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Suitability of CMS-based Interspecific Eggplant (*Solanum melongena* L.) Hybrids as Rootstocks for Eggplant Grafting

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Authors' contributions

This work was carried out in collaboration between all authors. Author KK designed the study, performed the statistical analysis, wrote the protocol, wrote the first draft of the manuscript and managed the literature searches. Authors KK, AM, FB and DR managed the analyses of the study. All authors read and approved the final manuscript.

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ABSTRACT

Aims: The objective of the study was to determine the suitability of five newly developed CMS-based interspecific eggplant hybrids as eggplant rootstocks.
Place of Study: This study was conducted in an experimental field of the Hellenic Agricultural Organization "Demeter" (HAO "Demeter"), in Thessaloniki, Greece.
Methodology: In the grafting experiment the Greek eggplant cultivars 'Langada' (L), 'Emi' (E) and 'Tsakoniki' (T) were used as scions. The interspecific rootstocks *viz*., F_1(cmsLxSI), F_1(cmsExSI), F_1(cmsTxSI), F_1(cmsExSG) and F_1(cmsTxSG) were previously developed after crossing the respective CMS eggplant lines (cmsL, cmsE and cmsT) to the wild species *S. integrifiilum* (SI) and *S. gilo* (SG). Self-grafted plants of the three eggplant scions were used as controls. For each of the 18 scion/rootstock combinations nine plants were grafted by using the cleft grafting technique and

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plant survival rate was recorded. The grafted plants were transplanted in the field and arranged according to the completely randomized experimental design. The number of early and total fruits and weight of early and total yield as well as some important fruit characteristics (weight, length and diameter, ratio of length to diameter, penducle length, number of penducle prickles) were recorded on per plant basis. In addition, some aspects of external fruit morphology (color, shape, presence of stripes) were also recorded.

Results: Plant survival in the hetero-grafting combinations was high (94.0%) and comparable to the self-grafted controls (96.3%). While early production was not affected by grafting, total production was improved by certain rootstocks. F_1(cmsTxSI) and F_1(cmsExSG) had an overall positive effect on all scions and increased total fruits by 41.4% and 31.0%, respectively, and total yield by 36.8% and 35.8%,respectively. F_1(cmsLxSI) combined well with cv. 'Langada' increasing total fruits by 34.3% and total yield by 53.8%. Interestingly, both self- and hetero-grafting resulted in morphological alterations of the fruit which varied with respect to the scion/rootstock combination.

Conclusion: The grafting compatibility between the eggplant scions and the interspecific rootstocks was very high. A differential response to grafting of each eggplant cultivar was apparent for most of the studied yield and fruit characteristics with possible underlying scion x rootstock interactions. From a practical point of view, F_1(cmsTxSI) and F_1(cmsExSG) indicate high potential as eggplant rootstocks and may be considered for further evaluation.

Keywords: Rootstock breeding; Solanum gilo; Solanum integrifolium; Solanum melongena.

1. INTRODUCTION

Eggplant (*Solanum melongena* L.) is an important vegetable species worldwide cultivated; however, its susceptibility to a wide range of soil-borne diseases causes significant economic losses [1]. A common reliable and environmentally friendly approach to overcome soil-borne disease losses is grafting eggplant onto resistant rootstocks [2–6]. Grafting principally confers resistance against different diseases, but may also improve the response of the scion to abiotic stresses and enhance the quality of the harvested product [7–10]. Moreover, selection of the appropriate rootstock can lead to an increased vigor and thereby increased yield of the eggplant scion [11,12]. Finally, some rootstocks appear to prevent the uptake of heavy metals by the scion or limit their concentrations below safety levels [13].

However, several problems may be encountered at various stages of grafting resulting in increased cost or reduced effectiveness of the process. Such problems may be the low germination rate or irregular germination of the rootstock [14–16], the risk of losing the resistance by continuously using certain rootstocks [17], grafting induced epigenetic changes in the scion which lead to altered fruit phenotype [18–20], the reduced vigor of the scion caused by rootstock/scion incompatibility [12], the high cost of hybrid rootstocks [21,22] and the potential deterioration of quality and quantity of the harvested product [22]. Finally, in one documented case grafting of eggplant onto *Datura metel*, caused poisoning due to high concentration of alkaloids in the fruit [23].

These problems may be addressed by rootstock breeding *via* the continuous development and evaluation of new rootstocks. The interspecific hybrids of eggplant seem to be a valuable pool of a large number of candidate rootstocks as they are usually characterized by a high degree of heterosis [12,16,24]. Indeed, the high degree of crossability between eggplant and wild *Solanum* species along with the large number of available *Solanum* accessions [1,25–27] provide that a vast number of interspecific combinations can be produced and evaluated as eggplant rootstocks. Another important benefit of using hybrid rootstocks, especially for the private sector, is the protection of breeder's rights.

The utilization of CMS eggplant lines in the crosses would facilitate interspecific rootstock breeding because hand emasculation of the female parent is not necessary and the resulting seed would be of perfect purity. In a previous study we developed the CMS lines of three Greek eggplant cultivars *viz*. 'Langada', 'Emi' and 'Tsakoniki' [28]. Subsequently, these lines were crossed as female parents to the wild species *S. integrifolium* and *S. gilo* (=*S. aethiopicum* groups Aculeatum and Gilo, respectively) aiming to the efficient and economical production of new eggplant rootstocks and breeding materials [29].

The resulting interspecific hybrids are potentially valuable rootstocks for eggplant grafting because both wild parents carry the dominant allele of resistance to the destructive soil-born pathogen *Fusarium oxysporum* f. sp. *melongenae* [30,31]. Moreover, the interspecific hybrids of *S. integrifolium* with eggplant were found to be tolerant to *Ralstonia solanacearum* (=*Pseudomonas solanacearum*) [32], highly vigorous [12] and have been used on a commercial scale as eggplant rootstocks [33]. In addition, in preliminary studies it was shown that the CMS-interspecific hybrids were produced in a more efficient way than the conventional method and had a very high germination rate [29,34,35].

The aim of this study was: 1) to evaluate the grafting compatibility between three Greek eggplant cultivars 'Langada', 'Emi' and 'Tsakoniki' (scions) and five CMS-based interspecific hybrids between eggplant and the wild species *S. integrifolium* and *S. gilo* (rootstocks) and 2) to study the effect of grafting on yield and fruit morphology of the eggplant scion.

2. MATERIALS AND METHODS

2.1 Plant Material

Three Greek eggplant cultivars *viz.* 'Langada' (L), 'Emi' (E) and 'Tsakoniki' (T) were used as scions and five interspecific hybrids *viz.* F_1(cmsLxSI), F_1(cmsExSI), F_1(cmsTxSI), F_1(cmsExSG) and F_1(cmsTxSG) were used as rootstocks. These cultivars were selected because they are very popular and have a considerable share in the local market. In addition, the fruits of these cultivars present considerable morphological differences (Table 1). The interspecific rootstocks were previously obtained *via* hybridization of the respective CMS eggplant lines (cmsL, cmsE and cmsT) to the wild species *S. integrifolium* (SI) and *S. gilo* (SG) [29,34,35]. Furthermore, self-grafted plants of each eggplant cultivar were used as controls. The plant material used in the grafting experiments is presented in Table 2. The resulting scion/rootstock combinations were cultivated during 15 June 2014-1 September 2014 in an open field in Hellenic Agricultural Organization "Demeter" (HAO "Demeter") and standard cultivation practices were applied. The plants were arranged in the experimental field according to the completely randomized design. The 18 scion/rootstock combinations were considered as treatments and the surviving 7-9 grafted plants per combination were used as replications.

2.2 Grafting

For the grafting experiment seeds of the scions (eggplant cultivars) and rootstocks (interspecific hybrids) were sown at the same time (2 May 2014) and the seedlings were grown for 30 days. For each rootstock/scion combination nine plants were grafted by using the cleft grafting method [2] and immediately transferred to a closed transparent plastic box with high humidity (about 100%), where they remained for 7-9 days until the complete union of the scion and the rootstock. Subsequently, the grafted plants were acclimatized for 2-3 days by gradually opening the box lid and then transferred to standard conditions until transplanting in the experimental field. In total, nine plants were grafted for each scion/rootstock combination and the survival rate of the grafted plants was calculated at 5 and 10 days after grafting (DAG).

2.3 Plant Productivity

In order to study the effect of grafting on scion yield the grafted plants were harvested three times at 12 days interval and the fruits of each harvest were counted and weighed. Weight of early yield (kg per plant) and number of early fruits was calculated by the sum of the first and second harvest and weight of total yield (kg per plant) and total number of fruits was calculated from the sum of all three harvests.

Table 1. Fruit characteristics of the eggplant cultivars 'Langada', 'Emi' and 'Tsakoniki'

Cultivar	Size	Shape	Commercial maturity		Physiological maturity	
			Color	Stripes	Color	Stripes
'Langada'	large	cylindrical	dark purple	absent	brownish yellow	absent
'Emi'	large	obovate	dark purple	absent	brown	absent
'Tsakoniki'	medium	cylindrical	medium purple	white	brown	yellow

Table 2. The plant material used in the grafting experiments

Eggplant scion	Rootstock
cv. 'Langada'	cv. 'Langada'
	F_1(cmsLxSI)
	F_1(cmsExSI)
	F_1(cmsTxSI)
	F_1(cmsExSG)
	F_1(cmsTxSG)
cv. 'Emi'	cv. 'Emi'
	F_1(cmsLxSI)
	F_1(cmsExSI)
	F_1(cmsTxSI)
	F_1(cmsExSG)
	F_1(cmsTxSG)
cv. 'Tsakoniki'	cv. 'Tsakoniki'
	F_1(cmsLxSI)
	F_1(cmsExSI)
	F_1(cmsTxSI)
	F_1(cmsExSG)
	F_1(cmsTxSG)

2.4 Fruit Morphology

To study the effect of grafting on the morphology of the fruit, the main quantitative (measurable) characteristics of the fruit (weight, length and diameter, ratio of length to diameter, penduce length, number of penducle prickles) were measured in three fruits per plant obtained from the second or third harvest. In addition, some characteristics of external morphology of the fruit (color, shape, presence of stripes) were recorded at commercial and post-commercial maturity.

2.5 Statistical Analysis

Statistical analysis of the experimental data was conducted with the statistical package SPSS 17.0. Analysis of variance was carried out separately for each eggplant scion and significantly different means were separated by the Duncan's multiple range test (α=0.05).

3. RESULTS AND DISCUSSION

3.1 Grafting Success

In the present study, the overall grafting compatibility between the new interspecific rootstocks and the eggplant scions was very high. That was apparent by the survival rate of the hetero-grafted plants, which was very high and similar to the self-grafted controls. At 5 DAG complete survival (100.0%) of the grafted plants was observed in all scion/rootstock combinations, with the exception of 'Emi'/F_1(cmsTxSG) and 'Tsakoniki'/F_1(cmsLxSI) where a slightly lower percentage was recorded (88.9%) (Table 3). The percentage of surviving plants at 10 DAG slightly decreased, due to the loss of few plants in some combinations. At this stage, complete survival was observed in self-grafted 'Emi' and 'Tsakoniki' as well as 9 of the 15 combinations of the interspecific rootstocks (Table 3). Finally, all the grafted plants that were transplanted in the field survived until the end period of observations i.e. at about 90 DAG. Pooled grafting data indicated that three eggplant scions had similar and high survival rates, which ranged from 98.6 to 100.0% at 5 DAG and from 92.6 to 96.3% at 10 DAG. Grouping according to the interspecific rootstocks showed that grafting on F_1(cmsTxSI) was the most successful (100.0% survival in all grafting stages) followed by F_1(cmsExSG) (100.0% at 5 DAG and 96.3% at 10 DAG). The lowest percentage of plant survival was recorded with F_1(cmsTxSG) (96.3% at 5 DAG and 88.9% at 10 DAG). Finally, hetero-grafted plants had very high overall survival rate (98.5% at 5 DAG and 94.1% at 10 DAG), similar to that of the self-grafted controls (100.0% and 96.3%, respectively) (Table 3).

Grafting success in the genus *Solanum* depends on the compatibility between the scion and the rootstock [36]. The results of the present work indicated that the genetic makeup of the interspecific rootstocks did not affect the post-grafting healing processes. This is further supported by the comparison with data from previous studies which employed a variety of commercial or experimental rootstocks. For example, Gisbert et al. [12] reported that the percentage of successful grafting of eggplant onto the wild species *S. incanum*, *S. aethiopicum*, *S. melongena* x *S. incanum* and *S. melongena* x *S. aethiopicum* was 100, 50, 80 and 100%, respectively. Further, in a two-year experiment Bletsos et al. [11] achieved somehow lower percentages of survival of eggplant seedlings grafted onto *S. torvum* (80.8 and 84.4%) and *S. sisymbriifolium* (77.2 and 74.8%). In another work, the average rates of successful grafting of eggplant cultivars onto *S. torvum* and *S. sisymbriifolium* were 92.8 and 89.5%, respectively [37].

3.2 Plant Productivity

In the present study early yield of the hetero-grafted plants was not significantly improved in comparison to the self-grafted control. In the grafting combinations of ‘Langada’, ‘Emi’ and ‘Tsakoniki’ the range for the number of early fruits per plant was 3.6-4.5, 2.6-3.9 and 3.1-5.3, respectively, and for the weight of early yield per plant was 0.7-1.22, 0.8-1.2 and 0.7-1.3 kg, respectively (Table 4). The only significant differences were observed between the combination ‘Tsakoniki’/F_1(cmsLxSI) which formed 3.1 early fruits weighing 0.7 kg, and ‘Tsakoniki’/F_1(cmsTxSI) and ‘Tsakoniki’/ F_1(ExSG) which produced 5.2 and 5.3 early fruits, respectively and yielded 1.0 and 1.3 kg, respectively (Table 4). Despite the non-significant differences, a positive trend in early yield was recorded in all scion/rootstock combinations involving F_1(cmsTxSI) and F_1(cmsExSG) and a negative trend in the combinations involving F_1(ExSI) and F_1(TxSG). Improvement of earliness is desirable as it ensures better prices for the producer. The inability to improve earliness *via* grafting may be due to the environmental factors of the present study (open field); Khah et al. [38] studied the effects of grafting on eggplant production and reported significant differences in earliness in the greenhouse environment but not in the open field. Although replication over years or environments could have detected potential genotype x environment interactions, it was previously shown that the ranking of different grafting treatments for early and total yield and fruit weight did not change over two years of experimentation [39].

Table 3. Percentage of plant survival (%) at 5 and 10 days after grafting (DAG) from self-grafted plants of the eggplant cultivars ‘Langada’, ‘Emi’ and ‘Tsakoniki’ and plants grafted onto five eggplant interspecific hybrids

Scion	Rootstock	No of grafted plants	Percentage of plant survival (%)	
			5 DAG	10 DAG
cv. ‘Langada’	cv. ‘Langada’	9	100.0	88.89
	F_1(cmsLxSI)	9	100.0	100.0
	F_1(cmsExSI)	9	100.0	88.89
	F_1(cmsTxSI)	9	100.0	100.0
	F_1(cmsExSG)	9	100.0	88.89
	F_1(cmsTxSG)	9	100.0	88.89
cv. ‘Emi’	cv. ‘Emi’	9	100.0	100.0
	F_1(cmsLxSI)	9	100.0	100.0
	F_1(cmsExSI)	9	100.0	88.89
	F_1(cmsTxSI)	9	100.0	100.0
	F_1(cmsExSG)	9	100.0	100.0
	F_1(cmsTxSG)	9	88.89	77.78
cv. ‘Tsakoniki’	cv. ‘Tsakoniki’	9	100.0	100.0
	F_1(cmsLxSI)	9	88.89	77.78
	F_1(cmsExSI)	9	100.0	100.0
	F_1(cmsTxSI)	9	100.0	100.0
	F_1(cmsExSG)	9	100.0	100.0
	F_1(cmsTxSG)	9	100.0	100.0
Grafting grouped according to scions				
	cv. ‘Langada’	54	100.0	92.59
	cv. ‘Emi’	54	98.15	94.44
	cv. ‘Tsakoniki’	54	98.15	96.30
Grafting grouped according to rootstocks				
	F_1(cmsLxSI)	27	96.30	92.59
	F_1(cmsExSI)	27	100.0	92.59
	F_1(cmsTxSI)	27	100.0	100.0
	F_1(cmsExSG)	27	100.0	96.30
	F_1(cmsTxSG)	27	96.30	88.89
	Total self-grafted	27	100.0	96.30
	Total hetero-grafted	135	98.52	94.07

In terms of total yield the effect of grafting onto the interspecific hybrids was more pronounced. Self-grafted ‘Langada’ set 8.8 total fruits per plant; whereas, ‘Langada’/F_1(cmsLxSI) set 11.8 total fruits (Table 4). In addition, ‘Langada’/ F_1(cmsLxSI) yielded in total 4.7 kg per plant outperforming the rest of the combinations of ‘Langada’ (2.5-4.0 kg). These values represent an increment of 34.0% for the number of total fruits and 54.0% for total yield with respect to the self-grafted ‘Langada’. Similarly, grafting ‘Emi’ onto the interspecific hybrids also affected total yield. While, on per plant basis, self-grafted ‘Emi’ set the fewest total fruits (6.2) and produced the lowest yield (2.6 kg); ‘Emi’/F_1(cmsExSG) produced the most of total fruits (9.8) and ‘Emi’/F_1(cmsTxSI) the highest yield per plant (4.2 kg). That corresponded to an increment of 57.0 and 60.0% over the control, respectively (Table 4). ‘Tsakoniki’/F_1(TxSI) was superior for the number of total fruits per plant (12.1) compared to the rest of the combinations of ‘Tsakoniki’ (8.1-10.0 fruits). However, significant differences for yield were observed only between the worst performing combinations of ‘Tsakoniki’ i.e. ‘Tsakoniki’/F_1(cmsLxSI) and ‘Tsakoniki’/ F_1(cmsTxSG) and the best performing one i.e. F_1(cmsExSG) (Table 4). Total yield per plant ranged from 3.1-3.3 kg in the hetero-grafted plants, while the control yielded 2.5 kg. Again, a more pronounced overall positive effect of F_1(cmsTxSI) and F_1(cmsExSG) on total production of all scions was noticed, while F_1(cmsLxSI) combined well only with ‘Langada’.

Preferably, the grafted plants should be more productive in order to compensate for their high cost. The positive effect of grafting on eggplant production could be attributed to the better intake of water and nutrients due to the vigorous root system of the rootstock [5,40]. Increased production of endogenous hormones from the rootstock may also account for the increased growth and yield of the grafted scion [40]. Since the interspecific hybrids produce these hormones to a greater extent [41], it is possible that scions grafted onto the interspecific rootstocks are exposed to higher levels of such hormonal stimuli. Post-grafting changes at the transcriptional level may also promote the vegetative growth of the scion as it was demonstrated in grapevine [42]. It is worth noting that in some scion/rootstock combinations the increment (in percent) in total yield was greater in comparison to the increment in the number of fruits (Table 4), probably due to the increased fruit weight (Table 5). Bletsos [5] also reported that grafting of ‘Tsakoniki’ onto *S. torvum* significantly increased total yield but not the number of fruits. Gisbert et al. [12] found that grafting eggplant on the interspecific hybrid *S. melongena* x *S. aethiopicum* had a positive effect on both yield and number of fruits.

F_1(cmsExSI) and F_1(cmsTxSG) were found to be less suitable as eggplant rootstocks. That was evidenced by the lack of significant improvement in scion yield, despite the fact that some negative effects were partially overcome at a later stage as indicated by total production measurements (Table 4). Perhaps, moderate performance of these rootstocks was caused by some kind of scion/rootstock incompatibility expressed after the healing process [43]. Similar moderate or poor performance was reported after using eggplant scions with the wild species rootstocks *S. habrochaites, S. incanum*, *S. aethiopicum*, *S. macrocarpon* and attributed to scion/rootstock incompatibility [12,16]. Grafting incompatibility is usually attributed to the low taxonomic affinity between the rootstock and the scion [43] and the consequent differences in tissue structure, physiology, biochemistry and rate of development [44]. However, the reduced compatibility observed here appears to depend more on the rootstock *per se* rather on the genetic affinity between the rootstock and the scion. This can be inferred by the fact that the ‘Emi’ performed well with the rootstock F_1(cmsTxSI) but not with F_1(cmsExSI), despite sharing half of its nuclear genome with the latter. Similarly, ‘Tsakoniki’ did not combine well with F_1(cmsTxSG), but performed well with F_1(cmsExSG) (Table 4). A possible explanation is that differences in the vigour of the scion and the rootstock result in incomplete union at the grafting surface and consequently in the reduced yield of the scion [36,44].

The results regarding plant productivity indicated that some interspecific rootstocks may combine well with a variety of scions e.g. F_1(cmsTxSI) and F_1(cmsExSG), while others may participate in a limited range of productive combinations e.g. F_1(cmsLxSI), which also holds true for other plant species [43]. These different trends may represent a kind of rootstock x scion (R x S) interactions which is worth studying in detail in future works. Such R x S interactions determine the positive or negative influence of the rootstocks on the performance and fruit quality of the scions [45]. Another note of interest is that the positive effects of F_1(cmsTxSI) and F_1(cmsExSG) followed diverse patterns among the eggplant scions. In particular, in 'Langada'/F_1(cmsTxSI) and 'Tsakoniki'/ F_1(cmsTxSI) the increase in total fruit number was more pronounced than the increase in fruit weight; while, the opposite was observed in 'Emi'/F_1(cmsTxSI). An inverted pattern was observed with F_1(cmsExSG) combined with the same scions (Table 4). These diverse patterns may also arise from the R x S interactions mentioned above. These results further support the opinion that newly developed rootstocks should be evaluated with as many scions as possible in order to identify the most productive combinations and to exclude the unfavourable ones [46,47].

3.3 Fruit Morphology

Fruit penducle length in self-grafted 'Langada' was 4.8 cm, significantly shorter than 'Langada'/F_1(cmsExSG) (6.6 cm) (Table 5). In addition, 'Emi'/'Emi' and 'Emi'/F_1(cmsTxSG) had significantly longer penducle (7.7 and 7.3 cm, respectively) than 'Emi'/'F_1(cmsLxSI) (5.6 cm). In 'Tsakoniki' fruit penducle length ranged from 5.4 to 6.0 cm with no significant differences (Table 5).

In the scion/rootstock combinations of 'Langada' the heavier fruits were recorded in 'Langada'/F_1(cmsExSG) (317.6 g) and the lowest in 'Langada'/F_1(cmsTxSI) (258.4 g); the former being significantly different from the self-grafted control (252.7 g) (Table 5). Also, the fruits of self-grafted 'Emi' weighed on average 309.9 g, while the hetero-grafted plants produced similar or heavier fruits (291.7-400.1 g) which were not significantly different from the control. However, 'Emi'/F_1(cmsTxSI) produced significantly heavier fruits in comparison to 'Emi'/F_1(cmsExSI) and 'Emi'/F_1(cmsExSG). Fruit weight of 'Tsakoniki' was apparently not affected by grafting and ranged from 191.2 to 221.3 g (Table 5). In eggplant the attributes of fruit morphology, such as size, shape and color, are genetically predetermined and characterized by a high degree of inheritance [48,49]. However, in this work grafting caused a variety of alterations in fruit morphology. These differences may be explained by the different degree of scion/rootstock compatibility. This is implied by the fact that combinations with indications of increased compatibility (increased number of fruits and yield), also had increased fruit weight and vice versa (Tables 4 and 5). In previous studies, increased fruit weight was reported in grafted eggplant [5,50,51] and tomato [14,52,53] and was attributed to the vigorous root system of the rootstocks. Conversely, a decrease in fruit weight of eggplant was observed with various rootstocks of low grafting compatibility [12]. A notable exception in the present work was the combination 'Emi'/F_1(cmsExSG), with increased total yield but decreased fruit weight (Tables 4 and 5). Perhaps, in that case the increased number of fruits resulted in a higher competition for photosynthetic assimilates and thus lower fruit weight.

Hetero-grafting also affected the dimensions of the fruit and each eggplant scion responded differently indicating a genotypic effect. 'Langada'/F_1(cmsExSI) and 'Langada'/ F_1(cmsExSG) produced fruits having length of 18.0 and 18.9 cm, respectively, significantly shorter with respect to 'Langada'/F_1(LxSI) (23.9 cm, Table 5). However, these differences were not significant in comparison to the control (21.4 cm). Also, no significant differences were observed in the grafting combinations of 'Emi' and 'Tsakoniki' for fruit length which ranged from 14.5 to 17.2 cm and 17.6 to 19.9 cm, respectively (Table 5). Fruit diameter ranged from 4.8 cm in 'Langada'/F_1(cmsExSI) to 6.8 cm in 'Langada'/ F_1(cmsExSG); the latter being significantly greater from the rest of the combinations. Fruits of 'Langada'/F_1(cmsExSG) also had significantly greater diameter/length ratio (0.37) which ranged from 0.24 to 0.28 in the rest combinations (Table 5). Furthermore, no significant differences were recorded in the graftings of 'Emi' and 'Tsakoniki' for fruit diameter which ranged 7.2 to 7.9 cm and 5.2 to 5.8 cm, respectively, and diameter/length ratio which ranged from 0.46 to 0.54 and 0.26 to 0.32, respectively (Table 5). Finally, no significant differences were recorded for the number of fruit calyx prickles which ranged from 0.6 to 2.2 in 'Langada', 1.0 to 2.9 in 'Emi' and 0.2 to 0.7 in 'Tsakoniki' (Table 5). A important note was that grafting 'Langada' onto F_1(cmsLxSI) and F_1(cmsExSG) affected a different dimension of the fruit (length and diameter, respectively; Table 5). Similar grafting-related changes in the dimensions of the fruit are frequently observed and were reported in various solanaceous species including eggplant [12,16,50], tomato [52] and pepper [19,54]. These alterations may be due to the different degree of vigour of the rootstocks [12], changes in the concentration of growth regulators [55] or grafting-induced epigenetic changes in the scion [19].

Table 4. Early and total number of fruits and yield weight (kg) per plant in self-grafted plants of eggplant cultivars 'Langada', 'Emi' and 'Tsakoniki' and plants grafted onto five interspecific eggplant hybrids

Scion	Rootstock	Early yield		Total yield	
		Number of fruits per plant	Yield weight (kg) per plant	Number of fruits per plant	Yield weight (kg) per plant
cv. 'Langada'	cv. 'Langada'	3.75±0.67[a,b]	0.95±0.20	8.75±1.26b	2.84±0.52b
	F_1(cmsLxSl)	4.38±0.56 (16.67)[c]	1.22±0.14 (28.90)	11.75±1.22a (34.29)	4.37±0.33a (53.77)
	F_1(cmsExSl)	3.63±0.80 (-3.33)	0.72±0.15 (-24.62)	8.00±0.82b (-8.57)	2.51±0.31b (-11.67)
	F_1(cmsTxSl)	4.50±0.33 (20.0)	1.14±0.08 (19.73)	10.50±0.85ab (20.0)	3.52±0.22ab (23.87)
	F_1(cmsExSG)	3.75±0.31 (0.0)	1.11±0.09 (17.37)	10.0±0.53ab (14.29)	3.96±0.30a (39.33)
	F_1(cmsTxSG)	3.71±0.97 (-0.95)	0.90±0.25 (-5.39)	8.57±0.84b (-2.04)	2.68±0.34b (-5.53)
cv. 'Emi'	cv. 'Emi'	3.0±0.37	0.96±0.09	6.22±0.32b	2.61±0.18b
	F_1(cmsLxSl)	2.63±0.60 (-12.50)	0.80±0.16 (-16.20)	7.63±1.07ab (22.55)	2.97±0.34b (13.63)
	F_1(cmsExSl)	3.25±0.37 (8.33)	0.94±0.11 (-1.42)	6.88±1.22ab (10.49)	2.81±0.50b (7.40)
	F_1(cmsTxSl)	2.89±0.56 (-3.70)	1.16±0.25 (21.09)	8.0±0.91ab (28.57)	4.19±0.28a (60.46)
	F_1(cmsExSG)	3.89±0.54 (29.63)	1.16±0.15 (20.92)	9.78±0.98a (57.14)	3.57±0.29ab (36.64)
	F_1(cmsTxSG)	2.75±0.31 (-8.33)	0.90±0.10 (-5.60)	7.0±1.10ab (12.50)	2.78±0.31b (6.21)
cv. 'Tsakoniki'	cv. 'Tsakoniki'	4.11±0.56ab	0.85±0.12b	8.22±1.04b	2.53±0.35ab
	F_1(cmsLxSl)	3.14±0.59b (-23.55)	0.68±0.13b (-20.28)	8.14±1.30b (-0.96)	2.30±0.23b (-8.85)
	F_1(cmsExSl)	3.63±0.46ab (-11.82)	0.77±0.15b (-9.97)	8.75±1.46b (6.42)	3.10±0.53ab (22.62)
	F_1(cmsTxSl)	5.27±0.62a (28.26)	0.97±0.11b (14.33)	12.09±0.99a (47.05)	3.18±0.24ab (26.03)

Scion	Rootstock	Early yield		Total yield	
		Number of fruits per plant	Yield weight (kg) per plant	Number of fruits per plant	Yield weight (kg) per plant
	F_1(cmsExSG)	5.22±0.55a (26.98)	1.31±0.10a (53.50)	10.0±0.74ab (21.60)	3.32±0.08a (31.44)
	F_1(cmsTxSG)	4.78±0.32ab (16.22)	0.87±0.06b (1.50)	9.33±0.78ab (13.51)	2.30±0.31b (-9.11)

[a]*Mean±Standard error.*

[b]*Comparisons were made separately for each scion group. Means followed by different letters in the same column differ significantly according to the Duncan's test (a=0.05).*

[c]*Difference (in percent) from the respective control is given in parentheses.*

Table 5. Quantitative morphological characteristics of the fruit in self-grafted plants of eggplant cultivars 'Langada', 'Emi' and 'Tsakoniki' and plants grafted onto five interspecific eggplant hybrids

Scion	Rootstock	Penducle	Fruit				
		Length (cm)	Weight (g)	Length (cm)	Diameter (cm)	Diameter/Length	Calyx prickles
cv. 'Langada'	cv. 'Langada'	4.79±0.61[a,b]	252.66±18.70ab	21.07±0.60abc	5.36±0.30ab	0.25±0.01a	0.71±0.36
	F_1(cmsLxSI)	5.87±0.32ab	286.34±13.62bc	24.50±0.73c	5.69±0.19ab	0.24±0.01a	1.60±0.43
	F_1 (cmsExSI)	5.44±0.48ab	212.58±11.22a	18.0±2.02a	4.66±0.36a	0.27±0.02a	1.13±0.58
	F_1 (cmsTxSI)	5.86±0.17ab	258.38±11.06ab	22.61±0.69bc	5.76±0.21bc	0.26±0.01a	1.57±0.59
	F_1 (cmsExSG)	6.61±0.25b	317.60±11.86c	18.72±0.83ab	6.79±0.23c	0.37±0.02b	2.22±0.57
	F_1 (cmsTxSG)	5.64±0.40ab	239.66±13.41ab	20.50±1.19abc	5.52±0.23ab	0.28±0.02a	0.64±0.20
cv. 'Emi'	cv. 'Emi'	7.70±0.37b	309.90±23.71ab	16.0±0.91	7.76±0.40	0.49±0.03	2.0±0.45
	F_1(cmsLxSI)	5.56±0.53a	300.22±15.91a	14.50±0.59	7.73±0.38	0.54±0.03	2.67±1.07
	F_1 (cmsExSI)	6.33±0.29ab	291.72±11.38a	15.11±0.48	7.29±0.39	0.48±0.02	2.22±0.49
	F_1 (cmsTxSI)	6.75±0.44ab	400.13±28.48b	17.21±0.70	7.91±0.28	0.46±0.02	2.92±0.68
	F_1 (cmsExSG)	6.27±0.23ab	333.22±24.08ab	14.92±0.49	7.24±0.17	0.49±0.02	1.77±0.56
	F_1 (cmsTxSG)	7.25±0.30b	314.11±15.78ab	15.69±0.82	7.68±0.34	0.50±0.03	1.0±0.38
cv. 'Tsakoniki'	cv. 'Tsakoniki'	5.46±0.26	202.38±8.46ab	19.92±0.57	5.32±0.16	0.27±0.01	0.69±0.36
	F_1(cmsLxSI)	5.96±0.24	210.69±10.12ab	19.65±0.77	5.17±0.14	0.27±0.01	0.30±0.21
	F_1 (cmsExSI)	5.58±0.32	221.32±17.18ab	19.50±1.19	5.76±0.33	0.32±0.04	0.42±0.26
	F_1 (cmsTxSI)	5.69±0.23	200.26±13.80ab	19.31±0.48	5.28±0.12	0.28±0.01	0.50±0.18
	F_1 (cmsExSG)	5.59±0.28	263.49±19.64b	19.71±1.09	5.27±0.10	0.28±0.02	0.18±0.10
	F_1 (cmsTxSG)	5.41±0.32	191.97±9.37a	17.61±0.60	4.95±0.15	0.26±0.02	0.21±0.11

[a]*Mean±Standard error.*

[b]*Comparisons were made separately for each scion group. Means followed by different letters in the same column differ significantly according to the Duncan's test (a=0.05)*

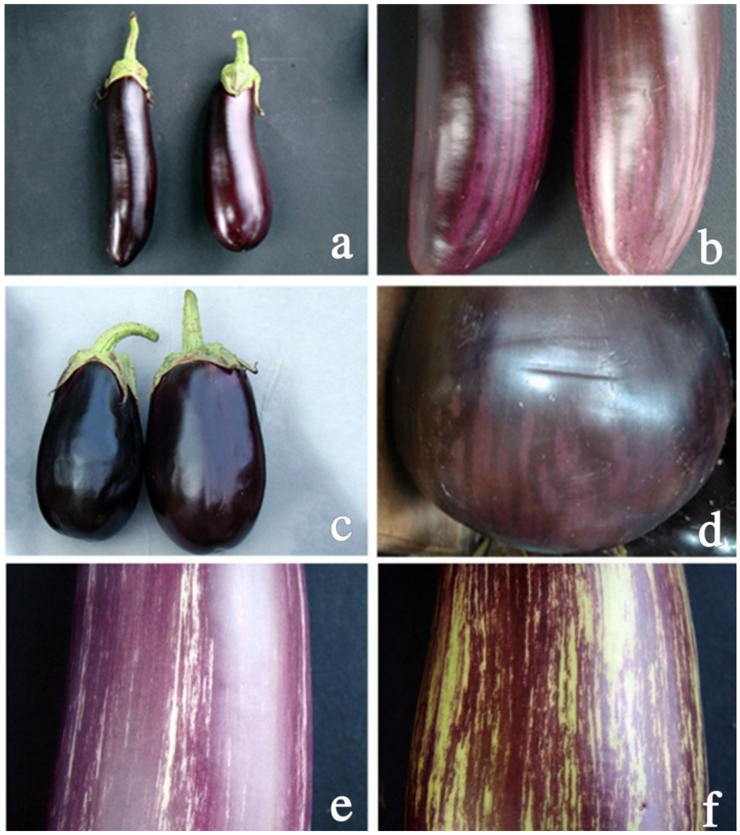

Fig. 1. Typical fruit in self-grafted 'Langada' (left) and club-shaped fruit in 'Langada'/F_1(cmsExSG) (right) (a). Fruit with stripes at post commercial maturity in 'Langada'/F_1(cmsLxSI) (b). Typical obovate (left) and obovate to ellipsoid (right) fruits in self-grafted 'Emi' (c). Fruit with stripes at post commercial maturity in 'Emi'/F_1(cmsExSI) (d). Typical fruit coloration with purple and white stripes in self-grafted 'Tsakoniki' (e) and fruit with purple and light green stripes in 'Tsakoniki'/F_1(cmsTxSI) (f)

Fruits in the grafted plants of 'Langada' had the typical dark purple color during commercial maturity (Tables 1 and 6, Fig. 1.a). However, at a later stage of ripeness a non-typical striped pattern was visible along the fruit surface in some combinations. These stripes were of lighter and darker shades of purple (Fig. 1.b). That pattern was present in all of the plants in 'Langada'/F_1(cmsTxSG) and at a lower frequency (3 : 8 or 4 : 9) in combination with other rootstocks. Interestingly, striped fruits were also observed in two self-grafted plants of 'Langada' (Table 6). Moreover, two plants in 'Emi'/F_1(cmsExSI) also had striped fruits at post-commercial maturity, which was not observed in the rest of the scion/rootstock combinations of 'Emi' (Table 6, Figs. 1.c and 1.d). In 'Tsakoniki', both the self- and hetero-grafting combinations had the typical fruit coloration with purple and white stripes (Tables 1 and 6, Fig. 1.e) with the exception of 'Tsakoniki'/F_1(cmsExSI) where three plants produced fruits with green and purple stripes (Fig. 1.f).

Fruit shape was also affected by grafting in 'Langada' and 'Emi'; however, only fruits with the typical shape was observed in 'Tsakoniki'. In particular, one plant in 'Langada'/F_1(cmsExSI) and two plants in 'Langada'/F_1(cmsTxSG) produced club-shaped fruits instead of the expected cylindrical shape (Tables 1 and 6, Fig. 1.a). Moreover, changes in fruit shape were also recorded in the grafting combinations of 'Emi' with the exception of 'Emi'/F_1(cmsExSG). Two self-grafted plants and one plant from 'Emi'/F_1(cmsLxSI) formed fruits having quite obovate to ellipsoid shape instead of the typical obovate (Tables 1 and 6, Fig. 1.c). However, the most frequent change observed in the fruit shape was the more elongated obovate observed after using the rootstocks F_1(cmsLxSI), F_1(cmsExSI), F_1(cmsTxSI) and F_1(cmsTxSG) with frequencies 1 : 9, 2 : 8, 1 : 9 and 2 : 7, respectively (Table 6).

It appears that some of the morphological changes in fruit shape and color observed in the present work were due to the grafting process itself. Such alterations are not unusual after self-grafting, despite the common genetic background of the scion and the rootstock [56]. These changes were observed in self-grafted 'Langada' and 'Emi', concerned different fruit characteristics and had a different incidence among the eggplant scions (Table 6), indicating a genotypic effect of the scion. Perhaps, 'Langada' and 'Emi' were more sensitive to the grafting process, while 'Tsakoniki' is more tolerant. Gisbert et al. [16] reported an irregular fruit cross-section in self-grafted eggplant, whereas, alterations in fruit phenotype were also observed in self-grafted tomato [57] and pepper [46]. In addition, the genetic background of the cultivars used here may also account for the segregation of these novel fruit phenotypes; 'Langada' and 'Tsakoniki' originated from local landraces via mass selection and thereby they can be considered as mixtures of inbred lines. Perhaps, some of the inbred lines that constitute each cultivar responded differentially in the grafting stress and produced the segregating phenotypes. In that case it would be possible to isolate lines that retain the original phenotype and lines that exhibit different phenotypes after grafting, an easy and rapid approach for diversification of fruit appearance in eggplant.

On the other hand, some alterations in fruit morphology were exclusively observed in the hetero-grafted plants, indicating an effect of the interspecific rootstock. These changes concerned fruit shape in 'Langada' and fruit color in 'Emi' and 'Tsakoniki' (Table 6, Fig. 1). It was interesting to note that the greater frequency of changes in fruit shape was observed in combination with the least productive rootsotcks (Tables 4 and 6). Hence, it is possible that the changes in fruit shape are another manifestation of a latent scion/rootstock incompatibility [16]. Nevertheless, the changes in the color of the fruit of 'Langada' and 'Emi' were evident at a post-commercial maturity stage and therefore are not considered as quality deteriorations.

Table 6. Color and shape characteristics of the fruit in self-grafted plants of eggplant cultivars 'Langada', 'Emi' and 'Tsakoniki' and plants grafted onto five interspecific eggplant hybrids

Scion	Rootstock	N[a]	Surface coloration		Fruit shape
			At commercial maturity	Post-commercial maturity	
cv. 'Langada'	cv. 'Langada'	8	UDP[b]	6 UDP : 2 DLPS	Cyl[c]
	F_1(cmsLxSI)	9	UDP	4 UDP : 5 DLPS	Cyl
	F_1(cmsExSI)	8	UDP	3 UDP : 5 DLPS	7 Cyl: 1 CS
	F_1(cmsTxSI)	9	UDP	4 UDP : 5 DLPS	Cyl
	F_1(cmsExSG)	9	UDP	4 UDP : 5 DLPS	7 Cyl: 2 CS
	F_1(cmsTxSG)	8	UDP	DLPS	Cyl
cv. 'Emi'	cv. 'Emi'	9	UDP	UDP	7 Ob: 2 ObE
	F_1(cmsLxSI)	9	UDP	UDP	7 Ob: 1 EOb: 1 ObE
	F_1(cmsExSI)	8	UDP	6 UDP : 2 DLPS	6 Ob: 2 EOb
	F_1(cmsTxSI)	9	UDP	UDP	8 Ob: 1 EOb
	F_1(cmsExSG)	9	UDP	UDP	Ob
	F_1(cmsTxSG)	7	UDP	UDP	5 Ob: 2 EOb
cv. 'Tsakoniki'	cv. 'Tsakoniki'	9	MPWS	MPWS	Cyl
	F_1(cmsLxSI)	7	MPWS	MPWS	Cyl
	F_1(cmsExSI)	9	MPWS	MPWS	Cyl
	F_1(cmsTxSI)	9	6 MPWS:3 MPGS	6 MPWS: 3 MPGS	Cyl
	F_1(cmsExSG)	9	MPWS	MPWS	Cyl
	F_1(cmsTxSG)	9	MPWS	MPWS	Cyl

[a]N=number of examined plants per scion/rootstock combination
[b]UDP=Uniform dark purple, DLPS=Dark and light purple stripes, MPWS=Medium purple and white stripes, MPGS=Medium purple and white stripes
[c]Cyl=Cylindrical, Cs=Club shaped, Ob=Obovate, ObE=Obovate to ellipsoid, EOb=elongated obovate

In ‘Tsakoniki’ the alterations in fruit color were probably caused by a different mechanism rather than scion/rootstock incompatibility as they were exclusively observed after grafting onto F_1(cmsTxSI) i.e. the best performing rootstock for that cultivar (Tables 4 and 6). The replacement of the typical white stripes by light green stripes in the affected plants was indicative of chlorophyll presence, which is a novel phenotype for ‘Tsakoniki’ (Fig. 1). In eggplant, fruit coloration depends on the concentration of pigments during fruit maturation, a process controlled by the coordinated regulation of biosynthetic and regulatory genes [58]. Novel color phenotypes including one with green and purple stripes were identified in the reciprocal backcross progenies of a ‘Black Beauty’ color mutant along with indications of complex genetic control [59]. Perhaps, in the grafted plants studied in the present study the regulation of pigment related gene network was altered due to grafting resulting in differentiated pigment formation and distribution on the fruit.

Some studies have progressed towards that direction of understanding the mechanisms underlying grafted-induced changes in fruit morphology. A possible explanation is that these changes occur through the mechanism of RNA silencing. The silencing signal is transported over long distances by siRNAs via the phloem tissue and affects gene expression at a remote point of the plant [18,60]. It is possible that silencing signals produced by the rootstock changed the gene expression of the scion resulting in altered phenotypes [61,62]. Recently, it was reported that DNA methylation in the leaves and fruits of grafted eggplant trended to vary in comparison to the non-grafted control [63].

4. CONCLUSION

The newly developed CMS-based interspecific hybrids were proved highly compatible rootstocks for the three eggplant cultivars used as scions. A differential response to grafting was observed in the scions comprising both significant positive and non-significant positive and negative effects on early and total yield. Also, both self-grafting and grafting on certain rootstocks caused changes in fruit morphology of the scion and these alterations were distinct for each scion/rootstock combination. From a practical point of view, F_1(cmsTxSI) and F_1(cmsExSG) are the most promising rootstocks, because of their high grafting compatibility and excellent performance in combination with all of the eggplant scions. F_1(cmsLxSI) performed well only with ‘Langada’ and could be evaluated with eggplant cultivars or F_1 hybrids of similar phenotype. Finally, F_1(cmsExSI) and F_1(cmsTxSG) are of limited value because they were the less productive rootstocks and caused more changes in the morphology of the fruit. The fact that these interspecific hybrids are easily produced by utilizing CMS eggplant lines renders them as materials of potential commercial interest. In our recent research, the selected rootstocks continue to be evaluated in various environments (open field and greenhouse) and in combination with more eggplant cultivars and F_1 hybrids. The effect of these rootstocks on the composition and nutritional value of the eggplant fruit should also be studied. Finally, an introgression breeding program is planned in order to transfer fusarium wilt resistance from the interspecific rootstocks to susceptible Greek eggplant cultivars.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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