X-RAY-INDUCED DEFICIENCIES OF CHROMOSOME 11 IN THE TOMATO[1]

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IDENTIFICATION of the linkage group of chromosome 11 of the tomato by use of the trisomic ratio method has so far been unsuccessful. A trisomic with distinctive phenotype (hereafter designated as 1-134) had been earlier identified cytologically as triplo-11 (RICK *and* BARTON 1954). But other features of 1-134 are anomalous: it had been recovered only once in very large aneuploid progenies of triploids, yet the extra chromosome is transmitted to a relatively high proportion of its progeny; the offspring of 1-134 consistently include triplo-7 and triplo-10. These characteristics suggested that 1-134 might be a tertiary trisomic—a condition also indicated by our recent discovery of rare pentavalents in its PMC's and by trisomic ratios for *cm* encountered in progenies of both 1-134 and triplo-10 (RICK and DEMPSEY, unpublished). Corroboration of the true nature of 1-134 at pachytene would be highly desirable, but such analysis is complicated by problems of a tertiary trisomic and by a condition of general asynapsis characteristic of 1-134.

Since our trisomic collection presumably did not include true triplo-11, the problem of detecting the linkage group corresponding to chromosome 11 was approached by use of X-ray-induced deletions. The most likely candidate was linkage group V, since its tested genes (a_1, *f*, j_1) have not yielded trisomic ratios with any of the primary trisomics (RICK and BARTON 1954 and unpublished).

MATERIALS AND METHODS

Pollen of normal nonmutant tomatoes was treated with various doses of X-rays from a G. E. dental unit, filtered with ½ mm of aluminum at 90 kv and an intensity of 300r/min. Immediately after treatment the irradiated pollen was applied to stigmas of a stock of ms_2 a_1 *hl*, the latter two genes conditioning easily identified seedling characters of group V and ms_2, a male sterility that prevents the procreation of any selfed contaminants, which could be highly distracting in such tests. Doses of 5,000, 10,000, and 20,000r were used, but results clearly demonstrated 5,000r to be the most efficient dose.

The immediate progeny of these treatments were grown and searched for individuals with the recessive marker characters. Such individuals were grown

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to maturity for full observation of their phenotypes, tests of fertility, and examination of their chromosomes. For the latter purpose, standard acetocarmine smears were made. Anthers were fixed under aspiration in 3:1 alcoholic acetic and prestained in alcoholic HCl-carmine (LEE 1921) as adapted by DR. S. R. SNOW.

EXPERIMENTAL RESULTS

This exploratory test proved fruitful beyond expectation. Slightly less than two percent of the progeny of the 5,000r treatment were mutant for one or both markers, and, in terms of reproductive rate, roughly one mutant seedling appeared for every two fruits harvested. This dose evidently had the merits of reducing pollen viability only slightly yet yielding deletions at a workable rate. Classification of the progeny at this dose is summarized in Table 1.

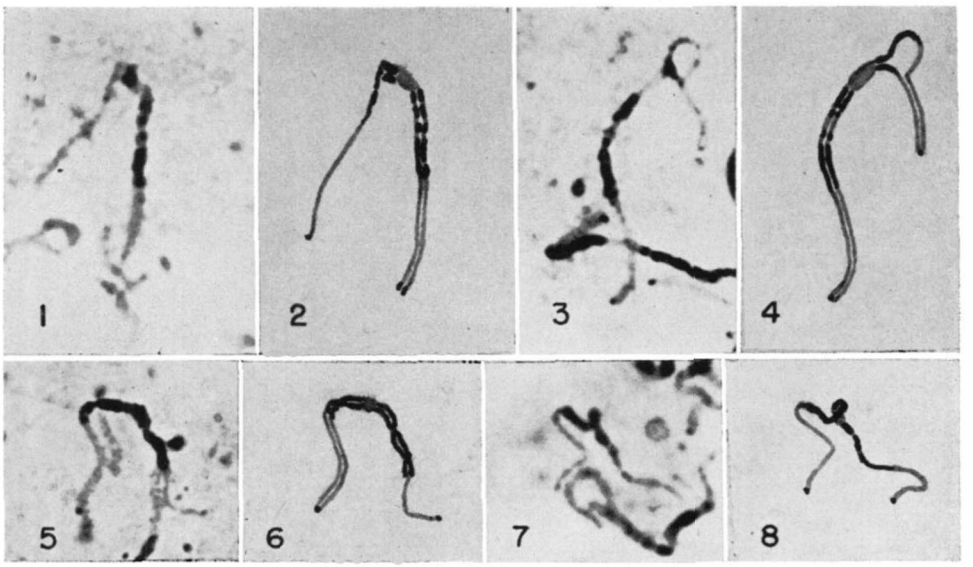
TABLE 1

Phenotypic classification of progeny from tomato pollen treated with 5,000r

	+ +	+ *hl*	a_1 +	a_1 *hl*
Number	2,312	19	16	10
Percentage	98.1	0.8	0.7	0.4

The mutant seedlings, retained and grown to maturity, could be segregated into phenotypic classes for "syndrome" characters of the same nature as those upon which trisomic identifications are based. Representatives of each of these classes were examined cytologically with results that were consistent with the phenotypic identifications. Of the + *hl* group, all except some weak abnormal seedlings conformed to an elongate, erect stature, and relatively vigorous condition. Preparations revealed terminal deficiencies with the achromatic region and most of the chromatic zone of the short arm of chromosome 11 missing for three individuals, and an interstitial deficiency including a short segment of the achromatic region and some of the adjacent chromatic section in the same arm for a fourth plant. Representative deficiencies of both types are illustrated in Figures 1 to 4. The regions missing in the interstitial deficiency could be detected by the loop formed by the normal chromatid (Figures 3 and 4). The plant with the latter aberration displayed more vigor and proved more fruitful than the other three, but otherwise conformed with them in phenotype.

The a_1 + plants were remarkably uniform for a broad rugose leaf, short internodes, and considerable vigor. All four cytologically studied plants lacked the achromatic portion of the long arm of one homologue of chromosome 11. In one plant the break appeared to be at the junction of the chromatic and achromatic, two lacked two chromomeres of the chromatic and one lacked one chromomere. A typical example of this type of loss is illustrated in Figures 5 and 6. The majority of the deletions are therefore terminal and all of the breaks occur in or near the proximal chromatic regions. These examinations leave no doubt that group V



FIGURES 1–8.—Tomato pachytene chromosomes showing heterozygous deficiencies for chromosome 11 2,000 ×. Odd-numbered figures are photomicrographs. Even-numbered figures are interpretive camera-lucida drawings. (1 and 2) + *hl* terminal deficiency; (3 and 4) + *hl* interstitial deficiency; (5 and 6) a_1 + terminal deficiency; (7 and 8) univalent in haplo-11.

belongs on chromosome 11 with a_1 in the achromatic of the long arm and *hl* in either the chromatic or achromatic, but close to the junction between the two in the short arm. Chromosome 11 is therefore the first of the tomato set to have the centromere approximated in its linkage group.

The a_1–*hl* plants were, predictably, haploid and monosomic, one of the former and nine of the latter. The phenotypes of these two chromosomal deviants are remarkably well defined. This haploid, like others described for the tomato, had the appearance of a diminutive, dainty diploid. The others conformed uniformly to a weak plant type with few, upright branches, with small, nonpendant leaves having a reduced number of segments, and with flowers tending to be fasciated. The chromosome number 23 was counted in somatic and meiotic plates of three plants in this group, and the univalent was identified as chromosome 11 in pachytene for two plants (Figures 7 and 8). The figures showed no evidence of translocation. Since all the plants of this group conformed in all the aforementioned details to a unique phenotype, including a_1 and *hl*, it can be safely assumed that all were haplo-11. These plants represent the first monosomics reported for tomatoes and one of the very few instances for diploid plants in general.

DISCUSSION

Interest centers particularly upon the production and survival of tomato monosomics. It was heretofore assumed that such tomato aneuploids would be inviable because they failed to appear in the progeny of haploids and asynaptics, whose

disturbed meiosis could be expected to yield N-1 gametes at high frequencies (RICK and BUTLER 1956). The success of our present efforts is most likely vested in averting the elimination in gametogenesis by treating mature pollen. Thus, although asynaptics and haploids yield a high proportion of deficient microspores, none apparently survive gametogenesis. Transmission in matings with haplo-11 might shed light on this problem, but all pollinations thus far attempted have failed to yield progeny. It is interesting in this light that irradiation of pollen also produced monosomics (but of translocation type) in *Petunia hybrida*, whose chromosome number, seven, is the lowest known in the Solanaceae (RICK 1943). Tests are in progress to determine if other tomato monosomics are viable. As with haplo-11, they might logically be sought for the shortest chromosomes of the complement.

Another point of interest concerns the position of the induced breaks. Although the examined sample of eight plants is small, it is doubtless significant that all breaks occurred in or very near the proximal chromatic zones of chromosome 11. A similar high propensity for breakage in this region was found for all tomato chromosomes by GOTTSCHALK (1951) and BARTON (1954). The latter reported a very much higher frequency of breaks in the chromatic zones than in the achromatic following treatment of mature pollen by X-rays and ultraviolet. In tomato material treated premeiotically and examined in pachytene, the former discovered more than twice as many breaks in the chromatic zone but a still higher frequency within the centromere. The short interval between treatment and examination undoubtedly accounts for the much higher survival of centromere breaks in GOTTSCHALK's experiments than in BARTON's or ours. The tomato results contrast sharply with the findings of SAX (1940) in Tradescantia and LONGLEY (1950) in Zea of only slightly higher induced break frequencies near the centromere. The differentiation of tomato chromosomes into chromatic and achromatic regions might account for this striking difference between species.

SUMMARY

The tomato linkage group V, including the markers a_1 and *hl*, was identified with chromosome 11 by means of the radiation-induced deficiency method. Terminal deficiencies were induced in both arms and an interstitial deficiency in one arm of chromosome 11, and plants monosomic for this chromosome were also cytologically identified in the progeny. The gene a_1 resides in the achromatic region of the long arm and *hl* in either the achromatic or chromatic close to the junction of the two in the short arm of chromosome 11. The significance of survival of tomato monosomics in this test is discussed.

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