Cytogenetical Studies on the Genus *Oryza*

VIII. Cytogenetics on the Allotriploids, *sativa*(4x)-*punctata*, *sativa*(4x)-intermediate form and *sativa*(4x)-*officinalis*

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Cytogenetical studies on allotriploids, *sativa*(4x)-*punctata*[AAB], *sativa*(4x)-intermediate form[AAC] and *sativa*(4x)-*officinalis*[AAC] were carried out. At MI of all allotriploids used in this experiment, except PF, 26 failing in chromosome pairing, 12II+12I were mostly observed. The univalents observed at MI of PMCs in PF, 25 may result from a gene or genes which cause disturbance in the pairing of the homologous chromosomes.

Introduction

Recently, transfer of useful genes from wild species to cultivated plants has been attempted by many geneticists and plant breeders, and their studies have been reported on alien addition lines of common wheat with the chromosomes of rye (Riley and Chapman 1958; Evans and Jenkins 1960; Mukade et al. 1970), and Haynaldia (Hyde 1953), of tetraploid wheat with the chromosomes of Aegilops squarrosa (Alston 1970), and Agropyron (Mochizuki 1962), and of Avena sativa with the A. hirtula chromosomes (Thomas 1968).

In order to use the useful gene(s) of such wild species as *Oryza officinalis* (CC), intermediate form (CC) and *O. punctata* (BB), the authors are trying to isolate alien addition lines from the progenies of the crosses between allotriploids (AAC and AAB) and cultivated rice (AA). For this purpose, several allotriploids having AAB or AAC genomic constitutions were produced.

This paper deals with the results of cytogenetical studies of allotriploids.

Material and Methods

Eight allotriploids, *sativa*(4x)-*punctata*, *sativa*(4x)-intermediate form and *sativa*(4x)-*officinalis* (6 lines), were used as materials in the present experiment (Table 1).

Emasculation was made by hot-water treatment (43°C for 7 min.).

F₁ seeds were sterilized and sown on the artificial culture medium in test tube. The cultured seedlings were transplanted into pots.

In order to promote flower initiation, the plants were subjected to short-day conditions (about 9 hours of day length).

The root-tips were pretreated with 0.002 M of 8-oxyquinoline at 18–20° C for 2–3 hours. After fixing with acetic-alcohol (1:3), the root-tips and pollen-mother-cells were stained with aceto-carmine.

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Table 1. Cross-combinations of *Oryza* species used in the present experiment

<table>
<thead>
<tr>
<th>PF, plant number</th>
<th>Cross-combination</th>
<th>Genomic cross combination</th>
<th>2n</th>
</tr>
</thead>
<tbody>
<tr>
<td>PF, 13*</td>
<td>Sekitori (4 x)</td>
<td><em>O. punctata</em> (W 1515)</td>
<td>AAAAA × BB</td>
</tr>
<tr>
<td>PF, 14*</td>
<td>Shinriki (4 x)</td>
<td>Intermediate (W 1527)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 15</td>
<td>Norin 18 (4 x)</td>
<td><em>O. officinalis</em> (W 0006)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 16*</td>
<td>Sekitori (4 x)</td>
<td><em>O. officinalis</em> (W 0006)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 17*</td>
<td>Sekitori (4 x)</td>
<td><em>O. officinalis</em> (W 0065)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 18</td>
<td>Norin 18 (4 x)</td>
<td><em>O. officinalis</em> (W 0065)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 19</td>
<td>Sekitori (4 x)</td>
<td><em>O. officinalis</em> (W 1267)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 20</td>
<td>Shinriki (4 x)</td>
<td><em>O. officinalis</em> (W 1267)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 21</td>
<td>Sekitori (4 x)</td>
<td><em>O. officinalis</em> (W 0564)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 22*</td>
<td>Shinriki (4 x)</td>
<td><em>O. officinalis</em> (W 0564)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 23*</td>
<td>Shinriki (4 x)</td>
<td><em>O. officinalis</em> (W 1302)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 24</td>
<td>Shinriki (4 x)</td>
<td><em>O. officinalis</em> (W 1306)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 25*</td>
<td>Shinriki (4 x)</td>
<td><em>O. officinalis</em> (W 1263)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 26*</td>
<td>Sekitori (4 x)</td>
<td><em>O. officinalis</em> (W 1281)</td>
<td>AAAAA × CC</td>
</tr>
<tr>
<td>PF, 27</td>
<td>Shinriki (4 x)</td>
<td><em>O. officinalis</em> (W 1134)</td>
<td>AAAAA × CC</td>
</tr>
</tbody>
</table>

* used for cytological observation

Table 2. Results of artificial cross-pollination between *O. sativa* (4 x) and wild species

<table>
<thead>
<tr>
<th>PF, plant number</th>
<th>Cross combination</th>
<th>Number of flowers Pollinated</th>
<th>Number of perfect grains obtained</th>
<th>Number of imperfect grains obtained</th>
<th>Number of grains germinated</th>
<th>Number of seedlings died soon after germination</th>
<th>Number of selfed individuals</th>
<th>Number of true F1 plants survived</th>
</tr>
</thead>
<tbody>
<tr>
<td>PF, 13</td>
<td>Shinriki (4 x) × W 1514</td>
<td>44</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>PF, 14</td>
<td>Sekitori (4 x) × W 1527</td>
<td>167</td>
<td>3</td>
<td>38</td>
<td>18</td>
<td>1</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>PF, 15</td>
<td>Norin 18 (4 x) × W 0006</td>
<td>22</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>PF, 16</td>
<td>Sekitori (4 x) × W 0006</td>
<td>109</td>
<td>2</td>
<td>10</td>
<td>9</td>
<td>2</td>
<td>7</td>
<td>20</td>
</tr>
<tr>
<td>PF, 17</td>
<td>Sekitori (4 x) × W 0065</td>
<td>86</td>
<td>33</td>
<td>24</td>
<td>4</td>
<td>2</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>PF, 18</td>
<td>Norin 18 (4 x) × W 0065</td>
<td>8</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>PF, 19</td>
<td>Sekitori (4 x) × W 1267</td>
<td>49</td>
<td>11</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>PF, 20</td>
<td>shinriki (4 x) × W 1267</td>
<td>21</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>PF, 21</td>
<td>Sekitori (4 x) × W 0564</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>PF, 22</td>
<td>Shinriki (4 x) × W 0564</td>
<td>29</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>PF, 23</td>
<td>Shinriki (4 x) × W 1302</td>
<td>18</td>
<td>6</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>PF, 24</td>
<td>Shinriki (4 x) × W 1306</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>PF, 25</td>
<td>Shinriki (4 x) × W 1263</td>
<td>8</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>PF, 26</td>
<td>Sekitori (4 x) × W 1281</td>
<td>24</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>PF, 27</td>
<td>Shinriki (4 x) × W 1134</td>
<td>18</td>
<td>1</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

Total 632 8 127 79 7 8 64
Results and Conclusion

Results of crossing

In 1972, the artificial hybridization was tried between *O. sativa* (4x) and the above mentioned wild species.

Out of 632 flowers pollinated in total, eight of them developed into perfect grains, while 127 of them developed imperfectly to various degrees. All greins thus obtained were grown under sterile condition, and the seedlings were later transplanted into pots. From the 79 germinated seeds, 64 matured plants were raised which were determined to be true hybrids (Table 2). Ho and Li (1965) obtained allotriploids by a backcross, (*O. sativa* × *O. officinalis*) × *O. sativa*, which were derived from un reduced gametes of the F₁ hybrids, but their cross-pollination ratio was very low.

Morphological characters

The results obtained on each character are shown in Table 3. Awn length of each PF₁ plant was similar to wild species but the awn color was that of the cultivated rice. Though the spikelet length and width of the PF₁ plants could not be compared with those of the parents, due to the complete sterility of the former, the spikelets were similar to the cultivated rice. Color of the flower and empty glumes of the PF₁ plants and the cultivated rice was yellowish brown in contrast with the black color of the wild species. Stigma color of the PF₁ plants was intermediate (light purple) of the cultivated rice (colorless) and the wild species (purple). The size of the ligules of the PF₁ plants was larger than that of the cultivated rice, whereas that of the wild species was smaller than both of them. Both the flag-leaf length and width of each PF₁ plant were respectively longer and wider than those of the wild species except the PF₁ 13. Stem, first internode and plant height in the PF₁ plant were generally thicker or longer than those of the cultivated rice and wild species. The plant type of the PF₁ plant was similar to that of the cultivated rice, while the panicle shape and deciduousness were intermediate of the both parents.

In general, increase in the size of the vegetative portions of the PF₁ plants may be the effects of hybridization and/or polyploidization, while in the qualitative characters, such as color and plants type, those of cultivated rice showed dominance.

Cytological observations

Three species and one form used in the present experiment, i.e., *O. sativa*, *O. punctata*, *O. officinalis* and intermediate form, have the genome of AA (Morinaga 1943), BB (Katayama 1967), CC (Morinaga and Kuriyama 1959) and CC (Ogawa and Katayama 1973), respectively. Therefore, the genomic constitutions of the allotriploids produced in this experiment, namely, sativa(4x)-punctata, sativa(4x)-officinalis and sativa(4x)-intermediate form, are AAB, AAC and AAC, respectively.

As shown in Fig. 1, the number of chromosomes counted in somatic cells was 36 in all the allotriploids. (PF₁ 13 to 25) : At pachytene stage, there was some difficulty in the identification of all the chromosomes deriving from both parents. At diakinesis, in most of the microsporo-
Table 3. Parental characters contrasted with those of F₁ plants

<table>
<thead>
<tr>
<th></th>
<th>Shinriki</th>
<th>Sekitori</th>
<th>W 1514</th>
<th>W 1527</th>
<th>W 0065</th>
<th>PF₁ 13</th>
<th>PF₁ 14</th>
<th>PF₁ 17</th>
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</thead>
<tbody>
<tr>
<td>Awn length (cm)</td>
<td>awnless</td>
<td>awnless</td>
<td>5.6</td>
<td>0.9</td>
<td>0.5</td>
<td>2.3</td>
<td>2.9</td>
<td>4.4</td>
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<tr>
<td>Awn color</td>
<td>yellow</td>
<td>purple</td>
<td>black</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
</tr>
<tr>
<td>Spikelet length (mm)</td>
<td>7.0</td>
<td>7.1</td>
<td>5.8</td>
<td>6.0</td>
<td>5.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spikelet width (mm)</td>
<td>3.5</td>
<td>3.0</td>
<td>2.1</td>
<td>2.0</td>
<td>2.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spikelet length/width</td>
<td>2.0</td>
<td>2.4</td>
<td>2.8</td>
<td>3.0</td>
<td>2.0</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Spikelet color of the tip</td>
<td>yellow</td>
<td>brown</td>
<td>black</td>
<td>black</td>
<td>black</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
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<tr>
<td>Spikelet color of the flower glumes</td>
<td>yellow</td>
<td>yellow</td>
<td>black</td>
<td>black</td>
<td>black</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
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<tr>
<td>Spikelet color of the empty glumes</td>
<td>yellow</td>
<td>yellow</td>
<td>black</td>
<td>black</td>
<td>black</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
</tr>
<tr>
<td>Spikelet deciduousness</td>
<td>not deciduous</td>
<td>not deciduous</td>
<td>deciduous</td>
<td>deciduous</td>
<td>deciduous</td>
<td>intermediate</td>
<td>intermediate</td>
<td>intermediate</td>
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<tr>
<td>Stigma color colorless</td>
<td>colorless</td>
<td>purple</td>
<td>purple</td>
<td>purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
</tr>
<tr>
<td>Leaf shape of the ligules medium</td>
<td>colorless</td>
<td>colorless</td>
<td>small</td>
<td>small</td>
<td>small</td>
<td>large</td>
<td>large</td>
<td>large</td>
</tr>
<tr>
<td>Leaf color of the ligules medium</td>
<td>colorless</td>
<td>colorless</td>
<td>colorless</td>
<td>colorless</td>
<td>colorless</td>
<td>colorless</td>
<td>colorless</td>
<td>colorless</td>
</tr>
<tr>
<td>Leaf auricle medium</td>
<td>medium</td>
<td>medium</td>
<td>glabrous</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
<td>medium</td>
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<tr>
<td>Leaf length of the flag-leaf (cm) 29.8</td>
<td>34.8</td>
<td>29.9</td>
<td>19.0</td>
<td>17.0</td>
<td>19.0</td>
<td>27.0</td>
<td>29.2</td>
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</tr>
<tr>
<td>Leaf width of the flag-leaf (cm) 1.1</td>
<td>1.6</td>
<td>1.4</td>
<td>1.7</td>
<td>1.5</td>
<td>1.6</td>
<td>2.0</td>
<td>1.7</td>
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<tr>
<td>Leaf color of the leaf-sheath green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
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<tr>
<td>Leaf color of the leaf-blade green</td>
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<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
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<tr>
<td>Stem length of the internode (cm) 21.4</td>
<td>17.2</td>
<td>17.9</td>
<td>12.0</td>
<td>14.0</td>
<td>22.0</td>
<td>18.0</td>
<td>23.5</td>
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</tr>
<tr>
<td>Stem color of the internode green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
<td>green</td>
</tr>
<tr>
<td>Stem color of the node green</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
<td>light purple</td>
</tr>
<tr>
<td>Plant type erect</td>
<td>erect</td>
<td>semi-spreading</td>
<td>spreading</td>
<td>spreading</td>
<td>erect</td>
<td>erect</td>
<td>erect</td>
<td></td>
</tr>
<tr>
<td>Plant height (cm) 85</td>
<td>99</td>
<td>87</td>
<td>66</td>
<td>72</td>
<td>112</td>
<td>98</td>
<td>112</td>
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<tr>
<td>Panicle shape closed</td>
<td>closed</td>
<td>semi-spreading</td>
<td>spreading</td>
<td>semi-spreading</td>
<td>semi-spreading</td>
<td>semi-spreading</td>
<td>semi-spreading</td>
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</tr>
<tr>
<td>Panicle length (cm) 18.7</td>
<td>21.9</td>
<td>17.0</td>
<td>21.0</td>
<td>16.0</td>
<td>14.0</td>
<td>24.0</td>
<td>21.0</td>
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<tr>
<td>Plant number</td>
<td>No. of cells observed</td>
<td>Trivalent</td>
<td>Bivalent</td>
<td>Univalent</td>
<td></td>
<td></td>
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<tr>
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<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
<td></td>
</tr>
<tr>
<td>PF₁, 13</td>
<td>216</td>
<td>0.0</td>
<td>0-1</td>
<td>11.9</td>
<td>9-13</td>
<td>12.2</td>
<td>10-18</td>
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<td>PF₁, 14</td>
<td>233</td>
<td>0.0</td>
<td>0-1</td>
<td>11.7</td>
<td>6-14</td>
<td>12.5</td>
<td>8-24</td>
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<td>PF₁, 16</td>
<td>228</td>
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<td>0-1</td>
<td>11.4</td>
<td>6-10</td>
<td>13.3</td>
<td>10-24</td>
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<tr>
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<td>240</td>
<td>0.0</td>
<td>0-1</td>
<td>11.8</td>
<td>10-14</td>
<td>12.3</td>
<td>8-16</td>
<td></td>
</tr>
<tr>
<td>PF₁, 22</td>
<td>245</td>
<td>—</td>
<td>—</td>
<td>12.0</td>
<td>10-13</td>
<td>12.0</td>
<td>10-16</td>
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<tr>
<td>PF₁, 23</td>
<td>264</td>
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<td>0-1</td>
<td>11.9</td>
<td>1-13</td>
<td>12.1</td>
<td>10-34</td>
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<tr>
<td>PF₁, 25</td>
<td>243</td>
<td>0.0</td>
<td>0.1</td>
<td>12.0</td>
<td>10-13</td>
<td>12.0</td>
<td>10-16</td>
<td></td>
</tr>
<tr>
<td>PF₁, 26</td>
<td>132</td>
<td>—</td>
<td>—</td>
<td>1.1</td>
<td>0-12</td>
<td>33.8</td>
<td>12-36</td>
<td></td>
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</tbody>
</table>

cytes some bivalents, although varied in number, were observed. In the PF₁, 13 to PF₁, 25, over 200 PMCs were observed at MI of each PF₁ (Table 4). The mean number of bivalents per PMC was 11.4 to 12.0, which was close to the haploid chromosome number of the diploid Oryza species (Table 4).

In this experiment, the bivalents should be originated from the chromosome pairing between two A genomes, because O. sativa, one of the parents, is autotetraploid. Ho and Li (1965), however, pointed out that there were only 6.86 bivalents per cell instead of 12 pairs derived from O. sativa chromosomes in allotriploids, (O. sativa × O. officinalis) × O. sativa. When most of the homologous chromosomes in these allotriploids formed bivalents, the univalents oriented themselves dispersely on either side of the equatorial plate at MI (Fig. 2). When the bivalents began to migrate to the poles, the univalents lagged on the equatorial plate. Later, the intact univalents might move randomly to the opposite poles or might be separated into two chromatids. The second division proceeded relatively regular. At the end of microsporogenesis, tetrads were formed. Each sporad would have 12 chromosomes of A genome and 0 to 12 extra chromosomes of B or C, and was almost non-functional.

In addition to the divisions mentioned above, these PF₁ plants frequently showed irregular meiotic behavior of the chromosomes, i.e., short spindle (Fig. 3), non-simultaneous division at second division (Fig. 4), restitution nucleus, and abnormal sporads (Fig. 6) etc. (PF₁, 26): In the PF₁, 26, 36 univalents or 1 bivalent and 34 univalents were observed from diakinesis to MI (Table 4, Fig. 5), and 72 chromatids were counted at AI. This plant showed asynapsis.

Asynaptic and desynaptic genes which control the chromosome pairing at MI of PMCs have been reported in a number of crop plants, such as, Zea (Beadle 1933), Triticum (Li et al. 1945), etc. Most of the asynapsis or desynapsis are controlled by a single recessive gene.

In the present experiment, Sekitori (4x) was used as female parent of PF₁, 26 as same as that of PF₁, 14, PF₁, 16 and PF₁, 17. These 3 PF₁ plants, except PF₁, 26, formed about 12 bivalents at MI as expected from the genomic constitution. And also Ogawa (1976) described that the chromosome pairing was normal in the F₁ hybrids between O. officinalis...
(W 1281) and O. officinalis (W 1267 and W 1291) or intermediate form (W 1525). Though there is no datum available on the chromosome pairing in the F₁ hybrid between W 1281 and a species having A genome, W 1281 from the facts mentioned above, is assumed to have the asynaptic or desynaptic gene(s) preventing the pairing of the homologous chromosomes. Additional studies are necessary to clarify this problem.
Cytogenetical Studies on the Genus *Oryza*. VIII.

**Literature Cited**


イネ属の異質三倍体に関する細胞遺伝学的研究

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近年、耐病虫性など野生種のもの有用な遺伝子を栽培植物に導入することを目的とした新しい育種技術の確立が試みられ、すでに実用品種の育成に成功した例もある。

野生イネのもつ有用遺伝子を栽培イネに導入する試みは、これからのイネ育種を進める1方法として、充分考慮されるべき問題の1つである。

本報告は異質染色体添加型植物を作出するための基礎として、まず栽培イネの人為同質4倍体を育成し、これに近縁野生2倍種を交雑して、えられた異質3倍体 *sativa*(AA)−*puncta*(B), *sativa*(AA)−intermediate(C)および *sativa*(AA)−*officinalis*(C)に従って行った細胞遺伝学的・形態学的研究の結果をまとめたものである。

体細胞で2n=36の染色体数を数えられ、いずれの個体も明らかに異質3倍体であることを確認した。

減数分裂は、PF26を除いて、各体細胞で大体類似しており、MIでは大部分の細胞で12Ⅱ+12Ⅰを示す分裂像を、また、Alでは1個染色体による分裂異常が観察された。

一方、PF26はMIで12Ⅱ+34Ⅰまたは36Ⅰを示し、明らかに相同染色体間の不対合現象を観察され、以後の分裂に種々の異常が認められた。この染色体不対合がasynapsisであるか、desynapsisであるかは不明であるが、供試した同質4倍体の細胞質と *O. officinalis* (W 1281)の核との何れか一方、または両者に不対合を誘起する遺伝的要因がある可能性が考えられ、その解明は今後の検討に期待したい。