PARTHENOCARPY IN A TOMATO DEFICIENT FOR A PART OF A CHROMOSOME AND IN ITS ANEUPLOID PROGENY¹

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INTRODUCTION

A VERY small tomato plant occurred in F_1 from diploid dwarf d_1d_1 parents, grown in the field at Riverside, California, for a study of male sterility. The mutant was very slow-growing, compared with normal sibs, but was perfectly developed and apparently healthy. It had extremely short internodes and very small leaves (fig. 1). It flowered freely and produced very small yellow (*ry*) fruit in abundance throughout the season,

FIGURE 1.—Deficient tomato plant (right) and diploid of the same family (left), in the field.

although there was, on the average, very little pollen, many anthers being completely empty. The fruit was spherical or obovoid and sometimes pointed at the stylar end. Only two of the fruits formed in the field without artificial pollination were seedy; these contained two and four seeds respectively.

After transfer to the greenhouse, nearly all the anthers of the mutant plant contained some normally matured pollen, although in flowers which had just opened about 75 percent of the pollen grains were empty; and of those grains which appeared to be normal, a great many germinated

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before anthesis. The mutant set fruit freely without artificial pollination; most of these fruits were seedless or contained one or two seeds. When artificially selfed, the fruits averaged about eight seeds each. The male-fertile diploid sibs of the mutant were very fruitful and normally seedy; the male-sterile sibs, whose pollen seldom becomes fully mature, had little or no fruit (LESLEY and LESLEY 1939).

Pollen mother cells of the mutant were studied from acetocarmine smears and from permanent smears fixed in Navashin's fluid and stained in gentian violet. Many pollen mother cells had degenerated long before anthesis, and those which underwent reduction did so at very different rates. Occasionally the shortening of the chromosomes also occurred very unevenly, since newly paired threads and fully shortened, dumb-bell-shaped pairs were found in some nuclei. These indications of internal unbalance were associated with other abnormalities in reduction. At diakinesis, there were 11 normal pairs and one unequal pair of homologues. Figure 2, A to D, shows that one of the unequal homologues is about a third shorter than the other. This size difference may be seen at first metaphase. Apparently the mutant plant was a deficiency heterozygote. It has been pointed out by STADLER (1933) that in a deficient maize plant the unpaired portion of the chromosome shortens more slowly than the paired portion. It is, therefore, difficult to be sure of the exact difference between the two homologues in the deficient tomato, but it is certainly considerable.

The unequal homologues were never seen to be attached at both ends at early diakinesis and were very often quite unpaired or very weakly joined at later diakinesis and first metaphase (fig. 2B, C). In the few figures seen at diplotene, the longer homologue was closely associated with the shorter throughout its length (fig. 2D). At first anaphase, the unequal homologues usually passed to opposite poles; often, before any of the other chromosomes had divided, they lay at opposite poles of the spindle. They very often lay diagonally across the plate (fig. 2C), and were sometimes in the cytoplasm at one side of the spindle. Both unequal homologues frequently passed to the same pole. Occasionally other chromosome pairs showed weakened pairing. The two chief causes of pollen abortion in the mutant plant were (1) abnormal early development of the pollen, largely dependent on environmental conditions, since in most of the smears made in the greenhouse the pollen cells were far less abnormal than in those made in the field, and (2) abnormal distribution of the members of the unequal pair of homologues.

The A or nucleolar pair of chromosomes may be heteromorphic as a result of addition of genetically inert material to the longer member, and tomato races exist which seem to differ only in the size of the A chromosomes (LESLEY and LESLEY 1935). The heteromorphic pair in the mutant plant

described above is not associated with the nucleolus; the extreme dwarfing, defective pollen, and parthenocarp of the plant indicate that euchromatin is involved.

TRISOMIC AND TETRASOMIC DERIVATIVES OF THE DEFICIENT PLANT

The seeds obtained from selfing the mutant gave 61 diploids, six trisomics, one tetrasomic, and four runt-like plants which died before their chromosomes were examined. No plants like the original mutant occurred. The trisomic type had two long chromosomes that were nearly always closely paired and one short chromosome similar to the shorter homologue

EXPLANATION OF FIGURES 2-4

Chromosomes in pollen mother cells of tomato.

FIGURE 2.—Meiosis in the deficient plant. Unequal homologues: A, paired at diakinesis; B, unpaired and at opposite sides of the nucleus (four pairs moved to the right); C, at opposite poles at first metaphase; D, at diplotene and early diakinesis. $\times 3070$.

FIGURE 3.—A, trivalent in a deficient trisomic; B, trivalent in a primary trisomic from a deficient trisomic selfed; C, ring trivalent from the secondary trisomic; D, typical unpaired chromosome from this secondary; E, typical unpaired chromosome from a deficient trisomic; F, diakinesis in a deficient tetrasomic plant. (A typical tetravalent is near the center of the nucleus.)

FIGURE 4.—A and B, typical ring and chain trivalents in a secondary originating from a double trisomic, triplo-BC; C, diakinesis in a hybrid between this secondary and a plant with an extra C fragment.

of the heteromorphic pair of the parent. The short chromosome was often separate, or it was more or less closely joined to the long pair (fig. 3A). If the original mutant had been the result of duplication, one would have expected that the normal diploid progeny would have two short chromosomes and that the trisomic would have two short and one long chromosome. The erratic behavior of the shorter homologue, both in the original mutant and in the trisomic, indicates that it does not undergo enough crossing over to insure association at metaphase. Evidently the longer chromosome of the unequal pair is normal and the shorter one is deficient. The appearance of the heteromorphic pair at pachytene in the deficient plant indicates that the deficiency is terminal. Terminal deficiencies have been described in *Zea mays* (McCLINTOCK 1931) but rarely occur in *Drosophila* (STURTEVANT and BEADLE 1939).

Since the trisomic type contained one deficient chromosome in addition to 12 normal pairs, it will be termed "deficient trisomic." The deficient trisomic plant was slightly smaller than its diploid sibs and had shorter internodes but was equally fruitful. The leaves were smaller, although not so small as those of the deficient diploid or original mutant plant, and the lamina was inclined to roll upward. Meiosis in deficient trisomic plants was about like that in the most fertile primary trisomics of the tomato. Frequent lagging and occasional omission of the deficient chromosome were observed. Rarely, all three members of the trisome were separate at diakinesis. Throughout the season an abundance of normal-looking pollen was present in anthers from pollen-fertile deficient trisomic plants.

The deficient diploid, as female parent, crossed with normal diploid gave two fruits, which together contained 47 seeds. In the F_1 grown in the field, there were 21 diploids, five deficient trisomics, and one plant almost as small as the deficient diploid and resembling it but less fruitful. This plant appeared to be a secondary trisomic since its pollen mother cells contained a ring composed of two normal-sized and one distinctly larger chromosome (fig. 3C). Since the large chromosome had a median attachment constriction, it was probably formed by duplication of the longer limb of the normal chromosome of this pair. The larger chromosome of the trivalent group was often separate at first metaphase (fig. 3D).

Only one other secondary has been found in our tomato cultures; in it, the altered chromosome was shorter than the normal chromosomes in the ring (fig. 4A, C). This secondary originated from a double trisomic (triplo-BC $\times$ diploid). Primary trisomics, diploids, a plant trisomic for a fragment of the C chromosome, and a tetraploid occurred also in the same family. This secondary showed little resemblance to its trisomic sibs. In *Datura*, secondaries most frequently occur in progenies of related trisomics, rarely in those of diploids. Reversed crossing over has been suggested as an ex-

planation of the occurrence of secondaries (BELLING and BLAKESLEE 1924). In a trisome at diakinesis, two of the homologous chromosomes are usually closely paired, and the third is either weakly attached to one member of the pair (fig. 3B) or entirely separate, presumably because in one member of the trisome crossing over has been greatly reduced or has failed to occur. The occurrence of a secondary in the progeny of the deficient diploid ♀ × diploid ♂ suggests that when a secondary chromosome is formed in a diploid, the chromosome involved has already been altered in such a way as to reduce crossing over with its homologues.

Evidence has been presented by RHOADES (1940) which indicates that numerous secondaries of chromosome 5 of maize arose at meiosis as a result of the instability of the centromere of a telocentric chromosome. He is not certain whether the misbehavior of the centromere consists of failure to divide or of a transverse instead of a longitudinal division; but since UP-COTT (1937), KOLLER (1938), and DARLINGTON (1940) have observed transverse division of the centromere in lagging chromosomes, RHOADES suggests that the latter is the more likely theory. Since the deficient diploid tomato plant produced a secondary trisomic among its few progeny and only one other has been found in the tomato and since the deficient chromosome tends to behave abnormally, it seems possible that the deficient chromosome is telocentric.

The occurrence of deficient trisomics from deficient diploid × diploid is explained by the frequent passing of both members of the heteromorphic pair to the same pole.

In the two progenies from deficient trisomics selfed, there were 42 diploids, 34 deficient trisomics, five primary trisomics, three deficient tetrasomics, and one runt. One primary and two deficient trisomics produced very little fruit and proved to be male sterile. The primary type is so much like the deficient trisomic that in families segregating for leaf characters, it is usually possible to differentiate them only by cytological examination. The tetrasomics were almost as small and stunted as the deficient diploid. A deficient tetrasomic selfed gave one tetrasomic, 11 trisomics, and one diploid. The deficient chromosome is probably transmitted to about 50 percent of the progeny from selfing a deficient trisomic and is transmitted, although much less frequently, by the pollen.

In the deficient tetrasomic, meiosis was far more regular than in the deficient trisomic, but the pair of deficient chromosomes showed weakened association, as did the pair of C fragments described in an earlier paper (LESLEY and LESLEY 1929). About 40 percent of the pollen grains in freshly opened flowers were found to be empty. At the same time, about five percent of the pollen grains in freshly opened flowers of diploid derivatives of the deficient diploid were empty. Loss of unpaired deficient chro-

mosomes would result in haploid gametes and would account for the occurrence of diploid progeny from tetrasomic female $\times$ diploid male. Quad-rivalents were frequent at diakinesis and first metaphase. The deficient

FIGURE 5 (above).—Tomatoes cut in half to show relative seediness of basal fruits (two lower rows) and apical fruits (two upper rows) of different types: vertical row A, deficient; B, deficient tetrasomic; C, diploid; D and E, deficient trisomic.

FIGURE 6 (below).—A deficient trisomic with a basal cluster of small seedless fruits (at right of label) and apical clusters of more or less seedy fruits.

chromosomes were usually attached to the two ends of a chain, as in figure 3F. Theoretically, a ring of four chromosomes might occur, but this was not found.

The very small size of the deficient diploid seems to indicate that a monosomic condition of certain genes, resulting from the deficiency, is by no means equivalent to a disomic condition in its effect on the growth of the plant. As yet, no gene has been located in the chromosome concerned in the deficiency. The primary trisomic from the deficient trisomic resembles triplo-J, which is probably a primary type, in being brachytic and unusually fruitful for a trisomic; but in a tendency to parthenocarpy it perhaps more closely resembles triplo-C and the trisomic containing a small C fragment. The deficient chromosome and the small C fragment may possibly be complementary parts of the C chromosome.

PARTHENOCARPY

Tomato trisomics vary in fruitfulness according to type and gene constitution, but when grown in the field, they are usually distinguishable from diploids by their unfruitfulness. Even when the extra chromosome present is less than normal in size, as in the deficient trisomic, an appreciable reduction in fruitfulness usually results. The deficient diploid, however, and its male-fertile deficient trisomic, deficient tetrasomic, and primary trisomic progeny were scarcely less fruitful than their diploid sibs, which were very fruitful. The unusual fruitfulness of these chromosomal mutants is apparently due to their tendency to parthenocarpy.

The fruits of the deficient diploid and of the deficient tetrasomics, both on seedlings and on plants grown from cuttings, which set without artificial pollination, were usually seedless. The secondary trisomic produced only two fruits, both seedless. In seedlings and cuttings of deficient trisomics and of primary trisomics derived from selfing the deficient diploid or from crossing it with a diploid dwarf, d_1d_1 , the fruits which developed from the first or basal inflorescence of the main shoot and of the large branches originating from the lower nodes were largely parthenocarpic. The apical fruits that set on the later-developed shoots were mostly seedy (fig. 5). Some fruits were intermediate, having some seedless loculi. The seediness of basal and apical fruits of deficient trisomics and their diploid sibs is shown in table 1. As a general rule, fruits that were deficient in seed content contained more seeds in the apical half than in the basal half (fig. 5, compare D and E). Seediness of fruit tended to increase gradually from the basal to the apical regions of the plant. Diploid sibs of the trisomics and tetrasomics in most families had fewer basal fruits than the deficient trisomics, and most of these fruits were seedy. For example, in six families, the mean number of fruits on the basal inflorescence of the 97 diploid plants

was 1.7, and that of the 119 trisomic plants was 4.3; the corresponding mean proportions of basal flowers that set fruit were .23 and .37. Basal seedless fruits averaged much smaller than seedy fruits (fig. 6) but were variable in size and sometimes as large as seedy fruits.

Parthenocarpny was much more frequent in fruits that matured in summer than in those that matured in November, at Riverside. Parthenocarpic fruits occur on diploid plants, especially in the greenhouse (BOUQUET 1931). In our cultures such fruits occurred occasionally on diploid plants, but much less frequently than on the trisomics. The larger parthenocarpic fruits found on the deficient diploid and on its aneuploid derivatives were solid; the smaller fruits, which were less common, were hollow and contained no pulp. The hollow type was perhaps more frequent than the solid on diploid plants.

When unopened buds of the deficient diploid plant or of the deficient trisomic were emasculated, none set fruit even under greenhouse conditions that were very favorable to fruit setting. Application of male-sterile pollen, which mostly fails to mature and hence rarely germinates, did not cause fruit setting in these types. The parthenocarpny of the deficient diploid and of the deficient trisomic depends, therefore, on the presence of some pollen capable of germination and, in the terminology of WINKLER (1908), is stimulative. On the deficient tetrasomic, fruit set fairly readily without pollination (after emasculation); parthenocarpny in this case is vegetative. Fruits that set without pollination required about half as long again to reach maturity as seedy fruits on the same plant. They attained only about a quarter of the size of seedy fruits on the same plant and had a dull appearance. It seems probable that the presence of seedless basal fruit on deficient trisomics in midseason is due to a similarly slow development. When any of the parthenocarpic types were pollinated with male-fertile pollen, the fruits were seedy.

The smaller amount of pollen deposited naturally on the stigma seems to be favorable for the parthenocarpic development of fruit. Parthenocarpny was more common in the types having less viable pollen. This condition was confined to the basal fruits of the trisomic types but extended to all the fruits of the deficient diploid and of the deficient tetrasomics. In the deficient diploid, much less than 25 percent of the pollen was capable of germination. In the tetrasomic, although 40 percent of the grains appeared to be good, most of them contained an extra chromosome. And in the trisomic, probably more than 50 percent of the pollen contained an extra chromosome, the remainder being normal haploid. Other trisomic tomatoes, such as triplo-A and triplo-H, have only 50 percent or less of normal haploid pollen, but these types are distinctly unfruitful and non-parthenocarpic. Apparently all the parthenocarpic types have an especial

TABLE 1

Seediness of basal and apical fruits per plant in deficient trisomic and diploid tomatoes. All the basal fruits (those that set on the first or basal inflorescence) were examined, but only a part of the apical fruits (those that set on inflorescences that developed later).

PLANT PARENTAGE AND NO.	BASAL FRUITS			APICAL FRUITS		
	SEEDLESS (PARTHENO- CARPIC)	PARTIALLY SEEDY	SEEDY	SEEDLESS (PARTHENO- CARPIC)	PARTIALLY SEEDY	SEEDY
Deficient trisomic C ₃₇₆₋₂						
selfed						
Trisomic plant no.						
2	0	0	3	0	0	10
3	11	0	0	2	2	1
4	3	1	0	0	5	0
11	10	1	11	0	13	5
14	6	2	0	0	2	8
15	13	0	0	0	2	8
17	3	2	0	0	5	11
20*	3	4	1	2	9	1
21	0	0	0	0	6	4
22*	8	0	0	5	2	0
23	2	0	4	0	0	10
24	1	0	0	0	2	10
30	4	0	0	0	0	10
32	2	0	0	3	2	3
Diploid plant no.						
1	0	0	2	0	0	14
5	0	0	3	0	1	9
7	0	0	2	0	0	10
8	0	0	0	0	0	10
9	0	0	0	0	0	10
10	0	0	0	0	0	10
12	0	0	0	0	0	10
16	0	0	0	0	0	10
18	0	0	0	0	0	11
19	0	1	2	0	1	14
25	0	0	3	0	0	10
26	0	1	0	0	0	10
27	0	0	1	0	0	10
28	0	0	1	0	0	11
29	0	0	1	0	0	10
31	0	0	6	0	0	10
33	0	0	5	0	0	10
34	0	0	2	0	0	10
Deficient tetrasomic X						
diploid C ₄₂₃						
Trisomic plant no.						
1	3	0	6	0	0	10
4	0	3	9	0	1	9

* Plant male sterile.

TABLE 1—*Continued*

PLANT PARENTAGE AND NO.	BASAL FRUITS			APICAL FRUITS		
	SEEDLESS (PARTHENO- CARPIC)	PARTIALLY SEEDY	SEEDY	SEEDLESS (PARTHENO- CARPIC)	PARTIALLY SEEDY	SEEDY
6	0	0	7	0	0	10
8	0	0	10	0	3	7
10	0	2	7	1	1	10
13	0	0	11	0	0	10
Diploid plant no.						
7	0	0	8	0	0	10
9	0	0	7	0	0	10
12	0	0	5	0	0	10

tendency to fruit setting. This occurs under the stimulus of a small amount of viable pollen or, in the deficient tetrasomics, even without pollination.

Trisomic plants of different genotypes varied widely in their tendency to parthenocarp. On some trisomics even the basal fruits were seedy; on others, not only the basal but most of the apical fruits that ripened in midsummer were parthenocarpic. In a small F_1 family, C 423 (table 1), from a dwarf d_1d_1 deficient tetrasomic with basal parthenocarp crossed with a standard D_1D_1 diploid, most of the trisomic progeny, although having plenty of basal fruits, were nonparthenocarpic. A similar condition occurred in C 422, an F_1 of a parthenocarpic primary trisomic crossed with the same standard diploid, and in a small F_2 family from C398-2, a standard D_1d_1 deficient trisomic. These three families contained the genes R , Y , and D_1 that were not present in families in which all the trisomics were partially parthenocarpic.

A primary trisomic plant, of which the basal fruits were mostly parthenocarpic, and a nonparthenocarpic primary trisome were selected from family C 422 and were crossed with the same parthenocarpic deficient trisomic. It appears from table 1 that parthenocarp was more frequent in the progeny of the parthenocarpic primary trisomic parent.

It is not known why most of the basal fruits on certain deficient trisomic plants were parthenocarpic. The fruiting of White San Pedro fig, described by CONDIT (1938), is somewhat analogous, the first crop being parthenocarpic and the second nonparthenocarpic. Evidently in the tomato the fruits of the deficient diploid and of its aneuploid progeny are seedy if conditions are favorable for fertilization. Since growth-promoting substances cause tomatoes to set parthenocarpically (GUSTAFSON 1936), it is possible that the deficient diploid and its trisomic and tetrasomic derivatives have a higher auxin content than the diploids. Unlike the partheno-

carpic fruits which GUSTAFSON produced with auxins, the seedless fruits in our cultures were, as a rule, smaller than the seedy fruits. Presumably these seedless fruits did not receive so much growth-promoting substance as the seedy fruits.

Seedlessness might result from the effect of high temperature on pollen (SMITH and COCHRAN 1935). HAWTHORN (1937) reports that in Texas certain derivatives of Large Cherry $\times$ Bonny Best varieties of tomato produced seedy fruits early in the season, then seedless fruits during a period of very high temperature, and seedy fruits again late in the season. LOEHWING² finds that, in general, high temperature and long day favor parthenocarpy and that in most tomato varieties, day lengths in excess of 12 hours are necessary to the parthenocarpic development of fruits. The

TABLE 2

Parthenocarpy in progenies of a parthenocarpic primary trisomic tomato and of a nonparthenocarpic primary trisomic sib, both crossed with the same parthenocarpic deficient trisomic. P = parthenocarpic; SP = slightly parthenocarpic; NP = nonparthenocarpic.

	TRISOMIC PROGENY			DIPLOID PROGENY		
	P	SP	NP	P	SP	NP
Parthenocarpic primary trisomic $\times$ nonparthenocarpic deficient trisomic, 39010.1	12	10	1	0	5	13
Nonparthenocarpic primary trisomic $\times$ nonparthenocarpic deficient trisomic, 39010.1	6	9	6	0	0	20

average mean daily temperature at Riverside in June 1939 was 71.1°F; this was 5.8° lower than the average in July, but the setting of the parthenocarpic fruit of the deficient trisomic probably occurred during June, or mainly then.

The parthenocarpic tendency of the deficient diploid plant and its aneuploid progeny indicates that the same chromosome is involved in all. Apparently in the whole chromosome the gene balance is favorable to parthenocarpy. This favorable effect is increased by the presence of an extra whole chromosome of this type, as in the simple trisomic. In the deficient chromosome, the gene balance is even more favorable to parthenocarpy, owing to the loss of genes unfavorable to it. On this hypothesis, the balance of genes in the deficient diploid, the deficient trisomic, the deficient tetrasomic, and in the primary trisomic is more favorable to parthenocarpy than in the diploid.

² PROFESSOR W. F. LOEHWING, UNIVERSITY OF IOWA. Unpublished data.

SUMMARY

A heterozygous deficient tomato plant originated in F_1 from diploid dwarf parents, probably from the egg cell of a deficient female gametophyte and a normal male gamete. The deficient diploid plant was very small but set seedless fruit abundantly without artificial pollination. The deficiency is equivalent to about one-third of the length of the chromosome and appears to be terminal. At diplotene the unequal homologues were closely associated, and at diakinesis they were attached at one end or were separate. The pollen, especially under field conditions, was scanty and mostly abnormal.

The aneuploid derivatives of the deficient plant included a primary trisomic, a deficient trisomic, a deficient tetrasomic, and a secondary trisomic. These, like the deficient, were relatively fruitful and had a tendency to parthenocarp. No deficient diploids were identified in progenies from the deficient diploid plant.

Either a deficiency of part of a chromosome or the addition of the deficient chromosome or of the whole chromosome to the normal complement causes a tendency to parthenocarp.

In deficient trisomic and primary trisomic plants, the basal fruits tend to be parthenocarpic. The fruits that set on inflorescences that develop later are less likely to be parthenocarpic, and apical fruits are generally seedy. Diploid plants sometimes have a few basal parthenocarpic fruits but can usually be distinguished from trisomics by the scarcity of basal fruit and a greater tendency to seediness.

Parthenocarp is stimulative except on the deficient tetrasomic, which sets fruit without pollination. These fruits, like the parthenocarpic fruits on the deficient trisomic, were, on the average, much smaller than the seedy fruits and required about half as long again to reach maturity. When artificially pollinated, all types of plants as a rule produced seedy fruits.

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