Aneuploids in some artificially induced polyploids of cultivated plants

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ABSTRACT


Artificially induced autotetraploid barley stocks (Hordeum vulgare), autotetraploid sugarbeet populations (Beta vulgaris) and amphipolyploid wheat-rye derivatives (4x Triticum x Secale cereale) were studied for chromosome number and chromosomal stability. In barley euploid plants produced 42 — 66 % aneuploid plants, which varied in growth and vigour from very poor to almost normal along with low fertility. In populations of sugarbeet aneuploidy occurred in about 42 — 44 %. Growth of aneuploid plants also ranged from very poor to almost normal. In some 6x Triticales aneuploids were encountered in lesser number (16 %).

From the results obtained it seems that inducing polyploidy affects chromosomal stability. The resulting aneuploids are less vigorous and less fertile than euploids and therefore unsuitable to grow in a commercial crop. To give reliable results tetraploid crops should be cleaned as much as possible of aneuploids, which can be done by mechanical selection. As long as chromosomal stability has not been completed by genetical selection mechanical selection has to be repeated in each generation.

It is thought that aneuploidy as a result of induced polyploidy is governed by gene-like acting newly arising gene interaction. Furthermore, though partial sterility is also the result of aneuploidy, fertility per se may be subdued to factors others than governing aneuploidy.

INTRODUCTION

In many cases artificially induced polyploids of cultivated plants have shown greater variation in morphology and yield than the diploids they were derived from. Three of these crops were studied for chromosome number and chromosomal stability. The informations yielded on the cytogenetic properties of the polyploids are reported and discussed herewith.

MATERIALS AND METHODS

The species investigated were:

- Autotetraploid barley (Hordeum vulgare L.), which as a diploid is a homozygous, self-fertile plant.
- Autotetraploid sugarbeet (Beta vulgaris L.), which as a diploid is a heterozygous, self-sterile plant.
- Amphidiploid hexaploid ryewheat (Triticale), derived from 4 × Triticum × Secale cereale crosses.

Chromosome counts on cereals were accomplished using root tips and the Feulgen staining method, and on sugarbeets applying the orcein technique of Tjio and Levan (1950), modified by Rommel (1963), on young leaves.

RESULTS

Hordeum vulgare.

In autotetraploid barley (4 × = 28 chromosomes) euploid plants produced progenies with 42—66% aneuploid plants besides the expected euploids (Rommel, 1961 and Table I). When the seeds were divided into three seed classes according to their endosperm development, 83% of the class I seed was made up out of euploids, while the class III seed contained 35% euploids only (Helgason and Rommel 1963). The aneuploid plants showed great variation in morphological appearance ranging from very poor to almost normal growth. Among 197 aneuploid plants with chromosome numbers ranging from 27 - 31, 13% died without developing heads.
These plants are sometimes called "dwarfs" (Reinbergs and Shebeski 1961). 13% developed heads, but were completely sterile, and 74% developed heads and set seed, but with an average seed set well below that of the euploid plants from the same crop.

**Beta vulgaris.**

In autotetraploid sugar-beet populations (4x = 36 chromosomes) 32—41% of the plants were found to be aneuploids (Rom-mel 1963 and Table I).

Many aneuploids were poor in growth of leaves as described by Levan (1942) and could be easily recognized within a population. The average weight of aneuploid roots seldom reached that of euploid roots. The percentage of seedlings, which did not survive the winter months, was much higher among aneuploids than among euploids.

**Triticale.**

Small samples of 42-chromosome ryewheat were searched for chromosome off-numbers. The results are presented in Table I. Though the samples were small, aneuploids were found in each one of them. These plants proved to be more sterile than the euploid ones.

**TABLE I**

*Euploid and aneuploid plants in three different polyploids*

<table>
<thead>
<tr>
<th>Species and variety</th>
<th>No. of plants</th>
<th>Euploids in %</th>
<th>Aneuploids in %</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hordeum vulgare</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁ Edda × Ricardo *</td>
<td>393</td>
<td>52.4</td>
<td>47.6</td>
</tr>
<tr>
<td>F₁ Edda × Anodium *</td>
<td>1148</td>
<td>50.5</td>
<td>49.5</td>
</tr>
<tr>
<td><em>Beta vulgaris</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B 742 MM</td>
<td>540</td>
<td>59.0</td>
<td>41.0</td>
</tr>
<tr>
<td>E 646 — 23</td>
<td>519</td>
<td>60.1</td>
<td>39.9</td>
</tr>
<tr>
<td>B 742</td>
<td>365</td>
<td>60.3</td>
<td>33.7</td>
</tr>
<tr>
<td>J 8413</td>
<td>312</td>
<td>68.3</td>
<td>31.7</td>
</tr>
<tr>
<td>E 646</td>
<td>305</td>
<td>67.2</td>
<td>32.8</td>
</tr>
<tr>
<td><em>Triticale 6x</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. durum × S. cereale</td>
<td>32</td>
<td>83.3</td>
<td>16.7</td>
</tr>
<tr>
<td>T. dicoccoides × S. cereale</td>
<td>32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4x wheat × S. cereale</td>
<td>38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Derived from euploid plants.
DISCUSSION

Aneuploidy was found in all three crops studied, i. e. none of the artificially induced polyploids was stabilized on the newly established chromosome level. Not only that plants with deviating chromosome numbers occurred right after the induction of polyploidy, but from generation to generation euploid plants gave raise to aneuploids besides the expected euploids (Rommel, 1961 and unpublished results). Extensive studies by other workers using crops like autotetraploid rye (Müntzing 1943, Hagberg and Ellerström 1959, Ellerström and Sjödin 1963, see literature there), or autotetraploid maize (Randolph 1935, Alexander 1957, Shaver 1962 a. o.) have yielded the same results.

While in diploids at least the loss of a chromosome seems to be lethal, many polyploids will tolerate the loss or gain of one or more chromosomes.

Without referring to any particular chromosome it can be said that this gain or loss of one or more chromosomes disturbs plant development in an unfavourable way. The chances for any aneuploid to fail in any stage of its development are much higher than for any euploid plant. Either the seed will not fully develop, or the plant will not reach the reproductive stage, or will not set seed, or will be highly sterile. These features make aneuploid plants unsuitable to grow in any crop, and their elimination seems desirable.

With respect to euploidy, genetical selection has not been widely explored. Selections, made on account of meiosis or fertility, failed to stabilize the plants on the euploid level. Therefore, once a relationship between certain morphological characters and aneuploidy has been established, these characteristics can be used to select mechanically for higher percentage of euploids. Mechanical selection has to be repeated in each generation. The most secure elimination of aneuploids is based on chromosome counts, herewith not considering the number of plants, which possess the euploid chromosome number, but in reality are aneuploids. To carry out chromosome counts on a large scale is time consuming, whereas mechanical selection can be done in much shorter time. Tetraploid rye or tetraploid barley seed lots can be cleaned of a considerable amount of aneuploids (Hagberg and Ellerström 1959, Helgason and Rommel 1963), thus reflecting in the stand and seed yield of
the varieties. Because a similar seed selection cannot be applied to autotetraploid sugarbeet (Rommel 1964), a field of tetraploid beet roots will represent the original amount of aneuploids, while seed beets grown from roots selected on account of weight can represent an almost pure stand of euploid plants.

In studies on inheritance and evaluation of polyploids the presence of aneuploids has to be considered, and crops used for the studies should be cleaned of aneuploids as much as possible to give true and reliable results. Many studies, which were based on selections within a variety using such visual features as seed size, root size and better fertility versus highly sterile plants in fact to a large amount can be interpreted as selections for euploid versus aneuploid plants.

Apparently inducing polyploidy seems to affect chromosomal stability, which indicates that the production of functional aneuploid gametes must be primarily conditioned by polyploidy. In the polyploid plants the off-number gametes result from meiosis disturbances, which seem to be genetically controlled (Roseweir and Rees 1962). But when all polyploids show genetically controlled production of aneuploid gametes, then we may conclude that the process of putting two complete sets of genomes into a new organism can result in new gene-like acting factors. If we find one gene controlling meiosis disturbances, we have to expect many other gene interactions. One factor may control meiosis disturbances, resulting in euploid and aneuploid zygotes, the latter ones including viable and inviable combinations, leading to a certain degree of sterility. Another factor is thought to control fertility per se. This would explain, why meiosis disturbances can be correlated with chromosomal stability, but not always with fertility (Riley 1960, Shaver 1962).

CONCLUSIONS

When comparing the chromosomal stability of the artificially induced polyploids with the chromosomal stability of some natural induced polyploids such as wheat (Riley and Kimber 1961), or oats (McGinnis 1962), the level of aneuploidy in the crops investigated is far too high to be tolerated. Mechanical selection for eu-
Ploidy should be applied wherever possible. Genetical means to raise euploidy in polyploid crops should be more explored. Nevertheless, it seems that such a low level of aneuploidy, which will not affect the yield of the crop cannot be reached by combination and selection but has to be forced onto by mutational steps.

**RESUMEN**

Aneuploidía en algunos poliploides artificiales de plantas cultivadas.

Se estudiaron variedades de cebada autotetraploide (*Hordeum vulgare*) producida artificialmente, poblaciones de remolacha azucarera autotetraploide (*Beta vulgaris*) y descendencias de Triticales anfipoliploides (4x *Triticum x Secale cereale*), en relación con el número de cromosomas y la estabilidad cromosómica. En cebada las plantas euploides produjeron del 42 — 66% de individuos aneuploides, de crecimiento y vigor variable: desde muy pobre a casi normal, al lado de una fertilidad baja. En poblaciones de remolacha la aneuploidía se presentó en una frecuencia del 42 — 44%. También el porte de las plantas aneuploides oscilaba entre muy pobre y casi normal. En varios 6x Triticales se encontraron aneuploides pero en una proporción más baja (16%).

Los resultados obtenidos parecen indicar que la poliploidía inducida afecta la estabilidad cromosómica. Los aneuploides resultantes son menos vigorosos y fértiles que los euploides, y por tanto inapropiados para constituir un producto comercial. Para conseguir buenos resultados prácticos hay que limpiar en lo posible de aneuploides las variedades tetraploides, y eso puede hacerse por selección mecánica. En tanto no se consiga una estabilidad cromosómica por selección genética, la selección mecánica debe repetirse en cada generación.

Se ha pensado que la aneuploidía como resultado de la poliploidía inducida está gobernada por una interacción génica —surgida por la aneuploidía— que actuaría a modo de gene. Además, aunque una esterilidad parcial es también el resultado de la aneuploidía, la fertilidad *per se* puede depender de otros factores distintos de los que gobiernan la aneuploidía.
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