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Cytogenetic Studies on the F_1 Hybrid *Solanum indicum* × *S. torvum*

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Summary. The F_1 hybrid *Solanum indicum* × *S. torvum* could be maintained only under special conditions. Meiosis was highly irregular: about 45% of chromosomes remained as univalents and wherever pairing was observed, it appeared to be loose. A maximum number of three higher chromosome associations other than bivalents, including 'Y' and 'spoon' type associations, indicate extensive chromosome repatterning. Occasional occurrence of twelve bivalents per PMC suggests that, notwithstanding the extreme divergence, the species have retained sufficient ancestral chromosome homoeologies. Chromosome distribution at anaphase-I was highly irregular and precocious division of chromosomes was observed frequently. This hybrid was 100% sterile and the dropping off of immature flower buds was observed.

Key words: *Solanum indicum* – *Solanum torvum* – F_1 *Solanum* hybrid – Meiosis – Sterility

Introduction

Based on crossability relationships, spinous *Solanums*, which are of considerable economic importance, are classified into two groups: one group consists of *S. melongena* and its wild forms, *S. indicum, S. surattense* (*S. xanthocarpum*) etc. and the other comprises *S. torvum, S. hispidum, S. ferox, S. khasianum*, etc.. Members of the former group intercross freely in one or reciprocal directions and members of the latter group are cross-infertile both among themselves and with the members of the former group. All reported cases of hybridization belong to the members of the former group (Sarvayya 1936; Hagiwara and Iida 1939; Tatebe 1939; Bhadhuri 1951; Magoon et al. 1962; Zutshi 1967; Rajasekaran 1969, 1970a, 1970b, 1971; Rajasekaran and Sivasubramanian 1971; Rangaswamy and Kadambavanasundaram 1974; Veerabhadrarao 1977; Veerabhadrarao and Rao 1977b, 1977c; Reayatkhan et al. 1978; Shamim Baksh 1979). Veerabhadrarao (1977), however, obtained the hybrid *S. indicum* × *S. torvum*, which could not be maintained beyond the few-leaved stage. He thought that the intergenomic association could be lethal. With a view to elucidating the chromosome relationships of species belonging to both the groups, some of the locally available species were inter-crossed and our observations on the F_1 *S. indicum* × *S. torvum* are reported here.

Material and Methods

Seed material of *S. indicum* L. and *S. torvum* Swartz was collected from plants occurring wild. The method used for crossing was that employed previously by Veerabhadrarao and Rao (1977a). A standard propionic carmine procedure was followed for pollen mother cell (PMC) smears.

Results and Discussion

Out of 25 controlled pollinations made, only one was successful. The solitary fruit obtained contained 95 seeds; 78 of which were shrivelled. Out of the remaining 17 seeds 15 germinated and only one of them gave the interspecific hybrid, the rest became maternal diploids. In the reciprocal direction, i.e. *S. torvum* × *S. indicum*, 90 crosses were made without success. The F_1 *S. indicum* × *S. torvum* was stunted in growth and no active growth was observed after the 2-leaved stage. After a regular application of fertilizers (urea and di-ammonium phosphate) and sprays of 0.001% gibberellic acid (aqueous), active growth could be induced. *S. indicum* was a small prostrate and highly-spreading herb with purple flowers on 3-4 flowered cymose inflorescences and solitary yellow fruits whereas *S. torvum* was an erect shrub, often reaching 3 to 4 metres in height. The F_1 hybrid resembled the pistillate parent in having more spines per unit area and spiny calyx; it resembled the staminate

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parent in being erect and possessing highly lobed leaves, many flowered inflorescences and white flowers. However, flowers were smaller than in both the parents.

Chromosome synapsis was very poor in the hybrid, while the parental materials showed regular meiosis with the formation of twelve bivalents (2 n = 24). In the F_1, chromosomes at pachytene remained unpaired along a greater part of their lengths. However, some chromosomes could be seen running parallelly in close juxtaposition in some nuclei. It was not possible to determine whether such regions represent true pairing of the partially homoeologous chromosomes or two strands running parallel to each other without any synaptic significance.

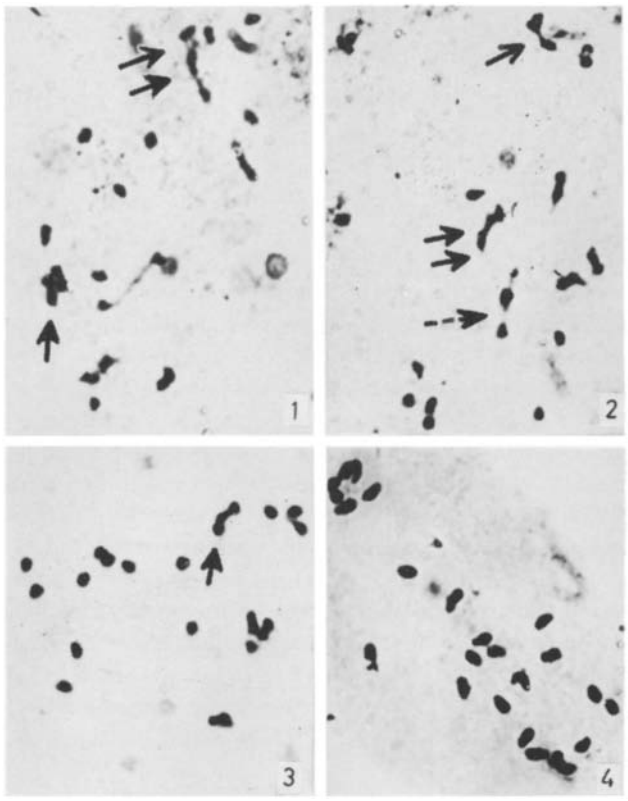
Various types and kinds of chromosome associations encountered in the F_1 are summarized in Tables 1 and 2. Chromosome associations in the hybrid ranged from $2_{IV} + 5_{II} + 6_I$ and $1_{IV} + 2_{III} + 1_{II} + 12_I$ to $2_{II} + 20_I$ per PMC. Only two out of 151 PMCs analyzed showed the occurrence of 11 to 12 bivalents per PMC. Univalents ranged from 0 to 20 per PMC and the percentage of chromosomes remaining unpaired was 44.56 (Figs. 1-4, Table 1).

The F_1 hybrid showed a mean chiasma frequency per bivalent of 0.66 and 0.62 at diakinesis and metaphase-I, respectively. Corresponding values obtained in the parents *S. indicum* and *S. torvum* were 1.68 and 1.66, and 1.69 and 1.64, respectively.

Table 1. Types of chromosome associations observed in the F_1

Number of cells analysed	
Diakinesis	87
Metaphase – I	64
Percentage of chromosomes forming	
Quadrivalents	3.97 (0-2)
Trivalents	6.04 (0-2)
Bivalents	45.41 (0-12)
Univalents	44.56 (0-20)
Frequency of higher chromosome associations/cell	a (0-3)
Mean frequency of bivalents/PMC at diakinesis	5.57
Percentage of ring bivalents/total bivalents	8.30
Mean frequency of bivalents/PMC at metaphase-I	5.38
Percentage ring bivalents/total bivalents	7.60

Figures in parentheses indicate range
[a] Mean frequencies given in Table 2

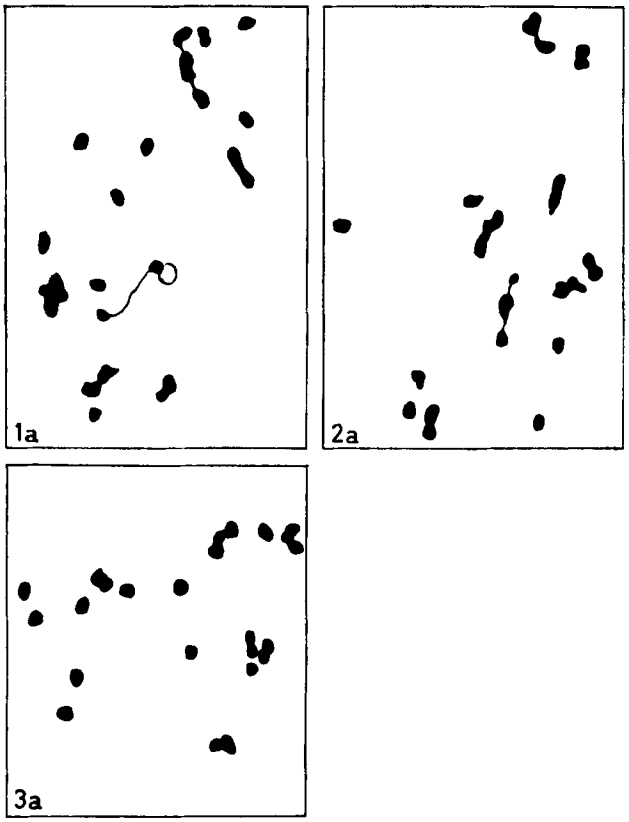


Figs. 1-4. Meiosis in the F_1 hybrid *S. indicum* × *S. torvum* (all figures × 1500). 1 Diakinesis – $1_{IV} + 1_{III} + 4_{II} + 9_I$ (ring of four-single-arrow; chain of three-double arrow); 2 Diakinesis – Metaphase-I – $2_{III} + 6_{II} + 6_I$ ('spoon' trivalent-single arrow; chain trivalent-double arrow; a heteromorphic bivalent-broken arrow. Note that in the heteromorphic bivalent, one of the chromosomes in satellited and the other is non-satellited); 3 Diakinesis – Metaphase-I – $1_{III} + 5_{II} + 11_I$ (chain trivalent – arrow); 4 Irregular chromosome distribution at anaphase-I.

Table 2. Frequencies of various types of higher chromosome associations observed at diakinesis and metaphase-I in the F_1

Total PMCs	Association of threes				Association of fours				
	Types			Total	Types				Total
	--- >– ○–				---- >– ○-- □				
151	54	13	6	73 (0.48)	24	2	1	9	36 (0.24)

Figures in parentheses indicate mean frequency



Figs. 1a-3a. Explanatory diagrams for Figs. 1-3

All the above cytogenetical observations point to the fact that the genomes of *S. indicum* and *S. torvum* diverged to a very great extent during the evolutionary process. On average, about 45% of the total chromosomes remained as univalents indicating highly reduced homologies. A maximum number of three higher chromosome associations than bivalents per PMC suggests that the constituent genomes differ at least by three interchanges. Moreover, special types of higher associations such as 'Y' and 'spoon' (Fig. 2, Table 2) suggest that for some interchanges there were interstitial break points. These are supported by the fact that heteromorphic bivalents occurred frequently (Fig. 2) which suggest gross chromosomal differences between species. Chromosome association at diakinesis-metaphase-I appeared to be loose which again indicates greatly reduced chromosome homologies between the two species.

Later stages of meiosis were abnormal. Chromosome segregation at anaphase-I was very irregular, ranging from 11:13 to 5:19. No PMC with 12:12 distribution was observed. In each PMC 2 to 13 laggards were observed; some of them divided precociously. No PMC in second meiotic division could be observed. This hybrid was 100% sterile and flower-buds generally dropped off long before maturity. Such dropping off of immature flower-buds was also observed in the F_1 hybrid *S. zuccagnianum* × *S. melongena* by Rajasekaran and Sivasubramanian (1971) who attributed the same phenomenon to high sterility. Sterility in the present case could be explained by extensive chromosome repatterning, very poor chromosome pairing, high incidence of univalents, abnormal chromosome segregation at anaphase-I and prececious division of univalents.

All the above cytogenetic observations on the F_1 hybrid between *S. indicum* and *S. torvum* prove that the species are strictly reproductively isolated. Even obtaining and maintaining the hybrid was very difficult. Thus the separation of these species into different groups by Bhadhuri (1951) and Veerabhadrarao (1977) is easily justified.

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