Theor Appl Genet (1985) 70:265–270



# New hybrids of *Hordeum parodii* with *Hordeum vulgare, H. bogdanii, Agropyron caninum* and X *Triticosecale* *

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Received December 4, 1984; Accepted December 19, 1984
Communicated by G. S. Khush

**Summary.** Hybrids were produced from crossing *Hordeum vulgare, H. bogdanii, Agropyron caninum* and X *Triticosecale* onto *H. parodii* (6x or 4x). The rates at which hybrids were produced, expressed in terms of plantlet establishment as percent pollinated florets, ranged from 0.47%, (6x *H. parodii* × 6x X *Triticosecale* cv. 'Welsh') to 6.3% (4x *H. parodii* × 2x *H. vulgare* cv. Betzes). Based on frequencies of paired configurations at MI, autosyndetic pairing appeared to be promoted by the presence of a *Secale cereale* genome but suppressed by the genome of *H. vulgare.*

**Key words:** *Hordeum* – *Agropyron* – X *Triticosecale* – Interspecific and intergeneric hybrids – Chromosome pairing

## Introduction

In recent years, increased interest has been observed in wild relatives of cultivated plants, due to a distinct possibility of their use as alien genetic material for improvement of existing cultivars.

In the genus *Hordeum,* 36 species have been listed recently by Baum et al. (1984), although Bothmer et al. (1981) listed only 28 species. Among these species there are at least two species complexes which are each represented by three cytotypes (2x, 4x, 6x). These include *H. brevisubulatum* s.l. and *H. parodii.* Two other complexes which have been studied in the past, although not in great detail, include *H. brachyantherum* s.l. (or *H. jubatum*) and *H. murinum.* Based on these studies, it was shown that the three American hexaploid species of *Hordeum,* namely *H. lechleri, H. procerum* and *H. arizonicum,* each possesses the two genomes of *H. brachyantherum,* the third genome in each case being unknown (Rajhathy et al. 1964). The species complexes associated with *H. brevisubulatum* and *H. parodii* have not been studied in any detail.

*Hordeum parodii,* a native of South America (mainly found in Argentina) is represented by three cytotypes (2x, 4x, 6x) but the genome relationships of these cytotypes are not known. Only recently this species, particularly the hexaploid *H. parodii,* has been utilized for interspecific and intergeneric hybridization (Subrahmanyam 1978a; Jacobsen and Bothmer 1981; Fedak 1983; Fedak and Armstrong 1981). These studies, however, did not elucidate the genomic constitution of hexaploid *H. parodii.* Polyhaploids of hexaploid *H. parodii* have been studied (Subrahmanyam 1977) and on the basis of exclusive bivalent formation in the hexaploid and low pairing in the polyhaploid, an allopolyploid genomic structure has been suggested. A hemizygous ineffective diploidizing genetic control of homoeologous chromosome pairing has also been suggested (Subrahmanyam 1978b). If the species is a true allopolyploid, there should be no requirement for a diploidizing system because the need for the latter would arise only in a segmental allopolyploid. Considerable pairing in a *H. parodii* × *S. cereale* hybrid also suggested homoeology between two or possibly all the three genomes of hexaploid *H. parodii* (Fedak and Armstrong 1981). Further study of interspecific and intergeneric hybrids involving *H. parodii* is required to establish the genomic constitution and meiotic pairing control mechanism.

In the present study, tetraploid and hexaploid *H. parodii* have been used successfully for hybridization with four other species from three different genera to produce five different hybrids for the first time. Morphology and meiosis of these hybrids was examined. Another hybrid between *H. parodii* (6x) and *S. cereale* cv. 'Petkus' was also produced and examined, the results for which are part of another study and are being published separately but will be utilized for the relevant discussion in this paper also.

## Materials and methods

### *Plant material*

The details of species and taxa used as parents with their accession numbers, chromosome numbers and the sources are given in Table 1.

* Contribution No. 759 Ottawa Research Station

*Plant culture*

The plants were grown from seed in a controlled environment cabinet at a temperature of 20 °C/15 °C day/night and 16 h days provided by a combination of fluorescent and incandescent lamps supplying illumination at the intensity of 800 micro Einstein $m^{-2}$ $s^{-1}$. The plants were vernalized as seedlings for 8 weeks at 4 °C and 8 h days prior to planting in a growth cabinet.

*Crossing*

*Hordeum parodii,* whether hexaploid or tetraploid, was always used as the female parent and their spikes were emasculated two days prior to anthesis and bagged with dialysis tubing. Pollen from the other parent in each case, was collected and applied to emasculated spikes by means of a small brush. At 24 and 48 h after pollination, $GA_3$ at 75 ppm was applied to the pollinated florets with a hypodermic syringe. At 15 days after pollination, the hybrid embryos were excised and plated on a $B_5$ medium modified by the exclusion of 2,4-D. When shoots appeared, seedlings were moved into diffuse and eventually into strong light and were raised in the same manner as the parental material.

*Cytological methods*

Spikes of hybrid plants were fixed in Carnoy's solution (6 parts ethanol : 3 parts chloroform : 1 part glacial acetic acid) for at least 24 h and squashed in acetocarmine. For better staining, anthers of appropriate meiotic stages, were immersed in Snow's solution (Snow 1963) overnight before they were squashed.

## Results

*Synthesis of hybrids*

Data on seed set, embryo yield and plantlets raised through embryo culture techniques for five different interspecific and intergeneric hybrids are presented in Table 2. The most difficult species to cross onto 6x *H. parodii* was X *Triticosecale* cv. 'Welsh', where hybrids were produced at the rate of 0.47% of pollinated florets. The seeds obtained from this cross had very few embryos and these were poorly differentiated. The hybrids that were made most readily were those from the cross 4x *H. parodii* × *H. vulgare* cv. 'Betzes' at 6.3% of pollinated florets compared to 1.8% when the hexaploid form of *H. parodii* was crossed with 'Betzes'. Although the embryos from the cross 6x *H. parodii* × *A. caninum* were not produced at a very high frequency, they were usually well differentiated and germinated readily.

*Morphology of hybrids*

In terms of hybrid morphology there was no particular overall pattern, the hybrids being intermediate or resembling a maternal or paternal parent. The hybrid between 6x *H. parodii* and *H. bogdanii* was somewhat intermediate to the parents, having slightly awnletted and slightly pubescent lemmas. The hybrids from both cytotypes of *H. parodii* crossed to 'Betzes' were somewhat similar in morphology. They resembled the paternal (a typical two-rowed cultivar) parent in spike structure, having one floret per spikelet and three spikelets per rachis node with lateral spikelets being rudimentary. The awn development on lemmas of central florets and on outer glumes of all florets was greater than on 'Betzes'. The hybrids of 6x *H. parodii* × *S. cereale* were tall and vigorous with profuse tillering. Whereas the floral structure of *H. parodii* consisted of a simple foret per spikelet and that of *Secale* consisted of two florets per spikelet, the hybrid was somewhat asymmetrical in structure having one or two florets per spikelet but one spikelet per rachis node. The 6x *H. parodii* × 'Welsh' hybrid resembled the latter parent in spike structure, having two florets per spikelet plus a third rudimentary one. The pubescent neck and extruding anthers were quite prominent. The 6x *H. parodii* × *A. caninum* hybrid had a very long, lax spike with two florets per spikelet. The secondary floret was smaller than the primary and subtended by a fairly long pedicel. The outer glumes were longer than those on the paternal parent and on occasional rachis nodes a third vestigal glume was present.

*Meiosis in hybrids*

Considerable variation in bivalent frequency was observed among the hybrids involving *H. parodii* and other species and genera (Table 3). A higher chiasmata frequency was detected in the hybrid of tetraploid *H. parodii* with *H. vulgare* cv. 'Betzes' [0.93 (Fig. 1)] compared to the hybrid of hexaploid form with 'Betzes' [0.06 (Fig. 2)]. The latter hybrid, however, only had 26 chromosomes instead of the expected 28. Hybrids of 6x *H. parodii* with the two cultivars of *Secale* had different amounts of autosyndetic pairing. The hybrid with Prolific had a chiasmata frequency of 5.10 compared to 8.60 for the hybrid with 'Petkus'. The bivalent frequency of 4.20 in the hybrid between 6x *H. parodii* and *H. bogdanii* (Fig. 3) may be indicative of some homology between the genome of the latter and one of the genomes in 6x *H. parodii.* In some cells the bivalent frequency was as high as eight. Similarly, a slightly higher bivalent frequency (5.72) in the hybrid between 6x *H. parodii* and *A. caninum* (Figs. 4 and 5) may be indicative of homology between one genome of each species. The bivalent frequency was as high as 11 in some cells of this hybrid. In addition, occasional heteromorphic bivalents may be an indication of homoeologous pairing between chromosomes of different parental genomes. The hybrid between 6x *H. parodii* and 6x X *Triticosecale* cv. 'Welsh' may be regarded as a

**Table 1.** Species used for hybridization

| Species | Ploidy level | Chromosome no. (2x) | Source |
|---|---|---|---|
| 1. *Hordeum parodii* Covas, s. l | 6x | 42 | Research Stn. CEF, Ottawa (CHC[a] 1451) |
| 2. *Hordeum parodii* Covas, s. l | 4x | 28 | Research Stn., CEF, Ottawa (CHC[a] 1529) |
| 3. *Hordeum vulgare* L. cv. 'Betzes' | 2x | 14 | Research Stn. CEF, Ottawa |
| 4. *Hordeum bogdanii* Wil. | 2x | 14 | USDA, Logan, Utah |
| 5. *Agropyron caninum* (L.) Beav. | 4x | 28 | USDA, Logan, Utah |
| 6. X *Triticosecale* Wittmack cv. 'Welsh' | 6x | 42 | Univ. of Manitoba, Winnipeg |

[a] Canadian-Scandinavian *Hordeum* collection (CHC)

**Table 2.** Frequency of seed set, embryo and plantlet yield from pollinating *H. parodii* with four species

| Hybrid combinations | Florets pollinated | Seeds obtained | Embryos excised | Plantlets obtained (%) |
|---|---|---|---|---|
| 1. *H. parodii* (6x)×*H. vulgare* (2x) cv. 'Betzes' | 55 | 5 | 3 | 1 (1.8) |
| 2. *H. parodii* (6x)×*H. bogdanii* (2x) | 36 | 2 | 2 | 1 (2.7) |
| 3. *H. parodii* (6x)×*A. caninum* (4x) | 128 | 13 | 12 | 6 (4.7) |
| 4. *H. parodii* (6x)×X *Triticosecale* (6x) cv. 'Welsh' | 213 | 7 | 7 | 1 (0.47) |
| 5. *H. parodii* (4x)×*H. vulgare* (2x) cv. 'Betzes' | 32 | 8 | 6 | 2 (6.3) |

**Table 3.** Chromosome pairing in interspecific and intergeneric hybrids involving *Hordeum parodii*

| Hybrid | Chromosome no. of $F_1$s | No. of PMCs examined | Average chromosome associations at metaphase I | | | | | | | c[c] value |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | I | Rod IIs | Ring IIs | Total IIs | III | IV | Xta | |
| 1. *H. parodii* (6x)×*H. vulgare* (2x) cv. 'Betzes' | 26 | 110 | 25.88 (24 – 26) | 0.06 (0 – 1) | – | 0.06 (0 – 1) | – – | – – | 0.06 (0 – 1) | 0.002 |
| 2. *H. parodii* (6x)×*H. bogdanii* (2x) | 28 | 92 | 19.25 (12 – 24) | 3.34 (1 – 6) | 0.86 (0 – 4) | 4.20 (2 – 8) | 0.11 (0 – 1) | – | 5.38 (3 – 12) | 0.192 |
| 3. *H. parodii* (6x)×*Agropyron caninum* (4x) | 35 | 88 | 22.45 (13 – 35) | 5.07 (0 – 10) | 0.66 (0 – 3) | 5.72 (0 – 11) | 0.26 (0 – 2) | 0.08 (0 – 1) | 7.15 (0 – 13) | 0.255 |
| 4. *H. parodii* (6x)×X *Triticosecale* (6x) | 42 | 120 | 25.88 (12 – 31) | 2.88 (0 – 9) | 3.91 (0 – 8) | 6.79 (3 – 12) | 0.86 (0 – 3) | 0.24 (0 – 2) | 13.14 (9 – 25) | 0.312 |
| 5. *H. parodii* (4x)×*H. vulgare* (2x) cv. 'Betzes' | 21 | 82 | 19.19 (11 – 21) | 0.87 (0 – 5) | 0.02 (0 – 1) | 0.89 (0 – 5) | 0.01 (0 – 1) | – – | 0.93 (0 – 5) | 0.066 |
| 6. *H. parodii*[a] (6x)×*Secale cereale* (2x) cv. Petkus | 28 | 86 | 16.66 (12 – 24) | 2.49 (0 – 6) | 2.83 (1 – 6) | 5.32 (2 – 8) | 0.20 (0 – 2) | 0.03 (0 – 1) | 8.60 (3 – 15) | 0.307 |
| 7. *H. parodii*[b] (6x)×*S. cereale* cv. 'Prolific' | 28 | 94 | 19.20 (12 – 28) | 3.00 (0 – 5) | 0.35 (0 – 1) | 3.35 (2 – 5) | 0.70 (0 – 2) | – | 5.10 | 0.182 |

[a] Reproduced from Gupta and Fedak (1985)
[b] Reproduced from Fedak and Armstrong (1981)
[c] Ratio of observed chiasmate arm associations to total possible arm associations per PMC

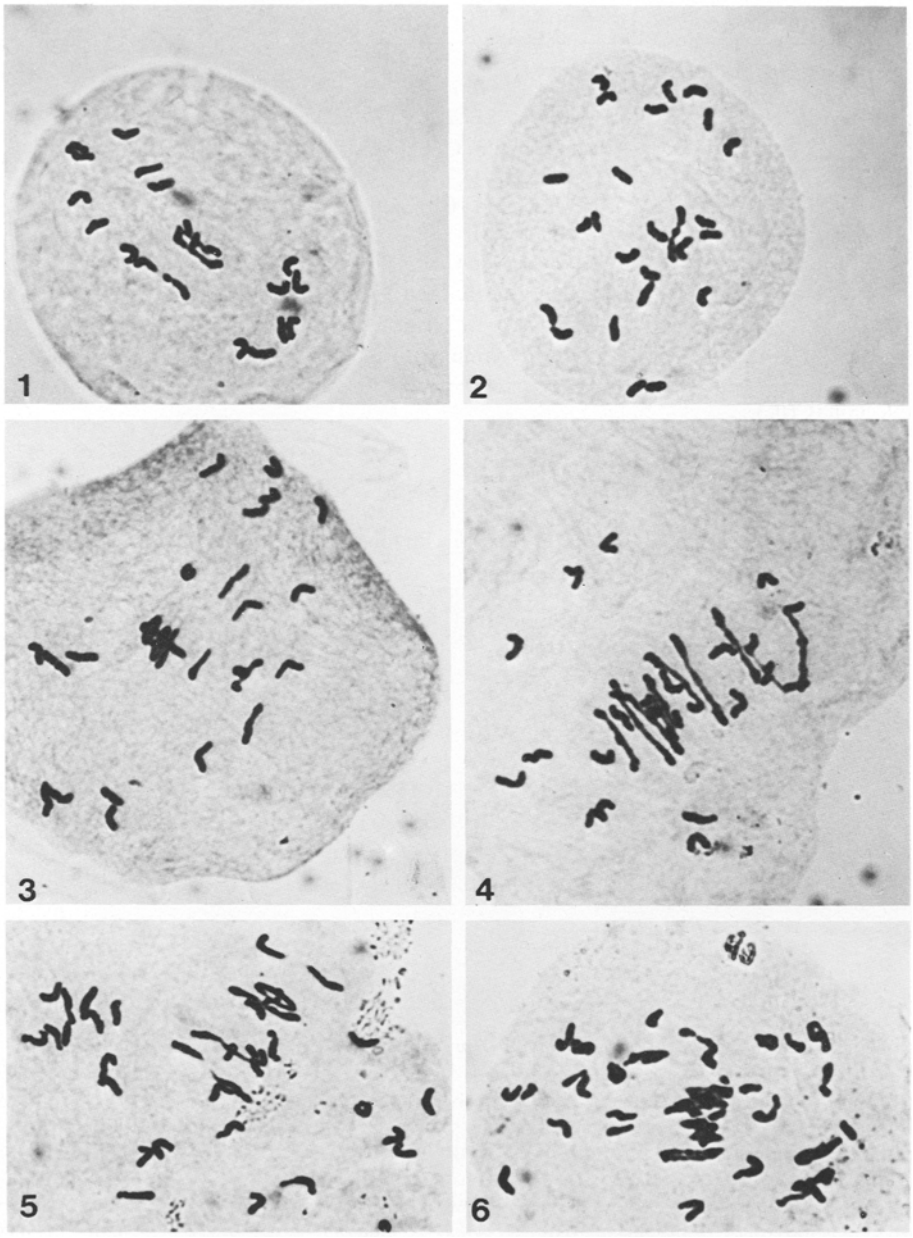


**Fig. 1.** MI in *H. parodii* (4x)×*H. vulgare* (2x) cv. 'Betzes' hybrid showing $3^{II}+15^{I}$

**Fig. 2.** MI in *H. parodii* (6x)×*H. vulgare* (2x) cv. 'Betzes' hybrid (with 2n=26) showing $1^{II}+24^{I}$

**Fig. 3.** MI in *H. parodii* (6x)×*H. bogdanii* (2x) hybrid with $6^{II}+16^{I}$, 3 bivalents have already disjoined

**Fig. 4.** MI in *H. parodii* (6x)×*A. caninum* (4x) hybrid with $10^{II}+15^{I}$

**Fig. 5.** MI in *H. parodii* (6x)×*A. caninum* (4x) hybrid with $5^{II}+25^{I}$

**Fig. 6.** MI in *H. parodii* (6x)×X *Triticosecale* (6x) cv. 'Welsh' hybrid with $1^{III}+5^{II}+29^{I}$

trigeneric hybrid composed of genomes for *Hordeum*, *Secale* and *Triticum*. A considerable amount of autosyndetic pairing was observed in this hybrid (Fig. 6) with an average bivalent frequency of 6.79 and as high as 12 in some cells.

## Discussion

It may be seen from the results of meiotic pairing in the hybrids examined, that the pairing, although ranging from a value of 0.06 chiasmata per cell to 13.14 chiasmata per cell, is not very different than what has been observed in certain hybrid combinations involving *H. parodii*.

In most of the earlier studies, where meiosis was studied either in polyhaploid *H. parodii* or in hybrids involving this species, the pairing was attributed to autosyndesis (Subrahmanyam 1978b; Fedak and Armstrong 1981). This pairing may be compared with the pairing in polyhaploid *Triticum aestivum* and its hybrids with unrelated species (McGuire and Dvorak 1982). In most of the latter cases, the pairing is much lower than that observed in the case of *H. parodii*. This, perhaps, is the basis of a suggestion of hemizygous ineffective genetic control for diploid-like meiotic behaviour in *H. parodii* (Subrahmanyam 1978b). The pairing in two *H. parodii*× *H. vulgare* hybrids (one involving 4x and the other involving 6x *H. parodii*), however, was much lower than the one observed

in polyhaploids of *H. parodii,* suggesting that not only the genome of *H. vulgare* is absent in *H. parodii,* but also that *H. vulgare* genome suppresses the pairing between homoeologous genomes of *H. parodii.* This holds true for the tetraploid as well as hexaploid *H. parodii,* although the suppression effect seems to be more pronounced in the hexaploid. Since the hybrid with 6x *H. parodii* had only 26 chromosomes instead of expected 28, one could also argue that the observed meiotic behaviour could be partly due to the two missing chromosomes, but we see very little possibility of this in view of other available information.

In the remaining three hybrids with *H. bogdanii, A. caninum* and X *Triticosecale,* it can be noticed that chiasmata frequency increased with increase in ploidy level of the hybrid. In order to compare the chromosome pairing in hybrids with different ploidy levels, the c value, suggested by Driscoll et al. (1979), has been calculated in each case. In this connection, chiasmata frequencies in hybrids involving *H. bogdanii* and *A. caninum* may be compared. It will be seen from Table 3 that the values of c in the two hybrids may not differ significantly suggesting that the pairing is either between the homoeologous chromosomes of different genomes of *H. parodii* or between the chromosomes of *H. parodii* and the homoeologous (but not homologous) H genome in the other parent in both cases. Although the total possible chiasmate arm associations in these two hybrids may be the same, the available extra genome in the hybrid *H. parodii* × *A. caninum* (2n = 35), may help chromosomes to find their homoeologues for pairing more readily. This may perhaps account for a slightly higher c value in this hybrid.

A similar comparison can also be made between the data collected for the first time in a hybrid between *H. parodii* and a 6x X *Triticosecale* ('Welsh') and those already available for the hybrid *H. parodii* × *S. cereale.* Although the chiasmata frequency per cell is higher in the former, it can be easily explained on the basis of difference in ploidy level such that the values of c in the two cases are largely similar, although in a previous report by Fedak and Armstrong (1981), the pairing in *H. parodii* × *S. cereale* was relatively low, suggesting genotypic differences in the rye genome promoting chromosome pairing (Lelley 1976). It will also be noticed that in these two cases, the frequencies of ring bivalents are much higher than in other hybrid combinations, where the ring bivalents were rather rare. However, this pairing in these two cases is higher than in the other hybrids and can be attributed to the effect of rye chromosomes promoting heterogenetic or homoeologous chromosome pairing. Therefore, a rye genome in single dose, when received even in the constitution of triticale gametes can still promote the pairing in the same manner as the rye genome alone does. The effect of the rye genome in promoting homoeologous pairing between wheat chromosomes has already been suggested in several studies (Feldman 1966; Lelley 1976; Dvorak 1977).

In wheat, a dosage effect has been shown for the influence of the rye genome on homoeologous pairing (Miller and Riley 1972; Gupta and Priyadarshan, unpublished), such that two doses of rye induced some homoeologous pairing in the haploid wheat complement while the effect of three doses was more pronounced. It appears that the extent of chromosome pairing in this case actually depends on the ratio between the number of wheat genomes to those of rye. In the genus *Hordeum,* however, although a dosage effect is observed, it has an opposite effect. As can be seen in the present study, a single dose of rye promotes pairing but in an earlier study, Rajhathy (1967) reported complete asynapsis in a 4x Petkus rye × *H. jubatum* hybrid (ratio of barley : rye genomes = 1 : 1). It is, however, interesting to note that the presence of two doses of rye genome does not always cause asynapsis because in a 6x (*H. depressum* × *H. compressum*) × 4x Svalof rye (*S. cereale*) hybrid considerable pairing was observed. In the latter hybrid (2n = 35) the ratio of *Hordeum : Secale* genomes was 3 : 2 and 1 : 1 which may explain the difference [a mean of only 7.4 univalents was observed in the hybrid with 2n = 35 Schooler (1967)].

From the above discussion it is obvious that genome analysis in polyploid *Hordeum* species may be difficult by conventional meiotic analysis of interspecific hybrids for the following reasons: First, the genomes of each of several polyploid species of *Hordeum* including *H. jubatum, H. brachyantherum, H. parodii, H. lechleri,* and *H. arizonicum* are at least partly related. Second, that the genetic control for diploid-like meiotic behaviour in these polyploids is not entirely like that in *Triticum,* but it is hemizygous ineffective (Subrahmanyam 1978 b) leading to some degree of pairing (which is higher than in bread wheat) in polyhaploids and in hybrids with related and unrelated species. Third, the S and H genomes known to the present in polyploid *Agropyron* and *Elymus* are also related to some extent showing pairing in hemizygous condition in hybrids, as in a hybrid between *H. brevisubulatum* s.l. (2x) and *A. spicatum* examined recently by Dewey (personal communication). Fourth, although the genomes of polyploid *Hordeum* are related (homoeologous) with each other and with the H and possibly the S genome found in *Agropyron* and *Elymus,* they are not as closely related to the genomes in the genus *Triticum,* as evident from the study of meiosis in intergeneric hybrids between *Triticum* and *Hordeum* (Fedak 1984 b). Fifth, the occasional presence of trivalents and quadrivalents in hybrids involving *Hordeum* species also suggests that structural differences like translocations are present between different H genomes and also between several S and H genomes. The underlying reason for difficulty in genome analysis in most cases is due to the inability to distinguish between auto- and allosyndesis.

*Acknowledgements.* The authors are grateful to CIDA/NSERC of Canada for the award of a research associateship to the senior author (PKG), during the tenure of which the work was undertaken.

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