

Apomictic progeny derived from intergeneric *Hordeum-Triticum* hybrids

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ABSTRACT: Intergeneric hybrids between *Hordeum vulgare* cv. Manker \times *Triticum turgidum* cv. Cocorit 71, and *H. vulgare* cv. Manker \times *T. aestivum* cvs. Bonza and Chinese Spring were backcrossed to their respective wheat parent cultivars in attempts to produce backcross-1 seed. The backcross chromosome composition was expected to be $2n = 5x = 35$ HAABB for the *T. turgidum* backcross, and $2n = 7x = 49$ HAABBDD for the *T. aestivum* backcross. From each cross, however, apomictic plants were obtained that were of similar genetic composition to the F_1 hybrids: $2n = 3x = 21$ for *H. vulgare* \times *T. turgidum*; and $2n = 4x = 28$ for *H. vulgare* \times *T. aestivum*. The significance and details of these observations are discussed.

INTERGENERIC hybridization efforts, other than crosses that produce hybrid *Triticum-Secale*, have increased during the 1970s, motivated partially by the work of Kruse in Denmark. Although wheat can be crossed with apomictic *Agropyron scabrum*¹, pseudogamous seed formation of agricultural utility in intergeneric hybrids within the *Triticeae* seems limited to the observation of Kruse⁵ for the *Triticum aestivum* \times *Avena sativa* cross. Instead of a hybrid with 42 chromosomes, a euploid *T. aestivum* plant was recovered that exhibited electrophoretic variations.

In our experiments euploid plants from intergeneric crosses also occurred, but since the possibility existed for confounding results by other processes⁷, an absolute confirmation of apomixis remained elusive. Recently while backcross-1 (BC_1) progenies from (*Hordeum vulgare* - *T. turgidum*) \times *T. turgidum* and (*H. vulgare* - *T. aestivum*) \times *T. aestivum* were being advanced, cytological confirmation of apomixis was possible. The details are reported here.

Materials and Methods

The intergeneric hybrids between *Hordeum vulgare* \times *Triticum turgidum*, and *H. vulgare* \times *T. aestivum* were maintained under growth chamber conditions of 14 hours day, 15°C day/10°C night, and 45 percent relative humidity. The hybrids were a product of CIMMYT's intergeneric hybridization program in wheat, and have been reported elsewhere⁸⁻¹⁰. Hybrid spikes were meiotically analyzed using Feulgen or 2 percent propionic-orcein⁹, and other spikes were used for

backcrossing to the respective wheat parental cultivar⁸⁻¹⁰. For somatic analyses of backcross-1 plants, the schedule of Mujeeb et al.⁶ was followed; details of these results are presented in Mujeeb-Kazi and Rodriguez⁸⁻¹⁰. Each BC_1 plant was meiotically analyzed and maintained under greenhouse conditions of approximately 15 hours natural daylight, 20°C day/12°C night, 60 percent relative humidity day/45 percent relative humidity night. The BC_1 plants that possessed $2n = 3x = 21$ from (*H. vulgare* - *T. turgidum*) \times *T. turgidum* and $2n = 34x = 28$ from (*H. vulgare* - *T. aestivum*) \times *T. aestivum* were cytologically analyzed for confirmation of the apomixis phenomenon.

Results and Discussion

The meiotic relationships in the *H. vulgare* \times *T. turgidum* hybrid were 19.26 univalents, 0.39 bivalents, 0.46 ring bivalents, 0.02 trivalents, with a chiasmata frequency of 1.21 per cell. The *H. vulgare* cv. Manker \times *T. aestivum* cv. Bonza hybrid had a mean chromosome pairing relationship of 23.87 univalents, 1.40 bivalents, 0.45 ring bivalents, 0.09 trivalents, 0.03 quadrivalents with a chiasmata frequency of 2.60 per cell. The mean pairing for the hybrid between cv. Manker \times cv. Chinese Spring was 23.85 univalents, 1.36 bivalents, 0.24 ring bivalents, 0.25 trivalents, 0.05 quadrivalents, with 2.63 chiasmata per cell. The chromosome pairing details are reported elsewhere⁹. There were 11 BC_1 seed obtained from the cv. Manker - cv. Chinese Spring \times cv. Chinese Spring combination, and one seed from cv. Manker - cv. Bonza \times cv. Bonza. The spikes of cv. Manker - cv. Cocorit 71 (*T. turgidum*) \times cv. Cocorit 71 set eight BC_1 seed of which seven germinated.

Two BC_1 plants from the *H. vulgare* - *T. aestivum* \times *T. aestivum* combination, one with cv. Bonza and one with cv. Chinese Spring, had chromosome counts of 28 and 27 instead of the expected $2n = 7x = 49$, HAABBDD. Of the seven BC_1 plants from *H. vulgare* - *T. turgidum* \times *T. turgidum*, six were of the HAB, $2n = 3x = 21$ composition, with one having the expected $2n = 5x = 35$, HAABB backcross combination. The presence of these plants with 28, 27, and 21 chromosomes provides the apomictic confirmation, since this is the sole phenomenon that operates to yield such a progeny. The F_1 hybrids were all male sterile, unable to set seed without the influence of backcross pollen. Seventy-five F_1 spikes were bagged to serve as controls; of these, 25 had florets treated with gibberellic acid (75 ppm). In both cases no seed set occurred. Once this was determined, representative spikes were indiscriminately pollinated to produce BC_1 seed. No effort was made to record the spike crossed data.

Gametic instability is frequently observed in F_1 hybrids and backcross progeny of the barley \times wheat, and intraspecific wheat combinations^{2-4,7,10}. This explains the 27 chromosomes of the apomictic plant derived from the Chinese Spring backcross. If such an unreduced egg-cell had been fertilized by *T.*

aestivum pollen, a 48-chromosome plant would have resulted, and an unreduced egg-cell with 29 chromosomes would have yielded a BC_1 plant with 50 chromosomes upon pollination with *T. aestivum*. Such BC_1 plants have been obtained^{9,10}.

The mechanism of origin of the apomictic progeny or the backcross progeny is the function of unreduced egg-cell formation. This is a partial mode of reproduction possible in facultative apomicts¹. Parthenogenetic development of the unreduced egg-cells would yield uniform maternal offspring genetically identical with the mother plant as in vegetative reproduction, maintaining the same meiotic genetic recombination status. This is apparent from the meiotic chromosome pairing relationships of the three F_1 ancestors and the apomictic hybrid progeny in Table I. The U-hybrids¹ (i.e., unreduced-egg), if fertilized by *T. turgidum* or *T. aestivum*, yield the $2n = 5x = 35$ pentaploid or $2n = 7x = 49$ heptaploid seed if aneuploidy is not involved on the maternal side. The apomictic and BC_1 were generally well filled and had copious endosperm, suggesting male gamete-polar nuclei triploid fusion in all cases, leaving the unreduced egg-cell either to be fertilized or triggered for parthenogenetic seed formation.

The meiotic analyses of the three BC_1 apomictic plant types indicate a close similarity of chromosome pairing to their respective F_1 hybrid ancestor (Table I). This observation sheds light on how maternal "euploids", instead of F_1 hybrids, may be produced when new intergeneric combinations are attempted. These "euploids" would maintain the maternal chromosome complement and have normal meiotic behavior. To what extent apomictic frequency exists would be left to the individual investigator's judgment. A euploid plantlet from intergeneric hybridization should be given its share or origin via pseudogamoapomixis instead of being classified as an outcross or a selfed product due to an error component.

The apomixis results have been of practical value in propagating the *H. vulgare* \times *T. turgidum* hybrid. Of the two original F_1 plants, clonal propagation was ineffective because of slow tillering. Now, from the seven BC_1 plants, six are cytologically similar to the F_1 ancestor. These have been backcrossed to cv. Cocorit 71. It has yet to be determined whether the progeny from this backcross with Cocorit 71 is still composed of a high frequency of the HAB, $2n = 3x = 21$, F_1 *H. vulgare* \times *T. turgidum* composition, or whether the expected (*H. vulgare*-*T. turgidum*) \times *T. turgidum* BC_1 progeny will possess a $2n = 5x = 35$ HAABB chromosome composition. The former will aid in providing additional F_1 hybrid progeny, with the latter types serving for barley addition line development on successive backcrossing to *T. turgidum* and routine cytological evaluation as proposed at the *T. aestivum* level⁹.

The *H. vulgare* \times *T. aestivum* hybrids were fair tillering and propagating them as clones was more convenient than propagating the *H.*

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Table I. Mean chromosome pairing relationships in hybrids of *H. vulgare* cv. Manker × *T. turgidum* cv. Cocorit; *H. vulgare* cv. Manker × *T. aestivum* cvs. Bonza, Chinese Spring, and of their apomictic derived progeny by backcrossing to the respective male parent cultivar

F ₁ or BC ₁ hybrid combination detail	Somatic count		Mean meiotic relationship				Mean chiasmata freq. per cell	
<i>H. vulgare</i> × <i>T. turgidum</i> ⁹	2n = 3x = 21, HAB	19.26 _t	0.39II	0.46II(.)*	0.02III		1.21	
(<i>H. vulgare</i> – <i>T. turgidum</i>) × <i>T. turgidum</i>	2n = 3x = 21, HAB	19.31 _t	0.39II	0.45II(.)	0.03III		1.20	
<i>H. vulgare</i> × <i>T. aestivum</i> cv. Bonza ⁹	2n = 4x = 28, HABD	23.87 _t	1.40II	0.45II(.)	0.09III	0.03IV	0.01VI	2.60
(<i>H. vulgare</i> – cv. Bonza) × cv. Bonza	2n = 4x = 28, HABD	23.84 _t	1.41II	0.43II(.)	0.10III	0.04IV		2.58
<i>H. vulgare</i> × <i>T. aestivum</i> cv. Chinese Spring ⁹	2n = 4x = 28, HABD-1	23.85 _t	1.36II	0.24II(.)	0.25III	0.05IV		2.63
(<i>H. vulgare</i> – cv. Chinese Spring) × cv. Chinese Spring	2n = 4x = 27, HABD-1	22.99 _t	1.30II	0.22II(.)	0.24III	0.04IV		2.61

(.)* = ring bivalent

vulgare × *T. turgidum* hybrids. Recovering the low frequency of apomicts in the (*H. vulgare*-*T. aestivum*) × *T. aestivum* BC₁ population merely serves to confirm the apomictic phenomenon.

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