Intergeneric hybridization between *Agropyron tsukushiense* and *Hordeum bulbosum* (4x)$^1$

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ABSTRACT

In order to obtain polyhaploids in the genus *Agropyron* by “the bulbosum method”, nine species were pollinated by *Hordeum bulbosum* (4x). Among progenies obtained by embryo culture, six plants did not show the elimination of any chromosomes derived from *H. bulbosum* and were intergeneric hybrids between *A. repens* or three ecotypes of *A. tsukushiense* and *H. bulbosum*.

Out of six hybrids obtained, two plants of *A. tsukushiense* EE-4 or ST-1 × *H. bulbosum* (4x) (2n=34 or 2n=35) were examined morphologically and cytologically. These hybrids were shorter, but had numerous tillers. They were completely sterile. The spike morphology resembled the female parent rather than the intermediate between the parents. Several characteristics of the pollen parent were also observed in these hybrids.

The average chromosome pairing per cell at MI of PMCs in *A. tsukushiense* EE-4 and ST-1 × *H. bulbosum* hybrids was 2.811 ± 28.41 and 4.611 ± 25.81, respectively. The loosely associated bivalent formation, a rare occurrence of the cells with more than seven bivalents, and the absence of multivalent association in these hybrids suggest a lack of segmental homology among the chromosome complements of three genomes of *A. tsukushiense* and two of *H. bulbosum*.

The production of these intergeneric hybrids suggests that the genome balance hypothesis proposed in interspecific hybrids of *Hordeum* can not be applicable to the intergeneric hybrids between *Agropyron* and *H. bulbosum*.

1. INTRODUCTION

In the genome analysis of polyploid species, polyhaploid plants of the species in question provide critical information concerning the genome structure of polyploid species. “The bulbosum method” (Jensen 1977), crossing with the pollen of *Hordeum bulbosum* Linn. followed by embryo culture during which chromosomes of the pollen parent are eliminated, is useful for the production of polyhaploids in the tribe Triticeae. So far, polyhaploids of *Triticum aestivum* Linn., *Aegilops crassa* Boiss. (6x) and *Ae. triuncialis* Linn. were produced by this method (Barclay 1975, Chapman and Miller 1977, Shigenobu and Sakamoto 1977).

$^1$) Contribution No. 20 from the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University, Kyoto.
Agropyron, a perennial genus of the tribe Triticeae, consists of many genetically complicated polyploid species. In order to obtain haploids in the genus Agropyron, the following nine species were pollinated by 39 strains of tetraploid *H. bulbosum* and hybrid embryos obtained were cultured aseptically: *A. caninum* (L.) Beauv. (4x), *A. cristatum* (L.) Gaertn. (4x), *A. desertorum* (Fisch.) Schult. (4x), *A. elongatum* (Host) Beauv. (2x), *A. intermedium* (Host) Beauv. (6x), *A. repens* (L.) Beauv. (6x), *A. semicostatum* Nees (4x), *A. trichophorum* (Link) Richt. (6x), and *A. tsukushiense* (Honda) Ohwi (6x). However, only several intergeneric hybrid plants between *A. repens* or *A. tsukushiense* and *H. bulbosum* were obtained instead of polyhaploids of female parents.

The present paper mainly reports the morphological and cytogenetic studies of intergeneric hybrids between *A. tsukushiense* and *H. bulbosum* (4x) and discusses some problems of "the bulbosum method" for producing haploid plants.

2. MATERIALS AND METHODS

In the present successful intergeneric crosses, *A. repens* (6x; stock no. A-20, collected in Quebec, Canada) and nine strains of *A. tsukushiense* (6x), including three ecotypes: six strains of the common type (CT-2, CT-6, CT-10, CT-12, 7805 and 7806), two of the early ecotype (EE-2 and EE-4) and one of the small ecotype (ST-1), were used as the female parent. Those strains of *A. tsukushiense* were collected in Japan and Taiwan. The strains of *Hordeum bulbosum* (4x) used as the pollen parents were HB-1 and HB-7, which were collected in Turkey by the Botanical Mission of University of Kyoto (1959), and HB7946, which was collected in Iraq by the Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia (1970). All strains have been maintained at the Plant Germ-plasm Institute, Kyoto University.

All plants grown in pots were kept outdoors but several plants of *A. tsukushiense* were grown in a glasshouse. Two hand-emasculated lowest florets of each spikelet of the female parents were enclosed in paraffin-paper bags and were pollinated four days after by brushing stigma with newly dehisced anthers of *H. bulbosum*.

The embryos of hybrid seeds were cultured with the modified medium of that used by Brink et al. (1944), adding 10 g agar, 1 g yeast extract and 0.1 g Vitamin B₃ per 1,000 ml of solution. The immature seeds about 14 days after pollination were taken from the spikes. After sterilization with 70% alcohol for 30 seconds and ca. 7% calcium hypochlorite solution for 10 minutes, the removal of the top half of the seed as described by Kasha and Kao (1970) was performed. Then the seeds with stigmatic ends cut off were planted on the medium in test tubes. The embryos were incubated at 22°C in the dark until they germinated. After 2–3 weeks, when visible roots and shoots appeared,
Hybrids of Agropyron × Hordeum bulbosum (4x)

they were grown in continuous light. Then the seedlings were transplanted in pots and they were placed in a growth cabinet with 20 hours of light at 25°C and four hours of darkness at 22°C thereafter. They were finally transferred to a glasshouse at 4-6 months after pollination.

For counting somatic chromosome numbers the aceto-carmine squash technique was used. In order to examine chromosome pairing of the plants obtained, the anthers were fixed in Farmer’s solution (3 ethanol : 1 acetic acid) and stored in a refrigerator. Chromosome pairing was observed at MI of PMCs using the aceto-carmine squash technique. Photomicrographs were taken from temporary preparations.

3. RESULTS

1. Intergeneric crosses

Seed set induced from intergeneric crosses between two species of Agropyron and three strains of H. bulbosum (4x) producing F₁ progenies undertaken during 1976-1979 is shown in Table 1. The highest percentage of seed set, 54.6%, was observed in the crosses of A. tsukushiense ST-1 × H. bulbosum HB-1. A large number of seeds were obtained when A. repens, A. tsukushiense EE-4 and ST-1 were used as female parents.

The seeds produced from intergeneric crosses developed vigorously for two weeks after pollination, but they thereafter began to show a sign of abortion. Therefore, embryo culture was applied to most of the seeds obtained. In some cases the majority of produced seeds was underdeveloped even if the per-

<table>
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<tr>
<th>Female parents</th>
<th>Male parents</th>
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<td>B</td>
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<tr>
<td>Agropyron repens</td>
<td>163</td>
<td>55</td>
<td>33.7</td>
<td>185</td>
<td>29</td>
<td>15.7</td>
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<tr>
<td>A. tsukushiense CT-2</td>
<td>182</td>
<td>23</td>
<td>12.6</td>
<td>485</td>
<td>9</td>
<td>1.9</td>
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<tr>
<td>CT-6</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>245</td>
<td>16</td>
<td>6.5</td>
<td>—</td>
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<td>—</td>
<td>186</td>
<td>18</td>
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<td>CT-12</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>90</td>
<td>0</td>
<td>0</td>
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<td>—</td>
<td>119</td>
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<tr>
<td>EE-2</td>
<td>96</td>
<td>10</td>
<td>10.4</td>
<td>201</td>
<td>24</td>
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<td>3</td>
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<td>895</td>
<td>89</td>
<td>9.9</td>
<td>103</td>
<td>34</td>
<td>33.0</td>
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<tr>
<td>ST-1</td>
<td>379</td>
<td>207</td>
<td>54.6</td>
<td>451</td>
<td>164</td>
<td>34.1</td>
<td>—</td>
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</table>

A: No. of florets pollinated, B: No. of seeds set, C: Percent of seeds set.
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percentage of seed set was high. Of the total 517 embryos cultured, 107 (20.7\%) developed into seedlings (Table 2), but a few produced callus. The majority of seedlings, however, showed no further growth.

Among 46 seedlings transplanted in pots, 10 plants were finally obtained as shown in Table 2, while the remaining seedlings died in the early stage of growth. By the investigation of somatic chromosome numbers, six plants were intergeneric hybrids between *Agropyron* and *H. bulbosum*, but two plants obtained from *A. tsukushiense* ST-1 were not hybrids but identical with the female parent. The somatic chromosome number of one plant from *A. tsukushiense* EE-4 × *H. bulbosum* HB7946 and one from *A. tsukushiense* ST-1 × *H. bulbosum* HB-7 can not be determined yet, because of its weak growth. One plant obtained from *A. tsukushiense* EE-4 × *H. bulbosum* HB-7 was 2n=34, indicating the elimination of one chromosome. One plant from *A. tsukushiense* EE-4 × *H. bulbosum* HB7946 was 2n=35, but has not headed yet. Somatic chromosome numbers of two plants obtained from *A. tsukushiense* ST-1 × *H. bulbosum* HB-7 were 2n=35 and 2n=33, respectively. The latter indicated the elimination of two chromosomes. This plant showed very weak growth in the tillering stage and died after nearly two years. One plant from *A. tsuku-

Table 2. Plants obtained from intergeneric crosses between two species of *Agropyron* and three strains of *H. bulbosum* (4x) using embryo culture technique

<table>
<thead>
<tr>
<th>Female parents</th>
<th>Male parents</th>
<th>No. of embryos cultured</th>
<th>No. of seedlings obtained</th>
<th>Percent of embryos giving seedlings</th>
<th>No. of plants obtained</th>
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<tr>
<td><em>Agropyron repens</em></td>
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<td>51</td>
<td>2</td>
<td>3.9</td>
<td>1</td>
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<tr>
<td></td>
<td>HB-7</td>
<td>27</td>
<td>0</td>
<td>0</td>
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<tr>
<td><em>A. tsukushiense</em></td>
<td>CT-2</td>
<td>22</td>
<td>2</td>
<td>9.1</td>
<td>1</td>
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<tr>
<td></td>
<td>HB-1</td>
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<td>33.3</td>
<td>0</td>
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<td>HB-7</td>
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<td>3</td>
<td>18.8</td>
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<td>5</td>
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<td>HB-7</td>
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<td>4</td>
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<td></td>
<td>HB7946</td>
<td>3</td>
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<td>11</td>
<td>16.7</td>
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<td>6.3</td>
<td>2</td>
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<td></td>
<td>ST-1</td>
<td>140</td>
<td>25</td>
<td>17.9</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>HB-7</td>
<td>95</td>
<td>50</td>
<td>52.6</td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>517</strong></td>
<td><strong>107</strong></td>
<td><strong>20.7</strong></td>
<td><strong>10</strong></td>
<td></td>
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</table>
Hybrids of Agropyron × Hordeum bulbosum (4x)

shiense CT-2 × H. bulbosum HB-1 was 2n = 35 (Fig. 1a). One plant from A. repens × H. bulbosum HB-1 was 2n = 34 (Fig. 1b) indicating the elimination of one chromosome. This plant was vigorous and produced numerous tillers but does not head yet.

2. Intergeneric hybrid between A. tsukushiense EE-4 and H. bulbosum HB-7

The growth of this hybrid (2n = 34) was subnormal. The plant was shorter than the parental plants. The date of first flowering of A. tsukushiense EE-4, H. bulbosum HB-7 and the F₁ plant in the glasshouse was April 21st, May 23rd and May 20th, respectively. Thus the F₁ plant started to bloom as late as the pollen parent. It was completely sterile with small and nondehiscent anthers. A marked characteristic of this plant was the vigorous tillering, which was commonly observed in the hybrid between Agropyron and H. bulbosum. The length of the top internode and flag leaf was shorter than the parental plants, while the length of spike was intermediate between the parents. The average rachis nodes per spike in nine spikes produced in 1977 and 1978 was 16.4. The F₁ plant was clearly less vigorous than the parents showing negative heterosis.

The spike morphology of the hybrid resembled the female parent rather...
than the intermediate between the parents, as shown in Fig. 2a. The spike of
_A. tsukushiense_ consists of solitary spikelets at each node of the rachis, while
that of _H. bulbosum_ is composed of three spikelets with a single floret at each
rachis node. The spike of the hybrid plant had 1, 2 or 3 spikelets at each
rachis node with the average 1.3 spikelets per rachis node. Several characteris-
tics of the pollen parent were observed in the hybrid. For example, the leaf
sheath of _H. bulbosum_ is densely pilose, while _A. tsukushiense_ is glabrous.
The leaf sheath of the hybrid plant was pilose as that of the pollen parent.
_H. bulbosum_ has a bulbous swelling at the base of the culm. The base of culm
of the hybrid was also bulbous, although the degree of swelling in F₁ was less than the pollen parent.

Chromosome pairing at MI of PMCs of the hybrid plant was analyzed only in 19 cells (Table 3), because most collected anthers contained no pollen mother cells. Of 19 cells, 5 and 7 cells (in total 63.1%) showed 3III + 28I, and 4III + 26I (Fig. 3a), respectively. No multivalents were observed. The average chromosome pairing per cell was 2.8III + 28.4I. Of 53 bivalents observed, 42 (79.2%) were rod-shaped association with a terminal chiasma.

Chromosome pairing at MI of PMCs of A. tsukushiense EE-4 showed 21I in most cells (53 cells, 80.3%) examined (Fig. 3b), and 1IV + 19I and 20I + 2I were found in eight (12.1%) and five (7.6%) cells, respectively. The average chromosome pairing was 0.1IV + 20.7I + 0.2I. Of 1,365 bivalents observed, 1,256 (92.0%) were ring-shaped association.

Chromosome pairing at MI of PMCs of H. bulbosum HB-7 is shown in Table 4 and Fig. 3c. It formed various numbers of quadrivalents and bivalents, and occasionally one sexivalent, quinquevalent and trivalent together with some univalents at MI. The average chromosome pairing was 0.061Iv + 0.004Iv + 1.80Iv + 0.016Iv + 9.74Iv + 0.90Iv. Of 2,396 bivalents observed, 1,974 (81.3%) were ring-shaped association. In spite of varying multivalent formations this strain showed relatively high pollen fertility (72.1%).

3. Intergeneric hybrid between A. tsukushiense ST-1 and H. bulbosum HB-7

The growth and flowering of this hybrid (2n=35) were nearly normal with vigorous tillers. Plant height of the hybrid was intermediate between the parental plants. The date of first flowering of A. tsukushiense ST-1, H. bulbosum HB-7 and the F₁ plant were May 21st, May 23rd and May 21st, respectively. Thus the F₁ plant started to bloom at the same time as the parents.
The F₁ plant was completely sterile. The length of the top internode and spike was intermediate between the parents, while the length of flag leaf was longer than the parental plants. The average number of rachis nodes per spike in 20 spikes produced in 1978 was 26.2.

The spike morphology of the hybrid resembled the female parent rather than intermediate between the parents as shown in Fig. 2b. The spike of the hybrid had 1, 2 or 3 spikelets at each rachis node with the average 1.8 spikelets per rachis node. Several characteristics of the pollen parent were also observed.
in this hybrid, such as pilose leaf sheath and bulbous swelling at the base of culm as observed in the hybrid of *A. tsukushiense* EE-4 × *H. bulbosum* mentioned above.

Chromosome pairing at MI of PMCs of the hybrid is shown in Table 5. Of 51 cells examined, 17 and 12 cells (in total 56.8%) showed 4II + 27I (Fig. 3d) and 5II + 25k, respectively. No multivalents were observed. The average chromosome pairing per cell was 4.6II + 25.8k. Of 235 bivalents observed, 172 (73.2%) were rod-shaped with a terminal chiasma.

Chromosome pairing at MI of PMCs of *A. tsukushiense* ST-1 showed 21II and
The growth of this hybrid (2n=35) was somewhat weak in spite of numerous tillering. The plant height of *A. tsukushiense* CT-2, *H. bulbosum* HB-1 and the F_1 plant was 93.7, 114.5 and 54.1 cm, respectively. Thus the F_1 plant was very shorter than the parental plants. The date of first flowering of the parental plants in the glasshouse was May 11th and May 12th, respectively. On the contrary, in the F_1 plant only one spike headed on June 2nd, far later than both parents, but did not flower. It was completely sterile. The length of the top internode and spike were shorter than the parental plants, while the length of the flag leaf was intermediate between the parents. The number of rachis nodes in one spike produced in 1980 was 24, but out of them, 9 had degenerate spikelets. The F_1 plant showed remarkable negative heterosis.

The spike morphology of this hybrid resembled the female parent rather than intermediate between the parents as shown in Fig. 2c. The spike of the hybrid had 1, 2 or 3 spikelets at each rachis node with the average 1.5 spikelets per rachis node. Several characteristics of the pollen parent were also observed in this hybrid, such as pilose leaf sheath and bulbous swelling at the base of culm as observed in two hybrids mentioned above. Because of no further heading, meiosis of this plant could not be observed.
4. DISCUSSION

In order to establish the genome relationships between Agropyron and Hordeum, natural and artificial intergeneric hybrids have been reported by many investigators (Stebbins et al. 1946, Boyle and Holmgren 1955, Dewey 1971 and others). However, the genome relationships between those two genera are not well understood yet. Therefore, intergeneric hybrids between those two genera provide more informations on this problem.

In the present study six intergeneric hybrids were obtained from crosses between A. repens or A. tsukushiense and H. bulbosum. In two hybrids of A. tsukushiense X H. bulbosum (2n=34 and 2n=33) and one of A. repens X H. bulbosum (2n=34), one or two chromosomes were eliminated. It is not clear that the eliminated chromosomes were derived from either male or female parent.

The average chromosome pairing per cell at MI of PMCs in A. tsukushiense EE-4 and ST-1 X H. bulbosum hybrids was 2.8II + 28.4I and 4.6II + 25.8I, respectively. A. tsukushiense is an allohexaploid whose genome constitution comprises three different genomes (Matsumura 1948, Sakamoto 1964). On the basis of the observation that H. bulbosum (4x) chromosomes formed one to seven quadrivalents autosyndetically with a mode at five quadrivalents per cell, Berg (1936) assumed H. bulbosum (4x) to be an autotetraploid. On the other hand, H. bulbosum HB-7 used in this experiment formed varying degree of multivalents with a mode at one quadrivalent per cell as shown in Table 4. This result indicates that the frequency of quadrivalent formation in HB-7 was lower than that of Berg’s materials. Judging from the formation of zero to six quadrivalents and an additional tri-, quinque- or sexivalent in HB-7 (Table 4), the autosyndesis of genomes derived from H. bulbosum in the intergeneric hybrid between A. tsukushiense and H. bulbosum is expected to form zero to six bivalents with the average about two bivalents per cell. Therefore, the formation of a maximum five or nine bivalents in two intergeneric hybrids shown in Tables 3 and 5 may be partly due to allosyndesis of A. tsukushiense and H. bulbosum chromosomes. However, the loosely associated bivalent formation (79.2% and 73.2%, respectively), a rare occurrence of the cells with more than seven bivalents (only five cells), and the absence of multivalent association in these hybrids suggest a lack of segmental homology among the chromosome complements of three genomes of A. tsukushiense and two of H. bulbosum.

Sakamoto (1961 and unpublished) indicated that three ecotypes of A. tsukushiense, used in the present study, differentiate cytogenetically with each other with one reciprocal translocation. Cytogenetic studies were conducted in two hybrids with A. tsukushiense EE-4 and ST-1. The intergeneric hybrid between A. tsukushiense ST-1 and H. bulbosum HB-7 formed more bivalents.
at MI than in the hybrid between *A. tsukushiense* EE-4 and *H. bulbosum* HB-7. This difference is probably ascribed to the small number of PMCs examined (only 19 cells) in the latter combination.

Cytological studies dealing with selective elimination of *H. bulbosum* chromosomes have been undertaken in interspecific hybrids of *Hordeum*. So far, it has suggested that the control over selective chromosome elimination resides in genetic factors on *H. vulgare* chromosomes and the genome balance between *vulgare* and *bulbosum* chromosomes, where the genome ratio of the parents of 1 vulgare: 1 bulbosum and 1 vulgare: 2 bulbosum mainly produced haploids and hybrids, respectively (Subrahmanyam and Kasha 1970, Ho and Kasha 1975). However, only polyhaploids in *T. aestivum* × *H. bulbosum* (2x or 4x) (the parental genome ratio is 3 : 1 or 3 : 2) or in *Ae. crassa* (6x) × *H. bulbosum* (4x) (3 : 2) were produced (Barclay 1975, Miller and Chapman 1976, Chapman and Miller 1977, Shigenobu and Sakamoto 1977). In the present study six intergeneric hybrids of *A. tsukushiense* (6x) or *A. repens* (6x) × *H. bulbosum* (4x) were produced even though the parental genome ratio is 3 : 2. Thus, the genome balance hypothesis that stable hybrids are obtained by increasing the *bulbosum* genomes found in *Hordeum* hybrids can not be applicable to the intergeneric hybridization between *Triticum*, *Aegilops* or *Agropyron* and *H. bulbosum*.

In *H. bulbosum* (4x) × *H. vulgare* (4x) the chromosome elimination in F₁ progenies was controlled by some heritable factors involved in *H. bulbosum* (Fukuyama and Takahashi 1975, Fukuyama and Kurozumi 1977). However, the crosses of *A. tsukushiense* and *Ae. crassa* (6x) with the pollen of *H. bulbosum* HB-7 produced intergeneric hybrids in the former combination and a polyhaploid in the latter. This suggests that controlling factors of chromosome elimination may reside in *A. tsukushiense* and *Ae. crassa* (6x).

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**REFERENCE**


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