TRISOMIC TYPES OF THE TOMATO AND THEIR RELATION TO THE GENES¹

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INTRODUCTION

The tomato provides rather favorable plant material for study of the effects of changes in chromosome number. Haploid ($n=12$), diploid, auto-triploid, and autotetraploid forms are known. Eleven of the twelve primary simple-trisomic types expected and two tetrasomic types have been identified, and some double and triple-trisomic types are viable. Moreover, in the same race, the simple-trisomic types and three or four which contain a chromosome fragment in addition to the normal complement can be identified phenotypically. MACARTHUR (1931) refers to twenty pairs of genes now under investigation. The loci of fifteen of these are reported to be in seven different chromosomes. In *Zea mays* the number of known genes is vastly greater but the simple-trisomic types ($n=10$), according to MCCLINTOCK and HILL (1931), are not easily distinguishable externally from diploids.

In the present paper two new simple-trisomic and two tetrasomic types of the tomato are described, more evidence is presented concerning the location of known mutant genes, and an attempt is made to interpret some of the phenotypic effects associated with the presence of extra chromosomes in simple-trisomic types.

As in a previous paper (LESLEY 1928) the twelve chromosomes of the haploid set will be designated by the first twelve letters of the alphabet. Triplo-A then denotes a simple-trisomic plant containing an A chromosome in addition to the normal complement of twelve pairs, and triplo-DF a double trisomic containing a D and an F chromosome in addition to

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the normal diploid complement. The term *non-hybrid* is again applied to plants of the two closely similar races of Dwarf Aristocrat in which the triploids used as parents occurred.

NEW SIMPLE-TRISOMIC AND TETRASOMIC TYPES

For comparison with other field-grown simple-trisomic types, non-hybrid plants of triplo-F, triplo-G, triplo-H and triplo-I are shown in figures 1 to 4.

FIGURE 1.—Triplo-F non-hybrid.

In one instance a single seed from triploid $\times$ diploid gave rise to two seedlings. One of these proved to be normal triplo-B, the other was a "runt" or budless plant. Presumably they originated from two distinct megaspore mother cells, of which two or more in a single ovule were observed by M. M. LESLEY (1926) in diploid, triploid, and double-trisomic tomato plants. Two other runs in F_1 triploid $\times$ diploid were found to have 26 chromosomes in their root tips but other 26 and even 27-chromosome F_1 plants developed normally. The fact that the observed multiple megaspore mother cells did not always mature synchronously suggests that possibly the runt condition was due in part to competition. Some

cause other than chromosome unbalance is indicated also by the occurrence of runts from diploid parents.

As triplo-I (figure 4) contains the locus of the *Rr* gene pair, a somewhat fuller description than that already published (LESLEY 1928, p. 25) seems desirable. Compared with diploid Dwarf Aristocrat (figure 7), the surface of the leaf lamina is more even and the texture is more leathery. The margin of the folioles is less indented and the foliolules are fewer in number. The color of the leaves is somewhat grayer green, with more purple along

FIGURE 2.—Triplo-G non-hybrid.

the midribs and in the axils of the leaflets. In the seed bed it is easily distinguishable from the diploid by the appearance of the first true leaves. The flesh, especially of the walls and placentae, of the fruit of *RRR* triplo-I plants tends to be paler red than that of *RR* diploids. Like other trisomic types, triplo-I grows more slowly than the diploid. It is one of the less fruitful and less fertile trisomic types. Non-hybrid plants seldom set fruit in the field at Riverside without hand pollination.

Further study of the type thought to be a secondary of triplo-I (LESLEY

1928, figure 17) has led to the conclusion that it is identical with the primary triplo-I.

The simple-trisomic type shown in figure 5 was first identified in an F_2 progeny of triploid $\times$ diploid. It was notable for the compound or much-branched character of its inflorescences. This branching was similar to that caused by the recessive mutant gene *s* (compound inflorescence) which CRANE (1915) showed to be a simple recessive to *S* (simple inflorescence). The mean number of nodes between successive inflorescences was

FIGURE 3.—Triplo-H non-hybrid.

2.8, approximately the same as in a diploid *SS* race, as compared with about 4 in Grape Cluster (*ss*). It is believed that the plant in figure 5 is *SS* and that it represents a new simple-trisomic type. The new trisomic type has shorter internodes and more purple in the buds, and is probably less fruitful in proportion to the number of flowers produced than the diploid. In the young seedling stage this type is not easily distinguished from the diploid. It is most like triplo-E among the other simple trisomics but differs in having the compound inflorescence, more purple in the buds and a less hairy surface. An F_3 triplo-J plant gave an F_4 from uncontrolled

pollination in which not only the 3 trisomic but also the 24 diploid progeny had a tendency to be compound. This can scarcely be explained by accidental cross-pollination and is being studied further.

In the F_1 progeny of triplo-BC $\times$ diploid Dwarf Aristocrat, a new simple-trisomic type appeared which bore no special resemblance to either the triplo-B or the triplo-C plants occurring in the same progeny. It contained an extra chromosome apparently of normal size (not a fragment),

FIGURE 4.—Triplo-I non-hybrid.

and is therefore believed to be a primary. Triplo-K (figure 6) has not been found in the F_1 progenies of triploid $\times$ diploid, perhaps owing to its close resemblance in general appearance to the diploid. The leaves are smaller, darker green, and more curled. The flower is smaller, the style more slender, and the number of loculi in the ovary about one-third less than in the diploid. A similar reduction in number of loculi occurs in triplo-D. In floral characters triplo-K suggests the small-fruited types of tomato

which grow wild in western Mexico and in Peru. Triplo-K is less fruitful and the fruits contain fewer seeds of normal size than the diploid.

The existence of 11 different simple-trisomic types agrees with the conclusion of LINDSTROM and KOOS (1931) from the absence of pairing among the chromosomes of the haploid that the basic number of chromosomes is 12.

FIGURE 5.—Triplo-J hybrid.

The frequency of transmission of an extra B chromosome by the pollen was 23 percent (LESLEY 1928); by the ovules it varied from 27 percent to 32 percent, and in selfing from 37 to 54 percent. The frequency of transmission of the D chromosome in selfing was as high as 45 percent. Furthermore, the D chromosome probably was transmitted more frequently than any other by the eggs of triploids. Not unexpectedly, therefore, the tetrasomic types tetra-B and tetra-D were found in the progeny of triplo-B

and triplo-D hybrids selfed, respectively. One tetra-B plant was shown to have 11 bivalent and 1 quadrivalent chromosomes in its pollen mother cells, and several other closely similar plants occurred in the same progeny. (The author is indebted to his wife, Doctor MARGARET M. LESLEY, for the chromosome counts reported in this paper.) The tetra-B plant had the distinctive characteristics of triplo-B but to a somewhat greater degree. Unlike its triplo-B sibs, it was unfruitful in the field without hand pollination.

FIGURE 6.—Triplo-K non-hybrid.

Two tetra-D plants were identified by chromosome number in the progeny of triplo-D selfed. The presence in this progeny of 13 percent of apparently tetrasomic plants indicates at least that amount of pollen transmission of the D chromosome. The tetra-D plants also had the characteristics of triplo-D to an increased degree. Although less fruitful than triplo-D sibs, both the tetra-D plants identified produced a few seeds of normal size.

TRISOMIC INHERITANCE

The extra chromosome of triplo-A contains the locus of the gene *d* (dwarf), as already reported (J. W. LESLEY 1926). C49-1a was a triplo-A

plant (it was probably a double trisomic but the other extra chromosome was not identified). The ratio of standard to dwarf from selfing C49-1a (table 1) shows that this plant was probably *Ddd*. The small F_1 progenies C77 and C79 (table 1) originate from two *dd* (diploid) plants pollinated by a single flower of C49-1a, the triplo-A (*Ddd*) plant. This flower was staminate and entirely without a gynaecium. As was expected, the extra A chromosome was not transmitted by the pollen and no other trisomics occurred, but instead of standard and dwarf plants in the ratio 1:2 in the

FIGURE 7.—Diploid Dwarf Aristocrat.

diploid progeny, C77 contained 11 standard and 10 dwarf, and C79 contained 8 standard and 6 dwarf. If the numbers are combined the odds against such a departure from the 1:2 ratio in simple sampling are 115 to 1. Apparently an aberrant somatic cell division in C49-1a resulted in the loss of an A chromosome or, more probably, part of an A chromosome containing *d*, and also prevented the development of the gynaecium.

Inheritance of flesh color of fruit (*R*, red; *r*, yellow) in the progenies of triplo-I was trisomic (table 1). The individual progenies are small owing to the low yield of viable seed obtained from triplo-I fruits. On the whole the ratios are nearly those expected in trisomic inheritance and leave no

TABLE 1
Trisomic inheritance of habit (D, standard; d, dwarf), foliage and stigma color (L, normal green; l, lutescent) and flesh color of fruit (R, red; r, yellow) in the tomato. The numbers expected are printed in italics under the observed numbers.

PARENTAGE	THEORETICAL GENETIC CONSTITUTION OF PARENTS	DIPLOID PROGENY												TRISOMIC PROGENY §											
		D	d	C	c	A	a	L	l	R	r	Y	y	D	d	C	c	A	a	L	l	R	r	Y	y
Triplo-A selfed* (C49-1a)	<i>Ddd</i>	71	44†	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dwarf Aristocrat diploid × triplo-A* (staminate flower) (C77)	<i>dd × Dd</i>	71	44†	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dwarf Champion diploid × triplo-A* (staminate flower) (C79)	<i>dd × Dd</i>	8	6	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Triplo-B selfed	<i>DdYyCc</i> and <i>DdCcAaLlRrYy</i>	19	6	17	8	19	6	23	2	13	0	11	2	27	9	27	9	26	10	35	0	13	4	12	5
Triplo-I selfed	<i>RrrYy</i> and <i>DdCcAaLlRrYy</i>	34	6	29	11	31	9	32	7	58	44	72	30	5	2	6	1	5	2	6	0	1	2	3	0
Triplo-I selfed	<i>RRrYy</i>	30	10	30	10	30	10	29	10	57	45	77	25	5	2	5	2	5	2	5	1	2	1	2	1
Triplo-I selfed	<i>RRrYy</i> and <i>RRr</i>	..	..	..	..	..	..	..	..	19	2	16	5	..	..	..	..	..	..	..	..	..	..	..	..
Triplo-I selfed	<i>RRrYy</i> and <i>RRr</i>	..	..	..	..	..	..	..	..	19	2	16	5	..	..	..	..	..	..	..	..	7	0	6	1
Triplo-I selfed	<i>RRr</i> (all)	..	..	..	..	..	..	..	..	90	12	68	24	..	..	..	..	..	..	..	..	all	..	5	2
Triplo-I × diploid	<i>RrrYy × rrYy</i> and <i>Rrr × rr</i>	..	..	..	..	..	..	..	..	109	14	..	..	..	..	..	..	..	..	..	..	all	..	..	..
Triplo-I × diploid	<i>RRr × rr</i>	..	..	..	..	..	..	..	..	34	39	10	2	..	..	..	..	..	..	..	..	13	7	1	0
Triplo-I × diploid	<i>RRr × rr</i>	..	..	..	..	..	..	..	..	24	49	8	4	..	..	..	..	..	..	..	..	4	0	..	..
Triplo-I × diploid	<i>RRr × rr</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	all	..	..	..

* Probably a double trisomic of which the other extra chromosome was not identified.

† Including trisomic progeny.

‡ Assuming that 25 percent of the total number of plants were triplo-A.

§ Including about from 0 to 10 percent of tetrasomic plants.

doubt that the locus of the *Rr* pair of genes is in the I chromosome. The total numbers obtained from selfing parents of theoretical genetic constitution *Rrr* or *RRr* agree very nearly with the trisomic expectation. Two plants of constitution *Rrr* were backcrossed with *rr* diploids. Owing to the deficiency of recessive-type (yellow-fleshed) diploids in both progenies (table 1), the *R:r* ratio was nearer that from disomic inheritance and the odds against a difference as great or greater between the observed and the expected ratios in simple sampling are 60 to 1. LINDSTROM (1926) found evidence of linkage between the *Rr* pair of genes and some of the genes for size of fruit. Consequently an overbalance of genes with a resultant effect on fruit size might be expected in triplo-I. The few data available indicate that the fruit size of non-hybrid triplo-I and diploid Dwarf Aristocrat is approximately the same, but some difference might be found in other races. It is possible also that an overbalance of genes for increased fruit size exists, but its effect is neutralized by the deficiency of viable seeds and lack of vigor of triplo-I compared with the diploid. However, there is other evidence that the grade of a character is not necessarily changed by the presence of an extra chromosome carrying a major gene for that character.

A triplo-B F_1 plant, C218-4, from green triploid (*LLL*) $\times$ lutescent (*ll*) diploid was selfed. The observed *L:l* ratio among the diploid and trisomic progeny (table 1) approaches closely that expected if the triplo-B parent was *Lll*, and differs from a disomic (3:1) ratio by nearly six times the probable error. The locus of the *Ll* pair therefore is believed to be in the B chromosome.

From the presence of the locus of the *Dd* gene pair in the A chromosome, it may be assumed to contain the loci of the gene pairs *Pp*, *Oo*, and *Ss*, which are linked with it. The direct evidence in table 2 and in a previous publication (LESLEY 1928, table 8) and the indirect evidence of linkage relations, which is wholly consistent with the direct evidence, lead to the following negative inferences. The locus of the *Yy* gene pair is not in chromosomes A, B, C, D, or I and is probably not in E, F, H, or J. The *Cc* locus is not in chromosomes A, B, C, D, E, F, or I and probably not in J. The *Aa* locus is not in chromosomes A, B, D, F, or I.

DISCUSSION OF THE CHARACTERISTICS OF TRISOMIC TYPES

The flesh color of the fruit of triplo-I suggests the presence of the locus of the *Rr* gene pair in an unexpected manner. *Rrr* plants, grown in the field or in the greenhouse, have slightly paler red flesh than *Rr* diploids, especially at the proximal and distal ends. In the field, pale areas occur

TABLE 2

Disomic inheritance of habit (D, standard; d, dwarf), leaf form (C, cut leaf; c, potato leaf), anthocyan in stem (A, purple; a, non-purple), foliage and stigma color (L, normal green; l, lutescent), flesh color of fruit (R, red; r, yellow) and skin color of fruit (Y, yellow; y, non-yellow). The numbers expected are printed in italics under the observed numbers.

PARENTAGE	THEORETICAL GENETIC CONSTITUTION OF PARENTS	DIPLOID										TRISOMIC AND TETRASOMIC PROGENY													
		D	d	C	c	A	a	L	l	R	r	Y	y	D	d	C	c	A	a	L	l	R	r	Y	y
Triplo-C selfed	<i>Rr</i>	..	..	..	..	..	..	..	..	24	10	..	..	..	..	..	..	..	..	..	..	5	2	..	..
Triplo-C×diploid	<i>DdCcYy</i> × <i>ddccyy</i>	23	10	16	17	..	..	..	..	26	8	16	17	3	3	4	1	..	..	..	..	5	2	1	3
Triplo-D selfed	<i>Rr</i>	17	16	16	17	..	..	..	..	..	..	16	17	3	3	3	2	..	..	..	..	..	2	2	
Triplo-D selfed	<i>Rr</i>	..	..	..	..	..	..	..	..	39	6	..	..	..	..	..	..	..	..	..	15	5	..	..	
Triplo-D selfed	<i>DdCcAaLLRrYy</i>	76	21	74	25	72	27	71	27	70	26	69	27	61	18	61	16	51	26	58	21	56	13	51	
2n+D/2 selfed	<i>Dd</i>	73	24	74	25	74	25	74	24	72	24	72	24	59	20	58	19	58	19	59	20	52	17	52	
Triplo-E selfed	<i>Rr</i>	91	24	..	..	..	..	..	..	..	..	..	..	4	1	..	..	..	..	..	..	..	..	..	
Triplo-F selfed	<i>CcYy</i> and <i>DdCcAaLLRrYy</i> <i>RrYy</i> × <i>rryy</i>	86	29	..	..	..	..	..	..	..	..	..	..	4	1	..	..	..	..	..	..	..	..	..	
Triplo-H×diploid	<i>RrYy</i>	..	..	..	..	..	..	..	..	26	9	..	..	..	..	..	..	..	..	..	..	3	0	..	..
Triplo-J selfed	<i>RrYy</i>	14	5	34	12	14	5	13	6	10	7	30	14	7	5	13	4	8	4	9	3	1	0	1	0
Triplo-J selfed	<i>RrYy</i>	14	5	34	12	14	5	14	5	13	4	33	11	9	3	13	4	9	3	9	3	1	0	1	0
Triplo-J selfed	<i>RrYy</i>	..	..	..	..	..	..	..	..	21	23	24	20	..	..	..	..	..	..	..	..	..	..	..	..
Triplo-J selfed	<i>RrYy</i>	..	..	..	..	..	..	..	..	22	22	22	22	..	..	..	..	..	..	..	..	..	..	..	..
Triplo-J selfed	<i>CcYy</i>	..	..	..	..	..	..	..	..	24	13	30	7	..	..	..	..	..	..	..	..	7	1	7	1
Triplo-J selfed	<i>CcYy</i>	..	..	..	..	..	..	..	..	28	9	28	9	..	..	..	..	..	..	..	5	2	5	2	2
Triplo-J selfed	<i>CcYy</i>	..	..	23	8	..	..	..	..	..	..	27	4	..	..	5	0	..	..	..	..	..	2	3	3
Triplo-DF selfed	<i>DdCcAaLLRr</i> diploid Triplo-D Triplo-F	..	..	23	8	..	..	..	..	..	..	..	23	8	..	4	1	..	..	..	..	..	4	1	0
Triplo-DF selfed	<i>DdCcAaLLRr</i> diploid Triplo-D Triplo-F	19	6	17	8	18	7	20	5	15	6	15	6	17	3	13	7	14	6	12	8	16	2	15	3
Triplo-DF selfed	<i>DdCcAaLLRr</i> diploid Triplo-D Triplo-F	..	..	..	..	..	..	..	..	..	..	..	..	13	9	17	5	17	5	13	4	2	0	2	0

on the fruit which resemble externally those caused by sunburn. Apparently *R* is completely dominant over *r*, but is incompletely dominant over *rr*. A similar paleness of flesh color was often seen in the fruits of *RRR* and *RRr* plants. Apparently modifying genes are present in the I chromosome, whose effect upon color is cumulative and opposed to that of *R*. The flesh color of *rrr* plants is yellow like that of *rr* diploids. Except in style length and sepal shape, *Ddd* plants of triplo-A are not more dwarf-like than *Dd* diploids, and *ddd* plants of triplo-A are distinctly less dwarf-like than *dd* plants of triplo-E or triplo-K (compare LESLEY 1928, figures 6, 7 and 12, and figure 6 in present paper). The presence of an extra gene is not indicated by the shade of green of *LLL* plants of triplo-B. A gene *O* for non-elongated (spherical or oblate) fruit shape is partially dominant to *o*, a gene for elongated fruit shape, and is linked with dwarf (LINDSTROM 1927). The fruit shape indices (equatorial diameter divided by length) of *OO* diploid, *OOO* triplo-A and *OO* triplo-D plants of Dwarf Aristocrat were 1.2, 1.4 and 1.0 respectively. A similar relation was found in the shape of *Oo* diploid, *OOo* triplo-A and *Oo* triplo-D hybrids.

The effect of an extra D chromosome on fruit shape therefore was as great as that of an extra A chromosome carrying *O*, a major gene for that character. A triplo-D F_1 plant, C150-3, from the cross Dwarf Aristocrat triploid $\times$ Red Pear diploid, had elongated slightly pyriform fruits. Its diploid F_2 progeny consisted of 35 non-elongated and 10 elongated-fruited plants. All the 22 triplo-D progeny had elongated fruit. The progeny from

TABLE 3

Frequency distribution of shape index of fruit of diploid standard, diploid dwarf and triplo and tetra-D, all progeny of a triplo-D hybrid (C218-1).

SHAPE INDEX	DIPLOID		
	STANDARD	DWARF	TRIPLO AND TETRA-D
0.52	..	..	1
0.57	..	..	0
0.62	..	..	1
0.67	..	..	8
0.72	..	..	5
0.77	1	1	12
0.82	0	2	4
0.87	0	2	2
0.92	1	1	..
0.97	2	2	..
1.02	12	0	..
1.07	8	1	..
1.12	14	..	..

selfing another triplo-D hybrid, C218-1, are classified in table 3. In the progenies of these triplo-D hybrids inheritance of elongated fruit shape seems to be disomic.

It appears from the foregoing that the characteristics of the simple-trisomic types give, at the most, a rather uncertain clue to the position of known mutant genes. In simple-trisomics an extra chromosome containing a mutant gene may have no more or even less effect on the grade of the character concerned than an extra chromosome not containing the locus of the mutant gene pair. The elongated fruit shape of triplo-D seems to be due to non-mutant genes which are cumulative in effect. If these genes had mutated to non-elongated, triplo-D plants with spherical fruits might have appeared in these cultures, and inheritance of elongated shape from triplo-D would in some cases be trisomic.

The D chromosome probably does not contain the locus of the *Dd*, *Rr*, *Yy*, *Cc*, *Aa* or *Ll* gene pairs, but the presence of genes for fruit size is suggested by the small size (weight) of the fruit of triplo and tetra-D. The mean weight per fruit of 10 fruits of each plant for part of the progeny of C218-1 (triplo-D) grown in the field is shown in table 4. The difference is 4.16 times the probable error and is significant. Since the fruits of triplo-D and even tetra-D contain abundant seeds of normal size, the size of their fruit can scarcely be limited by deficiency of seed. However, the small fruit size may possibly depend on the slower growth and lack of vigor of triplo and tetra-D and not on an overbalance of genes for small size.

TABLE 4

Mean weight per fruit of diploid and of triplo and tetra-D, all progeny of a triplo-D hybrid (C218-1).

	NUMBER OF PLANTS	MEAN WEIGHT PER FRUIT AND PROBABLE ERROR GRAMS	VARIANCE σ^2
Diploid	92	22.3 $\pm$ 4.09	36.71
Triplo and tetra-D	58	14.2 $\pm$ 3.41	25.50

Pyriform fruit shape appeared in the progeny from selfing the triplo-D hybrid C218-1. The fruit of the parent was predominantly plum-shaped (ellipsoid) but slightly pointed at the distal end. A classification of the progeny based on the predominant shape of several fruits from each plant, is shown in table 5. All the pyriform-fruited progeny were elongated. Among the 30 diploids having elongated fruit only 2 were pyriform, but among the 73 triplo and tetra-D plants, all of which were elongated, 35 were pyriform. These figures suggest that pyriform shape, in the strict sense, is not determined by a single pair of genes. The large proportion

of triplo and tetra-D pyriform-fruited plants is apparently due to an overbalance of genes in the D chromosome which influence the pyriform character. These genes may either determine pyriform shape directly or, by reducing the number of loculi or the size of the fruit, may affect the expression of the pyriform character.

TABLE 5

Fruit shape and growth habit of diploid and of triplo and tetra-D, all progeny of a triplo-D hybrid (C218-1).

	STANDARD	DWARF
Diploid non-elongated	64	1
Diploid plum-shaped	8	1
Diploid obovoid	2	17
Diploid pyriform	0	2
Triplo and tetra-D plum-shaped	13	1
Triplo and tetra-D obovoid	20	4
Triplo and tetra-D pyriform	27	8

The suggestion, in table 5, of linkage between dwarf and pyriform is weakened by the uncertainty experienced in distinguishing standard and dwarf habit among the triplo and tetra-D plants.

The difference in mean weight between diploid non-elongated and diploid elongated was five times the probable error. Since larger size and non-elongated shape of fruit came from the same parent in the original cross Dwarf Aristocrat $\times$ a small-fruited dwarf yellow pear race, this result agrees with LINDSTROM's (1929) finding of an association between genes for size and shape of fruit.

SUMMARY

Two new simple-trisomic types of tomato are described, of which triplo-J was found in F_2 from triploid $\times$ diploid, and triplo-K in F_1 from triplo-BC $\times$ diploid. Probably 11 of the 12 primary simple-trisomic types expected have been identified.

In the simple-tetrasomic types tetra-B and tetra-D the characteristics of the corresponding simple trisomics are accentuated.

The I chromosome contains the locus of the *R_r* pair of genes. The B chromosome probably contains the locus of the *Ll* gene pair.

In simple-trisomics, the grade of a character may be no more affected by an extra chromosome containing a known mutant gene than by an extra chromosome not containing a mutant gene for that character. Consequently, the characteristics of the simple-trisomic types may indicate the position of non-mutant genes rather than of the known major genes.

The small fruit size of triplo and tetra-D may be due to an overbalance

of genes for fruit size in the D chromosome, which does not contain the locus of any of the 3 gene pairs known to be linked with genes for fruit size.

Evidence is given that pyriform fruit shape is not determined by a single pair of genes and that the D chromosome contains genes which influence the expression of this character.

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