BULL. BOT. SURV. INDIA
Vol. 16, Nos. 1-4 : pp. 35-39, 1974

GENETIC SYSTEM AND EVOLUTIONARY TRENDS IN *SOLANUM NIGRUM* COMPLEX II: CYTOMORPHOLOGICAL STUDIES OF THE HYBRIDS BETWEEN HEXAPLOID INDIAN *SOLANUM NIGRUM* LINN. AND *SOLANUM NODIFLORUM* JACQ.

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ABSTRACT

Cytomorphological characteristics of Indian hexaploid *S. nigrum* and *S. nodiflorum* and of their F_1 hybrids were studied. The parents differed significantly in several morphological and cytological characters. The hybrids were highly sterile and did not set seed. They showed a wide range of meiotic irregularities. In several pollen mother cells, trivalents and quadrivalents were recorded, although in a very low frequency, in addition to a large number of univalents and bivalents. Occasionally bridges with or without fragments were recorded. The results of these investigations show that chromosomal differences as well as genic differences have played an important role in reproductive isolation and morphological differentiation of the two species.

INTRODUCTION

Cytotaxonomists in general and those dealing with the genus *Solanum* in particular have considered the *S. nigrum* complex of special interest from several points of view (*see* D'Arcy, 1974). The interrelationships of the members of the *S. nigrum* complex have often been a puzzle to the evolutionary biologists (Stebbins, 1950; Bhaduri, 1951; Tandon and Rao, 1966; Chennaveeraiah and Patil, 1968; Usha and Kaul, 1974). The authors, therefore, selected this complex to study its biosystematics, mainly with a view to unravelling the nature of sterility barriers and the phyletic relationships among the species of the complex. Cytomorphology and nature of sterility barriers of interspecific hybrids of some species of *S. nigrum* complex has been described in an earlier paper of this series by the authors (Rao, Khan and Khan, 1975). The present paper describes the cytomorphology of the hybrids between Indian hexaploid *S. nigram* and *S. nodiflorum*.

MATERIALS AND METHODS

Several reciprocal cross pollinations were attempted between Indian hexaploid *S. nigrum* and *S. nodiflorum*. Meiosis was studied in squashes of pollen mother cells fixed in Carnoy's fluid. The preparations were made permanent with butyl alcohol (*see* Swaminathan, Magoon and Mehra, 1954; Bhaduri and Ghosh, 1954). Pollen fertility was determined by stainability in acetocarmine.

OBSERVATIONS

Morphology of the parents: The plants of Indian hexaploid *S. nigrum* and *S. nodiflorum* were morphologically compared under identical experimental conditions and found that the two populations differed significantly in several morphological characters (Fig. 1). In Indian hexaploid *S. nigrum* the fruits are larger and purplish black while in *S. nodiflorum* they are small and shiny bluish black (Fig. 2). The gametic chromosome number of the Indian hexaploid *S. nigrum* is 36 whereas that of *S. nodiflorum* is 12. A detailed comparative account of morphological characters of the two species is presented in the following Table (p. 36).

Hybridization: Several reciprocal cross pollinations were made between Indian hexaploid *S. nigrum* and *S. nodiflorum*. However, the crosses were successful only when the species with higher chromosome number was used as the female parent.

Out of 66 cross pollinations made only 25

mature fruits were obtained with a total number of 10 seeds. All the 10 seeds were sown but only four germinated and developed into adult plants.

Morphology of the hybrids: Morphological characters of the hybrids, Indian hexaploid *S. nigrum* × *S. nodiflorum*, were studied and compared with those of the parents (Fig. 1). The data are presented in the Table. The hybrids resembled the hexaploid parent in general morphological features. As compared to the parents, the hybrids were taller and bore large, thick and dark green leaves. They flowered profusely and produced very small purplish black fruits (Fig. 2) without seeds. The hybrids were sterile and the percentage of pollen fertility was 1.95 whereas in Indian hexaploid *S. nigrum* it was 74.70 and in *S. nodiflorum* 71.50 (Figs. 3-5). The F1 hybrids were tetraploid, as expected, with 2n = 48 chromosomes in their pollen mother cells.

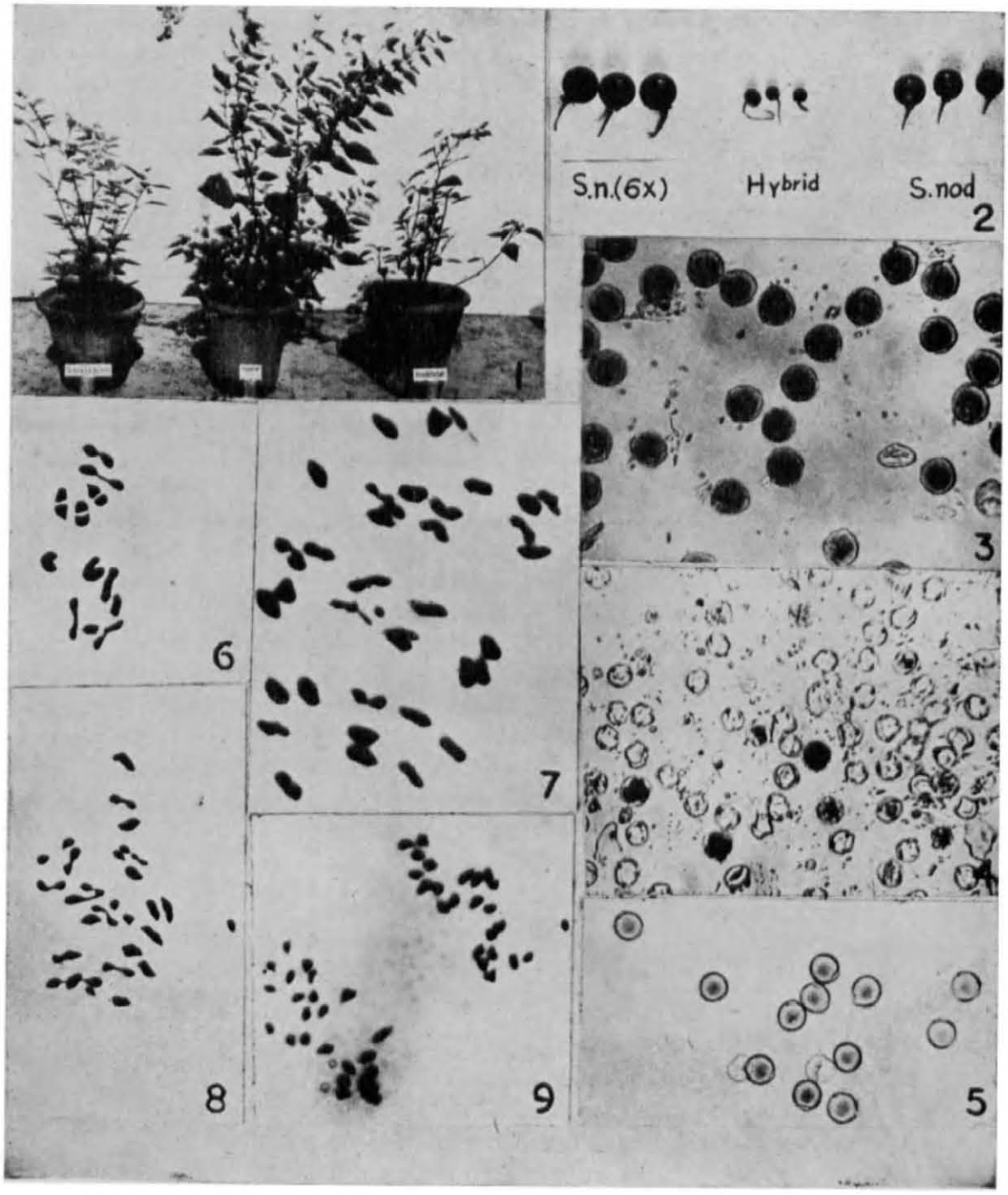
Table: Comparison of morphological characters of Indian hexaploid *S. nigrum* (used as female parent), *S. nodiflorum* and their F_1 hybrids

Characters	Indian hexaploid *S. nigrum*	*S. nodiflorum*	F_1 hybrid
Habit	Erect and branched	Erect and branched	Erect and branched
Height (cm)	78.00–95.00	40.00–90.00	98.00–111.00
Stem	Thick and green with occasional ribs	Slender and dark green without prominent ribs	Thick and dark green with prominent ribs
Leaf	Thick and ovate-lanceolate with sparsely dentate margin. Petiole marginate	Thin and ovate with ill defined margin. Petiole marginate	Thick and ovate with dentate margin. Petiole marginate
Length of petiole (cm)	1.80–5.60	1.40–4.50	1.40–8.50
Length of lamina (cm)	6.50–14.30	5.90–11.00	5.00–14.50
Breadth of lamina (cm)	3.70–8.00	3.50–7.00	3.00–11.20
Thickness of leaf (μ)	35.10–81.40	25.90–57.30	31.40–49.90
No. of flowers per inflorescence	3–8	3–5	2–7
Diameter of corolla (mm)	7.50–15.00	5.00–8.00	9.20–14.50
No. of fruits per inflorescence	3–8	2–5	0–1
Diameter of fruit (mm)	7.00–9.00	4.00–6.00	1.00–2.50
Colour of fruit	Purplish black	Shiny bluish black	Purplish black
No. of seeds per fruit	21–66	3–70	—
Diameter of pollen grain (μ)	18.00–32.40	12.60–25.20	9.00–30.60
Percentage of pollen fertility	74.70	71.50	1.95
Gametic chromosome number	36	12	24

Cytology of the parents: Meiosis was normal in Indian hexaploid *S. nigrum* and *S. nodiflorum*. At diakinesis and metaphase I, 12 bivalents were seen in *S. nodiflorum* (Fig. 6) while 36 bivalents were observed in Indian hexaploid *S. nigrum* (Fig. 7). The chiasma frequency per bivalent at metaphase I was 1.59 in the former species and 1.03 in the latter.

Cytology of the hybrids: The hybrids

showed irregular meiosis. Bivalents and univalents were most frequent at diakinesis and metaphase I. However, trivalents (Fig. 8) and quadrivalents were also recorded in a very low frequency. The mean pairing of chromosomes at diakinesis was 6.64 univ-



Figs. 1-9 : 1. Plant of hexaploid *S. nigrum* (left), *S. nodiflorum* (right) and their F_1 hybrid (middle). 2. Fruits of hexaploid *S. nigrum* (left), *S. nodiflorum* (right) and their F_1 hybrid (middle). 3. Pollen of hexaploid *S. nigrum*. 4. Pollen of F_1 hybrid. 5. Pollen of *S. nodiflorum*. 6. and 7. MI in *S. nodiflorum* and hexaploid *S. nigrum* showing 12 II and 36 II respectively. 8. MI in F_1 hybrid showing 16 II + 7I+3III. 9. AI in F_1 hybrid showing 24 chromosomes at each pole

ents, 17.00 bivalents, 1.60 trivalents and 0.64 quadrivalents. The bivalents in pollen mother cells ranged from 13 to 22 whereas the univalents, trivalents and quadrivalents ranged from 3 to 12, 0 to 5 and 0 to 2 respectively. The mean chiasma frequency per bivalent was 1.50.

At metaphase I, the frequency of chromosome association per cell was 9.08 univalents, 16.20 bivalents, 1.52 trivalents and 0.48 quadrivalents. The bivalents ranged from 13 to 18 whereas the univalents, trivalents and quadrivalents ranged from 1 to 20, 0 to 4 and 0 to 2 respectively. At metaphase I, the chiasma frequency per bivalent was lower (1.03) than that at diakinesis (1.50).

Anaphase I was irregular in 80% of the pollen mother cells and was often characterised by lagging chromosomes and unequal number of chromosomes at poles. The behaviour of the univalents was erratic. Bridges, with or without fragments, were recorded very rarely at anaphase I. In 20% of the cells, the distribution of chromosomes at anaphase I was normal with 24 chromosomes at each pole (Fig. 9). At telophase I and II, laggards were recorded in only 4% of the cells. Micronuclei were not observed at telophase I but were recorded at telophase II in 12% of the cells. Occasionally pentads were recorded.

DISCUSSION

The cytological analysis of interspecific or intergeneric hybrids has been of immense value in determining the probable relationships and origin of many species of plants (Goodspeed, 1934; Sax, 1935; de Wet and Harlan, 1972). This is inspite of the instances where synapsis and asynapsis are controlled by genetic (Riley and Chapman, 1958; Kimber and Riley, 1963; Riley, 1966; Taylor, 1967) and environmental factors (Sax, 1935).

The hybrids Indian hexaploid *S. nigrum* × *S. nodiflorum* were sterile and showed irregular meiosis with several univalents, bivalents and a few multivalents. The presence of univalents as early as diakinesis and a large number of them at metaphase I suggest lack of significant homology between chromosomes of the parents due to structural differences as well as genic (*see* Rangasamy and Kadambavanasundaram, 1974) and other factors (Magoon, Hougas and Cooper, 1958). The formation of as many as 22 bivalents and a few multivalents in the hybrids could be partly due to auto-synaptic and partly to allo-synaptic associations of chromosomes. The low chiasma frequency of the hybrids as compared to the parents and the occasional occurrence of bridges with or without fragments can be attributed to structural differences between the chromosomes of *S. nodiflorum* and the hexaploid form of *S. nigrum*.

S. nodiflorum differs significantly in several morphological characters from the Indian hexaploid *S. nigrum*. These morphological differences seem to be due to the accumulation of genic factors. Therefore, it appears that the structural differences as well as genic differences have played an important role in the reproductive isolation and morphological distinction of the two species from each other (*see* Venkateswarlu and Krishna Rao, 1972).

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