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The effect of grafting on pollen fertility and seed production of diploid interspecific hybrid and tetraploid eggplant genotypes

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Abstract: *Solanum melongena* is susceptible to diverse diseases and parasites, in particular the wilts (bacterial, *Fusarium* and *Verticillium*), nematodes, and some insects. *Solanum torvum* is robust to *Verticillium* and some bacterial wilts and root-knot nematode. It was reported that interspecific hybrid plants originated out of the hybridization of these species were sterile. In our previous studies that have been carried out to overcome this interspecific hybridization barrier, only from Faselis F_1 that was used as the female parent, many interspecific hybrid seeds were obtained and 9.07% of the seeds grew into plants in vitro. The percentage of pollen viability and germination of tetraploid interspecific hybrid (amphidiploid) genotypes that have been produced by in vitro colchicine treatment, were 6.8 and 3.4 fold of its source diploid genotype, respectively. However, the increment was not high enough to overcome the interspecific hybridization barrier between *S. torvum* and *S. melongena*. In this study, the changes in pollen fertility of diploid interspecific hybrids and tetraploid plants, which have grafted on Pala or Faselis F_1, were investigated. Pollen viability and germination percentage in diploid genotypes were not affected by grafting, although they increased significantly (51.54% and 119.73%, respectively) in tetraploid genotypes by grafting. It was determined that the fertile diploid rootstock used for the tetraploid genotypes that produced by chromosome doubling from cultured eggplants could increase the number of seeds per fruit. It was concluded that some fertile diploid varieties can be used as rootstocks in order to increase pollen viability, germination rate and seed yield of tetraploid genotypes with low pollen yield obtained from cultivated eggplant by chromosome doubling.

Key words: Rootstock, *Solanum melongena*, *Solanum torvum*, pollen germination, pollen viability, seed formation

1. Introduction

Solanum melongena L. (cultivated eggplant) is a member of the *Solanaceae* family and is one of the Old World species. Eggplant, whose homeland is India, is cultivated in temperate and tropical Asian countries and worldwide today (Daunay, 2008). With an average production of 846, 466 t between 2016 and 2020, Turkey is the country that produces the most eggplant after China (~34.52 million t, India (~12.65 million t), and Egypt (~1.3 million t) in the world (FAO, 2022). In accordance with the data in 2021 approximately 31.8 million t of vegetables are produced in Turkey. Eggplant has a share of 832,938 t in this production (TUIK, 2022). In this context, eggplant is an important vegetable in Turkey. Cultivated eggplant is sensitive to many diseases and pests, such as wilts (bacterial, *Fusarium* and *Verticillium*), nematodes, and some insects (Osman et al., 2018). It is stated that *Solanum torvum* Sw. (wild eggplant) is robust to wilt (*Verticillium*, bacterial) and root-knot nematode (Yang et al., 2014). It has been reported that the plants obtained from the crossing of *S. torvum*, which has many resistance features, and *S. melongena* has been sterile or self-incompatible (Collonnier et al., 2003; Çürük and Dayan, 2018; Daunay et al., 2019). In a study, when 'Faselis F_1' (*S. melongena*) and *S. torvum* were crossed, pollen viability was found to be 92.93% in Faselis F_1, 43.84% in *S. torvum*, and between 0% and 3.01% depending on the genotype of the interspecific hybrid genotype (Çürük and Dayan, 2018). In addition, pollen germination rates were determined as 70.18%, 35.74%, and 0.0%–1.36% in Faselis F_1, *S. torvum*, and the hybrids obtained from "Faselis F_1 × *S. torvum*", respectively. Fruit could not be obtained as a result of the backcrossing of the interspecific hybrid plants with the pollen of *S. torvum* or Faselis F_1. Besides, the ratios of pollen viability and germination of the amphidiploid plant were greater than its origin diploid plant (Çürük and Dayan, 2018). Also, the flowers of the amphidiploid plant produced more pollen than the flowers of their diploid plant. Although the percentage of

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pollen viability (3.10%) and germination (1.97%) of this amphidiploid genotype were 6.8 and 4.3 times higher than the source genotype, respectively, the hybridization barrier has not been overcome.

Since grafting or budding is widely used for vegetative propagation of plants, intensive research has been carried out on the subject and significant knowledge has been gained. However, according to Liu et al. (2010), gene transmission between rootstock and scion by grafting/budding is not well-known. Liu et al. (2010) have reported that Darwin (1868) specified diverse cases in which the shoots of fruit tree scion which was grafted onto a rootstock, displayed features of scion and rootstock. According to the authors, Darwin reports that this change is related to a molecule termed 'gemmules', that transmits freely between the cells of rootstock and scion and transfers inheritable material which can self-replicate. Unfortunately, these views of Darwin were generally accepted as wrong, since it was thought that there was no exchange of genetic material between the rootstock and the scion. For more than a hundred years, the changes that occur at the graft point have been defined as a kind of chimera. And the chimeric plants have been considered as plants consisting only of a mixture of cells or tissue carrying different genetic material, without any exchange of genetic material between the rootstock and the scion. It has been reported that the reaction of the scion to the day length, and the rate of male/female flower formation, were affected depending on the rootstock used in cucurbits (Takahashi et al., 1982). Then, it has been stated that the pollen production of heat susceptible tomatoes increased compared to the nongrafted ones, at high temperatures (37/27 °C), when it grafted on a rootstock of eggplant (Abdelmageed and Gruda, 2009). Therefore, the flower-related characteristics of the plant may change with the use of rootstock.

In this investigation, the variations in pollen fertility and seed production in consequence of grafting of hybrids (*S. melongena* × *S. torvum*), autotetraploid and amphidiploid eggplant genotypes with low fertility onto fertile eggplant cultivars 'Pala' or Faselis F_1, were studied.

2. Material and method

2.1. Material

A total of 4 genotypes namely 2 diploid hybrids (Au2/I-6, Au4/I-10) of 'Faselis F_1 and *S. torvum*', 1 autotetraploid (Kol53) and 1 amphidiploid (U4/IV-I-4), were used as scions in the study. The autotetraploid Kol53 genotype was produced by in vitro application of 0.05% colchicine to Faselis F_1 buds, and amphidiploid U4/IV-I-4 genotype was obtained by in vitro application of 0.03% colchicine to the buds of 'Faselis F_1 × *S. torvum*' hybrid (Çürük and Dayan, 2018). These diploid and tetraploid genotypes were cultivated in a temperature-controlled greenhouse. Eggplant cultivars, Pala and Faselis F_1 were used as rootstock. After the seeds of the genotypes were pregerminated at 30 °C, germinated seeds were planted in 0.5 L pots with a mixture of peat and perlite (2:1) and grown in the greenhouse.

2.2. Production of ungrafted seedlings and grafted plants

It is not possible to propagate the interspecific diploid and tetraploid genotypes to be used in the experiment by seed due to low pollen production and sterility. Therefore, nongrafted seedlings of the sterile genotypes were propagated by cuttings in order to increase the number of plants and flowers, to obtain enough pollen in order to examine the viability and germination status of pollens of these sterile interspecies hybrids.

The buds/scions of diploid and tetraploid genotypes were grafted on fertile diploid rootstocks, Pala and Faselis F_1, that were planted and cultivated as mentioned above. Grafted plants were grown in the temperature-controlled greenhouse.

2.3. Planting and cultivation conditions

The grafted and nongrafted seedlings were planted on September 2013, in 5 L plastic pots filled with a mixture of peat and perlite (2:1) and cultivated in the greenhouse. When these seedlings reached a certain size, the plants were transferred to 16 L plastic pots containing the same mixture and these pots were placed in the heated glasshouse at 0.9 m between the row and 0.5 m between plants within the row. The plants were irrigated by drip irrigation system or hand watering when the irrigation was necessary according to the plant and peat/perlite mixture moisture content observations in the pots. The applied $N:P_2O_5:K_2O$ were 250:75:300 kg ha^{-1} in total. Humidity and temperature values in the greenhouse were measured and recorded with a data logger (HOBO U14) every 30 min. Average relative humidity and temperature in the glasshouse were 58.19% and 22.08 °C, respectively, during cultivation.

2.4. Investigated parameters

The viability of the pollen was determined by TTC containing 6% sucrose and 1% of 2,3,5 triphenyl tetrazolium chloride, and its germination was carried out by the agar method. Pollens were germinated in glass Petri dishes at 25 ± 1 °C in media containing 50 mg L^{-1} boric acid, 5% sucrose, and 1% agar (Khan and Isshiki, 2008). Since the amphidiploid U4/IV-I-4 genotype did not flower sufficiently, pollens were taken only from the flowers of Au2/I-6 and Au4/I-10 (interspecific diploid) and Kol53 (tetraploid) on 14–15 May 2014 and on 24–25 May 2014. These pollens were viewed almost 5 h after they were incubated at 22 °C in TTC or on a germination medium, under a light microscope. Viability and germination ratios (%) were figured out by examining, total of 200 pollen from each genotype in 4 replicates (approximately 50 pollens × 4 replicates). Since pollen viability and germination rate of Kol53 from tetraploid individuals were higher than other genotypes, selfing was done on May 20–23, 2014. Furthermore, pollens of this genotype were used for crossing the flowers of another amphidiploid genotype (U4/IV-I-4). Since the viability and germination ratios of pollen of diploid interspecific hybrid plants were very low, they were not used as paternal. The flower buds of the Kol53 genotype used as the maternal were emasculated 12–24 h before the petals opened and then closed. Besides, 12–24 h after this process, the female organs of the maternal were pollinated with the pollen of the paternal, and the flower petals were closed again. The number of pollinated flowers at the beginning, flowers setting fruit, and the fruit-setting rate (%) was determined approximately 1 week after hybridization.

The fruit weight (g), width (cm), and length (cm) were determined when the fruit ripened. Fruits were harvested when they matured, and the seeds were fermented with fruit juice for 1 week, then the number of seeds in the fruit was counted.

2.5. Statistical analysis

The experiment was carried out according to a completely randomized design and the data were analyzed accordingly (Bek and Efe, 1989). In each application, 3 replicates and 2 (ungrafted Kol53) or 3 plants were used per replicate. Pollen viability and germination experiments were performed in 4 replicates, with approximately 50 pollens per replicate. Data that were expressed as a percentage, were angular transformed (Bartlett, 1947) for variance analysis. The means were compared at the 5% significance level according to the Honestly Significant Difference (Tukey's HSD) test when the treatments were found significant by the variance analysis. Data were back-transformed for the presentation of the means.

3. Results

3.1. Pollen viability and germination

Pollen viability was calculated by considering only red-stained, and pink plus red-stained pollens in TTC, and the average values obtained from two experiments of these characteristics of diploid genotypes are given in Table 1. According to the analysis of variance with average data of two experiments conducted on different dates, as no red-stained or germinated pollen was observed, there was no effect of rootstock and diploid scion genotypes on these variables. When the pollen viability was determined based on pink plus red-stained pollen, the 'rootstock × scion' interaction was significant. Accordingly, 1.63% pink-stained pollen was determined in the nongrafted Au4/I-10 genotype propagated by cuttings. However, these pink-stained pollens did not germinate.

Pollen viability and germination means obtained from the tetraploid genotype Kol53 are presented in Table 2. According to the average of two TTC tests, based on red staining, performed on different dates, 51.54% higher pollen viability was detected in grafted compared to ungrafted plants. Although higher viability was determined depending on pink plus red staining, the same statistical groups were detected. With respect to pollen germination rate, Kol53 genotype grafted on Pala showed 119.73% higher germination than nongrafted one. However, when Faselis F_1 was used as rootstock, the difference between grafted and ungrafted Kol53 in terms of pollen germination was not significant.

3.2. Selfing and hybridization of grafted tetraploid plants

Kol53 tetraploid genotype grafted on Pala or Faselis F_1, which has high viability and germination rate according to pollen TTC and germination tests was selfed. Also, it was used as a paternal partner for the crossing of the amphidiploid U4/IV-I-4 genotype, which is ungrafted or grafted on the same rootstocks. The results are given in Table 3. Fruit setting did not occur in 17 crosses made by crossing of the U4/IV-I-4 genotype grafted onto Pala or Faselis F_1 or ungrafted, using pollens of Kol53 genotype grafted on the same rootstocks. However, when flowers of Kol53 grafted onto Pala were pollinated with the pollens of Kol53 grafted on Faselis F_1 or vice versa, the fruit set was 100.00%. Besides, when 7 and 9 flowers of Kol53 grafted onto Pala and Faselis F_1

Table 1. The average values of pollen viability and germination ratios (%) obtained from two experiments carried out on two different dates (14–15 May 2014 and 24–25 May 2014) in diploid genotypes.

Rootstock	Genotype	Red stained pollen viability (%)	Pink plus red stained pollen viability (%)	Pollen germination (%)
Pala	Au4/I-10	0.00	0.00[b]	0.00
Pala	Au2/I-6	0.00	0.00[b]	0.00
Faselis F_1	Au4/I-10	0.00	0.00[b]	0.00
Faselis F_1	Au2/I-6	0.00	0.00[b]	0.00
Ungrafted	Au4/I-10	0.00	1.63[a]	0.00
Ungrafted	Au2/I-6	0.00	0.00[b]	0.00

The difference among values in a column followed by same letters is not significant by Honestly Significant Difference test ($p \leq 0.05$).

Table 2. The average values of pollen viability and germination ratios (%) obtained from two experiments performed on two different dates (14–15 May 2014 and 24–25 May 2014) in tetraploid genotype, Kol53, ungrafted or grafted on Pala or Faselis F_1 eggplant cvs.

Rootstock	Red stained pollen viability (%)	Pink plus red stained pollen viability (%)	Pollen germination (%)
Pala	60.05^{a}	66.03^{a}	10.62^{a}
Faselis F_1	59.21^{a}	62.53^{a}	7.05^{ab}
Ungrafted	39.35^{b}	44.75^{b}	4.90^{b}

The difference among values in a column followed by same letters is not significant by Honestly Significant Difference test ($p \leq 0.05$).

Table 3. In tetraploid genotypes, the flower number used in pollination or selfing, fruit setting (%), fruit characteristics, and seed formation.

Maternal genotype	Paternal genotype	Number of pollinated flowers	Number of flowers set fruit	Fruit setting (%)	Number of developed fruit	Average fruit weight (g)	Average fruit diameter (cm)	Average fruit length (cm)	Number of seeds per fruit
U4/IV-I-4 grafted onto Pala	Kol53 grafted onto Pala or Faselis F_1	6.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
U4/IV-I-4 grafted onto Faselis F_1	Kol53 grafted onto Pala or Faselis F_1	6.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ungrafted U4/IV-I-4	Kol53 grafted onto Pala or Faselis F_1	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kol53 grafted onto Pala	Kol53 grafted onto Faselis F_1	3.00	3.00	100.00	3.00	85.02	4.73	7.60	3.00
Kol53 grafted onto Pala	Kol53 grafted onto Pala	7.00	7.00	100.00	6.00	141.42	4.87	13.10	4.67
Kol53 grafted onto Faselis F_1	Kol53 grafted onto Pala	4.00	4.00	100.00	4.00	139.56	4.10	14.10	0.25
Kol53 grafted onto Faselis F_1	Kol53 grafted onto Faselis F_1	9.00	8.00	88.89	7.00	152.07	4.66	14.27	0.00

(respectively) were selfed, the fruit set was 100.00% and 88.89% (average 94.45%). The average weight and length of the fruits formed from the pollination of the flowers of Kol53 grafted onto the Pala with pollens of Kol53 grafted on Faselis F_1 were lower than the fruits obtained from other pollination combinations. When the flowers of Kol53 grafted onto genotypes Pala or Faselis F_1 were used as a pollen source, it was determined that an average of 4.11 seeds formed in each fruit (37 seeds from 9 fruit) of Kol53 grafted onto Pala. On the other hand, when flowers of Kol53 grafted on Faselis F_1 were pollinated with the same pollen source, an average of 0.09 seeds formed per fruit (1 seed from 11 fruit). According to the T-test, the difference between these two means was found to be significant (t (18) = 2.42, p = 0.026). It can be interpreted that the use of Pala as rootstock may give a better result than Faselis F_1, in terms of seed setting.

4. Discussion

In our study, it was observed that rootstock and scion had no effect on red-stained pollen viability and germination rate in interspecific diploid genotypes (Table 1). This result supports the findings of the study conducted by Kombo and Sarı (2019) in watermelon grafted onto *Cucurbita* rootstock. Kombo and Sarı (2019) reported that the rootstock, NUN-9075 (*Cucurbita maxima* × *Cucurbita moschata*), did not significantly change the pollen viability and germination rate of the fertile Crimson sweet watermelon cultivar compared to the control. The results obtained from the diploid interspecific hybrid genotypes regarding pollen fertility in our study indicated that substances such as water, nutrients, plant growth regulators, protein, and/or genetic material that can increase pollen viability of the scion were not sufficiently transferred from diploid fertile rootstocks to sterile diploid interspecific genotypes. As a matter of fact, it has been reported in some studies that protein and/or mRNA are transported with various substances from the rootstock to the scion and these transported substances change the scion characteristics (Gómez et al., 2005; Kudo and Harada, 2007; Davis et al., 2008; Rasool et al., 2020). Moreover, it has been reported that sterility in genotypes obtained by hybridization of *S. melongena* with *S. torvum* species is virtual sterility (pollen stainability < 5%) (Plazas et al., 2016; Çürük and Dayan, 2018; Daunay et al., 2019). It can be suggested that the failure of overcoming the sterility may be due to using the limited number of interspecific genotypes in grafting, or it may not be easy to overcome such a high sterility by grafting on fertile genotypes. Thus, more diploid interspecific hybrid genotypes should be tested by grafting on different fertile eggplant varieties. As a matter of fact, Dayan and Çürük (2022) reported that pollen viability and germination rates of some interspecific diploid genotypes which grafted onto some rootstocks with higher pollen fertility, increased significantly, while some genotypes did not change significantly.

In the study with the tetraploid Kol53 genotype, it was observed that pollen viability and germination rate increased significantly in grafted plants compared to ungrafted ones, especially when the Pala was used as rootstock (Table 2). These results are compatible with the results of Abdelmageed and Gruda's (2009) study in eggplant, but not compatible with Kombo and Sarı's (2019) study in watermelon. The reason why the Pala cultivar used as a rootstock in our study significantly increased pollen viability and germination rate may be due to the fact that Pala is a stronger growing cultivar (Çürük et al., 2009; Dayan and Çürük, 2022). It may stem from the transfer of water, mineral matter, plant growth regulator, protein, and/or mRNA-like substances, which may increase the pollen fertility of the scion by forming stronger vascular bundles connections between the Pala and tetraploid Kol53 (Gómez et al., 2005; Kudo and Harada, 2007; Davis et al., 2008; Rasool et al., 2020). In addition, since the tetraploid Kol53 genotype was obtained by chromosome doubling of the Faselis F_1 cultivar, the substances that came from the rootstock may not be very different when it was grafted on Faselis F_1. However, when this tetraploid genotype is grafted onto a fertile cultivar that has a different genetic structure, such as Pala, it can be concluded that the pollen viability and germination rate of the scion may increase, since various compounds, which are uptaken from rootstock to scion. As a matter of fact, Abdelmageed and Gruda (2009) reported that the high-temperature sensitive tomato cultivar grafted onto eggplant produced a higher amount of pollen per flower under high-temperature conditions (37/27 °C) compared to the nongrafted one and tomato cultivar grafted on the tomato rootstock.

It was observed that grafting combinations used in grafted tetraploid genotypes had a positive effect on fruit set and seed production (Table 3). Çürük et al. (2009) reported that the Pala formed more vigorous plants compared to Faselis F_1, and when grafted on a vigorous rootstock such as *S. torvum*, it produced taller plants compared to Faselis F_1. Therefore, the Pala cultivar is thought to be compatible with the Kol53 genotype grafted onto it, resulting in higher seed formation by supporting vigorous growth and providing various compounds (plant growth regulators, protein, mRNA, etc.) and increasing pollen yield. Lardizabal and Thompson (1990) reported that grafting and some plant growth regulators used in potatoes increased the number of seeds, and Kombo and Sarı (2019) stated that NUN-9075 rootstock had a similar effect in watermelon. However, Khah (2011) reported that one species of tomato used as rootstock for eggplant reduced the number of seeds obtained from the fruit in glasshouse conditions, while another species did not. In light of this information, it is possible to state that grafting affects the number of seeds depending on the rootstock/scion combination used.

5. Conclusion

Grafting (on fertile Faselis F_1 and Pala cultivars) in 2 interspecific diploid genotypes did not affect pollen viability and pollen germination. But, the Pala cultivar used as rootstock significantly increased both pollen viability and germination rate in the tetraploid Kol53 genotype. Grafting of the sterile amphidiploid U4/IV-I-4 genotype and of the tetraploid Kol53 genotype that has high pollen viability onto diploid fertile Faselis F_1 and Pala cultivars did not enable hybridization of these genotypes. Furthermore, when the tetraploid Kol53 genotype grafted on diploid fertile cultivars was pollinated in various combinations, a very high fruit set was achieved, but the number of seeds in the fruits was low. However, grafting the tetraploid Kol53 genotype onto Pala increased the number of seeds formed in the fruit compared to the grafting ones on Faselis F_1. In the study, it was concluded that some fertile diploid varieties can be used as rootstocks in order to increase pollen viability, germination rate, and seed yield of tetraploid genotypes with low pollen yield produced from cultivated eggplant by chromosome doubling.

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