NOVEL COMPENSATING TRISOMICS OF THE TOMATO: CYTOGENETICS, MONOSOMIC ANALYSIS, AND OTHER APPLICATIONS[1]

GURDEV S. KHUSH AND CHARLES M. RICK

Department of Vegetable Crops, University of California, Davis, California 95616

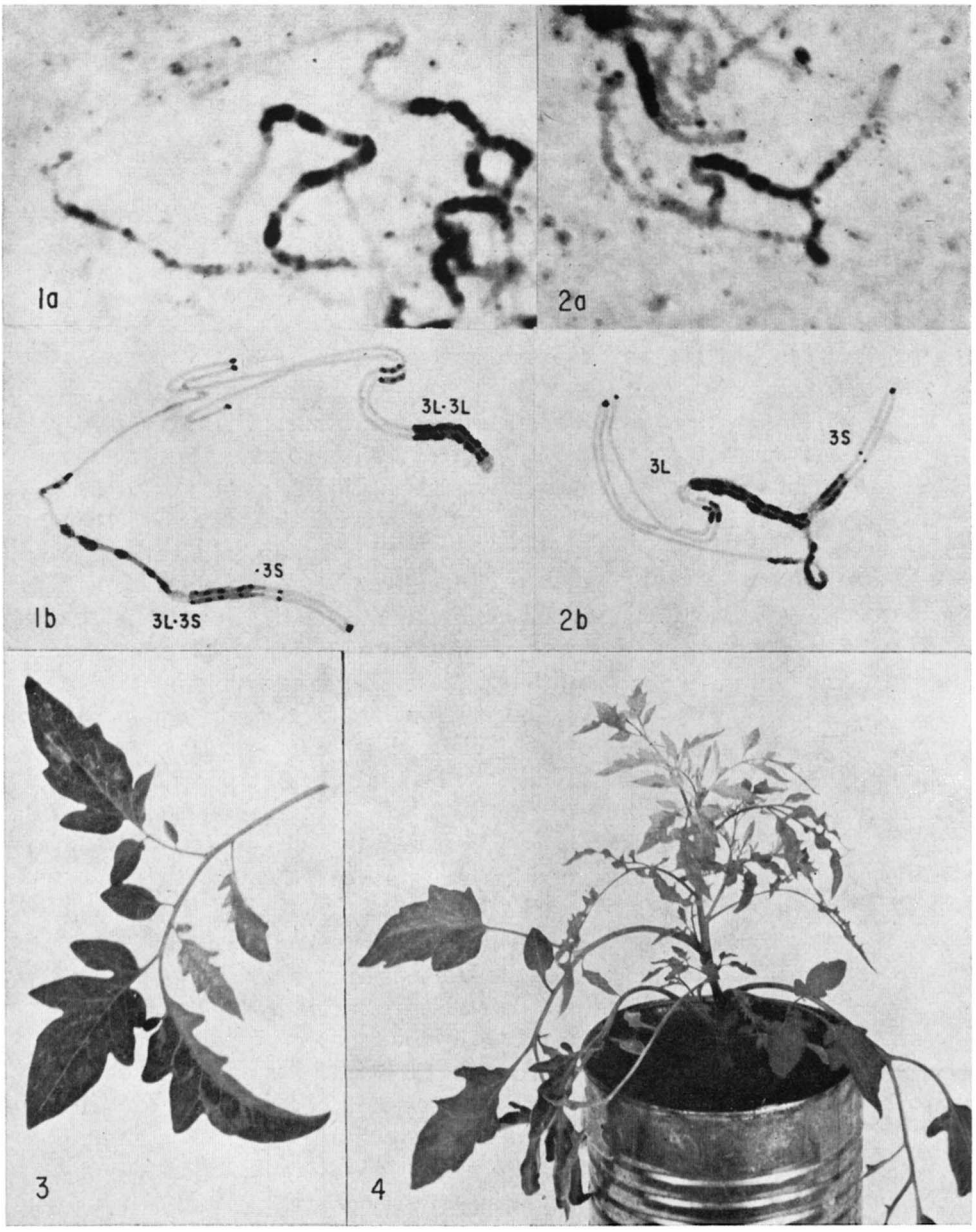
Received February 1, 1967

THE feasibility of applying monosomic analysis to the tomato (*Lycopersicon esculentum*) has been explored by utilizing chromosomal deficiencies induced by radiation (RICK and KHUSH 1961, 1966; KHUSH and RICK 1966, 1967; KHUSH, RICK, and ROBINSON 1964). Although useful in the immediate generation of their production, the monosomics or deviants lacking only part of a chromosome fail to transmit their karyotype excepting a single deficiency in the heterochromatin of 9L. The basically diploid condition of the tomato genome thus permits certain types of deficiency to survive in the sporophyte but almost never in the gametophyte. Although the diploid nature of the tomato is advantageous for many types of genetic analysis, such narrow transmission tolerance severely limits monosomic analysis, requiring tedious, large-scale progeny tests every time deficiencies for a specific region are sought. In attempting to circumvent this obstacle, we have been seeking deviant chromosomal types that might be transmissable but also useful for monosomic analysis. A type of compensating trisomic that fits this requirement as well as two examples of another, previously undescribed type of compensating trisomic, form the substance of this article.

The concept of a "compensating" trisomic was formulated by BLAKESLEE and his colleagues (see review by AVERY *et al.* 1959) as a sporophyte in which the loss of a normal chromosome is compensated by the presence of the two arms in new, translocated associations. Several of the kinds discovered in *Datura stramonium* included trisomics in which the deficiency was corrected by two tertiary chromosomes, by a secondary and a tertiary chromosome or by a telocentric and a tertiary. Since such compensating trisomics are useful for locating genes on specific chromosomes, various types were synthesized until at least two combinations were obtained for each of the 12 Datura chromosomes.

The three compensating trisomics to be described were first detected by virtue of their deviating gross morphology in progenies of various origin. An acquaintance with the phenotypes of the primary tomato trisomics and other trisomic types often permits a reasonably good guess as to the chromosomal constitution of new variants. Details as to the origin, techniques used, and other matters will be presented with each example.

[1] Research supported in part by Public Health Service Grant GM 06209.



FIGURES 1 to 4.—Compensating trisomic for chromosome 3 (2n — 3S·3L + ·3S + 3L·3L). FIGURES 1 and 2.—The chromosome 3 complex at pachytene of meiosis. In each figure *a* is the photomicrograph, *b* an interpretative drawing. Approximately 2,000×. FIGURE 1.—At bottom of figure the telocentric ·3C is paired with 3S of the normal chromosome, the remainder of 3 being unpaired except that the distal end of 3L is paired with one arm of 3L·3L. Most of 3L·3L is internally paired, the distal portion of one arm nonhomologously with itself. FIGURE 2.—Here 3L·3L and ·3S are paired respectively with 3L and 3S of the normal chromosome. FIGURES 3 and 4.—Sporophytic parts of the trisomic heterozygous for *ru,sy* carried on the normal chromo-

Compensation by an Isochromosome and a Telocentric

Amongst the progeny of the tertiary monosomic haplo-3S-11L (KHUSH and RICK 1966) appeared a plant that displayed several morphological features of triplo-3. Since we were seeking the corresponding tertiary trisomics in the progenies of tertiary monosomics, we tentatively scored this plant as triplo-3S-11S. When a small progeny of this plant was grown, it was surprising to find that its trisomic type was transmitted at a much higher rate than that previously observed for triplo-3.

Cytological examination of this plant at diakinesis revealed not the presence of the pentavalent expected in a tertiary trisomic, but the following configurations: (1) A highly heteromorphic trivalent, (2) a distinctly heteromorphic bivalent and a ring-shaped univalent, or, rarely (3) a heteromorphic bivalent and a very small univalent. These observations ruled out the possibility that this trisomic might have been either a primary, secondary, tertiary, or telosomic trisomic. Pachytene analysis demonstrated that this plant had only one normal chromosome 3, with the other one replaced by an isochromosome for the long arm of 3 and a telocentric for the short arm (Figures 1, 2). This trisomic type can therefore be represented by the formula 2n − 3S·3L + 3L·3L + ·3S.

Inasmuch as the absence of normal chromosome 3 is balanced by the presence of the two arms of 3 in new associations, this trisomic is effectively a compensating type. As far as we are aware, only one such trisomic was previously reported in the literature—a plant of *Triticum monococcum* found by LUTHER SMITH (1947) in the offspring of a spike on a plant grown from an X-rayed dormant seed. The plant was identified at diakinesis as a trisomic in which one normal chromosome was replaced by a telocentric for one arm and an isochromosome for the other, but this identification could not be confirmed by pachytene configurations, which, via exact identification of the chromosomes, provide a much more critical test than diakinesis.

As a result of the unique constitution of this plant, genetic ratios in its progeny segregating for marker genes of chromosome 3 should be entirely different from those expected for primary, secondary, tertiary, or telosomic trisomics. The single normal chromosome 3 present in this type can only be received from the male parent; the unbalance wrought by the extra 3L in complements, including 3L·3L, is tolerated by gametogenesis only on the female side. In order to make it heterozygous for marker genes, the trisomic is therefore used as the female parent. One consequence of this situation is that, except for certain recombination products, all the 1n gametes, female as well as male, produced by such a heterozygous trisomic should carry the marker genes, and all the diploids in F_2 or backcrosses to the respective marker stocks should be homozygous for the markers. All the

---

some. FIGURE 3.—Leaf with mosaic pattern resulting from elimination of ·3S. The gene *ru* conditions reduced leaf area and *sy* intensifies the chlorosis. Note that the two effects are not expressed independently. 0.5×. FIGURE 4.—Plant in which the first three leaves have normal phenotype, all subsequent growth is *ru,sy* presumably as a result of complete loss of ·3S. 0.2×.

trisomic progeny should be phenotypically normal. By detecting such modified ratios, SMITH (1947) was able to associate one of the seven linkage groups of diploid wheat with the chromosome in the aforementioned trisomic.

Since all the tomato linkage groups have been assigned to their respective chromosomes (RICK, DEMPSEY, and KHUSH 1964; KHUSH and RICK 1966), use of this compensating trisomic for the aforementioned purpose would be superfluous. But because it produces telosomic trisomics for 3S (Table 1), this trisomic can be exploited to determine the arm location of markers on chromosome 3. Thus normal alleles on 3S should cover recessive genes on the short arm but not the long arm of its trisomics. To determine the arm location of *ru*, a dwarf chlorophyll mutant known to be linked on chromosome 3 (BOYNTON and RICK 1965), the trisomic was made heterozygous for this gene. Six heterozygous trisomics were grown, and in the examination of their vegetative portions, another useful feature of this trisomic was encountered. Leaves of each of the heterozygous trisomics had patches of mutant (*ru*) tissue varying in size from a minute speck to an entire leaflet. One plant of the group became entirely mutant except for the first true leaf. It was suspected that the mutant tissues were deficient for the 3S telocentric, implying in turn that *ru* is situated on this arm. Cytological examination of this plant confirmed our prediction, as it proved to be haplo-3S-triplo-3L—one of a group of haplo-triplo disomics described elsewhere (KHUSH and RICK 1967).

The somatic elimination of the 3S telocentric provides an excellent opportunity for determining arm location of 3S markers. By providing the critical information in the F_1 trisomics, this method in effect corresponds to monosomic analysis. Arm locations of all known markers of chromosome 3 can be determined by use of this trisomic. A mosaic pattern is expected for markers of 3S, not for those of 3L. Another chlorophyll mutant, *sy*, of chromosome 3 was located on 3S by this technique. The trisomic was made heterozygous for *ru,sy*, and all patches of F_1 trisomic leaf tissue that showed the subnormal size of *ru* also exhibited the chlorosis characteristic of *sy* (Figure 3).

It therefore follows that *sy* is also situated on 3S; had the *ru* patches not also been *sy* in phenotype, *sy* would have been located on 3L. One trisomic plant of this family lost the telocentric after producing three normal leaves and became entirely *ru,sy* (Figure 4). Use of either *ru* or *sy* along with the marker to be located serves to detect the tissues deficient for the telocentric 3S.

A test cross progeny of 2n − 3S·3L + 3L·3L + 3S was grown to test the breeding behavior of this trisomic. As shown in Table 1, 56.3% of the plants were diploid and all were of *ru* phenotype. The parental karyotype was transmitted to 40.5% of the progeny, and all such plants were ru^+. In addition, five plants (2.7%) carried 3S in addition to the normal diploid complement, and, as expected, each was ru^+. The n + 3S gametes from which they were generated are undoubtedly produced by nondisjunction of 3S and the normal chromosome 3. Cytological preparations show that 3S is almost always paired with normal 3 (Figures 1, 2), thereby accounting for the low frequency of nondisjunction and low frequency of 2n + 3S individuals in the progeny. Another product—namely an n + 3L·3L gamete and the corresponding 2n + 3L·3L zygote,

TABLE 1

Progeny of the test cross between a compensating trisomic for chromosome 3 and the diploid marker stock

Constitution for chromosome 3:
[3S·3L (*ru*), 3L·3L, ·3S (*ru*+)] × [3S·3L (*ru*), 3S·3L (*ru*)]

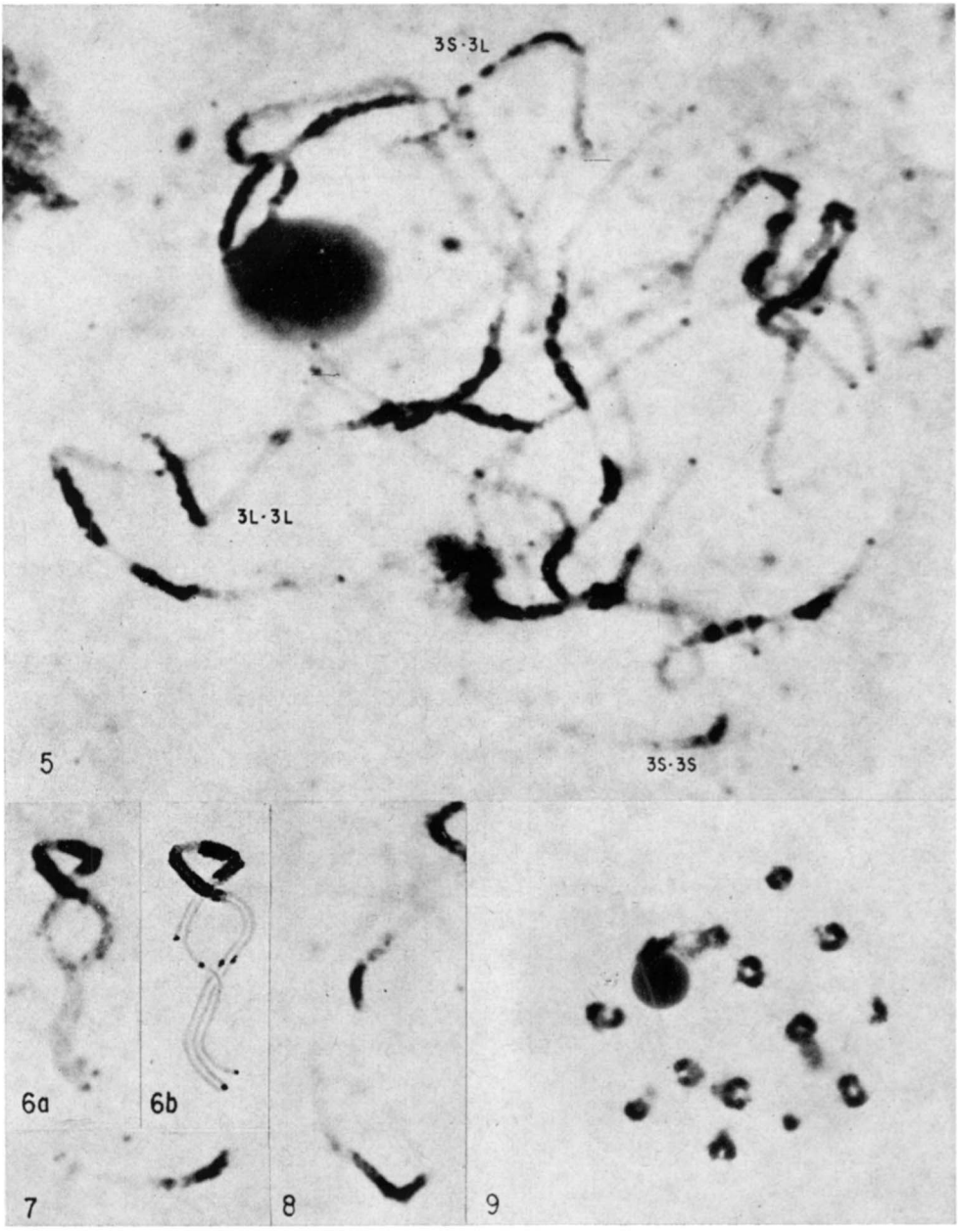
Expected type	Constitution for chromosome 3	Phenotype	Observed	
			No.	Percent
Diploid	3S·3L (*ru*), 3S·3L (*ru*)	ru	103	56.3
Compensating trisomic (parental type)	3S·3L (*ru*), 3L·3L, ·3S (*ru*+)	+	74	40.5
Telotrisomic	3S·3L (*ru*), 3S·3L (*ru*), ·3S (*ru*+)	+	5	2.7
Secondary trisomic	3S·3L (*ru*), 3S·3L (*ru*), 3L·3L	ru	0	0
Compensating trisomic (double iso-trisomic)	3S·3L (*ru*), 3S·3S (*ru*+/*ru*+), 3L·3L	+	1	0.5

might be expected in the progeny, but none has been recovered. Since 3L·3L is frequently observed as a univalent, it should undergo nondisjunction with normal 3. The results indicate, however, that gametes, zygotes, or both with an extra 3L·3L are inviable. Those gametes that receive 3L·3L instead of normal 3 would be expected to abort as a result of the deficiency for 3S. In one additional plant of this family two isochromosomes—3S·3S and 3L·3L—replaced a normal 3. Conversion of the telocentric ·3S into 3S·3S in one of the compensating trisomics probably accounts for the origin of this plant.

From the above description it is evident that the unique features of 2n − 3S·3L + 3L·3L + ·3S make it an exceptionally useful cytogenetic tool. Thanks to its chromosomal constitution, diagnostic morphology, high transmissibility, and the somatic instability of the telocentric ·3S, it permits the determination of arm location of markers of chromosome 3 simply by observing F_1 trisomic plants. A model has thereby been provided for conducting monosomic analysis of a basic diploid. As far as we are aware, this is the only instance in which a trisomic has been used in monosomic analysis of a diploid species.

Compensation by two Isochromosomes

Two examples of a new kind of compensating trisomic appeared in our progenies in addition to the three kinds in Datura (all including tertiary or translocated chromosomes) described by AVERY *et al.* (1959) and the fourth type described above for the tomato. In both of these, a normal chromosome is replaced by the two isochromosomes for the arms of that chromosome. One of these, 2n − 3S·3L + 3S·3S + 3L·3L, originated as mentioned above in the progeny of 2n − 3S·3L + ·3S + 3L·3L. Since ·3S is unstable, presumably because its centromere is terminal, it became converted into iso-3S (3S·3S). The extra chromatin in this new compensating trisomic exactly equals normal chromosome 3, hence the genetic complement is equivalent to the primary trisomic, triplo-3, from which the plant is indeed phenotypically indistinguishable.



FIGURES 5 to 9.—Photomicrographs of chromosomes of double iso-trisomics at pachytene of meiosis. Approximately 2,000×. FIGURE 5.—Complete complement of double iso-3 (2n — 3S·3L + 3S·3S + 3L·3L). All elements of the 3 complex are univalents. The long (right) arm of the normal (3S·3L) chromosome is entirely paired nonhomologously with itself in fold-back fashion. Both isochromosomes are completely paired internally. The centromere of 3L·3L is subterminal in the respect that it is flanked by two chromomeres of heterochromatin of one of the paired strands, while that of 3S·3S is terminal. FIGURES 6 to 9.—Double iso-7 (2n — 7S·7L + 7S·7S

The other compensating trisomic of this type is 2n − 7S·7L + 7S·7S + 7L·7L, which was discovered amongst the progeny of a plant deficient for 6S. A remarkably close resemblance to triplo-7 called our attention to this plant, and upon routine cytological examination its actual structural nature was discovered.

Although various associations of the trisomes are seen in meiotic prophase of these double iso-trisomics, the elements tend to remain dissociated in contrast to those of the preceding type of compensating trisomic. The configuration most frequently seen in pachytene is the normal chromosome disposed as a univalent and the two identical arms completely paired within each isochromosome (Figure 5—double iso-3; Figures 7 and 8—double iso-7). The centromere of such internally paired isochromosomes appears in a terminal (Figures 5, 8) or subterminal (Figures 5, 7, 8) position, as if it were resisting fold-back forces. Similar disposition of centromeres was observed by KHUSH and RICK (1967) in haplo- triplodisomics. The typical configuration in diakinesis is a single rod univalent formed by the normal chromosome and two small rings formed by the isochromosomes (Figure 9—double iso-7). In a few cells the normal chromosome is paired with one or both isochromosomes. In an example of this phenomenon (Figure 6), 7L is paired nonhomologously with normal 7 in the proximal region, but distally with the two other 7L's in a triple association.

Progeny tests on these trisomics have not yet been made, but it can be predicted with reasonable confidence that, in addition to parental types, both should yield secondary trisomics in their progeny. From 2n − 3S·3L + 3S·3S + 3L·3L, 2n + 3S·3S almost certainly should be obtained, but not 2n + 3L·3L for reasons of extreme unbalance as previously ascertained (KHUSH and RICK 1967). The progeny of double iso-7 will very likely include 2n + 7S·7S and probably 2n + 7L·7L.

DISCUSSION

Synthesis of compensating trisomics. In view of the previously delineated advantages of compensating trisomics for monosomic analysis and other potential applications discussed below, it is worthwhile to consider the feasibility of intentionally synthesizing them. It appears theoretically feasible to accomplish this by mating appropriate secondary and telo-trisomics in such combinations that the female parent contributes the less transmissible element. A compensating trisomic for chromosome 10 might thereby be prepared by first crossing the presently available stock of 2n + 10L·10L as female with 2n + ·10S. Amongst the progeny

---

+ 7L·7L). FIGURE 6.—a. "Bivalent" formed by pairing between 7S·7L and 7L·7L, showing nonhomologous pairing between ·7S and the proximal portion of one strand of 7L.—b. Interpretive drawing of a. FIGURE 7.—Univalent 7S·7S completely paired internally. Centromere position is subterminal. FIGURE 8.—Group showing complete internal pairing within univalent 7S·7S (top) and within univalent 7L·7L (bottom). Centromere of the former is subterminal, that of the later, terminal. FIGURE 9.—Complete figure at diakinesis, showing 11 pairs and three univalents. All univalents are in the periphery, the rod univalent of 7S·7L at 3 o'clock, ring univalents of 7S·7S and 7L·7L at 5 and 7 o'clock, respectively. Approximately 800×.

should appear individuals of the constitution 2n + 10L·10L + ·10S, which should be a good source for the functional gamete, n — 10S·10L + 10L·10L + ·10S, and consequent 2n — 10S·10L + 10L·10L + ·10S zygote—the desired compensating trisomic. The method is currently limited by the fact that only a few secondary trisomics and still fewer telo-trisomics are now available. The extreme sensitivity of male gametophytes to aneuploidy in the tomato would likely limit the number of combinations that can be synthesized.

Another method that might prove more rapid and direct is that of synthesis in the immediate products of chromosome breakage, by which the double iso-7 compensating trisomic reported here might have originated. The simplest conceivable situation would be for the centromere to be ruptured transversely by a single break, yielding two telocentrics, whose unstable centromeres would probably misdivide later to provide the required set of two isochromosomes for the arms of the same chromosome. Mature pollen, which our previous research has proved withstands many kinds of breakage and unbalance, would be the best stage for treatment. Presumably the method only requires large-scale irradiation of pollen followed by screening of the progeny for plants of primary trisomic phenotype, among which compensating types could be readily identified by their characteristic configurations at diakinesis. This method should be superior to the preceding one because it would not be limited by tolerances of the male gametophyte.

Applications. In addition to monosomic analysis that we have demonstrated to be feasible with 2n — 3S·3L + 3L·3L + ·3S, several unique properties of the compensating trisomics suggest other, new applications in cytogenetic research, which, insofar as we are aware, have not been proposed previously. The requirements of the following two suggested uses should be met by any of the known types of compensating trisomics, although in certain respects the double iso-trisomics are superior.

1. *Transfer of single chromosomes from wild to cultivated species:* This application exploits the peculiar transmission characteristics of this group of trisomics. As revealed in our experience and that of the Datura group, purely haploid gametes produced by compensating trisomics can consist solely of unmodified chromosomes, whereas extra-chromosomal gametes may include various combinations of normal and modified chromosomes. In the following procedure, advantage is also taken of the fact that extra chromosomes are seldom transmitted by the male parent.

The scheme outlined in Figure 10 essentially proposes a series of backcrosses between *Solanum pennellii* as the wild parent and *L. esculentum* as the cultivated, recurrent parent, to which such a chromosome substitution might be desired. The appropriate compensating trisomic of *L. esculentum* (double iso-7 serving as an example) is used as the female parent in the original cross and in each of the backcrosses. The diploid wild species is used as male parent in the original cross, thereafter, compensating trisomic derivatives, which should be readily identifiable by their phenotype. With selection, the peculiar transmission features mentioned above guarantee transmittal of solely isochromosomes from the female parent and the unmodified wild chromosome from the male parent for the

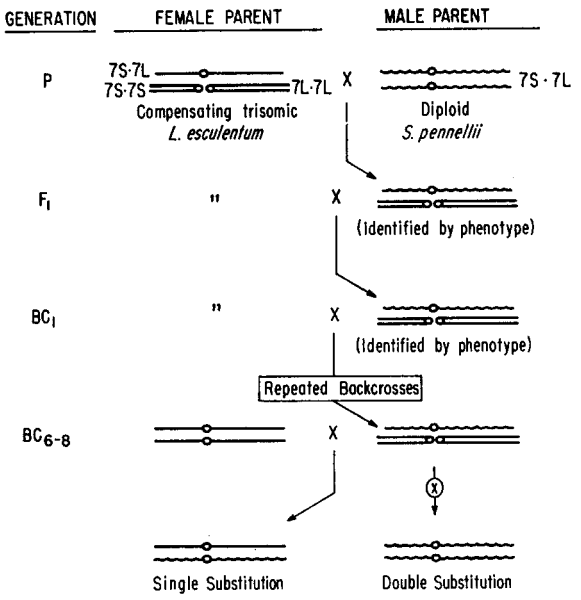


FIGURE 10.—Prosposed scheme for substituting chromosome 7 of a wild species (*Solanum pennellii*) in the complement of *L. esculentum*.

chromosome concerned, a rapid return to the recurrent parent being expected for all other chromosomes. Assuming random assortment and equal transmission probabilities, approximately 85% of BC_6 (94% of BC_8) segregants should be homozygous for all *esculentum* chromosomes excepting No. 7.

Selfing at any generation results in fixation of the wild chromosome in homozygous condition (double substitution) in all diploid progeny. Likewise a cross between the diploid *esculentum* parent and a trisomic derivative should yield diploids which are exclusively heterozygous (single substitution).

This method offers several advantages over the traditional method of using chromosomes that are multiply marked with recessive genes for the recurrent parent. In the first place, the latter presupposes the availability of many, non-epistatic markers suitably placed on the desired chromosome; the synthesis of an appropriate compensating trisomic might be simpler—certainly it is more rapid. In the second place, the double substitution product can be obtained in a single diploid plant from only one generation of selfing in the compensating trisomic method, whereas two generations, requiring many separate progeny tests, are needed for the marker gene method.

This proposed method presupposes that no genetic exchanges will take place between the substituted wild chromosome and the isochromosomes of the cultivated parent. While such crossovers cannot be completely discounted, they should be minimal because (1) the isochromosomes tend strongly to pair internally, (2) chromosomes in the *esculentum-pennellii* hybrid tend to pair autosyndetically (RICK and KHUSH 1962), and (3) recombination rates tend to be reduced in the same hybrid (RICK and KHUSH 1966).

2. *Location of marker genes:* The special advantages of compensating trisomics for the assignment of marker genes to their respective chromosomes have been demonstrated by AVERY *et al.* (1959) and SMITH (1947). When heterozygous for genes in such a fashion that the normal element of the trisome carries the recessive allele, such trisomics, except for crossovers, will yield diploid progeny that are entirely homozygous for the marker, and a very small progeny will suffice to discriminate against the normal 3:1 ratio.

But the compensating trisomics provide the additional advantage of detecting arm locations of the markers—a useful feature that apparently escaped the attention of previous workers. Arm assignments can be made because compensating trisomics throw related secondary, tertiary or telo-trisomics, according to their constitution. Since these off-types must result from nondisjunction, they are anticipated at a low frequency. Thus in Datura, 2n − 1·2 + 1·9 + 2·5 yielded 2n + 1·9 and 2n + 2·5 in its progeny. Similarly the 2n − 3S·3L + ·3S + 3L·3L tomato reported here threw 2n + ·3S (Table 1). As an example of the proposed use a marker on 7S when tested against double iso-7 would show the following kinds of segregation. For reasons just presented most of the diploid progeny should show the recessive phenotype, thus revealing the presence of the marker on 7. Among the progeny that are secondaries for 7L (2n + 7L·7L), a normal disomic ratio should be observed. The remaining trisomics—secondaries for 7S and double iso-7, both of which carry an extra 7S·7S—should be exclusively of normal phenotype. Crossing over might carry the recessive gene into one arm of the critical secondary, but never into both. Thus, in this unique and hitherto unreported type as well as other compensating trisomics, three kinds of ratios would be obtained, each depending upon the chromosomal constitution of its group and each giving key information about the chromosome and arm location of the respective gene. For these reasons a set of 11 compensating trisomics in the tomato (a primary trisomic would suffice for chromosome 2 because its short arm is heterochromatic and genetically inert) would be much more useful for gene location than any other trisomic types.

SUMMARY

Two new types of compensating trisomics are reported in which a normal chromosome of the tomato complement is replaced by either (1) an isochromosome for one arm and a telocentric for the other arm or (2) two isochromosomes, one for each arm. In the single example encountered of the former (2n − 3S·3L + 3L·3L + ·3S), the telocentric usually pairs with the normal 3S·3L chromosome, 3L·3L either associating with these elements in a trivalent or pairing internally as a univalent. A heterozygote of the same karyotype was synthesized with the recessive genes *ru* and *sy* on 3S·3L. Losses of ·3S resulted in somatic variegation in such plants obtained and in a complete conversion to *ru, sy* in one plant, thereby revealing that both genes reside on 3S. Such a compensating trisomic therefore provides a model for the application of monosomic analysis to strictly diploid species. Since haploid gametes of this aneuploid will survive if only they possess 3S·3L, all of its diploid progeny were *ru/ru*, and all of the aneuploid

progeny were ru^+, comprising the parental trisomic type, the telosomic trisomic 2n + 3S and one compensating double iso-trisomic.

In the second category the absence of a normal chromosome is compensated by two isochromosomes, one for each arm, examples having been found for tomato chromosomes 3 and 7. Since the extra chromatin is exactly equal to a single normal chromosome, this type is phenotypically identical with the corresponding primary trisomic. The three chromosomes are dissociated as univalents in the majority of figures of these trisomics. Considering the segregations theoretically expected for a recessive gene located on the single normal chromosome, all or nearly all of the diploid progeny should be homozygous for that gene, the secondary trisomics for the arm in which the marker is not located should segregate normally, and the remainder of the aneuploids should be of normal phenotype. This unique situation of three different patterns of segregation within one progeny should index a gene not only to its respective chromosome, but to the arm as well. A scheme is presented for utilizing such double iso-trisomics for efficient chromosome substitution from a wild parent. Methods of synthesizing these types of compensating trisomics are also discussed.

LITERATURE CITED

AVERY, A. G., S. SATINA, and J. RIETSEMA, 1959 Blakeslee: The Genus Datura. Ronald Press, New York.

BOYNTON, J. E., and C. M. RICK, 1965 Linkage tests with mutants of Stubbe's groups I, II, III, and IV. Rep. Tomato Genetics Coop. **15**: 24–27.

KHUSH, G. S., and C. M. RICK, 1966 The origin, identification and cytogenetic behavior of tomato monosomics. Chromosoma **18**: 407–420. —— 1967 Haplo-triplo-disomics of the tomato: origin, cytogenetics, and utilization as a source of secondary trisomics. Biol. Zbl. **86** (In press).

KHUSH, G. S., C. M. RICK, and R. W. ROBINSON, 1964 Genetic activity in a heterochromatic chromosome segment of the tomato. Science **145**: 1432–1434.

RICK, C. M., W. H. DEMPSEY, and G. S. KHUSH, 1964 Further studies on the primary trisomics of the tomato. Canad. J. Genet. Cytol. **6**: 93–108.

RICK, C. M., and G. S. KHUSH, 1961 X-ray-induced deficiencies of chromosome 11 in the tomato. Genetics **46**: 1389–1393. —— 1962 Preferential pairing in tetraploid tomato species hybrids. (Abstr.) Genetics **47**: 979–980. —— 1966 Chromosome engineering in Lycopersicon. Heredity (Suppl.) **20**: 8–20.

SMITH, L., 1947 A fragmented chromosome in *Triticum monococcum* and its use in studies of inheritance. Genetics **32**: 341–349.