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Evaluation of crossability studies between selected eggplant accessions with wild relatives *S. torvum*, *S. anguivi* and *S. aethopicum* (Shum group)

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Wild relatives of eggplants represent a good source of variation for breeding programmes, in particular for traits related to biotic and abiotic stresses and also fruit quality traits. However, wild species remain largely unexploited for eggplant breeding compared to other crops like tomato. Seven cultivated eggplant accessions (SM001-02, SM001-04, SM001-06, SM001-07, SA002-02, SA002-03 and SMA003-03) were crossed with three wild accessions (ST004-03 (*Solanum torvum*), San005-01 (*Solanum anguivi*) and SA002-08 (*Solanum aethiopicum*)) in an open field using completely randomized design. The success of fruit and seed set as well as seed germination depended on the cross combination and the direction of the cross. In this regard, no fruit set was recorded when the wild accessions were used as female parents. The highest fruit set and mean number of seeds/fruit was obtained from the crosses Sm001-07 × ST004-03 (6%; 264 seeds) and Sm001-07 × San005-01 (5.7%, 114 seeds), respectively. The germination of hybrid seeds was recorded in only three crosses, SM001-07 × ST004-03, SM001-07 × San005-01 and SA002-02 × San005-01 with germination range from 3.3 to 16.6%. However, plantlets from these seeds did not survive after two weeks of germination. The hybridity of the putative interspecific F1 hybrids (through tissue culture) was confirmed with a morphological marker. These hybrids obtained will contribute to broadening the genetic background of cultivated eggplant species used in this study and to the genetic enhancement of this crop.

Key words: Crossability, eggplant, fruit set, germination, introgression, seed set, wild relatives.

INTRODUCTION

Cultivated eggplants (*Solanum* species) are popular vegetable crop worldwide especially in Africa and Ghana, where their leaves and fruit are consumed almost on daily basis (Daunay et al., 2001). All parts of the plant are useful to the populace; the fruits and leaves are used in

cooking vegetable soup and stews and have been reported to be good source of dietary fibre, vitamins (vitamins A, B1 and B6) and provides substantial quantities of minerals especially phosphorus, potassium, calcium and magnesium (Okmen et al., 2009; Raigón et

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et al., 2008). The roots, leaves and inflorescences are also indicated for the treatment of several diseases such as glaucoma, convergence insufficiency, heart diseases, arteriosclerosis, bronchitis, itch, body aches and asthma (Igwe et al., 2003; Grubben and Denton, 2004; Johnson et al., 2010; Okon et al., 2010). Studies by Nagoaka et al. (2001), Shamin et al. (2004), Aliero (2007), and Chinedu et al. (2011) revealed the presence of high levels of steroidal glycoalkaloids, tannins sesquiterpenoids and other essential bioactive compounds that act as analgesic, anti-inflammatory, anti-hypertensive and antimicrobial in the treatment and/or prevention of these diseases (Plazas et al., 2016). In spite of these advantages, the genetic diversity of cultivated eggplants is narrow compared to their wild relatives such as *Solanum insanum*, *Solanum anguivi* and *Solanum dasyphyllum* for cultivated *Solanum melongena*, *Solanum aethiopicum* and *Solanum macrocarpon*, respectively (Furini and Wunder, 2004; Vorontsova et al., 2013). This narrow genetic base can be attributed to evolution bottlenecks and intensive selection of few desired traits during domestication; a limitation to obtaining major breeding advances (Meyer et al., 2012). To broaden the genetic base of cultivated eggplant species, there is a need to crossbreed them with their wild relatives.

Eggplant wild relatives represent immeasurable source of genetic variation for the development of novel cultivars to address the challenges posed by biotic and abiotic stresses (Vorontsova et al., 2013; Mutegi et al., 2015; Kouassi et al., 2016). They grow in the wild under different environmental conditions such as deserts, waterlogged and swampy areas with varying degree of temperatures and thus become resistant to most biotic and abiotic conditions (Knapp et al., 2013; Lester et al., 2011; Davidar et al., 2015). The fact that wild eggplant species can grow under varying environmental conditions compared to their cultivated counterparts may play a pivotal role towards the breeding of eggplant cultivars that can withstand climate change (Dempewolf et al., 2014). Further, wild relatives have been reported to contain high levels of antioxidants especially phenols (Kaushik et al., 2015). For instance, wild tomato and eggplant species have been reported to contain higher concentrations of phenolic acid compared to their cultivated relatives which is of interest for developing new eggplant varieties with improved bioactive properties (Meléndez-Martínez et al., 2010; Meyer et al., 2015). In this regard, fruits of *S. torvum*, *S. anguivi* and *S. aethiopicum* Shum gp. are regularly used in many Ghanaian food preparations because of the belief that they are very nutritious and contain medicinal properties (antioxidants) (Akoto et al., 2015; Oppong et al., 2015). Their fruits are harvested from the wild and nutritionally contain high levels of iron among other nutrients that can significantly reduce iron deficiency in the country (Welch, 2008; Oyeyemi et al., 2015).

Moreover, studies by Clain et al. (2004) and Gousset et

al. (2005) have also shown that some wild species such as *S. torvum* have high levels of resistance to pests, nematodes and pathogens (Collonnier et al., 2003; Clain et al., 2004; Gousset et al., 2005). This suggests the potential to introgress stress resistance genes into cultivated eggplants to enhance their resistance to pests and diseases. Another wild species, *S. anguivi* is of great interest for breeding, given its resistance to bacterial wilt disease (*Ralstonia solanacearum*) (Schipper, 2000) and high number of fruits per inflorescence. A successful cross between *S. melongena* and *S. anguivi* may eventually result in the development of eggplant variety that is resistant to disease and high yielding (Schipper, 2000). However, the utilization of wild species for eggplant breeding has been underutilized (Kaushik et al., 2015). Eggplant breeders have underexplored the potential of wild species for eggplant breeding compared to other crops like tomato (Hajjar and Hodgkin, 2007; Díez and Nuez, 2008) and hence no commercial varieties containing introgressions from wild related species have been released (Plazas et al., 2016).

Although, there are several reports regarding interspecific hybridization of eggplant and their wild relatives, the hybrids produced are highly sterile, with a few cases of partially fertile or fertile hybrids (Lester and Kang, 1998; Behera and Singh, 2002; Daunay and Hazra, 2012; Rotino et al., 2014; Davidar et al., 2015; Devi et al., 2015; Plazas et al., 2016). Even though the challenges and potential of hybrids produced using interspecific hybridization of cultivated and wild relatives of eggplant is known, information regarding interspecific hybridization of eggplant species using local cultivars and their wild relatives is not readily available in Ghana. Lack of this information hampers efforts to develop nutritious and stress resistant varieties of eggplant. There is therefore a need to evaluate crossability of populations of cultivated cultivars and wild eggplant species. The objective of this study was to evaluate the crossability of selected high yielding eggplant cultivars with their wild relatives (*S. torvum*, *S. anguivi* and *S. aethiopicum* (Shum group)).

MATERIALS AND METHODS

Plant material

Accessions of eggplant from three species *S. melongena* (4), *S. macrocarpon* (1) and *S. aethiopicum* (2) originating from central, western, Greater Accra and Eastern regions of Ghana were used as cultivated eggplant parents, while *S. torvum* (ST003-03), *S. aethiopicum* (SA002-08) and *S. anguivi* (San005-01) were utilized as wild parents. Table 1 shows the accessions, collection sites, and status.

Selfing of eggplant accessions

Both cultivated and wild accessions were selfed by covering healthy flower buds, a day to anthesis to maintain homozygosity.

Table 1. Eggplant accessions used in hybridization studies.

Accession	Species	Ploidy level	Collection site	Region	Status
SM001-04	<i>S. melongena</i>	2n=24	Mankesim	Central	Cultivated
SM001-06	<i>S. melongena</i>	2n=24	Dome	Greater Accra	Cultivated
SM001-02	<i>S. melongena</i>	2n=24	Juabuso	Western	Cultivated
SM001-07	<i>S. melongena</i>	2n=24	Abura	Central	Cultivated
SA002-03	<i>S. aethiopicum</i> (Gilo group)	2n=24	Bunso/PGRRI	Eastern	Cultivated
SA002-02	<i>S. aethiopicum</i> (Gilo group)	2n=24	Bunso/PGRRI	Eastern	Cultivated
Sma003-03	<i>S. macrocarpon</i>	2n = 24, 36	Ajumako Besease	Central	Semi-wild
ST003-03	<i>S. torvum</i>	2n = 24, 48	Atonsu	Ashanti	Wild
SA002-08	<i>S. aethiopicum</i> (Shum gp.)	2n=24	Bunso/PGRRI	Eastern	Wild
San005-01	<i>S. anguivi</i>	2n=24	Atonsu	Ashanti	Wild

The covers were removed when the developing fruit had reached a suitable size, and tagged. Thereafter, fully ripe and tagged fruits of all the accessions were harvested individually. Seeds were then extracted from their fruits and air dried under a shade to a moisture content of 8%. These were nursed and used for the hybridization studies.

Nursery preparation, transplanting and field establishment

Seeds of all accessions were germinated in wooden boxes containing sterile black soil. The seedlings were transplanted into experimental pots after four weeks at the research field of the Faculty of Agriculture, Kwame Nkrumah University of Science and Technology, Ghana situated at longitude 01° 33W and latitude 06° 41 N.

Seedlings were transplanted at spacing 60 × 60 cm², with three plantlets per accession in four replicates. In all, a total number of 120 plantlets from all the accessions were grown. Fertilizer application was done one week after transplanting using NPK (15:15:15) at the rate of 10 g/plant (312 kg/ha) while urea was applied at the rate of 10 g/plant when flowering began. Irrigation was carried out three times a week during the first four weeks after transplanting and daily thereafter. However, at flowering, watering was done twice daily (morning and evening). Developing weeds were hand weeded two to three times a month.

Hybridization and germination of hybrid seeds

Cross-pollinations were carried out between the seven cultivated eggplant cultivars (maternal parents) and the three wild relatives (paternal parents) (Table 1). The parents were crossed using reciprocal crossing. The young buds were emasculated in the morning (6 to 9 am) one day to anthesis to prevent accidental self-pollination. The emasculated flowers were then bagged to prevent pollination by any unknown source. Thereafter, pollen collected from the wild accessions was dusted on the stigma of the emasculated flowers on the same day. Pollinated flowers were then covered again with brown paper bags to prevent any other pollen getting in contact with the stigma. Each flower was labeled showing the cross details.

The crossed fruits were harvested at full ripe stage, seeds extracted and stored for raising F1 populations. The seeds were then nursed in trays containing growing substrate. However, few seeds were cultured *in-vitro* using MS medium (with vitamins supplemented with phytigel (3.5 g/L), sucrose (30 g/L), indole-3-acetic acid (0.5 mg/L), benzylaminopurine (2 mg/L) and incubated

in the growth chamber under standard conditions. Seedlings from germinated seeds were transplanted in plastic pots containing growing substrate and covered with plastic cups for acclimatization.

Data collection and analysis

Data taken included number of buds pollinated per cross, fruit set (%), number of seeds/fruit and germination (%) of F1 seeds. Number of pollinated buds and number of seeds per fruit were obtained by counting the number of flower buds pollinated and seeds extracted from each cross and fruit, respectively. Fruit set (%) was calculated by dividing the number of developing fruits by the total number of pollinated buds expressed as percentage. Percentage germination was obtained by dividing the number of hybrid seeds that germinated by the total number of seeds sowed and expressed as percentage.

RESULTS

Interspecific hybridization and fruit set

Table 2 shows the result of crosses between cultivated eggplant cultivars and wild eggplant accessions. A total of 3,640 interspecific crosses were performed using *S. melongena* (4), *S. aethiopicum* (2, Gilo group) and *S. macrocarpon* (1) accessions as cultivated eggplants and *S. torvum*, *S. anguivi* and *S. aethiopicum* (Shum group) as wild accessions (Tables 1 and 2). Although reciprocal hybridizations were also conducted, no success was achieved and therefore was not included in the results. The number of crosses performed depended on the number of healthy flower buds available for pollination. In this respect, it was observed that accessions SM001-06, SM001-02 and SA002-02 produced flowers profusely, while accession SMA003-03 produced few flowers. Hence, the number of hybridization obtained in accession SM001-06 was found to be more than twice higher than that observed in accession SMA003-03. Moreover, the number of days for a crossed flower to wither and drop (abort) varied among the accessions. Generally, flower abortion is preceded by gradual senescence of the

Table 2. Hybridization studies between cultivated eggplant and wild eggplant accessions.

Female (♀)	Male (♂)	No. of crosses	Fruit setting (%)	No. of seeds/fruit	Germination (%)
Sm001-02	ST004-03	200	4.0	0.00	Nil
Sm001-02	San005-01	300	0.0	0.00	Nil
Sm001-02	SA002-08	111	2.7	100.00	Nil
Sm001-04	ST004-03	150	4.0	40.00	Nil
Sm001-04	San005-01	150	0.0	0.00	Nil
Sm001-04	SA002-08	120	2.5	15.67	Nil
Sm001-06	ST004-03	280	1.4	0.00	Nil
Sm001-06	San005-01	250	0.0	0.00	Nil
Sm001-06	SA002-08	200	2.5	201.67	Nil
Sm001-07	ST004-03	133	6.0	264.00	16.6
Sm001-07	San005-01	173	5.7	114.00	16.6
Sm001-07	SA002-08	150	1.3	45.00	Nil
SA002-02	ST004-03	462	1.5	0.00	Nil
SA002-02	San005-01	150	4.6	50.00	3.3
SA002-03	ST004-03	200	1.5	0.00	Nil
SA002-03	San005-01	300	3.3	0.00	Nil
SMA003-03	ST004-03	142	2.8	1.00	Nil
SMA003-03	San005-01	95	3.1	0.00	Nil
SMA003-03	SA002-08	74	1.3	0.00	Nil

sepals of the flower (change from green to yellow and brown thus wilting) within five days after pollination. However, accessions such as SM001-02 was noted to wilt within three days after pollination while, accessions SMA004-03 and SM001-07 were observed to abort without necessarily undergoing senescence, while others abort as a result of pest infestation (Plate 1A to E). Besides, the longevity of a pollinated flower bud was dependent on the length of style. Flowers with long styles were observed to have higher longevity compared to that of medium length styles flowers (Plate 1F).

Moreover, fruit development among the different cross combinations varied. Developing fruits from SM001-07 × ST004-03 showed no pigment while that of cross SM001-07 × San005-01 was pigmented (Plate 2). In addition, developed fruits were observed to be smaller than their female parents but bigger than the male parents. For instance, in the cross SM001-07 × ST004-03, putative hybrid fruit resembled *S. torvum* fruit in size and shape compared to *S. melongena*, but the fruit colour was similar for both parents (Plate 3). The hybridized fruits presented small and round fruits like that of *S. torvum* (ST004-03) that contrast the semi-long and big fruits in *S. melongena* (SM001-07) (Plate 3). The leaf and flower morphology provided further evidence for the success of the hybrid plants. Hybrid leaves showed intermediate lobbing between the strong lobed *S. torvum* accession and the weak lobbed *S. melongena* accession. Similarly, flower colour was bluish violet in hybrid flowers and deep bluish violet in *S. melongena*, while *S. torvum* showed white flowers (Plate 3).

The result revealed that percentage of fruit set of eggplant among the various interspecific test crosses was generally low, though all the crosses under study produced fruits except, SM001-02 × San005-01, SM001-04 × San005-01 and SM001-06 × San005-01 (Table 2). Among the three wild accessions used, fruit set was comparatively higher in ST003-03 followed by San005-01 and SA002-08 (Table 2). The highest percentage fruit set (6%) was recorded in SM001-07 × ST004-03 cross and the lowest (1.3%) was observed in the crosses SMA003-03 × SA002-08 and SM001-07 × SA002-08, respectively (Table 2). Some hybridized fruits developed to maturity (40 days after pollination) while others were affected by diseases such as fruit rot (Plate 4).

Number of seeds/fruit

Seeds were obtained from the fruits of crosses, SM001-02 × SA002-08 (100), SM001-04 × ST004-03 (40), SM001-04 × SA002-08 (16), SM001-06 × SA002-08 (202), SM001-07 × ST004-03 (264), SM001-07 × SA002-08 (114), SM001-07 × San005-01 (45), SA002-02 × ST004-03 (50) and SMA003-03 × ST004-03 (1). However, no seed was recorded in the other test crosses, although fruit formation was noted in accessions SM001-02, SM001-06, SA002-02, SA002-03 and SMA003-03 with ST004-03, respectively (Table 2 and Plate 5). The highest mean number of seeds/fruit was observed in cross SM001-07 × ST004-03 (264 seeds) followed by SM001-06 × SA002-08 (202 seeds). The lowest number

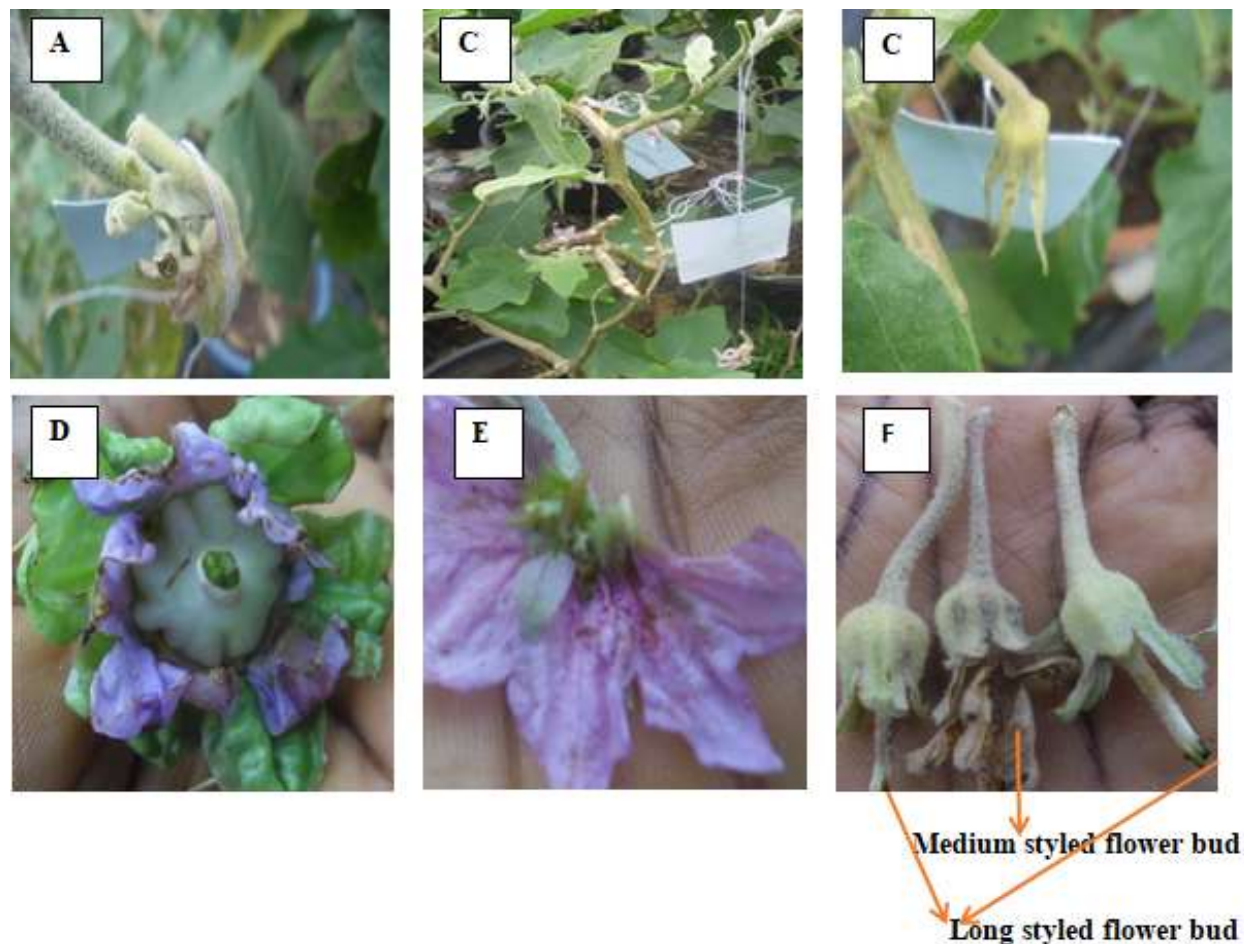


Plate 1. Flower senescence and abortion in eggplant hybridization. (A) Flower undergoing senescence four days after pollination. (B and C) Freshly aborted flower (SM001-02 × ST004-03), detached from mother plants. (D) Aborted flower caused by fruit borer. (E) Longevity of medium and long styled flowers five days after pollination.

of seeds/fruit was recorded in the cross combination, SMA003-03 × ST0003-03 (Table 2).

Seed germination

The percentage seed germination among the various crosses was very low and few combinations produced viable seeds (Table 2). Few apparently normal looking seeds, more or less of the same size in appearance as selfed parents were observed. Also most hybrid seeds were empty when cut open and subsequently weighed less than selfed seeds of the respective female parents. Although, the crosses SM001-02 × SA002-08, SM001-04 × ST004-03, SM001-04 × SA002-08, SM001-06 × SA002-08, SM001-06 × SA002-08, SM001-07 × ST004-03, SM001-07 × San005-01, SM001-07 × SA002-08, SA002-02 × San005-01 and SMA003-03 × ST004-03 produced seeds, no germination was observed except the cross combinations SM001-07 × ST004-03 (16.6%),

SM001-07 × San005-01 (3.3%) and SA002-02 × San005-01 (16.6%), respectively (Table 2). While fruits from the crosses SM001-07 × ST004-03, SM001-06 × SA002-08 and SA002-02 × San005-01 produced a relatively high number of seeds (264, 201.67 and 114 seeds, respectively), only 16.6% of 264 and 114 seeds obtained from the crosses germinated. However, plantlets from these seeds did not survive after two weeks of germination (Table 2).

DISCUSSION

Hybridity confirmation

The putative interspecific hybrids showed intermediate morphological traits between the two parents for corolla colour, leaf blade lobbing and fruit shape. These traits are qualitative and considered as the most important characters to identify a particular plant variety. Qualitative

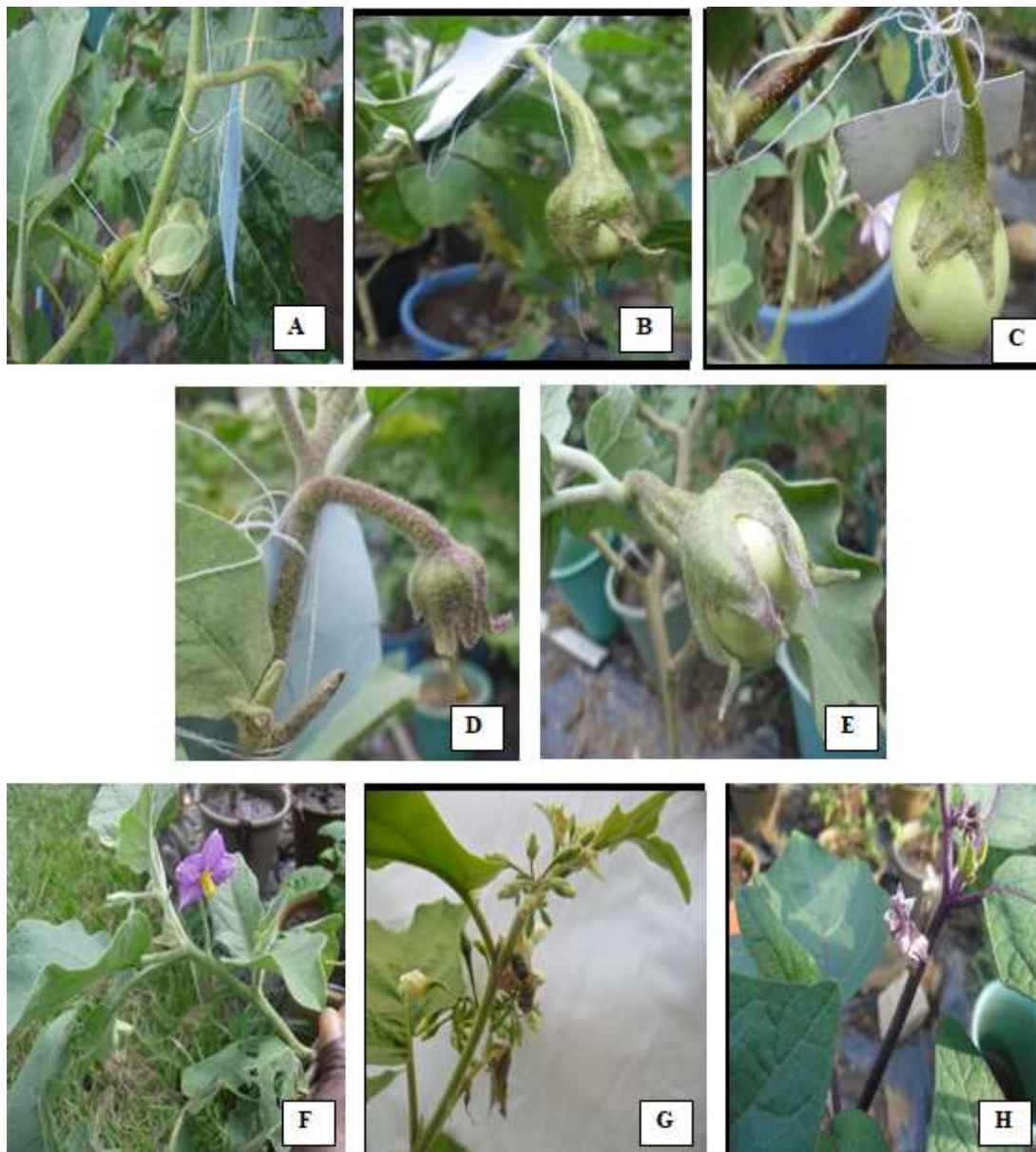


Plate 2. Different stages in fruit development between interspecific crosses (A and D) Developing fruit 9 days after pollination (B and E) Developing fruit 21 days and (C) 40 days after pollination in the cross SM001-07 × ST004-03 and SM001-07 × San005-01; and (F, G and H) plants of accessions SM001-07, ST004-03 and San005-01, respectively.

traits are mostly genetically controlled; thus, they are less independent to the environmental response (Sinha and Mishra, 2013; Bashar et al., 2015). The utilization of morphological trait such as prickliness in hybridity confirmation has been reported by Plazas et al. (2016) in their study of interspecific hybridization between eggplant and their wild relatives. Similarly, in cotton, morphological characters of the putative hexaploid plants such as the shapes and sizes of leaves, bolls and bracts were observed to be intermediate between the cross *G. hirsutum* and *G. anomalum* (Zhang et al., 2014).

Hybridization between cultivated eggplant species and their wild relatives

Findings from the crossability studies indicate that accessions of cultivated *S. melongena*, *S. aethiopicum* (Gilo group) and *S. macrocarpon* are crossable with the wild *S. torvum*, *S. anguivi* and *S. aethiopicum* (Shum group) in one direction; although the crossing success varied among the different cross combinations. This phenomenon of hybridization success in only one direction has been ascribed varyingly to unilateral

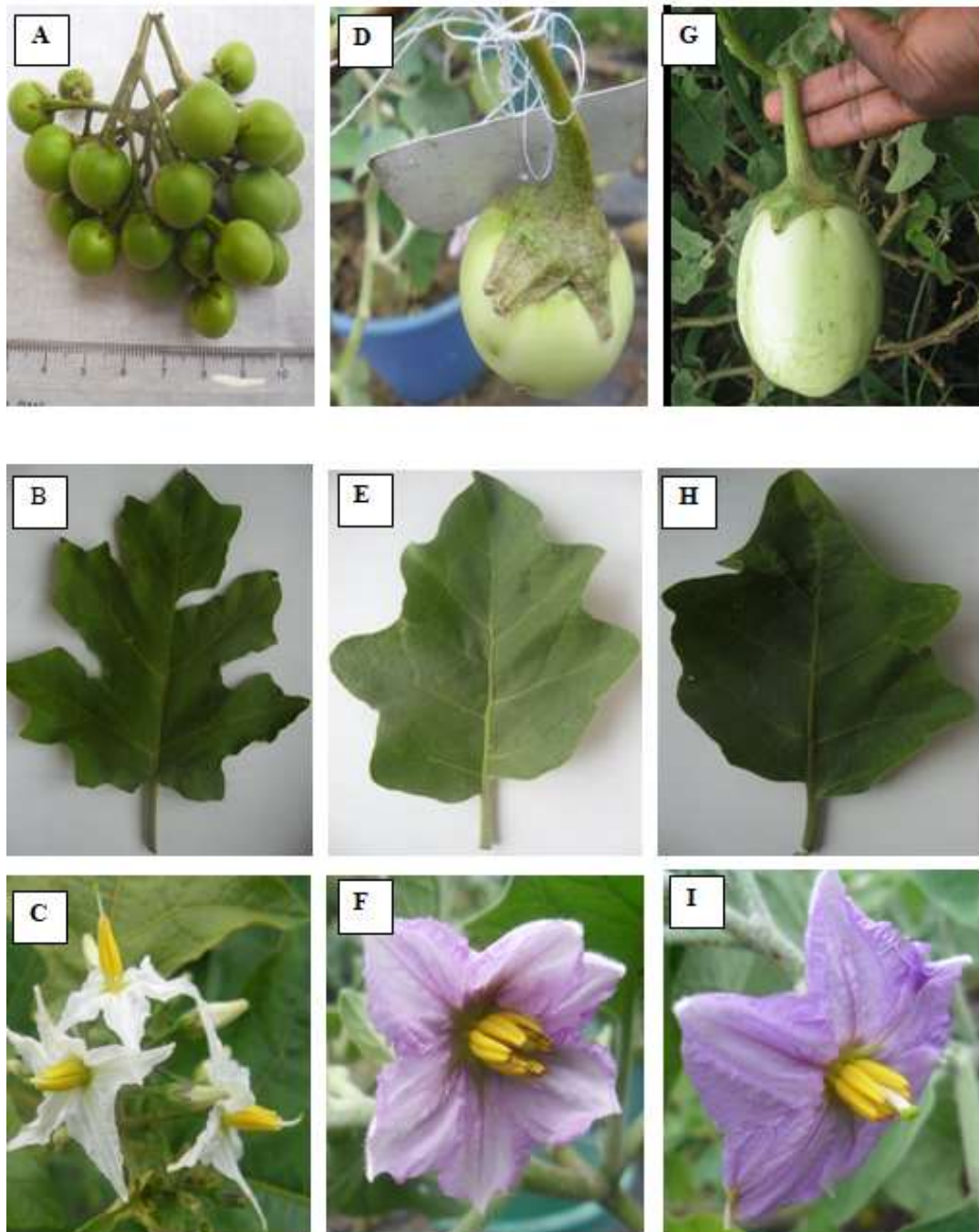


Plate 3. Plant morphology of interspecific hybrid and parental accessions. (A, B and C) Fruit, leaf and inflorescence of male parent (ST004-03). (D, E and F) Fruit, leaf and flower of interspecific hybrid (ST004-03 x SM001-07). (G, H and I) Fruit, leaf and flower of female parent (SM001-07).

incompatibility (UI), interspecific incompatibility (IC), unilateral hybridization (UH), unilateral inhibition (UI), unidirectional crossability, and one-way isolation among others with the basic principle of inhibition of pollen growth by cells of the pistillate parent or the incompatible relationship between embryo and endosperm leading to embryo abortion during the early stages of development

(Abdalla and Hermsen, 1972; Kitashiba and Nasrallah, 2014). Although UI is generally exhibited in self-compatible (SC) x self-incompatible (SI) species which has resulted in the generalization of SI being controlled by genes of the S-locus that are responsible for recognition of self-pollen by the stigma (Franklin-Tong and Franklin, 2000); there are various examples where

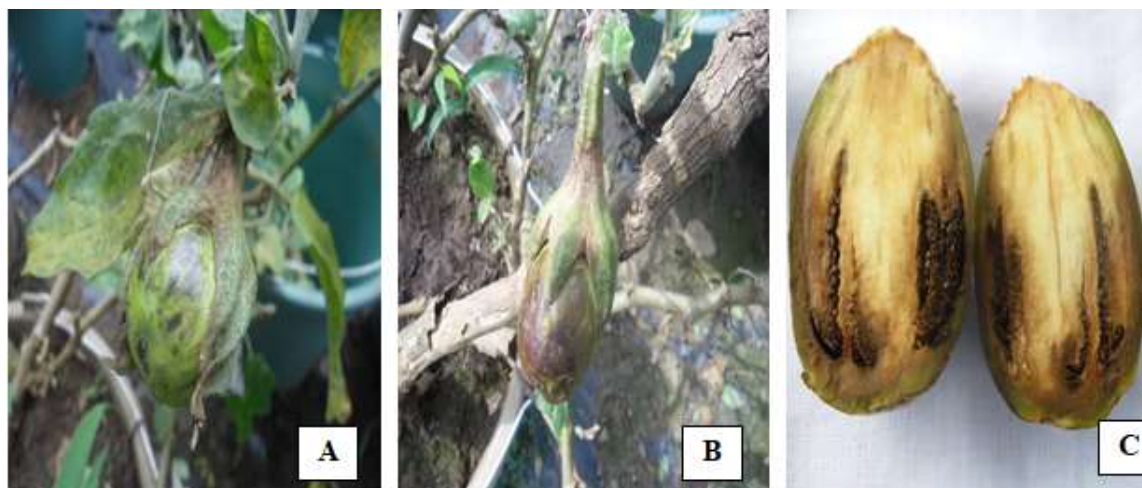


Plate 4. Hybridized (SM001-06 × ST004-03) fruit 32 days after pollination (B), Fruit showing rot (C) Cut fruit.



Plate 5. Seeded and parthenocarpic fruits of eggplant hybrids. (A) Seeded fruit of cross SM001-07 × ST004-03. (B and C) Fruits of crosses SA002-02 × ST004-03 and SMA003-03 × ST004-03 devoid of seeds.

one way cross has been observed not only in SC × SI species, but also between two SC or two SI species (Abdalla, 1970; Abdalla and Hermesen, 1972; Camadro and Peloquin, 1981). Lewis and Crowe (1958) explained that, self-compatible species might have evolved from self-incompatible ones by mutation in a sequence SI Sc Sc' SC. In this respect, a homologous Sc Sc species would be self-compatible and produce pollen which would be compatible on SI styles but displays in its styles the same inhibition. Mutation from Sc to Sc' (intermediate stage of self-compatible style) does not inhibit the pollen of SC and produces pollen compatible with SI styles. Whereas mutation from Sc' to SC leads to self-compatibility phenotype which shed pollen that are inhibited by SI species.

McClure et al. (1989) and Sijacic et al. (2004) also attributed unilateral incompatibility in *Solanum* and other Solanaceae to the S-RNase-based, gametophytic type, in which S-specificity is determined by S-RNases in the

pistil and S-locus F-box proteins (SLFs) in pollen. Li and Chetelat (2014) further emphasized that pollen rejection in UI involves biochemical mechanisms related to SI (self-incompatibility). According to Li and Chetelat (2014), ui1.1, a pollen UI factor in tomato, encodes an S-locus F-box protein that is homologous to an SI gene that in *Petunia* determines pollen specificity. Thus, pollen rejection in UI involves biochemical mechanisms related to SI. Though eggplants are self-pollinated plants and thus pollen does not need a pollinator to transfer it in the field, they are partly self-incompatible species which may explain their unilateral hybridization behaviour (Sękara and Bieniasz, 2008). In this regard, the use of *S. melongena* as female parent is usually preferred due to its numerous advantages such as allowing the 100% recovery of the cytoplasm of the cultivated parent, easier manipulation of flowers, more regular fruit set, greater number of seeds/fruit and absence of dormancy in the seeds (Behera and Singh, 2002; Devi et al., 2015; Plazas

et al., 2016). Kumchai et al. (2013), Rotino et al. (2014), Devi et al. (2015), and Kouassi et al. (2016) have reported on crossing successes and/or failures between cultivated and wild eggplant species which is in consonance with the finding of this study.

Besides, incompatibility (UI), the degree of success of interspecific sexual hybridization between eggplants and their wild relatives also depends on the species involved in the crossability studies (Plazas et al., 2016). Differences in the ploidy level among eggplant species (cultivar) used in this study might have contributed to the hybridization success or failure (Lester and Seck, 2004; Fontem and Schippers, 2004; Schippers, 2004; Yang et al., 2014).

Fruit set among hybridized accessions

The generally low fruit set observed in crosses between cultivated and wild eggplant species may be due to adverse weather conditions during flowering period (Okie and Weinberger, 1996), inadequate developmental stage of flower bud when emasculation was carried out (Hjeltnes and Stanys, 1998), loss of nutritive and protective functions of perianth (Badr and Crane, 1965), possible damage of pistil during emasculation (Okie and Hancock, 2008; Okie and Weinberger, 1996), acceleration of ovule degeneration (Hedhly et al., 2009) or the use different genetic background of parental cultivars (Yang et al., 2014; Kumchai et al., 2013). The results of fruit set (1.3 to 6%) in this study are in agreement with the findings of Manzur et al. (2015) and Plazas et al. (2016) who recorded fruit set success of 3 and 7% for the crosses Pas × P15 and Bie × P15 (*C. annuum* and *C. chinese* accessions, respectively) and the 3.3% of cross *S. melongena* × *S. torvum*, respectively; but significantly lower than the value obtained for cross *S. melongena* × *S. anguivi* which recorded 14.7% hybridized fruits (Plazas et al., 2016). However, no fruit set was observed when *S. melongena* cultivars SM001-02 SM001-04 and SM001-06 were crossed with the wild species, San005-01 (*S. anguivi*). The sterility in these hybrids may be attributed to irregular chromosome associations at diakinesis and metaphase I as well as concomitant abnormal disjunction of chromosomes at anaphase of meiosis (Singh and Rao, 1986; Nwofia and Ene-oblong, 2001).

The relative high percentage of fruit set with *S. torvum* compared to other wild accessions in this study contrasts report by Plazas et al. (2016) who obtained a higher fruit set with *S. anguivi* compared to *S. torvum*. Such differences observed by different workers could be linked to the use of different accessions of wild species and differences in conditions under which hybridization studies were carried out. While crosses were performed in the open field in this study, Plazas et al. (2016) conducted their crosses in a greenhouse (controlled

environment). Besides, these wild species as well as *S. melongena* belong to different gene pools and therefore may respond differently to fruit set (Syfert et al., 2016).

Seed set

Hybridized fruits borne in clusters or solitary were either parthenocarpic or seeded. Seed formation was possible in all *S. melongena* accessions except the crosses SM001-02 × ST004-03 and SM001-06 × ST004-03. Other seeded fruits were obtained from crosses SA002-02 × ST004-03 and SMA003-03 × ST004-03 in *S. aethiopicum* and *S. macrocarpon* accessions, respectively. While hybridized fruits of cultivars SM001-02, SM001-06, SA002-02, SA002-03 and SMA003-03 with ST004-03 were observed to be parthenocarpic. This may be attributable to allelic incompatibility at fertilization and the development of normal fruit (Behera and Singh, 2002). Similar findings have been reported by Devi et al. (2015), Plazas et al. (2016), Kouassi et al. (2016), and Chu et al. (2016) in the crossability studies between cultivated *S. melongena* and *A. hypogea* species and their wild relatives, respectively. Highest mean number of seeds/fruit was recorded in the cross combination SM001-07 × ST004-03 (264 seeds) while the lowest (1.00 seed) was observed in SMA003-03 × ST0003-03. Differences among genotypes of a given species have been reported to play an important role in obtaining interspecific hybrids in eggplant (Behera and Singh, 2002; Kumchai et al., 2013; Devi et al., 2015). Moreover, the success or failure of crosses between related plant species may be due to endosperm breakdown, which is cited frequently as the cause of seed failure in both interploidy crosses within a species and interspecific crosses (Bushell et al., 2003).

Seed germination

Seed germination among the tested crosses was very low and only few seeds germinated when sown in sterilized black soil in trays. Similar observation was reported by Hao et al. (2009) who studied the viability of seeds obtained by crossing *S. melongena* × *S. torvum* using potting mix. However, in an experiment conducted by Kumchai et al. (2013), hybrid seeds sown in conventional potting mix did not show any sign of germination. This differential response to germination in potting mix could be explained by the different genetic background of parental lines despite the same species combination. Moreover, the abnormal seeds (empty seeds, seeds with different appearance, low weight) obtained from the interspecific crosses might have also contributed to the low germination observed; such seeds have been reported to contain under-developed embryo and/or endosperm which prevent germination (Escobar-

Guzman et al., 2008).

The germination percentage of hybrid seeds ranged between 3.3 (SA002-02 × San005-01) to 16.6% (SM001-07 × San005-01 and SM001-07 × ST004-03) which contrast report by Plazas et al. (2016) who observed high germination range of 25 (*S. melongena* × *S. dasyphyllum*) to 92% (*S. melongena* × *S. insanum*). The low germination of hybrid seeds in sterilized black soil was probably due to the different genetic background of parental accession as well as the germination medium. While Plazas et al. (2016) used wild species from primary and secondary gene pools, this study utilized species from secondary and tertiary gene pools. Moreover, seeds were soaked in gibberellic acid solution and germinated in petri dishes on a layer of hydrophilic cotton covered with filter paper, while, in this work, hybrid seeds were germinated in trays containing sterilized black soil. Although, few seeds from the interspecific crosses germinated in potting mix, seedlings did not survive after two weeks. This may be ascribed to hybrid lethality (a type of reproductive isolation), a genetically controlled event that occur at the seedling stage in interspecific hybrids (Mino et al., 2002), and results in the abortion of a zygote after fertilization in the embryo sac and/or cell death in the tissue of hybrid seedlings after germination (Adachi, 2001). *In-vitro* germinated seeds were transferred to the plant house for acclimatization and weaning and subsequently transferred to the field for further growth. Based on these results, it can be concluded that interspecific hybridization of cultivated eggplant species with the wild relatives is possible. The success in obtaining hybrids depended on the eggplant accessions/genotypes involved in the crossing as well as the direction of the cross. Fruit set and average number of seeds/fruit was appreciably high in the crosses Sm001-07 × ST004-03 and Sm001-07 × San005-01. Although the cross SA002-02 × San005-01 was better in seed germination compared to the other crosses, the germination percentage was significantly low when compared to the two crosses. Moreover, the results revealed that, hybridization of eggplant species may be hampered by the presence of pre-fertilization barriers such as the non-germination of pollen grains leading to failure of fruit set as recorded in the accessions SM001-02, SM001-04 and SM001-06 with wild San005-01 and post-fertilization barriers with the formation of abnormal/empty seeds, lack of vigor and hybrid sterility as observed in crosses SM001-06 × ST004-03, SA002-02 × ST004-03 and SA002-03 × ST004-03. The low seed germination recorded in the crosses can be resolved by plant tissue culture techniques which have been successfully used to regenerate interspecific hybrids through embryo rescue, ovule culture and seed culture. Finally, the information obtained from the hybridization studies will contribute towards the production F1 hybrids and subsequent plant generations in the development of new cultivars with enhanced quality traits.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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