cytological characteristics of these hybrids are given below.

Phenotypic features of F_1 hybrids

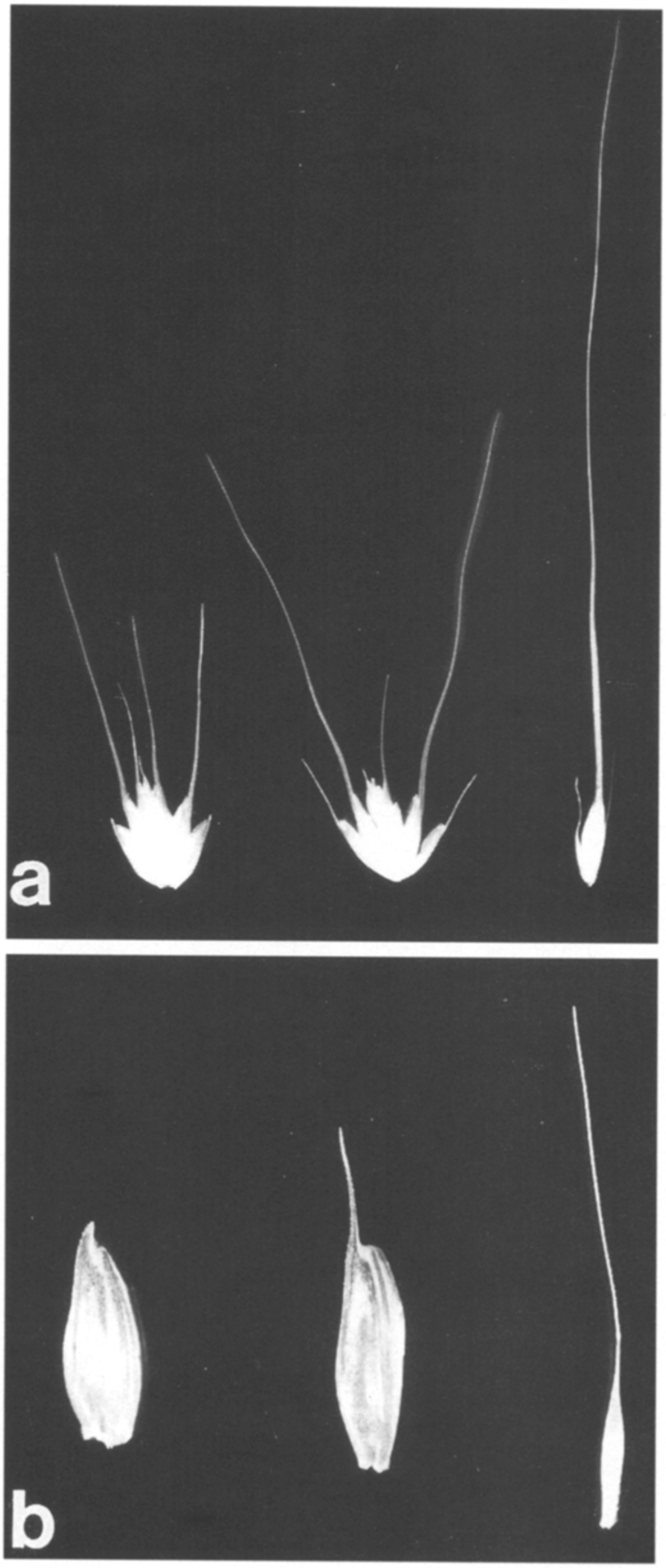
The F_1 hybrids had wheat-like morphology, were vigorous in growth, and tillered profusely. Although the hybrid plants were vigorous, they were highly or totally sterile. The spike morphology of the wheat parent dominated in the hybrids. Spikelets of the Fk × 'Luther' hybrids were similar to those of Fk (Fig. 1a). However, awn length and outer glumes were intermediate between the two parents (Fig. 1a, b). About 2% of the florets in some of the hybrids were pistilloid, where one or more of the anthers were transformed into pistils.

Using pollen from Fk for backcrossing onto F_1 hybrids, a BC_1 progeny of 2 plants was raised. Both died before maturity. This nevertheless showed that the hybrids had some female fertility.

Meiotic characteristics

Chromosome pairing and chiasma frequency in PMCs of 7 of the euploid F_1 hybrids are given in Table 1, and some representative cells are shown in Fig. 2a–f. Considerable variation in pairing among hybrids was observed. Generally, the hybrids with CS as the maternal parent showed less pairing than those involving Fk. Moreover, pairing varied from cell to cell within a hybrid. For example, Fig. 2a shows 4 PMCs from the same anther; the lowermost PMC has only univalents (see also Fig. 2b), but the upper 3 cells have various degrees of pairing with both rod and ring bivalents.

Fig. 1a, b Spikelet and glume morphology of wheat × barley hybrids and the parental species. **a** *Left to right*: Spikelets of Fk, Fk × 'Luther' hybrid, and 'Luther' barley. Note wheat-like morphology of the hybrid spikelet and intermediate awn length in the hybrid glumes. **b** *Left to right*: Glumes of Fk, Fk × 'Luher', and 'Luther' barley



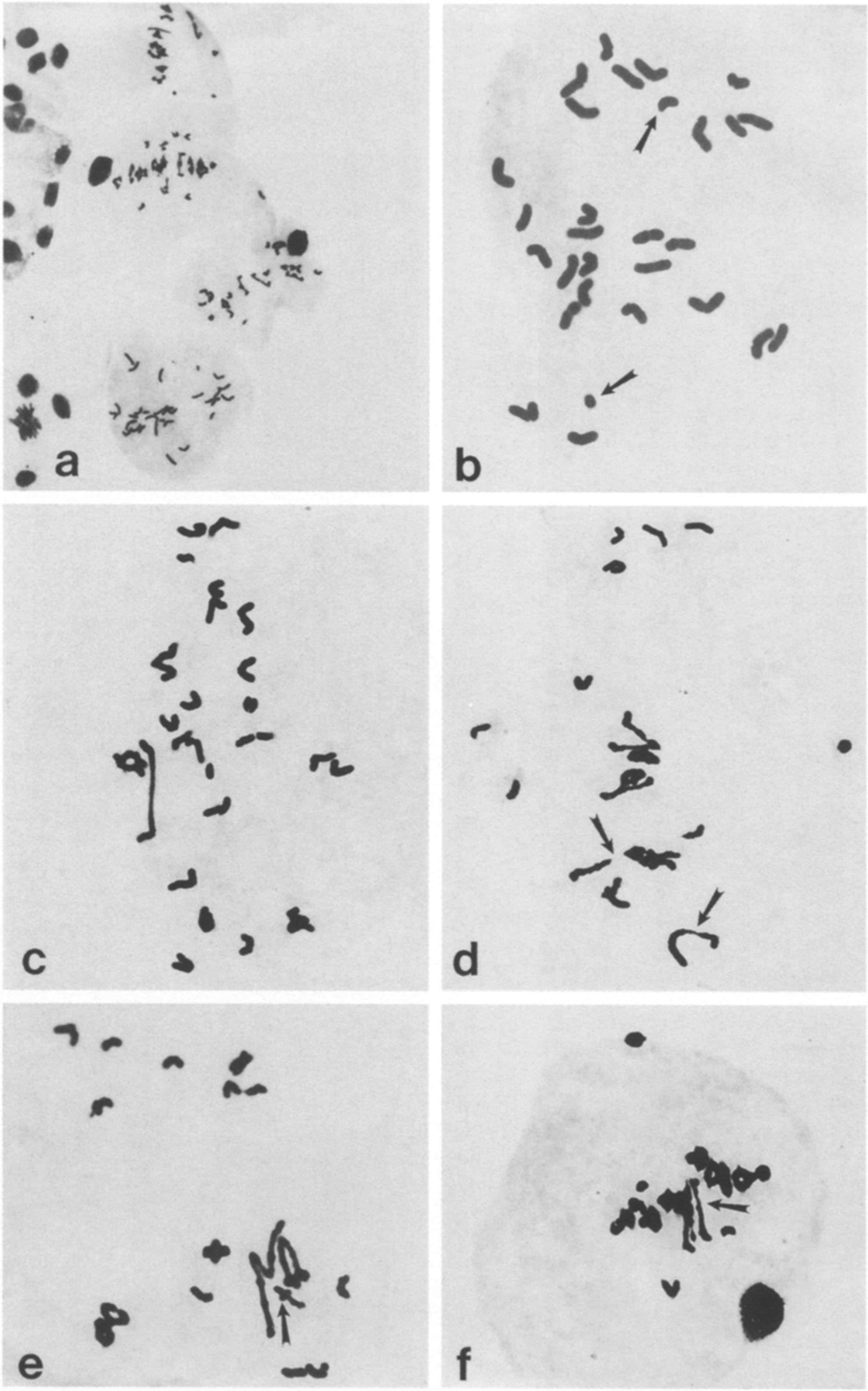


Fig. 2a–f Meiotic stages in PMCs of wheat × barley hybrids. **a** PMCs from a single anther showing varying degrees of pairing at metaphase I. Note complete lack of pairing in the lowermost cell and various frequencies of ring and rod bivalents in the upper three cells. **b** A meta-anaphase cell with 27 univalents and 2 fragments (*arrowed*), unequal arms of the same chromosome separated by misdivision. **c** Meta-anaphase I with 1 rod bivalent and 26 univalents (some misdivided); note the misdividison products at the center. **d** Metaphase I with 2 III + 3 ring II + 3 rod II + 10 I (one iso-ring). Note heteromorphic rod bivalents (*arrows*); one is separated. **e** An incomplete cell at metaphase I with 1 IV + 1 III + 3 ring II + 1 rod II + 11 I. Note the heteromorphic rod bivalent (*arrow*) and asymmetrical trivalent and quadrivalent. **f** Metaphase I with 9 ring II + 3 rod II + 4 I. Note a heteromorphic rod II (*arrow*)

Table 1 Chromosome pairing at metaphase I in seven wheat × barley hybrids ($2n = 4x = 28$)

Hybrid[a]	Number of cells scored	Mean and range of chromosome configurations						Chiasma frequency per cell
		IV[b]	III	II			I	
				Ring	Rod	Total		
1	50	–	0.06 (0–1)	0.60 (0–2)	0.84 (0–5)	1.44 (0–6)	24.94 (12–28)	2.16 (0–7)
2	50	0.02 (0–1)	0.08 (0–1)	0.74 (0–4)	1.02 (0–6)	1.76 (0–7)	24.16 (14–28)	2.72 (0–9)
3	50	0.04 (0–1)	0.06 (0–1)	1.42 (0–7)	1.74 (0–6)	3.16 (0–11)	21.32 (6–28)	5.08 (0–16)
4	50	–	0.10 (0–1)	0.96 (0–5)	1.40 (0–7)	2.36 (0–9)	22.98 (10–28)	3.52 (0–11)
5	50	0.10 (0–1)	0.24 (0–2)	2.24 (0–10)	1.44 (0–5)	3.68 (0–12)	19.50 (4–28)	6.72 (0–22)
6	50	–	–	0.80 (0–3)	0.80 (0–4)	1.60 (0–5)	24.80 (18–28)	2.40 (0–6)
7	25	0.08 (0–1)	0.20 (0–2)	2.20 (0–11)	1.48 (0–4)	3.68 (0–12)	19.76 (4–28)	6.60 (0–23)

[a] Hybrids nos. 1 and 2 were with 'Chinese Spring' and others with 'Fukuhokomugi'

[b] All quadrivalents were chain-or alternate–type

Nearly seven chiasmata per PMC were formed in some hybrids (Table 1). The frequency of ring bivalents was surprisingly high (Fig. 2f). Conspicuously heteromorphic bivalents were frequently observed (e.g., Fig. 2d–f); asymmetrical trivalents and quadrivalents were also found (Fig. 2e).

Numerous disjunctional abnormalities, including anaphase bridges, laggards, first-division and second-division restitutions, abnormal microspore tetrads, and endoreduplications, were observed, which resulted in a few seemingly normal pollen grains. Multipolar spindles, in conjunction with restitution, resulted in tetrads with microspores of different sizes, including some with unreduced chromosome number. Some highly abnormal tetrads are shown in Fig. 3a–d. Pollen stainability varied from 1.5% to 6.0%. Although anther development seemed to be normal and some pollen grains appeared normal, the anthers failed to shed pollen, resulting in male sterility of the hybrids.

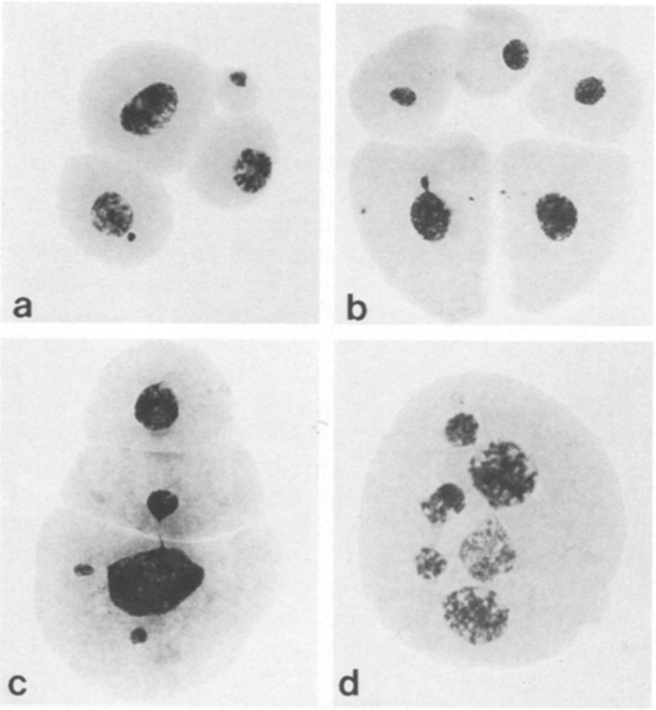


Fig. 3a–d Abnormal microspore "tetrads" and other products of meiotic division. Note unequal-sized microspores, apparently some with unreduced chromosome number. **a** A "tetrad" with two equal-sized microspores (one with a micronucleus), one large and one very small "microspore." **b** A "pentad" with two equal-sized microspores and three much smaller "microspores". **c** A highly abnormal "linear tetrad" with one apparently unreduced microspore due to second division restitution. Note two micronuclei in the large microspore, and remnants of a bridge. **d** An abnormal "polyad" with microspores of varying sizes

Discussion

Since Kruse (1973) successfully crossed common wheat with barley, several workers have produced hybrids between these two grain crops (Fedak 1985, 1992 and references therein; Koba et al. 1991). Better crossing success was achieved when barley was used as the female parent, and relatively few hybrids with wheat cytoplasm have been produced (see Fedak 1992). Crossability is known to be under genotypic control and hence the success of hybridization depends at least partly on the wheat cultivar used. The crossability inhibiting genes (*Kr*) pose a major obstacle to hybridizing wheat with related genera. CS, with three crossability genes *kr1*, *kr2*, and *kr3* in chromosomes of the homoeologous group 5 (Snape et al. 1979; Falk and Kasha 1981; Fedak and Jui 1982), has been considered to be highly crossable. In our breeding work we have consistently found Fk to be highly crossable, more so than CS. Fk also has a much better plant type than CS and is therefore a better choice for wide hybridization work. Our crossing success with barley might be attributable to the presence of crossability genes in Fk, better plant vigor, and pre- and post-pollination treatments with growth regulators.

Some barley characteristics, e.g., better awn development on lemmas and glumes, were expressed in F_1 hybrids, despite the presence in them of three genomes of the wheat parent and only one of barley. Undesirable characters such as pistilloidy are assoicated with barley × wheat hybrids (with barley as female parent), presumably because of an unfavorable interaction between the wheat nucleus and barley cytoplasm (Islam et al. 1975; Fedak 1985). In our wheat × barley hybrids, however, pistilloidy was rarely noticed. Such hybrids offer better prospects for intergeneric gene transfer.

The F_1 hybrids produced by earlier workers showed very little pairing between the parental chromosomes (Fedak 1985, 1992), thus imposing serious restrictions on transferring genes from barley into wheat. Substantial elevation of pairing in 3 of the Fk × 'Luther' hybrids reported in the present study appears promising from the standpoint of plant breeding. Certain genotypes of alien species are known to suppress the activity of *Ph1* (located in the long arm of chromosome 5B) that normally suppresses pairing between homoeologous chromosomes in wheat (Riley et al. 1968; Sears 1976; Dvořák 1977; Knott and Dvořák 1981; Jauhar 1992, 1993). It is likely that the barley genotype or the genotypic combinations of the parental species we used somehow suppressed the activity of *Ph1* and brought about extensive homoeologous pairing. Alternatively, *Ph1* may have been lost at the premeiotic mitotic stage and was absent in some PMCs, which consequently showed extensive homoeologous pairing. However, there was no evidence of aneuploidy among the cells scored and it seems unlikely that chromosome 5B was lost.

A large proportion of the pairing observed in the ABDI hybrids may be due to intergenomic chromosome pairing within the wheat complement, as observed earlier by Sethi et al. (1986) in F_1 hybrids between the *ph1b* 'Chinese Spring' and the barley cultivar 'Tuleen 346'. However, the occurrence of heteromorphic bivalents and multivalents and, more importantly, the formation of up to 12 bivalents in the ABDI hybrids would indicate pairing among wheat and barley chromosomes. The total pairing observed exceeds the amount of pairing that can be accounted for by autosyndesis within the wheat complement, even in *ph1b*-euhaploids (Jauhar et al. 1991). Some autosyndetic pairing may also have occurred within the barley complement. Chromosome banding would, therefore, provide clear evidence of pairing between wheat and barley chromosomes. Although C- or N-banding of meiotic chromosomes could not be done, it is highly likely that wheat × barley pairing occurred because 24 of the 28 chromosomes paired in some cells. Using various barley telocentrics, Islam and Shepherd (1988) showed evidence of occasional pairing between wheat and barley chromosomes. They also induced pairing in some triple monosomic stocks having 19 pairs of wheat chromosomes, a marked barley chromosome arm, a related wheat chromosome and a single dose of wheat chromosome 5B with *ph1b* mutation (Islam and Shepherd 1992).

No colchicine-induced amphidiploids could be produced from the wheat × barley hybrids reported in the present study or from those reported by earlier workers (see Fedak 1992). However, restitutions during first or second meiotic division seemed to produce unreduced gametes on the male side and possibly also on the female side (although megasporogenesis was not studied). The occasional fusion of unreduced gametes could result in the production of amphidiploids, albeit in low frequency. Six of the seven disomic addition lines of 'Betzes' barley in the CS background (Islam et al. 1978) and some addition lines of the BYDV (barley yellow dwarf virus)-resistant barley accession CI3208-4 in CS (McGuire and Qualset 1990) have been produced.

The occurrence of pairing between wheat and barley chromosomes, when appropriate genotypes of the two cereal crops are crossed, offers an opportunity for the production of wheat-barley exchange chromosomes and for intergeneric gene transfers from barley to wheat and vice-versa. Because there are indications that F_1 hybrids have low levels of female fertility, backcrossing onto the Fk parent may facilitate incorporation of desirable segments of the barley genome into wheat.

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