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INTERRELATIONSHIPS AMONG DIPLOID SPECIES OF THE *SOLANUM NIGRUM* L. COMPLEX[1]

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ABSTRACT

A few diploid species of the *Solanum nigrum* L. complex were selected with a view to finding out the relationship among them as revealed by crossability studies and pairing behaviour of chromosomes of their hybrids. Cytomorphology of the species was studied. The reciprocal crosses between *S. douglacii* and *S. americanum*, diploid *S. nigrum*, *S. nodiflorum*, *S. noidiflorum* ssp. *nutans* and *S. sarcachoides* were not successful. It is suspected that *S. douglasii* is distantly related to the other species. The reciprocal crosses between *S. nodiflorum* ssp. *nodiflorum* and *S. douglasii* produced several fertile reciprocal hybrids of identical morphological features with normal meiosis, whereas the other reciprocal crosses between *S. nodiflorum* ssp. *nutans* and *S. douglasii* have failed. A possible explanation for such behaviour is offered. On the basis of pairing behaviour of chromosomes of the hybrids between *S. nodiflorum* spp. *nodiflorum* and *S. douglasii* it is suspected that the two species have close genetic relationship with each other.

INTRODUCTION

One of the most wide spread and variable species of the genus *Solanum* is that centering around the type species, *Solanum nigrum* L. Therefore, the species *S. nigrum* has been considered as *S. nigrum* complex. Members of the complex are highly variable phenotypically and form a polyploid complex based on X=21. The complex consists of a group of plants in which a series of closely related diploid species support the superstructure of polyploids whose members often cannot be separated morphologically from diploids. Even though the *S. nigrum* complex has been the subject of study throughout the world (see Henderson, 1974), significant information is not immediately known regarding the phyletic relationships among the species of the complex (see Schilling and Heiser, 1979). For present work a few diploid species of the complex were selected with a view to finding out the relationship among them as revealed by crossability studies and pairing behaviour of chromosomes of their hybrids.

MATERIALS AND METHODS

In present study the following species were used: *Solanum americanum* Mill., *S. douglasii* Dun., *S. nigrum* L. (2X), *S. nodi florum* Jacq., *S. nodiflorum* Jacq., ssp. *nodiflorum*, *S. nodiflorum* Jacq. ssp. *nutans* R. J. Henderson and *S. sarachoides* Sendt.

The seeds of the species, except *S. nigrum* and *S. sarachoides*, were obtained from Dr. R. J. Henderson, Queensland Herbarium, Queensland, Australia. The seeds of diploid *S. nigrum* were collected from local populations growing in and

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around Delhi. A stock of *S. sarachoides* was raised from seed supplied by Dr. J.M. Edmonds, Cambridge University Botany School, Cambridge, England.

Several reciprocal cross pollinations were made among the species. For cytological studies flower buds were fixed in Carnoy's fluid and meiosis was studied from propiono-carmine squashes of pollen mother cells (Swaminathan *et al.*, 1954). The slides were made permanent by butyl alcohol schedule (Bhaduri and Ghosh, 1954).

OBSERVATIONS

Results of hybridization :

The reciprocal crosses between *S. nodiflorum* ssp. *nodiflorum* and *S. douglasii* produced fruits with viable seeds, but failed to produce fruits between *S. douglasii* and *S. americanum, S. nigrum* (2x) *S. nodiflorum, S. nodiflorum* ssp. *nutans,* and *S. sarachoides*. One hundred flowers of *S. nodiflorum* ssp. *nodiflorum* were pollinated with pollen of *S. douglasii*. Sixty five mature fruits were obtained with a total number of 200 seeds, the germination percentage was 72.

Cytomorphology of the parents and hybrids :

Description of morphological characters of the species is given in Table I. The hybrids (F_1) between *S. nodiflorum* ssp. *nodiflorum* and *S. douglasii* were erect and exhibited a more luxurious growth as compared to parents (Table II, Fig. 1) and flowered abundantly, but they were late in flowering and continued to grow for longer period than the parents. The fruits were bluish black. The mean number of seeds per fruit was 76. The pollen fertility was 84%. The reciprocal hybrids were morphologically alike. A detailed comparative account of morphological features of the parents and hybrids is given in Table 2.

The species *S. americanum, S. nigrum* (2x), *S. nodiflorum* Jacq. ssp. *nutans* and *S. sarachoides* showed normal meiosis with 12 bivalents at metaphase I and the frequency of chiasmata, per bivalent, in the species is 1.23, 1.13, 1.33 and 1.20, respectively. The subsequent course of meiosis was normal

S. nodiflorum ssp. *nodiflorum* and *S. douglasii* showed normal meiosis with 12 bivalents (Figs. 2, 3). In the former the frequency of chiasmata, per bivalent- at diakinesis and metaphase I was 1.82 and 1.33, respectively, while in the latter it was 1.84 at diakinesis and 1.25 at metaphase I. In both the species the fruther stages of meiosis were normal. The hybrids between the two species showed normal chromosome pairing at diakinesis and metaphase I (Fig. 4). Univalents and multivalents were absent. The number of ring bivalents, per cell, decreased from diakinesis to metaphase I and this was followed by an increase in number of rod bivalents. The frequecy of chiasmata, per bivalent, wàs less at metaphase I (1.20) than at diakinesis (1.78). At anaphase I, the distribution of chromosomes was normal with 12 chromosomes at each pole (Fig. 5). The subsequent stages of meiosis were regular. Tetrads were normal and size of pollen was uniform.

DISCUSSION

The close similarity of morphological features of *S. nodiflorum* ssp. *nodiflorum* and *S. douglasii,* and their ready reciprocal crossability with each other producing fertile reciprocal hybrids of identical morphological characters may indicate the close genetic relationship of the two species. The occurrence of 12 bivalents in all pollen mother cells of the hybrids, at diakinesis and metaphase I, may be due to allosyndetic pairing and thereby

TABLE I

COMPARISON OF MORPHOLOGICAL CHARACTERS OF DIPLOID SPECIES OF THE *SOLANUM NIGRUM* COMPLEX

Characters	*S. americanum*	*S. nigrum* (2x)	*S. nodiflorum*	*S. nodiflorum* ssp. *nutans*	*S. sarachoides*
Habit	Erect and short with spreading branches	Erect and branched	Erect and branched	Erect and tall with sprawling branches	Short and semi-erect with drooping branches
Height (cm)	59.40(42.50–79.50 68.00)	(61.60–98.00)	89.00(52.30–100.50)	91.23(61.40–141.00)	25.00(18.40–32.00)
Stem	Angular and dark green without prominent ridges	Cylindrical and green Ridges glabrous or somewhat pubescent	Cylindrical and dark green without prominent ridges	Cylindrical and green with smooth ridges	Cylindrical and green with eglandular hairs of unequal length.
Leaf	Thin and ovate with entire margin. Petiole marginate	Thick and ovate with toothed margin. Petiole marginate	Thin and ovate with ill-defined. margin. Petiole marginate	Thin and ovate to elliptic with ill-defined dentate margin	Thick, pale green and ovate with ill-defined toothed margin. Eglandular hairs are present on upper surface. Retiale marginate
Petiole length (cm)	1.66(1.20–2.80)	3.12(1.20–4.80)	3.27(1.50–4.70)	3.18(1.40–4.10)	0.96(0.60–1.20)
Lamina length (cm)	6.60(4.10–7.80)	8.60(4.40–11.	8.12(5.60–11.10)	8.10(5.40–11.30)	3.00(250–5.60)
Lamina breath (cm)	2.93(2.10–4.20)	4.54(2.80–5.90)	5.00(3.30–6.90)	3.86(3.10–5.80)	1.94(1.50–2.50)
Inflorescence	Umbelliform	Racemiform	Umbelliform	Umbelliform	Simple cymes
Peduncle	Unbranched and erect	Unbranched, short and erect	Unbranched or rarely branched, short and erect	Unbranched, short and erect	Unbranched, short and bifurcate
Pedicel	Deflexed in flower, but erect in fruit	Decurved to ascending in flower and decurved in fruit	Decurved to erect in flower and erect to pendulous in fruit	Erect in flower and strongly curved in fruit	Decurved in flower, but pendulous in fruit
Flowers/inflorescence	6(3–8)	4(3–5)	5(3–6)	6(3–7)	4(3–6)

TABLLE I—(Contd.)

Characters	*S. americanum*	*S. nigrum* (2x)	*S. nodiflorum*	*S. nodiflorum* ssp. *nutans*	*S. sarachoides*
Calyx	Not embracing the fruit	Not embracing the fruit	Not embracing the fruit	Not embracing the fruit	Embracing about half of the fruit
Corolla diameter (mm)	10.00(8.00–11.00)	6.31(5.00–7.00)	7.00(5.00–8.00)	6.14(5.00–8.00)	7.00(6.00–10.00)
Fruits/inflorescence	6(3–8)	4(2–5)	5(2–6)	5(2–7)	4(2–5)
Fruit diameter (mm)	7.00(6.00–8.00)	6.03(4.00–8.00)	7.12(4.00–8.00)	6.23(4.00–8.00)	7.00(5.00–8.00)
Fruit colour	Purplish black	Shiny bluish black	Shiny bluish black	Shiny purplish black	Greenish brown
Seeds/fruit	52(22–60)	64(11–72)	63(3–70)	68(13–72)	22(7–29)
Pollen grain diameter (μ)	24.90(18.60–27.90)	24.16(18.60–24.80)	21.98(15.50–24.80)	22.46(12.40–27.90)	24.00(21.70–27.90)
Pollen fertility (%)	89.46(83.50–96.00)	82.46(68.50–89.01)	80.43(71.50–89.40)	78.25(72.50–88.00)	76.00(74.00–81.12)
Chromosome number (n)	12	12	12	12	12

N.B. : The range of values is given in parentheses.

TABLE II

COMPARISON OF MORPHOLOGICAL CHARACTERS OF *Solanum nodiflorum* spp. *nodiflorum*, *S. douglasii* AND THEIR F_1 HYBRIDS

Characters	*S. nodiflorum* ssp. *nodiflorum*	*S. douglasii*	Hybrids
Habit	Erect and tall with sprawling braches	Erect, tall and bushy	Erect, tall and bushy
Height (cm)	87.56 (65.60-106.00)	84.00 (48.00-95.00)	(130.60 96.70-178.0)0
Stem	Cylindrical and green with smooth ridges	Angular and green with rough ridges	Angular and green with smooth ridges
Leaf	Thin, ovate to elliptical with highly dentate margin. Petiole marginate.	Thick and ovate to narrowly elliptical with entire margin. Petiole marginate.	Thick and ovate to narrowly elliptical with entire margin. Petiole marginate.
Petiole length (cm)	3.14 (1.30-4.10)	3.06 (1.30-4.90)	3.84 (1.50-5.60)
Lamina length (cm)	7.24 (5.40-11.20)	8.12 (3.00-10.20)	9.10 (5.00:11.40)
Lamina breadth (cm)	4.98 (3.20-6.20)	5.00 (3.40-6.60)	5.20 (3.20-6.90)
Flowers/inflorescence	6 (5-7)	7 (3-8)	6(3-8)
Corolla diameter (mm)	6.50 (5.00-7.00)	10.12 (8.00-12.00)	10.10 (8.00-12.00)
Fruits/inflorescence	6 (3-7)	6 (4-8)	6 (5-8)
Fruit diameter (mm)	6.42 (4.00-8.00)	7.98 (5.00-9.00)	7.24 (4.00-9.00)
Fruit colour	Shiny purplish black	Dull black	Bluish black
Seeds/fruit	68 (9-85)	78 (8-95)	76 (19-92)
Pollen grain diameter (μ)	22.10 (21.70-24.80)	23.25 (15.50-27.90)	23.50 (18.60-24.80)
Pollen fertility (%)	82.30 (72.02-85.60)	84.12 (67.42-91.12)	84.00 (69.56-89.00)
Chromosome number (n)	12	12	12

N. B: The range of values is given in parentheses.

suggesting the close identity of genomes of the two species. Thus the studies on crossability and karyomorphology of *S. nodiflorum* spp. *nodiflorum* and *S. douglasii*, and their hybrids may indicate a close genetic link of the two species.

Several reciprocal cross pollinations between *S. douglasii* and *S. americanum*, dihloid *S. nigrum*, *S. nodiflorum*, *S. nodiflorum* ssp. *nutans*, and *S. sarachoides* were not successful even though they possess the same chromosome number. Many bio-

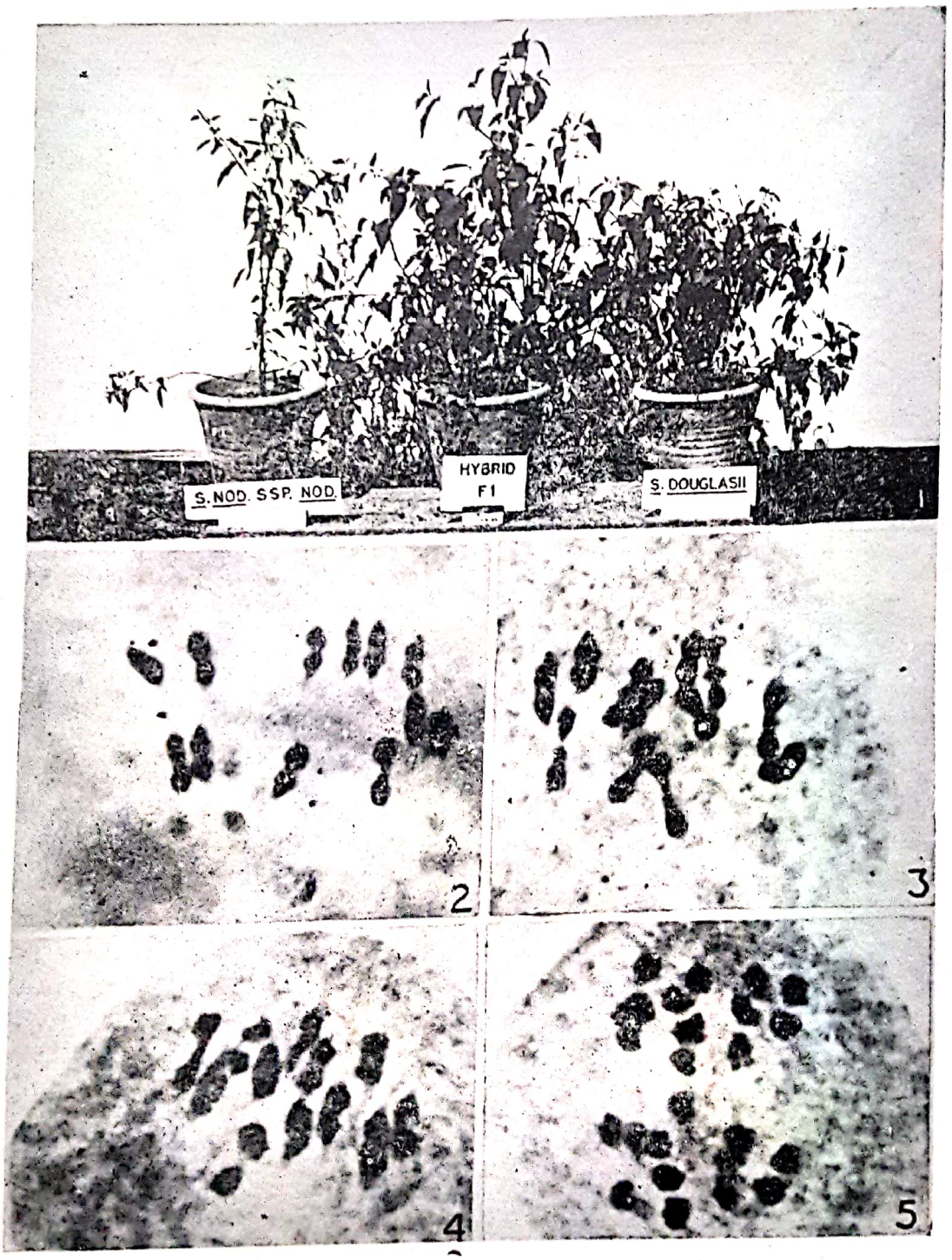

Fig. 1. Plants of *S. nodiflorum* ssp. *nodiflorum* (left), *S. douglasii* (right) and their F_1 hybrid (middle). Fig. 2. M_1 in *S. nodiflorum* ssp. *nodiflorum* showing 12_{II}. Fig. 3. M_1 in *S. douglasii* showing 12_{II}. Figs. 4 & 5. Meiosis in F_1 hybrids of the cross *S. nodiflorum* ssp. *nodiflorum* x *S. douglasii*. Fig. 4. M_1 showing 12_{II}. Fig. 5. A_1 showing 12 chromosomes at each pole.

systematists claim that species are natural populatio/ns which are genetically distinct and reproductively isolated from other species while being potentially interfertile among them (Mayr, 1942; Stebbins- 1950; Dobzhansky, 1951; Löve, 1960; Huxley, 1963). Therefore, the reproductive isolation between *S. douglasii* and the other species as indicated by failure of cross pollinations may suggest that the former is distantly related to the latter.

A feature worthy of mention here is the divergent crossing behaviour of sub-species of *S. nodiflorum* with *S. douglasii*. The reciprocal cross pollinations between *S. nodiflorum* ssp. *nodiflorum* and *S. douglasii* produced several fertile reciprocal hybrids of identical morphological characters with normal meiosis, whereas all the reciprocal crosses between *S. nodiflorum* ssp. *nutans* and *S. douglasii* failed. The reason for such crossing behaviour of sub-species of *S. nodiflorum* with *S. douglasii* is not immediately known, but a possible explanation is that the basic species, that is, *S. nodiflorum* might have undergone extensive local adaptations by developing a heterogeneous internal genetic system and this in turn might have produced gradually the successful genotypes or sub-species with cross incompatibility system with *S. douglasii*.

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