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# Intergeneric Hybrids Between *Triticum crassum* and *Hordeum vulgare**

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**Summary.** Intergeneric hybrids between *Triticum crassum* (2n = 6x = 42) and *Hordeum vulgare* cv. 'Bomi' were obtained at a frequency of 15% of pollinated florets. Meiotic chromosome pairing in the hybrids was not different from that observed in a polyhaploid of *T. crassum* indicating negligible pairing between chromosomes of the two species and secondly that the genome of *H. vulgare* had no effect on intergenomic pairing in *T. crassum*.

**Key words:** Intergeneric hybrids – Embryo culture – Homoeologous chromosome pairing – *Triticum* – *Hordeum*

## Introduction

Phylogenetic relationships among different species and genera have been determined mainly on meiotic chromosome pairing in interspecific and intergeneric hybrids. Recently, viable intergeneric hybrids have been successfully produced from crosses of wheat (*T. aestivum* L.) and barley (*H. vulgare* L.) by means of embryo culture techniques (Kruse 1973; Islam et al. 1975; Fedak 1977; Thomas et al. 1977; Mujeeb et al. 1978). Other *Hordeum-Triticum* combinations successfully hybridized were *H. chilense* × *T. aestivum* (Martin and Chapman 1977) and *T. timopheevi* × *H. bogdanii* (Kimber and Sallee 1979). During the study of wide crosses in cereals, viable hybrids have been obtained between a hexaploid *T. crassum* and *H. vulgare* cv. 'Bomi'. Since chromosome pairing in haploids of both parental species has already been reported (Sadasaviah and Kasha 1971; Shigenobu and Sakamoto 1977), chromosome pairing in the hybrids can be interpreted on the basis of the genomic relationships between the two species. This paper reports meiotic pairing of the hybrids in comparison with that of both parental haploids.

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## Materials and Methods

Seeds of *T. crassum* (Boiss.) Aitch and Hensl. (2n = 6x = 42 with M, D and $D^2$ genomes) were obtained from Dr. E.R. Kerber, Agriculture Canada Research Station, Winnipeg, Manitoba. They were germinated on moistened filter paper in petri dishes. The seedlings were potted and vernalized for eight weeks at 4°C with a 16-h photoperiod. They were transplanted to a soil-proroot mixture in pots and grown in a growth room at day/night temperatures of 20/15°C and light intensity of 600 microeinsteins $m^{-2}$ $sec^{-1}$. Spikes of *T. crassum* were emasculated and covered with dialysis tubing prior to pollination with *H. vulgare* L. cvs. 'Bomi' and 'Emir'. At 24 and 48 h after pollination $GA_3$ at a concentration of 75 p.p.m. was applied to individual florets by means of a hypodermic syringe. The embryos were excised from developing seeds at 15 days following pollination and placed on a modified $B_5$ medium as previously described (Fedak 1977, 1980). The embryos were cultured in a dark incubator maintained at 25°C. With the initiation of root growth the culture vials were placed under a fluorescent light to stimulate coleoptile growth. At the three leaf stage, seedlings were transplanted to pots and returned to the growth chamber.

Somatic and meiotic chromosomes were stained with Snow's solution (Snow 1963) and prepared by the standard acetocarmine squash method. A detailed meiotic analysis was carried out on two of the three intergeneric hybrids that were produced.

## Results

### *Production of Hybrids*

Hybrids between *T. crassum* × *H. vulgare* cv. 'Bomi' were produced quite readily (Table 1). Three seedlings were obtained from the five cultured embryos which were obtained from pollinating 20 florets. This represents a seed set of 25% and seedlings were obtained at a frequency of 15% of pollinated florets.

The morphology of the hybrid plants was predominantly *Triticum*-like as previously reported for other hybrids between the two genera. Vegetatively the hybrid plants were nearly twice as tall as the maternal parent (60 cm vs. 30 cm), more vigorous, and more profuse in tillering. The

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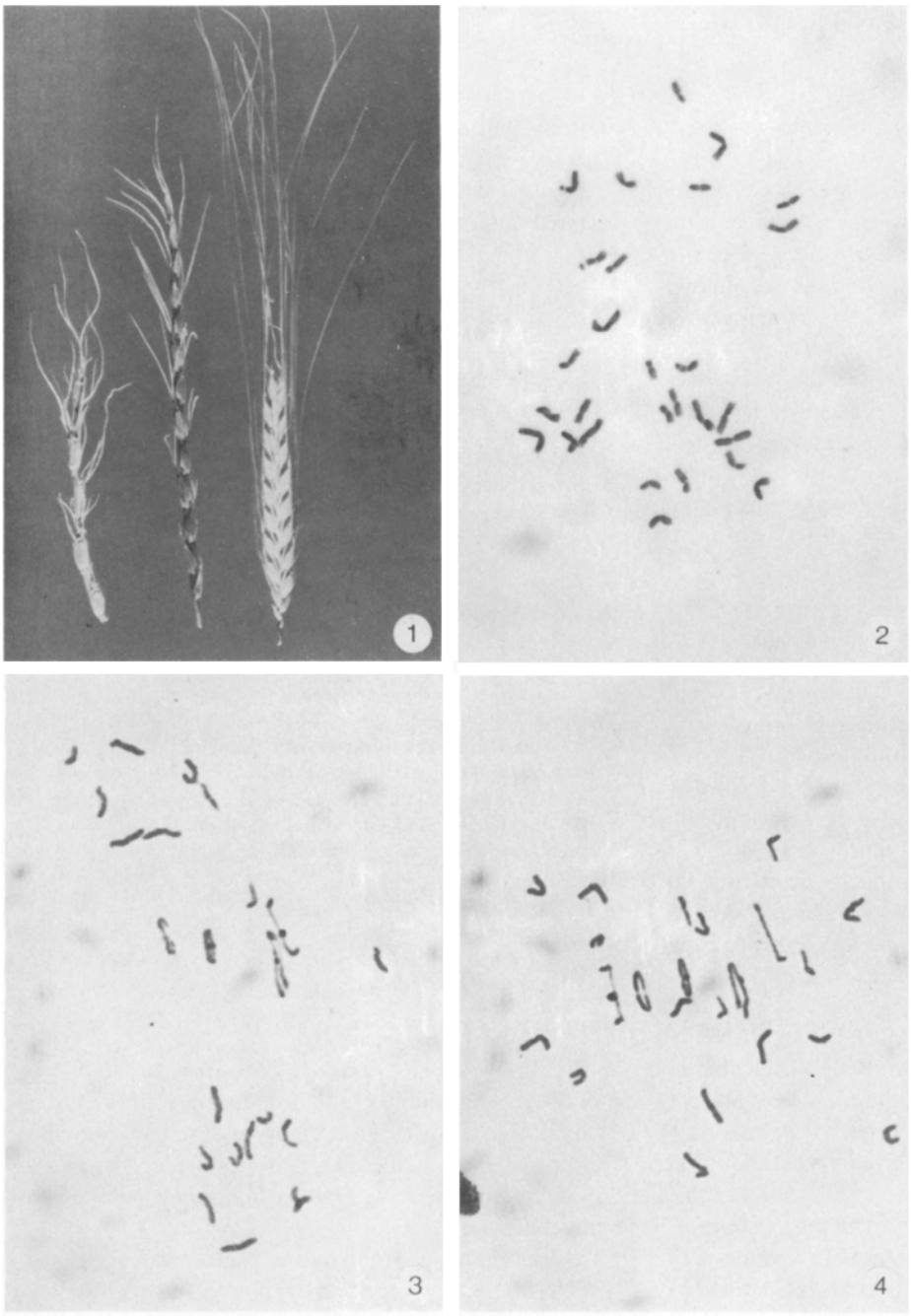
**Table 1.** Seed set and embryos cultured from intergeneric crosses between *Triticum crassum* and *Hordeum vulgare*

| *H. vulgare* male parents | Florets pollinated | Seeds set | Embryos cultured | Plantlets obtained |
|---|---|---|---|---|
| cv. Bomi | 20 | 5 | 5 | 3 |
| cv. Emir | 100 | 0 | – | – |

spikes of the hybrid plant as shown in Fig. 1 were much longer with many more, at times twice as many, spikelets. The lemma awns on the terminal florets of the hybrid were equal in length to those on the maternal spike. however, those on lower florets were nearly twice as long. The floret structure of the hybrid spike was similar to *T. crassum* with four florets per spikelet but those of the hybrid were larger. The hybrid spikes were completely sterile.




**Figs. 1-4.1** (L-R). *T. crassum; T. crassum* × *H. vulgare* hybrid; *H. vulgare* cv. 'Bomi'; **2** somatic metaphase of *T. crassum* × *H. vulgare* hybrid; **3, 4** meiotic metaphase in *T. crassum* × *H. vulgare* hybrids; Fig. 3. Meiocyte with $1^{III} + 3^{II} + 19^{I}$; Fig. 4. Meiocyte with $1^{III} + 6^{II} + 13^{I}$

**Table 2.** Mean chromosome pairing at first metaphase of meiosis in intergeneric *Triticum crassum* X *Hordeum vulgare* hybrids compared to haploids of parental species

| Genotype | Mean configurations | | | | Xta/cell | No. of cells |
|---|---|---|---|---|---|---|
| | I | II | III | IV | | |
| *T. crassum* X *H. vulgare* no. 2 observed | 19.13 | 3.87 | 0.36 | 0.01 | 5.43 | 230 |
| *T. crassum* X *H. vulgare* no. 4 observed | 17.71 | 4.56 | 0.37 | 0.02 | 6.25 | 130 |
| Average of hybrids 2 and 4 | 18.62 | 4.12 | 0.36 | 0.01 | 5.73 | 360 |
| *T. crassum* polyhaploid[a] | 10.47 | 4.81 | 0.28 | 0.02 | 6.34 | 184 |
| *H. vulgare* haploid[b] | 6.90 | 0.04 | | | 0.04 | 589 |
| Sum of haploids | 17.37 | 4.85 | 0.28 | 0.02 | 6.38 | 773 |

[a] Shigenobu, T.; Sakamoto, S. (1977)
[b] Sadasaviah, R.S.; Kasha, K.J. (1971)

*Cytology of Hybrids*

The two hybrids obtained from the intergeneric cross between *T. crassum* and *H. vulgare* cv. 'Bomi' had a somatic root tip chromosome number of 2n = 28. As shown in Figure 2 the expression of satellites of one species was being suppressed by the other. Only two satellited chromosomes were observed instead of the expected number of four.

Chromosome pairing at MI in the PMCs of the hybrids is shown in Table 2 together with data from haploids of the parental species. Meiotic configurations were observed in both hybrids (Figs. 3, 4). The number of bivalents per cell ranged from 0 to 9 and 3 out of 360 cells showed one quadrivalent configuration. The mean chromosome pairing per cell as an average of both hybrids was $18.62^{I} + 4.12^{II} + 0.36^{III} + 0.01^{IV}$.

## Discussion

The crossability between *T. crassum* and *H. vulgare* cv. 'Bomi' at 15% was exceptionally high compared to crossability between other species combinations from the same two genera. For example, hybrids between *T. aestivum* and *H. vulgare* were obtained at a frequency of only 0.23% of pollinated florets (Fedak 1980). Similarly, the haploid of *T. crassum* was obtained at a very low frequency by means of the *H. bulbosum* (2n = 28) technique (Shigenobu and Sakamoto 1977). In the latter a seed set of 46.25% was obtained following pollination but only one out of 85 cultured embryos grew for a seedling frequency of 0.3%.

The high crossability may be under the control of specific crossability genes. Genes that control crossability have been identified in *T. aestivum* and assigned to specific chromosomes. The major genes in 'Chinese Spring' that facilitate crossability with *Secale cereale* are located on chromosomes 5A and 5B (Riley and Chapman 1967) as are the genes that permit crossability with *H. bulbosum* (Snape et al. 1979). In the latter combination, additional minor genes that enhance crossability with *H. bulbosum* are located on chromosomes 1B, 1D, 2D, 3A, 4A, 4B and 6D while chromosome 5D carries gene(s) that significantly depress crossability. Genes in 'Chinese Spring' that permit crossability with *H. vulgare* cv. 'Betzes' are located on chromosomes 5A, 5B and 5D (Fedak unpublished). It was more difficult to identify chromosomes in 'Chinese Spring' that had an enhancing effect on crossability with 'Betzes' since crossability between the two species was very low (~ 1%) and no clear indication of enhancement was observed among D genome chromosomes. It is conceivable that in *T. crassum*, in the absence of A and B genomes, the D genome chromosomes with enhancing effects, 1D, 2D and 6D that are present in two doses (D and $D^2$ genomes) confer high crossability on that species.

The average chiasma frequency in the two intergeneric hybrids obtained in the present investigation was compared to chromosome pairing reported for haploids of *H. vulgare* (Sadasaviah and Kasha 1971) and the polyhaploid of *T. crassum* (Shigenobu and Sakamoto 1977). In *H. vulgare*, a diploid species, the observed chromosome pairing in the haploid was of the non-homologous type while in the polyhaploid of *T. crassum* the observed pairing was presumed to be homoeologous, at least between the D and $D^2$ genome chromosomes. The frequency of paired configurations in the intergeneric hybrid was quite similar to the sum of paired combinations in parental haploids that in fact was not greatly different from paired configurations in the polyhaploid of *T. crassum* since the haploid of *H. vulgare* contributed only 0.04 bivalents to the total (Table 2). This indicates that chromosome pairing in the hybrid was limited to certain homoeologous genomes, probably between the D and $D^2$ genomes of *T. crassum*, occasionally the M genome and at some very low frequency perhaps the *H. vulgare* genome. The very low frequency of trivalents and quadrivalents indicated no simultaneous pairing of chromosomes from more than two of the four genomes, implying either a lack of homoeology between all genomes or a lack of expression of homoeology as by a meiotic pairing control mechanism. These results also imply that the presence of the *H. vulgare* genome in the hybrid does not affect the *T. crassum* meiotic pairing control mechanism since chromosome pairing in the intergeneric hybrid

was not appreciably different from pairing in the *T. crassum* polyhaploid.

The level of chromosome pairing in barley-wheat hybrids reported thus far is low or negligible. The chiasma frequency in various varietal combinations of *H. vulgare* × *T. aestivum* has ranged from 1.5-1.8 in 'Betzes' × 'Chinese Spring' hybrids (Fedak 1977; Cauderon et al. 1978) to 0.55 in 'Marker' × 'Tobari 66' (Mujeeb et al. 1978). In other species combinations the pairing has been variable, ranging from 0.91 chiasma per cell in *T. timopheevi* × *H. bogdanii* (Kimber and Sallee 1979) to 2.23 in a hybrid from *H. chilense* × *T. aestivum* (Martin and Chapman 1977). The polyploid wheat species listed above have genome constitutions of ABD or AB but no duplicated genomes as does *T. crassum*. The D and $D^2$ genomes of the latter are homoeologous and even considering the chromosomal differentiation that has taken place; cells with seven bivalents should be expected at MI in the polyhaploid. Since an average of 4.81 bivalents were observed it leads to the supposition that meiotic pairing control genes have reduced the expression of existing homoeology. The observed chromosome pairing in hexaploid is the end result of the promotive and repressive effects of major and minor genes. The major meiotic pairing control gene of wheat (*Ph*) located on chromosome 5BL would not be present in *T. crassum*. However, other genes with similar but weaker activity are present in the D genome. A gene located on $5D^L$ has a weak pairing promoting function (Feldman 1966) as has a gene on the 3D$\alpha$ arm while the opposite arm, 3D$\beta$, has a strong effect on restricting the pairing of homoeologues (Mello-Sampayo and Canas 1973). Activation of the function of the latter genes could be under the control of chromosome 5B. It has been shown that the degree of suppression of pairing of homoeologous chromosomes can be proportional to the number of doses of the 5B gene present (Feldman 1966). The dosage effect of minor genes has not been reported but may function in the same way. In the polyhaploid of *T. crassum* with two doses of the D genome and thus two doses of the pairing suppressor gene on chromosome arm 3D$\beta$, the bivalent frequency is reduced from the expected number of seven. The lack of pairing between chromosomes of *H. vulgare* and *T. crassum* in the intergeneric hybrid may also be a consequence of the double dose of the 3D$\beta$ gene.

The intergeneric hybrids between *T. crassum* and *H. vulgare* have been synthesized quite readily and have been vegetatively quite vigorous but thus far completely sterile. Attempts at chromosome doubling by conventional means have failed and the hybrids have not set any seed when backcrossed by the parental strains. Chromosome doubling attempts through in vitro callus culture of hybrid tissue have shown some promise (Nakamura et al. 1981) and are presently in progress. This unique hybrid offers an additional potential for the transfer of genetic traits from the genus *Triticum* to cultivated barley in addition to studies of genomic and evolutionary relationships between the genera.

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