

THE TOLERANCE OF EXTRA CHROMOSOMES BY PRIMITIVE TOMATOES¹

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THE unexpected composition of the progeny of a triploid plant of the Red Cherry variety of tomato (*Lycopersicon esculentum*) attracted our attention to the possibilities of greater tolerance of aneuploidy in primitive than in highly selected horticultural varieties. Previous experience with the latter varieties revealed striking morphological manifestations, reduced vigor, and decreased fertility caused by a single extra chromosome and an upper limit of three extra chromosomes tolerated (LESLEY 1928; RICK and BARTON 1954).

Progenies in the following studies were derived from open pollination of polyploids or from crosses between the polyploids and diploid staminate parents of the corresponding variety. For the intended comparisons the nature of the pollination is inconsequential since the rate of transmission of extra chromosomes through tomato pollen is negligible.

Triploid plants of Red Cherry had been sought as a source of specific primary trisomics of that variety, and one triploid was found as an unfruitful plant in a commercial culture in San Diego County in October, 1958. From 51 fruits that were naturally set on this plant, approximately 200 seeds were harvested, and the progeny were grown in 1959. Following our procedures for raising trisomic stocks and F₁ hybrids, we sowed the seeds in a greenhouse culture, later transplanted the seedlings to nursery flats, and, before transplanting to the field, discarded 23 plants of greatest vigor. Identification of trisomics of large-fruited tomatoes in the seedling stage, learned from ten years experience, has proven highly effective in greatly reducing the proportion of undesired diploids. Separations of such trisomics as triplo-1,2,8,9, and 10 are often 100 percent accurate as verified by the phenotypes of subsequently developed mature plants. It was unfortunate, however, for purposes of the present study that any seedlings had been eliminated, for further experience cast doubt on the accuracy of seedling identification in this variety.

As the retained members of this family grew in the field, phenotypic identification of trisomic types was attempted, but without success. Previous research (LESLEY 1928; RICK and BARTON 1954) showed that each tomato chromosome in

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triplicate conditions such a distinct syndrome of morphological changes that each of the 12 primary trisomics of large-fruited tomatoes can be easily identified, even in complexly segregating populations. To the contrary, within the Red Cherry family, deviations from diploid morphology were not so strongly expressed and many plants were encountered with atypical associations of characters.

Chromosome counts were next made in an attempt to solve the problems presented by this population. Most of the counts were made in acetocarmine smears of PMC's, but for plants of greatly reduced vigor it was necessary to make counts in mitotic figures of shoot meristems and leaf primordia prepared according to BALDWIN'S (1939) technique. Contrast was enhanced by mordanting with four percent iron alum following fixation in both methods and preceding HCl hydrolysis in the latter method. As the counts were made, the source of identification difficulties soon became apparent: 29 of the 55 retained plants were multiply trisomic, 25 were singly trisomic, and only one was diploid. The average vigor of plants with two and even three extra chromosomes was far greater than that noted previously in var. San Marzano and other large-fruited tomatoes. The survival of a single plant with four extra chromosomes was unmatched by any previous experience in tomatoes (Table 1).

With the aid of exact chromosome counts, classification of the single trisomic plants was simplified, although morphological deviations of several of the plants were so slight or atypical that they could not be typed accurately. A precise comparison between Red Cherry and other tomatoes in the degree of morphological deviation resulting from trisomy was not attempted. Though worthwhile, such a study would entail quantitative comparisons in replicated plantings of elaborate scale. Even though such data have not been obtained it can be stated with assurance that extra chromosomes cause far less anatomical modification in Red Cherry than in large-fruited tomatoes.

TABLE 1

Frequencies of transmission of extra chromosomes to the progeny of triploids and multiple trisomics of two tomato varieties

Chromosome number	Progeny of triploids				Progeny of multiple trisomics			
	San Marzano* No.	Percent	Red Cherry No.	Percent	San Marzano No.	Percent	Red Cherry No.	Percent
2N	303	38.7	26†	27.6	310	88.3	72	51.4
2N + 1	342	43.7	32	34.0	39	11.1	52	37.1
2N + 2	131	16.7	25	26.6	2	0.6	16	11.4
2N + 3	7	0.9	10	10.6
2N + 4	1	1.1
Total	783	...	94	...	351	...	140	...
Heterogeneity								
Chi-square	50.28*** (5 d.f.)				84.67*** (3 d.f.)			

* Data of RICK and BARTON (1954).

† Twenty-three of these plants were discarded before planting time, probably including some trisomic individuals (see text).

*** Significant at 0.001 level.

In the 1960 season another family of the same parentage was grown, which was secured from a clone of the original triploid plant. This new family, from which no seedlings were eliminated, included seven single trisomics, three doubles, four triples and only two diploids. The low frequency of diploids lent support to the belief that the seedlings discarded in 1959 probably included many with unbalanced chromosome number.

The combined data of both triploid progenies are presented in Table 1 in comparison with similar statistics for the progeny of San Marzano triploids obtained by RICK and BARTON (1954). The 23 uncounted Red Cherry seedlings are arbitrarily classified as diploids. Such treatment provides the greatest possible bias toward least tolerance of extra chromosomes. If, in spite of such bias, a statistical difference can be proved, any extra chromosomes that might have been present in the discarded lot would have served only to reinforce the difference. A heterogeneity χ^2 test, in fact, reveals a highly significant difference between the two sets of data. Extra chromosomes are therefore better tolerated by Red Cherry than by large-fruited varieties.

Higher transmission is also encountered in the offspring of multiply trisomic plants of Red Cherry. In 1960 three complete families were grown, each representing the natural progeny of plants having 26, 26, and 27 chromosomes. In previous years progenies were grown of 19 plants with 26 chromosomes and one with 27 in var. San Marzano. The tallied data are presented in Table 1. Plants with two or more extra chromosomes are considered as one group and entered as $2N + 2$. The difference, again highly significant statistically, reveals a higher transmission in Red Cherry. Single trisomics were proportionally more than three times, and multiple trisomics nearly 20 times as abundant in the Red Cherry progenies. The following composition of a typical Red Cherry family (60L684, the progeny of a triple trisomic) might be of interest: 18 diploids, five triplo-4, six triplo-10, five triplo-12, and 12 multiple trisomics.

Another feature common to the Red Cherry triploid and multiple trisomics and different from that of San Marzano polyploids is the higher fertility of the former. Whereas the mean number of normal seeds per fruit from the Red Cherry triploid was four, the corresponding count for San Marzano triploids is 0.5. Relatively large progenies were obtained from naturally set fruits of Red Cherry multiple trisomics whereas much smaller progenies were yielded from comparable plants of San Marzano, despite attempts to improve yields by hand pollination. Finally, progeny were obtained from five triple trisomics of Red Cherry whereas the total issue of numerous plants of San Marzano with the same chromosome number was only three plants.

Cytological abnormalities were frequently observed among the plants with higher chromosome numbers. Three plants, two having 26 and the other having 27 chromosomes, exhibited asynapsis. Nearly all chromosomes were unpaired at the first meiotic division in the former two plants, while those of the latter were paired to a variable extent. Spindle abnormalities in the majority of the sporocytes were characteristic of the single plant with 28 chromosomes; as many as five spindles and nine polar groups were counted in its second meiotic division figures.

Abnormal meiotic products were associated with strong clumping of chromosomes in the first division of another double trisomic. These distinctive abnormalities might have been caused by unbalance for particular combinations of chromosomes or they might be a general property of greater unbalance in tomatoes. The available facts do not give a clue as to the more likely of these alternative explanations.

DISCUSSION

The literature reveals little knowledge of genetic influence on tolerance of extra chromosomes. The fact that most studies on trisomics have been conducted with a single genotype or closely related genotypes of a species accounts for the paucity of such data. Comparisons cannot readily be made therefore between the trisomic series established in the highly selected cultigens, *Antirrhinum*, *Matthiola*, *Spinacea*, and *Zea* and those found in wild or primitive forms of *Datura*, *Nicotiana*, and *Oenothera*. More comparable, however, are the two series in *Hordeum*—one established from translocation heterozygotes in a cultivated variety of *H. vulgare* by RAMAGE (1960) and the other from triploids in wild *H. spontaneum* by TSUCHIYA (1958). Vigor, fertility, and transmission of extra chromosomes were higher in the latter. An unexpected disagreement with the tomato findings is provided by the stronger expression of trisomic phenotypes in wild barley. Although TSUCHIYA (1960) attributes the higher sterility in the cultivated series mainly to cytological abnormalities resulting from translocations, the low fertility found in trisomics that were recently derived from triploid cultivated barley by other workers (RAMAGE, personal communication) reveals that genotype is a more important factor.

In tomatoes Soost (1958) has revealed a remarkable exception to the previously understood tolerance of extra chromosomes in tomatoes. He synthesized sesquidiploid hybrids with two sets of *L. esculentum* and one of *L. peruvianum* chromosomes and, in their first and second generation progeny, discovered plants with nearly the complete range of numbers from diploid to triploid. Within the limits of the small families studied, all unbalanced types appeared to survive. This tolerance is attributed to either a characteristic of the wild parent or hybridity. Such indifference to extra chromosomes has been matched in higher plants only by such wild forms as *Collinsia heterophylla* (DHILLON and GARBER 1960) and *Clarkia unguiculata* (MOORING 1960).

Although tolerance of chromosomal unbalance in the above examples has been attributed to various causes, they share a common element: a wild or primitive genotype. Primitiveness also provides the most reasonable explanation for tolerance of extra chromosomes in the present example. Red Cherry is the oldest among currently cultivated tomato varieties. Although somewhat ameliorated beyond the feral var. *cerasiforme*, it is a much closer approximation of the latter than of the large-fruited cultivated sorts.

Primitive or wild forms undoubtedly possess such tolerance as part of their plasticity and ability to withstand various unfavorable situations. *L. esculentum*

var. *cerasiforme* is a familiar and outstanding example of an aggressive, weedy form, which has spread rapidly and become established throughout the tropics of the world. Despite widespread cultivation, the large-fruited tomatoes have a comparatively poor record for escape and establishment in the wild. As to the fundamental causes and a more explicit genetic explanation for extra-chromosomal tolerance, only calculated guesses can be made. It would be of interest in this connection to test the tolerance of several recognized wild tomato species.

The limits of chromosomal unbalance in the tomato are most likely determined by sporophyte viability. Although many unbalanced gametes are inviable, the detectable abortion of embryo sacs cannot nearly account for the infertility of triploids. The extreme weakness of plants having the highest aneuploid chromosome numbers is itself good evidence of zygotic elimination.

SUMMARY

Plants of the tomato variety Red Cherry tolerate more extra chromosomes than those of large-fruited varieties, as verified by statistical differences in the progeny of triploids and of multiple trisomics. Fertility is likewise less reduced and gross morphology less modified by aneuploidy in this variety. Based on these findings and others reported in the literature, this tolerance is attributed to the greater viability and plasticity of wild or primitive races.

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