

Nuclear and non-nuclear interactions in F₁ hybrid populations of three *Solanum* species in the subgenus *Leptostemonum*, section *Melongena* (Solanaceae)

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Abstract: Reciprocal crosses involving *Solanum gilo* Raddi, *S. anguivi* Lam. and *S. macrocarpon* L., subg. *Leptostemonum* (Dunal) Bitter sect. *Melongena* Dunal were produced in order to assess inherent nuclear and non-nuclear influences on hybrid fitness, the extent of genomic change, and species compatibility. Hybrids expressed intermediacy and overlaps in leaf, petiole, petal, and plant height dimensions. Maternal influence was dominant in growth habit, leaf shape and texture, flower colour, and fruit size, while paternal control was limited to fruit colour in *Solanum gilo* × *S. macrocarpon*. Pollen viability was reduced from 97.3%-86.5% in parents to 53.8%-20.5% in hybrids. *S. gilo* × *S. macrocarpon* produced single-flowered inflorescence, whereas the reciprocal *S. macrocarpon* × *S. gilo* developed the ability to perennate, indicating the heterogeneity of the parental genome. Fruits of the hybrids were intermediate or smaller, and had fewer seeds. They were wrinkled in *S. gilo* × *S. macrocarpon*, with many aborted seeds. Meiosis was irregular, with few laggards, and isolated uni- and bivalent chromosomes associated with foreign genes in the parent species. Conversely, multivalent and chromosome clumps revealed the extent of homogenization of the parental genomes and species affinity. The maternal genome exerted profound influence on hybrid phenotype and fitness, and should inform and direct future hybridization efforts.

Key words: Genotype, hybrid fitness, hybridization, maternal-paternal influence, meiosis, *Solanum*

Introduction

The genus *Solanum* L. consists of over 2000 species distributed worldwide (Omidiji, 1983; Knapp, 1991), is the largest in Solanaceae, is one of the largest among all flowering plants (Olmstead & Palmer, 1997), and is of economic importance to farmers across Africa (Gbile, 1985; Gruben & Denton, 2004). The species are a ready source of vegetables (Gbile, 1979; Omidiji, 1982), tubers (Okoli, 1988), and medicinal herbs (Caicedo & Schaal, 2004), and contain unique

alkaloids and other biochemical constituents used for the treatment of diverse ailments (diabetes, cholera, bronchitis, high blood pressure) and as laxatives (Daunay & Chadha, 2004; Lester & Seck, 2004).

Despite their economic importance, most species are cultivated at subsistence levels across Africa (Manoko & Van der Weerden, 2004). They constitute one of the main vegetables and are often regarded as staple crops, especially among the major ethnic groups in Nigeria. The wild harbours a greater

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number of unidentified species, which constitute the weed populations. These have become burdensome to farmers (Edmonds, 1977; Bukenya-Ziraba, 2004) and horticulturists alike, and their control and eradication often attract huge investment. They have also been linked to crop failure (Gbile, 1979; Omidiji, 1982) and reductions in farm income.

The domesticated species are consumed as leafy and/or fruit vegetables that are rich in essential minerals and vitamins (Bukenya-Ziraba, 2004), and are recommended as a dietary staple or supplements for nursing mothers, the young, the aged, and anaemic patients (Jansen, 2004). A number of experimental plots maintained by research institutes across Africa, including the Nigerian Institute of Agricultural Research and Training (IAR&T) and the Nigerian Institute of Horticultural Research (NIHORT)—both in Ibadan, Nigeria—serve as reservoirs of germplasms for some important *Solanum* vegetables, and provide extension services to farmers concerning essential practices for optimizing land resources and yield.

An extensive review of *Solanum* species in Africa was carried out by Grubben and Denton (2004) and attempts are being intensified to catalogue natural populations in order to identify pure stocks for backcrosses that may lead to stabilization of hybrid populations with improved vigour. The use of interspecific crosses as a breeding strategy (Ugborogho & Oyelana, 1999; Masuelli et al., 2006; Oyelana & Ugborogho, 2008) has become an important means of improving existing genetic stocks and the productivity of members of this genus. Many of these hybrids possess excellent agronomic qualities, such as good number of harvestable leaves, efficient nutrient utilization (Fontem & Schippers, 2004), and resistance to pests and disease (Caicedo & Schaal, 2004). The preference for and selection of genotypes with desirable agronomic qualities and the ability to adapt to extreme environmental and soil conditions have prevented hybrid stability in nature, reducing chances for backcrosses and/or the exchange of genes between related hybrids.

Solanum species have been characterized morphologically and cytologically. The analyses reveal extensive variation in chromosome number, including a number of aneuploid, aneusomatic, and mixoploid

hybrids (Gavrilenko et al., 1999). Ugborogho and Oyelana (1999), and Oyelana and Ugborogho (2008) assessed phenotypic variation in some hybrids, reflecting an emerging expansion of the genus' genome. Correlations between certain leaf characters and species ploidy level (Levin et al., 2005) have also been used to distinguish the tetraploids ($2n = 48$) from diploids ($2n = 24$) and triploids ($2n = 36$). Mutations (inversions and deletions) have been suggested in some species (Ugborogho & Oyelana, 1999) as being part of the genome of several hybrids, resulting in their low productivity and non-fitness. These chromosomal mutations are recent phenomena (Oyelana, 2005; Oyelana & Ogunwenmo, 2005) in a few domesticated species, with opportunity for speciation.

Hybrid genotype selection for economic benefits may have altered the distribution and genomic structure of *Solanum* species, leading to genetic erosion of traditional and local cultivars (Daunay & Chadha, 2004). Consequently, a number of reciprocal crosses involving 3 representative species from the subg. *Leptostemonum* (Dun.) Bitt. sect. *Melongena* Dun. were produced to determine the mode of inheritance of characters from parents to hybrids and assess the patterns of chromosome pairing and behaviour at meiosis, as well as the effects of parental gene interactions on hybrid fitness and maternal or paternal influence on hybrid phenotypes.

Materials and methods

Description of parent species

Three representative species from the subg. *Leptostemonum* (Dun.) Bitt. sect. *Melongena* Dun. (Table 1) were studied. Plants were erect, woody shrubs with profuse branches. Leaves were simple, broad, and deeply lobed in *Solanum gilo* Raddi, shallowly lobed in *S. anguivi* Lam. and deeply and variously lobed in *S. macrocarpon* L. They were acute at the apices and obovate in *S. gilo* and *S. anguivi*, but obovate to oblanceolate in *S. macrocarpon*. Inflorescence was raceme with pink flowers in *S. gilo*, umbellate white flowers in *S. anguivi*, and purple flowers in *S. macrocarpon*. Fruits were yellow, oblong, and 198.3 mm long in *S. gilo*, but round, red, and 7.7 mm long in *S. anguivi* and yellow and 29 mm long in *S. macrocarpon* (Figure 1a-c).

Table 1. Taxonomic classification of the *Solanum* subgenus *Leptostemonum* section *Melongena*.*

Subgenus <i>Leptostemonum</i> (Dunal) Bitter	
Section <i>Melongena</i> Dun.	
Series <i>Incanifloria</i> Bitt.	
Sub-series <i>Euincana</i> Bitt.	<i>S. melongena</i> L.
Series <i>Macrocarpa</i> Dun.	<i>S. macrocarpon</i> L.
Series <i>Afroindica</i> Bitt.	<i>S. anguivi</i> Lam.
Series <i>Aethiopica</i> Bitt.	<i>S. aethiopicum</i> L.
Series <i>Aethiopica</i> Bitt.	<i>S. gilo</i> Raddi

*Adapted from Gbile (1985)

Cultivation of species

The 3 parent species and their respective hybrids were cultivated in well-drained loamy soil in the biological garden of the University of Lagos, Lagos, Nigeria. Parent species were maintained for upwards of 12 weeks before crosses were produced.

Emasculation of flowers and pollination

Ten flowers per species were emasculated c. 18 h prior to anthesis and bagged, and pollen from freshly dehisced anthers (unbagged flowers) was rubbed on the stigmas to effect pollination. Pollen was applied to the stigmatic surfaces every hour for the entire

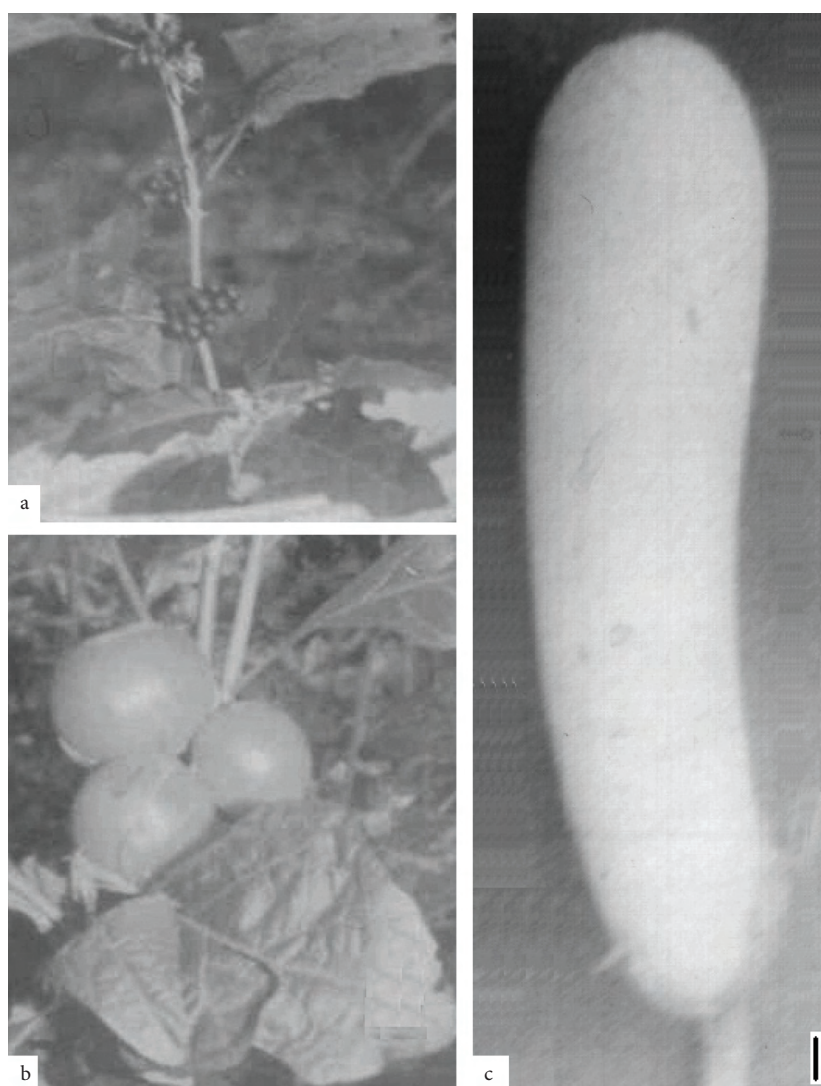


Figure 1. Mature plants and fruits: a. *Solanum anguivi*; b. *S. macrocarpon*; c. fruit of *S. gilo*. Scale bar = 10 mm.

duration of flower opening to ensure a high success rate. The pollinated flowers remained in bags to avoid contamination by any foreign pollen. The bags were later removed on the sixth day of pollination when the corollas had completely withered and the ovaries initiated growth. The same procedure was repeated for the reciprocal crosses.

Germination and screening of seedlings

The F₁ seeds were first sown in planting trays in the greenhouse and the emerging seedlings were allowed to sufficiently root before they were transferred into planting bags 1 week after germination. The young seedlings were left in planting bags for up to 3 weeks, after which time the successful seedlings were transferred to the field and grown in shade for another 2 weeks.

Field exposure

The seedlings were gradually exposed to the field environment and cultivated alongside the parent species. Watering was performed daily at 07:00 and 18:00 hours.

Morphometric analysis

Observation of growth habit, and detailed analysis of morphological and floral features were performed with a hand lens and/or stereomicroscope, while all the measurements were made with the aid of a metric ruler.

Cytological analysis

Cytological analyses included study of stomata, pollen size and viability, and the behaviour of chromosomes during meiosis. The techniques of Ugborogho et al. (1992) and Ogunwenmo (1999) were employed for the analysis of stomata and pollen viability, while meiotic chromosomes were assessed according to Ugborogho and Oyelana (1992).

Hybridization

Ten crosses were made per species and a success rate of over 65% was obtained in all, except *S. macrocarpon* × *S. gilo*, in which no fruit was produced. Reciprocal crosses were made as follows:

- ♀ *S. gilo* × ♂ *S. anguivi*;
- ♀ *S. anguivi* × ♂ *S. gilo*;
- ♀ *S. gilo* × ♂ *S. macrocarpon*;
- ♀ *S. macrocarpon* × ♂ *S. gilo*.

Results

Morphological characters

The hybrids were annuals, except the perennial *S. macrocarpon* × *S. gilo*. They were erect, with few to many spreading branches, becoming woody in *S. anguivi* × *S. gilo* and *S. macrocarpon* × *S. gilo*. Leaves were sparsely hairy and the shape and size were as described for the female parent. In the reciprocal, *S. macrocarpon* × *S. gilo*, leaves were hairy, following the male parent, though with the darker shade of green of the female parent. The stems and midribs of leaves were unarmed, as in the male parent in *S. gilo* × *S. anguivi*. Petiole length overlapped, but mean size was often closer to the female parent in the reciprocal crosses of *S. gilo* × *S. anguivi* and the male parent in crosses involving *S. gilo* × *macrocarpon*. Stipules were profuse at the nodes in *S. anguivi* × *S. gilo*. Stomata were anomocytic, with a few contiguous and sunken on the abaxial leaves of *S. macrocarpon* × *S. gilo* (Figure 2a-d) and *S. anguivi* × *S. gilo* (Figure 2e, f), respectively (Tables 2 and 3).

Inflorescence was raceme (*S. gilo* × *S. anguivi*, *S. macrocarpon* × *S. gilo*) as in the female parent, umbellate (*S. anguivi* × *S. gilo*) as in the male parent, or consisted of solitary flowers (*S. gilo* × *S. macrocarpon*) in the hybrids. Petals were pink as in the female (*S. gilo* × *S. anguivi*, *S. gilo* × *S. macrocarpon*) or male (*S. macrocarpon* × *S. gilo*) parent, but white as in the female parent in *S. anguivi* × *S. gilo*. Petal size was closer to that of the female parent in reciprocal crosses of *S. gilo* × *S. anguivi* or approached that of the parents in crosses involving *S. gilo* × *S. macrocarpon*. Pollen was regular, but viability reduced from 97.3%-86.5% in the parents to 53.8%-20.5% in the hybrids (Tables 2 and 3). A large number of flowers dropped while in buds and less than 25% opened for pollination in *S. macrocarpon* × *S. gilo*.

Fruits

Fruits were red, following the male parent, fairly globose (Figure 3a), and set many seeds in *S. gilo* × *S. anguivi* hybrids. They were yellow as in the male parent, but round as in the female parent, with few seeds in *S. anguivi* × *S. gilo* (Figure 3b, Table 2). The fruits were irregular and brown with a wrinkled pericarp in *S. gilo* × *S. macrocarpon* (Figure 3c). There were few seeds and many aborted. Hybrids did not

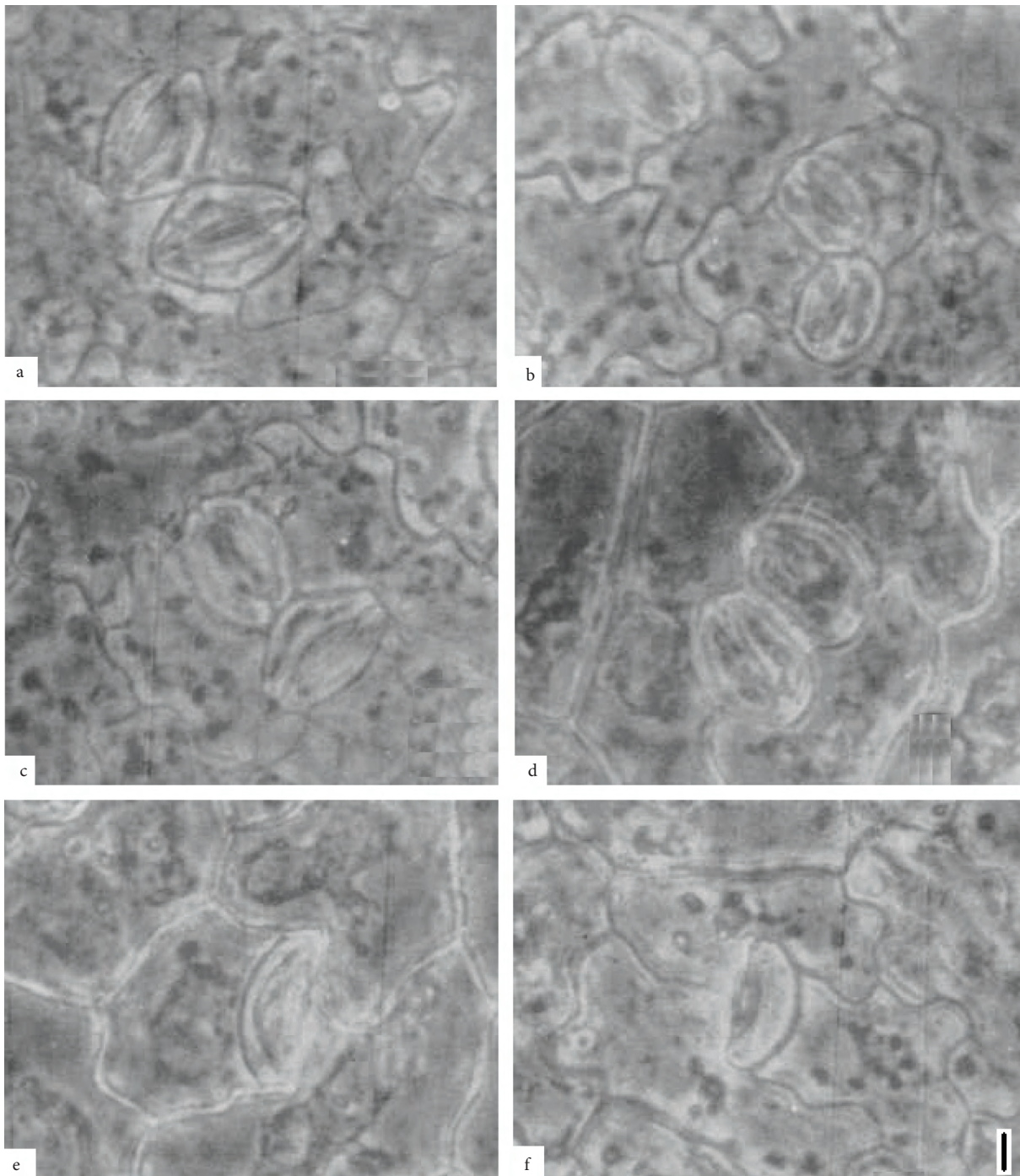


Figure 2. Stomata types: a, b, c, and d: Contiguous stomata types in the F₁ from *S. macrocarpon* × *S. gilo*.
e and f: Sunken stomata in the F₁ from *S. anguivi* × *S. gilo*.
Scale bar = 9 μm.

produce any fruits in *S. macrocarpon* × *S. gilo*, but remained in flower throughout the study. All attempts at hand pollinating were unsuccessful (Table 3).

Meiosis

Meiosis was regular, with 12 bivalents (Figure 4a) and a few tetravalents (Figure 4b) in *S. gilo* × *S.*

Table 2. Morphological characteristics of the F₁ hybrids from reciprocal crosses of *S. gilo* × *S. anguivi*.

Character	<i>S. gilo</i>	F ₁ <i>S. gilo</i> × <i>S. anguivi</i>	F ₁ <i>S. anguivi</i> × <i>S. gilo</i>	<i>S. anguivi</i>
Habit	Erect, many spreading branches	Erect, few moderately spreading branches	Erect, short woody stem, moderately spreading branches	Erect, many spreading branches, stem and leaves armed
Leaf L × B (cm)	14.9 × 13	14.2 × 11.2	7.8 × 6.6	10.05 × 8.8
Petiole L (cm)	4.5	4.4	2.0	2.8
Inflorescence	Raceme	Raceme	Umbellate	Umbellate
Colour of petals	Pink	Pink	White	White
Petal L × B (mm)	18.5 × 8.5	16.4 × 6.5	5.9 × 3.7	6.3 × 3.9
Fruit L × D (mm)	198.3 × 44	45 × 28	6.5 × 6.7	7.7 × 7.1
Fruit colour	Yellow	Red	Yellow	Red
Seeds per fruit	296	93	69	58
Pollen viability (%)	90	53.8	47.9	86.5
Pollen size (µm)	41.9	38.5	31.9	36.2
Abaxial stomata				
L × B (µm)	40.4 × 25.1	38.3 × 24.2	33.5 × 26.2	43.7 × 27.6
Adaxial stomata				
L × B (µm)	38.3 × 23.2	35.3 × 23.6	36.6 × 27.4	40.1 × 26.7

L: length; B: width; D: diameter.

Table 3. Morphological characteristics of F₁ hybrids from reciprocal crosses of *S. gilo* × *S. macrocarpon*.

Character	<i>S. gilo</i>	F ₁ <i>S. gilo</i> × <i>S. macrocarpon</i>	F ₁ <i>S. macrocarpon</i> × <i>S. gilo</i>	<i>S. macrocarpon</i>
Habit	Erect, many spreading branches	Erect, many spreading branches	Erect, many spreading branches	Erect, moderately spreading branches
Leaf (L × B, cm)	14.9 × 13	12.8 × 11.8	12.8 × 12.1	22.2 × 12.3
Leaf indumentum	Hairy	Hairy	Hairy	Glabrous
Petiole L (cm)	4.5	4.8	4.2	5.5
Inflorescence	Raceme	Solitary flowers	Raceme	Umbellate
Colour of petals	Pink	Light pink	Pink	Purple
Petal (L × B, mm)	18.5 × 8.5	16.3 × 7.2	18.1 × 8.3	18.3 × 8.4
Fruit (L × D, mm)	198.3 × 44.0	28.2 × 27.7	0	29.0 × 46.0
Fruit colour	Yellow	Brown (wrinkled)	-	Yellow
Seeds per fruit	296	16	0	107
Pollen viability (%)	90	34.2	20.5	97.3
Pollen size (µm)	41.9	35.5	36.6	34.4
Abaxial stomata				
(L × B, µm)	40.4 × 25.1	29.2 × 23.3	39.3 × 32.0	38.9 × 26.7
Adaxial stomata				
(L × B, µm)	38.3 × 23.2	32.4 × 26.8	37.0 × 33.6	41.0 × 28.1

L: length; B: width; D: diameter.

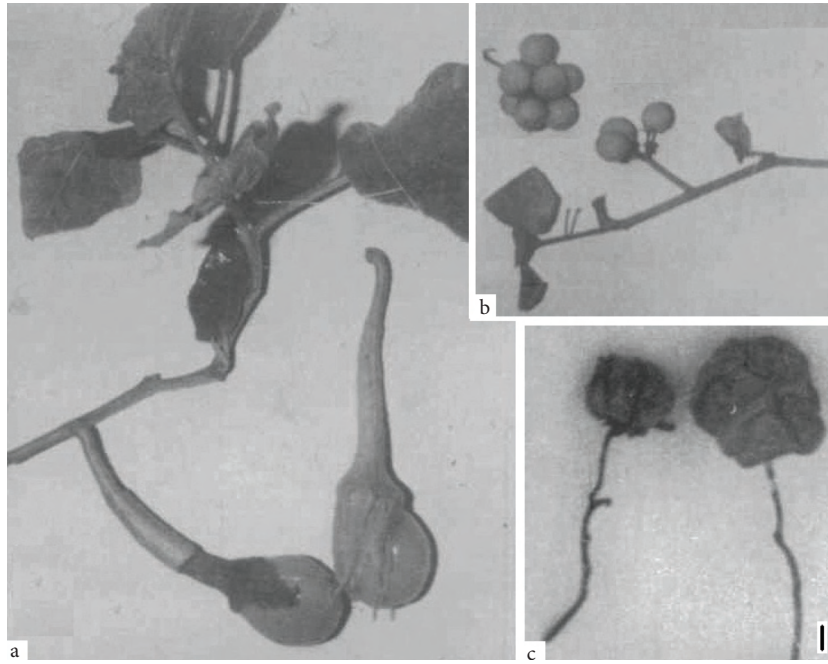


Figure 3. Fruits from the F_1 hybrids: a. F_1 fruits from *S. gilo* \times *S. anguivi*; b. F_1 fruits from *S. anguivi* \times *S. gilo*; c. F_1 fruits from *S. gilo* \times *S. macrocarpon*. Scale bar = 8 mm.

anguivi. It was irregular in the reciprocal *S. anguivi* \times *S. gilo*, with tetravalents (Figure 4c), clumps, and laggards in a few cells, as well as triads. Chromosomes aligned normally at the equator (Figure 4d) in *S. gilo* and migrated to the poles equally (Figure 4e, f) in *S. gilo* \times *S. anguivi*. Telophase and tetrads were also normal (Figure 4g) in *S. gilo* \times *S. anguivi*.

Though meiosis was regular in *S. macrocarpon* (Figure 5a), it was irregular in the hybrid *S. gilo* \times *S. macrocarpon*, with tri-, tetra-, and multivalency (Figure 5b-f), clumps, few laggards, 3-nuclei telophase (Figure 5g), and triads (Figure 5h). The reciprocal also had similar characteristics (Figure 6a-f) and tetrads, with unequal chromosome distribution in the microspores (Figure 6g). Table 4 shows the percentages of different chromosome configurations in the parents and hybrids.

Discussion

There was substantial variation in the level of fitness expressed by the different hybrid progeny. Variations were the outcome of parental genotype

interaction, strong maternal, and/or bi-parental non-nuclear factors. The fitness value of all the hybrids, except *S. macrocarpon* \times *S. gilo*, did not exceed that of their parents, as observed by Burgess and Husband (2004), and Campbell and Waser (2001) in the growth and survival of F_1 hybrids between red and white Mulberry and *Ipomopsis aggregate* \times *I. tenuituba*.

Nonetheless, a hybrid with perennating ability (*S. macrocarpon* \times *S. gilo*) and another with a solitary inflorescence (*S. gilo* \times *S. macrocarpon*) confirmed the observation by Burke et al. (1998), and Emms and Arnold (1997) that *Iris hexagona* \times *I. fulva* had fitness equal to or higher than that of their parents. Mating between genetically distinct populations or closely related species may introduce new genes or combinations in hybrids (Arnold et al., 2001; Oyelana & Ugborogho, 2008). Natural species may also harbour foreign genes from mixed populations (Ugborogho & Oyelana, 1999). If the composite genotypes of these new hybrids support their continued survival, then they may have acquired a competitive edge over other species, which may result in an evolutionary advantage in the future.

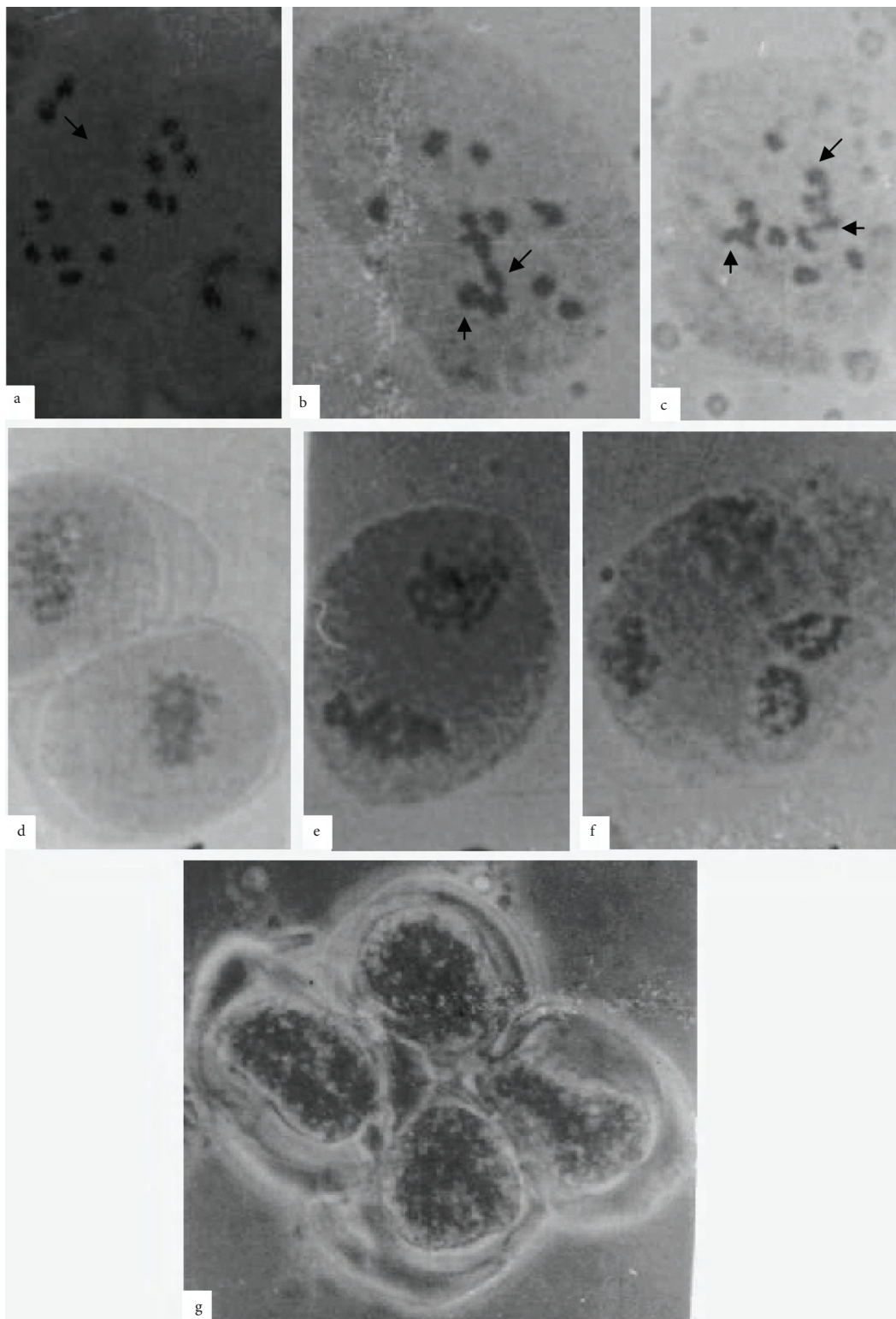


Figure 4. Meiotic chromosome configuration in the F₁ from *S. gilo* × *S. anguivi*: a. 12 II in parent (arrowed) - *S. gilo*; b. 8 II, 2 IV (arrowed) in *S. gilo* × *S. anguivi*; c. 6 II, 3 IV (arrowed) in the F₁ from *S. anguivi* × *S. gilo*; d. Equatorial metaphase in *S. gilo*; e. Anaphase I in *S. gilo* × *S. anguivi*; f. Anaphase II in *S. gilo* × *S. anguivi*; g. a tetrad in *S. gilo* × *S. anguivi*.

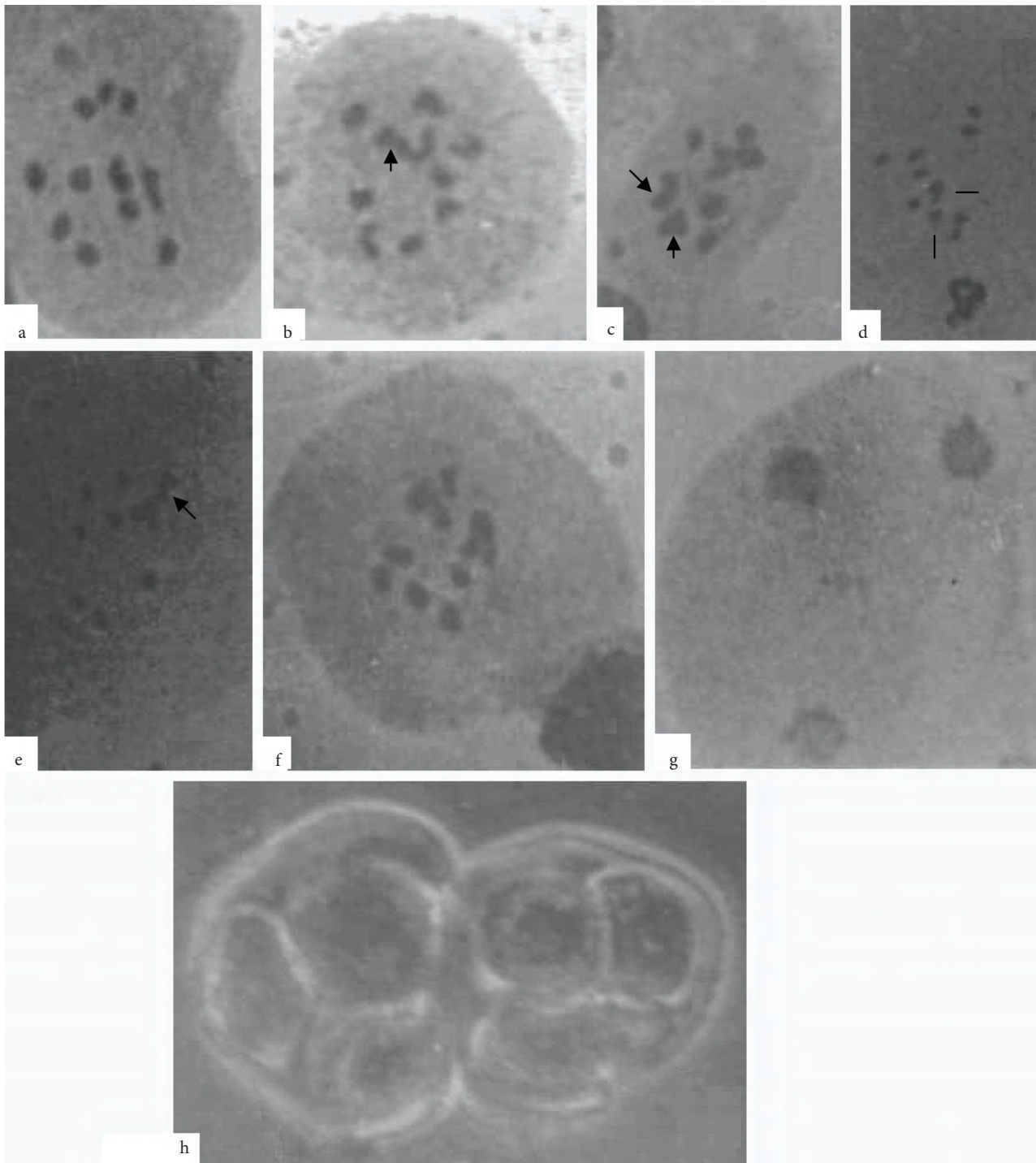


Figure 5. Meiotic chromosome configuration in the F_1 from *S. gilo* \times *S. macrocarpon*: a. 12 II in parent - *S. macrocarpon*; b. 8 II, 2 IV (arrowed) in *S. gilo* \times *S. macrocarpon*; c. 2 II, 4 III, 2 IV (arrowed) in *S. gilo* \times *S. macrocarpon*; d. 8 II, 2 IV (pointed) in *S. gilo* \times *S. macrocarpon*; e. 7 II, 2 V (arrowed) in *S. gilo* \times *S. macrocarpon*; f. 6 II, 2 VI in *S. gilo* \times *S. macrocarpon*; g. Telophase II showing 3 nuclei instead of 4 in *S. gilo* \times *S. macrocarpon*; h. A triad in *S. gilo* \times *S. macrocarpon*.

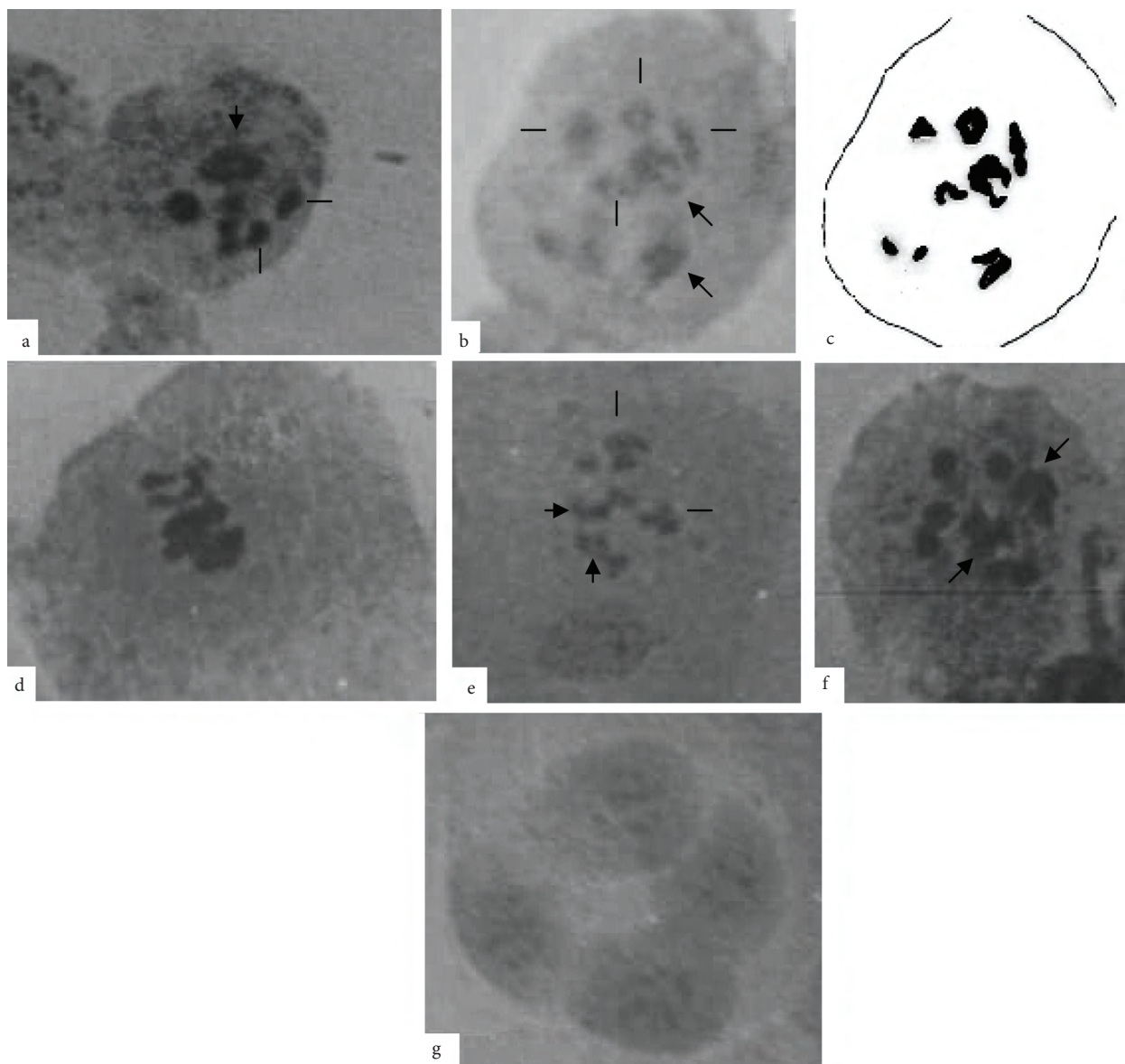


Figure 6. Meiotic chromosome configuration in the F₁ from *S. macrocarpon* × *S. gilo*: a. 3 II, 2 III (pointed), I IV, 1 VIII (arrowed); b. 2 II, 4 III (pointed), 2 IV (arrowed) (cf. drawing - c.); c. Drawing of b; d. Chromosome clump in the F₁; e. 1 II, 2 V (pointed), 2 VI (arrowed); f. 2 II, 2 IV, 2 VI (arrowed); g. Tetrad with unequal chromosome distribution.

The mode of inheritance of some traits in the hybrids consistently expressed the dominance or influence of the female parent, especially crosses involving *S. gilo* and *S. anguvi*; however, the venation pattern, and flower shape and colour of *S. macrocarpon* were consistently masked in the hybrids from crosses involving *S. gilo* and *S. macrocarpon*. Fitness relationships between hybrids may differ due to heterosis or inferiority, depending on which of

their features were expressed or masked (Burke & Arnold, 2001). Otherwise, epistasis or additive genetic effects (Arnold & Hodges, 1995; Burgess & Husband, 2004) and/or favourable allelic combinations (Rieseberg et al., 1996; Arnold et al., 1999) may contribute to observed morphological variation in leaves, petioles, petals, and pollen. In the same vein, low hybrid fertility may have been a consequence of negative genetic interactions (Coyne & Orr, 1998;

Table 4. Meiotic chromosomes of parent species and their respective hybrids.

Taxa	Number of cells	% Chromosome configuration				
		II	III	IV	Clumps	Laggards
<i>S. gilo</i>	40	88	10	2	0	0
<i>S. anguivi</i>	38	76	20	4	0	0
<i>S. macrocarpon</i>	42	64	25	10	1	0
<i>S. gilo</i> × <i>S. anguivi</i>	32	33	36	21	10	0
<i>S. anguivi</i> × <i>S. gilo</i>	41	47	21	12	16	0
<i>S. gilo</i> × <i>S. macrocarpon</i>	34	43	16	28	11	2
<i>S. macrocarpon</i> × <i>S. gilo</i>	52	56	24	12	8	0

II: Bivalent; III: trivalent; IV: tetravalent; V (pentavalent)-VIII (octavalent): rare.

Turelli et al., 2001) between parental genomes or a few emerging mutations inherent in some of the natural species (Ugborogho & Oyelana, 1999). If variation in hybrid fitness was a reflection of species genetic difference (Burgess & Husband, 2004), then low variability and reduced pollen viability, and pollen and stomata size overlaps are indicative of a similar genome or closeness of the parent species; hence, the relative ease of homogenization of the parental genomes in the hybrids. This might have promoted the cumulative effects of recessive alleles, resulting in low fertility and reduced vigour in the hybrids. Swamps of hybrids with little or no agronomic value (Omidiji, 1983; Knapp, 1991; Ugborogho & Oyelana, 1999) from crosses involving members of this genus abound. Many of the domesticated species are themselves products of age-long hybridization; hence, their interspecific hybridization may be mere backcrosses.

Increased gene flow between populations should enhance heterozygosity (Oostermeijer et al., 1995). Consistent low hybrid fertility, small fruits, poor fruit and seed set, and intermediate values of most morphological features suggest outbreeding depression. Such depression may occur if parent species adapted to local conditions or co-adapted gene complexes were disrupted (Fischer & Matthies, 1997; Montalvo & Ellstrand, 2001). We add that the “direction of gene flow” between individuals or groups (choice of crossing parents) is more germane to the success or failure of any breeding programme, as the present study highlights.

Semi-compatible genes, in form of laggards, and few isolated uni- and bivalent chromosomes in the genomes of hybrids could lead to new genetic combinations (Tovar-Sanchez & Oyama, 2004). This may also suggest the presence of some foreign genes in one or both of the crossing parents. This may have caused pairing errors that contributed to faulty microspores (pollen), and poor fruits and seed set in these hybrids. Similarly, chromosome clumps and multivalents in the hybrids suggest a similar genome in the parent species and their close proximity. Studies of chromosome patterns in hybrids have contributed to our understanding of the relationships and evolution (Schneeweiss et al., 2004) of *Solanum*.

Non-nuclear contributions or parental influence on fitness outside those of nuclear genes may include cytoplasmic effects (Levin, 2003), unequal contribution to endosperm (Haig & Westoby, 1991), and the influence of parental environment on the phenotype of offspring (Lacey, 1998; Wade, 1998). These parental effects are usually transmitted differentially and thus manifest themselves as fitness differences in reciprocal crosses (Shaw & Byers, 1998; Levin, 2003). Our reciprocal crosses revealed more maternal influence on growth habit, leaf shape and texture, flower colour, inflorescence type, and fruit shape, while paternal influence was limited to fruit colour (red and yellow) in the hybrids from reciprocal crosses of *S. gilo* × *S. anguivi*. Similarly, Burke et al. (1998) observed strong cytoplasmic effects on the

fitness of *Iris hexagona* × *I. fulva*, as did Campbell and Waser (2001), for reciprocal crosses between *Ipomopsis aggregata* and *I. tenuitula*.

The quality (genotype) of female parents was a major factor contributing to the fitness and survival of the hybrids, and should direct the flow of genes in subsequent breeding programmes involving member species.

References

- Arnold ML, Kentner EK, Johnson JA, Cornman S & Bouck AC (2001). Natural hybridization and fitness. *Taxon* 50: 93-104.
- Arnold ML, Bulger MR & Burke JM (1999). Natural hybridization: how low can you go and still be important? *Ecology* 80: 371-381.
- Arnold ML & Hodges SA (1995). Are natural hybrids fit or unfit relative to their parents? *Trends Ecol Evol* 10: 67-71.
- Bukenya-Ziraba R (2004). *Solanum anguivi* Lam. In: Gruben GJH & Denton OA (eds.) *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers/CTA.
- Burgess KS & Husband BC (2004). Maternal and paternal contributions to the fitness of hybrids between red and white Mulberry (*Morus*, Moraceae). *Am J Bot* 91 (11): 1802-1808.
- Burke JM & Arnold ML (2001). Genetics and the fitness of hybrids. *Annu Rev Genet* 35: 31-52.
- Burke JM, Carney SE & Arnold ML (1998). Hybrid fitness in the Louisiana Irises: analysis of parental and F₁ performance. *Evolution* 52: 37-43.
- Caicedo AL & Schaal BA (2004). Heterogeneous evolutionary processes affect 'R' gene diversity in natural populations of *Solanum pimpinellifolium*. *Proceedings of the National Academy of Sciences USA* 101 (50): 17444-17449.
- Campbell DR & Waser NM (2001). Genotype-by-environment interaction and the fitness of plant hybrids in the wild. *Evolution* 55: 669-676.
- Coyne JA & Orr HA (1998). The evolutionary genetics of speciation. *Philosophical Transactions of the Royal Society of London B* 353: 287-305.
- Daunay MC & Chadha ML (2004). *Solanum melongena* L. In: Gruben GJH & Denton OA (eds.) *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers /CTA.
- Edmonds JM (1977). Taxonomic studies on *Solanum* section *Solanum* (Maurella). *Bot J Linn Soc* 75: 141-178.
- Emms SK & Arnold ML (1997). The effect of habitat on parental and hybrid fitness: transplant experiments with Louisiana Irises. *Evolution* 51: 1112-1119.
- Fischer M & Matthies D (1997). Mating structure, inbreeding and outbreeding depression in the rare plant *Gentianella germanica*. *Am J Bot* 84: 1685-1692.
- Fontem DA & Schippers RR (2004). *Solanum scabrum* Mill. In: Gruben GJH & Denton OA (eds.) *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers/CTA.
- Gavrilenko T, Thieme R & Tiemann H (1999). Assessment of genetic and phenotypic variation among intraspecific somatic hybrids of potato, *Solanum tuberosum* L. *Pl Breed* 118: 205-215.
- Gbile ZO (1985). Taxonomic study of Nigerian species of *Solanum* L. I. Studies of the generic and infra-generic statuses. *Nigerian J Sci* 19 (1-2): 57-61.
- Gbile ZO (1979). *Solanum* in Nigeria. In: Hawkes JG, Lester RW & Skelding AD (eds.) *The ecology and taxonomy of the Solanaceae*. London: Academic Press.
- Gruben GJH & Denton OA (2004). *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers/CTA.
- Haig D & Westoby M (1991). Genomic imprinting in the endosperm: its effect on seed development in crosses between species, and differences between ploidies of the same species, and its implications for the evolution of apomixes. *Philosophical Transactions of the Society of London, B* 333: 1-13.
- Jansen PCM (2004). *Solanum anomalum* Thonn. ex Schumach. In: Gruben GJH, Denton OA (eds.) *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers/CTA.
- Knapp S (1991). A revision of the *Solanum* sessile species group (Section *Germinate* parte) (Solanaceae). *Bot J Linn Soc* 105: 179-210.
- Lacey EP (1998). What is an adaptive environmentally induced parental effect? In: Mousseau TA & Fox CW (eds.) *Maternal effects as adaptations*. New York: Oxford University Press.
- Lester RN & Seck A (2004). *Solanum aethiopicum* L. In: Gruben GJH, Denton OA (eds.) *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers/CTA.

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- Levin RA, Watson K & Bohs L (2005). A four-gene study of evolutionary relationship in *Solanum* section *Acanthophora*. *Am J Bot* 92(4): 603-612.
- Levin DA (2003). The cytoplasmic factor in plant speciation. *Syst Bot* 28: 5-11.
- Manoko ML & Van der Weerden GM. (2004). *Solanum americanum* Mill. In: Gruben GJH & Denton OA (eds.) *Plant Resources of Tropical Africa 2. Vegetables*. Wageningen: PROTA Foundations/Backhuys Publishers/CTA.
- Masuelli RW, Marfil CF, Davison J & Conai L (2006). Genomic instability in *Solanum tuberosum* × *S. kurtzianum* interspecific hybrids. *Genome* 49(2): 104-113.
- Montalvo AM & Ellstrand NC (2001). Non local transplantation and outbreeding depression in the shrub *Lotus scoparius* (Fabaceae). *Am J Bot* 88: 258-269.
- Ogunwenmo KO (1999). Evolutionary and taxonomic studies of *Ipomoea* L. sect. *Involucratae* Bak. & Rendle (Convolvulaceae) in Nigeria. *Feddes Repert* 110 (7-8): 499-514.
- Okoli BE (1988). Cytotaxonomic studies of five West African species of *Solanum* L. (Solanaceae). *Feddes Repert* 99 (5-6): 183-187.
- Olmstead RG & Palmer JD (1997). Implications for the phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. *Syst Bot* 22(1): 19-29.
- Omidiji MO (1983). Cytomorphological studies of *Solanum aethiopicum* x *S. macrocarpon* F₁ hybrid. *Cytologia* 48: 35-40.
- Omidiji MO (1982). Interrelationships of *Solanum* species in different series of the subgenus *Leptostemonum* (Dun) Bitt. *Crop Research* 22: 13-21.
- Oostermeijer JGB, Altenburo RGM & Den Nijs HCM (1995). Effects of outcrossing distance and selfing on fitness components in the rare *Gentiana pneumonanthe* (Gentianaceae). *Acta Bot Neerl* 44: 257-268.
- Oyelana OA (2005). Karyotypic analysis and meiotic chromosomes in eight taxa of *Solanum* species (Solanaceae). *Acta Satech* 2 (1): 24-29.
- Oyelana OA & Ogunwenmo KO (2005). Comparative assessment of induced mutants from *Solanum macrocarpon* L. (Solanaceae). *Acta Satech* 2 (2): 50-56.
- Oyelana OA & Ugborogho RE (2008). Phenotypic variations of F₁ and F₂ populations from three species of *Solanum* L. (Solanaceae). *Afr J Biotechnol* 7 (14): 2359-2367.
- Rieseberg LH, Sinervo B, Linder CR, Ungerer MC & Arias DM (1996). Role of gene interactions in hybrid speciation: evidence from ancient and experimental hybrids. *Science* 272: 741-745.
- Schneeweiss GM, Palomeque T, Colwell AE & Weiss-Schneeweiss, H. (2004). Chromosome numbers and karyotype evolution in *Holoparasitic orobanche* (Orobanchaceae) and related genera. *Am J Bot* 91 (3): 439-448.
- Shaw RG & Byers DL (1998). Genetics of Maternal and Paternal Effects. In: Mousseau TA & Fox CW (eds.) *Maternal effects as adaptations*. New York: Oxford University Press.
- Tovar-Sanchez E & Oyama K (2004). Natural hybridization and hybrid zones between *Quercus crassifolia* and *Quercus crassipes* (Fagaceae) in Mexico: Morphological and Molecular evidence. *Am J Bot* 91 (9): 1352-1363.
- Turelli M, Barton NH & Coyne JA. (2001). Theory and speciation. *Trends Ecol Evol* 16: 330-343.
- Ugborogho RE, Ogunwenmo KO & Aina, OI (1992). Epidermal morphology of six taxa of *Ipomoea* L. in Nigeria. *Feddes Repert* 103 (7-8): 543-550.
- Ugborogho RE & Oyelana OA (1999). A cytogenetic assessment of sterility in F₁ hybrid and its backcross from *Solanum gilo* x *S. aethiopicum* (Solanaceae). *J Sci Res Dev* 4: 61-70.
- Ugborogho RE & Oyelana OA (1992). Meiosis, pollen morphology and perianth stomata of some taxa of *Amaranthus* L. (Amaranthaceae) in Nigeria. *Feddes Repert* 103 (5-6): 363-373.
- Wade MJ (1998). The Evolutionary Genetics of Maternal Effects. In: Mousseau TA & Fox CW (eds.) *Maternal Effects as Adaptations*. New York: Oxford University Press.