

THE CYTOLOGY OF TRIPLOID AND TETRAPLOID
LYCOPERSICON ESCULENTUM.

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INTRODUCTION.

THE study of chromosome behaviour in the tetraploid tomato has resulted in a conflict of opinion.

In a recent account Humphrey (1934) states that at diplotene in the tetraploid *Lycopersicon esculentum* "the chromosomes usually appear as tetrasomes, but become separated into disomes at diakinesis and metaphase". On the other hand Kostoff and Kendall (1934) find that "in some cases the number of tetravalent chromosomes appears to be increased during metaphase". These statements not only conflict with one another; they also conflict with all previous accounts of chromosome association at meiosis in tetraploids as well as in diploids, and the theory of association by chiasmata which rests on these accounts. Moreover, Humphrey's account is irreconcilable with genetical results in the tomato. I therefore thought it worth while to undertake a re-examination of the tetraploid and compare it with the triploid, since material of both was available.

MATERIAL AND METHODS.

I am indebted to Dr F. W. Sansome of this Institution for providing me with both triploid and tetraploid material. The triploid plants arose from tetraploid \times diploid crosses and the tetraploids were F_2 plants from somatically doubled diploids, the parents differing by one or two factors only (Sansome, 1931). This material was therefore not completely homozygous, as was Humphrey's, who obtained the diploid from the haploid and the tetraploid from the diploid by somatic doubling. It is improbable, however, that such slight heterozygosity would be sufficient to cause an appreciable diminution in chiasma frequency.

The material was fixed during September 1934, buds being taken from different plants and smeared separately. I could detect no difference in chromosome behaviour between any of the triploids or any of the tetraploids. The smears were fixed in 2BE (La Cour, 1931) and stained

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by the gentian-violet iodine method. Smearing was somewhat difficult, as the anthers at the time of meiosis are rather small and the cells are apt to stick together in lumps. Nevertheless it was possible to get satisfactory results by staining for a short time (4-5 min.) and differentiating rapidly. Root tips were fixed in medium Flemming and cut at 8μ . Drawings were made by camera lucida and a Zeiss 2 mm. oil immersion objective with a $30\times$ compensating ocular. All the figures are $\times 4000$ reduced from $\times 5000$, except the photographs which were taken at $\times 3000$ and reduced to $\times 2400$.

MITOSIS.

The triploid plants had 36 and the tetraploid 48 chromosomes, as would be expected (Fig. 1). No aneuploidy was observed in any of the plants examined.



Fig. 1. Mitotic metaphases of the triploid (left) and tetraploid (right) *Lycopersicum esculentum*. $\times 4000$.

Since only material fixed in medium Flemming was available, the morphology of the chromosome complement was difficult to make out accurately. The chromosomes vary slightly in length and have median or submedian attachment constrictions. Two individual chromosomes only can be distinguished from the rest of the complement. One of these has two relatively large trabants attached terminally to the short arm. The other is longer, with a secondary constriction in the long arm. Both these types have been observed before (Darlington, 1932; Afify, 1933), and each occurs three times in the triploid and four times in the tetraploid.

THE FIRST MEIOTIC DIVISION.

Twenty cells of the diploid were analysed for comparative purposes. At diakinesis 34.2 per cent. of the bivalents have one chiasma and 65.8 per cent. have two, almost all of which are terminalised.

Observations of complete nuclei were confined to diakinesis and

metaphase in the triploid and to diakinesis alone in the tetraploid. I found it impossible to analyse a sufficient number of metaphases in the tetraploid to be statistically valuable, for the plates are very dense and the number of chromosomes high. In the triploid, the high percentage of univalents lying off the plate and the frequent occurrence of trivalents,

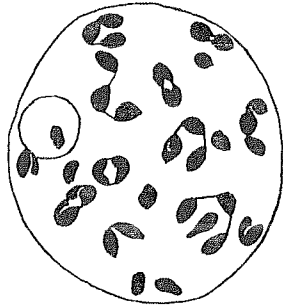


Fig. 2. Diakinesis in the triploid, showing five trivalents, seven bivalents and seven univalents. Three chromosomes, a bivalent and a univalent, are associated with the nucleolus. $\times 4000$.

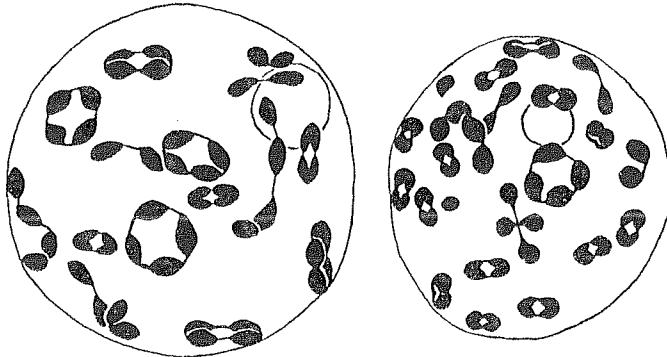


Fig. 3. Two cells of the tetraploid at diakinesis. Left, eight quadrivalents and eight bivalents. Two bivalents are associated with the nucleolus. Right, three quadrivalents, seventeen bivalents and two univalents. $\times 4000$.

as well as the smaller number of chromosomes, makes the metaphase plates less crowded and correspondingly easier to analyse.

At the diplotene stage, which I did not analyse statistically, the chromosomes are less contracted than at diakinesis and stain less deeply. The chiasmata are not yet terminalised.

At diakinesis (Figs. 2 and 3) terminalisation is usually complete, both in the triploid and the tetraploid. The chromosomes show the distribution typical of this stage, in which the majority arrange themselves

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on the surface of the nucleus, with the remainder distributed in the interior. This arrangement has given rise to the hypothesis that every chromosome repels every other chromosome, and that movements generated by this repulsion are limited by the surface of the nucleus and the occurrence of chiasmata. When equilibrium is reached, the configurations, whether univalent, bivalent, trivalent or quadrivalent, are nearly equidistant from one another. (This is not evident from a two-dimensional drawing.)

In the triploid there are three, in the tetraploid four chromosomes associated with the nucleolus. Owing to the small size of the chromosomes relative to the nucleolus, which stains rather deeply, I find it im-



Fig. 4. Side view of metaphase in the triploid, with eight trivalents, four bivalents and four univalents. Configurations drawn separately. Each configuration has two chiasmata. $\times 4000$.

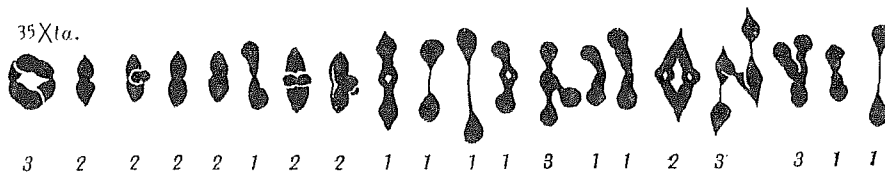


Fig. 5. Side view of metaphase in the tetraploid showing four quadrivalents and sixteen bivalents. The number of chiasmata is given beneath each configuration. $\times 4000$.

possible to determine whether these chromosomes are actually attached or not, except in rare cases (Fig. 2) when the chromosomes happen to lie at the side of the nucleolus. In cells less favourable than these, the fact that the chromosomes lie in close proximity to the nucleolus, either immediately above or immediately below, suggests that they are connected. This association is not invariable (Fig. 3, right) since one or more chromosomes may have broken free and been repelled at a slightly earlier stage than usual.

A further slight contraction of the chromosomes takes place after diakinesis, as the nucleolus disappears and the chromosomes arrange themselves on the metaphase plate (Figs. 4 and 5). Very little movement of chiasmata occurs since nearly all are already terminalised. Occasionally interstitial chiasmata persist to metaphase (Fig. 5).

Univalents, where they occur, lie off the plate; hence in the triploid, where they are frequent, side views of metaphase are much less compact and dense than those of the tetraploid.

For the determination of chiasma frequency at metaphase, side views were exclusively used, for only in these views can the configurations be accurately made out. In polar views (Fig. 6) it is impossible to distinguish between bivalents with one and those with two chiasmata.

In an organism with completely terminalised chiasmata, the number of different configurations possible is restricted. Darlington (1931) gives a diagram (Fig. 7) showing the twenty types of configuration possible in a tetraploid having complete terminalisation. Of the multivalents, types 7–10 are possible in a triploid. All these except type 10 have been found to occur in triploid *Lycopersicum* (Fig. 8). Similar trivalents also occur in the tetraploid (Fig. 9) but only rarely (Table VI).

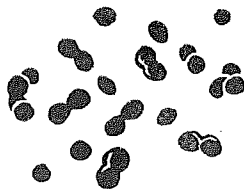


Fig. 6. Polar view of metaphase in the tetraploid, showing eight quadrivalents and eight bivalents. $\times 4000$.

Of the quadrivalents (types 11–20) all but two (types 19 and 20) were found at diakinesis (Fig. 10 A). At metaphase only six could be identified (Fig. 10 B). The two remaining types (16 and 18) might be expected to look like two bivalents if they were orientated normally and would be difficult to distinguish on a crowded plate.

MULTIVALENT ASSOCIATION OF CHROMOSOMES.

On the assumption that association at pachytene is in pairs, we must expect to find univalents much more frequently in the triploid than in the tetraploid, since whereas in the tetraploid two bivalents can be formed by the association of two pairs of threads along their entire length, with a chiasma between each pair, a similar association in the triploid would give rise to a bivalent and a univalent. The number of trivalents per cell in the triploid, on the other hand, would be expected to be greater than the number of quadrivalents per cell in the tetraploid, assuming the chiasma frequency to be approximately the same, since fewer chiasmata are required for the formation of trivalents. On the assumption of random distribution of chiasmata we should expect the number of multivalents

Configurations of chromosomes possible in tetraploid with only terminal chiasmata

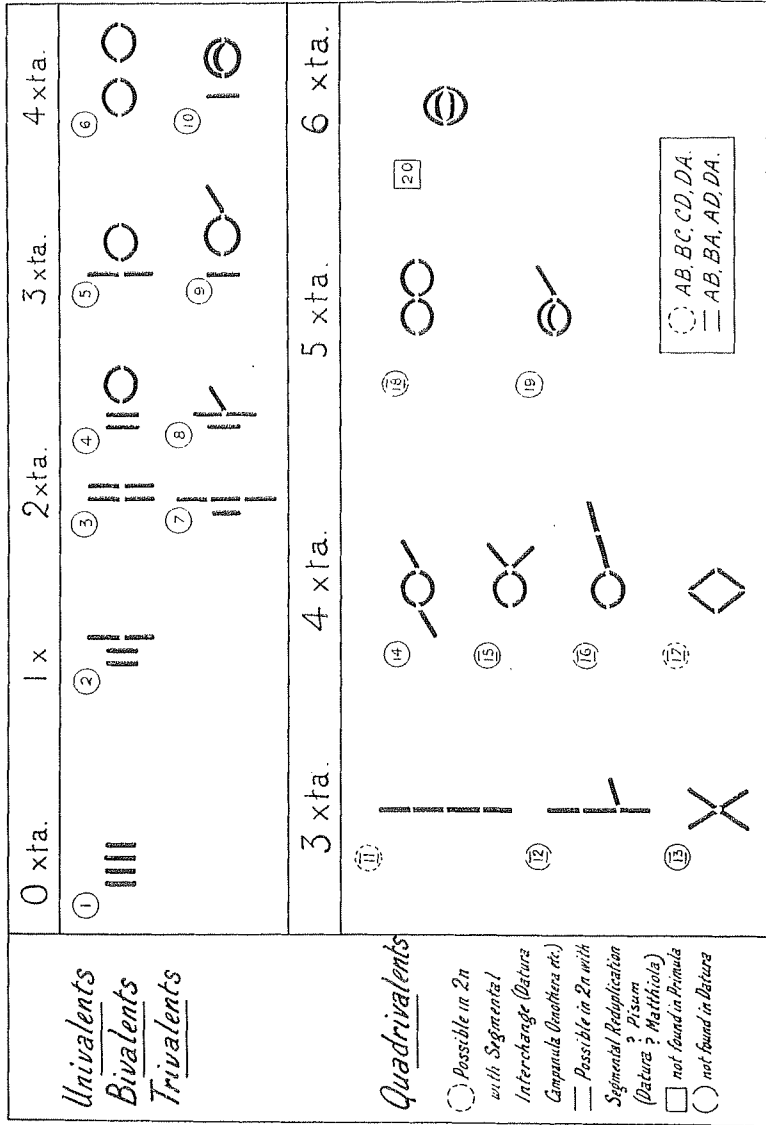


Fig. 7. Diagram showing configurations of chromosomes possible in a tetraploid with only terminal chiasmata. Certain of these associations of four are possible in diploid structural hybrids. Xta. = chiasmata. The numbers given are those necessary for the formation of the different types of association. Types 10, 19 and 20 have been found in *Lycopersicum esculentum* (from Darlington, 1931).

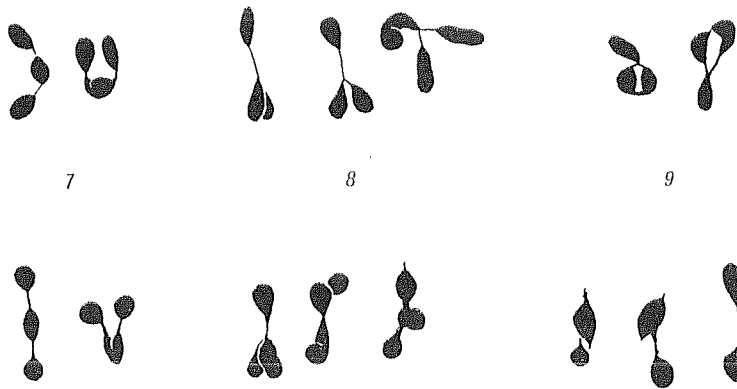


Fig. 8. Types of trivalent found in the triploid, numbered according to the preceding diagram. Above, diakinesis. Below, metaphase, showing different orientations upon the plate. $\times 4000$.



Fig. 9. Trivalents in the tetraploid. The first two at diakinesis, the last three at metaphase. $\times 4000$.

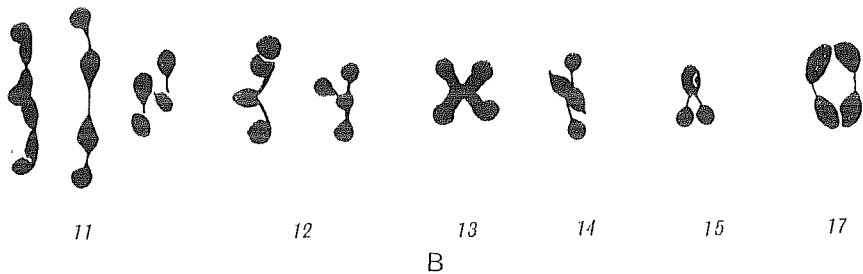
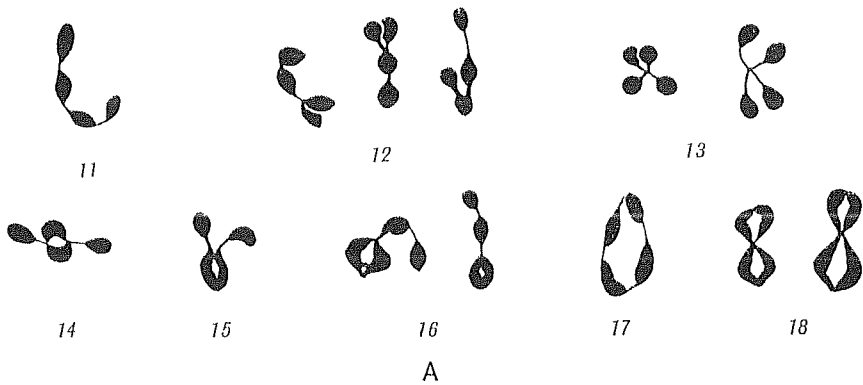


Fig. 10. Types of quadrivalent found in the tetraploid, numbered according to the diagram. A, diakinesis; B, metaphase. $\times 4000$.

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to vary from cell to cell, but to remain statistically constant at successive stages.

We find that these predictions are justified. Fifty cells of the triploid contain 365 univalents (Table I) as compared with 28 in the tetraploid

TABLE I.

Triploid. Fifty cells at diakinesis and metaphase.

	Univalents	Bivalents	Trivalents	Total Xta.
0 Xma.	356	—	—	—
1 Xma.	—	155	—	155
2 Xta.	—	195	221	832
3 Xta.	—	—	27	71
Total	356	350	248	1068
Total chromosomes	356	700	744	1800
$\frac{1}{2}$ Xta. per chromosome	—	—	—	1.19

TABLE II.

Tetraploid. Fifty cells at diakinesis.

	Uni- valents	Bi- valents	Tri- valents	Quadri- valents	Total Xta.
0 Xma.	28	—	—	—	—
1 Xma.	—	404	—	—	404
2 Xta.	—	390	3	—	786
3 Xta.	—	—	1	83	252
4 Xta.	—	—	—	110	440
Total	28	794	4	193	1882
Total chromosomes	28	1588	12	772	2400
$\frac{1}{2}$ Xta. per chromosome	—	—	—	—	1.57

TABLE III.

Numbers of multivalents per cell.

Triploid.										
No. of tri- valents	1	2	3	4	5	6	7	8	Mean	
No. of cells	—	—	5	13	17	10	5	—	4.9	
Tetraploid.										
No. of quadri- valents	1	2	3	4	5	6	7	8	Mean	
No. of cells	3	12	10	2	15	6	—	2	3.8	

(Table II). The number of trivalents in the triploid varies between three and seven per cell, whereas the number of quadrivalents in the tetraploid varies between one and eight (Table III). The mean number of multivalents per cell is 4.9 and 3.8 respectively.

The chiasma frequency per chromosome on the other hand is less in the triploid than in the tetraploid (Table IV). This would tend to reduce the number of multivalents per cell in the triploid. Evidently, however, the decrease is not sufficient to reduce the frequency to that of the tetraploid.

The chiasma frequency per chromosome is highest in the diploid (1.66). On this point I am unable to corroborate Afify's (1933) work on the same material. He states that 60 per cent. of the bivalents had one and 40 per cent. two chiasmata, which would give a chiasma frequency of 1.4. On the other hand Lesley and Lesley's (1929) illustrations agree with my results. They figure four cells at diakinesis which show 29.2 per cent. of the bivalents with one chiasma and 70.8 per cent. with two. This gives a chiasma frequency of 1.7, a value slightly higher than mine. The same difference applies to the triploid and tetraploid. M. M. Lesley (1926) frequently finds twelve trivalents where I have never found more than

TABLE IV.

Comparison of chiasma frequencies in diploids, triploids and tetraploids.

	<i>Drosophila melanogaster</i> (chromosome II)	Chiasmata not terminalised		Chiasmata terminalised	
		<i>Tulipa</i>	<i>Hyacinthus</i>	<i>Primula sinensis</i>	<i>Lycopersicum esculentum</i>
2x	2.13	2.1	2.7	1.9	1.66
3x	ca. 2.13	2.3	2.6	1.4 ±	1.19
4x	—	—	—	1.7 ±	1.56

seven. She illustrates three of the four possible types of trivalent, Nos. 7, 8 and 9, of which 9 appears most frequently. This configuration requires three chiasmata, whereas the others require only two. In the tetraploid, Lesley and Lesley (1930) find that the number of quadrivalents varies between seven and eleven at diakinesis (compare Table III). It appears that their observations throughout in the diploid, triploid and tetraploid can be accounted for on the consistent assumption that the chiasma frequencies of their plants are slightly higher than those of mine. These differences may be due to differences of genotype or to differences in external conditions, such as temperature, between California and England.

The differences in chiasma frequency between the diploid, triploid and tetraploid (Table IV) correspond with those for *Primula sinensis*, which also has completely terminalised chiasmata. The data for the estimations of the triploid and tetraploid were taken from the polar views illustrated by Dark (1931) and Darlington (1931) but as only one nucleus of each was illustrated the numbers can only be provisional. In

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organisms without terminalisation, such as *Tulipa* (Darlington and Mather, 1932) and *Hyacinthus* (Stone and Mather, 1932) in which there is no fusion of chiasmata at diakinesis or metaphase, the chiasma frequency of the diploid and triploid corresponds very closely. In *Drosophila* the chiasma frequency in the second chromosome has been worked out from genetical data (Mather, 1933). In the triploid the crossing-over frequency per chromosome is greater than in the diploid ($3x:2x=1.4$, Redfield, 1932) in the region of the spindle attachment, and less ($3x:2x=0.6$) on either side of this region. Considering the chiasma frequency of the chromosome as a whole, it seems that the value is approximately equal in the diploid and triploid.

The lower value for the triploid in *Primula sinensis* and *Lycopersicum esculentum* must be due to the fact that fewer chiasmata were formed at pachytene and not that a greater number of fusions has occurred. For in a trivalent with a triple chiasma it is still possible to conclude that two chiasmata have been formed, although fusion has taken place. In a bivalent, on the other hand, a single terminal chiasma may occur in the place of two, three or more interstitial ones. On this argument, the triploid should show a higher frequency than the diploid. Since we find that it is actually lower we must assume that the original chiasma frequency is lower than in the diploid.

In order to compare the behaviour of chiasmata of the diploid with that of the triploid and tetraploid, the number of half-chiasmata per chromosome must be calculated (Table V). This is a simple matter in the diploid, since the number of half chiasmata per chromosome is equal to the number of chiasmata per bivalent. In the case of certain types of trivalent and quadrivalent, however, there is more than one possible distribution of half-chiasmata among the chromosomes (Darlington and Mather, 1932).

Of the three types of trivalent observed, only the one requiring three chiasmata for its formation has more than one possibility. The three chromosomes may have 2, 2 and 2 half-chiasmata (with minimum variance in the distribution) or 1, 2 and 3 (with maximum variance) (see diagram, Fig. 11). Since there are very few of this kind of trivalent in the triploid (10.9 per cent., Table VI) the difference between the maximum and the minimum variance is small.

Among the quadrivalents in the tetraploid, types 14 and 15 only have more than one possibility. Type 14 has three different distributions, the chromosomes having 1, 1, 3, 3 or 2, 2, 2, 2, or 1, 1, 2, 4 half-chiasmata. Type 15 has four possibilities, 1, 1, 3, 3; 2, 2, 2, 2; 1, 2, 2, 3 or 1, 1, 2, 4

(see diagram, Fig. 11). Of these possibilities, the distributions with maximum and minimum variances only are included in the table. The difference

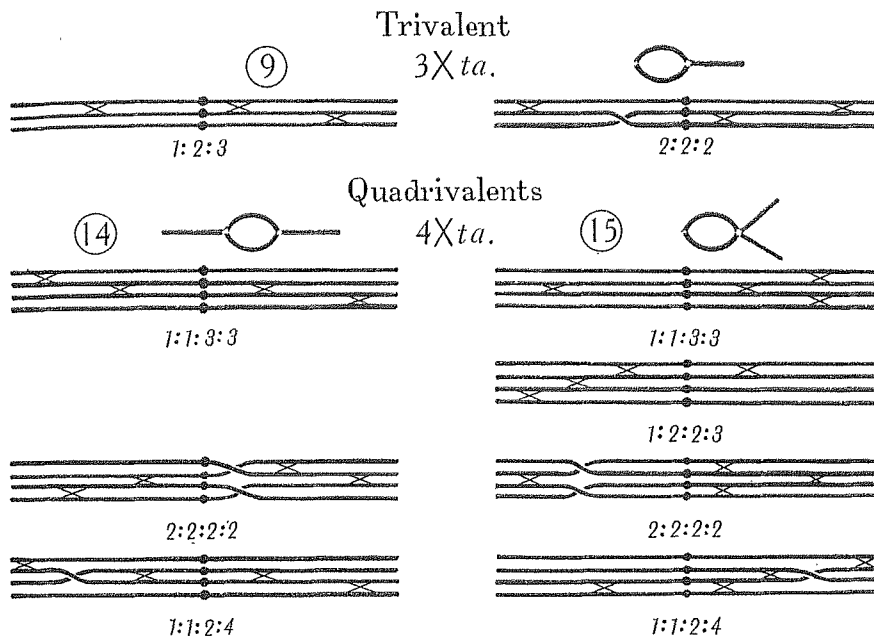


Fig. 11. Diagram illustrating the possible ways in which pachytene pairing and chiasma formation may take place to give configurations of the types shown. Crosses indicate the position of chiasmata. The order of two chiasmata on the same side of the spindle attachment may be reversed, without affecting the distribution among the chromosomes or the type of resulting configuration.

TABLE V.

Nos. of $\frac{1}{2}$ -Xta. ...	Nos. of $\frac{1}{2}$ -Xta. per chromosome.					Mean	Variance	$\frac{\text{Variance}}{\text{Mean}}$
	0	1	2	3	4			
Diploid:								
Nos.	—	82	158	—	—	1.66	0.216	0.13
Percentage	—	34.2	65.8	—	—	—	—	—
Triploid:								
Min: Nos.	356	750	694	—	—	1.19	0.548	0.46
Percentage	19.8	41.6	38.6	—	—	—	—	—
Max: Nos.	356	778	638	28	—	1.19	0.579	0.48
Percentage	19.8	43.2	35.4	1.6	—	—	—	—
Tetraploid:								
Min: Nos.	28	984	1384	4	—	1.56	0.265	0.17
Percentage	1.1	41.0	57.7	0.2	—	—	—	—
Max: Nos.	28	999	1361	5	7	1.56	0.279	0.18
Percentage	1.1	41.6	56.8	0.2	0.3	—	—	—

between these two estimations in this case also is not large, since these quadrivalents only constitute 3.6 per cent. of the total (Table VI).

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From these data, the mean half-chiasma frequency per chromosome and the variance were calculated (Table V) and the curves for the diploid, triploid and tetraploid drawn (Fig. 12), taking the mean of the variance. The variance is much higher in the triploid than in the diploid in proportion to the mean. This is conformable with the results of Darlington and Mather (1932) in *Tulipa* and may be accounted for in the same way,

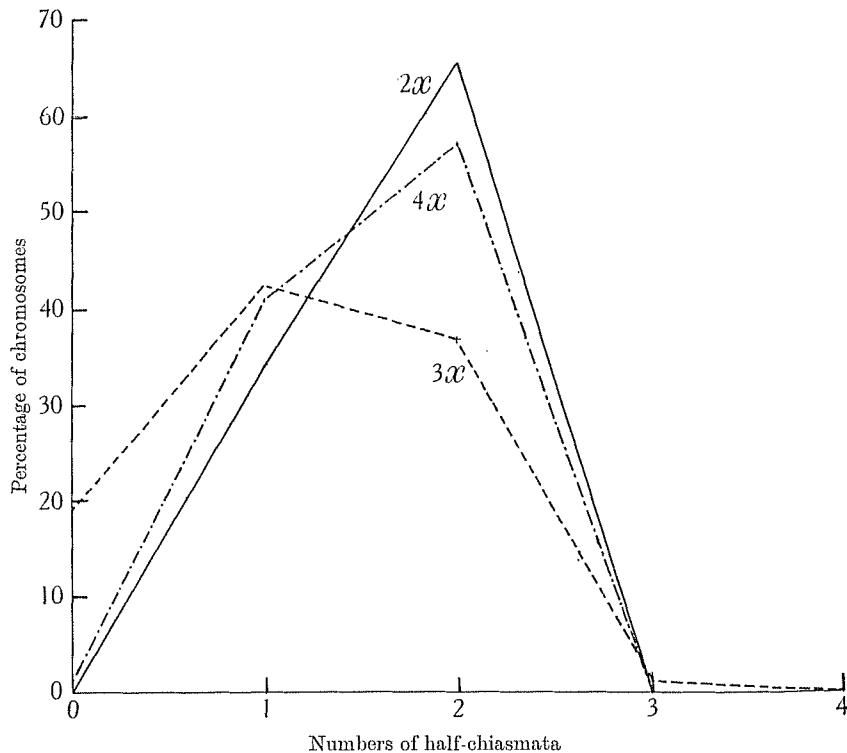


Fig. 12. Graph showing the numbers of half-chiasmata per chromosome. The values for the triploid and tetraploid are the mean of the maximum and minimum variance.

namely by the fact that the variance in triploids is the product of two kinds of variation: (1) the length of the chromosomes paired and (2) the chiasma frequency per length paired. In the tetraploid, the variance is less than in the triploid but greater than in the diploid, owing to incompleteness of pachytene pairing where changes of association occur (illustrated by Darlington, 1929; McClintock, 1930).

The different types of association (Table VI) correspond with those found in *Primula sinensis* (Darlington, 1931). The multivalents depend,

TABLE VI.
Frequencies of different types of configuration.

	Bivalents		Trivalents		Quadrivalents							
	1 Xma.	2 Xta.	2 Xta.	2 Xta.	3 Xta.	3 Xta.	3 Xta.	3 Xta.	4 Xta.	4 Xta.	4 Xta.	Total
Diploid:												
Nos.	82	158										240
Percentage	34.2	65.8										100
Triploid:												
Nos.	155	195	124	97	27	248						100
Percentage	44.3	55.7	50.0	39.1	10.9	100						
Tetraploid:												
Nos.	404	390	2	1	1	4	67	13	3	99	3	193
Percentage	50.9	49.1	50.0	25.0	25.0	100	34.7	6.7	1.5	51.3	1.5	100

TABLE VII.

Chromosome Nos. counted in metaphase II of tetraploid.

	20	21	22	23	24	25	26	27	28	Total	Number balanced gametes	Number unbalanced gametes	Percentage balanced
Kostoff and Kendall (1934)	2	1	7	15	187	12	4	2	1?	231	187	44	80.9
Lesley and Lesley (1930)	—	—	3	5	35	6	—	—	—	49	35	14	71.4
Upcott	—	—	4	16	63	13	4	—	—	100	63	37	63

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in the same way, upon the formation of chiasmata among sets of chromosomes changing partners at random at pachytene.

It follows from the chiasma theory of metaphase pairing that the frequencies of different types of quadrivalent will depend upon the frequency and distribution of chiasmata. Since the chiasma frequency in the diploid is 1.66, we must expect the average number of metaphase chiasmata in sets of four chromosomes to be between three and four. Furthermore, from the property of interference between chiasmata, the probability is that the commonest types of quadrivalent will be those without multiple chiasmata, since these are due to the formation of more than one chiasma in one arm. We find in fact the commonest types of quadrivalent to be those with three or four chiasmata distributed equally in all the arms. This predominance of symmetrical arrangements may also account for the rarity of trivalents in the tetraploid (Table II), for these involve essentially asymmetrical prophase arrangements of the four chromosomes.

Previous workers on the tetraploid *Lycopersicum* have illustrated various types of quadrivalent. Jørgensen (1928) illustrates Nos. 11, 12 and 17, and Lesley and Lesley (1930) Nos. 11, 17 and 18. Kostoff and Kendall (1934) show Nos. 11, 12, 15 and 17. These workers also find (their Fig. 3*b* and *c*) non-homologous association of parts of chromosomes at diakinesis and metaphase such as have never been seen before at this stage. I have seen no such configurations. Each type of configuration requires a different explanation. It is of course possible that there is a duplication or an inversion in their material, but the interpretation of such configurations is difficult in an organism with such small chromosomes as *Lycopersicum*.

Matsuda (1934) gives a diagram showing thirteen types of quadrivalent. Ten of these were given by Darlington in 1931 and the remaining three are impossible without the occurrence of some structural change, the assumption of which would allow for an indefinite number of possibilities.

THE SECOND MEIOTIC DIVISION.

Owing to the presence of univalents which lag on the equator after the chromosomes have passed to the poles, irregularities in the second division occur in the triploid, but are comparatively rare in the tetraploid. Fig. 13 shows two anaphases of the first division with six and seven univalents, some of which have divided while others have not. If the number of lagging univalents is great, a restitution nucleus is pro-

duced (Figs. 14 and 15) in which one instead of two plates is formed at second metaphase. These nuclei have 36 chromosomes, but may have one or two less if some of the univalents are lost in the cytoplasm.

A normal metaphase II is shown in Fig. 16, one nucleus having 15,

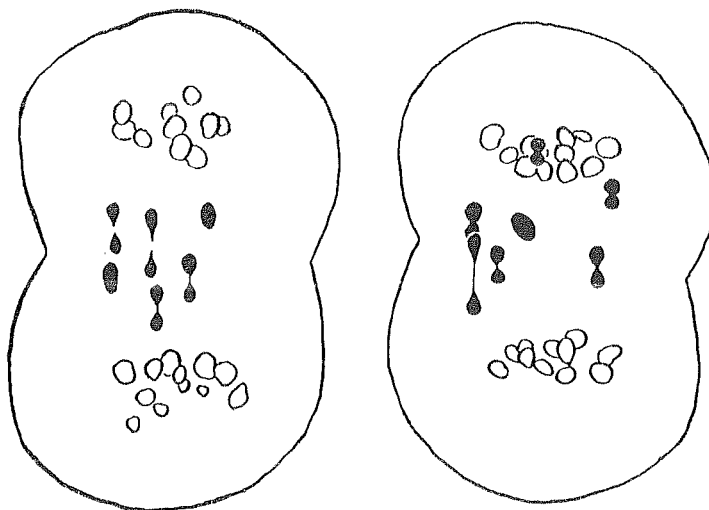


Fig. 13. Two anaphases of the first division of the triploid with six and seven univalents respectively, some of which have already divided. $\times 4000$.

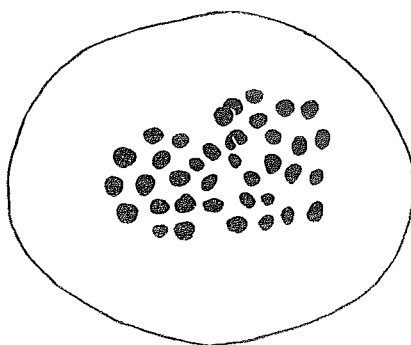


Fig. 14. Metaphase II of restitution nucleus in the triploid, showing 36 chromosomes. $\times 4000$.

the other 21 chromosomes. Other variations occur, including nuclei with 18 chromosomes each, according to the number and disposition of the univalents. At anaphase II there is further lagging of univalents (Fig. 17).

In the tetraploid, restitution nuclei would not be expected, since very few univalents are formed, and such nuclei were in fact not observed. The

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chromosome numbers of the two cells at metaphase II varies about a mean of 24. Table VII gives the variation of chromosome number in the two cells at this stage, together with similar results given by Kostoff and Kendall (1934) and Lesley and Lesley (1930).

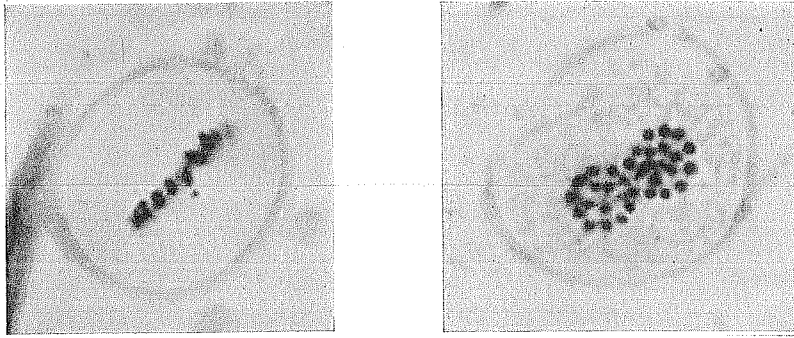


Fig. 15. Photographs of side and polar views of metaphase of restitution nuclei. $\times 2400$.

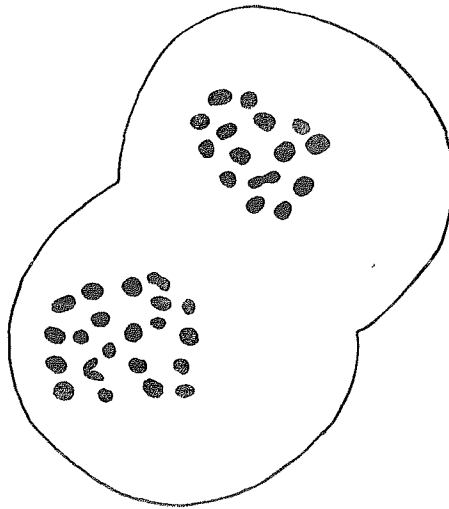


Fig. 16. Metaphase II in the triploid, showing nuclei with 21 and 15 chromosomes respectively. $\times 4000$.

Numerical disjunction occurs in 63 cells out of 100. The curve should theoretically be symmetrical on either side of the mean, the asymmetry being due to the occasional loss of a chromosome from cells which should have had 25.

The number of cells with 24 chromosomes is the summation of a series $24, 24+1-1, 24+2-2$, etc. Similarly with cells having more or

less chromosomes than 24. The proportion of genetically balanced gametes produced by plants examined will therefore be less than 63 per cent., the percentage of numerically balanced gametes observed. Since two-thirds are numerically balanced it may be assumed that about two-thirds of these are genetically balanced (an exact calculation cannot be made without additional assumptions). Hence it is probable that 40 per cent. of the gametes produced are balanced and, if all these gametes function, rather more than 20 per cent. of the zygotes. Since 25 per cent. of the pollen is bad (Jørgensen, 1928), a higher proportion than 40 per cent. of the functional male gametes will probably be balanced. Sansome (1933)



Fig. 17. Two pollen mother-cells of the triploid at anaphase II showing lagging univalents.
×4000.

found 20 per cent. seeds formed as compared with the diploid. The result seems adequately explained by the observations of non-disjunction.

The occurrence of this non-disjunction depends almost entirely upon the formation of quadrivalents and is characteristic of the behaviour of autotetraploids. It accounts for the rarity of such tetraploids in nature (Darlington, 1928).

Another consequence of the segregation of adjacent chromosomes to the same pole at the first division is that both divisions are reductional in respect of those parts of the chromosomes distal to the point at which crossing-over took place. The frequency of this double reduction depends directly on the frequency of quadrivalent formation, and determines the

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extent to which genes lying in these chromosomes will segregate according to the proportions of random chromatid segregation as calculated by Haldane (1930). The observations of quadrivalents described here therefore account for Sansome's (1933) observations of chromatid segregation.

CONCLUSIONS.

1. The multivalent configurations in the triploid and tetraploid *Lycopersicum esculentum* are of the types which would be expected, if they were determined by a random distribution of chiasmata.

2. They vary in frequency from cell to cell, but remain statistically constant at successive stages, as they would be expected to do on this assumption.

3. The configurations (contrary to the opinion of previous authors, but as is expected on analogy with all other cases of chiasma pairing) are constant between diplotene and metaphase.

4. The metaphase chiasma frequency is highest in the diploid and lowest in the triploid. This is attributed to a similar difference in original chiasma frequency rather than to a greater reduction in number in the triploid during terminalisation.

5. The curve of variance is higher in the polyploids than in the diploids, as has previously been found in *Tulipa* and *Hyacinthus*.

6. The formation of trivalents and univalents in the triploid gives rise to irregularities in the second division, and to the formation of restitution nuclei.

7. The formation of quadrivalents in the tetraploid leads to numerical non-disjunction which is reflected in reduced fertility.

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