CHROMOSOME NUMBER IN THE PROCENY OF TRIPIOID CLADIOLUS WITH SPECIAL REFERENCE TO THE CONTRIBUTION OF THE TRIPIOID

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In a previous report concerning the chromosome number in Gladiolus (3) and a later one (4) showing the relation of this factor to the hybridization of various species and varieties, one of the important objects in view has been the origin of the present-day commercial varieties. That certain of the species of this genus were concerned in the formation of these types has long been recognized (6), and, as Molean (51) pointed out some time ago, certain characters in the commercial types must have come from the South African species. In terms of chromosome number. this means that certain characters of the commercial totraploids have been derived from the South African diploid species. Whether this transfer was by means of amphidiploids, which might have been formed spontaneously after hybridization and then crossed again with other tetraploids, or whether triploids were involved, is a question. In the first study (3) it was appearent that triploids did occur among the commercial types and later (4) that the probable origin of these was from either a diploid-tetraploid or reciprocal cross, since over fifty per cent of such attempts were successful. Perhaps the most important observation in the recent study (4), however, was that such triploids were partially fertile when used as the seed parent in further crosses with either of the original parents or with other diploid and tetraploid forms.

Although the thought still persists among many that tripleids are sterile, an examination of the literature reveals that such is not the case. Progeny have been produced from crosses involving triploids, mostly as the seed parents, with diploids in apple (11) (34) (15), Petunia (16), Fragaria (48), Cenothera (12), Populus (10) (22),

Tulips (5) (19) (45), Zes (30), Impatiens (42), Allium (28), Datura (6) (59), Iilium (40), Grepis (33), tomate (27), and petate (36). It has also been reported that progeny have been produced from crosses between triploids and tetraploids in Petunis (16), Phleum (35) (18), and others. It would appear then that Gladiolus is not unusual in this respect.

Preliminary investigations (26) showed that not only did these <u>Cladiolus</u> triploids, when used as the seed parents, behave in a fashion similar to those already reported in the literature (5, 15, 19, 30, 34, 39, 45), but that some other type of chromosome behaviour was taking place. This report presents the occurrence and frequency of these observations.

MATERIAIS AND METHOUS

With the exception of the previously reported triploid variety

Chara (5), the triploids used in this study were produced through reciprocal crosses between various tetraploid commercial varieties and diploid
species. Using the triploids as the female parent, seeds were obtained
after crossing these with diploid species or some diploid hybrids, and
also with tetraploid commercial varieties, as well as some tetraploid
hybrids produced as the result of previous hybridization. Some examples
illustrating the parentage of these progeny are:

[Prof. Donders (60) x G.hirsutus (50)] x (G.tristis (50))

(G.tristis (50) x Prof. Donders (60)] x (G.tristis (50) x G.alatus (50))

(Miss Pleomington (60) x G.angustus (30)) x (Dr. Moody (60))

(Prof. Donders (60) x G.tristis (30)) x (G.primulinus (60) x

Princeps (60)]

In all, approximately 500 plants were obtained, and of these it was possible to obtain chromosome counts from 470.

All work was done in the greenhouse during the winter months. Seeds from the triploids were gathered in the late spring and planted in pots the following fall. The corms produced from these seeds were generally planted the next fall, if large enough, in separate pots and root tips collected from each. These tips were fixed in Navashin's solution and prepared for sectioning by the short butyl alcohol method. Tissue-met was used for the embedding process, and all sections were cut 12 microns thick. Staining was accomplished by the crystal violet-iodine technique. Observations were made with the sid of a 90x, 1.8 aprochromatic objective. Drawings were made with a camera lucida. All magnifications are listed with the plates.

In making the chromosome counts, it was impossible in a few cases to obtain a consistent number for some individuals. In recording these, it was necessary to list them as <u>t</u> the number which was found most frequently. The least inconsistent of these have been included in the graphs, while the more variable ones were entirely eliminated from consideration.

RESULTS AND DISCUSSION

It was presumed in all cases that the diploid male parent centributed only fifteen chromosomes and the tetraploid male only thirty chromosomes, because in all other crosses, such as diploid-diploid, diploid-tetraploid, tetraploid-diploid, and tetraploid-tetraploid, no irregularities in gametic chromosome contribution have been observed from a study of the resultant hybrids.

After the chromosome number of the triploid progeny had been determined, the contribution of the triploid seed parent, when crossed with the diploid, was ascertained by subtracting the haploid number of the pollen parent. This is shown graphically in Plate I, while the contribution of the triploid, when crossed with the tetraploid as the pellen parent, is shown in Plate II. In Plate III the total contribution in all cases is shown, thus combining the two previous graphs, since the triploid parent was common to both types of crosses.

to determine whether certain triploids might have reacted differently when crossed with various diploids and tetraploids; but there was no indication of this in the behaviour of any of the triploids in crosses with any one individual variety or species. For this reason, all triploid-diploid or triploid-tetraploid crosses were treated as a group rather than as individuals.

Triploid-Diploid Progeny. It is quite obvious from Plate I that there is a great variance in regard to the chromosome number of the functional gemetes of the triploid. From 18 to 55 chromosomes were contributed one or more times. Despite this wide distribution and variation as shown in the charts, it is possible to note three obvious frequencies, which probably indicates three different possible types of behaviour most frequently occurring in the triploid. The frequent contribution of approximately 24 indicates the moiosis must have been nearly normal, the frequency at 50 indicates gemetes like those of tetraploids, and 45 the contribution of the full triploid chromosome complement.

In Plate I, which shows the contribution in the triploid-diploid crosses, it is obvious that the 5n/2 number, or approximately that, was contributed in only a small per cent of the cases. One might expect it to be that of greatest frequency in view of the results previously reported in some other plants. In <u>Tulipa</u> (n-12) Bamford et al (5),

Hall (19), and Upcott (45) have found that a triploid, used as the female parent and crossed with a diploid, contributed from 12 to 22 chromosomes and in most cases from 15 to 18, which would be about the 5n/2 number. Nebel (54) has shown in a 3n x 2n cross in apple (n-17) that the chromosome number of the progeny ranged from 35 to 48 with the mode at 40.5, which would indicate that in most cases the triploid contribution would be somewhere near the 5n/2 number. Capinpin (12) in Oenothers (n-7) in a similar cross found the range to be 14 to 21 with the mode at 16, which again approximates the Sn/2 number from the tripleid. Bergstrom (10) and Johnsson (22) in Populus, Dermen (15) in apple, and Levan (28) in Allium all found similar results, with the progeny from 5n x 2n crosses having sometic chromosome numbers ranging from the diploid to the triploid. In all these instances, however, practically all of the triploid progeny fell within this group. In Gladiolus it must be emphasised that such a contribution occurs in only a small portion of the cases, and only a small portion of the progeny would have somatic chromosome numbers ranging from the diploid to the triploid.

The second most obvious contribution of the triploid female in triploid-diploid hybrids of <u>Gladiolus</u> was that of thirty chromosomes, which would make the resulting progeny full triploids with regard to chromosome number. A few such progeny have been found by McClintock (50) and Longley (29) in Zea, Levan (28) in Allium, and Sato (40) in <u>Lilium</u> in crosses involving a triploid parent. Bergstrom (10) in <u>Populus</u> and Dermen (15) in apple also found evidence of similar gametes from the triploid. Navashin (33) in <u>Crepis</u>, in crossing a triploid F₁ inter se and with other sister diploid plants, found that approximately twenty-sight per cent of the progeny were triploids. Then this type of behaviour

is not unusual in the case of triploids.

The contribution in <u>Gladiolus</u> of the full triploid number would seem to be the most common type of behaviour. This would then mean that the progeny receiving this number would be tetraploid in nature. This is not in general accord with the literature, although occasional tetraploid progeny from triploids have been reported. In <u>Solanum</u> (36), <u>Tulipa</u> (45), and <u>Populus</u> (10) (22) infrequent progeny have appeared with the full tetraploid chromosome number. This unusual behaviour of <u>Gladiolus</u> would make it possible to see how diploid characters could be transmitted to the tetraploids if this has been common in the past development of commercial <u>Gladiolus</u>.

Triploid-Tetraploid Progeny. Upon examining the contribution of the triploid (Plate II) in the triploid-tetraploid crosses, it is again obvious that the previous three types of behaviour, as found in the triploid-diploid crosses, still exist. This indicates that the triploid, regardless of the pollen parent used, is consistent in the types of gametes most frequently produced.

The twenty-four and the thirty chromosome contributions again appear in approximately the same proportions as in the triploid-diploid crosses, although the somatic chromosome number of the progeny would be higher because of the thirty chromosome contribution from the pollen parent. Only a limited number of 5n x 4n crosses have been previously reported; but longley (29) in Zea, Dermen (16) in <u>Petunia</u>, and Gregor and Sansome (18) in <u>Phlaum</u> found that the triploid contributed approximately the diploid number when used in such a cross.

The full triploid somatic number again was contributed in most of the cases. This would indicate that the progeny receiving this contribution would be pentaploid with regard to chromosome number. Dermen (16)

in <u>Petamia</u>, in a 3n x 4n cross, found one plant with the full pentaploid number of chromosomes; and Nordenskiold (35), using <u>Phlaum</u> in such a cross, found some of the progeny to be pentaploid. In neither of these cases, however, was the full triploid contribution a general feature of such a cross. This indicates that in <u>Gladiolus</u>, the triploid, regardless of the male parent, most generally contributes the full triploid chromosome number. This is particularly true when, out of 470 progeny observed (Plate III), 129 apparently resulted from such behaviour.

Instances of higher chromosome contribution than forty-five are also shown. This is comparable to the results shown by Nordenskiold (35) in Phleum.

To explain the results presented above, it is only necessary to remember that failure of pairing, unequal divisions, lagging chromosomes, and the formation of restitution nuclei have repeatedly been described as characteristic of triploids. Stout (43) in Hemorocallis, Capinpin (12) in Conothera, Dermen (15) in the Caldwin apple, Levan (28) in Allium, McClintock (50) in Zea, Satina and Blakeslee (58) in Datura, Sato (40) in Lilium tigrium, Belling (7) in Hyscinthus, and Skovsted (41) in cotton, and many others have observed these phenomena. Although no extensive observations have been made of the embryo sac behaviour in triploid Gladiclus, those of Westfall (47), Bellows (9), and Satina and Blakeslee (58) in other genera demonstrate that the meiotic and subsequent divisions are similar to the FMC behaviour so often described, although Jensen (21) observed that they are not apt to show such violent irregularities. One of these phenomena, or a combination of them, is all that is necessary to account for the variety and extent of chromosoms numbers present in the female gametes produced by the triploid. The number twenty-four could be the result of nearly normal meiosis, while the

number thirty would indicate the contribution of a diploid gamete, which is not uncommon in such hybrids. The numbers 18-25 and 25-27, as well as those from 28 to 29 and 31 to 35 could have resulted from lagging of chromosomes or unequal division of chromosomes during the meiotic and subsequent divisions.

It is apparent that the most frequent method of behaviour in triploid Gladiolus, in contrast to many other observations, is nonreduction or the formation of a restitution nucleus. This is also borne out by Derlington (14) who states, "Nearly all triploids that have been examined, for example, form restitution muclei whether they are the product of hybridization of two species or of self-fertilizing a diploid." This is not an uncommon behaviour because it has been observed frequently in triploids and in other hybrids by Kostoff (24) in Triticum. Crane and Darlington (13) in Rubus, Andersson and Gairdner (1) in Dianthus, Webber (46) in Nicotians, Lawrence (25) in Delphinium, Graze (17) in Veronica, and many others. However, the total range from 36 to 55 is due to other phenomena in addition to the formation of restitution muclei. Lagging and unequal division of chromosomes after non-reduction could account for gametes with chromosome numbers from 36 to 44 and from 44 to 55. It is also possible that lack of pairing, with the resultant irregular behaviour of univalents, might produce a gamete with greater than the diploid or triploid number of chromosomes, as has been suggested by Karpechenko (23). When those progeny receiving the numbers 30 to 44 and 44 to 55 are added to the 129 which received the full 45 chromosomes, it shows that over fifty per cent of all the progeny fell within this group, which basically are the result of the formation of restitution miclei.

From all this evidence of high chromosome number in the functional gametes of the triploids, it seems entirely possible that the characteristics of the diploids may have been transmitted to the tetraploids through the medium of hybridization which involved the formation of triploid hybrids. Navashin (55) has speken of "... the tendency of triploids to produce polyploid interspecific hybrids...." during his work on <u>Grepis</u>, and Crane (20) in a recent article states, "We are often unable to say how a particular polyploid arose, but it is clear that the functioning of unreduced germ cells is a frequent method and that in conjunction with hybridization it has played an important part, both in nature and in cultivation, in the origin of new forms and species."

Cladiolus, because of its extensive cultivation and hybridization, might well have followed this pattern.

chromosome number of these triploid progeny, another occurrence may explain some minor changes. These are the irregularities in somatic cell division illustrated in Plate VI. That these concerned tissues, as well as individual cells, is obvious, because in some cases certain areas in the root tips were found to have different chromosome numbers from that of the surrounding tissue. In one instance the epidermis within a limited area gave a consistent chromosome count of 88, while the area of the cortex between that and the stell contained only 75 chromosomes. In another case the epidermis and cortex continually differed in number throughout the observable portion of the root. There were also instances of single cells which possessed chromosome numbers well over 100. In addition to these irregularities, a persistent nucleolus was found in some cells, as shown in Plate VI. The presence of such a nucleolus has previously been reported in Gladiolus (32).

Cases of premature division of the chromosomes at metaphase also were found. In such cases some of the chromosomes preceded the others in moving toward the poles. Observations of such mitotic irregularities have been made previously by Mensinkai (32) in Gladiolus, Babu (2) in Groundmut, Stout (44) in Memerocallis, and others; but no special significance seems to be attached to the phenomena. These irregularities may indicate a certain degree of unbalance, either in chromosome number or in the rhythm of cell division.

Summery

- 1. Four hundred and seventy progeny were obtained from several triploid <u>Cladiolus</u>, when these were used as the seed parents in crosses with diploids and tetraploids. The somatic chromosome numbers of these progeny were determined to find the contribution of the triploids.
- 2. The triploids contributed every chromosome complement from 18 to 58 and other sporadic numbers up to 69. The majority of the triploid progeny fell into three main groups, the most important being that where the triploid seed parent contributed its full chromosome complement of 45.
- This behaviour could have come about through the formation of restitution nuclei during meiosis or subsequent divisions, with the accompanying unequal distribution of chromosomes. Both of these types of behaviour are characteristic of triploids.
- 4. Such behaviour in the triploid followed by hybridization offers one explanation for the transmission of characters from the diploid species to the tetraploid forms in Gladiolus.
- 5. Irregularities is mitotic cell division were observed in the root tips of several of the triploid progeny.

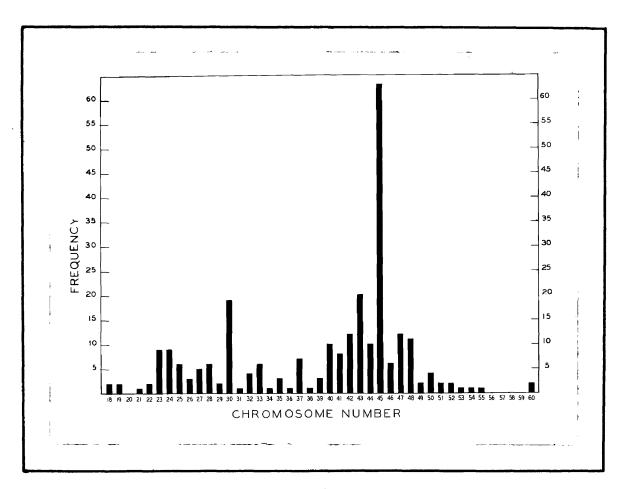
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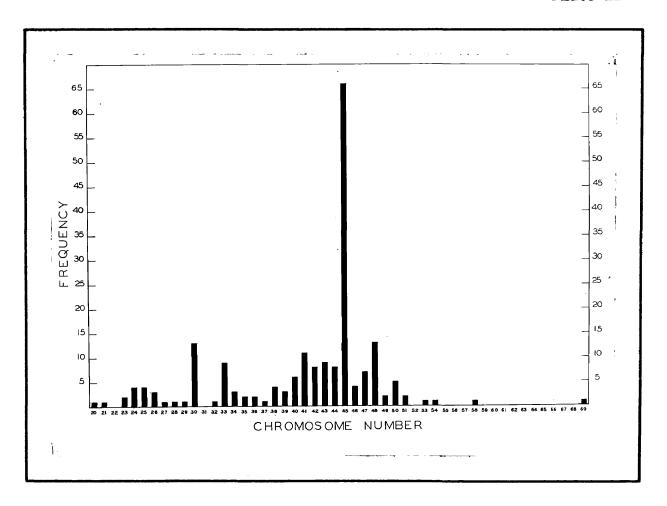
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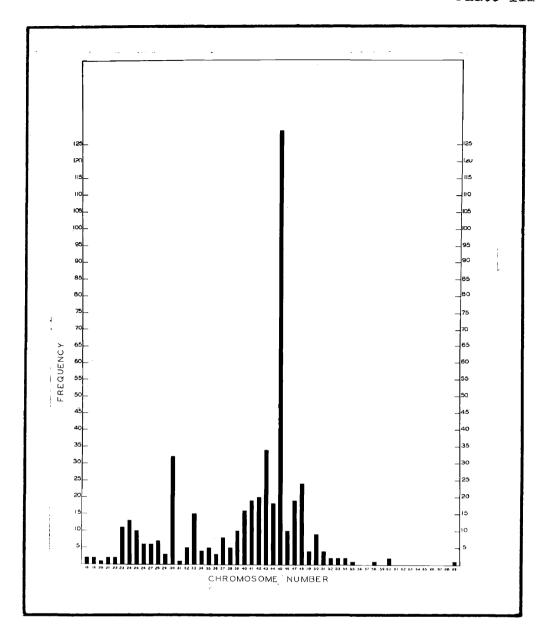
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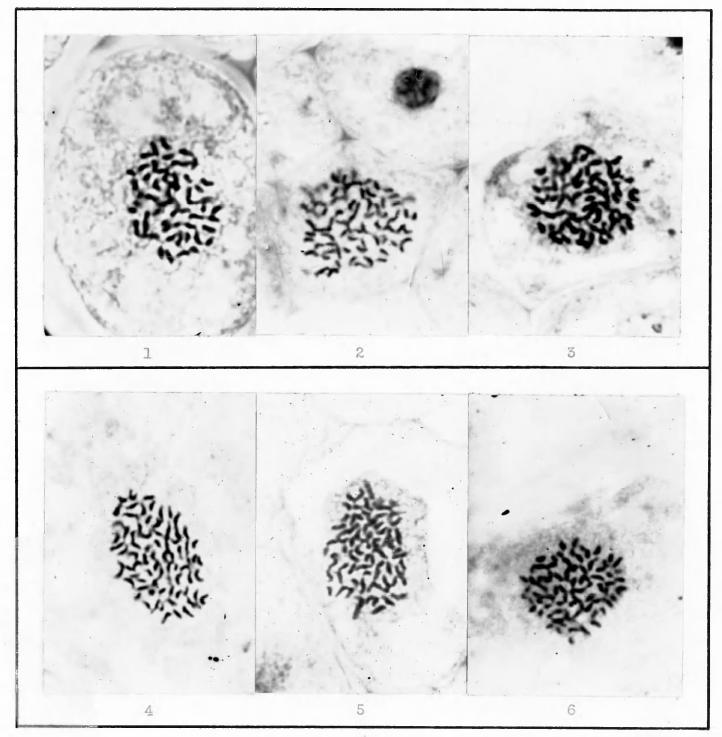
The chromosome contribution of the triploid in the triploid-diploid hybrids.



The chromosome contribution of the triploid in the triploid-tetraploid hybrids.



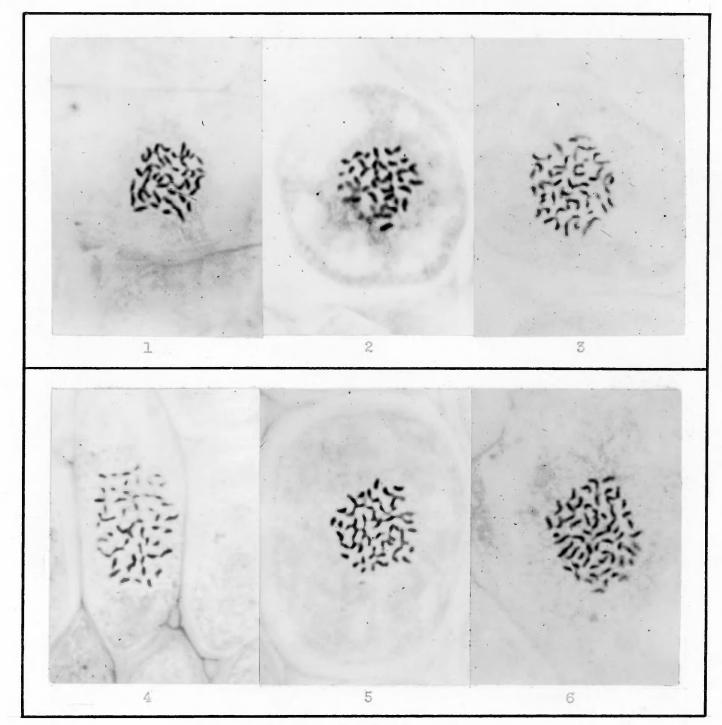
The chromosome contribution of the triploid in both triploid-diploid and triploid-tetraploid hybrids.



Chromosomes from Triploid-Tetraploid Progeny

- Fig. 1. (Edith Mason (60) x G. cuspidatus (30)) x (Edith Mason (60)), 55 chromosomes.
- Fig. 2. (Prof. Donders (60) x G. hirsutus (30)) x (Dr. Moody (60)), 71 chromosomes.
- Fig. 3. (Prof. Donders (60) x G. tristis var. concolor (30)) x (Prof. Donders (60)), 74 chromosomes.
- Fig. 4. (Prof. Donders (60) x G. undulatus (30)) x (Mrs. Francis King (60) x self (60)), 75 chromosomes.
- Fig. 5. (Edith Mason (60) x G. angustus (30)) x (Prof. Donders (60)), 77 chromosomes.
- Fig. 6. (Prof. Donders (60) x G. tristis var. concolor (30)) x (Dr. Moody (60)), 78 chromosomes.

 Mag. Approximately 2500



Chromosomes from Triploid-Diploid Progeny

Fig. 1. (Joost Vondel (60) x (G. tristis var. concolor (30) x G. hirsutus (30))) x

(G. tristis var. concolor (30) x G. hirsutus (30)),42 chromosomes.

Fig. 2. (Prof. Donders (60) x (G. tristis var. concolor (30) x G. callistus (30)))

x (G. tristis var. concolor (30) x self (30)),48 chromosomes.

Fig. 3. (Prof. Donders (60) x G. undulatus (30)) x (G. tristis var. concolor (30)

x G. watsonius (30)), 55 chromosomes.

Fig. 4. (G. tristis var. concolor (30) x Prof. Donders (60)) x (G. tristis var. concolor (30) x G. alatus (30)),57 chromosomes

Fig. 5. (Prof. Donders (60) x G. tristis var. concolor (30)) x (G. tristis var. concolor (30) x self (30)),60 chromosomes.

Fig. 6. (G. tristis var. concolor (30) x Prof. Donders (60)) x (G. tristis var. concolor (30)),60 chromosomes.

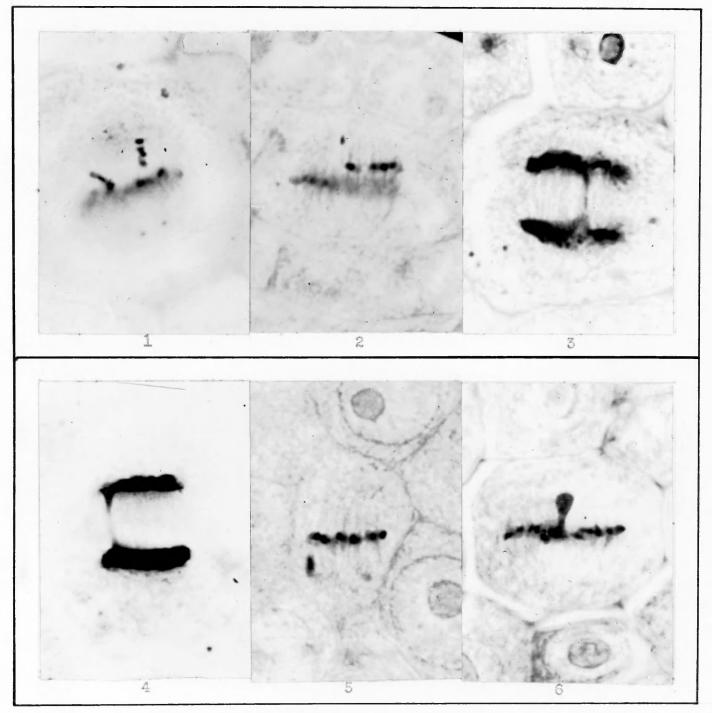
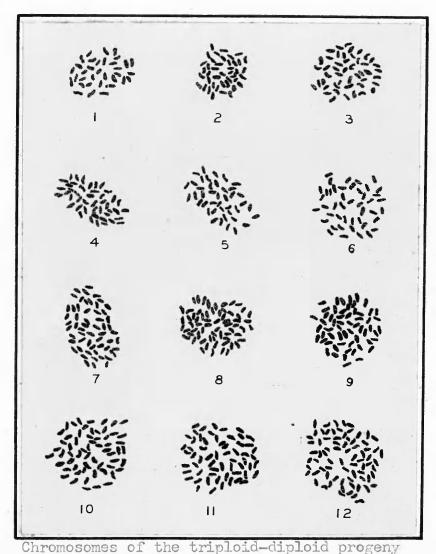


Fig. 1. Irregular mitotic division from the root tip of a triploidtetraploid hybrid.

- Fig. 2. Irregular mitotic division from the root tip of a triploid-diploid hybrid.
- Fig. 3. Chromatin bridge found in the root tip of a triploid-tetraploid hybrid.
- Fig. 4. Chromatin bridge found in the root tip of a triploid-tetraploid hybrid.
- Fig. 5. Irregular mitotic division from the root tip of a triploid-diploid hybrid.
- Fig. 6. A persistent nucleus found in a root tip cell of a triploid-diploid hybrid.

Magnification approximately 2500x



1. G. tristis var. concolor (30) x Prof. Donders (60) x G. tristis var. concolor (30) x G. hirsutus (30), 34 chromosomes.

2. Goost Vondel (60) x (G. tristis var. concolor (30) x G. hirsutus (30)) x [a. tristis var. concolor (30) x a. hirsutus (30)], 42 chromosomes.

3. Prof. Donders (60) x (G. tristis var. concolor (30) x G. callistus (30)) x [0. tristis var. concolor (30) x self (30)], 48 chromosomes. (G. angustus (30) x G. undulatus (30)) X (Prof. Donders (60) x

[G. blandus (30) x G. angustus (30], 45 chromosomes.

5. [Dillenberg (60) x G. undulatus (30)] X [G. tristis var. concolor (30), 43 chromosomes.

6. G. tristis var. concolor (30) x Prof. Donders (60) X G. tristis var. concolor (30), 45 chromosomes.

7. [Prof. Donders (60) x G. hirsutus (30)] X [G. tristis var. concolor (30)], 57 chromosomes.

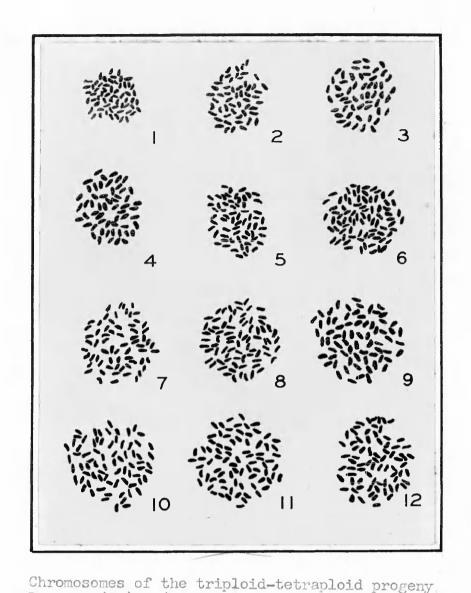
8. (Prof. Donders (60) x G. undulatus (30)) X (G. tristis var. concolor (30) x G. watsonius (30), 65 chromosomes.

9. G. tristis var. concolor (30) x Prof. Donders (60) X G. blandus (30) x G. angustus (30), 60 chromosomes.

10. [Prof. Donders (60) x G. tristis var. concolor (30)] X G. tristis var. concolor (30) x self (30), 60 chromosomes.

11. [Prof. Donders (60) x G. undulatus (30)] X [G. tristis var. concolor (30) x G. watsonius (30), 60 chromosomes.

12. (6. tristis var. concolor (30) x Prof. Donders (60) X G. tristis var. concolor (30) x G. watsonius (30)], 75 chromosomes.



1. (Prof. Donders (60) x (G. tristis var. concolor (30) x G. callistus (30)) x (Dr. Moody (60)), 60 chromosomes. 2. (Prof. Bonders (60) x G. tristis var. concolor (30)) x (Dr. Moody (60), 54 chromosomes. 3. [Prof. Donders (60) x G. undulatus (30) x [Dr. Moody (60)], 54 chromosomes. 4. (G. tristis var. concolor (30) x Prof. Donders (60)) x P. C. Hooft. (60)], 56 chromosomes. 5. (Prof. Donders (60) x (G. tristis var. concolor (30) x G. callistus (30)))x (Edith Mason (60)), 63 chromosomes. 6. (Prof. Donders (60) x G. undulatus (30)) x (Mrs. Francis King (60) x self (60)], 80 chromosomes. 7. (Prof. Donders (60) x G. tristis var. concolor (30)) x (Prof. Donders (60), 66 chromosomes. 8. [Prof. Donders (60) x G. angustus (30)] x [Joost Vondel (60)], 77 chromosomes. 9. (Prof. Donders (60) x G. angustus (30) x unnamed seedling (60) x G. primulinus (60), 71 chromosomes. 10. [Prof. Donders (60) x G. undulatus (30)] x [Prof. Donders (60)], 75 chromosomes. 11. [Prof. Donders (60) x G. angustus (30)] x [Prof. Donders (60)], 80 chromosomes. 12. (Prof. Donders (60) x G. angustus (30)) x (Joost Vondel (60)),

75 chromosomes.