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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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 Solanum incanum L. (SI × SM) and Solanum aethiopicum L. (SM × SA). The results are compared with non-grafted (BB control) and self-grafted (BB/BB) controls and with S. melongena ‘Black Beauty’ scions grafted onto Solanum torvum Sw., (STO) and Solanum macrocarpon L. (SMA) rootstocks. All treatments were grown in a soil naturally infested with root-knot nematodes (mostly Meloidogyne incognita (Kofoid and White) Chitwood), SI × SM and SM × SA 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 SI × SM 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 the SI × SMA 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.

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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,b; 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-borne pests, or that induce vigorous growth of the scion are used for improving eggplant production (Daunay, 2008). Because soil pathogens can cause important losses 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 and 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 (Solanum lycopersicum L.) hybrids (e.g., ‘Energy’, or ‘Kyn-dia’) as well as tomato S. lycopersicum × S. habrochaites S. Knapp and D.M. Spooner interspecific hybrids (e.g., ‘He Man’, ‘Beaumont’) are also commonly used as rootstocks for eggplant (Bletsos et al., 2003; Miguel et al., 2007; King et al., 2010). However, specific

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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 Giumfrida, 2006; Oda et al., 1996). Also, the wild species Solanum sisymbriifolium Lam. and the hmg eggplant Solanum integrifolium Poir. (=Solanum aethiopicum L. Acauleatum 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 (Solanum macrocarpon L.) are cultivated species of economic importance in Western Africa (Spichers, 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. melongena and resistant to R. solanaearum (Cappelli et al., 1995; Daunay et al., 1991; Hébert, 1985). Resistance to root-knot nematodes (RKN) has also been reported in S. aethiopicum Gilo group (Cappelli et al., 1995; Hébert, 1985).

Another species of interest as a source of variation for developing new eggplant rootstocks is Solanum incanum, which is the putative ancestor of eggplant (Lester and Hasan, 1991), and which has been reported as resistant to F. oxysporium f. sp. melongena (Yamakawa and Mohcuzuki, 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. and 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 S. integriolium rootstocks (Oda et al., 1996) and the accumulation of high amounts of nicotine in tomatoes from plants grafted onto Nicotiana tabacum have been reported (Yasinok et al., 2009). In the specific case of eggplant grafted onto Datura inoxia P. Mill., scopalamine 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 tri-

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Plant materials used for the eggplant grafting experiments, type of material, and their origin.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant material</td>
<td>Code</td>
</tr>
<tr>
<td>&quot;Black Beauty&quot;</td>
<td>BB</td>
</tr>
<tr>
<td>G7878</td>
<td>STO</td>
</tr>
<tr>
<td>BBS168</td>
<td>SMA</td>
</tr>
<tr>
<td>MM577 × ANS26</td>
<td>SI × SM</td>
</tr>
<tr>
<td>P470273 × P4143783</td>
<td>SM × SA</td>
</tr>
</tbody>
</table>

* For commercial seed the seed company and headquarters location is indicated; for germplasm accessions the province (if available) and country of origin are indicated.
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Table 2

<table>
<thead>
<tr>
<th>Rootstock</th>
<th>Plant height (cm; mean ± SE)</th>
<th>Leaf length (cm; mean ± SE)</th>
<th>Leaf width (cm; mean ± SE)</th>
<th>Leaf prickles (0–9 scale; mean ± SE)*</th>
<th>Shoot tip anthocyanin intensity (0–9 scale; mean ± SE)**</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB</td>
<td>87.4 ± 6.7</td>
<td>8.66 ± 1.31</td>
<td>7.83 ± 0.56</td>
<td>0.00 ± 0.00</td>
<td>1.1 ± 1.0</td>
</tr>
<tr>
<td>STO</td>
<td>144.5 ± 9.6</td>
<td>12.05 ± 0.68</td>
<td>9.61 ± 0.94</td>
<td>1.55 ± 0.09</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>SMA</td>
<td>108.3 ± 6.3</td>
<td>8.94 ± 0.69</td>
<td>11.17 ± 0.77</td>
<td>0.22 ± 0.14</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>SM × SMA</td>
<td>172.4 ± 8.9</td>
<td>13.50 ± 0.76</td>
<td>9.44 ± 0.80</td>
<td>4.77 ± 0.76</td>
<td>5.0 ± 2.8</td>
</tr>
<tr>
<td>SM × SA</td>
<td>156.9 ± 4.2</td>
<td>12.88 ± 0.60</td>
<td>9.11 ± 0.67</td>
<td>0.66 ± 0.86</td>
<td>2.2 ± 1.3</td>
</tr>
</tbody>
</table>

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

als per material, with 8–15 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 °C for 20 min. Plates were incubated in a growth chamber at 26 ± 2 °C 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 our research on grafting presented here (Table 2), these data are useful to estimate the vigour of the rootstocks used.

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 (SI × SM), and S. melongena × S. aethiopicum (SM × SA) rootstocks using the cleft procedure described by Lee (1994). Plants at the 3–4 leaf stage (25–35 d old) were subjected to grafting, as well as by the number of fruit per plant harvested during this period. Commercially mature fruit were harvested for 2 months, 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 plant−1 (taking into account only the plants alive at the end of the experiment) and as kg 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, SI × SM, and SM × SA 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 = 1–20%; 2 = 21–40%; 3 = 41–60%; 4 = 61–80% and 5 = 81–100%) (Oka 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 °C 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, Högåsm, Sweden) and reported as N × 6.25. For extraction of phenolics, 5 mL of juice were poured on 10 mL of an extracting solution of acetone (70%, v/v) and glacial acetic acid (0.5%, v/v) and left for 24h 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 (SOLAAAR 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.

### Table 3

<table>
<thead>
<tr>
<th>Rootstock</th>
<th>Germination (%)</th>
<th>a, b</th>
<th>Graft success (%)</th>
<th>a, b</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB</td>
<td>95 a</td>
<td>98 a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>STO</td>
<td>0 c</td>
<td>100 a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SMA</td>
<td>58 b</td>
<td>90 b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SI × SM</td>
<td>95 a</td>
<td>100 a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SM × SA</td>
<td>90 a</td>
<td>100 a</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*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.

### 3. Results

#### 3.1. Seed germination and graft success

Germination of seeds sown in Petri dishes with GA3 containing medium could be observed at 3–4 d after sowing for ‘Black Beauty’, SI × SM, and SM × SA, and at 8 d after sowing for SMA. At 15 d after sowing, ‘Black Beauty’ and the interspecific hybrids SI × SM and SM × SA exhibited very low 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, SI × SM, and SM × SA rootstocks, which had percentages of graft success that ranged from 98% (‘Black Beauty’) to 100% (STO, SI × SM, and SM × SA). 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 SI × SM and SM × SA 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 SI × SM and SMA and between SM × SA 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 SI × SM and SM × SA, respectively (100% survival) (Table 4).

The mean plant height among different treatments varied between 108.9 and 127.0 cm for the SMA and SI × SM rootstocks, respectively (Table 4). ‘Black Beauty’ scions grafted onto SI × SM, SM × SA and STO rootstocks were significantly taller than those grafted onto SMA rootstock. Plants with SI × SM 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).
Table 4

<table>
<thead>
<tr>
<th>Scion/rootstock</th>
<th>Plants dead before initiation of fruit set (%)</th>
<th>Plants dead at the end of the experiment (%)</th>
<th>Plant height (cm)</th>
<th>Stem diameter (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB control</td>
<td>16 ab</td>
<td>16 ab</td>
<td>114.5 bc</td>
<td>22.4 a</td>
</tr>
<tr>
<td>BB/BB</td>
<td>8 ab</td>
<td>12 ab</td>
<td>119.7 abc</td>
<td>24.5 a</td>
</tr>
<tr>
<td>BB/STO</td>
<td>4 b</td>
<td>8 ab</td>
<td>123.6 ab</td>
<td>24.6 a</td>
</tr>
<tr>
<td>BB/SMA</td>
<td>24 a</td>
<td>28 a</td>
<td>108.9 c</td>
<td>23.0 a</td>
</tr>
<tr>
<td>BB/SA × SI</td>
<td>0 b</td>
<td>0 b</td>
<td>127.0 a</td>
<td>23.7 a</td>
</tr>
<tr>
<td>BB/SA × SM</td>
<td>0 b</td>
<td>0 b</td>
<td>122.5 ab</td>
<td>22.7 a</td>
</tr>
</tbody>
</table>

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

Table 5

<table>
<thead>
<tr>
<th>Scion/rootstock</th>
<th>Plants with early fruit (%)</th>
<th>Early fruit (no./plant)</th>
<th>Total fruit (no./plant)</th>
<th>Fruit weight (g)</th>
<th>Yield/plant (kg)</th>
<th>Yield (kg/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB control</td>
<td>23.8 b</td>
<td>1.8 bc</td>
<td>11.6 bc</td>
<td>464 a</td>
<td>5.4 b</td>
<td>5.7 b</td>
</tr>
<tr>
<td>BB/BB</td>
<td>26.1 bc</td>
<td>1.4 bc</td>
<td>12.7 ab</td>
<td>440 a</td>
<td>5.7 b</td>
<td>6.3 b</td>
</tr>
<tr>
<td>BB/STO</td>
<td>37.5 abc</td>
<td>2.2 bc</td>
<td>14.4 ab</td>
<td>445 a</td>
<td>6.4 ab</td>
<td>7.7 ab</td>
</tr>
<tr>
<td>BB/SMA</td>
<td>15.8 c</td>
<td>0.6 c</td>
<td>7.6 c</td>
<td>446 a</td>
<td>3.4 c</td>
<td>3.2 c</td>
</tr>
<tr>
<td>BB/SA × SI</td>
<td>68.0 a</td>
<td>5.0 a</td>
<td>15.8 a</td>
<td>437 a</td>
<td>6.9 a</td>
<td>8.6 a</td>
</tr>
<tr>
<td>BB/SA × SM</td>
<td>48.0 ab</td>
<td>2.6 ab</td>
<td>15.0 ab</td>
<td>427 a</td>
<td>6.4 ab</td>
<td>8.0 a</td>
</tr>
</tbody>
</table>

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

Visual assessment of the roots at the end of the experiment revealed more vigorous root growth in STO, SI × SM, and SM × SA 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 SI × SM and SM × SA 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 SI × SM rootstocks (Table 5). Plants with SI × SM 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 SM × SA 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⁻¹ to 5.0 fruit plant⁻¹ for those with SMA and SI × SM rootstocks, respectively (Table 5). In the latter case, 'Black Beauty' grafted onto SI × SM 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 SM × SA 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 SI × SM rootstocks, while the total yield ranged between 3.4 kg plant⁻¹ (taking into account only plants alive at the end of the experiment) or 3.2 kg/m² (taking into account all plants, alive or dead, at the end of the experiment) for 'Black Beauty' grafted onto SI × SM rootstock and 6.9 kg plant⁻¹ or 8.6 kg/m² for those grafted onto SI × SM rootstock (Table 5). Plants with SI × SM rootstock had a significantly greater number of early fruit and yield in comparison to non-grafted 'Black Beauty' plants and those grafted onto SMA rootstock, and plants with SM × SA 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).

Table 6

<table>
<thead>
<tr>
<th>Scion/rootstock</th>
<th>Fruit length (cm)</th>
<th>Fruit width (cm)</th>
<th>Fruit length/ width ratio</th>
<th>Fruit curvature (1–9 scale)</th>
<th>Fruit cross-section (1–9 scale)</th>
<th>Fruit calyx length (0–9 scale)</th>
<th>Fruit calyx prickles (0–9 scale)</th>
<th>Seeds index (0–9 scale)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB control</td>
<td>13.16 ab</td>
<td>10.60 a</td>
<td>1.27 ab</td>
<td>1.33 a</td>
<td>5.00 abc</td>
<td>1.60 b</td>
<td>1.77 b</td>
<td>1.63 a</td>
</tr>
<tr>
<td>BB/BB</td>
<td>12.82 ab</td>
<td>10.53 a</td>
<td>1.25 bc</td>
<td>1.13 a</td>
<td>5.20 ab</td>
<td>1.60 b</td>
<td>1.63 b</td>
<td>1.40 a</td>
</tr>
<tr>
<td>BB/STO</td>
<td>13.45 a</td>
<td>9.91 a</td>
<td>1.37 a</td>
<td>1.13 a</td>
<td>4.73 bc</td>
<td>1.56 b</td>
<td>1.67 b</td>
<td>1.56 a</td>
</tr>
<tr>
<td>BB/SMA</td>
<td>11.77 c</td>
<td>10.62 a</td>
<td>1.13 c</td>
<td>1.06 a</td>
<td>5.40 a</td>
<td>2.26 a</td>
<td>3.06 a</td>
<td>1.23 a</td>
</tr>
<tr>
<td>BB/SA × SI</td>
<td>13.14 ab</td>
<td>9.73 a</td>
<td>1.38 a</td>
<td>1.20 a</td>
<td>4.53 c</td>
<td>1.27 b</td>
<td>1.50 b</td>
<td>1.30 a</td>
</tr>
<tr>
<td>BB/SA × SM</td>
<td>12.47 bc</td>
<td>10.10 a</td>
<td>1.24 bc</td>
<td>1.20 a</td>
<td>4.93 abc</td>
<td>1.27 b</td>
<td>1.43 b</td>
<td>1.40 a</td>
</tr>
</tbody>
</table>

* Measured in a column separated by different letters are significantly different (P<0.05) according to Duncan’s multiple range test.

* Measured on a 1–9 scale where 1 = none and 9 = U-shaped according to the European Eggplant Genetic Resources Network (EGGNET) descriptors (Prohens et al., 2005).

* Measured on a 1–9 scale where 1 = circular and 9 = very irregular according to EGGNET descriptors.

* Measured on a 0–9 scale where 0 = none and 5 = very many (>80) seeds per fruit visible in a longitudinal fruit section.
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 SI × SM 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 SM × SA 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 SI × SM 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 SI × SM 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 kg⁻¹) versus the non-grafted plants (4.3 g kg⁻¹). Total fruit phenolics content from plants with SMA rootstock was significantly higher (550 mg kg⁻¹) in comparison to that from non-grafted or from STO grafted plants (419 and 411 mg kg⁻¹, respectively).

Regarding the mineral composition, high fruit K content was evident (mean of 2366 mg kg⁻¹), followed by Na (382 mg kg⁻¹), Mg (257 mg kg⁻¹), P (221 mg kg⁻¹), Ca (170 mg kg⁻¹), and at much lower concentrations by Zn (1.88 mg kg⁻¹), Fe (1.34 mg kg⁻¹), and Cu (0.68 mg 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 kg⁻¹) in comparison to fruit from ‘Black Beauty’ grafted onto STO rootstock (0.86 mg 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,b; King et al., 2008, 2010; Lee, 1994; Lee and Oda, 2003; Rivero et al., 2003). Ideally, rootstocks should improve the yield, disease resistance and quality of a number of vegetable crops (Davis et al., 2008a,b; King et al., 2008, 2010; 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 synchronizing 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 days can be needed to attain germination with percentage rates that vary between 15% and 50% in S. insculpta L., S. torvum, S. integrifolium, S. surattense Burm., S. khasianum C.B. Clarke, S. santomosanum Craib and in hybrids of S. melongena × 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 Laterrt, 1991), even after GA3 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 (Dauñay, 2008). In our study, high germination rates (>90%) were obtained with seed for 'Black Beauty', SI × SM and SM × SA rootstocks. For SMA, the rates obtained (58%) were somewhat lower. S. torvum however, did not germinate under our GA3 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 SI × SM and SM × SA, 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, SI × SM, 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 SI × SM and SM × SA 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 × S. aethiopicum or S. melongena × 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 SI × SM and SM × SA 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, SI × SM and SM × SA 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 (Tzortzakis et al., 2006), our results agree with previous reports that consider this species as resistant or a poor host for M. incognita (Dauñay and Dalmasso, 1985; Hébert, 1985). It is remarkable that no plants grafted onto the interspecific hybrids SI × SM and SM × SA 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 SI × SM 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 SI × SM and SM × SA. 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 SI × SM 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 SI × SM and SM × SA rootstock 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., 2007; Davis et al., 2008a,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 calyces in eggplant landraces (Prohens et al., 2004). Similar to observations for fruit yield, weight and earliness in a diverse collection of germplasm, prior studies also demonstrated that envi-
vironment 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 Paiva, 1995; Moglia et al., 2008).

Divergence between allied eggplant species for fruit phenolic acid constituents and their total has been documented (Stommel and Whittaker, 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 SI × SM and SM × SA 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 SI × SM and SM × SA 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, SI × SM rootstock may be the best selection. Our results demonstrated that the use of interspecific hybrid rootstocks derived from fully compatible crosses with related species affords a valuable approach to improve eggplant production.

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