

HYBRIDS BETWEEN *HORDEUM VULGARE* L. AND *HORDEUM JUBATUM* × 4*x* *SECALE CEREALE*¹

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Summary. Trihybrids were produced by embryo culture from intercrossing of *Hordeum vulgare* L. and F_1 hybrid of *Hordeum jubatum* × 4*x* *Secale cereale*. Morphologically the plants resembled the pollen parent in sheath and peduncle pubescence characteristic of rye. Most of the plants had a somatic chromosome number of 21, consisting of 7 *H. vulgare*, 7 *H. jubatum* and 7 *S. cereale* chromosomes. Hybrids with the chromosome numbers of 17, 19 and 22 were also obtained. At metaphase I most PMCs contained unpaired chromosomes; a small degree of nonhomologous pairing expressed as bivalents, or secondary associations were observed.

The frequency of hybrid plants resulting from barley-rye crosses is very low and the hybrids are usually weak (Kruse 1967; Fedak 1977, 1978; Cooper et al. 1978; Thomas, Pickering 1979; Wojciechowska 1984). More viable are reported to be trigeneric hybrids of (barley × wheat) × rye (Fedak, Armstrong 1980; Clauss 1980). The incompatibility between barley and rye is compensated by wheat ABD or AB genomes, and normally growing and viable hybrids can be obtained (Clauss 1980).

Hordeum jubatum crosses relatively more easily with *H. vulgare* (Clauss, Kunert 1979) and with *Secale cereale* (Wojciechowska 1978; Clauss, Kunert 1981), than *H. vulgare* with *S. cereale*. The crossing of *H. jubatum* × 4*x* *S. cereale* was carried out simultaneously with the hybridization of *H. vulgare* with *S. cereale*. The hybrid production was easier in the first cross combination (Wojciechowska 1984).

The present paper deals with the morphology and cytology of *Hordeum vulgare* × × (*Hordeum jubatum* × 4*x* *Secale cereale*) trihybrids.

MATERIAL AND METHODS

Trihybrids were obtained via embryo culture from *Hordeum vulgare* (four cultivars of four-rowed diploid barley with spring growth habit — Menuet, Aramir, Trumpf, Emir) pollinated by F_1 hybrid of *H. jubatum* × 4*x* *S. cereale* (Wojciechowska

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Table 1. Chromosome numbers and configurations at MI of *H. vulgare* × *H. jubatum* × *4x S. cereale* hybrids

| Hybrid number | No cells | No chromo- somes in pmc's | % total cells | Primary associations | | | | | | X ta** | | | | Secondary associations** | | | | | | | | | | |
|---------------|----------|---------------------------------|------------------|----------------------|-----------------|--------------|-------------|------------|-------------|--------|------|------|-------|--------------------------|-----|------|-------|------|------|------|------|------|------|--|
| | | | | I* | | II** | | | | H/H | C/C | H/C | total | H-H | C-C | H-O | total | | | | | | | |
| | | | | H | C | H/H rod | H/H ring | C/C rod | C/C ring | | | | | | | | | rod | rod | | | | | |
| 54/1 | 100 | 22 | 4 | 14.5 (13-15) | 7.0 | | | | | | | | | | | | 1 | | | | 1 | | | |
| | | 21 | 72 | 12.6 (5-14) | 6.5 (4-7) | | | | | | | | | | | | | 38 | 4 | | | 22 | 64 | |
| | | 20 | 13 | | 12.7 (11-14) | 6.7 (6-7) | | | | | | | | | | | | 2 | | | | 2 | 4 | |
| | | 19 | 9 | | 12.0 | 7.0 | | | | | | | | | | | | | | | | | | |
| | | 18 | 2 | | 11.5 (11-12) | 6.5 (6-7) | | | | | | | | | | | | | | | | | | |
| | | | | | \bar{x} | | | | | | | | | | | | | 0.41 | 0.04 | | | 0.24 | 0.69 | |
| | | 61 | 21 | 88.5 | 13.9 (12-14) | 5.4 (5-7) | 1 | 2 | 42 | | | 3 | 42 | | | | | 16 | | | | | 16 | |
| 105 | | 20 | 3.3 | 13.0 | 5.0 | | | 2 | | | | 2 | | | | | 2 | | | | | 2 | | |
| | | 19 | 4.9 | 12.3 (12-13) | 4.7 (4-5) | | | 3 | | | | 3 | | | | | | 3 | | | | | 3 | |
| | | 18 | 1.6 | | 11.0 | 5.0 | | | 1 | | | 1 | | | | | 1 | | | | | 1 | | |
| | | 17 | 1.6 | | 10.0 | 5.0 | | | 1 | | | 1 | | | | | 1 | | | | | 1 | | |
| | | | | | \bar{x} | | | | 0.02 | 0.02 | 0.80 | 0.05 | 0.80 | | | | 0.85 | 0.26 | | | | | 0.26 | |
| | | 48 | 23 | 2.3 | 12.0 | 6.0 | | | | | | | | | | | | 1 | | | | 1 | 2 | |
| | | | 22 | 20.9 | 15.0 (15-16) | 6.8 (6-7) | | | | | | | | | | | | 1 | | | | 1 | 2 | |
| | | | 21 | 9.3 | 13.0 (10-14) | 7.0 | | | | | | | | | | | | | | | | | 2 | |
| | | | 20 | 18.6 | 11.9 (9-15) | 6.4 (5-7) | | | | | | | 1 | | | | | 2 | | | | 4 | 6 | |
| | | | 19 | 18.6 | 12.5 (11-13) | 5.7 (4-7) | | | | | | | | | | | | 1 | | | | 2 | 3 | |
| | | 18 | 20.9 | 11.7 (11-13) | 6.2 (5-7) | | | | | | | | | | | | | | | | | | | |
| | | 17 | 2.3 | 10.0 | 5.0 | | | | | | | | | | | | | | | | | 1 | | |
| | | 16 | 4.7 | 9.5 (9-10) | 6.5 (6-7) | | | | | | | | | | | | | | | | | | | |
| | | 14 | 2.3 | 8.0 | 6.0 | | | | | | | | | | | | | | | | | | | |
| | | | | \bar{x} | | | | 0.02 | 0.02 | 0.80 | 0.02 | 0.80 | | | | 0.02 | 0.16 | 0.02 | | 0.19 | 0.87 | | | |

| 189/1 | 111 | 25 | 0.9 | 18.0 | 7.0 | 4 | 8 | 7 | 10 | 20 | 27 | 47 | 1 | 20 | 1 | 11 | 1 | 32 |
|-------|-----|----|------|---------|-----------|------|------|------|------|------|------|------|------|------|------|------|------|----|
| | | 22 | 0.9 | 13.0 | 7.0 | | | | | | | | | | | | | |
| | | 21 | 58.6 | 12.8 | 6.2 | | | | | | | | | | | | | |
| | | 20 | 18.0 | (8-14) | (0-7) | | | | | | | | | | | | | |
| | | 19 | 16.2 | 12.8 | 6.3 | | | | | | | | | | | | | |
| | | 18 | 3.6 | (8-14) | (5-7) | | | | | | | | | | | | | |
| | | 17 | 1.8 | 12.0 | 6.3 | | | | | | | | | | | | | |
| | | | | (10-14) | (5-7) | | | | | | | | | | | | | |
| | | | | 12.0 | 6.0 | | | | | | | | | | | | | |
| | | | | (11-13) | (5-6) | | | | | | | | | | | | | |
| | | | | 11.0 | 4.0 | | | | | | | | | | | | | |
| | | | | (2-6) | (2-6) | | | | | | | | | | | | | |
| | | | | | \bar{x} | 0.04 | 0.07 | 0.08 | 0.09 | 0.18 | 0.26 | 0.44 | 0.28 | 0.01 | 0.15 | 0.04 | 0.34 | |
| 190/1 | 110 | 25 | 0.9 | 18.0 | 7.0 | | | | | | | | | | | | | |
| | | 23 | 1.8 | 13.5 | 5.5 | | | | | | | | | | | | | |
| | | 22 | 4.5 | (12-15) | (4-7) | | | | | | | | | | | | | |
| | | 21 | 45.5 | 13.6 | 5.8 | | | | | | | | | | | | | |
| | | 20 | 26.4 | (12-15) | (4-7) | | | | | | | | | | | | | |
| | | 19 | 18.2 | 12.8 | 6.5 | | | | | | | | | | | | | |
| | | 18 | 2.7 | 12.8 | 6.5 | | | | | | | | | | | | | |
| | | | | (9-14) | (3-7) | | | | | | | | | | | | | |
| | | | | 12.9 | 6.6 | | | | | | | | | | | | | |
| | | | | (11-14) | (5-7) | | | | | | | | | | | | | |
| | | | | 11.7 | 6.1 | | | | | | | | | | | | | |
| | | | | (8-13) | (5-7) | | | | | | | | | | | | | |
| | | | | 11.3 | 6.0 | | | | | | | | | | | | | |
| | | | | (11-12) | (5-7) | | | | | | | | | | | | | |
| | | | | | \bar{x} | 0.06 | 0.09 | 0.05 | 0.06 | 0.25 | 0.17 | 0.03 | 0.45 | 0.08 | 0.04 | 0.34 | | |

H = chromosomes of *H. vulgare* and *H. jubatum*; C = chromosomes of *S. cereale*; * = mean univalents in different pnc types; ** = number of bivalents, chiasma and secondary associations in different pnc types.

1982). Techniques of hybridization and embryo culture were described previously (Wojciechowska 1984).

Out of 15 obtained hybrids 11 were derived from pollination of cv. Menuet (Nos. 54/1, 2; 188; 189/1-5; 190/1-3), 2 from pollination of cv. Aramir (Nos. 57, 105) and 1 had cv. Trumpf (No. 64) and 1 cv. Emir (No. 415) as maternal forms.

The plants were grown in a glasshouse and did not require vernalization.

The cytological techniques employed for somatic chromosome counts and meiotic chromosome behaviour in PMCs were the same as used previously (Wojciechowska 1978, 1979).

The letters used for marking the chromosomes were as follows: V — *H. vulgare*, J — *H. jubatum*, H — *H. vulgare* and *H. jubatum*, C — *S. cereale*.

RESULTS

Hybrids with $2n=21$ and 22 tillered profusely and were very vigorous (Figs 1-2). In contrast, plants with $2n=17$, and 19 grew poorly like barley-rye seedlings (Wojciechowska 1984) and died at 2-4 leaf stage and at early-tillering.

Trihybrids were perennial in growth habit and male features predominated in their morphological characteristics. Features of rye were well manifested in sheath and peduncle pubescence. Spikes of the hybrids were shorter and had longer awns of lemmas than those of the male parent (Fig. 3). The arrangement of spikelets on the rachis was irregular. The spikelets consisted of three equally frequently as well as of two florets. Small, dry anthers contained sterile pollen grains. Pistillody was sporadically noted in florets.

Of 15 hybrids 10 had $2n=3x=21$ with 7 *H. vulgare*, 7 *H. jubatum* and 7 *S. cereale* chromosomes (VJC); 5 plants had $2n=17$ (Nos. 64 and 189/3), $2n=19$ (No. 189/2) and $2n=22$ (Nos. 57 and 105) consisting of 7 *S. cereale* and probably 7 *H. vulgare* and variable number of *H. jubatum* chromosomes. At mitosis and MI of PMCs the chromosomes of *Secale* distinguished by a larger size, however, *H. vulgare* chromosomes could be not distinguished from those of *H. jubatum*. At somatic metaphase, all plants had two SAT chromosomes of *H. vulgare*, moreover, in four plants one SAT chromosome of *H. jubatum* with the largest satellite was present. Also, in four plants one SAT chromosome of rye was visible (Fig. 4).

Meiocytes exhibited characteristic haploid meiosis. Some PMCs contained chromatid inclusion at cytoplasm (Fig. 5) and exhibited chromosome instability at MI. In four out of five studied plants most of PMCs had euploid chromosome number, i.e. the chromosome number was the sum of the parental gametic chromosome numbers (Table 1). In one plant (No. 105) the euploid number was 22 chromosomes. Among PMCs with unstable chromosome numbers most cells were hypoploid; 11.4 - 47.2% of the cells contained 4.8 - 33.3% less chromosomes than the euploid cells and 0.00 - 7.3% of the cells had 4.8 - 19.0% more chromosomes. In hypo- and hyperploid cells the chromosomes below and above the euploid number originated mostly from *Hordeum* (Table 2).

In anthers the meiotic divisions in PMCs were asynchronous. At early prophase

stages the terminal connections between chromosomes were more frequent than at a late prophase (Fig. 6). The results of metaphase I are presented in Table 1. Most of the chromosomes occurred as univalents, some formed end-to-end achiasmatic associations. The bivalents between *Hordeum* chromosomes and between rye chromosomes were most frequent in three plants — Nos. 54/2, 189/1, 190/1 (Figs. 7 - 11). Very few *Secale-Hordeum* heteromorphic bivalents were noted (Fig. 10). Meiotic doubtful associations, probably achiasmatic, were excluded when the chiasma frequency was determined. The mean chiasma frequencies ranging from 0.00 to 0.85 were generally low.

Table 2. Number and percentage of PMCs at MI with chromosomes of *Hordeum* (H) and *Secale* (C) below or above the euploid number

| Hybrid number | No of cells | Hypoploidy | | | | Hyperploidy | | | |
|---------------|-------------|------------|------|--------|------|-------------|-----|--------|-----|
| | | H | | C | | H | | C | |
| | | number | % | number | % | number | % | number | % |
| 54/1 | 100 | 23 | 23.0 | 3 | 3.0 | 4 | 4.0 | | |
| 54/2 | 64 | 7 | 11.5 | 1 | 1.6 | | | | |
| 105 | 43 | 33 | 76.7 | 16 | 37.2 | 2 | 4.7 | | |
| 189/1 | 111 | 29 | 26.1 | 23 | 20.7 | 2 | 1.8 | | |
| 190/1 | 110 | 45 | 40.9 | 11 | 10.0 | 7 | 6.4 | 1 | 0.9 |

The hypo- and hyperploid PMCs showed the chiasma frequencies similar to those of the euploid cells. Bivalents and rare univalents were mostly oriented at the equator of the cell, however, most of the univalents were scattered throughout the cell. Univalents organized at the equatorial region divided precociously. At telophase I the chromosomes grouped in two or more nuclei and usually some part of chromatin was randomly distributed in the cell (Fig. 12). The dyad cells mostly exhibited the nuclei and cells of unequal size and variable number of micronuclei (Fig. 13). Most of PMCs undergo the second meiotic division and tetrads (Fig. 14) or pentads and hexad are often asymmetrical, with a variable nucleus size and micronucleus number.

Trihybrids were found to be completely male sterile. Also, the female gametes were probably sterile, as a result of hybrid spike pollination with pollen of barley, rye, *H. jubatum* × 4x *S. cereale* and under open pollination no embryos and seeds were set.

DISCUSSION

The use of *Hordeum jubatum* as a bridging-species gave positive results. However, viable hybrids were only those, which had in the somatic tissues 7 *H. vulgare* chromosomes, 7 *S. cereale* and 7 or more *H. jubatum* chromosomes. Because of a small number of hybrids it was impossible to define whether the vitality of the hybrids (with $2n=21$ and 22) resulted from the balance or from the ratio of chromosome number of initial species or from other factors.

In trihybrids of *H. vulgare* × (*H. jubatum* × 4x *S. cereale*) the chromosomes of *H. jubatum*, probably like the ABD wheat genomes in (barley × rye) × wheat hybrids or AB genomes in barley × 6x *Triticale* (Clauss 1980, 1983), compensated a strong incompatibility between barley and rye.

Meiocytes of all studied plants were found to have nuclear instability. Hyper- and hypoploids cells were reported in several *Hordeum* hybrids e.g. *Hordeum* × *Secale* (Finch, Bennett 1980; Fedak, Nakamura 1982) or *Hordeum* × *Triticum* (Mujeeb et al. 1978). The chromosome instability may be due to incomplete expressions of the chromosome elimination mechanism (Finch, Bennett 1980; Fedak, Nakamura 1982).

In one of our plants all meiocytes were achiasmatic, while in four hybrids the chiasma frequency was variable but generally low (0.00 - 0.85). The chromosome pairing occurred mostly between rye chromosomes (0.00 - 0.80) and between *Hordeum* chromosomes (0.00 - 0.23). Nordenskiöld (1939) and Levan (1943) reported chiasma frequency in rye haploids equal to 0.03 or 0.33 (0.08 - 0.83). The chiasma frequency of nonhomologous rye chromosome pairing in our hybrids is very close to the data for haploid rye.

Probably, the pairing of not verified chromosomes of *H. vulgare* and *H. jubatum* was also partly of nonhomologous type especially between *H. vulgare* chromosomes. Nonhomologous pairing was found in several haploids of *H. vulgare* (Sadasivaiah, Kasha 1971; Fedak 1979). Fedak (1979) reported the mean for haploid chiasma frequency per cell equal to 0.04 and 0.22 for *H. vulgare* × *S. cereale*. As far as we know, there are probably no data on the chromosome pairing in monoploids of *H. jubatum*. In the hybrid of *H. jubatum* × 2x *S. cereale*³ (2n=21, 7 *H. jubatum* + 14 rye chromosomes) the chromosome bivalent associations of *H. jubatum* were rare (0.00 - 0.05) and rather of achiasmatic type (Wojciechowska 1981).

Heteromorphic bivalents between chromosomes of *Secale* and *Hordeum* were very infrequent. Similar bivalents between chromosomes of *H. vulgare* and *H. jubatum* were not verifiable. Also, very low frequency of pairing was found in a barley-rye hybrid between chromosomes of barley and rye (Fedak 1979) and in hybrids of *H. jubatum* and 2x *S. cereale* between *H. jubatum* and *S. cereale* chromosomes (Wagenaar 1960; Kistner, Clauss 1978; Wojciechowska 1978).

The discussed trihybrids showed differences in their ability to chromosome pairing. For example, in two hybrids obtained from pollination of cv. Menuet: in one plant no primary associations were observed, whereas in the second hybrid 81.5% of PMCs exhibited one rye bivalent. The differences between the plants are probably due to heterozygosity of rye (rye pollen were collected from several plants).

The trihybrids were completely sterile. Attempts to double their chromosome number by colchicine and tissue culture methods have been unsuccessful.

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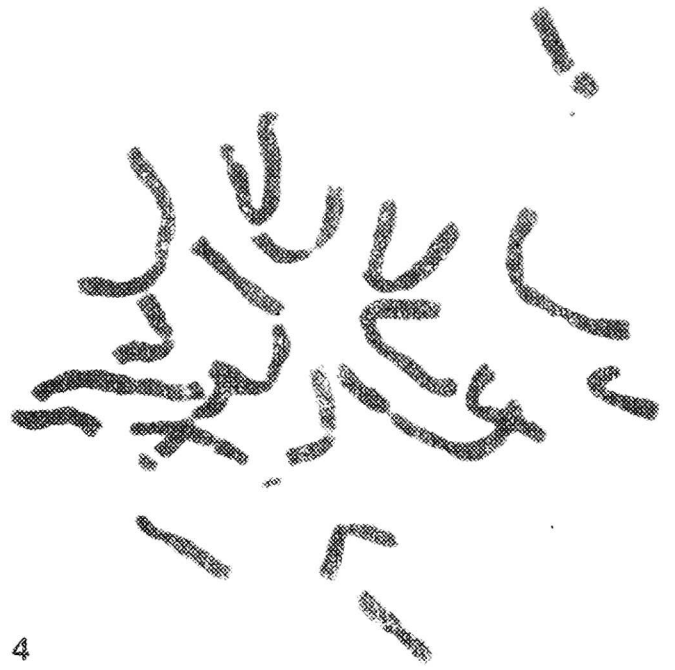
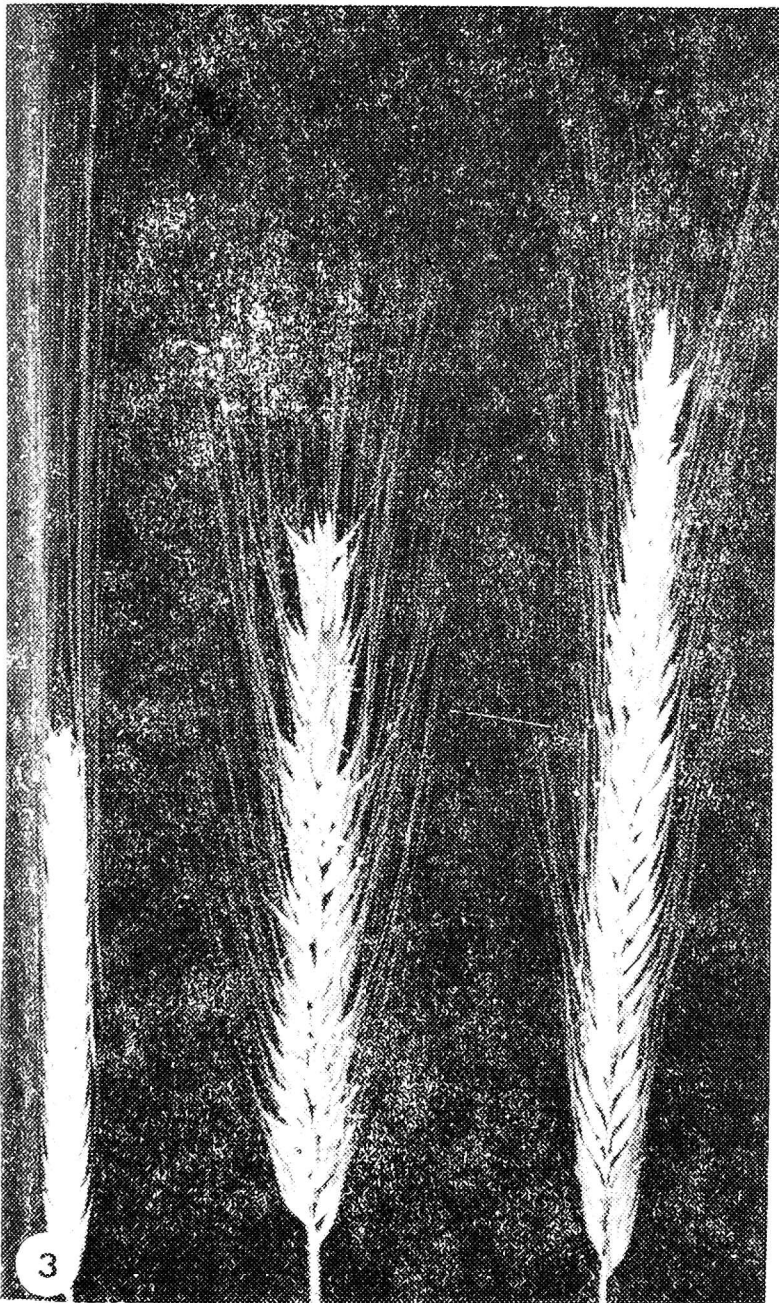
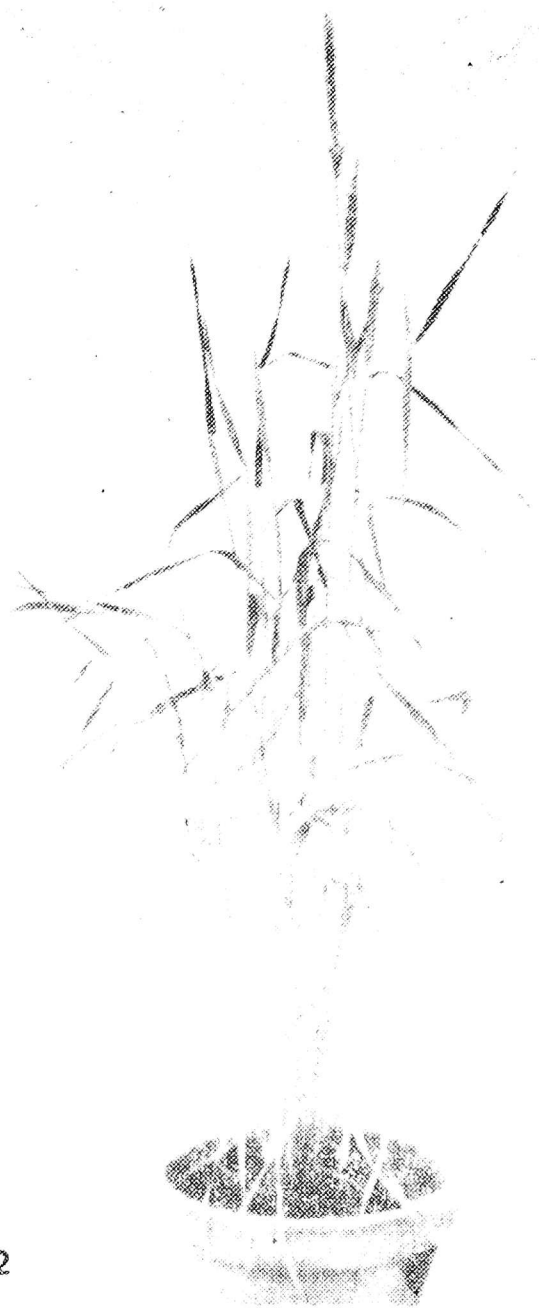
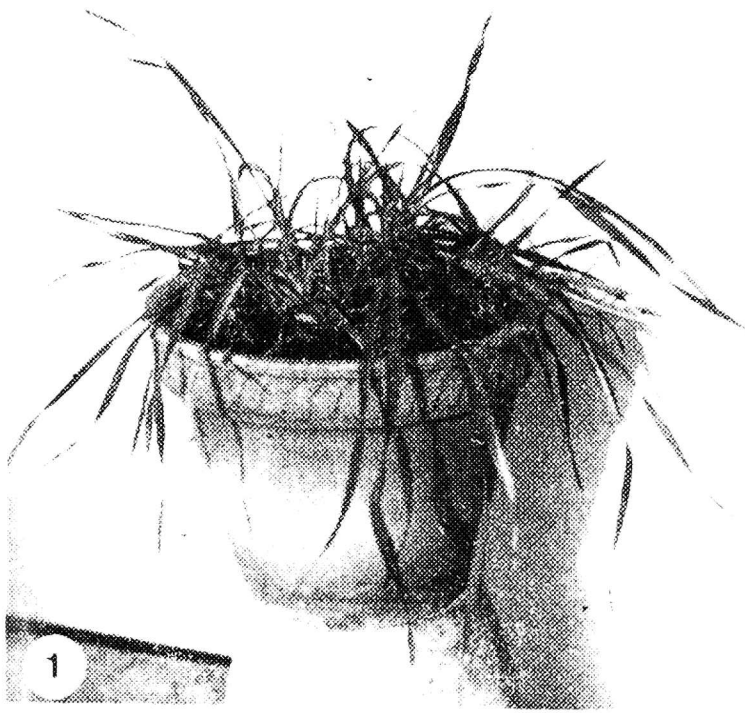
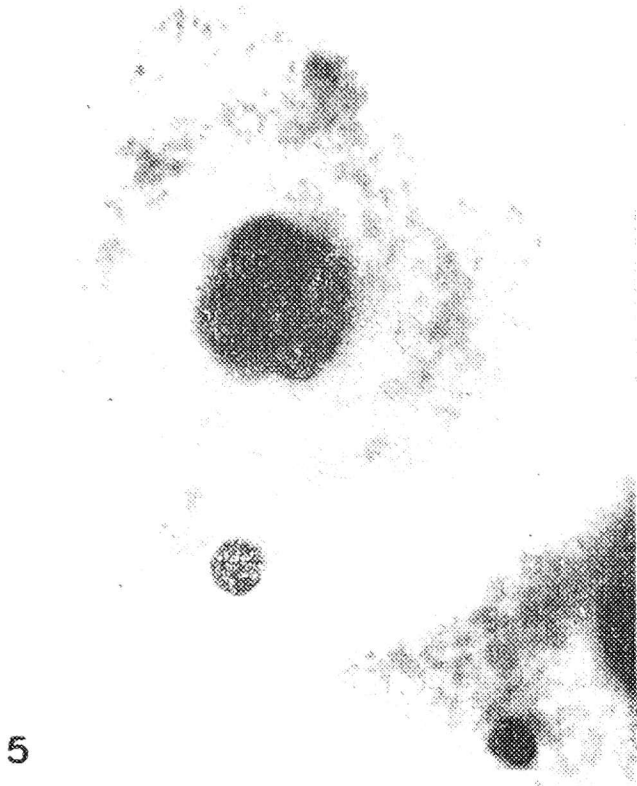
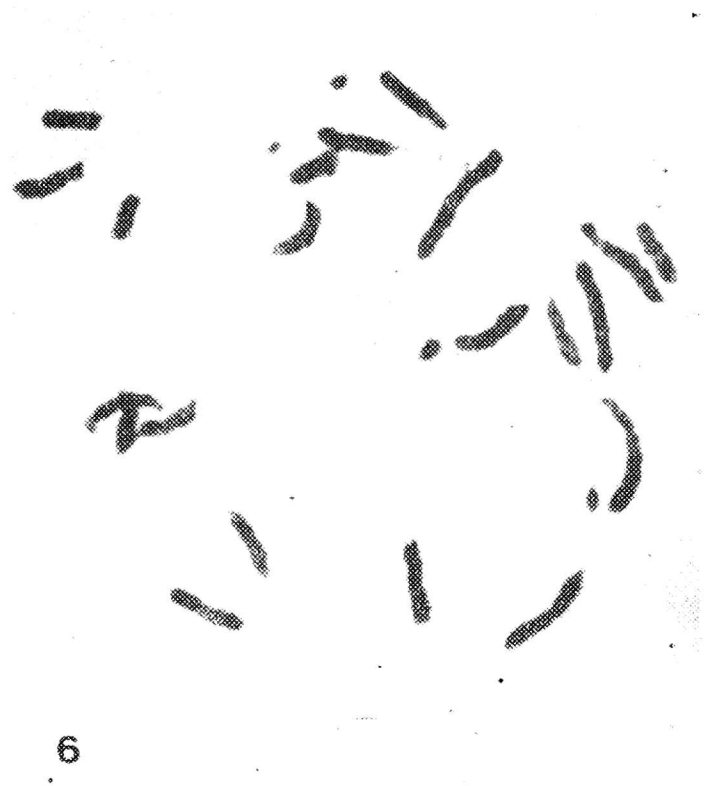


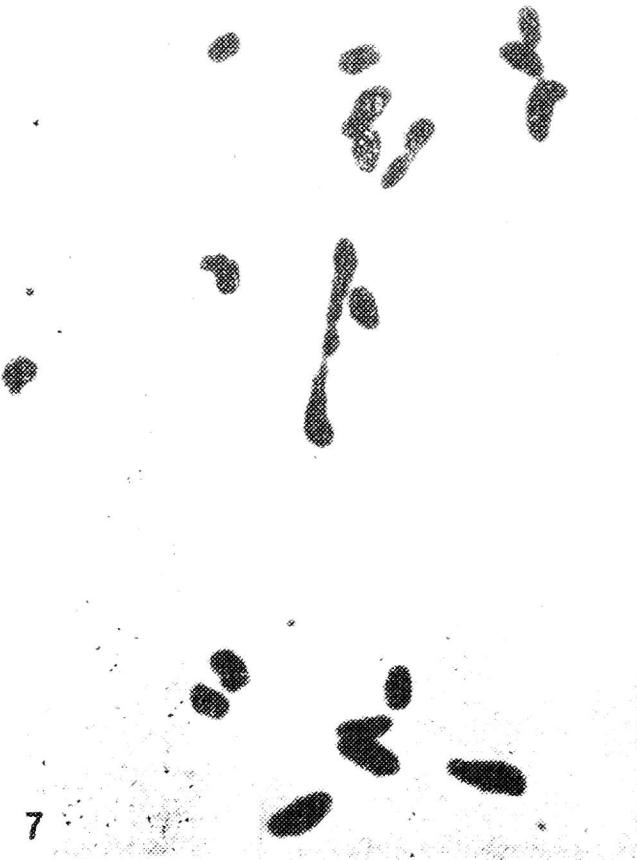
Plate 1. Figs. 1 - 4. 1 - 2 - *H. vulgare* \times (*H. jubatum* \times 4*x* *S. cereale*) plants, 3 - L ft to right: Spikes of *H. vulgare* (σ), *H. vulgare* \times (*H. jubatum* \times 4*x* *S. cereale*) hybrid, *H. jubatum* \times 4*x* *S. cereale* (δ), 4 - Mitotic chromosomes of *H. vulgare* \times (*H. jubatum* \times 4*x* *S. cereale*), $2n=21$ with 4 SAT chromosomes (2 *H. vulgare* + 1 *H. jubatum* + 1 *S. cereale*)



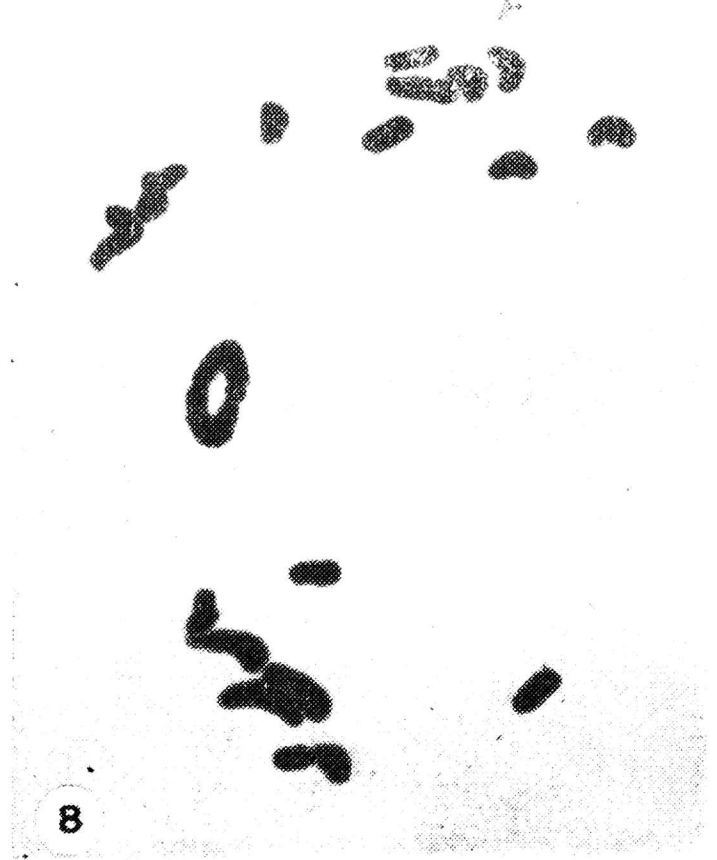
5



6



7



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Plate 2. Figs. 5 - 8. PMCs of *H. vulgare* × (*H. jubatum* × 4x *S. cereale*) hybrids
 5 - Inclusions in cell cytoplasm, 6 - Pachytene/diploten stage, 7 - MI: 1HC + 1C/H-s-s +
 1C/H-s-e + 1H/H-e-e + 1C/H/H-s-e-e, 8 - MI: 1HC + 1C/C-s-s + 1C/H-s-e +
 1C/H/H-s-e-s + 1C/H-e-e

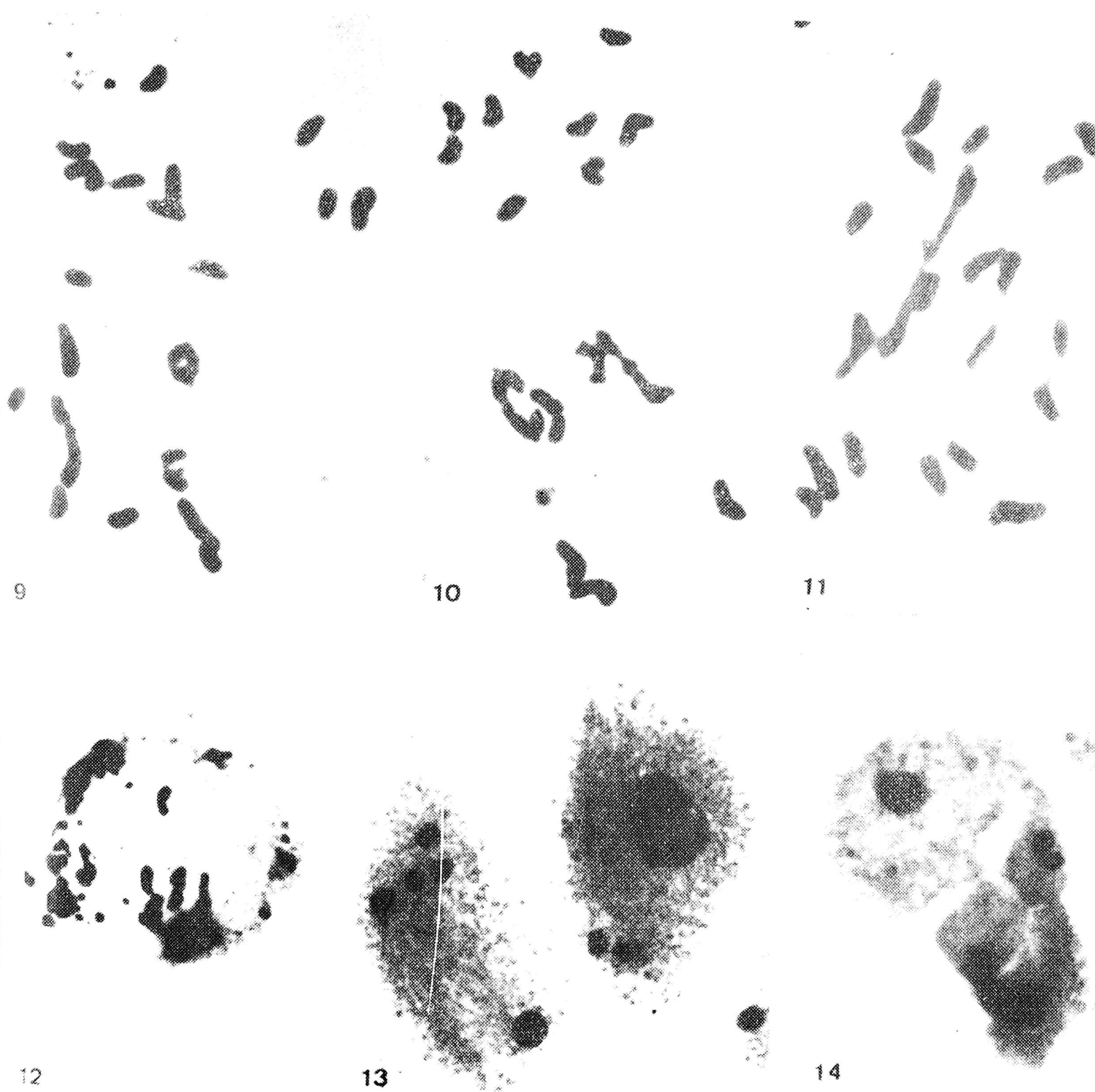


Plate 3. Figs. 9 - 14. Meiosis in PMCs of *H. vulgare* × (*H. jubatum* × 4*x* *S. cereale*) hybrids
 9 - MI: 1IIIH + 1C/H-s-s + 1H/H-e-e + 1H/C/H-e-e-e + 1C/C-s-e + 1H/C/H-e-e-s, 10 -
 MI: 1IIC + 2IIH + 1IIC/H + 1C/C-s-e + 1H/H-e-e. 11 - MI: 1IIC (note loose connections of
 one chromosome of C bivalent with C and H univalents) + 1H/H-e-e + 1H/H/C-e-e-e at equatorial
 plate, 12 - Telophase I, 13 - Dyad cells, 14 - Tetrad asymmetrical cells

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MIESZANŃCE MIĘDZY *HORDEUM VULGARE* L.
I *HORDEUM JUBATUM* × 4x *SECALE CEREALE*

Streszczenie

Trójgatunkowe mieszańce — *H. vulgare* × (*H. jubatum* × 4x *S. cereale*) — otrzymano w wyniku przekrzyżowania jęczmienia uprawnego z rośliną pokolenia F_1 *Hordeum jubatum* × 4x *Secale cereale*, przy zastosowaniu hodowli in vitro niedojrzałych zarodków. Cechy morfologiczne mieszańców były bardziej zbliżone do formy ojcowskiej z charakterystycznymi cechami żyta, omszenia liści i dokłosa. Większość roślin posiadała $2n=21$ (7 chromosomów *H. vulgare* + 7 *H. jubatum* + 7 *S. cereale*), ponadto kilka mieszańców wykazywało $2n=17$, $2n=19$ i $2n=22$. W metafazie I przeważająca liczba KMP zawierała niekonjugujące chromosomy; biwalenty formowały się bardzo rzadko; obserwowano też wtórne asocjacje chromosomów.

ГИБРИДЫ МЕЖДУ *HORDEUM VULGARE* L.
И *HORDEUM JUBATUM* × 4x *SECALE CEREALE*

Резюме

Трёхвидовые гибриды, *H. vulgare* × (*H. jubatum* × 4x *S. cereale*) были получены в результате скрещивания культурного ячменя с растением поколения F_1 *Hordeum jubatum* × 4x *Secale cereale* при применении культуры in vitro незрелых зародышей. Морфологические признаки гибридов были более близки к отцовской форме с характерными признаками ржи, овлосением листьев и предколосья. Большинство растений имело $2n=21$ (7 хромосом *H. vulgare* + 7 *H. jubatum* + 7 *S. cereale*) и кроме того, несколько гибридов имело $2n=17$, 19 и 22. В метафазе I преобладающее число материнских клеток пыльцы содержало неконъюгационные хромосомы, биваленты образовывались редко. Наблюдались также вторичные ассоциации хромосом.