THE OCCURRENCE OF PARTHENOGENETIC DIPLOIDS IN TETRAPLOID MAIZE

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Chromosome doubling within species and varieties of plants has contributed extensively to the origin of stable new forms among both cultivated and wild species. But the reverse process involving a reduction in chromosome numbers comparable to the reduction which occurs in the origination of parthenogenetic haploids from diploids is unknown among autopolyploids, with the possible exception of a case reported by Hakanson in Oenothera. Evidence that this reverse process may occur is available from the results of intercrosses between intraspecific tetraploid and diploid races in which the tetraploid was the seed parent. Belling and Blakeslee obtained diploids as well as triploids in a cross of this kind in Datura, and Gairdner and Darlington noted the occurrence of a diploid plant from a similar cross in Campanula persicifolia. In experiments with tetraploid maize extending over a period of years diploid individuals have been noted at infrequent intervals in the progenies of tetraploid plants, but the possibility was not excluded that these were due to admixtures of diploid seed at planting time or to contaminations of some other sort.

Last year in experiments with tetraploid maize designed primarily to determine their frequency of occurrence 23 parthenogenetic maternal diploids were discovered among 17,165 individuals and their identity as such was definitely established by genetic tests and by direct cytological examination. Crosses were made between tetraploid stocks in which genes for recessive endosperm and seedling characters were contributed by the seed parent and their dominant alleles were contributed by the pollen parent. Any parthenogenetic maternal individuals originating pseudogamously from such crosses would exhibit the recessive characters of the seed parent and would therefore be readily distinguishable from the hybrids which would exhibit the dominant characteristics contributed by the pollen
parent. An attempt was not made to plan these crosses to aid in the identification of paternal as well as maternal parthenogenetic diploids, by introducing genetically unlike recessive seedling genes in both parent stocks.

Data were obtained from four different crosses, in each of which the seed parent was a green plant ($A_1 b \ p l \ r^e$) with colorless aleurone ($r^e$) and white endosperm ($y_1$). In the first cross sugary endosperm ($sul$) also was involved.5 The pollen parent of the first two crosses had purple plant color ($A_1 B P I$) colored aleurone ($R$) and starchy ($Sul$) yellow ($Y_1$) endosperm. The pollen parent of the third cross was a dilute sun-red plant ($A b \ pl \ rr$) with yellow endosperm ($Y_1$), and that of the fourth cross was a sun-red plant ($A B \ pl \ r^e$) with yellow endosperm ($Y_1$). The genotype of each of the crosses and the number of parthenogenetic maternal diploids and hybrid tetraploids obtained from each were as follows:

<table>
<thead>
<tr>
<th>No.</th>
<th>Cross Description</th>
<th>Maternal 2N</th>
<th>Tetraploid 4N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$A_1 \ b \ pl \ r^e \ y_1 \times A_1 \ B \ Pl \ R^e \ Sul \ Y_1$</td>
<td>3</td>
<td>904</td>
</tr>
<tr>
<td>2</td>
<td>$A_1 \ b \ pl \ r^e \ y_1 \times A_1 \ B \ Pl \ R^e \ Y_1$</td>
<td>2</td>
<td>530</td>
</tr>
<tr>
<td>3</td>
<td>$A_1 \ b \ pl \ r^e \ y_1 \times A_1 \ b \ pl \ r^e \ Y_1$</td>
<td>17</td>
<td>15,615</td>
</tr>
<tr>
<td>4</td>
<td>$A_1 \ b \ pl \ r^e \ y_1 \times A_1 \ B \ Pl \ r^e \ Y_1$</td>
<td>1</td>
<td>93</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23</td>
<td>17,142</td>
</tr>
</tbody>
</table>

The first, second and fourth crosses were from hand-pollinated ears; the third cross was produced in an isolated plot, the seed parent being detasseled before pollen was shed. The $F_1$ populations were grown exclusively from seeds with hybrid endosperm, i.e., seeds exhibiting the dominant endosperm characters of the pollen parent.

The 23 individuals classed as maternal diploids were with respect to the contrasting characters contributed to the cross by the parent stocks genotypically like the tetraploid seed parent; they lacked anthocyanin color as seedlings and mature plants, and when selfed or crossed with appropriate tester stocks, exhibited the recessive endosperm and aleurone characters of the seed parent. The reduced size of their stomata and pollen indicated that they were diploid. They produced abundant good pollen, were highly self-fertile, crossed readily with other diploids and like diploids were highly cross-sterile with tetraploids.

Among 20 of the 23 exceptional plants in which accurate chromosome counts were made there were 15 plants with 20 chromosomes, 1 with 21 chromosomes, 3 with 22 chromosomes and 1 with 24 chromosomes. Since in tetraploid maize aberrant individuals with one or a few chromosomes more or less than the typical number 40 occur not infrequently,6 it was anticipated that numbers greater than 20 would appear in some of the maternal diploids. These aberrant extra-chromosome plants furnish a readily available source of trisomic stocks, which would be especially favorable for a study of the phenotypic characteristics of the different trisomics provided
they originate from uniform inbred tetraploid stocks. They also furnish
direct evidence of the frequency with which normal 20-chromosome gametes
and functional extra-chromosome gametes are produced by the ovules of
tetraploid plants.

In general the parthenogenetic maize diploids resembled in appearance
and breeding behavior the diploid stocks from which their maternal tetra-
ploid parents were derived. But a critical study of these relationships has
not yet been made.

It is anticipated that these maternal diploids will provide valuable ma-
terial for a new approach to the study of the cytogenetic, physiological and
morphological consequence of direct chromosome doubling. It has been
suggested by various workers that certain of the characteristics which dis-
tinguish autotetraploids from their parental diploids may have resulted
from genotypic changes induced by chromosome doubling and are not due
merely to the presence of the doubled number of chromosomes. This
problem and others like it can be attacked by comparing maternal diploids
extracted from autotetraploid stocks with the tetraploid parent and with
the original diploid stock from which the tetraploid originated.

The occurrence of fertile parthenogenetic diploids in populations of auto-
tetraploid plants is highly significant from the evolutionary standpoint,
since these diploids are capable of establishing new races with the reduced
chromosome number. Admixture with the parental tetraploid does not
occur to any appreciable extent and seed is produced abundantly by the
diploid from its own pollen to the exclusion of that from the tetraploid
parent, according to the results of mixed pollen experiments with maize.6
Equal significance cannot be attached to the occurrence of parthenogenetic
diploids among allotetraploids which are of hybrid origin, because they are
sterile.7

It would be inappropriate to discuss here the various conditions under
which new species and horticultural varieties of plants originate by chromo-
some doubling or by the reverse process of halving the number of chromo-
somes. However, as a result of the discovery of fertile parthenogenetic
diploids in the progeny of autotetraploid maize, the conclusion is inescap-
able that the evolutionary trend among autopolyloids is not necessarily
unidirectional, the forms with low numbers being always primitive and
those with high numbers being always derived from them as has been
generally believed. It is now apparent that the trend may be in either
direction. Polyploids which have arisen by direct chromosome doubling
may in turn give rise to new forms with lower chromosome numbers. Ma-
ternal diploids occurred in tetraploid maize with a frequency in the ratio of
approximately 1:750. If parthenogenetic diploids occurred with a similar
frequency among autotetraploids generally there would be ample oppor-
tunity for new diploid races to originate from them.
These experiments were aided by a grant to the senior author by the Committee on Effects of Radiation upon Living Organisms of the National Research Council.

Hakansson (Hereditas 5, 93–96 (1924)) discovered a 14-chromosome plant in the progeny of Oenothera gigantea, which was thought to have originated from the union of 7-chromosome gametes. But it is possible that the plant was a parthenogenetic diploid.

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Appendix.—Since this article was submitted for publication the current number of Hereditas was received, in which there was a paper by Heribert Nilsson (Hereditas, 25, 1–8 (1939)) describing diploid derivatives of Oenothera gigantea, an autotetraploid form of Oe. Lamarckiana (cf. footnote 2). These derived diploids definitely exhibited certain characteristics of Oe. gigantea as well as certain characteristics of Oe. Lamarckiana and for this reason were appropriately designated Oe. diplo-gigantea.

THE SYNTHESIS AND DESTRUCTION OF VITAMIN B₁ BY PHYCOMYCES

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In an earlier communication¹ data relative to the in vivo synthesis of vitamin B₁ by the isolated pea root have been presented. For a fuller understanding of the physiological economy of the vitamin, some insight also into the modes of disappearance of the substance is indispensable.

The accumulated evidence now permits us to present a picture both of in vivo synthesis of the vitamin by Phycomyces Blakesleeanus and of a mechanism by which the vitamin molecule is broken down by the latter organism.

The experimental techniques were similar to those described in earlier communications.¹ ² Stock cultures of Phycomyces Blakesleeanus and of Phytophthora cinnamomi were maintained on malt agar. The experimental cultures were, in all cases, made up with 10 cc. of medium (MgSO₄.7H₂O... 0.5 gm.; KH₂PO₄... 1.5 gm.; asparagin... 4.0 gm.; dextrose... 100 gm.; distilled water... 1 liter) to which was added the desired amount of vita-