

Full Length Research Paper

# Phenotypic variation of F<sub>1</sub> and F<sub>2</sub> populations from three species of *Solanum* L. (Solanaceae)

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**Emerging chromosome types in some *Solanum* species underscore inherent potentials and possible new and expanded genome. Interspecific crosses involving the varieties of *Solanum melongena* L., *Solanum macrocarpon* L. and *Solanum aethiopicum* L. were carried out to assess species phylogenetic relationships and the extent of evolutionary changes with a view to improving the agronomic characters in the hybrids. The dimensions of leaves, petals and fruits in the F<sub>1</sub> hybrids were intermediate in values between parents while parental influence was significant in such characters as growth habit, inflorescence types and colour of flowers. Pollen viability was depressed from 97.3 – 71% in parents to 56.8 - 48.8% in the F<sub>1</sub> and consistently lowered from 48.6 – 38.2% in the F<sub>2</sub> hybrids but restored (63.8%) in an F<sub>2</sub> plant. Fruits were few on inflorescence, small sized with generally fewer seeds in the F<sub>1</sub> (67 - 132) and F<sub>2</sub> (52 – 135) hybrids compared with the parents (87 – 384). A single flowered inflorescence from a cross (*S. melongena* 'Melongena' x *S. aethiopicum*) revealed a novel gene and possible selective ecological advantage over other hybrids. The incomplete restoration of some of the masked characters in the F<sub>2</sub> hybrids suggests a near-complete homogenization of parental genomes and/or chromosomal disharmony through silent genomic changes. These might have prevented sufficient chromosomal rearrangement and full homology for improved vigour in many of the F<sub>2</sub> hybrids.**

**Key words:** *Solanum*, genome, phenotype, taxonomy, evolution, interspecific hybridization, pollen viability, hybrid fertility fruit set.

## INTRODUCTION

Members of the genus *Solanum* L. are as varied morphologically as they are diverse in number (Knapp, 1991a; Levin et al., 2005) and ecogeographically distributed (Nee, 1979; Whalen, 1984; Wunderlin et al., 1993). The genus is made up of over 2000 species, constituting one of the large genera of angiosperms found in both the temperate (Gbile, 1985) and tropical (Okoli, 1988) regions of the world. Some species are habitat specific and inhabit the mountain zones, particularly the highlands of Mambilla, Obudu, Vogel peak and Jos Plateau across the savanna and arid belts of Nigeria (Heine, 1963; D'Arcy, 1979). The domesticated species are often diploids (2n =

24), with many wide-spread escape in the wild (Oyelana, 1997). This last group expresses unique adaptive features which confer a competitive advantage over other common angiosperm species (Cipollini et al., 2002), generally regarded as weeds (Gbile, 1979).

The genus provides enormous food resources as vegetables and tubers (Omidiji, 1982) and medicinal source of unique alkaloids and other biochemical constituents for the treatment of ailments (Caicedo and Schaal, 2004).

The taxonomy of the group has remained challenging due to species' large size (Knapp, 1991b; Edmond, 1986; Oyelana, 1997), overlapping ecogeographical distribution (Levin et al., 2005), morphological plasticity (Edmond, 1977), similar genomes (Okoli, 1988; Omidiji, 1982; Sangowawa, 1986) and existence of swamps of natural hybrids (Omidiji, 1982, 1983; Knapp, 1991a; Ugborogho and Oyelana, 1999; Oyelana, 1997). These factors have generated a number of inconsistencies and misconcep-

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tions on past attempts at taxonomically resolving the complexities associated with the genus.

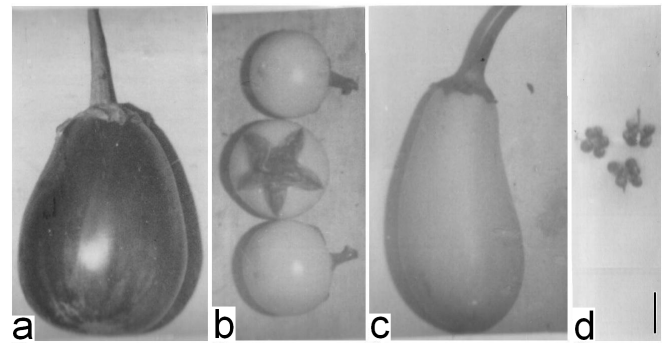
The diploid chromosome complements of  $2n = 24$  and 48 are widely reported with similar genomes (Oyelana, 2005; Oyelana and Ugborogho, 1997; Sangowawa, 1986; Okoli, 1988). Chromosome sizes overlapped considerably. Karyotypic assessment revealed few emerging chromosomes (submetacentric and subtolocentric), which according to Ugborogho and Oyelana (1999) may have evolved from breaks and rearrangement of chromosome arms. The similar genomes may not sufficiently explain the expression of diverse morphological features and wide spread habitats for many of these species. This raises possibilities for silent genomic changes in some members of this genus. This position is readily corroborated with the existence of dissimilar chromosomes and cases of hybrid break down from crosses between related species (Masuelli et al., 2006; Gavrilenko et al., 1999; Ugborogho and Oyelana, 1999), meiotic irregularities from pairing errors (Oyelana and Ugborogho, 1997), somatic instability (Omidiji, 1982) and emergence of few aneuploid races (Oyelana, 1997).

Gavrilenko et al. (1999) reported a number of cytological differences among few of the established hybrids from intraspecific crosses involving *Solanum tuberosum* L. These included extensive chromosome number variation (aneuploid, aneusomatic and mixoploid) in the hybrids. Though, most of these hybrids represented the expected chromosome number of  $2n = 48$ , the frequency of aneuploids reached 50%. Some hybrids equally carried structurally rearranged chromosomes and exhibited a high frequency of aberrant anaphase. These cytological aberrations may have provided the basis for the expression of rare traits or features in the emerging hybrids. These inherent potentials could be explored in species' hybridization with the ultimate aim of improving the existing genetic stock. Interspecific hybridization in nature (Arnold et al., 1999; Rieseberg and Ellstrand, 1993) is believed to play a prominent role in the evolution of new taxa (Rieseberg, 1995, 1997; Cattell and Karl, 2004). Thus, interspecific hybridization of three *Solanum* species was carried out with a view to exploring species' inherent potentials for possible improvement of their agronomic values and assess species' relationship.

## MATERIALS AND METHODS

### Description of the natural species

The species were shrubs, annual, rarely perennial, erect with woody stems except *Solanum aethiopicum*, a herb. Branches were generally profuse and spreading in the three species. Leaves were simple, deeply and variously lobed and hairy in *S. melongena*, glabrous in *S. macrocarpon* but dentate, shallowly lobed and glabrous in *S. aethiopicum*. Inflorescence was raceme in *S. melongena*, simple umbellate in *S. macrocarpon* and cymose and leafopposed in *S. aethiopicum*. Flowers (3 – 8) were usually pink in *S. melongena*, purple in *S. macrocarpon* and white in *S. aethiopicum*. Fruits were subglobose and purple in *S. melongena* 'Melongena' (Figure



**Figure 1.** Fruits of parent species of *Solanum*; **a.** *S. melongena* 'Melongena'; **b.** *S. macrocarpon*; **c.** *S. melongena* 'Golden'; **d.** *S. aethiopicum*, Scale bar = 20 mm.

1a) but yellow in *S. melongena* 'Golden' (Figure 1c) while they were generally round in the other two species, appearing yellow when ripe in *S. macrocarpon* (Figure 1b) and red in *S. aethiopicum* (Figure 1d). The species were all diploid with  $2n = 24$  (Figure 4a).

### Emasculation and pollination of flowers

Hand pollinated flowers were emasculated 18 h prior to anthesis and bagged. Pollen from freshly dehisced anthers from designated male parents were applied on the stigmatic surfaces of the already emasculated flowers with the help of a small brush. The pollinated flowers were immediately bagged to eliminate any foreign pollen. The bags were later removed as soon as the ovaries initiated growth and the petals completely withered. The same procedure were repeated for the  $F_1$  flowers.

### Cultivation and morphometric analysis

The three crossing species were first raised in the biological garden of the University of Lagos for three months before flowers were emasculated and crosses effected. The  $F_1$  and  $F_2$  hybrid seedlings were nursed in the greenhouse for four weeks and subsequently transferred to the garden and cultivated alongside the parent species. Detailed observations of growth, morphological and floral features and dimensions were made using a hand lens, stereomicroscope and a metre rule

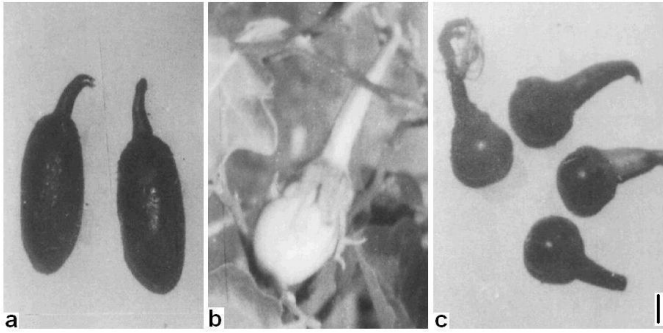
### Cytological analysis

Cytological features including stomata, pollen and mitotic chromosomes were assessed based on the techniques of Oyelana (2005) and Ugborogho and Oyelana (1992). Measurements of micromorphological features were done with the help of an eye piece graticule at x40 objective on a Microscope.

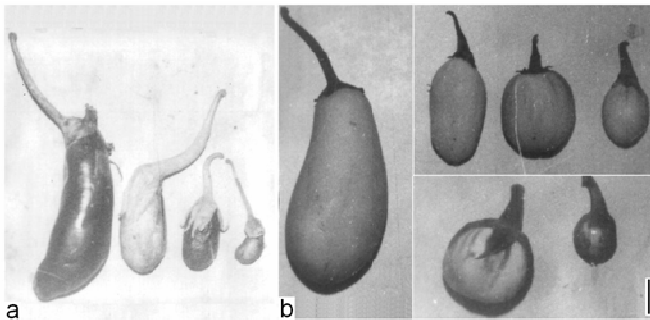
### Hybridization

For the groups listed below; ten, twelve and eleven crosses were made respectively and above 80% success rate was recorded for each cross.

- ♀ *S. melongena* 'Melongena' x ♂ *S. macrocarpon*
- ♀ *S. macrocarpon* x ♂ *S. melongena* 'Golden'
- ♀ *S. melongena* 'Melongena' x ♂ *S. aethiopicum*



**Figure 2.** F<sub>1</sub> fruits; **a.** F<sub>1</sub> fruits from *S. melongena* 'Melongena' x *S. macrocarpon*; **b.** F<sub>1</sub> fruit from *S. macrocarpon* x *S. melongena* 'Golden'; **c.** F<sub>1</sub> fruits from *S. melongena* 'Melongena' x *S. aethiopicum*; Scale bar: a = 18 mm, b = 8 mm, c = 5 mm.



**Figure 3.** F<sub>2</sub> fruits; **a.** F<sub>2</sub> fruits from *S. melongena* 'Melongena' x *S. macrocarpon*; **b.** F<sub>2</sub> fruits from *S. macrocarpon* x *S. melongena* 'Golden'; Scale bar = 10 mm.

## RESULTS

### ♀ *S. melongena* 'Melongena' x ♂ *S. macrocarpon*

#### Morphological characters

Table 1 shows the details of morphological features of the parent species and their respective F<sub>1</sub> and F<sub>2</sub> hybrids. The F<sub>1</sub> hybrids were intermediate for the sizes and dimensions of leaves and length of petioles while the shape and texture of leaves were as described for the female parent. They were vigorous in growth and characterized by many and well spread branches. Two of the four plants in the F<sub>2</sub> were erect with well-spread branches as in the female grandparent (F<sub>2</sub>A) while the remaining two (F<sub>2</sub>B) were moderately spreading as in the male grandparent. The texture of leaves and lobing characteristics in the second group (F<sub>2</sub>B) were equally similar to the male grandparent. In both groups of F<sub>2</sub> hybrids (F<sub>2</sub>A and B), the dimensions of most of the morphological features, especially the leaves, overlapped with those of the parents and grand-parents. Stomata were anomocytic in both the F<sub>1</sub> and F<sub>2</sub> hybrids as in the parents and their sizes greatly overlapped.

#### Inflorescence and floral characters

Inflorescence was raceme in the F<sub>1</sub> hybrids, flowers were pink like the female parent and dimensions of petals (length and breadth) were intermediate to both parents. The raceme type with cluster of pink and light pink flowers was found in all the F<sub>2</sub>. The pedicel length overlapped and sizes varied between 5.6 and 5.8 mm in both groups of F<sub>2</sub> plants. Pollen were regular in both F<sub>1</sub> and F<sub>2</sub> hybrids and sizes overlapped. The average viability was 48.8% in the F<sub>1</sub> and between 45.2% and 38.2% respectively for pink and light pink flowers in F<sub>2</sub>.

#### Fruits

Fruits were oblong, purple with rough crisply pericarp in the F<sub>1</sub> hybrids (Figure 2a), and set fewer seeds (58 – 76) compared to the female (354 – 468) and male (88 – 102) parents. In the F<sub>2</sub>, the plants were characterized by globose fruits, purple in the set of plants with pink flowers (Figure 3a) but yellow/light purple in the light pink flowers. Table 1 shows details of seed set, sizes of fruits and other morphological and floral features for both the F<sub>1</sub> and F<sub>2</sub> plants.

#### Mitotic chromosomes

The parents, F<sub>1</sub> and F<sub>2</sub> hybrids were diploid with 2n = 24.

### ♀ *S. macrocarpon* x ♂ *S. melongena* 'Golden'

#### Morphological characters

The F<sub>1</sub> hybrids were intermediate in values for several features (Table 2). They were erect with spreading branches like the male parent. The F<sub>2</sub> individuals were made up of six erect plants with many spreading branches in one like the F<sub>1</sub> hybrids, few spreading branches in another two and few to many moderately spreading branches in the remaining three. Leaves were hairy in the F<sub>1</sub> hybrids and four of the six F<sub>2</sub> plants as in the male parent while they were glabrous to sparsely hairy in the remaining two F<sub>2</sub> plants. The values for most morphological features in both the F<sub>1</sub> and F<sub>2</sub> individuals overlapped. Stomata were anomocytic.

#### Inflorescence and floral characters

Inflorescence was umbellate (2 – 4 flowers) in the F<sub>1</sub> hybrids but subumbellate (2 – 5 flowers) in four of the six F<sub>2</sub> hybrids and raceme (3–5 flowers) in the remaining two plants. Flowers were pink in the F<sub>1</sub> but pink to light pink in the F<sub>2</sub>. Pollen were regular in both the F<sub>1</sub> and F<sub>2</sub>, and their sizes overlapped. The average pollen viability was 51.8% in the F<sub>1</sub> but respectively 63.8 and 48.6% for F<sub>2</sub> raceme and subumbellate flowers (Table 2).

**Table 1.** Growth and morphological characters of *S. melongena* 'Melongena', *S. macrocarpon* and their F<sub>1</sub> and F<sub>2</sub> hybrids.

Character	<i>S. melongena</i>	F <sub>1</sub> Hybrids	F <sub>2</sub> Hybrids	<i>S. macrocarpon</i>	
Habit	Erect 1.5 - 1.8 m, branches many and spreading.	*Erect 1.2 - 1.4 m, branches many and spreading .	*Erect branches many and spreading ( <sup>2</sup> / <sub>4</sub> ); Erect and moderately spreading ( <sup>2</sup> / <sub>4</sub> )	Erect 1.0 - 1.2 m, branches few and moderately spreading.	
Leaf length (cm)	18.0	19.2	Plants with profuse branches= 18.3; Plants with moderate branches = 20.1	23.3	
Leaf breadth (cm)	12.4	14.2	Plant with profuse branches= 14.2; Plant with moderate= branches 16.2	15.0	
Petiole length (cm)	9.0	7.8	Plant with profuse branches= 6.2; Plant with moderate= branches 7.2	5.5	
Inflorescence	Raceme	*Raceme	*Raceme	Umbellate	
Color of Petals	Pink	*Pink	*Pink to Light pink	Purple	
Petal length (mm)	18.0	17.0	Pink Flowers= 16.0; Light Pink Flowers= 16.5	15.0	
Pedicel length (mm)	6.8	6.2	Pink Flowers= 5.8; Light Pink Flowers= 5.6	7.6	
Fruit	Length (mm)	129.0	84.0	Purple fruit= 82.0; Light Purple= 62.0	25.0
	diameter( mm)	75.5	35.0	Purple fruit= 44.0; Light purple= 35.0	48.0
Fruit Color	Purple	*Light Purple	*Purple ( <sup>2</sup> / <sub>4</sub> ); Light Purple ( <sup>2</sup> / <sub>4</sub> )	Yellow	
Number of seeds per fruit	354 (376) 468	58 ( 67) 76	Purple fruit= 112; Light Purple= 52	88 (92) 102	
Pollen	viability (%)	71	48.8	Pink flower = 45.2; Light pink flower =38.2	71.5
	size (µm)	36.1	34.3	Pink flower= 34.2; Light pink flower= 34.3	34.2
Stomata	abaxial	34.3 x 26.9	34.1 x 25.6	38.3 x 24.4	30.3 x 23.6
L/B	adaxial	34.9 x 26.5	33.3 x 24.7	31.6 x 25.1	39.4 x 28.5

\*Dominant.

## Fruits

Fruits were globose and cream yellow with the calyces almost accrescenting in the F<sub>1</sub> hybrids (Figure 2b). Fruit shape, colour and degree of calyx accrescence varied among the six F<sub>2</sub> hybrids. One was characterized by globose-oblong and light yellow fruit, three had oblong and yellow fruits while the remaining two had round and cream yellow fruits (Figure 3b). The percentage of seed set and sizes of fruits are shown in Table 2.

## Mitotic chromosomes

The parents and, F<sub>1</sub> and F<sub>2</sub> hybrids were diploids with 2n = 24 (Figure 4a and b).

♀ *S. melongena* 'Melongena' x ♂ *S. aethiopicum*

## Morphological characters

The F<sub>1</sub> hybrids were erect. Branches were profuse

and spreading as in the female parent while leaves were glabrous on both surfaces like the male parent. Stomata were anomocytic (Table 3).

## Inflorescence and floral characters

In the F<sub>1</sub>, the inflorescence consisted of solitary flowers inserted directly on stems (Figure 2c); a significant deviation from both parents (Table 3). The flowers were pink and pollen viability was 56.8%.

**Table 2.** Growth and morphological characters of *S. macrocarpon*, *S. melongena* 'Golden' and their F<sub>1</sub> and F<sub>2</sub> hybrids.

Character	<i>S. macrocarpon</i>	F <sub>1</sub> Hybrid	F <sub>2</sub> Hybrids	<i>S. melongena</i>
Habit	Erect 1.0 - 1.5 m, broad leaves and moderately spreading	*Erect 1.0 - 1.3 m, broad leaves and spreading	*All erect; branches many and spreading = $\frac{1}{6}$ ; branches few and spreading = $\frac{2}{6}$ ; braches few and moderately spreading = $\frac{3}{6}$ .	Erect 1.5 - 1.8m, branches many and spreading
Leaf indumentum/length (cm)	Glabrous leaves/ 22.2	* Hairy leaves/ 16.8	Hairy = $\frac{4}{6}$ / 19.7; Sparsely hairy = $\frac{2}{6}$ / 15.4	Hairy leaves / 14.7
Leaf breadth (cm)	15.3	13.6	Hairy = 11.8; Sparsely hairy = 12.2	10.6
Petiole length (cm)	5.5	7.9	Hairy = 7.3; Sparsely hairy = 6.7	5.6
Inflorescence (flower number)	Umbellate (2 - 4)	*Umbellate (2 - 4)	Raceme (3-5) = $\frac{2}{6}$ ; Subumbellate (2-5) = $\frac{4}{6}$	Raceme (2 - 4)
Color of petals	purple	*Pink	*Mixture of pink and light pink flowers	Deep pink
Petal length (mm)	18.0	15.8	Raceme = 14.6; Subumbellate = 15.0	18.0
Petal breadth (mm)	8.4	6.4	Raceme = 5.8; Subumbellate = 6.4	5.8
Pollen	Viability (%)	51.8	Raceme = 63.8; Subumbellate = 48.6	58.4
	Size (µm)	34.4	Raceme = 33.5; Subumbellate = 35.7	36.4
Fruit	Length (mm)	38	Deep yellow = 85; light yellow = 42; cream yellow(short calyx) = 34; (calyx accrescent) = 39	126.0
	Diameter (mm)	41.0		63.3
Fruit color	Brown	*Cream yellow	*Deep yellow = $\frac{1}{6}$ ; light yellow = $\frac{2}{6}$ ; cream yellow = $\frac{3}{6}$	Yellow
Number of seeds per fruit	107	132	Deep yellow = 135; light yellow = 89; cream yellow = 63	384
Stomata (L/B)	abaxial	33.8 x 25.5	Hairy leaf = 36.4 x 24.5; Sparsely hairy 36.1 x 25.3	34.5 x 26.9
	adaxial	41.0 x 28.1		32.9 x 26.7

\*Dominant.

## Fruits

Fruits were all round and purple in the F<sub>1</sub> (Figure 2c), and sizes ranged between 4.5 and 7.0 mm and with an average of 85 seeds per fruit (Table 3).

## Mitotic chromosomes

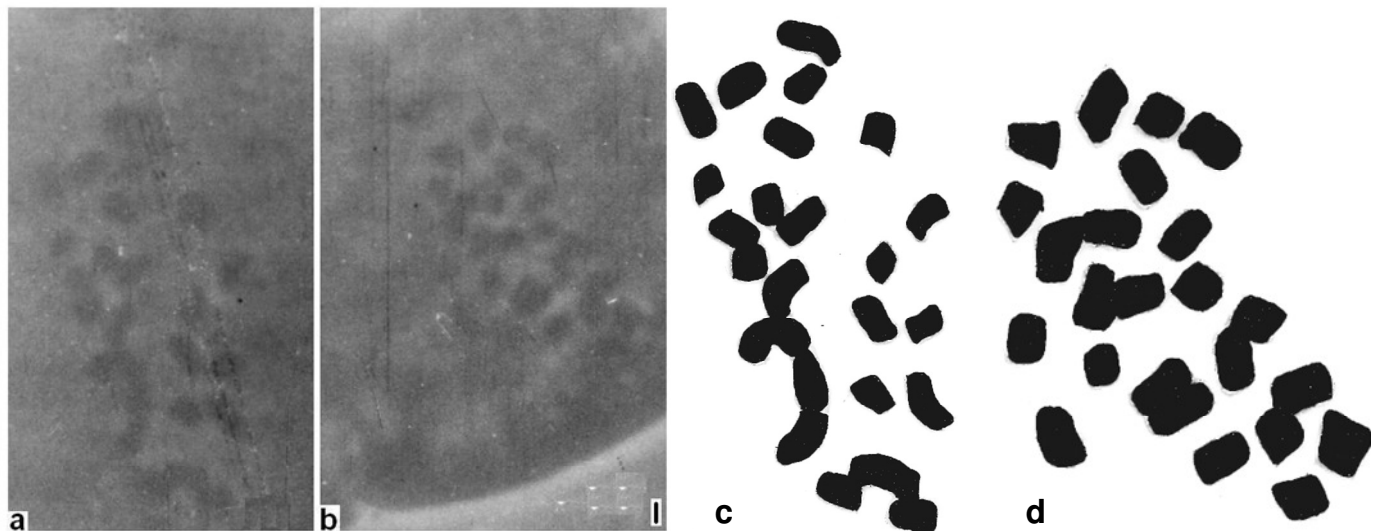
The parents and F<sub>1</sub> hybrids were diploids with 2n = 24.

## DISCUSSION

Leaf size, petiole length, plant height and growth habits of F<sub>1</sub> hybrids were intermediate, though few traits like flower colour and inflorescence type in few instances, expressed dominance. Hybrids are generally identified on the basis of morphological (Schwarzbach et al., 2001; Lexer et al., 2003) or ecological (Archibald et al., 2004) intermediacy. The intermediate phenotypes expressed in the F<sub>1</sub> hybrids may suggest harmonious gene interaction of complement of recessive and

dominant alleles in the crossing parents. By extension, it also supports the claim of similar genomes operative in members of this genus.

This closeness might have resulted from natural inter- and intra-specific hybridization. The existence of swamps of natural hybrids (Omidiji, 1982, 1983; Knapp, 1991a) reinforces this assertion. The same views were expressed for several closely related members of other angiosperms (Rieseberg, 1997; Cattell and Karl, 2004). A number of hybrid zones have been identified which consisted of populations of hybrid plants with unique adaptive



**Figure 4.** Somatic chromosomes; **a.** *S. melongena* 'Golden',  $2n = 24$ ; **b.**  $F_1$  hybrid between *S. macrocarpon*  $\times$  *S. melongena* 'Golden'; **c, d.** drawings of a and b respectively. Scale bar = 3  $\mu$ m.

**Table 3.** Growth and morphological characters of *S. melongena* 'Melongena', *S. aethiopicum* and their  $F_1$  hybrids.

Character	<i>S. melongena</i>	$F_1$ hybrid	<i>S. aethiopicum</i>
Habit	Erect, many branches and spreading 1.5 - 1.8 m	*Erect, many branches and spreading 1.3 - 1.6 m	Erect, few branches and moderately spreading 0.5 - 0.8 m
Leaf length (cm)	18.0	16.9	8.6
Leaf breadth (cm)	12.4	11.9	4.6
Petiole length (cm)	9.0	8.5	1.7
Inflorescence	Raceme	Single flowers	Simple cyme
Color of petal	Pink	* Pink	White
Petal length (mm)	18.4	12.3	7.1
Petal breadth (mm)	6.8	6.4	3.9
Fruit	length (mm)	128.6	5.8
	diameter (mm)	75.4	6.2
Fruit color	Purple	*Purple	Red
Number of seeds per fruit	376	85	87
Pollen	viability (%)	71	56.8
	size ( $\mu$ m)	36.1	31.9
Stomata	abaxial ( $\mu$ m)	34.3 x 26.9	36.1 x 25.7
	L/B	34.9 x 26.5	32.5 x 26.2
			37.1 x 26.8
			32.5 x 25.3

\*Dominant.

features and outstanding competitive advantage over the endemic natural populations (Hijmans et al, 2007). Height was greatly reduced and branches were few and moderately spreading in the  $F_1$  hybrids. The vigour that often characterize hybrids (Moore and Buchanan, 1985; Pico et al., 2003, 2004) was significantly absent in these  $F_1$  hybrids. The intermediacy of values for both morphological and floral features and low quality yield

could have been due to hybrid depression as a number of prominent characters and fitness of the crossing parents were not sufficiently expressed in the  $F_1$  hybrids. Hybrid fitness according to Burgess and Husband (2004) is largely dependent on the magnitude of parental nuclear and non-nuclear contributions since the genetic disparity between crossing species is expected to contribute to the fitness or success of hybrids.

Non-nuclear effects were evident in some features, especially among the  $F_1$  hybrids. The inflorescence type, flower and fruit colour, and growth habit were largely as described for the maternal parent. The influence of extra nuclear factors have been reported in many plant species (Donohue and Schmitt, 1998; Galloway, 2001; Lacey and Herr, 2000) and were found to significantly determine the phenotype and fitness of hybrids, including seed set, germination, survival, adaptation and fertility (Burgess and Husband, 2004). Campbell and Waser (2001) attributed the survival of *Ipomopsis aggregate* x *Ipomopsis tenuituba* to the genetic composition of the maternal parent.

Fertility was greatly depressed in the  $F_1$  hybrids in spite of the high values recorded in the parental species. This occurrence has been linked to a negative genetic interaction between disparate parental genomes (Turelli et al., 2001, Coyne and Orr, 1998), and hybrids are largely expected to be of low pollen viability and reduce fertility than parent species. In similar vein, Ugborogho and Oyelana (1999) alluded to negative chromosomal interaction through inversions and/or deletions as highly significant to the fitness and success rate of several *Solanum* hybrids. This was responsible for the depression in pollen viability, small sized fruits and low seed set observed in their hybrids. In several experimental crosses, hybrid depression was often expressed in low pollen viability (Ugborogho and Oyelana, 1999; Burke and Arnold, 2001), small fruit size (Keller and Waller, 2002), low seed germinability (Omidiji, 1982), seedlessness (Edmond, 1977) and fruitless inflorescence (Wunderlin et al., 1993). Cheptou et al. (2000) and Fishman (2001) equally ascribed fitness disadvantage in hybrids to probable expression of recessive deleterious alleles in the homozygous condition. Other opinions linked hybrid depression to inefficient utilization of nutrients (Heschel et al., 2005) and poor adaptation to environment, including low drought resistance level (Heschel et al., 2002; Heschel and Hausmann, 2001; Chapin et al., 1993).

Despite the fitness disadvantage and depression in many of the  $F_1$  hybrids, a novel case emerged from a cross *S. melongena* 'Melongena' x *S. aethiopicum*. This hybrid was characterized by single flower-inflorescence attached directly on the stem, a significant deviation from the usual raceme and cyme inflorescences in both parent species. This unique feature may be of evolutionary advantage as insect pollinators may act selectively on it creating an adaptive complex which may confer ecological advantage. This development affirms the views of Rieseberg (1997), Arnold (1997) and Arnold et al. (2001) that mating between genetically distinct populations or closely related species may introduce new genes or gene combinations in hybrid species leading to speciation.

The  $F_2$  hybrid populations exhibited low variability than expected, especially in such features as flower color, fruit size and colour, number of seeds in fruits, degree of pollen viability, hybrid fertility and growth habit. Largely, many of these features remained depressed in the  $F_2$ .

However, pollen viability was restored (63.8%) in one  $F_2$  plant but remained largely depressed (38.2 – 48.8%) in the others. Hybrid fertility was also not fully restored in many as some of the  $F_3$  fruits were characterized by fewer seeds.

The loss of several morphological features, low hybrid variability and non-restoration of many masked features in the  $F_2$  populations suggest a near complete homogenization of the genomes of the crossing parents, and which is also an indication of closeness and/or similar origin for the crossing species. The homogenization of the genomes may have afforded a number of recessive genes to appear in homozygous condition, and this may equally have accentuated significantly, the effects of a number of inherent chromosomal aberrations (Oyelana, 2005; Oyelana and Ugborogho, 1997). This occurrence may have significantly prevented sufficient chromosomal rearrangement for full restoration of homology and vigor in many of these  $F_2$  hybrids. The accumulation of these mutations as observed in few natural species (Force et al., 1999) manifested as pollen inviability, reduced or loss of morphological features, low fertility, small sized fruits, low seed set and poor yield in the emerging hybrids.

The evolutionary changes that might have given rise to the diversity of the natural species are attributable to structural chromosomal mutations. This was evident in the performance of both the  $F_1$  and  $F_2$  hybrids. The age long practice of breeding for the purpose of improving the genetic stock of existing vegetables including many *Solanum* species afforded free exchange of genes, and consequently, the breakdown of species reproductive barriers. The ease with which genomes homogenized in these hybrids can be ascribed to this phenomenon. The negative impact of deletions and inversions underscores the need to re-introduce new genes through backcross to related genera or wild species from similar lineage in order to enrich and stabilize the existing genomes.

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