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Allozyme variation in the eggplant, *Solanum melongena* L. (Solanaceae)

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Abstract Enzyme electrophoretic studies were made in cultivated *Solanum melongena* L. (eggplant) and similar wild and weedy forms, several of which have been thought to be different species/taxa. Twenty-nine accessions of *S. melongena*, 33 accessions of weedy forms (referred to as "insanum") and 2 accessions of wild forms (referred to as "incanum") were surveyed for 29 isozyme loci. In *S. melongena*, 22 of the 29 loci were monomorphic, and nearly all of its genes were either also monomorphic or in similar frequencies in insanum and incanum. The results demonstrate that the three taxa have a very close genetic relationship. The high genetic identities between them (0.913–0.967) suggests that they are conspecific even though they include extensive morphological diversity.

Key words *Solanum melongena* · Insanum Incanum · Allozymes · Genetic diversity Interrelationships

Introduction

Solanum melongena L., popularly known as eggplant, brinjal or aubergine, is a widely grown vegetable of Asia, parts of Europe and Africa. Several advanced cultivars and numerous landraces are cultivated in India for their young, unripe fruits, which are consumed fresh, dried or pickled. There is consensus that India or Indochina is the centre of eggplant diversity with China as a probable secondary centre (Bhaduri 1951; Vavilov 1951; Zeven and Zhukovsky 1975; Lester and Hasan 1991).

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A number of wild and weedy taxa that are morphologically similar to eggplant are found in India. Their identity, taxonomic status and relationships are highly confusing. Taxonomic entities like *Solanum incanum*, *S. insanum*, var 'Potangi' and var 'Travancore' have been identified among the nearest relatives of *S. melongena* (Mital 1950; Bhaduri 1951). *S. incanum* from India has often been treated as a distinct species (Clark 1883 as *S. coagulans*; Duthie 1911). The identity of this form has, however, been brought into question. Hepper and Jaeger (1985) selected a neotype of *S. incanum* from the Middle East. Lester and Hasan (1990, 1991) pointed out that some of the plants described as *S. incanum* from India do not conform to the neotype and treated *S. incanum* as a solely African and Middle Eastern species. *S. insanum* has been treated as a species (Roxburgh 1832) or a variety of *S. melongena* (Prain 1903; Duthie 1911). Deb (1989) proposed the merger of *S. melongena* and *S. insanum* under *S. incanum*. Lester and Hasan (1991) treated eggplant cultivars and wild and weedy forms found in India and Indochina as 'Groups' in the *S. melongena* complex. *S. insanum* was placed by these workers in a group separate from the rest of the weedy forms. *S. incanum* from India, *S. incanum* from Africa and S. W. Asia, *S. insanum*, var 'Potangi' or hybrids between two to three of the above taxa have been proposed from time to time to be the progenitor of eggplant (Bhaduri 1951; Khan 1979; Lester and Hasan 1991).

Much of the ambiguity regarding eggplant origin and relationships stems from the fact that most of the eggplant workers have studied only a small number of collections from South Asia. Further, with a few exceptions (Pearce and Lester 1979; Sakata et al. 1991), all evidence regarding its taxonomic affinities is from morphological comparisons, crossability estimates, F_1 fertility determinations and chromosome pairing analyses (Mital 1950; Bhaduri 1951; Baksh 1979; Narsimha Rao 1979; Lester and Hasan 1991). However, morphological characters for taxonomic delimitation in section *Melongena* have been highly confusing because of large intra- and interspecific diversity. Crossability studies

have not provided unambiguous estimates of genetic proximity because *S. melongena* can be crossed not only with putative progenitors but even with distantly related species belonging to a number of other sections of the genus (Narsimha Rao 1979; Khan 1979; Omidiji 1982, 1986).

Eggplant collections have been evaluated mostly for morphological and agronomic characters (for example, Vadivel and Bapu 1988; Anonymous 1990). These studies have revealed a large diversity in vegetative, floral and fruit characters, and have led to the classification of cultivars into several phenotypic groups (Martin and Rhodes 1979). However, there are no comparable studies on the genetic diversity.

The present electrophoretic study on 64 collections of *S. melongena* and related wild and weedy forms from South Asia was undertaken to obtain a more accurate estimate of their interrelationships as well as an overview of the genetic diversity in eggplant.

Material and methods

Materials

Table 1 lists the collections of the three taxa of the *S. melongena* complex used for the present investigation. Since, as detailed in the Introduction, the nomenclature of the wild and weedy forms existing in India and its neighbouring countries is controversial, we have used tentative epithets to designate them. Plants identified as *S. incanum* by most Indian workers have been named as "incanum" while those identified as *S. insanum* have been designated as "insanum". However, to facilitate communication, reference has also been made to the species/groups of other workers to which the present taxa correspond. *S. melongena*, insanum and incanum constitute the *S. melongena* complex.

S. melongena

These are cultivated forms that include primitive landraces and relatively advanced named cultivars. They correspond to Groups G and H of Lester and Hasan (1991).

The named cultivars are tall, erect and nonprickly; leaves are large (up to 27 cm); fruits are large (up to 731 g), solitary and purple. The landraces represent a highly varied assemblage constituting erect to suberect, nonprickly to highly prickly plants; the leaves are large to small (minimum 4 cm); fruits are purple, white, green or variegated, from large to as small as 23 g.

Table 1 Plants examined

Taxon	Number of accessions	Location	Source[a]
I. *S. melongena* complex			
1. *S. melongena*	29[b]	India, Bangladesh, USA, Japan	1, 2, 3
2. Insanum	33	India, Sri Lanka	1, 2
3. Incanum	2	India	1, 2
II. Other species			
4. *S. incanum*	1	Zambia	4
5. *S. virginianum*	8	India	1, 2
6. *S. macrocarpon*	1	Brazil	4

[a] 1, Collections of JLK; 2, germ plasm collections of National Bureau of Plant Genetic Resources, New Delhi; 3, commercial cultivars from US market; 4, USDA Southern Regional Plant Introduction Station, Georgia, USA

[b] Includes 9 named cultivars and 20 landraces

Insanum

These are weedy forms. Some accessions, being semierect and highly prickly with small leaves and fruits, matched the description of *S. insanum sensu* Roxburgh (1832), Prain (1903 as *S. melongena* var *insanum*) and Lester and Hasan (1991 as *S. insanum sensu stricto*, Group E). However, we prefer to treat the nonprickly weedy forms with large leaves and fruits (Group F of Lester and Hasan 1991) also under this 'species' since a continuous range of variants exists that practically obliterates a clear distinction between the different weedy groups (personal observation of JLK).

Plants are erect to decumbent; prickly or prickleless; leaves are relatively small (4.5–14.9 cm); fruits are often one per inflorescence, sometimes more, small (3.5 g–35 g), globose, ovoid or oblong, white, green or purple, often variegated, bitter and inedible.

Incanum

These conform to the wild form *S. incanum sensu* Clark (1883 as *S. coagulans*) and Duthie (1911) and treated similarly by Indian workers. These correspond to Group F (in part) of Lester and Hasan (1991) but are not weedy; probably truly wild.

A number of accessions conforming to incanum were available in the N.B.P.G.R. germ plasm collection. However, we restricted the present investigation to the two accessions that had been collected from truly wild situations.

Electrophoretic patterns among the above-mentioned taxa of *S. melongena* complex were generally very uniform. Thus, it became necessary to use materials from other species of section *Melongena* to confirm the present genetic interpretations. These materials are also listed in Table 1.

Four to eight seeds of each accession were sown in paper cups containing moist vermiculite. Four seedlings were transplanted at the fully expanded cotyledon stage (8–30 days after sowing depending upon species) into plastic cells containing standard soil mix. The seedlings were germinated and maintained throughout the study at 12 h of daylight at 30 °C and 12 h of night at 25 °C.

Electrophoresis

Enzyme analysis was done on seedling leaf tissue. However, for esterase, the best results were obtained from roots, while for alcohol dehydrogenase, activity was only observed in 24-h flooded roots. Generally, two randomly selected seedlings from each accession were analysed for different enzyme systems. Fifteen enzyme systems were examined.

About 1.5 cm^2 young leaves (or 20–30 mg young roots for esterase and alcohol dehydrogenase) were crushed in cold extraction buffer (Gottlieb 1981a), and horizontal starch gel electrophoresis was carried out. Four gel/electrode buffer systems were used: (A) System I of Gottlieb (1981a) for aspartate aminotransferase (ATT, EC 2.6.1.1), phosphoglucose isomerase (PGI, EC 5.3.1.9), phosphoglucomutase (PGM, EC 2.7.5.1), triose-phosphate isomerase (TPI, EC 5.3.1.1), leucine aminopeptidase (LAP, EC 3.4.1.-), glutamate dehydrogenase (GDH, EC 1.4.1.2), esterase (EST, EC 3.1.1.1) and alcohol dehydrogenase (ADH, EC 1.1.1.1); (B) the morpholine-citrate pH 6.5 system of Wendel and Weeden (1989) for malate dehydrogenase (MDH, EC 1.1.1.37) and 6-phospholuconate dehydrogenase (6-PGD, EC 1.1.1.44); (C) System IV of Gottlieb (1981a) for isocitrate dehydrogenase $NADP^+$ (IDH, EC 1.1.1.42), shikimate dehydrogenase (SKDH, EC 1.1.1.25) and malic enzyme (ME, EC 1.1.1.40); (D) the Tris-citrate pH 7.0 system of Wendel and Weeden (1989) for aconitase (ACO, EC 4.2.1.3) and peroxidase (PRX, EC 1.11.1.7). Standard recipes for visualising the enzymes were used (Gottlieb 1981a; Soltis et al. 1983; Wendel and Weeden 1989) except for EST, which was

modified to include in a 100 ml of 100 m*M* sodium phosphate, 90 mg α-napthyl acetate, 90 mg β-napthyl acetate and 90 mg Fast Blue RR. Specificity of the staining solutions for the individual enzymes was confirmed by excluding/altering substrate/cofactor from the recipe; in all cases this resulted in blank gels.

Genetic interpretation

Genetic interpretations were based on electrophoretic patterns and enzyme subunit structure (Weeden and Gottlieb 1980; Gottlieb 1981b, 1982, 1983; Wendel and Weeden 1989). Isozyme loci were designated by Arabic numerals; the locus which produced the product migrating most anodally was designated as *1*, the next as *2* and so forth. Similarly, the allele which produced the product with greatest mobility was designated as *a*, the following ones *b*, *c*, etc. Genetic statistics of Nei was performed using GeneStat-PC (Lewis 1992). Statistics not included in this programme were performed manually.

Results

The 15 well-resolved enzyme systems reported here included isozymes specified by approximately 29 loci. EST and PRX exhibited 4 and 5 isozymes, respectively, which were similar to the electrophoretic patterns described in *Lycopersicon* (Rick et al. 1974; Tanskley and Rick 1980). However, because the isozymes of both enzymes were variable in activity, only 1 PRX and 2 EST isozymes were scored. In *S. melongena*, 23 genes were monomorphic and 6 were polymorphic with 2 or 3 alleles per locus (Tables 2, 3). But the distribution of polymorphism was very limited, with 7 accessions accounting for all the diversity. Two of the polymorphic accessions were named cultivars while the rest were landraces. Thus, for most part, accessions of *S. melongena* exhibiting very distinctive morphologies could not be distinguished on these tests.

The insanum accessions showed more variability with 8 of the 29 loci being polymorphic and polymorphisms present in 23 of the 33 accessions (Tables 2, 3). Accessions conforming to *S. insanum sensu stricto* had the same alleles at the highest frequency at all polymorphic loci as the other insanums and had no unique alleles.

No heterozygous individuals were found for 22 loci in either of the taxa. Fifteen individuals were heterozygous for *Pgi2* and *Pgm2* in *S. melongena*, and 34 were heterozygous for these genes and *Idh*, *Est1*, *Skdh*, *Adh1* and

Table 2 Allelic frequencies of 29 isozyme loci in *S. melongena* complex (*N* the number of accessions/number of individuals assayed for each locus)

Locus		*S. melongena*	Insanum	Incanum
Aat1	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Aat2	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Aat3	N	29/66	33/77	2/4
a		1.0	31.0	1.0
Aco1	N	15/25	20/35	1/2
a		1.0	1.0	1.0
Aco2	N	15/25	20/35	1/2
a		1.0	1.0	1.0
Adh1	N	29/66	33/74	2/4
a		–	0.09	–
b		1.0	0.91	1.0
Adh2	N	29/66	33/74	2/4
a		1.0	1.0	1.0
Est1	N	29/66	33/74	2/4
a		–	0.01	–
b		1.0	0.99	1.0
Est2	N	29/66	33/74	2/4
a		1.0	1.0	1.0
Gdh	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Idh	N	29/66	33/77	2/4
a		1.0	0.88	1.0
b		–	0.12	–
Lap	N	29/68	33/77	2/4
a		0.03	–	–
b		0.94	1.0	0.5
c		0.03	–	–
d		–	–	0.5
Mdh1	N	29/66	33/74	2/4
a		1.0	1.0	1.0
Mdh2	N	20/00	33/74	2/4
a		1.0	1.0	1.0
Mdh3	N	29/66	33/74	1/2
a		–	0.10	–
b		0.99	0.31	–
c		0.01	0.59	1.0
Mdh4	N	29/66	33/74	2/4
a		0.99	0.31	–
b		0.01	0.69	1.0
Me	N	27/37	28/51	2/4
a		1.0	1.0	1.0
6Pgd1	N	29/66	33/77	2/4
a		1.0	1.0	1.0
6Pgd2	N	29/66	33/77	2/4
a		1.0	1.0	1.0
6Pgd3	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Pgi1	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Pgi2	N	29/66	33/77	2/4
a		–	0.08	–
b		0.01	0.36	–
c		0.99	0.55	1.0
d		–	0.01	–
Pgm1	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Pgm2	N	29/66	33/77	2/4
a		0.92	0.90	0.38
b		0.08	0.10	0.62
Prx	N	26/51	33/64	2/4
a		0.02	–	–
b		0.98	1.0	0.75
c		–	–	0.25
Skdh	N	29/66	33/77	2/4
a		1.0	0.99	1.0
b		–	0.01	–
Tpi1	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Tpi2	N	29/66	33/77	2/4
a		1.0	1.0	1.0
Tpi3	N	29/66	33/77	2/4
a		1.0	1.0	1.0

Table 3 Summary statistics for genetic data

Species/ taxa	Total alleles/ 29 loci	Mean alleles/ locus	Number of polymorphic loci	Proportion polymorphic loci	Mean no. alleles/ polymorphic locus	Heterozygosity	
						Observed	Expected
S. melongena	36	1.24	6	0.21	2.17	0.006	0.013
Insanum	40	1.38	8	0.28	2.38	0.016	0.073

Mdh3 in insanum. In both taxa, the observed heterozygosity was lower than expected (Table 3).

S. melongena and insanum were nearly identical (Table 2). They were fixed for the same alleles at the monomorphic loci, and at the polymorphic loci, the same alleles were present at similar frequencies. The exceptions were *Mdh3* and *Mdh4*, which appear to be a pair of duplicated loci, and *Pgi2*. The only *S. melongena* alleles not present in insanum were at *Lap* and *Prx*, and the insanum accessions had alleles not present in *S. melongena* only at *Adh1*, *Est1*, *Idh*, *Mdh3*, *Pgi2* and *Skdh*. In every case, the alleles found in only one or the other were at a low frequency. The calculated Nei genetic identity $\bar{I}$ between them was $\bar{I} = 0.963$.

The incanum accessions were too few to provide confident estimates of the gene frequencies. The alleles recorded here (Table 2) were obviously the most frequent ones, while it is probable that low-frequency alleles went undetected. Nevertheless, genetic proximity of this taxon with *S. melongena* and insanum was evident by the presence in the three taxa of the same monomorphic genes or, at polymorphic loci, the same alleles at high frequencies at 25 of the 29 loci (Table 2). Incanum, however, had 2 alleles at *Lap* and *Prx* not found in *S. melongena* and insanum. The genetic identity of incanum with *S. melongena* was $\bar{I} = 0.913$ and with insanum it was $\bar{I} = 0.967$.

Discussion

Interrelationships within the *S. melongena* complex

The present study clearly establishes the close phylogenetic relationships between cultivated *S. melongena* and superficially similar weedy and wild forms existing in S. Asia. These taxa have previously been treated as either distinct species, *S. melongena*, *S. incanum* and *S. insanum*, or as varieties of one or two of the above species (Roxburgh 1832; Clark 1883; Prain 1903; Deb 1989). Electrophoretic results strongly favour their conspecific treatment. *S. melongena* and insanum (weedy forms) were monomorphic for the same alleles at 19 of the 29 loci investigated. Furthermore, the two taxa had the same alleles at the highest frequency at 8 of the 10 polymorphic loci. The genetic identity of the two taxa was $\bar{I} = 0.963$. The electrophoretic patterns of incanum (wild forms) accessions were also very similar with those of the above two taxa. Consequently, its genetic identity with *S. melongena* was $\bar{I} = 0.913$ and with insanum, $\bar{I} = 0.967$. Earlier studies on a large number of plants have shown that such high $\bar{I}$ values are obtained either between populations that are conspecific or between species that are related as progenitor and recent derivative (Gottlieb 1977, 1984; Crawford 1989).

Earlier conclusions of close phylogenetic relationships among components of the *S. melongena* complex have been based mostly on crossability studies. Fertile hybrids between *S. melongena* on the one hand and *S. incanum* and *S. insanum* on the other have been reported by Bhaduri (1951), Baksh (1979), Narsimha Rao (1979), Zohary (1983) and Lester and Hasan (1991). However, the results from crossability studies have not been definitive because the same crosses made by different workers have yielded different results. Thus, while Zohary (1983) produced fully fertile F_1 hybrids between *S. incanum*, collected from Israel, and *S. melongena*, Lester and Hasan (1990, 1991) obtained only partially fertile (53–60% pollen stainability) hybrids from a similar cross even though they also used a collection of *S. incanum* from Israel. Interestingly, the latter authors regarded the Indian *S. incanum* as only a form of *S. melongena* because the hybrids between the two are highly fertile.

Genetic variation in *S. melongena*

The present electrophoretic data for this species is based on 29 accessions, including both relatively advanced named cultivars and landraces. As mentioned earlier, they represent a wide diversity of morphological and agronomic attributes available in this species. Enzymatically, they seem to be extremely uniform. Alleles were fixed among all 29 accessions at 23 of the 29 loci. Even among the polymorphic loci the frequency of the alleles other than the most frequent ones was as low as 0.01–0.08 (Table 2). Polymorphism was actually confined to only 7 accessions, the rest being monomorphic at all loci. All these figures indicate the highly uniform genetic architecture of eggplants. Unlike potato, in which allozyme polymorphism is high enough to enable the identification of cultivars on the basis of electrophoretic patterns (Martínez-Zapater and Oliver 1986), eggplant has a very narrow genetic base. This conclusion is in line with some of the hypotheses on the origin of *S. melongena*. As mentioned earlier, *S. melongena* is suggested to have originated from an African species, *S. incanum*. Migration of *S. incanum*, or its derivative wild ancestor of *S. melongena*,

into South and Southeast Asia is supposed to have taken place either by human agency through land routes or by sea dispersal of fruits (D'Arcy and Pickett 1991; Lester and Hasan 1991). In any case, the basic gene pool from which the cultivated forms arose must have been very small.

Genetic variation in wild and weedy forms

Weedy forms of the *S. melongena* complex are genetically more diverse than cultivars. Thus, twenty-two accessions of insanum possessed 1 or the other polymorphic locus compared to 7 accessions of *S. melongena*. Furthermore, in insanum, the total number of alleles for the 29 loci, the number of polymorphic loci and the mean number of alleles per polymorphic locus were higher than their corresponding figures for *S. melongena* (Table 3). Unfortunately, the sample size of our wild forms (incanum) was too small to reflect the entire allelic diversity that may be available in this taxon. Still 2 alleles not present in *S. melongena* were located in these materials. An allozyme survey made in *Capsicum* (McLeod et al. 1983) revealed similar lower levels of genetic variability in cultivars than in their wild putative ancestral species. In the *S. melongena* complex, while the wild incanum is generally accepted as a progenitor of *S. melongena*, the weedy insanum has been variously treated as a progenitor, a derivative or a complex of both progenitor and derived forms (Prain 1903; Bhaduri 1951; Lester and Hasan 1991). Whether the allelic richness of insanum is due to its being more ancient and ancestral to *S. melongena* or a reflection of its derived nature, perhaps by natural cross pollination of cultivars with some wild forms, can be determined only after a more intensive sampling and analysis of the natural populations is done. It is of interest to mention that Omidiji (1986) obtained *S. insanum*-like derivatives from crosses between *S. melongena* and *S. anomalum* (section *Torva*), leading the author to suggest that interspecific hybridization may have been involved in the origin of *S. insanum*. Though the present allozyme data do not support the separation of its various morphoforms into distinct groups as suggested by Lester and Hasan (1991), the likely possibility of insanum being a conglomeration of ancestral and derived forms needs to be examined further.

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