A CYTOLOGICAL AND GENETICAL STUDY OF PROGENIES OF TRIPLOID TOMATOES[1]

JAMES W. LESLEY
University of California, Citrus Experiment Station, Riverside, California

Received May 9, 1927

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INTRODUCTION

Perhaps the most familiar kind of mutation is that which appears to involve a change at a specific locus in a chromosome, commonly called a gene mutation. No change of a quantitative kind is visible in the chromosomes. Mutant characters of this kind were used by MENDEL in his famous "Experiments in plant hybridization." As a general rule, such mutants can be made to breed true. Another kind of mutation is that associated with a change in the number of chromosomes. Usually one or more complete sets of extra chromosomes are present as in polyploids or a smaller number is present in addition to the normal complement. As a rule, except in the case of certain types of polyploidy, these chromosomal mutants are genetically inconstant and cannot be made to breed true.

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[1] Paper No. 164, UNIVERSITY OF CALIFORNIA, Citrus Experiment Station, Riverside, California.

Doubtless chromosomal mutants were found by the hybridists and earlier geneticists and, before the advent of the chromosome theory, these must have been a source of much perplexity both from their elusive character and from their peculiar mode of inheritance. Probably in many cases they were thought to be the result of accident or disease. Recent work seems to have brought to light an essential similarity between chromosomal and gene mutations. According to the theory of gene balance which we owe chiefly to BRIDGES (1921), the characteristics of mutants of both kinds are an expression of a certain gene balance. While a gene mutant appears to result from a qualitative change at a certain locus in the chromosome and a chromosomal mutant from a quantitative change occasioned by the change in chromosome number, in both the genes play an essential part in determining the mutant characters.

While a diploid plant contains $2n$ chromosomes, where n represents the number of pairs present in the heterotype division up to the beginning of the anaphase, a triploid contains $3n$ chromosomes, or n sets each consisting of 3 chromosomes which tend to attract one another. According to a recent list (LESLEY, MARGARET M., 1926), triploidy has been reported in Oenothera, Morus, Uvularia, Datura, Canna, hyacinth and tomato; to this, maize (RANDOLPH and MCCLINTOCK 1926), Primula (IINUMA 1926) and Crepis (NAVASCHIN 1926) may now be added. Apparent triploid plants originating from species crosses followed by parthenogenesis as in the polyploid roses studied by TÄCKHOLM (1922) are not necessarily triploids in the strict sense.

A triploid plant is usually a replica of the corresponding diploid but is distinguished by the larger size of the organs, cells and nuclei. Usually the pollen is scanty and contains many empty grains. Little viable seed is produced.

BLAKESLEE (1924) has shown that the progeny of a triploid Datura includes a remarkable series of forms with one or more extra chromosome. Although different in origin, these forms are undoubtedly of the same nature as certain of the mutants which regularly appear among the progeny of normal Datura plants.

A triploid tomato plant which chanced to appear in a commercial variety was the starting point of the present work. As in the case of Datura, crosses between triploid and diploid tomato plants gave rise to a series of variant types comparable with chromosomal mutants. The number of chromosomes has been determined and the characteristics and genetic behavior of certain of these types have been studied with the special object of throwing some light on the composition of the individual chromosomes.

ACKNOWLEDGMENTS

The writer is deeply indebted to his wife, Doctor MARGARET MANN LESLEY, for much help especially in the cytological work. He has also received valuable suggestions from Professor ROY E. CLAUSEN, Division of Genetics, UNIVERSITY OF CALIFORNIA. For advice in the preparation of this manuscript the writer is indebted to Professor E. B. BABCOCK, Division of Genetics, UNIVERSITY OF CALIFORNIA, and to Doctor HOWARD B. FROST, Citrus Experiment Station, UNIVERSITY OF CALIFORNIA.

METHODS

Chromosome number was, as a rule, obtained from smears of pollen mother cells, stained by Belling's method. The most generally favorable stage for counting was the second metaphase but cells in which both plates are countable are sometimes difficult to find; diakinesis was often used and occasionally interkinesis and second anaphase. First metaphase and anaphase often gave useful indications. In exceptional cases to be noted later, chromosomal counts were obtained from sections of root tips and of anthers fixed in chrom-acetic-urea and stained in Heidenhain's iron-alum haematoxylin. In no case was a constant discrepancy found between chromosome number in the root tips and in the pollen mother cells, but the occasional presence of tetraploid pollen mother cells in diploid or trisomic plants previously reported by M. M. LESLEY (1925) was confirmed. Although the chromosomes are only about 1μ in diameter at the second metaphase, their relatively small number and their shortness in the later phases of meiosis and in root tips, make the tomato fairly favorable material for chromosome counting.

In many first-metaphase plates there is some gradation in chromosome size; in particular one large bivalent is often seen at the periphery and smaller ones in the center of the plate. These differences, however, are not constant and are probably due to slight differences in stage of development; they were not detected in root tips.

The pollen was examined in acetocarmine. Mixed samples were taken from what appeared to be typical healthy and ripe anthers. The grains which were round and full of stained material were counted as "good" and those which were irregular in outline, imperfectly filled or empty were counted as "bad." Very few burst grains were found. In the same plant and even in individual anthers of the same flower the variability both in quantity of pollen and in proportion of good grains greatly exceeded that of random sampling.

Unless otherwise stated, all flowers in both self- and cross-pollination were inclosed in paper bags and the usual precautions taken in pollination. Field cultures were for the most part grown in the experimental grounds of the Division of Genetics, at Berkeley, and greenhouse cultures at the CITRUS EXPERIMENT STATION, Riverside.

ORIGIN OF TRIPLOIDS AND F_1 PROGENY

The normal tomato plant was found by WINKLER (1910) to contain 24 chromosomes in the root tips and 12 pairs at diakinesis in the pollen mother cells. In 1923 a single triploid plant was found among 29 plants of Livingston's Dwarf Aristocrat, grown from commercial seed. The root tips contained 36 chromosomes and a study of the prophases of meiosis in the pollen mother cells by M. M. LESLEY (1926) showed at diakinesis, as a rule, 12 trivalents. The morphological characteristics of this plant have been briefly described in a previous paper (LESLEY and MANN 1925). The stems, leaves and flowers were more or less gigantic but the fruits were undersized and few in number. In 1924 a second triploid plant identical in appearance with the first occurred among 85 plants from the same lot of seed (figure 3). A third appeared among 104 plants also from commercial seed of a rather similar variety, Dwarf Champion, and a fourth in a commercial planting of an early strain of Stone, a variety of standard habit. Altogether among 200 plants of Dwarf Aristocrat 2 plants (1 percent) and among 280 plants of Dwarf Champion 1 plant (0.4 percent) were triploid. Some of the giant unfruitful plants known to commercial tomato growers as "he" plants or "fruitless hybrids" are undoubtedly triploids, others perhaps are trisomics as is noted below (p. 36).

A triploid plant may originate from a cross between a tetraploid and a diploid. Tetraploid tomato plants were obtained by WINKLER (1916) from shoots arising from the callus of a graft between *Solanum nigrum* and tomato. He reports regular 24+24 reduction in the pollen mother cells but only 5 percent of good pollen. No tetraploid plant has been found in the course of the present study. Recently M. M. LESLEY (1925) has found islands of tetraploid cells in roots and groups of tetraploid pollen mother cells which are believed to have originated from tetraploid islands in the meristems of shoots. She also found diploid pollen mother cells of tomato in which the reduction division was suppressed with resulting dyad formation (unpublished data). In each case a diploid gamete would be formed, which, when fertilized by a normal (haploid) gamete, would give a triploid plant. Probably triploids have arisen in both ways.

The two triploid plants of Dwarf Aristocrat used in practically all the breeding work showed the dwarf habit, rather dark green foliage and smooth scarlet fruit characteristic of this variety. Numerous attempts were made to obtain seed from self-fertilization but without success. Seeds from a few fruits which set on one plant late in the season without hand-pollination gave rise to plants of standard habit and therefore resulted from vicinism. Seed was produced very sparingly from diploid ♀×triploid ♂, and therefore the failure to obtain seed from self-fertilization seems to be due to defective pollen. Indeed very little mature pollen is found in the anthers of the triploid and a very large proportion of the grains are empty or clearly degenerate (table 5). Triploid Datura produced very little good pollen but gave some progeny from self-fertilization. Seed was readily obtained from triploid tomato ♀ × diploid ♂. In 56 fruits obtained from crosses of this type the mean number of viable seeds per fruit was about 4, as compared with about 50 in diploid Dwarf Aristocrat selfed.

Since pollination with a diploid proved to be the most effective method of obtaining progeny a choice of diploid pollen parents had to be made. Clearly the identification of forms with extra chromosomes was of primary importance. How greatly identification of a trisomic form may be hindered by differences resulting from the segregation of genes has been clearly pointed out by CLAUSEN and GOODSPEED (1924). In the present case, therefore, since self-fertilization had failed, the triploids were crossed with a diploid plant *of the same variety.*

The progeny of triploid×diploid Dwarf Aristocrat will be referred to as the non-hybrid F_1. This term is not strictly correct since the triploid and diploid plants were probably not genotypically identical. The two diploid plants used appeared to be typical of the variety, were similar in appearance and probably belonged to the same pure line, but both may have differed genotypically from the triploids. Among the 10 plants with the diploid chromosome number which appeared in the non-hybrid F_1, the only obvious variation was in foliage color. In the non-hybrid progenies there was rarely any difficulty in identifying healthy diploid plants in the field or greenhouse. It appears, therefore, that the genotypic differences in the non-hybrid progeny were not sufficient to obscure the differences associated with the presence of extra chromosomes. Small hybrid F_1 progenies were also grown from triploid crossed with the varieties Globe, Red Pear, and Magnus, for comparison of the hybrid with the corresponding non-hybrid forms.

The F_1 triploid × diploid progenies contained a most striking diversity of types, varying in plant size, color and shape of foliage, flower structure, fruit shape and other characters. Part of these plants were grown in the field and part in the greenhouse. Certain characteristics, especially of foliage, were more evident in the field than in the greenhouse, so that the identification of types, particularly by foliage, was sometimes difficult (see figures 7 and 8). BLAKESLEE and FARNHAM (1923) report a similar experience with the Poinsettia mutant of Datura.

CHROMOSOME NUMBER OF F_1 PROGENY OF TRIPLOID × DIPLOID

Table 1 shows the chromosome number of the hybrid and non-hybrid progenies of triploid ♀ × diploid ♂. M. M. LESLEY (1926) has shown that in the pollen mother cells of triploid tomato the unpaired chromosomes are distributed at random at the heterotypic division, and consequently it might be expected that the chromosome number in the microspores would show approximately a binomial distribution. Such a distribution was also found by BELLING and BLAKESLEE (1922) in the pollen mother cells of Datura and by BELLING (1924) in hyacinth. It is at least not improbable that the chromosome number of the eggs in these triploids has a similar distribution. It is evident from table 1 that, in tomato, the chromosome number of the progeny has quite a different distribution. In a binomial series, 30-chromosome plants would be the most frequent, but no 30-chromosome plant appeared and no gamete with more than 3 extra chromosomes has given a viable zygote. Some of the counts are not decisive but the data certainly warrant the conclusion that the 25-chromosome plant or simple trisomic is the most frequent and suggest that the

TABLE 1

Chromosome number of F_1 progeny of triploid × diploid tomato.

Number of chromosomes	2n	2n+1	2n+1 or 2n+2	2n+2	2n+3
Frequencies observed	7	26(2)	–	7	2
	3(3)	9(3)	5(3)	7(3)	
Total frequencies	10	35	5	14	2

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[2] Including one plant with additional fragment.

[3] Based on fewer counts.

double trisomic, diploid and triple trisomic are next in order. Since chromosome counts were obtained from only about half the population, these data represent only a sample of the F_1 progeny grown. Probably the frequency of 26- and 27-chromosome plants is underestimated since, as a rule, they produce few or even no buds and relatively few counts were made from root tips. On the other hand a few plants which were obviously diploid were not examined cytologically. One plant was found to contain a whole extra chromosome and an additional fragment.[4] This and other fragment-containing types which occurred in the progeny of double trisomics will be described in another paper. No plant was found to have less than 24 chromosomes.

Presumably the numerous, more or less undersized and abortive seeds which are to be found in the fruit of triploids, represent the inviable combinations with high chromosome number, if indeed the eggs with high chromosome numbers ever became fertilized.

A correlation was found between seed size and chromosome number similar to that observed by FROST (1919) in Matthiola. Non-hybrid F_1 seeds were arbitrarily grouped into "large" and "small." The chromosome numbers of the resulting plants are shown in table 2. The data indicate that "small" seeds give rise to a larger proportion of 26- and 27-chromosome plants. One "large" seed however gave rise to a 26-chromosome plant that was extremely abnormal in development.

TABLE 2

Seed size and chromosome number of F_1 plants from triploid×diploid tomato.

SIZE OF SEED	NUMBER OF SEEDS	DIPLOID (PERCENT)	TRISOMIC (PERCENT)	ONE EXTRA CHROMOSOME[5] (PERCENT)	MORE THAN ONE EXTRA CHROMOSOME[5] (PERCENT)
"Large"	28	21	79	57	14
"Small"	22	5	95	50	32

As a result of numerous attempts, only 2 plants have been obtained from diploid pollinated by triploid. These originated from diploid×triploid Dwarf Champion and both F_1 plants were diploid.

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[4] The number of chromosomes in this plant, and in the 27-chromosome and some 26-chromosome plants was determined from root tips by Doctor M. M. LESLEY.

[5] Excluding plants with extra chromosomes of which the number was not positively determined.

Discussion of chromosome number

WINKLER (1916) first suggested that hyperdiploid forms were likely to differ more than tetraploids from the normal on account of unbalance in chromosome number.

In the progeny of Datura triploid×self and triploid×diploid, BLAKESLEE and BELLING (1924) found no plant with more than 3 extra chromosomes, although the distribution of the chromosomes in meiosis in the pollen mother cells was approximately binomial. As all combinations with more than 27 chromosomes were absent, it was concluded that an unbalance exceeding 3/24 was inconsistent with viability. In the progenies of the triploid *Oenothera semigigas*×*O. Lamarckiana* and *O. biennis*, VAN OVEREEM (1920) found plants with chromosome number ranging in unbroken series from 14 (diploid) to 20. In the progeny of *O. semigigas*×mut. *velutina*, DE VRIES and BOEDIJN (1924) found a similar range of chromosome number with a mode in the 15-chromosome class. In this species, unbalance in chromosome number appears to have no obvious relation to viability; this seems to point to a certain similarity of its chromosomes at least in genes affecting viability. Presumably the greatest unbalance in chromosome number in these plants is 3/14 and 4/14, for, if 7 is the basal number, a 20-chromosome plant would be less unbalanced than one with 17 or 18 chromosomes.

A glance at table 1 at once suggests that in tomato, as in Datura, viability has some relation to unbalance of chromosome number and is at least an approximate measure of it. It appears that an unbalance of 3/24 is the maximum consistent with viability and that, as a rule, the greater the unbalance, the less the chance of viability of gamete or zygote. It is probable that 27-chromosome plants occur more frequently in the F_1 from triploid×diploid in tomato than in Datura, since 2 such plants were found among 66 F_1 plants in tomato while BLAKESLEE and BELLING (1924) mention only 1 among a much larger F_1 progeny in Datura. This suggests that Datura is more sensitive to changes of numerical chromosome balance than tomato.

BRIDGES (1923) found in Drosophila that triplo-X or triplo-IV or haplo-IV flies were viable but that no triplo-II or triplo-III appeared in the progeny of triploids. Since the numerical chromosome unbalance is the same in triplo-IV and triplo-III, it appeared that the size of the extra chromosome had to be taken into account. According to BRIDGES (1922) the effect of extra chromosomes on development depends on their internal gene balance. It is inferred that the internal gene balance differs in the chromosomes of the same and of different species. Except in the cases of polyploidy and of replication of the same chromosome, viability will depend, not on the unbalance in terms of chromosome number, but rather on the gene unbalance of the individual chromosomes and combinations of chromosomes. This hypothesis explains why a gamete of Oenothera can sustain an unbalance of 3/7 but a gamete of tomato probably only an unbalance of 3/12.

BEHAVIOR OF EXTRA CHROMOSOMES

The mode of origin of the triploid×diploid F_1 and the presence of trisomes in meiosis of 25- and 26-chromosome plants suggest that the tomato plants with extra chromosomes are, in BLAKESLEE'S (1921a) terminology, simple, double and triple trisomics. Although double trisomics were less extensively studied than simple trisomics the evidence indicates no great difference in the behavior of the extra chromosomes in these two groups. Neither has any constant difference in the behavior of the extra chromosome been observed in different simple-trisomic types.

In diakinesis the arrangement of the set of 3 chromosomes in the pollen mother cells of a simple trisomic is the same as that found by M. M. LESLEY (1926) in her study of the prophases of the triploid tomato. Either 11 pairs and 1 trivalent, the latter arranged in a single row or in a triangle (figure 2A), are present, or less frequently 12 pairs and 1 unpaired chromosome (figure 1A). Usually one member of the set of 3 chromosomes lags during the formation of the first metaphase plate, as commonly one monovalent is seen outside the plate in lateral view of the first metaphase. Sometimes however, the association typical of diakinesis is maintained and 11 pairs and 1 fairly compact trivalent appear; the latter has sometimes been seen as a compact row of 3 in lateral view. In polar views, accordingly, 12 bivalents and 1 monovalent (figure 2B) or 11 bivalents and 1 trivalent (figure 1C) were found. One or two laggards are common in the early first anaphase (figure 1D). It is probable that the unpaired chromosome usually passes without division into one of the second-metaphase plates, as 12+13 (figure 2C) is more common that 13+13 at that stage. A lagging chromosome is usually included in one of the second-metaphase plates, as it is exceptional to find 12+12 at that stage. Sometimes, however, during interkinesis one or two (figure 2D) micronuclei or karyosomes are seen with membranes and chromatin in a condition similar to interkinesis. In such a case the lagging chromatin doubtless fails to reach the second-metaphase plates and forms microcytes

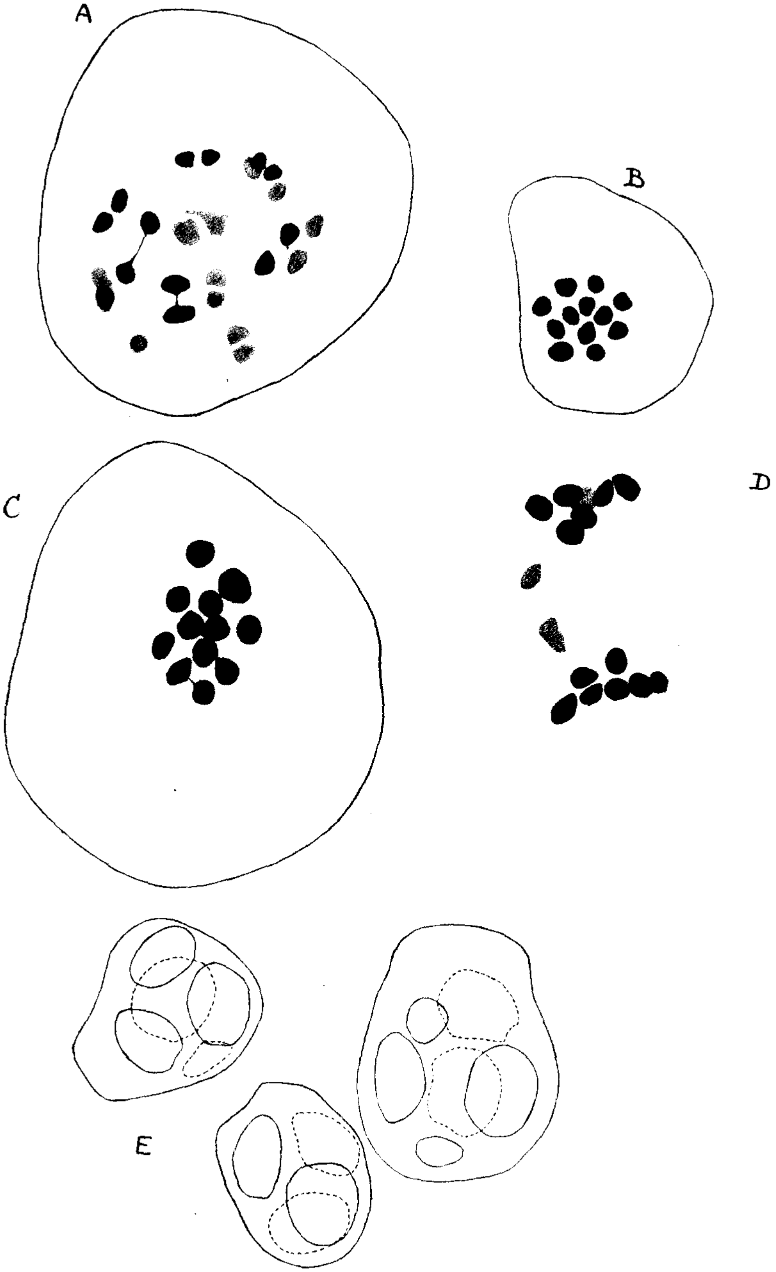

FIGURE 1.—Pollen maturation in diploid and simple trisomics. A, triplo-A, diakinesis, 12 bivalents (pairs) and 1 univalent; B, diploid, 1st metaphase, 12 bivalents; C, triplo-A, 1st metaphase, 11 bivalents and 1 trivalent; D, triplo-E, late 1st anaphase, 2 laggards from division of unpaired chromosome (polar groups not countable); E, triplo-A, tetrad (below), pentad (left), hexad (right). A, C, D×4000; B, E×2200.

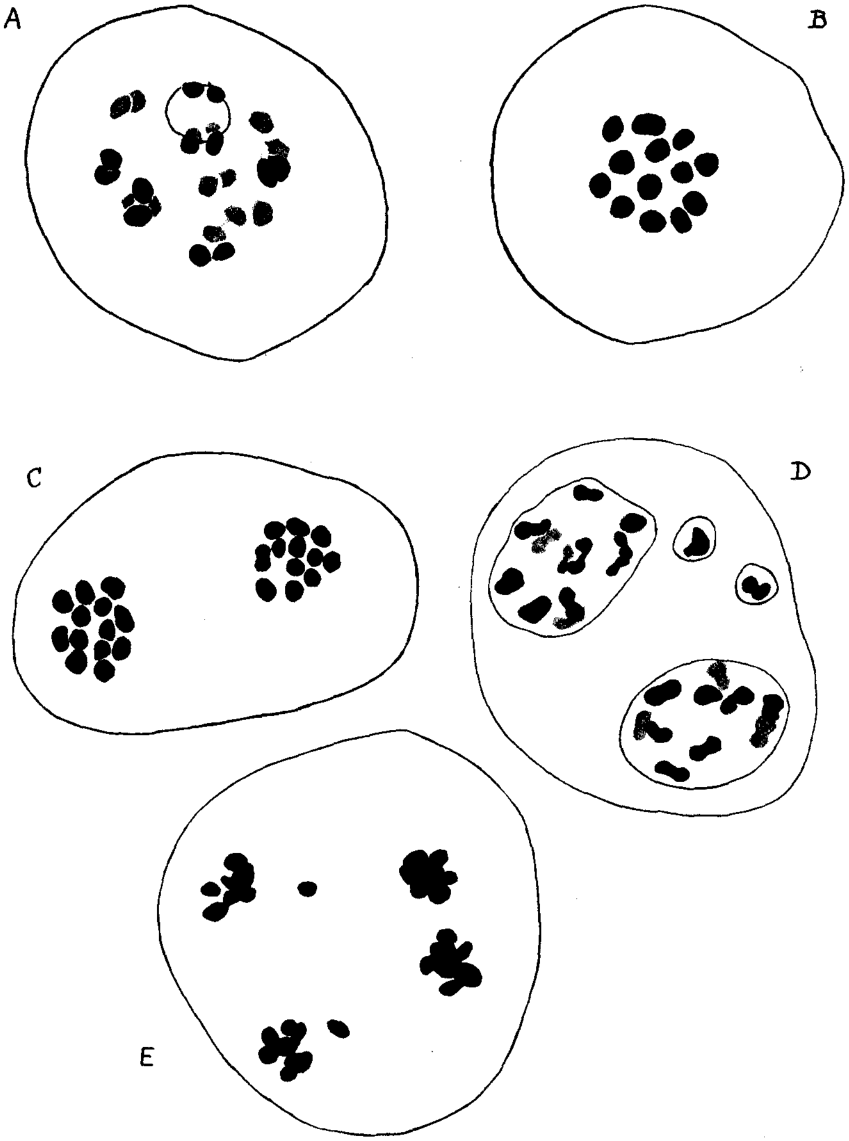

FIGURE 2.—Pollen maturation in simple trisomics. A, triplo-C, diakinesis, 11 bivalents and 1 trivalent; B, triplo-A, 1st metaphse, 12 bivalents and 1 monovalent; C, triplo-C, 2nd metaphase, 12+13; D, triplo-C, interkinesis showing micronuclei (chromosome count not clear); E, triplo-A, ate 2nd anaphase, 2 laggards from division of unpaired chromosome in 1st division. ×3050.,

(figure 1E). In the second anaphase, after assortment in the heterotypic division, the unpaired chromosome divides so that 13+13 and 12+12 result; or after division at the first anaphase, assortment occurs forming 12+13, 12+13. As before, the unpaired elements often lag during the second anaphase and 2 laggards are seen in one plate or 1 in each (figure 2E). Since 12+13 is more common than 13+13 at the second metaphase, it was surprising to find 1 laggard in each second anaphase plate more commonly than 2 laggards in one plate. Apparently lagging in the second anaphase is more common in the process of *assortment* of the 2 unpaired elements than in the *division* of 1 or, in other words, in the second division assortment is slower than the completion of the process of division. It is evident from the above statement that there is much variation in chromosome behavior during meiosis. While the process tends to follow a certain rule there is no constant behavior of the chromosomes even in material prepared on the same day and from the same anther. Such irregularity seems to be characteristic of meiosis where unpaired chromosomes are present.

The microspore groups or "tetrads" of a simple trisomic may contain 1 or 2 microcytes (figure 1E). Owing to the compact arrangement of the microspores, the counting of microcytes was usually made after much shrinkage had been allowed to occur. The occurrence of micronuclei at interkinesis noted above indicates that some microcytes originate in the heterotype division. From 4.5 percent to 7.6 percent of "tetrads" containing microcytes were counted in 3 different simple trisomic types (table 3). Probably the proportion differs significantly in these types although considerable variation was found in different samples from the same type. In the "tetrads" of double trisomics 3 microcytes were often present.

TABLE 3

Microcytes in pollen "tetrads" of trisomic tomatoes.

NAME	NUMBER OF "TETRADS" EXAMINED	PENTADS AND HEXADS, PERCENT
Triplo-A	513	4.5
Triplo-B	426	7.1
Triplo-C	1154	7.6

GENERAL CHARACTERISTICS AND NAMING OF TRISOMICS

All the trisomic plants which have appeared either in the F_1 progeny of triploids or in the progeny of trisomics show certain general characteristics which serve to distinguish them from diploids. They are slower-growing, and more or less distinct in foliage. They have a tendency to pollen sterility and unfruitfulness which is more marked under field than under greenhouse conditions. Although even simple trisomics are distinguished from diploids by their smaller size up to the time when the first fruits set, later in the season certain of them may exceed diploids in plant size, doubtless on account of their unfruitfulness. Most of the trisomic types are later in flowering, show some difference from diploids in the size or structure of the floral organs and produce fewer viable seeds. These peculiarities are in general more marked in double and triple than in simple trisomics, especially the slower rate of growth, pollen sterility and diminished seed production. In the chromosomal mutants of Matthiola, according to FROST (paper in preparation) hybrid forms are much more fertile than non-hybrid. So in tomato, certain double-trisomic hybrids set seed more freely and were probably more vigorous and more fertile than the corresponding non-hybrids. When the trisomic hybrid type can readily be identified, it is therefore preferable to the non-hybrid for breeding work, but the differences introduced by segregation of genes from hybrid parents increase the difficulty of recognizing extra-chromosome types, especially those containing chromosome fragments.

An attempt has been made to point out some of the most conspicuous features in which certain trisomic types differ from the diploid. Only a beginning has been made in the description of these types. Some of the simple trisomic plant types are by no means easy to distinguish from diploids (see figures 6 and 12). In tobacco the discovery by CLAUSEN and GOODSPEED (1924) of the simple trisomic "Enlarged" was made by the use of a correlation table. So in the tomato, the distinguishing characteristics of certain trisomics, such as rate of growth, number of loculi in the fruit, and foliage color are of a quantitative nature and so variable as to make identification difficult to one unfamiliar with the types, especially where only a small number of plants are observed.

In the naming of trisomics, a modification of the method used by BRIDGES (1921) is adopted here. The capital letters of the alphabet are used to distinguish the individual chromosomes. The haploid number of chromosomes in the tomato is 12 but as yet only nine different types each with 1 whole extra chromosome have been found. Accordingly the letters A to I are used to name these 9 chromosomes. A simple trisomic (25 chromosomes) may then be triplo-A, which means that the A-chromosome is present in triplicate, the remainder being made up of 11 normal pairs. A double trisomic may be triplo-AB, which means that the A- and B-chromosomes are present in triplicate, the balance consisting of 10 normal pairs.

DESCRIPTION OF TRISOMIC TYPES

Since the distinguishing characteristics of trisomic types may be masked in hybrid progenies, the non-hybrid progeny of triploid Dwarf Aristocrat was used as the basis for the following descriptions.

FIGURE 3.—Triploid (left) and diploid (right) plants of Dwarf Aristocrat tomato.

The diploid form of Dwarf Aristocrat shows the characteristics of stem and leaf which combine to make the dwarf habit. The stem is short and stiff, giving the plant a rather erect habit until borne down by the weight of the fruit. The leaves are dark green, thick and leathery in texture and deeply rugose, and the leaflets are nearly sessile on the rachis (figures 5 and 6). The style length is about 5 mm and the top of the stigma is

TABLE 4

Shape and number of loculi ("cells") in fruit of diploid and non-hybrid trisomic tomatoes.
(For explanation of terms, see figure 4, legend)

	NUMBER OF FRUITS MEASURED	MEAN E. D.	MEAN $\frac{\text{E. D.}}{\text{L}}$	MEAN $\frac{\text{L}}{\text{P. D.}}$	NUMBER OF FRUIT CUT	MEAN NUMBER OF CELLS PER FRUIT	STANDARD DEVIATION OF NUMBER OF CELLS
Diploid	47	4.7	1.2	1.2	87	4.4	1.4
Triplo-A	9	5.4	1.4	1.4	8	5.4	
Triplo-C	4	5.2	1.5	1.7	50	8.8	2.6
Triplo-D	14	3.9	1.0		15	3.3	
Triplo-G	6	5.2	1.5	1.4	3	8.0	
Triplo-H					10	6.5	
Triplo-I	7	6.2	1.3	1.3	7	7.7	

usually about level with the apex of the staminal column (figure 21B); this arrangement probably tends to insure self pollination. As a rule pollen is abundantly produced but exceptionally nearly sterile anthers are found. This type set an abundance of fruit in the field without artificial pollination. The color of the fruit is scarlet. Table 4 shows the results of certain measurements of fruits all of which developed in the same season on plants growing in the greenhouse. The meaning of the terms used is shown in figure 4. The values of the ratios of mean equatorial diameter

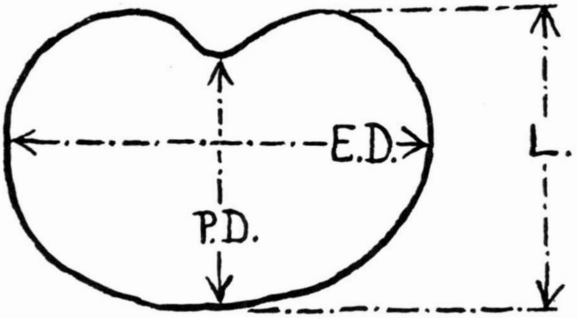

FIGURE 4.—Diagram of fruit. E.D. = equatorial diameter; P.D. = polar diameter; L. = length.

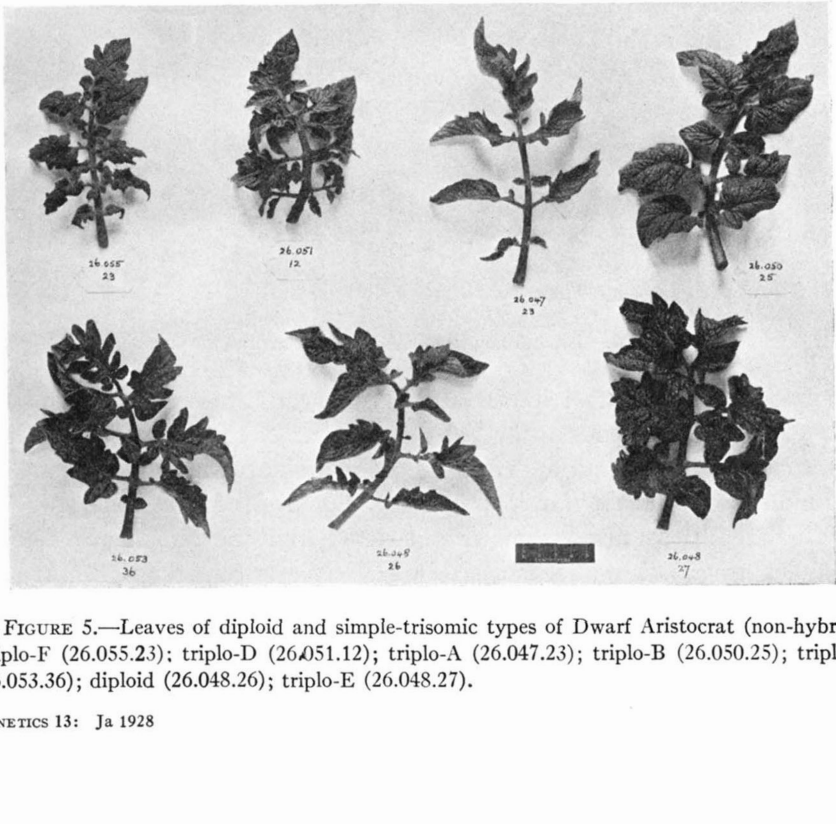

FIGURE 5.—Leaves of diploid and simple-trisomic types of Dwarf Aristocrat (non-hybrid). Triplo-F (26.055.23); triplo-D (26.051.12); triplo-A (26.047.23); triplo-B (26.050.25); triplo-C (26.053.36); diploid (26.048.26); triplo-E (26.048.27).

to length and of length to polar diameter show that the fruit of the diploid is slightly oblate and has shallow polar depressions (figure 25). As a rule it is fairly free from corrugations or longitudinal grooves. The number of loculi or "cells" in the fruit is also shown in table 4, and figure 24D shows a transverse section.

Simple-trisomic types

Triplo-A (figures 5, 7 and 8)

Like the other trisomic types, triplo-A is slower-growing than the diploid and is probably intermediate between the more rapidly growing trisomic types such as triplo-B and the slower types such as triplo-D. The young foliage tends to be paler than that of the diploid. The leaflets appear to be farther apart, are more acuminate and have fewer deep but more shallow irregular incisions and a more undulate margin. The terminal leaflet is often somewhat twisted and the smaller leaflets or foliolules are much reduced in size. The style is remarkably short; the stigma is about 2 mm below the apex of the staminal cone and often malformed, infolded or without a distinct disc (figure 21A). Under field conditions triplo-A has less pollen and more empty grains than the

FIGURE 6.—Diploid non-hybrid (Dwarf Aristocrat), in field.

FIGURE 7.—Triplo-A non-hybrid (Dwarf Aristocrat), in field.

FIGURE 8.—Triplo-A non-hybrid (Dwarf Aristocrat), in greenhouse.

diploid (table 5). On 88 plants of this type not one fruit set in the field without hand pollination. Only 9 fruits were measured; these were distinctly larger and more oblate and had deeper polar depressions and more cells (figure 24C and table 4) than the diploid fruits.

TABLE 5

Pollen sterility.

	IN FIELD			IN GREENHOUSE		
	Number of grains examined	Bad grains (percent)	Bad grains (percent in total)	Number of grains examined	Bad grains (percent)	Bad grains (percent in total)
Diploid Dwarf Aristocrat	225	12				
"	285	13				
"	231	9	11	177	3	3
Triploid Dwarf Aristocrat				155	75	
"				108	92	87
Triploid Dwarf Champion				84	80	80
Triplo-A, hybrid				202	14	
"	307	66		202	6	
"	334	51	58	139	20	8
Triplo-B, hybrid	272	35				
"	249	33				
"	674	30	31	176	26	26
Triplo-C, non-hybrid	383	64				
"	264	84				
"	957	54				
"	337	70	63	119	17	17
Triplo-D, non-hybrid	252	74	74	135	39	39
Triplo-E, non-hybrid	350	25	25			
Triplo-F, hybrid	274	49				
"	302	26	37			
Triplo-G, non-hybrid	83	27	27			
Triplo-H, non-hybrid	76	27	27			
Triplo-A?, hybrid				295	31	31

A triplo-A hybrid type of standard habit has been described elsewhere (J. W. LESLEY 1926). It has been shown that the extra chromosome present is associated with the locus of the dwarf-standard pair of genes and that the *Ddd* plant, although standard, shows a suggestion of the dwarf character in the greater thickness and rugosity of the leaflets and the shorter style.

Triplo-B (figure 9)

This seems to be one of the more rapidly growing simple-trisomic types. The plant has a characteristic pale olive-green color and metallic cast, especially under field conditions; this difference from the diploid color may be due to the denser coating of trichomes. The leaflets have a greater tendency to downward or inward rolling of the edges, and the rachis of the leaflets has less tendency to curling than with the diploid (figure 5). The spread of the calyx and corolla is smaller and the stamens shorter than in the diploid. An outstanding characteristic is the length of the style, which is about 1 mm greater than that of the diploid; as a rule the stigma projects considerably beyond the relatively short stamens (figure 22). In the field the quantity of pollen, in proportion to the small size of the stamens, is nearly equal to that of the diploid, and the quality (table 5) was superior to that of triplo-A and among the best of the trisomics. Triplo-B plants often set a few fruits in the field and in the greenhouse without hand pollination.

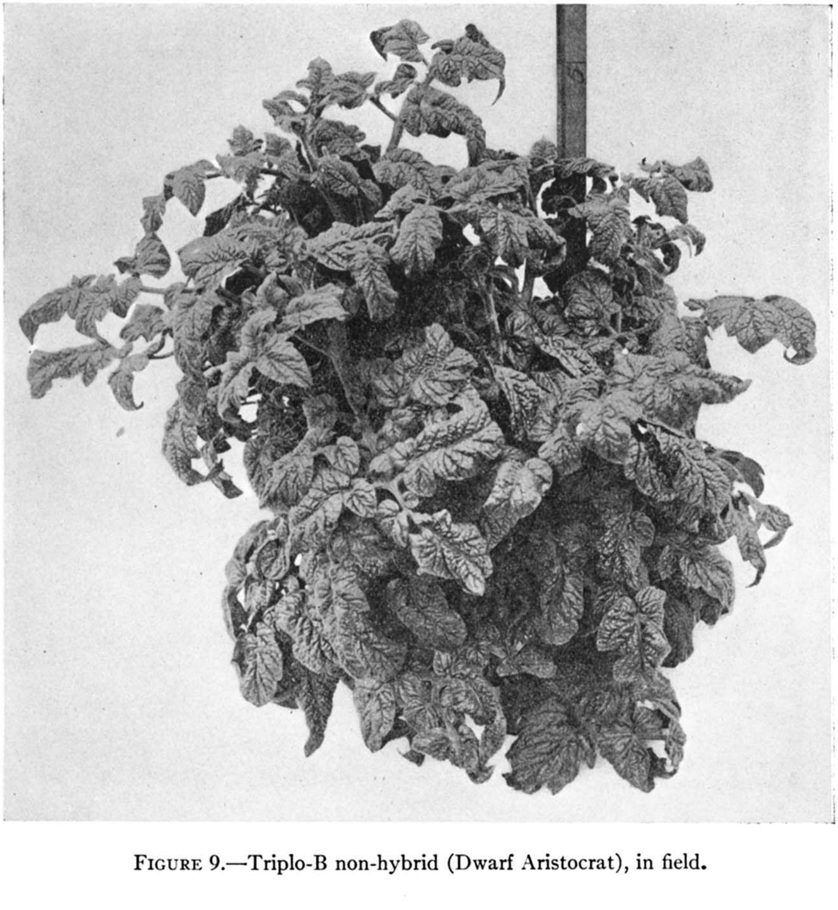

FIGURE 9.—Triplo-B non-hybrid (Dwarf Aristocrat), in field.

Triplo-C (figure 10)

This type is intermediate among the simple trisomics in rate of growth, or about equal to triplo-A. The foliage, especially in young plants, is somewhat duller green and the stem is thicker and stiffer and the internodes shorter than in the diploid. The leaflets appear closer together (figure 5) and the edges more uprolled. The peduncles are shorter than those of the diploid. The pollen was scanty and probably inferior in quality to triplo-B in field (table 5) but not in greenhouse plantings. The style appears to be especially variable in length but is on the average shorter than that of the diploid. An interesting characteristic of this type is the greatly increased fasciation of the flower. The number of stamens and other floral organs is much increased; table 4 shows that the

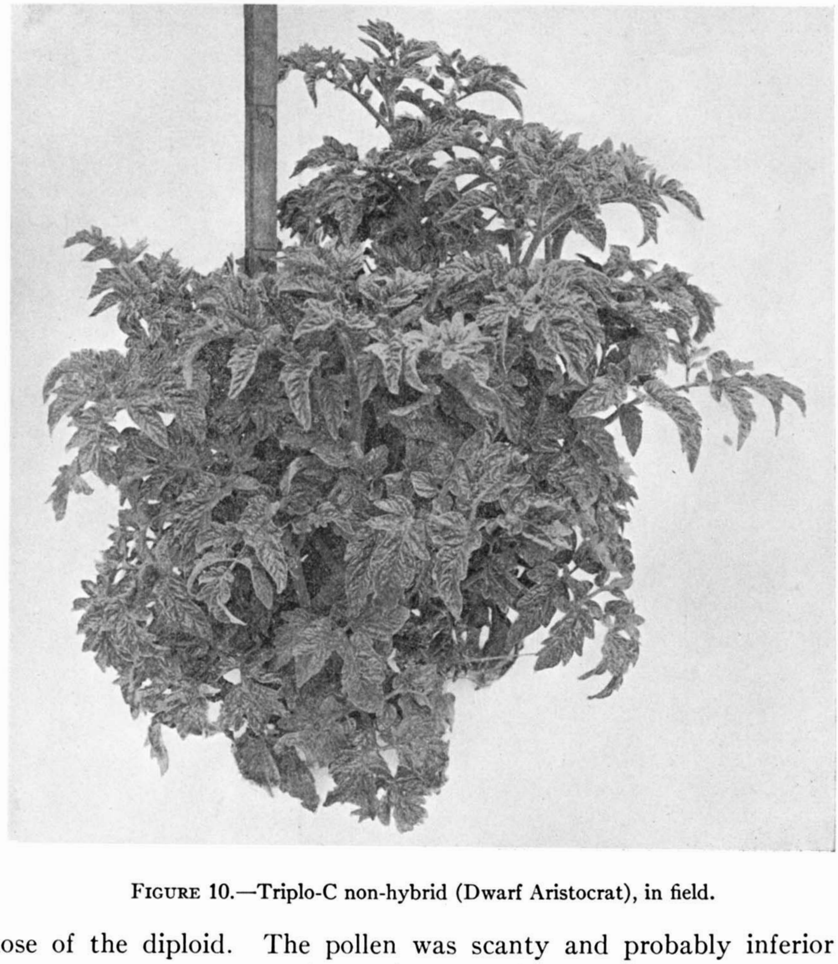

FIGURE 10.—Triplo-C non-hybrid (Dwarf Aristocrat), in field.

number of loculi in the ovary is more variable but the mean is twice that of the diploid. The interior of some fruits (figure 24A) suggests that of the most highly fasciated varieties such as Trophy. In the field 23 plants of this type set no fruit. Under greenhouse conditions and without artificial pollination, the diploid sets some fruits which are as a rule nearly seedless. Unlike other simple-trisomic types triplo-C sets fruit under these conditions quite as readily as the diploid.

FIGURE 11.—Triplo-D non-hybrid (Dwarf Aristocrat), in field.

Triplo-D (figure 11)

This type is one of the slower-growing simple trisomics and, especially in the field, is far behind the diploid in plant size, previous to fruit setting. The stem is relatively thin, and the leaflets are smaller, narrower and with more deep incisions than in the diploid (figure 5). Most characteristic of this type is the downward (inward) curling of the rachis and of the rachillae, especially of the terminal leaflet. This feature is more marked under field conditions, where the plant presents a compact, almost cushion-like appearance. The sepals are longer and more recurved (figure 23B) and the stamens more tapering than in the diploid. The quantity of pollen is only slightly less than in the diploid but the quality is probably much inferior (table 5). The flower shows *less* tendency to fasciation than the diploid, and the fruit has fewer loculi, is smaller and distinctly less oblate in shape (table 4 and figures 24E and 25). In the field among 25 plants of this type one set a single fruit without hand pollination. In the greenhouse, after hand pollination, triplo-D set fruit and viable seed nearly as freely as the diploid.

FIGURE 12.—Triplo-E non-hybrid (Dwarf Aristocrat), in field.

Triplo-E (figure 12)

This is one of the relatively fast-growing trisomics and in general most nearly resembles the diploid. The leaves however are darker green and have shorter petioles and broader, less acuminate leaflets, giving the leaf a more rounded and less spaced appearance (figure 5). The rachis and rachillae, especially of the terminal leaflet, are more curled and in the field the plant forms a compact, almost pillarlike mass of vegetation. The flower and fruit closely resemble the diploid but the ripe fruit seems to be firmer and contains fewer viable seeds. In the field among some 30 plants of this type, 1 set a single fruit without artificial pollination.

FIGURE 13.—Triplo-F hybrid (Dwarf Aristocrat×Globe F_2 plant), in field.

Triplo-F (figure 13)

This type is one of the slower-growing simple trisomics. Young plants are much paler green but later the color tends to approach the normal diploid. The leaflets (figure 5) have fewer deep incisions or lobes but more serration. The surface of the leaves has more fine rugosity and is more velvety than that of the diploid. In the field the pollen appears to be of relatively good quality (table 5) or about equal to triplo-B. Six field-grown plants set no fruit.

Triplo-G (figure 14)

This is one of the more rapidly growing trisomics, like triplo-B and triplo-E. The stems are weaker and the plant is more decumbent in habit than the triplo-C. The leaflets are narrower and comparatively free from both lobing and serration. Observation of a few specimens indicates that the fruit is more oblate and has a deeper basin (stylar-end depression) than the diploid.

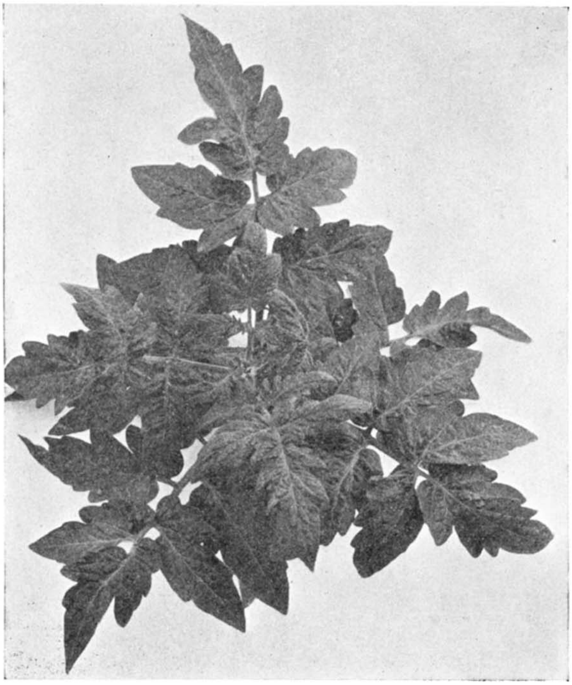

FIGURE 14.—Triplo-G non-hybrid (Dwarf Aristocrat), in greenhouse.

Triplo-H (figure 15)

Only one plant of this type has appeared. It has fewer foliolules and narrower, more acute leaves than the diploid. The leaflets are almost free from lobing and serrations, giving the foliage a very distinctive appearance. The leaf surface unlike that of triplo-I is as rugose as with the diploid. The flower is probably larger than that of the diploid.

Triplo-I (figure 16)

This type resembles the preceding in having fewer foliolules and less lobing or serration than the diploid. It is distinguished from triplo-H and from the diploid by its less rugose leaves and by paleness of the red flesh color of the interior of the fruit.

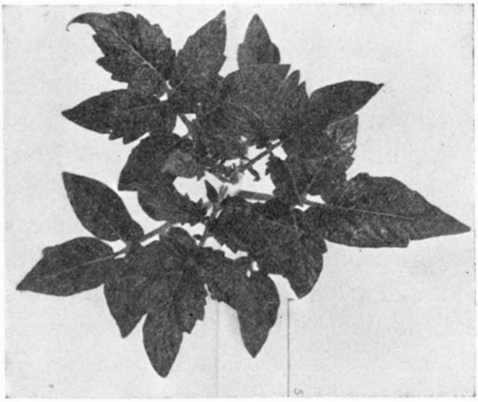

Figure 15.—Triplo-H non-hybrid (Dwarf Aristocrat), in greenhouse.

Double-trisomic types

Double trisomics are in general even slower-growing than simple trisomics and tend to have less good pollen and less viable seed. The 10

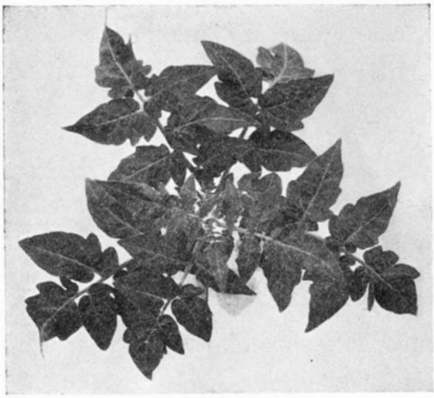

Figure 16.—Triplo-I non-hybrid (Dwarf Aristocrat), in greenhouse.

Figure 17.—A simple trisomic plant closely resembling triplo-I and perhaps a secondary of it.

non-hybrid double-trisomic plants found belonged to as many different types. This is not surprising since theoretically 9 simple trisomic types may give 36 combination double-trisomic types. Most of the non-hybrid double trisomics were planted in the field. On account of their slow growth and incomplete development, and the small number of plants of each type, adequate descriptions were not obtained. It might be expected that a double trisomic would show a combination of the characteristics of two simple-trisomic types. To some extent, this expectation was fulfilled. Thus one hybrid double trisomic had the curled foliage and small fruit of triplo-D and the pale green color of triplo-F. On selfing both of these types appeared in addition to diploids. One non-hybrid double trisomic was surprisingly like a diploid but had the projecting style and metallic green cast of triplo-B, and like triplo-C it set fruit freely in the greenhouse without pollination. The pollen was very scanty and to obtain progeny it was necessary to backcross to the diploid. The fruits contained but little more seed than the triploid. Among the progeny were triplo-B and triplo-C. A third double-trisomic type clearly suggested triplo-D by its curled foliage and calyx. In other double trisomics the characteristics of simple-trisomic types were not clearly recognized, in some cases perhaps, owing to blending and neutralization of the effects of the extra chromosomes.

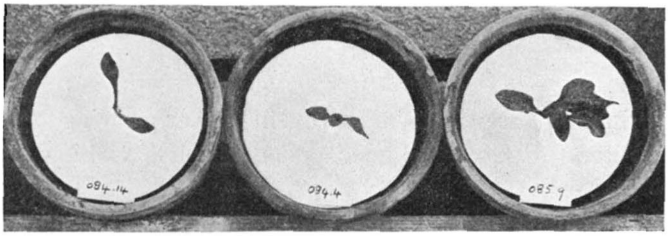

FIGURE 18.—Non-hybrid (Dwarf Aristocrat) "runts"; plants at right and center contained 26 chromosomes in root tips.

A few 26-chromosome plants which originated in the triploid × diploid F_1 and were therefore probably double trisomics, were termed "runts" on account of their imperfect development. The shoot failed to form a bud and consisted of a pair of cotyledons and usually one first leaf which was either tube-like or more normal (figure 18). Owing to the incomplete development and lack of distinctive characters, it is not certain whether they belonged to more than one genotype.

Triple-trisomic types

Two 27-chromosome types were found which, from their origin, were presumably triple trisomics. Although extremely slow-growing they were not "runts" but were perfect in development. Two plants of the remarkable type shown in figure 20 have occurred in the non-hybrid F_1. This type had almost entire leaves like triplo-H, an abnormal stigma like triplo-A and a fasciated ovary like triplo-C; the anthers contained extremely little pollen. The other type (figure 19) was pale green like triplo-F, and curled foliage like triplo-D and had almost entire leaflets like triplo H.

FIGURE 19.—Non-hybrid (Dwarf Aristocrat) 27-chromosome plant with some characteristics suggestive of triplo-D, triplo-F, and triplo-H.

FIGURE 20.—Non-hybrid (Dwarf Aristocrat) 27-chromosome plant with some characteristics suggestive of triplo-A, triplo-C, and triplo-H.

Discussion of trisomic types

According to BLAKESLEE and BELLING (1924), in Datura 11 or perhaps 12 different primary simple-trisomic types have been identified, each containing 1 extra chromosome of the normal haploid set of 12. DE VRIES and BOEDIJN (1924) report that the Oenothera mutants and the progeny of *semigigas*-forms of *O. Lamarckiana* and *O. biennis* having 15 chromosomes, fall into 7 groups corresponding to the haploid number of chromosomes in *O. Lamarckiana*. Accordingly if all of the 12 chromosomes of the haploid set in tomato are different in their effect, 12 primary simple-trisomic types may be expected to occur in the triploid×diploid F_1. Hitherto 9 such types, each with a single apparently whole extra chromosome, have been found. In view of the unequal frequency with which the corresponding types occurred in Datura and of the relatively small number of tomato plants studied, there is reason to think that more simple-trisomic types will be found.

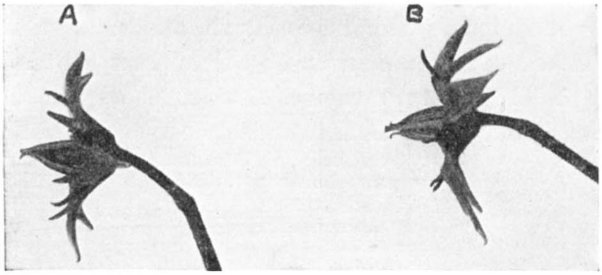

FIGURE 21.—Styles of non-hybrids (Dwarf Aristocrat). A, triplo-A, short; B, diploid, normal.

FIGURE 22.—Style of triplo-B non-hybrid (Dwarf Aristocrat), long.

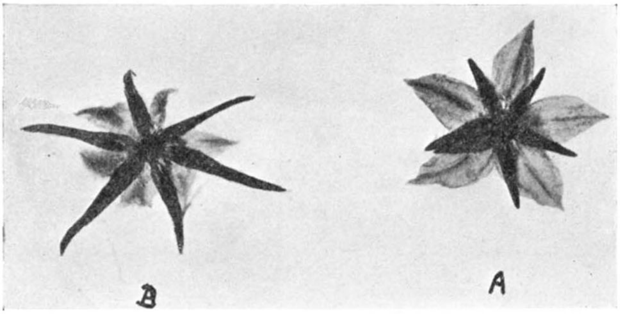

FIGURE 23.—Sepals of non-hybrids (Dwarf Aristocrat). A, diploid, normal; B, triplo-D, long.

For the present, it is preferable to regard these 9 types as homologous with primary mutants of Datura because they originated in the triploid ×diploid F_1, the number of simple-trisomic types found is less than the haploid number of chromosomes and the data (table 6) do not justify the conclusion that any of them is rare. Moreover the 9 types are quite distinct in character and only 1 of the 6 types tested gave trisomic ratios for dwarf. As will be noted later, 2 of them have occurred as mutants in the progeny of other trisomics but in each case the mutant type showed no special resemblance to the parent and belonged to another type previously recognized in the F_1 from triploid×diploid. Moreover there is some cytological evidence to suggest that these mutations resulted from

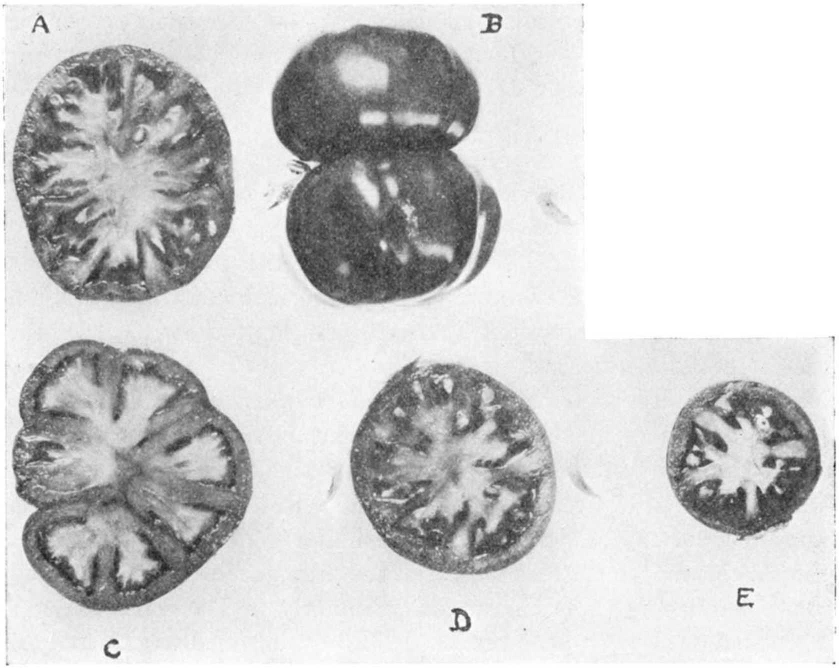

FIGURE 24.—Fruits of non-hybrids (Dwarf Aristocrat). B, triplo-C; transverse sections; A, triplo-C; C, triplo-A; D, diploid; E, triplo-D.

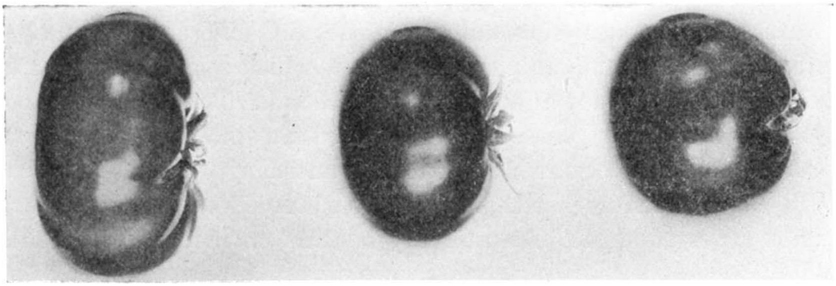

FIGURE 25.—Fruits of non-hybrids (Dwarf Aristocrat). Triplo-G (left); diploid (centre); triplo-D (right).

lagging of members of a normal chromosome pair. On the other hand one plant (figure 17) in the non-hybrid F_1, containing 1 apparently whole extra chromosome, although distinct, resembled triplo-I very closely. Whether this represents another primary type or whether it is a secondary or merely a result of gene mutation cannot as yet be stated. That chromosome fragmentation occurs is shown by the discovery by M. M. LESLEY (unpublished data) of a plant in the non-hybrid F_1 containing 1 whole extra chromosome and an additional fragment, and of other fragment-containing plants in the progeny of trisomics.

It is concluded that the characteristics of each of the 9 simple-trisomic types of tomato are due to the presence of a whole extra chromosome and it is inferred that at least 9 of the 12 chromosomes are different in effect. The fact that no simple-trisomic type has been found which is identical with the diploid, is consistent with the assumption that all of the 12 chromosomes are different.

In haplo-IV and in triplo-IV *Drosophila melanogaster*, BRIDGES (1921) observed a change in the grade of mutant characters due to the IV-chromosome genes, demonstrating clearly the relation between these characters and this particular chromosome. But he also found a change in the grade of mutant characters, the major genes for which were not in the IV-chromosome. This indicated the presence in the IV-chromosome of genes modifying these characters. Similarly in Datura, a single gene difference determines purple and white flower color but BLAKESLEE (1921a) found that in a homozygous purple race, the intensity of color differed widely in the trisomic mutants. Thus Glossy was darker and Cocklebur lighter than the normal. Since neither of these types proved to contain the extra chromosome with the major gene for purple color, the differences indicate the presence of modifying genes in different chromosomes. BRIDGES (1922) has advanced a hypothesis which appears to harmonize admirably with the known facts relating to the distribution and number of major and modifying genes. According to that author, a change in the grade of a character occurs if the extra chromosome present is unbalanced for the genes affecting that character. Now an outstanding feature of the trisomic types of tomato is that many of their distinctive characteristics strongly suggest those which are known to depend on gene differences. Thus the almost entire leaflets of the triplo-H suggest the potato-leaf character, which is a simple recessive to cut leaf. The pale green color of triplo-F is suggestive of the "yellow" foliage character, which according to PRICE and DRINKARD (1908) is a simple recessive to "green" in certain varietal crosses. Differences in number of loculi in the fruit similar to those seen in triplo-D and triplo-C have been shown by PRICE and DRINKARD (1908) and by WARREN (1924) to depend on gene differences. Compared with the diploid, fruit size is smaller in triplo-D and probably larger in triplo-A. According to LINDSTROM (1926), the evidence clearly indicates that hereditary factors for fruit size and fruit color depend on the same chromosomal mechanism.

Just such a similarity between the effects due to gene mutations and to the presence of extra chromosomes is to be expected according to BRIDGES' hypothesis of gene balance. Moreover, in tomato, a change in the grade of a given characteristic commonly occurs in more than one trisomic type, and in some cases the change is in opposite directions. For example triplo-H tends to have leaflets more nearly entire and triplo-D more dissected than the diploid. Triplo-F is paler green, and triplo-E darker green than the diploid. Triplo-D has fewer loculi in the fruit and triplo-C more than the diploid. This is in accordance with the known fact that number of loculi is not dependent on a single gene pair. Probably this is also true of foliage color and shape of leaflets. Where other evidence suggests that the number of genes influencing a characteristic is relatively small, it is simpler to suppose that the change of grade is due to the presence in the extra chromosome of a single gene influencing the grade of that character. In the case of fruit size, however, which undoubtedly depends on a large number of genes, BRIDGES' conception of gene balance is especially appropriate. Thus the small fruit size of triplo-D may well be due to an excess of modifiers in the minus direction in the internal gene balance of the D-chromosome.

Little is known of the genetic basis of growth rate but it is probably not genetically simple. Since trisomic types differ in rate of growth, it appears that the internal balance of genes affecting growth differs in different chromosomes. Thus the fact that triplo-B is nearer to the diploid in growth rate than triplo-D suggests that the internal balance of genes affecting growth is nearer to the normal (diploid) in the B-chromosome than in the D-chromosome. It seems to be a general rule, to which the tomato conforms, that *no* trisomic type is quicker-growing than the diploid, as if unbalance of chromosome number were never associated with acceleration of growth. In terms of + and − modifiers there is not an excess of plus modifiers in any of the chromosomes. Hence if genes affecting growth are involved, they cannot be adequately classified merely as + and − modifiers but must have more complex relations, perhaps of a complementary nature.

Attention has already been called to the very abnormal development of certain plants, probably double trisomics, which were termed "runts," and to the perfect development of other plants, probably triple trisomics. Clearly these facts cannot be explained on the basis of unbalance in chromosome number. According to BRIDGES' theory of gene balance, however, 2 extra chromosomes with a gene unbalance of the same kind would cause a greater disturbance than 3 extra chromosomes which tend to neutralize one another.

That some attributes of trisomics differ from any gene mutation known in tomato may mean that such mutations have not occurred or have not been preserved. It is possible that some effects due to extra chromosomes, such as curling of foliage and extreme imperfection of development, may not be attainable by any combination of genes in a diploid plant.

FREQUENCY DISTRIBUTION OF OCCURRENCE OF TRISOMIC TYPES

The frequency distribution of the simple trisomic types is shown in table 6. The data do not suggest the great predominance of any one type, and and the absence of three expected types is not surprising considering the small number of plants. Triplo-D, one of the least vigorous types, occurred most frequently, and triplo-H, which is probably one of the more vigorous, occurred least frequently. The chromosome number was not determined in every individual but in all determined cases without exception the same plant type was found to have the same number of chromosomes.

TABLE 6

Frequency of occurrence of simple-trisomic types in triploid×diploid F_1.

	TRIPLO-									TOTAL NUMBER OF F_1 PLANTS
	A	B	C	D	E	F	G	H	I	
Frequencies observed	5	4	5	6	4	3	5	1	3	91

The far more complete data of BLAKESLEE (1924) show that in the progeny of triploid Datura, the simple-trisomic types Echinus and Rolled occur less commonly than Globe and Buckling. In Oenothera DE VRIES and BOEDIJN (1924) found that *cana* occurred more often than *lata* among the 15-chromosome progeny of semigigas (triploid)×*velutina* (diploid). As already noted the 10 double- and 2 triple-trisomic tomato plants belonged to as many distinct types.

TRANSMISSION OF EXTRA CHROMOSOMES

If the extra chromosome of a simple trisomic is distributed to half of the gametes in meiosis, with equal viability of gametes and zygotes and with random mating, a simple-trisomic plant, if fertile, on selfing would give 25 percent simple-tetrasomic, 50 percent simple-trisomic and 25 percent diploid progeny; on backcrossing to a diploid, 50 percent simple trisomics and 50 percent diploids would result. That this expectation was not fulfilled is shown by the data from selfing and backcrossing six of the trisomic types shown in table 7.

Several reasons may be suggested for the failure of trisomic plants to transmit the extra chromosomes through the pollen to the full extent. In the pollen mother cells of a simple trisomic the frequent lagging of the unpaired chromosome and the presence of microcytes show that less than half the microspores of the tetrads contain the extra chromosome. But microcyte formation alone does not account for the deficiency in pollen transmission. For triplo-A, which failed entirely to transmit the extra chromosome through the pollen (table 7), had only 4.5 percent of tetrads containing microcytes (table 3), and triplo-B, which gave 23 percent pollen

TABLE 7

Transmission of extra chromosomes by trisomic parents.

	POPULATION NUMBER	NUMBER OF PLANTS	GERMINATION PERCENT	PERCENT TRIPLO-					
				A	B	C	D	E	F
Triplo-A hybrid selfed	25.063	47		23					
Triplo-A hybrid×diploid	25.065	88		24				1	
Do.	26.046	72	80	25					
Triplo-A hybrid×Dwarf Champion diploid	25.064	89		18					
Do.	26.047	67	81	33					
Diploid×triplo-A hybrid	25.062	43	80						
Triplo-B hybrid×diploid	26.050	83	93		27				
Diploid×triplo-B hybrid	26.049	90	100		23	1			
Triplo-B hybrid selfed	26.059	92	96		37				
Triplo-C non-hybrid selfed	26.052	61	67			7			
Triplo-C hybrid selfed	25.075	31				26			
Do.	26.056	54	75			20			
Diploid×triplo-C non-hybrid	26.053	52	84			10			
Triplo-D non-hybrid selfed	26.051	64	73				29		
Triplo-E non-hybrid selfed	25.074	33							
Do.	26.048	70	89					16	
Triplo-E hybrid selfed	25.072	53						21	
Do.	26.057	24	89					17	
Triplo-DF hybrid selfed	26.055	34	57				9		24
Triplo-C?×diploid	25.073				18				

transmission, had a *greater* proportion of tetrads containing microcytes than triplo-A. The pollen sterility of all trisomic types probably contributes to the low pollen transmission. Since the unbalance in chromosome number of 13-chromosome pollen is as great as that of a simple-tetrasomic plant, the proportion of inviable grains is probably greater among 13-chromosome than among 12-chromosome grains. Triplo-B had fewer "bad" pollen grains than triplo-A or triplo-C and correspondingly transmitted the extra chromosome more readily through the pollen. Triplo-C had less "bad" pollen than triplo-A and higher pollen transmission. Another possible cause of defective pollen transmission is competition between the pollen tubes. Thus BUCHHOLZ and BLAKESLEE (1922) found that, in the Globe mutant of Datura, tubes from pollen with the extra chromosome are slower-growing than those of normal pollen. Consequently the application of an excess of pollen may lead to selective fertilization.

While spore sterility may thus account for defective pollen transmission, it probably does not account for defective transmission through the eggs. BUCHHOLZ and BLAKESLEE (1922) found a larger proportion of aborted ovules from Globe×normal than from normal×normal. Some of these ovules apparently were fertilized and had suffered in competition for food with diploids. In tomato the relatively small number of viable seeds in the fruit of triploids and of trisomic types suggests that the small inviable seeds are those with extra chromosomes. Such zygotic sterility may well account for the deficiency of ovule transmission.

The frequency of transmission of the extra chromosome varied considerably in progenies of similar origin. Thus 26.048 (table 7), the progeny of triplo-E selfed, contained 16 percent, but 25.074, a small population from different seed of the same parentage, contained no trisomic plants. It should be mentioned that these 2 progenies were grown under somewhat different cultural conditions. Again 26.052, from non-hybrid triplo-C selfed, contained 7 percent trisomics, but 26.056 and 25.075, from hybrid triplo-C selfed and from the same seed sample, contained respectively 20 percent and 26 percent triplo-C. These data suggest that the hybrid triplo-C parent transmits the extra chromosome somewhat more readily than the non-hybrid. This may be due in part to the superior germination of the hybrid seed (26.056) compared with the non-hybrid (26.052). According to FROST (1919) it is probable that with the mutant forms of Matthiola, higher frequency of transmission of the extra chromosome is associated with higher percentage of seed germination within the same non-hybrid race.

The frequency of transmission seems to differ significantly in different trisomic types. In hybrids, it ranged from 37 percent from selfing in triplo-B to 20 percent in triplo-C and in non-hybrids from 29 percent in triplo-D to 7 percent in triplo-C. In Matthiola, FROST and MANN (1924) report that in selfing 4 different mutant types, the frequency of transmission by non-hybrids has varied from 25 to 50 percent; later results (FROST, unpublished data) suggest that F_1 hybrid forms tend to give a higher frequency than non-hybrid forms of the same mutant types.

In Datura, the frequency of transmission of the extra chromosome was found to be much lower through the pollen than through the eggs. Thus BLAKESLEE (1921b) reports that the Globe mutant gave about 25 percent transmission through the eggs but only about 3 percent through the pollen. Again CLAUSEN and GOODSPEED (1924) found 35.5 percent of ovule transmission but only 3.4 percent of pollen transmission of the trisomic form "Enlarged" of *Nicotiana tabacum*. In Matthiola on the other hand, FROST and MANN (1924) report that the chromosome or chromosome fragment present in the mutant Slender has been transmitted to nearly 20 percent of the progeny through the pollen. In tomato there seems to be little or no transmission of the extra chromosome through the pollen of triplo-A. For, a small population from diploid×triplo-A contained no trisomic plants and the percentage of trisomics in the progeny of triplo-A hybrid selfed was practically the same as that of triplo-A hybrid×diploids. On the other hand triplo-C transmitted the extra chromosome through the pollen to 10 percent of its progeny. A striking contrast with the results from Datura and Nicotiana was found in the case of triplo-B. Diploid×triplo-B hybrid (26.049, table 7) gave 23 percent triplo-B. The relatively little pollen sterility compared with other simple trisomic types of tomato and the relatively high seed germination in 26.049 are both likely to favour high frequency of transmission. When used as seed parent the same hybrid trisomic gave 27 percent triplo-B or only slightly more than when used as pollen parent. When selfed this plant gave 37 percent triplo-B, which agrees fairly closely with the expectation assuming independence of the processes of transmission through eggs and pollen.

Defective transmission of the extra chromosome, especially through the pollen accounts in part for the scarcity of tetrasomics. Furthermore tetrasomic zygotes are likely to be even less vigorous than trisomics and less able to survive competition with more balanced zygotes. No tetrasomic plants have been found in the progeny from selfing of triplo-A, triplo-C or triplo-E. From the high percentage of pollen transmission in triplo-B, tetrasomics might be expected in its progeny from selfing. Two remarkably slow-growing plants originated in that way. One of these failed to develop a normal shoot but several adventitious buds developed on the leaves and the flowers resembled triplo-B. Several fruits set from self-pollination. The other plant was normal in development but also far slower-growing than its trisomic sibs. Similarly in the progeny of triplo-D selfed, a single "runt" appeared. The chromosome number of these plants has not yet been determined but they are most probably tetrasomics.

MUTATIONS

No chromosomal mutations other than triploids have been observed by the writer in commercial plantings or in the progeny of plants which were known to be diploid. Two mutant trisomics have occurred, however, in the progeny of trisomic plants. One population (25.065, table 7) from triplo-A hybrid×diploid Dwarf Aristocrat contained 63 diploid, 24 triploid-A and in addition 1 triplo-E plant which must be considered as a mutant. A single mutant plant of triplo-C occurred among the progeny of diploid Dwarf Aristocrat×triplo-B hybrid (26.049, table 7). In simple trisomics the occasional presence of supernumerary laggards in the pollen mother cells points to irregular behavior of a normal pair of chromosomes and not merely of the extra chromosome. In diploids the occurrence of microcytes in the tetrads also suggests irregularities of chromosome distribution. As these irregularities seem to be more frequent in trisomics than in diploids, on the whole it is probable that the mutants resulted from a disturbance of maturation division in the trisomic parents. Since trisomic mutants tend to be unfruitful, some of the "he" plants or "fruitless hybrids" of the tomato grower may be of this nature. Since, however, these mutants have not been observed in the progeny of diploids and are likely to be crowded out in the seedbed probably the "he" plants are usually either triploids or the result of other causes such as mosaic disease.

TRISOMIC INHERITANCE AND LINKAGE

A modification of the Mendelian ratios should occur on breeding from a trisomic plant which is heterozygous for genes whose loci are in the extra chromosomes present. BLAKESLEE and FARNHAM (1923) have shown that the Poinsettia mutant of Datura gives trisomic ratios for flower color, and they conclude that the extra chromosome present contains the locus of the allelomorphic genes which determine purple or white flowers.

Trisomic inheritance of the dwarf character in the tomato has been reported by the present writer (1926). The A-chromosome was found to contain the locus of the genes which determine standard and dwarf. As table 8 shows, 5 other simple-trisomic types heterozygous for the standard-dwarf pair of genes have given apparent disomic ratios for dwarf and standard in accordance with expectation. This is also true of the progeny of C86-8 which belongs to a simple-trisomic type not identified.

Triplo-B, triplo-C and triplo-E hybrids and C86–8, all heterozygous for the pair of genes for cut-leaf and potato-leaf, gave disomic ratios for this pair of characters.

The non-yellow skin color of the fruit is due to the recessive member of a single pair of genes *Yy*. When flesh color is red, *yy* plants have crimson and *Yy* or *YY* plants scarlet fruit. Triplo-A plants gave approximately disomic ratios for skin color, which is in accordance with expectation, since dwarf and non-yellow skin depend on genes which are not linked. The data from other simple- or double-trisomic plants heterozygous for skin-color genes indicate that the locus of this pair of allelomorphs is probably not in the B, C,D, E or F chromosomes, since the ratios among the diploid progeny appear nearer to 3:1 than to the 8:1 ratio which would occur in trisomic inheritance.

A study of the combination of characteristics present in the simple-trisomic types may throw light on the distribution of the genes in the different chromosomes. The simplest case is that in which certain characteristics are peculiar to one only of the simple-trisomic types. For those characteristics, if due to genes, must depend either on a single gene or on linked genes present in that particular chromosome. From the preceding account of the trisomic types, however, it is evident that a change in the grade of a characteristic is usually not confined to one trisomic type. In tomato the I-chromosome probably contains genes which modify flesh color of fruit. Since triplo-I has nearly entire leaves, it may be inferred that, in this case, flesh color of fruit and leaf shape depend on the same gene or on genes which are linked. Again the characteristics of triplo-D suggest that certain genes for size and number of loculi in the fruit are linked. From breeding and correlation studies LINDSTROM (1926) has found evidence of linkage between the genes for dwarf habit and fruit size. Since the A-chromosome contains the locus of the gene for dwarf, triplo-A should accordingly differ from the diploid in size of fruit. The few fruits observed seemed to be distinctly larger than the diploid but more data are required to establish this. The relatively small size of seedless fruits and of the few-seeded fruits regularly produced by the

Table 8[6]

Inheritance of habit, leaf form and skin color of fruit.
(D = standard, d = dwarf habit; C = cut, c = potato leaf; Y = yellow, y = non-yellow skin of fruit.)

	HABIT AND LEAF FORM								SKIN COLOR OF FRUIT				THEORETICAL MONOHYBRID RATIOS				
													Disomic inheritance	Trisomic inheritance			
	Diploid progeny				Trisomic progeny				Diploid progeny		Trisomic progeny		Diploid and trisomic progeny	Diploid progeny		Trismoic progeny	
	DC	*Dc*	*dC*	*dc*	*DC*	*Dc*	*dC*	*dc*	*Y*	*y*	*Y*	*y*	*D*:*d*, *C*:*c* or *Y*:*y*	*D*:*d*	*C*:*c* *Y*:*y*	*D*:*d*	*C*:*c* *Y*:*y*
Triplo-A hybrid selfed	60		56		8		3		17	11			3:1	5:4	8:1	7:2	all dominants
Diploid×triplo-A hybrid	13		30						18	18			1:1	1:2	2:1	2:1	do
Triplo-B hybrid selfed	54	7	17	7	15	9	6	5	54	11	5	1	3:1	5:4	8:1	7:2	do
Triplo-B hybrid×diploid	37		24		15		7						1:1	1:2	2:1	2:1	do
Diploid×triplo-B hybrid	37		32		6		15						1:1	1:2	2:1	2:1	do
Triplo-C hybrid selfed	35	19	12	9	7	3	4		40	14			3:1	5:4	8:1	7:2	do
Triplo-E hybrid selfed	41	11	14	8	10	2	1		29	11			3:1	5:4	8:1	7:2	do
Triplo-DF hybrid selfed	17		5		11		1		14	8			3:1	5:4	8:1	7:2	do
Simple trisomic hybrids of unknown type: C86-2 selfed	38	9	9	5	5	2			26	13			3:1	5:4	8:1	7:2	do
C86-7 selfed	23	13	7	4					19	7			3:1	5:4	8:1	7:2	do
C86-8 selfed	33	9	7	7	5	2	2	2	42	12			3:1	5:4	8:1	7:2	do

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[6] The writer is indebted to Mr. C. W. Haney, Division of Genetics, University of California, for part of the observations contained in this table.

triploid, point to some degree of correlation between fruit size and seed production in tomato. If so, comparison of fruit size between trisomic types with few seeds such as non-hybrid triplo-A and the diploid is more difficult. CRANE (1915) has found some evidence of linkage between the genes for simple inflorescence and short, that is, oblate, fruit. MACARTHUR (1926) has shown that simple inflorescence and dwarf are linked. Hence triplo-A, which contains the locus of dwarf, should also contain factors modifying length of fruit. The scanty data available (table 4) suggest that this is in fact the case, since in triplo-A, ED/L is 1.44 as compared with 1.25 in the diploid. LINDSTROM (1926) has found good evidence of linkage between *Yy*, the genes for skin color of fruit, and certain major factors determining size of fruit. Hence the simple-trisomic type with the extra chromosome containing the locus of *Yy* should also contain major genes affecting fruit size. As noted above a type giving trisomic ratios for skin color of fruit has not yet been found.

CONCLUSION

The present paper represents only a beginning of the analysis of the progeny of triploid tomatoes. In particular much more light can be thrown on the composition of the individual chromosomes by a more detailed study of the types and by hybridization. The occurrence of chromosome fragmentation is of special interest and may also throw light on the distribution of the genes and on the problems of size and number of chromosomes.

The foregoing data appear to be wholly consistent with the chromosome theory of heredity. In infectious disease certain conditions, defined by ROBERT KOCH in 1882, are required to prove the causal nature of the infecting organism. A rather close analogy may be drawn between such a pathogenic organism and a chromosome. Extra chromosomes occurred invariably and exclusively in plants with certain variant characters, thus conforming to two of the famous canons. As in the case of obligate parasites the chromosomes have not been grown in culture apart from the host as the third canon requires, but they are transmitted to the progeny and reproduce identical symptoms. The simplest conclusion is that the relation between the extra chromosome and the characteristics of a trisomic plant is causal. To hypothecate an unknown underlying cause of which an extra chromosome is merely a symptom would seem to be gratuitous.

The occurrence of trisomic ratios in the progeny of a hybrid trisomic tomato plant is a further confirmation of the association between chromosome and gene. Evidently in the tomato unbalance in terms of chromosome number is an important factor influencing growth and viability. The effects of extra chromosomes on development are such as might result from differences in internal gene balance in different chromosomes, as defined by Bridges, and at present the most reasonable hypothesis is that certain of the effects associated with the presence of extra chromosomes are due to a change in the balance of the genes.

The visible effects caused by a single whole extra chromosome are in some cases small compared with those due to single gene differences. For example the effect of the E-chromosome in triplo-E is less striking than that of the gene causing potato leaf. On the other hand the effect of the D-chromosome in triplo-D is probably greater than that of certain genes. Indeed from its appearance, triplo-D would readily pass as a distinct variety, but owing to its partial sterility and genetic inconstancy, so characteristic of trisomic types, it can scarcely be of importance in the evolution of new varieties.

SUMMARY

1. Triploid plants have been found in 3 varieties of tomato. They probably originated from the fusion of diploid and haploid gametes.
2. In the F_1 from triploid×diploid, chromosome number did not have a binomial distribution but ranged from 24, the diploid somatic number, to 27, with the mode at 25 chromosomes. Degree of unbalance in chromosome number is therefore an important factor influencing viability.
3. The smaller seeds from triploid×diploid gave more 26- and 27-chromosome plants than the larger seeds.
4. From diploid×triploid, only 2 plants were obtained, both of which were diploid.
5. In meiosis in the pollen mother cells of a simple trisomic, the unpaired chromosome is not constant in its behavior. At diakinesis it may either form a trisome or lie separate. It frequently lags in the first and second anaphase. In the heterotype division it may undergo either assortment or division, more often the former. Correspondingly in the homotype division either division or assortment takes place, and probably assortment requires more time than completion of the process of division.
6. The proportion of tetrads containing microcytes varied from 4.5 percent to 7.6 percent in different simple-trisomic types. The presence of micronuclei at interkinesis in the pollen mother cells suggests that microcyte formation sometimes begins at that stage.

7. In general, compared with the diploid, simple-trisomic types are slower-growing and have a greater tendency to pollen sterility and unfruitfulness in the field. These differences are accentuated in double- and triple-trisomic types.

8. From the haploid number of chromosomes, 12 different simple-trisomic types are expected. Of these, 9 have been identified. At least 9 of the 12 chromosomes of the haploid set are therefore different in their effect on development.

9. The 9 simple-trisomic types are "primaries" in the terminology proposed by BLAKESLEE and are due to the presence of a whole extra chromosome of the normal set. Types containing fragments also occur.

10. No variation in chromosome number was found among individuals of the same type, when examined, they invariably proved to have the same number of chromosomes except in the case of tetraploid islands (p. 4).

11. Each of the simple-trisomic types has a distinctive combination of characteristics. In several cases two or more types differ from the diploid in the same characteristic but to a different degree and in different directions.

12. The double- and triple-trisomic types have, in some cases, combinations of the characteristics of simple-trisomic types.

13. Some of the effects of an extra chromosome are due to modifying genes present in it. Where the number of genes affecting a characteristic is large, the effects of an extra chromosome are probably the result of an internal gene balance of the extra chromosome, different from that of the normal chromosome complement.

14. Certain double trisomics are more abnormal in development than certain triple trisomics. Two extra chromosomes with an internal gene balance in the same direction may cause a greater disturbance of development than three extra chromosomes which tend to neutralize one another.

15. Among 35 simple-trisomic plants of 9 different types, no type predominated greatly in number of individuals.

16. The extra chromosome is transmitted to less than the expected proportion of the progeny. The observed proportion from selfing varied with different extra chromosomes. In two simple trisomic types the extra chromosome was transmitted through the pollen almost as frequently as through the eggs. Defective transmission through the pollen is in part due to irregularities in sporogenesis and in part perhaps to pollen sterility and selective fertilization. Defective transmission through the eggs is probably due, in part, to zygote sterility.

17. Tetrasomics probably occur, although rarely, in the progeny of certain simple trisomics.

18. Simple-trisomic types sometimes occur as mutants. In pollen mother cells of trisomics the occasional lagging of members of a normal pair and the occasional presence of microcytes in the tetrads of a diploid suggest how these mutants may arise.

19. Trisomic inheritance of the dwarf character has been found and the simple-trisomic type whose extra chromosome contains the locus of dwarf has been identified.

20. Evidence of linkage between genes may be obtained from a knowledge of the combinations of characteristics occurring in simple-trisomic types, especially when this information is supplemented by results of correlation studies and breeding experiments.

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