

## Polyploidy in *Solanum Melongena* Linn.

By

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### Introduction

In the course of genetical work with the diploid egg-plant *Solanum Melongena*, I found an abnormal plant whose occurrence lead me to undertake a cytological study of the plants used for breeding.

The material was obtained from the cultures grown at the Botanical gardens of the University of Michigan, Ann Arbor. The diploid plants investigated were

(1) J22, a dark purple variety, seeds of which were sent by Professor Kakizaki of the Saitama Agricultural Farm of Japan.

(2) 515B, an oval green fruited variety which came up amongst a culture of Messers Suttons "Long White" in 1925, and which has been breeding true since.

(3) F<sub>1</sub> hybrids between 515B and J22 which had medium purple skin colour together with the green flesh colour found in both parents. (My unpublished genetical work has shown these colours to be independently inherited.)

The abnormal plant that arose in a culture of the above cross was triploid as described in an earlier paper (E. K. Janaki Ammal, 1931). It was found to be highly sterile. After repeated selfings it produced one

fruit with 14 seeds all of which germinated and proved to have 44–48 chromosomes. Root tips and anthers were fixed in Flemming's fluid of medium strength and Karpechenko's (1924) modification of chrom-formal acetic. Sections of root tips were cut at a thickness of  $10\ \mu$  and anthers  $12\text{--}15\ \mu$  and stained with gentian violet (cf. Newton and Darlington 1926). All drawings were made at bench level with a Zeiss camera lucida with a Zeiss 1.5 objective N.A. 1.3 and Zeiss  $20\times$  eye piece to give a magnification of 4500, and reduced in reproduction to the scale given under each figure.

### Somatic Chromosomes

The somatic number in *Solanum Melongena* is 24 as first noted by Kojima (1925) in his study of 21 different races of *Solanum Melongena*. The chromosomes (Fig. 1) are of varying lengths. About five types could be picked out. The triploid plant had 36 chromosomes in the metaphase plate (Fig. 2) and some types of chromosomes represented twice in the diploid occurs three times in the triploid. The tetraploid with 48 chromosomes and aneuploids 44–46 show the same chromosome morphology. (Figs. 3 and 4).

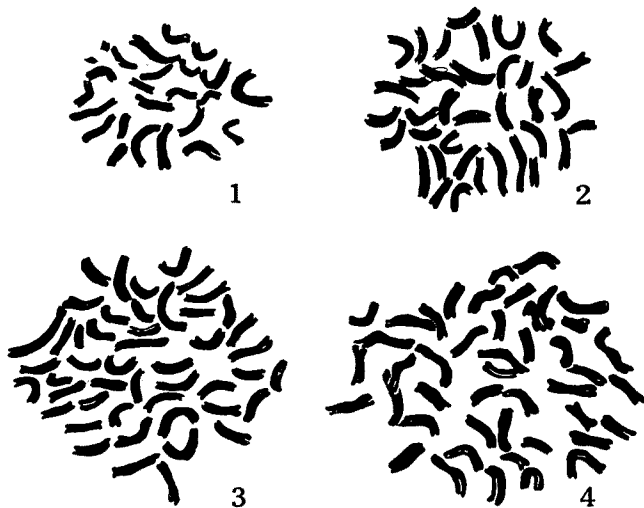


Fig. 1. Mitotic metaphase plate in a diploid *Solanum Melongena* showing 24 chromosomes. Fig. 2. Mitotic metaphase plate in the triploid *Solanum Melongena*. Fig. 3. Mitotic metaphase plate in the tetraploid progeny of the triploid showing 48 chromosomes. Fig. 4. Mitotic metaphase plate in an aneuploid progeny of the triploid with  $4x-3$  chromosomes.  $\times 3000$ .

### Meiosis in the Diploid

The early prophase stages have not been recorded because they do not differ in any way from that figured by Kojima, the artifact synizesis which presumably corresponds to zygotene (Darlington 1932) is observed in fixed material and when noted is found to occur simultaneously in all cells of the same anther. There is a fine gradation in the development of the pollen mother cells within one anther sac after this stage. This makes possible a study of the different stages of meiotic activity from P.M.Cs. of the same archesporium.

This serial development of P.M.Cs. have been noted in other Solanaceous plants, Lesley (1926) in Tomatoes, Goodspeed (1923) in *Nicotiana*, Janaki Ammal (1932) in *Nicandra physaloides*. There is a normal association of chromosomes side by side at the pachytene stage following synizesis. In this condition the material does not stain well and the chromosome configuration is not clearly indicated. At diplotene it is possible to observe that pairing is due to the random formation of chiasmata or the exchange of partners between chromatids, a condition now acknowledged as universal in the meiosis of homozygous plants and animals (Darlington 1931).

Fig. 5 shows the association in the twelve bivalents at early diakinesis. At least five different lengths occur, which may be represented thus:  $L_2 + 2I_2 + 4M_2 + 3m_2 + 2S_2$ . The single long chromosome is very conspicuous in all cells. Such a pair has been observed in tomatoes by Lesley (1926), in *Capsicum* by Kostoff (1926), in *Datura* by Belling and Blakeslee (1923) and in *Nicandra* by the writer. It appears to be a characteristic of some genera in the family Solanaceae and might be useful to indicate taxonomic affinities between the different genera of this family. There is apparently some movement of chiasmata between diplotene and metaphase. In this respect the long, medium and short chromosomes can be sharply distinguished. In the long type even the distal chiasmata remain interstitial at metaphase. In the median type distal interstitial chiasmata are terminalised between diplotene and metaphase while proximal ones remain interstitial. These two types correspond to types found in *Tulipa* (Darlington and Janaki Ammal 1932.) In the short type terminalisation is always complete at diplotene, i.e. before the decipherable stage as in *Fritillaria* fragments (Darlington 1930). Terminalisation therefore follows the same lines as in *Nicandra* and is weaker than in tomato and *Datura*.

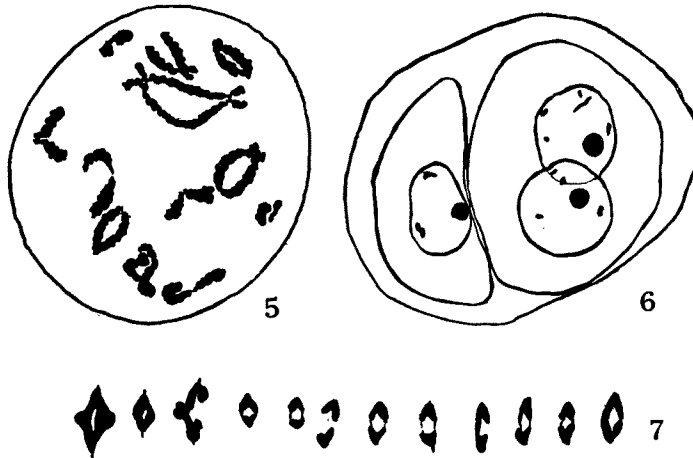


Fig. 5. Early diakinesis in a diploid *Solanum Melongena*.  $\times 3750$ . Fig. 6. Bivalents as seen in the first meiotic metaphase in the diploid.  $\times 3000$ . Fig. 7. Exceptional dyads found in diploid *Solanum Melongena*.  $\times 3750$ .

The spindle attachments are median in all chromosomes (Fig. 6) and the distribution during anaphase is regular. The second division is normal. Quadripartition of the pollen grains is by means of furrowing. In exceptional cases dyads have been observed (Fig. 7) due to irregularity in cytokinesis. This gives rise to pollen grains with 2 haploid nuclei, or perhaps single diploid nucleus.

### Meiosis in the Triploid

Early pachytene stages show that the chromatid threads are not of uniform thickness. Lesley (1926) noticed the same phenomenon in triploid tomatoes. She considers the thick and thin threads as paired and unpaired chromosomes and this is probably true here as well. According to Newton and Darlington (1929) longitudinal contraction following pairing may be different in those threads in which pairing occurs earlier. This would also lead to differences in the thickness of threads. In diplotene stages the 36 chromosomes are associated as trivalents and bivalents while a few remain unpaired. These last are generally the small chromosomes (Fig. 8) as expected if the chiasma frequency is proportional to the length of the chromosomes. End to end associations which are regarded as due to terminalised chiasmata

are generally seen in the small trivalents. Triple chiasmata are also frequent. The three longest chromosomes associate to form complex configurations in which chiasmata are all interstitial. These interstitial chiasmata persist to metaphase as in diploid (Fig. 9).

The configurations between diakinesis and metaphase are not very different and any changes that might occur are found only in the medium chromosomes in which some terminalisation takes place between diplotene and metaphase. The proportion of trivalents to bivalents found, agrees with that of other non-hybrid triploids like *Tulipa* (Darlington and Mather 1932), *Primula* (Dark 1932), *Hyacinthus* (Darlington 1929b), and their incomplete formation is sufficiently explained by the random formation of chiasmata in chromosomes with low chiasma frequency and is not due to lack of similarity or "affinity" between the chromosomes.

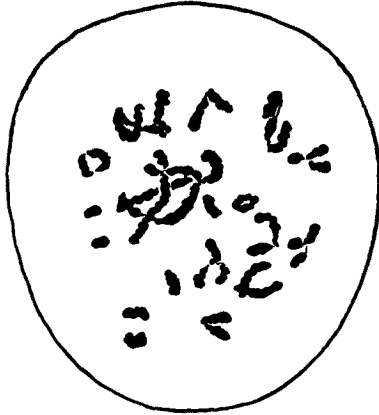


Fig. 8. The configuration of chromosomes during early diakinesis in the triploid *Solanum Melongena*.  $\times 3750$ .

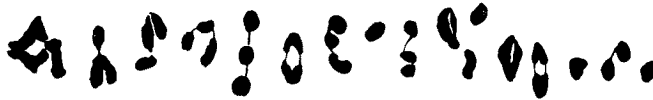


Fig. 9. The chromosomes from one P.M.C. at the first meiotic metaphase in the triploid.  $\times 3750$ .

Fig. 9 shows the chromosomes from the first metaphase of one cell with the complete set of 36 chromosomes. Observations from similar cells showed that the number distributed to the poles varies considerably. Unpaired chromosomes pass without division to the nearer poles and not much lagging is observed.

### The Progeny of the Triploid

Pollen sterility in the triploid was very high. After repeated selfings one single fruit with 14 seeds was obtained. A fertile diploid fruit will contain 1200-1500 seeds. It is interesting to note that the

development of anthocyanin on the fruit of the triploid hybrid was less than in normal  $F_1$  of the cross between green and purple. This seems to indicate that the triploid had two doses of green and one of purple.

The 14 seeds from the triploid were larger than those of the diploid, and germinated very easily. Root tips of 13 seedlings which survived showed them to have 44-48 chromosomes. There are therefore probably tetraploids and aneuploids with  $4x-2$ ,  $4x-3$  and  $4x-4$  chromosomes.

### Discussion

#### *Origin of triploidy in the egg-plant*

According to Jørgensen (1928) the triploid tomato Bals Fill Basket arose as a somatic sport from a plant which was probably diploid. Triploids however generally arise in nature as a cross between tetraploids and diploid plants of the same species as in the case of *Oenothera*, *Primula*, *Datura* and *Zea Mays*. They can also arise as a result of the failure of reduction in the archesporium of one of the two diploid parents and the consequent fusion of a reduced  $x$  with an unreduced  $2x$  germ cell—a method which is according to Darlington (1932) very frequent amongst dicots. The presence of exceptional binucleatic pollen grains in one of the diploid parents supports this conclusion. The triploid is the result of the fertilization of a normal  $x$  female germ by a diploid male germ which arose by the union of these two nuclei before fertilization. This will be a form of doubling in which reunion takes place not at the last division before meiosis but at the formation of the generative and tube nuclei in the pollen grain.

#### *The origin of tetraploid progeny from a triploid*

The distribution of 36 chromosomes at the first meiotic division in the triploid was apparently random and therefore a binomial frequency of chromosomes ranging from 12-24 is expected. Sterility in the triploid was high as is indicated by the few seeds produced (other fruits which fell off presumably had even fewer). The  $4x$  plants must have arisen by the chance fertilization of a 24 chromosome egg by a pollen grain with 24 chromosomes. The viability of gametes with a few chromosomes less than 24 are not impaired, which explains the existence of plants with  $4x-2$  and  $4x-4$  chromosomes following Darlington's convention by which  $x$  is the basic number and  $2n$  is the somatic number.

### Summary

1. The chromosomes of diploid ( $2x=24$ ) and triploid ( $3x=36$ ) *Solanum Melongena* were studied in somatic and meiotic divisions. The triploid arose from the functioning of a diploid pollen grain.
2. Long median and short chromosomes are distinguished at meiotic metaphase and differ at meiosis in two ways :—
  - (a) The shorter chromosomes have fewer chiasmata and consequently univalents of this type are commoner in the triploid (as in *Hyacinthus*).
  - (b) The shorter chromosomes have earlier and more complete terminalisation than the longer ones (as in *Fritillaria*).
3. The triploid when selfed gave two tetraploid and 11 tetraploid or nearly tetraploid seedlings. These evidently resulted from gametes to which all the extra set of chromosomes had passed at meiosis. This is compatible when the random segregation observed at meiosis for the triploid is less than 1% fertile.

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