Theor. Appl. Genet. 62, 149–153 (1982)

Hybridization and Fertility of Hybrid Derivatives of *Solanum melongena* L. and *Solanum macrocarpon* L.*

D. A. Schaff, G. Jelenkovic, C. D. Boyer and B. L. Pollack
Department of Horticulture and Forestry, Rutgers University, New Brunswick, N.J. (USA)

Summary. Eleven genotypes of *Solanum melongena* L. and one genotype tentatively identified as *Solanum macrocarpon* were reciprocally intercrossed. Three patterns of the crossability were determined: a) reciprocally crossable, b) reciprocally non-crossable, and c) unidirectionally crossable. In toto 524 F_1 interspecific hybrids were grown during one season under open pollination conditions in the field. A large proportion of the F_1 hybrids produced seed set. The highest degree of seed set was recorded in the reciprocal F_1 hybrid of *S. melongena* (cv. 'Burpee Hybrid') and *S. macrocarpon* (Acc. 21–73). In addition, a limited number of backcross progeny have been produced. The germinating seeds produced an F_2 generation of which some recombinants showed a considerably higher degree of fertility than the F_1. This finding suggests the possibility of the transfer of genes for resistance to two-spotted spider mite from *S. macrocarpon* to *S. melongena.*

Key words: Interspecific hybridization – *Solanum* – Eggplant

Introduction

An African accession of *Solanum* acquired by one of the authors (B. L. Pollack), presumably of *Solanum macrocarpon* L., designated as 21–73, has displayed a marked resistance to the two-spotted spider mite, *Tetranychus urticae* Koch, at the New Jersey Agricultural Experiment Station, Rutgers University. From the point of view of the genetic improvement of the cultivated *S. melongena* eggplant, the recognition of this genetic attribute of the 21–73 is of great practical importance. The cultivars of *S. melongena* L. are notoriously susceptible to the two-spotted spider mite and as yet no available source of resistance among the genotypes of this species has been identified. Hence, hybridization of the two species may provide a practical way of transferring the resistance into the cultivated genotypes.

Previous results of the crossability and production of F_1 hybrids between these two species have been fragmentary, inconclusive and often contradictory. A number of researchers have reported unidirectional crossability, i.e. crossability is feasible only when *S. melongena* genotypes were used as the female parent (Chopde and Wanjari 1974; Rajasekaran 1970, 1970b; Wanjari 1976), while a few reported successful hybridization only when *S. macrocarpon* genotypes were used as the female parent (Omidiji 1979; Rajasekaran 1970). The resulting interspecific F_1 hybrids, however, were completely sterile and set no seed upon selfing or backcrossing (Chopde and Wanjari 1974; Omidiji 1979; Rajasekaran 1970b, 1970c; Wanjari 1976). The crossability tests, as a rule, in all previous studies have been based on a very limited number of genotypes, usually one and not more than three.

In light of this information, the production of partially fertile F_1 hybrids, which would serve as a bridge for the transfer of the resistance, appeared to be a formidable task. Nevertheless, it was reasoned, that perhaps by using a wider range of variability in *S. melongena,* a particular combination of the parental genotypes may be found that would produce at least partially fertile F_1 hybrids. In other plant species, such an approach has been frequently used (Meister and Tjumjakoff 1928; Rangasamy and Kadambavansundaram 1973, 1974; Wall and York 1960).

The present paper reports crossability studies of various *S. melongena* genotypes with *S. macrocarpon* accession 21–73. In the combinations which produced F_1 hybrids, fertility tests have been conducted. Most of the hybrids displayed a low degree of fertility. Yet, this is the first report on the hybridization of these two species which resulted in at least partially fertile F_1 hybrids.

---

* This research was performed as part of NJAES Project No. 99201 (NE-9) supported by the New Jersey Agricultural Experiment Station and Regional Hatch Funds. Paper of the Journal Series of the New Jersey Agricultural Experiment Station. Please address reprint requests to Dr. C. Boyer

0040-5752/82/0062/0149/$ 1.00

Materials and Methods

Parental Material

One African accession of *S. macrocarpon* (21–73) and four genotypes of *S. melongena* ('Rayada,' 'Rosita,' 'Italian Long' and 'White') maintained at Cook College, and seven genotypes of *S. melongena* from commercial sources ('Jersey King' and 'Burpee Hybrid' from Burpee Seed Co., 'Classic,' 'Black Oval' and 'Hibush Special' from Harris Seed Co., 'Dusky' and 'Midnight' from Peto Seed Co.) were used. Seeds were germinated in coarse horticultural grade vermiculite and transplanted at the cotyledon stage into two-inch plastic pots containing soilless mix. These plants were later transplanted either into the field or into eight-inch pots to be grown in the greenhouse.

Pollination Technique

Reciprocal crosses were made between *S. macrocarpon* (21–73) and the eleven genotypes of *S. melongena.* These pollinations were made in 1978 and 1979 in both the field and the greenhouse. Pollinations were done as described by Narasimha Rao and Ponnaiya (1970). Crossed flowers were tagged with light weight tags for easy identification. The crossed flowers were not bagged because this practice may have deleterious effects on seed set (Beamish 1955; Wanjari 1976). The calyces were removed at the time of emasculation as a prevention to ovary inhibition as postulated by Villareal (1966). The majority of the backcross were attempted with the F_1 hybrid as the female parent. Meiotic chromosomes were observed in both parental species and F_1 hybrids using the cytological techniques described in Paris et al. (1978).

Pollen Stainability

An estimate of the pollen viability of a limited number of F_1 hybrids, F_2 and BC_1 progenies was obtained by the staining of the pollen grains with propionic carmine. Anthers from freshly picked flowers in the late bud stage or those just recently opened were used for this study. All pollen grains that were both plump and deeply stained were counted as viable. Poorly or nonstained grains were classified as nonviable.

Results

The results of the crosses attempted between *S. macrocarpon* (21–73) and the eleven genotypes of *S. melongena* are presented in Table 1. The combinations of crosses revealed three patterns of crossability: a) regardless of which species was used as the female parent, the cross was successful; b) the success of the cross depended on which species was used as the female parent (Hibush Special has been successfully crossed in both directions when pollinated without emasculation at the bud break stage); and c) the cross was unsuccessful regardless of which species was the female parent. The F_1 hybrids (Fig. 1) can be distinguished from selfs at the seedling stage by the appearance of spines on the mid-ribs of the second set of true leaves as well as other contrasting parental characteristics described in Table 2. There was a reciprocal difference in the crossability of the two species. Of the pollinations made using *S. macrocarpon* as the female parent, 21.4% set fruit, while only 4% of the reciprocal crosses set fruit (Table 1).

Table 1. Crossability of one genotype of *S. macrocarpon* (mac) with eleven genotypes of *S. melongena* (mel)

Parental genotypes	Flowers pollinated (number)	Fruit set (number)
(Mel × Mac)		
('Black Oval' × 21 – 73)	25	2
('Dusky' × 21 – 73)	18	1
('Burpee Hybrid' × 21 – 73)	18	1
('Classic' × 21 – 73)	23	4
('Italian Long' × 21 – 73)	20	1
('Hibush Special' × 21 – 73)	26	0
('Midnight' × 21 – 73)	19	0
('Rayada' × 21 – 73)	6	0
('Rosita' × 21 – 73)	21	0
('White' × 21 – 73)	20	0
('Jersey King' × 21 – 73)	31	0
Total	227	9 (4.0%)
(Mac × Mel)		
(21 – 73 – 'Black Oval')	5	1
(21 – 73 × 'Dusky')	10	2
(21 – 73 × 'Burpee Hybrid')	5	2
(21 – 73 × 'Classic')	5	2
(21 – 73 × 'Hibush Special')	5	2
(21 – 73 × 'Midnight')	5	3
(21 – 73 × 'Rayada')	5	1
(21 – 73 × 'Rosita')	9	1
(21 – 73 × 'White')	5	1
(21 – 73 × 'Italian Long')	6	0
(21 – 73 × 'Jersey King')	10	0
Total	70	15 (21.4%)

The F_1 hybrids were variable in vigor, phenotypic appearance and fertility. When the hybrids were selfed by hand, they produced no fruit set. All F_2 seed production from the F_1 hybrids occurred under open pollination conditions. The hybrids produced with *S. macrocarpon* as the female parent yielded a higher percentage of partially fertile F_1 seedlings than the hybrids produced with *S. melongena* as the female parent (Table 3). The former hybrids, however, produced predominantly parthenocarpic fruits, whereas the latter hybrids yielded a considerably larger proportion of plants with seeded fruit. Hence, the hybrids with *S. melongena* as the female parent displayed a higher degree of female fertility (Table 3).

Table 2. Phenotypic characteristics of *Solanum melongena* L., *S. macrocarpon* L. and their F_1 hybrid

Genotype	Leaf surface	Leaf shape	Spininess	Fruit shape	Immature fruit color
S. melongena	pubescent	length = width	small spines on calyx	oblong	purple
S. macrocarpon	globulous	length > width	spineless	round	green
F_1	pubescent	length > width	leaf mid-rib spiny; calyx very spiny	round	green or purple

Table 3. Summary of male and female fertility[a] of F_1 hybrids between *S. melongena* and *S. macrocarpon*

Cross combination	No. F_1 seedlings grown	% F_1 plants with fruit	% F_1 plants with seeded fruits	No. of F_2 seeds obtained	Pollen stainability
(Mel × Mac)					
('Black Oval' × 21 – 73)	47	37.0	30.5	96	10.35 ± 1.14
('Burpee Hybrid' × 21 – 73)	18	38.9	33.3	144	9.55 ± 0.55
('Classic' × 21 – 73)	54	38.9	14.8	31	10.59 ± 1.18
('Hibush Special' × 21 – 73)	4[b]	25.0	25.0	27	14.60 ± 3.60
('Dusky' × 21 – 73)	35	22.9	20.0	89	–
('Italian Long' × 21 – 73)	34	0	–	–	–
Total	192	28.3	18.9	387	10.13 ± 2.42
(Mac × Mel)					
(21 – 73 × 'Burpee Hybrid')	72	70.8	29.2	162	9.23 ± 5.07
(21 – 73 × 'Classic')	80	77.2	2.6	5	1.94 ± 0.68
(21 – 73 × 'Hibush Special')	46	58.7	6.5	4	2.20 ± 1.11
(21 – 73 × 'Dusky')	11	90.9	9.1	1	–
(21 – 73 × 'Midnight')	44	31.8	2.3	1	–
(21 – 73 × 'White')	55	32.7	9.1	13	–
(21 – 73 × 'Black Oval')	9	77.8	0	–	1.03
(21 – 73 × 'Rosita')	11	72.7	0	–	–
(21 – 73 × 'Rayada')	4	0	–	–	–
Total	332	59.2	9.9	186	1.74 ± 0.72[c]

[a] Fruit produced by open pollination; [b] Selected plants from previous cross; [c] Mean of (21 – 73 × 'Burpee Hybrid') not included

Fig. 1. F_1 hybrid from the cross between *Solanum macrocarpon* (21 – 73) × *Solanum melongena* cv. 'Classic'

Among the fifteen cross combinations, the most productive combination, when considering the production of F_2 seeds, was 'Burpee Hybrid' × 21–73 and its reciprocal. With a relatively small number of F_1 plants, an adequate number of F_2 seeds were secured from these F_1 hybrids.

The pollen stainability of the hybrids with *S. melongena* as the female parent was ten percent while their reciprocals (excluding 21–73 × 'Burpee Hybrid') was approximately two percent. The hybrid of 21–73 × 'Burpee Hybrid' showed approximately the same pollen stainability regardless of the parental combination of the cross (Table 3). Observations at meiosis in a limited number of F_1 hybrids revealed the chromosome number to be $2n = 2x = 24$ and the formation of twelve bivalents and an occasional multivalent (Fig. 2).

A similar pattern of female fertility in the F_1 hybrids was observed when the hybrids were used as

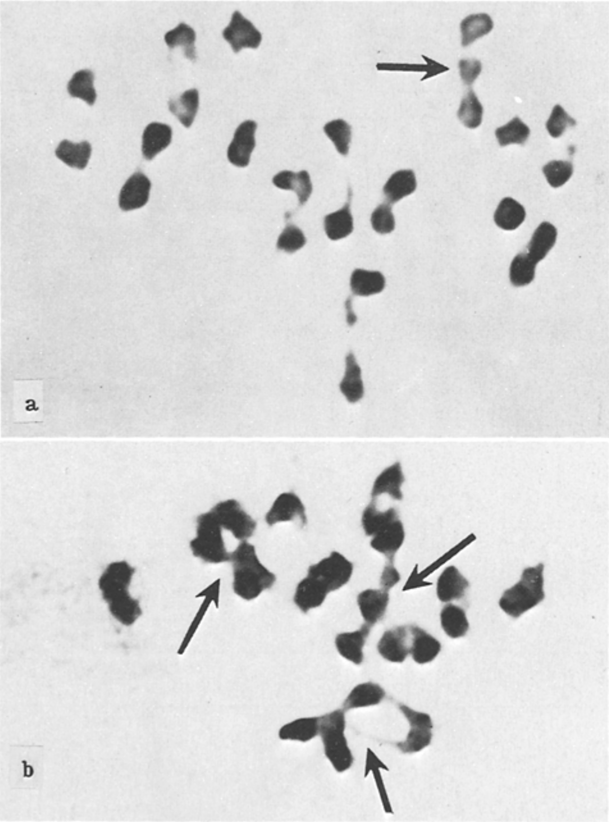

Fig. 2a and b. Meiotic chromosomes of the hybrid of *S. macrocarpon* (21 – 73) × *S. melongena* cv. 'Burpee Hybrid'. The parental genotypes and hybrid are $2n=2x=24$. **a** Metaphase I showing 12 bivalents: 11 rod bivalents and 1 ring bivalent. Also one bivalent shows non-terminalized chiasmata (arrow). **b** Premetaphase I showing multivalent associations (arrows): two quadrivalents, one trivalent, six bivalents and one univalent. The univalent is oriented to one quadrivalent and the trivalent

the female parent and backcrossed to both parents. On the hybrids in which *S. melongena* was the female parent, 163 backcross pollinations were made, 21 fruits set, and 78 seeds were recovered, six of which germinated. Out of 477 pollinations of the F_1 hybrids in which *S. macrocarpon* was the female parent, 35 fruits set but only four of these contained seed. Of the five seeds that were recovered, only one germinated. Of these seven backcross plants, two have failed to flower. The pollen stainability of the remaining five plants is shown in Table 4, and it ranged from 15.1–51.2%.

In the F_2 population obtained from open pollination of F_1 hybrids (Table 5), the phenotypic characteristics varied widely including spininess, flower color, spine color (when present), and flower size. The pollen stainability of the F_2 progeny grown in the greenhouse was highly variable (Table 6), the highest being 92.6%. This hybrid derivative has produced an abundance of seed and has given rise to an F_3 population.

Table 4. Pollen stainability of backcross progeny produced through the use of the F_1 hybrids between *S. melongena* and *S. macrocarpon* as the female parent and backcrossed to both parents

Cross combinations	% Stainable pollen	
	Plant 1	Plant 2
('Classic' × 21 – 73) × 'Classic'	25.8	51.2
('Classic' × 21 – 73) × 21 – 73	15.1	27.3
(21 – 73 × 'Burpee Hybrid') × 21–73	17.9	–

Table 5. Germinability of F_2 seeds produced under open pollination conditions from F_1 hybrids between *S. melongena* and *S. macrocarpon*

F_1 hybrid	F_2 seeds planted (number)	F_2 seedlings obtained (number)
(Mel × Mac)		
('Black Oval' × 21 – 73)	72	9
('Dusky' × 21 – 73)	54	4
('Burpee Hybrid' × 21 – 73)	83	13
('Classic' × 21 – 73)	29	10
('Hibush Special' × 21 – 73)	13	3
Total	251	39 (15.5%)
(Mac × Mel)		
(21 – 73 × 'Burpee Hybrid')	97	6
(21 – 73 × 'Hibush Special')	3	2
(21 – 73 × 'White')	13	1
(21 – 73 × 'Dusky')	1	–
(21 – 73 × 'Classic')	5	–
(21 – 73 × 'Midnight')	1	–
Total	120	9 (7.5%)
Total of Reciprocal Crosses	371	48 (12.9%)

Table 6. Pollen stainability of selected F_2 plants from the interspecific hybrids between *S. melongena* and *S. macrocarpon*

Parent	% Pollen stainability plant number				
	1	2	3	4	5
('Burpee Hybrid' × 21 – 73)	0	0.4	7.4	17.4	57.1
('Classic' × 21 – 73)	3.9	12.1	14.8	14.8	92.6
('Hibush Special' × 21 – 73)	2.4	2.4	3.0	11.9	–
(21 – 73 × 'Hibush Special')	0	0	5.7	16.2	–
('Black Oval' × 21 – 73)	11.3	15.6	16.7	41.0	–
('Dusky' × 21 – 73)	2.6	37.0	–	–	–
(21 – 73 × 'Burpee Hybrid')	14.7	–	–	–	–
(21 – 73 × 'White')	60.3	–	–	–	–

Discussion

The most interesting feature of the data presented in this paper is the ability of a large number of F_1 hybrids to produce seed set under open pollination conditions. This is unexpected and contrary to the previous reports dealing with hybridization of the two species (Chopde and Wanjari 1974; Omidiji 1979; Rajasekaran 1970, 1970b, 1970c; Wanjari 1976). The discrepancy could be attributed to either false authenticity of accession 21–73 or to the variability of the genotypes of *S. melongena.* Although there is no critical evidence on the taxonomy of the 21–73, the formation of multivalents in its F_1 hybrids with the *S. melongena* indicates that 21–73 belongs to a different species. The chromosome number is similar to that of *S. macrocarpon* ($2n=2x=24$). Moreover, the crossing behavior of this genotype with other *Solanum* species is similar to other genotypes of *S. macrocarpon* (Attavian 1981). Hence, all available evidence seems to indicate that 21–73 is, at least, related to *S. macrocarpon.* It is, therefore, most likely that the fertility is the result of the use of different genotypes of *S. melongena.* This speculation is further supported by the differing crossabilities of *S. macrocarpon* and *S. melongena* genotypes and variable seed production in the various F_1 hybrid combinations. The strategy of employing different genotypes of the same species to overcome crossability and sterility barriers in interspecific hybridization has been repeatedly used in plant hybridization (Meister and Tjumjakoff 1928; Rangasamy and Kadambavansundaram 1973, 1974; Wall and York, 1960). The possibility that the F_1 hybrids which produce seed set resulted from contamination in the crosses of the two species is ruled out by the distinctive phenotypic characteristics of the F_1 hybrids (Table 2).

Considering different combinations of crosses, the results indicate that the degree of crossability and fertility of the hybrids were dependent upon two factors: a) the genotype of *S. melongena* used and b) the direction of the cross. In general, the hybrids were more readily obtained with *S. macrocarpon* as the female parent, but higher fertility was observed when *S. melongena* was used as the female parent. These observations are in agreement with the results reported on the hybridization in other plant species (Meister and Tjumjakoff 1928; Rangasamy and Kadambavansundaram 1973, 1974; Wall and York 1960).

The origin of the F_2 progenies deserves further consideration. Although the F_2 progenies resulted under conditions of open pollination in the field, we strongly believe that they resulted from self-pollination. The opening of an anther in eggplant is porecidal and the opening of an anther usually precedes the opening of the flowers. As a consequence, selfing is a prevalent type of pollination in *S. macrocarpon* and *S. melongena.* In addition, the observed range of segregation in the F_2 would be expected in crosses of different taxa. However, the possibility of some outcrossing cannot be ruled out in the present studies.

Literature

Attavian, B.M. (1981): Cytogenetical and crossability studies of selected *Solanum* species and their hybrid derivatives. PhD Thesis, Rutgers University

Beamish K.L. (1955): Seed failure following hybridization between the hexaploid *Solanum demissum* and four diploid *Solanum* species. Am. J. Bot. **42,** 297–304

Chopde, P.R.; Wanjari, K.B. (1974): Interspecific hybrids in *Solanum.* Indian J. Genet. Plant Breed. **34 A,** 1318–1323

Meister, N.; Tjumjakoff, N.A. (1928): Rye-wheat hybrids from reciprocal crosses. J. Genet. **20,** 233–245

Narasimha Rao, N.; Ponnaiya, B.W.X. (1970): A note on the hybridization technique in *Solanum* species. Andhar Agric. J. **17,** 95–96

Omidiji, M.L. (1979): Crossability relationships between some species of *Solanum, Lycopersicon* and *Capsicum* cultivated in Nigeria. In: The Biology and Taxonomy of the Solanaceas. (eds. Hawks, G.J.; Lester, R.N.; Skelding, A.D., pp 599–604. London: Acad. Press

Paris, H.S.; Shifriss, O.; Jelenkovic, G. (1978): Idiogram of *Ricinus communis* L. J. Hered. **69,** 191–196

Rajasekaran, S. (1970): Sterility in an inter-varietal hybrid *Solanum melongena* L. × *S. melongena* var. 'bulsaresis Argikar'. Madras Agric. J. **57,** 194–196

Rajasekaran, S. (1970b): Ovule sterility of the F_1 hybrid *Solanum melongena* var. *bulsarensis* Argikar. Jpn. J. Genet. **45,** 163–166

Rajasekaran, S. (1970c): Cytogenetic studies on the F_1 hybrid of *Solanum macrocarpon* L. (*S. melongena* var. 'bulsarensis Argikar') × *S. melongena* L. Auara **2,** 21–28

Rangasamy, P.; Kadambavansundaram, M. (1973): Incompatibility in interspecific hybrid *Solanum indicum* L. × *S. melongena* L. Madras Agric. J. **60,** 1617–1621

Rangasamy, P.; Kadambavansundaram, M. (1974): Interspecific hybridization in *Solanum* – *Solanum melongena* L. × *Solanum indicum* L. Madras. Agric. J. **60,** 1687–1694

Villareal, R.L. (1966): Inheritance of resistance to *Verticillium albo-atrum* Rke. and Berth. in eggplant (*Solanum melongena* L.) crosses. PhD Dissertation, Rutgers University

Wall, J.R.; York, T.L. (1960): Gametic diversity as an aid to interspecific hybridization in *Phaseolus* and in *Cucurbita.* Am. Soc. Hortic. Sci. **75,** 419–428

Wanjari, K.B. (1976): Cytogenetic studies on F_1 hybrids between *Solanum melongena* L. and *S. macrocarpon* L. Hortic. Res. **15,** 77–83

Received October 15, 1981
Accepted January 5, 1982
Communicated by G. S. Khush and D. von Wettstein

D. A. Schaff
Department of Horticulture, Kansas State University
Manhattan, Kans. 66506 (USA)

Dr. G. Jelenkovic, Dr. C. Boyer, Dr. B. Pollack
Department of Horticulture and Forestry
Rutgers University
New Brunswick, N.J. 08903 (USA)