Eggplant relatives as sources of variation for developing new rootstocks: effects of grafting on eggplant yield and fruit apparent quality and composition

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ABSTRACT

We propose the utilization of eggplant (*Solanum melongena* L.) interspecific hybrids derived from crosses with closely related species as an approach for developing new improved rootstocks for eggplant. Here we investigate rootstock effects on fruit yield, apparent quality and proximate and mineral composition of *S. melongena* ‘Black Beauty’ (BB) scions grafted on interspecific hybrid rootstocks developed from crosses of *S. melongena* with *S. incanum* L. (SIxSM) and *S. aethiopicum* L. (SMxSA). The results are compared with non-grafted (BB control) and self-grafted (BB/BB) controls and with *S. melongena* ‘Black Beauty’ scions grafted onto *S. torvum* Sw. (STO) and *S. macrocarpon* L. (SMA) rootstocks. All treatments were grown in a soil naturally infested with root-knot nematodes (mostly *Meloidogyne incognita* (Kofoid & White) Chitwood). SIxSM and SMxSA interspecific hybrids had high germination (≥90%) and total graft success (100%). Contrary to what occurred with all other treatments, no plants from scions grafted onto these hybrid rootstocks died during the experiment. In particular, the SIxSM hybrid rootstock conferred the highest vigour to the scion, which resulted in the highest values for fruit earliness and early and total yield. Little difference was observed among treatments for apparent fruit quality traits, except for a greater fruit calyx length and prickliness of fruit grafted onto SMA rootstocks. A similar result was obtained for fruit composition where phenolics content was higher in fruit from plants grafted onto SMA rootstocks. Grafting eggplant onto interspecific eggplant hybrids, especially on the SIxSM hybrid, has proved advantageous for eggplant production, as the high vigour and good compatibility of the rootstock with scion results in improved early and total yield without negative effects on apparent fruit quality or

composition. Interspecific hybrids represent an alternative to the commonly used STO rootstock, which is a wild species with irregular germination.

Keywords: interspecific hybrids, *S. incanum, S. macrocarpon, S. melongena, S. torvum,* vigour

1. Introduction

Grafting of vegetable crops is used to provide resistance to soil pests and pathogens, to increase the tolerance to abiotic stresses, to improve water or nutrient uptake, or to enhance the vigour of the scion (Davis et al., 2008a, 2008b; King et al., 2008, 2010; Lee, 1994; Lee and Oda, 2003; Rivero et al., 2003). Lack of cultivars tolerant or resistant to increasingly important soil biotic and abiotic stresses, together with the prohibition of the use of methyl bromide for soil disinfestations, have led to a worldwide renewed interest in vegetable crops grafting (Bletsos, 2005; Davis et al., 2008a, 2008b; King et al., 2008; Miguel et al., 2004).

Eggplant (*Solanum melongena* L.) is widely cultivated in tropical and temperate regions around the world and is amenable to grafting (Bletsos et al., 2003; Daunay, 2008). Because soil pathogens can cause important loses in eggplant production, several rootstocks reported to be resistant or tolerant to soil pathogens, or that induce vigorous growth of the scion are used for improving eggplant production (Daunay, 2008). The wild relative *Solanum torvum* Sw., which has resistance to a wide range of soil borne pathogens (*Verticillium dahliae* Klebahn, *Ralstonia solanacearum* (Smith) Yabuuchi et al., *Fusarium oxysporum* (Schlechtend:Fr.) f. sp. *melongenae* Matuo & Ishigami, and

Meloidogyne spp. root-knot nematodes), is recommended for eggplant grafting (Bletsos et al., 2003; Daunay, 2008; Singh and Gopalakrishnan, 1997; King et al., 2010). However, its use is limited by difficulty in getting rapid and homogeneous seed germination (Ginoux and Laterrot, 1991). Some tomato (*S. lycopersicum* L.) hybrids (e.g., 'Energy', or 'Kyndia') as well as tomato *S. lycopersicum* × *S. habrochaites* S. Knapp & D.M. Spooner interspecific hybrids (e.g., 'He Man', 'Beaufort') are also commonly used as rootstocks for eggplant (Bletsos et al., 2003; Miguel et al., 2007; King et al., 2010). However, specific tomato-eggplant rootstock-scion combinations are only moderately compatible (Kawaguchi et al., 2008), and without an adequate selection of rootstock-scion combinations, deleterious effects may appear (Kawaguchi et al., 2008; Leonardi and Giuffrida, 2006; Oda et al., 1996). Also, the wild species *Solanum sisymbriifolium* Lam. and the hmong eggplant *Solanum integrifolium* Poir. (=*Solanum aethiopicum* L. Aculeatum group) have been tested as rootstocks for grafting of eggplant, although the results were not very promising due to poor performance (Rahman et al., 2002; Yoshida et al., 2004).

Other *Solanum* species and materials, as well as interspecific hybrids, could increase the sources of variation for developing eggplant rootstocks that are tolerant or resistant to biotic and abiotic stresses, or to enhance nutrient uptake and vigour. In this respect, the scarlet eggplant (*S. aethiopicum* Gilo, Shum, or Kumba groups) and the gboma eggplant (*S. macrocarpon* L.) are cultivated species of economic importance in Western Africa (Schippers, 2000). Both species are phylogenetically close to *S. melongena* (Furini and Wunder, 2004), are propagated by seed, and their germination is more uniform than that of the wild *S. torvum* (Ginoux and Laterrot, 1991). Materials of both species have been described as tolerant to *F. oxysporum* f. sp. *melongenae* and resistant to *R. solanacearum* (Cappellii et al., 1995; Daunay et al., 1991; Hébert, 1985). Resistance to root-knot nematodes (RKN) has also been reported in *S. aethiopicum* Gilo group (Cappellii et al., 1995; Hébert, 1985). Another species of interest as a source of variation for developing new eggplant rootstocks is *S. incanum* L., which is the putative ancestor of eggplant (Lester and Hasan, 1991), and which has been reported as resistant to *F. oxysporium* f. sp. *melongenae* (Yamakawa and Mochizuki, 1979). Furthermore, these species could provide tolerance to abiotic stresses such as drought and low or high temperatures, which are important breeding objectives in *S. melongena* (Daunay, 2008).

Interspecific hybrids are used as rootstocks in many vegetable crops since they can contribute several advantages including pathogen resistances from both parents, vigourous growth, and, in the cases where one of the parents is from the same species as the scion, a greater degree of rootstock-scion compatibility (Daunay, 2008; Lee and Oda, 2003; Miguel et al., 2007). Interspecific hybrids of *S. aethiopicum*, *S. macrocarpon*, and *S. incanum* with *S. melongena* have been obtained with different degrees of success (Behera and Singh, 2002; Bletsos et al., 2004; Daunay, 2008; Lester and Hasan, 1991; Schaff et al., 1982). In this respect, *S. melongena* and *S. incanum* are easily crossed and the fruit resulting from the crosses bear many seeds with high viability (Lester and Hasan, 1991). Hybrids of *S. melongena* with *S. aethiopicum* are more difficult to obtain by sexual crosses than those with *S. incanum*, but viable seeds are produced (Behera and Singh, 2002). On the contrary, hybrids between *S. melongena* and *S. macrocarpon* are difficult to obtain and few viable seeds are obtained per cross (Bletsos et al., 2004; Schaff et al., 1982). This suggests that while *S. melongena* × *S. incanum* and *S. melongena* × *S. aethiopicum* hybrids might be of interest as eggplant rootstocks, the use of *S. melongena* × *S. macrocarpon* hybrids as rootstocks does not seem to be economically viable at this time.

Apart from the productive advantages offered by grafting, a very important issue, which on many occasions remains overlooked, is the effect of grafting on fruit quality (Davis et al., 2008a). In this respect, the apparent quality characteristics and composition of the final product of grafted plants should remain unchanged or improved with respect to the non-grafted plants. In some cases, an improvement in fruit composition has been reported. For example, mini-watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) fruit from plants grafted onto a *Cucurbita moschata* Poir. × *Cucurbita maxima* Duch. interspecific hybrid rootstock had higher levels of K, Mg, lycopene and vitamin C in comparison to their respective control plants (Proietti et al., 2008). Deleterious effects may also appear as a consequence of grafting. For example, an enhanced incidence of fruit blossom end rot in tomato grafted onto *Solanum integrifolium* rootstocks (Oda et al., 1996) and the accumulation of high amounts of nicotine in tomatoes from plants grafted onto *Nicotiana tabacum* L. have been reported (Yasinok et al., 2009). In the specific case of eggplant grafted onto *Datura inoxia* P. Mill., scopolamine and atropine were accumulated in fruit at levels sufficient to cause poisoning (Oshiro et al., 2008).

In this work, we assess the potential vigour and influence on eggplant yield and fruit quality traits of *S. incanum* × *S. melongena* and *S. aethiopicum* × *S. melongena* interspecific hybrid rootstocks, as well as of *S. macrocarpon* rootstocks. The results are compared with those obtained from non-grafted, self-grafted, and *S. torvum* rootstock grafted plants. Our objective is to identify new potential rootstocks for eggplant as well as to validate our hypothesis that using interspecific hybrid rootstocks may be a good strategy for improving eggplant production.

2. Material and methods

2.1. Plant material

The eggplant cultivar Black Beauty (B and T World Seeds, Aiguesvives, France) was used as the scion variety as well as the ungrafted control. Five rootstocks that included materials corresponding to the three species *S. melongena*, *S. torvum*, and *S. macrocarpon* and to two interspecific hybrids, *S. incanum* × *S. melongena* and *S. aethiopicum* × *S. melongena*, were evaluated (Table 1). Hybridity of the interspecific hybrids was confirmed by evaluation with five SSR markers: CSM7, CSM12, CSM21, CSM40, and CSM54 (Manzur, 2009), which were homozygous for different alleles in the parents and heterozygous in the hybrids. Data for morphological characters of the aerial part of these materials used as rootstocks were obtained from the database of the germplasm bank of the Instituto de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV) of the Universidad Politécnica de Valencia (Valencia, Spain) from germplasm characterization data trials (one to five trials per material, with 8 to 15 plants per trial and material) performed previously to our research on grafting presented here (Table 2). These data are useful to estimate the vigour of the rootstocks used.

2.2. Seed germination

Seeds of all genotypes were surface-sterilized for the grafting trial and sown on Petri dishes as detailed in Gisbert et al. (2006). Gibberellic acid at 1 mg·L^{-1} was added to the sterile nutrient medium after filter sterilization. The pH of the medium was adjusted to 5.8 before sterilization at 120 ºC for 20 min. Plates were incubated in a growth chamber at 26 ± 2 ºC under a 16 h photoperiod with cool white light provided by fluorescent lamps (90 µmol m^{-2}·s^{-1}). In order to obtain uniform rootstock plantlets, and given that variability for seed germination rates and vigour was previously observed by us for some materials used in this work, seeds from all accessions were sown twice in two consecutive weeks. Germinated seeds were subsequently transferred to seedling trays with cell sizes of 85 mm x 85 mm x 80 mm depth filled with Neuhaus-Huminsubstrat N3 commercial substrate (Klasmann-Deilmann, Geeste, Germany). In addition, since seeds of *S. torvum* are known to be very variable in their germination behavior (Ginoux and Laterrot, 1991; Ibrahim et al., 2001) and materials of this species were not previously evaluated for their germination capacity in Petri dishes with nutrient medium, a large amount of seeds of this rootstock were also sown directly in seedling trays filled with the same commercial substrate aforementioned.

2.3. Grafting

The eggplant cultivar Black Beauty was grafted onto ‘Black Beauty’ rootstocks (self-grafted; BB/BB), *S. torvum* (STO), *S. macrocarpon* (SMA), *S. incanum* × *S. melongena* (SIxSM), and *S. melongena* × *S. aethiopicum* (SMxSA) rootstocks using the cleft procedure described by Lee (1994). Plants at the 3 to 4 leaf stage (40-50 d old) were used as rootsotcks. The ‘Black Beauty’ scion source plants selected for grafting had a lower development stage (2-3 leaves; 25-35 d old). For grafting, the stem for both the scions and the rootstocks at right angles was cut using a razor blade. Rootstocks were cut over cotyledons and had a total length of 6-7 cm. Scions of 1.5 to 2 cm with one or two small leaves were subjected to the rootstocks using a buddy tape. After grafting, plantlets were incubated within a plastic tunnel in a glasshouse with a mean air temperature of 24 ± 2 ºC and 70-85% relative humidity for 5 d. Plantlets were subsequently acclimatized outside of the plastic tunnel for 1 week in a glasshouse with extreme day and night temperatures of 30 and 18 ºC, respectively. Sixty plantlets of each rootstock were grafted.

2.4. Growing conditions

'Black Beauty' plants non-grafted (BB control), self-grafted (BB/BB) and grafted onto STO, SMA, SIxSM and SMxSA rootstocks were transplanted for the grafting trial on 30 June, 2009, to a soil (sandy loamy soil) naturally infested with root-knot nematodes (RKN) in the campus of the Universidad Politécnica de Valencia, Valencia, Spain (GPS coordinates of the field plot: lat. 39º 28' 55'' N, long. 0º 20' 11'' W) in a completely randomized design with 25 plants per treatment. The mean nematode (primarily *Meloidogyne incognita* (Kofoid & White) Chitwood, as observed in the microscope) concentration in the infested soil was 5017 nematodes/kg of soil (dry weight; average of 10 soil samples from different parts of the field). Plants were spaced 1 m between rows and 0.8 m apart within the row and drip irrigated. Fertilization was applied with drip irrigation throughout the growing cycle and consisted of 80 g/plant of a 10N-2.2P-24.9K plus micronutrients commercial fertilizer (Hakaphos Naranja;

Compo Agricultura, Barcelona, Spain). Standard horticultural practices for eggplant production in the Mediterranean coastal area of Spain were followed (Baixauli, 2001).

2.5. Plant survival, growth, earliness, yield, and fruit quality evaluation

Plant survival was measured at the initiation and conclusion of fruit harvest. Plant height and stem diameter were measured following the last harvest. Fruit harvesting began 50 d after transplanting. Earliness was determined as the percentage of plants in which commercially mature fruit (evaluated by the color and glossiness of the fruit) were harvested up to 57 d after transplanting, as well as by the number of fruit per plant harvested during this period. Commercially mature fruit were harvested for 2 months, with two harvests per week. Fruit were weighed immediately after harvesting. Total yield was calculated as $kg \cdot plant^{-1}$ (taking into account only the plants alive at the end of the experiment) and as $kg \cdot m^2$ (taking into account all the plant, i.e., including those alive and dead at the end of the experiment).

Apparent quality traits of ‘Black Beauty’ eggplant fruit were measured in 30 representative commercially mature fruit from non-grafted (BB control) and self-grafted (BB/BB) plants, and from plants derived from ’Black Beauty’ scions grafted onto STO, SMA, SIxSM, and SMxSA rootstocks. Fruit length/width ratios were calculated. Several traits were measured in an arbitrary scale according to the European Eggplant Genetic Resources Network (EGGNET) descriptors (Prohens et al., 2005). These traits included fruit curvature (1=none; 9=U-shaped), fruit cross-section (1=circular; 9=very irregular), fruit calyx length (1=very short [>10%]; 9=very long [>75%]), and fruit calyx prickles (0=none; 9=very many [>30]). In addition to these EGGNET descriptors, seed index (0=none; 5=very many [>80] seeds visible in a longitudinal fruit section) was measured.

At the end of the experiment, plants were uprooted and root growth and nematodes gall presence were visually rated. Root growth was assessed as high, medium, or low, according to a subjective scale. Galling index (GI) was assessed according to a 0-5 scale reflecting the percentage of galled roots (0=0%; 1=1% to 20%; 2= 21% to40%; 3= 41% to60%; 4= 61% to80% and 5= 81% to100%) (Oda et al., 2004).

2.6. Proximate composition and mineral content of fruit

Proximate composition and mineral content of fruit were measured in five samples from each treatment. For proximate composition traits three measurements per sample were made, while for mineral content two measurements per sample were taken. Each sample consisted of four transverse slices of similar weight from the central part (mid-way between stem and blossom ends) of the fruit of four commercially mature peeled fruit. Total soluble solids were determined by an N-20E refractometer (ATAGO, Japan) at 20 °C. Dry matter percentage was determined in samples dried at 105 ºC until constant weight as 100%×(dry weight/fresh weight). Protein concentration was estimated from N content obtained from the Kjeldahl method using a Kjeltec 2100 Distillation Unit (Foss Tecator, Högamäs, Sweden) and reported as N×6.25. For extraction of phenolics, 5 mL of juice were poured on 10 mL of a an extracting solution of acetone (70% v/v) and glacial acetic acid (0.5% v/v) and left for 24 h at room temperature. Content in phenolics was determined according to the Folin–Ciocalteu procedure (Singleton and Rossi, 1965). An aliquot of 1.3 mL of the supernatant of the extracted phenolic sample was mixed with 1 mL of diluted (10% v/v) Folin–Ciocalteu reagent (Sigma-Aldrich Chemie, Steinheim, Germany) and allowed to stand at room temperature for 5 min. After that, 1 mL of a sodium carbonate solution (60 g·L^{-1}) was added to the mixture. After 90 min at room temperature, absorbance was measured at 760 nm in a Jenway 6305 UV–VIS spectrophotometer (Jenway, Dunmow, UK). Chlorogenic acid (Sigma-Aldrich Chemie) was used as standard. The phenolic acid content was expressed as chlorogenic acid equivalents in mg·kg^{-1} per 100 g of fresh fruit flesh.

For mineral analyses, 2 g of the dried samples were calcined in a furnace at 450 °C for 2 h, after which they presented a light color, and were weighed. Ashed samples were dissolved in 2 mL of concentrated HCl (12N). The mixture was heated until the first vapors appeared and 2-3 mL distilled water was immediately added. Samples were mixed, filtered through Whatman #40 filter paper and the extract brought to 100 mL final volume with distilled water. P was analyzed by the molibdovanadate method using a Jenway 6305 UV–VIS spectrophotometer. K and Na were analyzed by flame photometry using a Jenway PFP7 flame photometer (Jenway, Essex, UK). Ca, Mg, Fe, Cu, and Zn were analyzed by atomic absorption spectrophotometry using a Thermo Elemental (SOLAAR AA Spectrometers, Cambridge, UK) spectrometer (MAPA, 1994). For Ca and Mg measurements, a solution of lanthanum oxide (5% w/v) was used, in standards and samples, to avoid interferences.

2.7. Data analysis

Data for each of the traits evaluated was analyzed via one-factor analysis of variance (ANOVA) using a fixed-effects model for the effect of rootstock treatment. For data expressed in percentage, the logarithmic transformation was applied, while for the number of early fruit per plant, we applied the square root transformation (Little and Hills, 1978). Significance of the treatment effects was obtained from the ANOVAs, and where the F-test proved significant (P =0.05), means were compared using the Duncan multiple-range test.

3. Results

3.1. Seed germination and graft success

Germination of seeds sown in Petri dishes with GA_3 containing medium could be observed at 3 to 4 d after sowing for 'Black Beauty', SIxSM, and SMxSA, and at 8 d after sowing for SMA. At 15 d after sowing, 'Black Beauty' and the interspecific hybrids SIxSM and SMxSA exhibited high percent germination (≥90%) (Table 3). SMA displayed significantly lower germination (58%), and no germination was obtained with this protocol for STO. However, it was possible to obtain the necessary number of STO plantlets for the grafting experiments using a large amount of STO seeds sown in commercial substrate. Similar to our results, the commercial seed supplier warns that even under good conditions, STO germination may be erratic.

The cleft grafting method proved highly efficient with success percentages ≥90% in all materials used (Table 3). No significant differences were found in the success rate among 'Black Beauty', STO, SIxSM, and SMxSA rootstocks, which had percentages of graft success that ranged from 98% (‘Black Beauty’) to 100% (STO, SIxSM, and SMxSA). In contrast, SMA had a significantly lower percentage of success (90%) with respect to the other rootstocks (Table 3). No overgrowth at the graft junction was observed for any rootstock-scion combination.

3.2. Plant survival and vigour

The survival rate between transplant and initiation of fruit set ranged from 76% for ‘Black Beauty’ grafted on SMA rootstock to 100% for those grafted on SIxSM and SMxSA rootstocks (Table 4). Although some plants died for the ungrafted and self-grafted ‘Black Beauty’, and STO treatments, the only significant differences in survival rate were between SIxSM and SMA and between SMxSA and SMA. Some plants corresponding to the self-grafted, STO, and SMA treatments died between the initiation of fruit set and the end of the experiment, but again the only significant differences in the survival rate at the end of the experiment were between SMA (72% survival) and SIxSM and SMxSA, respectively (100% survival) (Table 4).

The mean plant height among different treatments varied between 108.9 and 127.0 cm for the SMA and SIxSM rootstocks, respectively (Table 4). ‘Black Beauty’ scions grafted onto SIxSM, SMxSA and STO rootstocks were significantly taller than those grafted onto SMA rootstock. Plants with SIxSM rootstocks were also significantly taller than those of ungrafted ‘Black Beauty’ plants (Table 4). No significant differences among treatments were found at the end of the experiment for scion stem diameter (Table 4).

Visual assessment of the roots at the end of the experiment revealed more vigorous root growth in STO, SIxSM, and SMxSA grafted plants (strong root growth) in comparison to non-grafted and self-grafted plants (medium root growth) and plants derived from grafts with SMA rootstock (weak root growth). Galls were scarce in STO roots (GI=1) and abundant (GI=4) in all other treatments.

3.3. Earliness and yield

The first plants to flower and set fruit were from 'Black Beauty' grafted on SIxSM and SMxSA rootstocks. Fruit harvest for these plants began 50 d after transplanting, and fruit harvested until 57 d after transplant were considered as early harvest fruit. Percentage of plants with early fruit ranged from 15.8% for those with SMA rootstocks to 68.0% for plants with SIxSM rootstocks (Table 5). Plants with SIxSM rootstock had a significantly higher percentage of plants with early fruit in comparison to non-grafted or self-grafted 'Black Beauty' plants, or plants with SMA rootstock; also treatments with SMxSA rootstock had a significantly higher percentage of plants with early fruit in comparison to those grafted onto SMA rootstock. Early fruit per plant ranged from 0.6 fruit/plant to 5.0 fruit/plant for those with SMA and SIxSM rootstocks, respectively (Table 5). In the latter case, 'Black Beauty' grafted onto SIxSM rootstock had a significantly greater number of early fruit in comparison to non-grafted and self-grafted 'Black Beauty' plants or plants with STO or SMA rootstocks; also, plants with SMxSA rootstock had a significantly greater number of early fruit versus those with SMA rootstock grafts (Table 5).

Significant differences among treatments were also evident for total fruit number and yield, which followed a similar pattern. The total fruit per plant ranged between 7.6 and 15.8 for ‘Black Beauty’ respectively grafted onto SMA and SIxSM rootstocks, while the total yield ranged between 3.4 kg/plant (taking into account only plants alive at the end of the experiment) or 3.2 kg/m^2 (taking into account all plants, alive or dead, at the end of the experiment) for ‘Black Beauty’ grafted onto SMA rootstock and 6.9 kg/plant or 8.6 3.2 kg/m^2 for those grafted onto SIxSM rootstock (Table 5). Plants with SIxSM rootstock had a significantly greater fruit number and yield in comparison to non-grafted ‘Black Beauty’ plants and those grafted onto SMA rootstock, and plants with SMxSA rootstock had greater fruit number per plant and yield versus those grafted onto SMA rootstock. No significant differences among treatments were found for the mean fruit weight (average of 433 g/fruit).

3.4. Apparent fruit quality

No significant differences among treatments were found for the fruit width (average of 10.25 cm), fruit curvature (average of 1.18), and seeds index (average of 1.42) (Table 6). In contrast, differences among treatments were found for fruit length, which resulted in differences in the fruit length/width ratio. In this respect, fruit from ‘Black Beauty’ grafted onto SIxSM and STO rootstocks were significantly more elongated (length/width ratio of 1.38 and 1.37, respectively) than those from plants grafted onto SMA and SMxSA rootstocks or from self-grafted ‘Black Beauty’ plants which had fruit length/width ratios of 1.13, 1.24, and 1.25, respectively; also, fruit from non-grafted plants were significantly more elongated (fruit length/width ratios of 1.27) in comparison to those from plants with SMA rootstock (Table 6). Fruit from 'Black Beauty' grafted onto SMA rootstock were significantly more irregular, with a regularity fruit cross-section value of 5.40 versus those grafted onto STO or SIxSM rootstocks, with values of 4.73 and 4.53, respectively; fruit from self-grafted 'Black Beauty' plants were significantly more irregular in cross-section (5.20) versus those grafted onto SIxSM rootstock. Finally, fruit from 'Black Beauty' grafted onto SMA rootstock had significantly higher scores for calyx length (2.26) and calyx prickles (3.06) in comparison to the mean of the rest of treatments (averages of 1.46 and 1.60, respectively) (Table 6).

3.5. Fruit composition

When considering the proximate composition traits, no significant differences were found between treatments for fruit dry matter (average value of 5.7%) and soluble solids content (average value of 4.12%) (Table 7). However, we found that fruit protein content of self-grafted 'Black Beauty' plants was significantly higher (4.9 $g \cdot kg^{-1}$) versus the non-grafted plants (4.3 $g \cdot kg^{-1}$). Total fruit phenolics content from plants with SMA rootstock was significantly higher (550 $mg \cdot kg^{-1}$) in comparison to that from non-grafted or from STO grafted plants (419 and 411 $mg \cdot kg^{-1}$, respectively).

Regarding the mineral composition, high fruit K content was evident (mean of 2366 $mg \cdot kg^{-1}$), followed by Na (382 $mg \cdot kg^{-1}$), Mg (257 $mg \cdot kg^{-1}$), P (221 $mg \cdot kg^{-1}$), Ca (170 $mg \cdot kg^{-1}$), and at much lower concentrations by Zn (1.88 $mg \cdot kg^{-1}$), Fe (1.34 $mg \cdot kg^{-1}$), and Cu (0.68 $mg \cdot kg^{-1}$). No significant differences were found for mineral contents between graft treatments, with the exception of Fe, in which fruit from 'Black Beauty' grafted onto SMA had a significantly higher Fe content (2.66 $mg \cdot kg^{-1}$) in comparison to fruit from ‘Black Beauty’ grafted onto STO rootstock (0.86 $mg \cdot kg^{-1}$) (Table 7).

4. Discussion

Grafting has proved to be an efficient tool for increasing the yield, disease resistance and quality of a number of vegetable crops (Davis et al., 2008a, 2008b; King et al., 2008, 2010; Lee, 1994; Lee and Oda, 2003; Rivero et al., 2003). Ideally, rootstocks should improve the yield and/or quality of the produce. This can be achieved by using rootstocks that have resistance to soil diseases or pests, tolerance to abiotic stress, selective absorption of available soil nutrients, or that confer a high degree of vigour to the scion (Davis et al., 2008a, 2008 b; Lee, 1994; Lee and Oda, 2003; Rivero et al., 2003). Here, we have tested the effects of grafting the eggplant cultivar Black Beauty onto different species and interspecific rootstocks and have found that improvements in the production of eggplant can be achieved by using this technique. Benefits realized through rootstock grafts often justify the challenges that successful production of grafted plants requires including synchronization and good germination rates of the rootstock and scion, and high rates of graft success and stand establishment after transplant.

Seed germination is an important concern when using materials of wild species or from exotic species as rootstocks. Seeds of a number of wild *Solanum* species are known to emerge slowly, and about 30 d can be needed to attain germination with percentage rates that vary between 15% and 50% in *S. insanum* L. *S. torvum*, *S. integrifolium*, *S. surattense* Burm., *S. khasianum* C.B. Clarke, *S. sanitwongsei* Craib and in hybrids of *S. melongena* x *S. integrifolium* (Ibrahim et al., 2001). *S. torvum*, which is the most common *Solanum* eggplant relative used for grafting, exhibits long germination time and frequently has poor germination (Ginoux and Laterrot, 2001), even after GA_3 treatments (Ibrahim et al., 2001) which are known to promote germination in several *Solanum* species including *S. melongena*, *S. aethiopicum* and *S. macrocarpon* (Joshua, 1978). As a result, the difficulty in achieving rapid and homogeneous germination of *S. torvum* seeds limits their use as rootstock (Daunay, 2008). In our study, high germination rates (≥90%) were obtained with seed for 'Black Beauty', SIxSM and SMxSA rootstocks. For SMA, the rates obtained (58%) were somewhat lower. *S. torvum* however, did not germinate under our GA_3 treatment conditions. Germination of some seeds of this species in commercial substrate was achieved, but was irregular and erratic even under good germination conditions. In contrast, high germination percentages and uniformity of germination were achieved for the interspecific hybrids SIxSM and SMxSA, thus facilitating their use as eggplant rootstocks. In this respect, it is of interest to note that although the wild species *S. incanum* usually has low and irregular germination (Joshua, 1978), its interspecific hybrid with eggplant, SIxSM, has a high germination rate.

Grafting success depends on several factors that include graft union and graft compatibility, which in herbaceous plants, depends on the combination of scion and rootstock (Kawaguchi et al., 2008). Eggplant is grafted mainly by cleft or tube grafting techniques (Bletsos et al., 2003; Lee, 1994; Miguel et al., 2007). In our case using the cleft grafting approach, graft success rates of 90% for SMA, 98% for self-grafting, and 100% for grafting onto STO, and SIxSM and SMxSA rootstocks, were obtained. The results indicate that this procedure is highly efficient with these scion-rootstock combinations. The lower success rate obtained with SMA may indicate that, despite its phylogenetic proximity to eggplant (Furini and Wunder, 2004), some graft incompatibility might exist. Also, the fact that this species is less vigorous than other rootstocks that we tested, suggests that vigour may also account for this lower success rate. To our knowledge, no reports exist describing the success of eggplant grafts with interspecific hybrid rootstocks of *S. melongena* x *S. aethiopicum* or *S. melongena* x *S. incanum.* Successful grafting of eggplant varieties with the wild *S. torvum*, which is the phylogenetically most distant of the rootstocks used (Isshiki et al., 2008), has been reported (Bletsos et al., 2003; Rahman et al., 2002).

All plants with SIxSM and SMxSA rootstock grafts survived, whereas in all other treatments some plants died, especially for 'Black Beauty' scions grafted onto SMA rootstock. Physiological disturbances induced by vascular bundle discontinuities at the graft union may lead to growth inhibition and high mortality; however, in this case, soil that was heavily infested with nematodes may have been a major reason for the loss of plants. In fact, a high sensitivity to *M. incognita* has been reported for some accessions of *S. macrocarpon* (Afouda et al., 2008). At the end of the experiment, root vigour of plants grafted onto STO, SIxSM and SMxSA was higher than that of plants from the ungrafted and self-grafted 'Black Beauty' or SMA treatments. In all tested plants, a high amount of galling was evident, with the exception of *S. torvum* roots, which exhibited little galling. Although susceptibility to *M. incognita* has been described in accessions of *S. torvum* (Tzortzakakis et al., 2006), our results agree with previous reports that consider this species as resistant or a poor host for *M. incognita* (Daunay and Dalmasso, 1985; Hébert, 1985). It is remarkable that no plants grafted onto the interspecific hybrids SIxSM and SMxSA died, suggesting that these scion/rootstock combinations have a high rate of survival/tolerance to nematode infection despite having a galling index (GI) of GI=4 in a scale from 0 (no galled roots) to 5 (81-100% of galled roots).

Rootstock-scion interactions are commonly observed in different crops (Cohen et al., 2002; Leonardi and Giuffrida, 2006; Yetisir and Sari, 2003) and we have observed that rootstock source can have an important effect on eggplant vigour, earliness, yield and fruit quality characteristics. Plant height, which may be considered as an indicator of vigour was highest in plants with the interspecific hybrid SIxSM rootstock and lowest in those plants with SMA rootstock grafts, revealing that vigour of the rootstock is important in conferring scion vigour. In the absence of scion/rootstock incompatibility problems, grafted plants may also develop faster, thus contributing to earliness. In our study, greater earliness was observed in the most vigorous rootstocks, i.e., the interspecific hybrids SIxSM and SMxSA. Increased earliness has also been reported for eggplant grafted onto two tomato hybrids (Khan et al., 2006) and in melon plants grafted onto *Cucurbita* rootstocks (Cohen et al., 2002; Fita et al., 2004). We also found that grafted plants with SIxSM rootstocks had higher yield than non grafted plants and that grafted plants with SMA rootstocks had a much lower yield than other treatments, confirming that this latter rootstock has little value for improving eggplant yield. In contrast, interspecific SIxSM and SMxSA rootstocks demonstrated positive benefits for agronomic performance in grafted eggplant. In this respect, grafting tomato plants onto an interspecific tomato rootstock also resulted in higher vigour when compared with tomato plants self-grafted or grafted onto other cultivated tomato rootstocks (Leonardi and Giuffrida, 2006).

Our observations on yield and earliness are consistent with our previous results where plants with the highest yield entered much earlier into production than low yielding material (Raigón et al., 2008; Muñoz-Falcón et al., 2008a,b). Although replication over different environments may reduce potential bias in the results due to genotype × environment interaction, Muñoz-Falcón et al. (2008a) found that eggplant yield varied across environments but relative genotype rankings remained the same and genotype × environment interactions were non-significant. Environmental factors, as well as genotype × environment effects, were also nonsignificant for the yield attributes such as fruit weight and earliness. Hence relative rankings of even diverse material remained the same when grown in divergent environments. A recent report of eggplant grafted onto tomato rootstocks similarly demonstrated that rankings between treatments for early yield, total yield, and fruit weight, as well as disease incidence and severity were unchanged over multiple years of testing (Liu and Zhou, 2009).

Fruit quality is important for the marketability of fruit, and grafting can influence traits related to quality (Alexopoulos et al., 2005; Davis et al., 2008 a, 2008 b; López-Galarza et al., 2004; Proietti et al., 2008). Although we found no differences for most eggplant traits of apparent quality, differences were found for some relevant characters. For example, although fruit shape in eggplant is highly heritable and under genetic control (Muñoz-Falcón et al., 2008a), rootstocks influenced fruit length and fruit length/width ratios, possibly due to changes in the concentration of growth regulators induced by the rootstock. The presence of prickles and calyx length, which was significantly higher in grafted plants with SMA (which has few prickles) rootstocks, may be an indicator of stress in the scion. In fact, environmental stress conditions including cold or pest attack have been reported to induce the presence of prickles and longer calyxes in eggplant landraces (Prohens et al., 2004). Similar to observations for fruit yield, weight and earliness in a diverse collecgtion of germplasm, prior studies also demonstrated that environment and genotype × environment effects were non-significant for fruit shape (Muñoz-Falcón et al., 2008a).

Although few differences were found in fruit composition traits, higher fruit phenolic content was found in fruit of plants with SMA rootstocks in comparison to ungrafted plants. This higher phenolics concentration may be an additional indication of stress in this rootstock/scion combination, as stress conditions induce accumulation of phenolics (Dixon and Pavia, 1995; Moglia et al., 2008). Divergence between allied eggplant species for fruit phenolic acid constituents and their total has been documented Stommel and Whitaker, 2003). Phenolics content reported in the current study are within expectations reported for *S. melongena* and denote that exotic rootstocks have little or no effect on fruit phenolics content.

Although self-grafted plants had a more irregular cross section and slightly higher protein content than non-grafted plants, changes in proximate composition between grafted and non-grafted plants were generally not observed. Modification of fruit characteristics in self-grafted plants has been observed in other crops including tomato (Khan et al., 2006) and pepper (*Capsicum annuum* L.) (Gisbert et al., 2010) and indicates that grafting may induce modifications that are associated with growth regulator balance.

5. Conclusions

Interspecific hybrids SIxSM and SMxSA exhibited high and uniform seed germination and eggplant scions grafted onto them displayed good vigour, excellent survival despite nematode soil infestation, and high yield. These results, together with the lack of deleterious effects on apparent fruit quality traits or fruit composition from SIxSM and SMxSA rootstocks, indicates that both hybrids are an advantageous alternative to the presently used *S. torvum* rootstock. In particular, given the fact that hybrids between *S. melongena* and *S. incanum* are easier to obtain than hybrids between *S. melongena* and *S. aethiopicum*, SIxSM rootstock may be the best selection. Our results demonstrated that the use of interspecific hybrid rootstocks derived from fully compatible crosses of eggplant with related species affords a valuable approach to improve eggplant production.

Acknowledgements

This work was partially financed by the Ministerio de Ciencia y Tecnología (AGL2009-07257 and RF-2008-00008-00-00). The technical assistance of Nuria Palacios and Mariola Plazas is gratefully acknowledged.

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Table 1

Plant materials used for the eggplant grafting experiments, type of material, and their origin.

Plant material	Code	Species	Type of material	Origin[a]
'Black Beauty'	BB	*Solanum melongena*	Cultivated, commercial variety	B and T World Seeds, Aiguesvives, France
67878	STO	*Solanum torvum*	Wild	B and T World Seeds, Aiguesvives, France
BBS168	SMA	*Solanum macrocarpon*	Cultivated, local landrace	Ivory Coast
MM577 × ANS26	SIxSM	*Solanum incanum* × *S. melongena*	Wild (MM577); Cultivated, local landrace (ANS26)	Israel (MM577); Andalucía, Spain (ANS26)
PI470273 × PI413783	SMxSA	*S. melongena* × *Solanum aethiopicum*	Cultivated, local landrace (PI470273); Cultivated, local landrace (PI413783)	Kalimantan, Indonesia (PI470273); Burkina Faso (PI413783);

[a]For commercial seed the seed company and headquarters location is indicated; for germplasm accessions the province (if available) and country of origin are indicated.

Table 2

Plant characteristics for the rootstocks used (BB='Black Beauty'; STO=*Solanum torvum*; SMA=*Solanum macrocarpon*; SIxSM= *Solanum incanum* × *Solanum melongena*; SMxSA=*S. melongena* × *Solanum aethiopicum*). Data were obtained from the database of the germplasm bank of the Instituto de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV) of the Universidad Politécnica de Valencia (Valencia, Spain) from germplasm characterization data trials.

Rootstock	Plant heigth (cm; mean±SE)	Leaf length (cm; mean±SE)	Leaf width (cm; mean±SE)	Leaf prickles (0-9 scale; mean±SE)[a]	Shoot tip anthocyanins intensity (0-9 scale; mean±SE)[b]
BB	87.4±6.7	8.66±1.31	7.83±0.56	0.00±0.00	1.1±1.0
STO	144.5±9.6	12.05±0.88	9.61±0.94	1.55±0.69	0.0±0.0
SMA	108.3±6.3	8.94±0.69	11.17±0.77	0.22±0.14	0.0±0.0
SIxSM	172.4±8.9	13.50±0.76	9.44±0.80	4.77±0.76	5.0±2.8
SMxSA	156.9±4.2	12.88±0.60	9.11±0.67	0.66±0.86	2.2±1.3

[a]Measured on a 0 to 9 scale where 0=none and 9=very many (>20)prickles per leaf according to the European Eggplant Genetic Resources Network (EGGNET) descriptors (Prohens et al.,2005).

[b]Measured on a 0 to 9 scale where 0=absent (green shoot tip) and 9=very strong (dark purple shoot tip) according to EGGNET descriptors.

Table 3

Seed germination (in Petri dish) of the rootstocks used (BB='Black Beauty'; STO=*Solanum torvum*; SMA=*Solanum macrocarpon*; SIxSM= *Solanum incanum* × *Solanum melongena*; SMxSA=*S. melongena* × *Solanum aethiopicum*), and graft success on these rootstocks when using 'Black Beauty' eggplant as scion.

Rootstock	Germination (%)[a,b]	Graft success (%)[b]
BB	95 a	98 a
STO	0 c	100[c] a
SMA	58 b	90 b
SIxSM	95 a	100 a
SMxSA	90 a	100 a

[a]Percent of seeds germinated after 15 d of sowing.

[b]Mean values within a column separated by different letters are significantly different (P<0.05) according to Duncan's multiple range test.

[c]An adequate supply of plantlets of *S. torvum* rootstock for the grafting experiment were obtained after sowing a large amount of seeds in seedling trays filled with commercial substrate (see text for explanation).

Table 4

Plant survival and plant vigour traits of non-grafted ‘Black Beauty’ (BB control), self-grafted (BB/BB) and grafted onto *Solanum torvum* (BB/STO), *Solanum macrocarpon* (BB/SMA), *Solanum incanum* × *Solanum melongena* (SIxSM) and *S. melongena* × *Solanum aethiopicum* (BB/SMxSA) rootstocks.

Scion/Rootstock	Plants dead before initiation of fruit set (%)[a]	Plants dead at the end of the experiment (%)[a]	Plant heigth (cm)[a]	Stem diameter (mm)[a]
BB control	16 ab	16 ab	114.5 bc	22.4 a
BB/BB	8 ab	12 ab	119.7 abc	24.5 a
BB/STO	4 b	8 ab	123.6 ab	24.6 a
BB/SMA	24 a	28 a	108.9 c	23.0 a
BB/SIxSM	0 b	0 b	127.0 a	23.7 a
BB/SMxSA	0 b	0 b	122.5 ab	22.7 a

[a]Mean values within a column separated by different letters are significantly different ($P<0.05$) according to Duncan’s multiple range test.

Table 5

Earliness and yield traits of ‘Black Beauty’ eggplant from non-grafted plants (BB control), self-grafted (BB/BB) and grafted onto *Solanum torvum* (BB/STO), *Solanum macrocarpon* (BB/SMA), *Solanum incanum* × *Solanum melongena* (SIxSM) and *S. melongena* × *Solanum aethiopicum* (BB/SMxSA) rootstocks.

Scion/Rootstock	Plants with early fruit (%)[a,b]	Early fruit (no./plant)[a,b]	Total fruit (no./plant)[a,b]	Fruit weigth (g)[a,b]	Yield/plant (kg)[a,b]	Yield (kg/m^2)[a,c]
BB control	23.8 bc	1.8 bc	11.6 b	464 a	5.4 b	5.7 b
BB/BB	26.1 bc	1.4 bc	12.7 ab	440 a	5.7 ab	6.3 b
BB/STO	37.5 abc	2.2 bc	14.4 ab	445 a	6.4 ab	7.7 ab
BB/SMA	15.8 c	0.6 c	7.6 c	446 a	3.4 c	3.2 c
BB/SIxSM	68.0 a	5.0 a	15.8 a	437 a	6.9 a	8.6 a
BB/SMxSA	48.0 ab	2.6 ab	15.0 ab	427 a	6.4 ab	8.0 a

[a]Mean values within a column separated by different letters are significantly different ($P<0.05$) according to Duncan’s multiple range test.

[b]Data taking into account only the plants alive at the end of the experiment.

[c]Data taking into account all the plants (i.e., including those alive and dead at the end of the experiment).

Table 6

Apparent quality traits of 'Black Beauty' eggplant fruit from non-grafted (BB control), self-grafted (BB/BB) plants and from 'Black Beauty' grafted onto *Solanum torvum* (BB/STO), *Solanum macrocarpon* (BB/SMA), *Solanum incanum* × *Solanum melongena* (SIxSM) and *S. melongena* × *Solanum aethiopicum* (BB/SMxSA) rootstocks.

Scion/Rootstock	Fruit length (cm)[a]	Fruit width (cm)[a]	Fruit length / width ratio[a]	Fruit curvature (1-9 scale)[a,b]	Fruit cross-section (1-9 scale)[a,c]	Fruit calyx length (1-9 scale)[a,d]	Fruit calyx prickles (0-9 scale)[a,e]	Seeds index (0-9 scale)[a,f]
BB control	13.16 ab	10.60 a	1.27 ab	1.33 a	5.00 abc	1.60 b	1.77 b	1.63 a
BB/BB	12.82 ab	10.53 a	1.25 bc	1.13 a	5.20 ab	1.60 b	1.63 b	1.40 a
BB/STO	13.45 a	9.91 a	1.37 a	1.13 a	4.73 bc	1.56 b	1.67 b	1.56 a
BB/SMA	11.77 c	10.62 a	1.13 c	1.06 a	5.40 a	2.26 a	3.06 a	1.23 a
BB/SIxSM	13.14 ab	9.73 a	1.38 a	1.20 a	4.53 c	1.27 b	1.50 b	1.30 a
BB/SMxSA	12.47 bc	10.10 a	1.24 bc	1.20 a	4.93 abc	1.27 b	1.43 b	1.40 a

[a]Mean values within a column separated by different letters are significantly different ($P<0.05$) according to Duncan's multiple range test.
[b]Measured on a 1 to 9 scale where 1=none and 9=U-shaped according to the European Eggplant Genetic Resources Network (EGGNET) descriptors (Prohens et al., 2005).
[c]Measured on a 1 to 9 scale where 1=circular and 9=very irregular according to EGGNET descriptors.
[d]Relative to the fruit length; measured on a 1 to 9 scale where 1=very short (>10%) and 9=very long (>75%) according to EGGNET descriptors.
[e]Measured on a 0 to 9 scale where 0=none and 9= very many (>30) calyx prickles per fruit according to EGGNET descriptors.
[f]Measured on a 0 to 9 scale where 0=none and 5=very many (>80) seeds per fruit visible in a longitudinal fruit section.

Table 7

Proximate composition and mineral content (on a fresh weight basis) of ‘Black Beauty’ eggplant fruit produced from non-grafted (BB control), self-grafted (BB/BB) and grafted onto *Solanum torvum* (BB/STO), *Solanum macrocarpon* (BB/SMA), *Solanum incanum* × *Solanum melongena* (SIxSM) and *S. melongena* × *Solanum aethiopicum* (BB/SMxSA)rootstocks.

	Dry matter	Protein content		Total phenolics	Minerals ($mg \cdot kg^{-1}$)							
Scion/Rootstock	(%)[a]	($g \cdot kg^{-1}$)[a]	Soluble solids content (%)[a]	($mg \cdot kg^{-1}$)[a]	P[a]	K[a]	Ca[a]	Mg[a]	Na[a]	Fe[a]	Cu[a]	Zn[a]
BB control	5.7 a	4.3 b	4.02 a	419 b	229 a	2316 a	148 a	239 a	345 a	1.04 ab	0.50 a	2.58 a
BB/BB	5.8 a	4.9 a	4.16 a	447 ab	237 a	2443 a	161 a	296 a	356 a	1.26 ab	1.00 a	2.62 a
BB/STO	5.6 a	4.4 ab	4.12 a	411 b	186 a	2266 a	176 a	205 a	348 a	0.86 b	0.58 a	1.58 a
BB/SMA	5.9 a	4.8 ab	4.11 a	550 a	225 a	2562 a	185 a	286 a	534 a	2.66 a	0.94 a	1.60 a
BB/SIxSM	5.6 a	4.4 ab	4.14 a	481 ab	206 a	2127 a	151 a	198 a	356 a	1.08 ab	0.48 a	1.30 a
BB/SMxSA	5.8 a	4.7 ab	4.18 a	456 ab	242 a	2482 a	200 a	319 a	353 a	1.16 ab	0.58 a	1.60 a

[a]Mean values within a column separated by different letters are significantly different ($P<0.05$) according to Duncan’s multiple range test.

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	Dry matter	Soluble solids content	Protein content	Total phenolics	Minerals ($mg\cdot kg^{-1}$)							
Scion/Rootstock	(%)[a]	(%)[a]	($g\cdot kg^{-1}$)[a]	($mg\cdot kg^{-1}$)[a]	P[a]	K[a]	Ca[a]	Mg[a]	Na[a]	Fe[a]	Cu[a]	Zn[a]
BB control	5.7 a	4.02 a	4.3 b	419 b	229 a	2316 a	148 a	239 a	345 a	1.04 ab	0.50 a	2.58 a
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BB/SMA	5.9 a	4.11 a	4.8 ab	550 a	225 a	2562 a	185 a	286 a	534 a	2.66 a	0.94 a	1.60 a
BB/SIxSM	5.6 a	4.14 a	4.4 ab	481 ab	206 a	2127 a	151 a	198 a	356 a	1.08 ab	0.48 a	1.30 a
BB/SMxSA	5.8 a	4.18 a	4.7 ab	456 ab	242 a	2482 a	200 a	319 a	353 a	1.16 ab	0.58 a	1.60 a

[a]Mean values within a column separated by different letters are significantly different ($P<0.05$) according to Duncan’s multiple range test.