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GRAFTING COMPATIBILITY, SCION GROWTH, AND FUSARIUM WILT DISEASE INCIDENCE OF INTRASPECIFIC GRAFTED TOMATO

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ABSTRACT

The tomato (*Solanum lycopersicum* L.) is one of the most important vegetables grown globally. However, the production of tomatoes is restricted by *Fusarium oxysporum* f. sp. *lycopersici* (Fol). This study aims to investigate the ability of Fol-resistant tomato genotypes to be a rootstock for the susceptible cultivar. In this study, a tomato cultivar was grafted on rootstocks of the same species (intraspecific), and grafting compatibility, peroxidase gene expression, and fusarium wilt disease incidence of tomato scion was evaluated. A Fol-susceptible tomato 'Sidathip 3' (SDT3) was grafted onto four different Fol-resistant tomato genotypes and compared with self-grafted cultivar/cultivar and rootstock/rootstock. The survival rate of all grafted plants was 100% at 20 days after grafting (DAG) without significant differences in incompatibility evaluated at 42 days after grafting. The expression of the peroxidase gene (*Solyc02g084800.2*) using the qPCR technique was compared in self-grafted rootstock LE472/LE472 and SDT3/LE472. The expression level was three times higher in heterografted plants than in self-grafted ones at 15 DAG, indicating graft incompatibility. The rootstocks did not affect the height of the plant, the number of branches, the size of the fruit, or the yield of SDT3 scion. All intraspecific heterografted plants significantly controlled Fol when evaluated 60 days after inoculation. These results showed the usefulness of intraspecific grafting by using the proper rootstock genotypes to increase pathogen resistance in addition to stimulating growth and fruit yield.

Key words: Fol control, grafting compatibility, peroxidase, tomato rootstock resistance, *Solanum lycopersicum*

INTRODUCTION

The tomato (*Solanum lycopersicum* L.) is one of the most important vegetable species worldwide. However, tomatoes can be affected by pests and pathogens, including viruses, bacteria, fungi, and nematodes, resulting in annual yield losses (Bai & Lindhout 2007; Vitale et al. 2014). The biotrophic fungus *Fusarium oxysporum* f. sp. *lycopersici* (Fol) is the causal agent of vascular wilt disease in tomatoes. Disease symptoms appear initially in the lower leaves, followed by the wilting of the plants. When Fol penetrates tomato plants, it colonizes and blocks vascular tissues, causing browning and chlorosis of the leaves. The continued infection of Fol can cause the whole plant to wilt, collapse, and die, resulting from the accumulation of fungal mycelia in the vascular system, mycotoxin production, and repression of the host defense mechanism (Srinivas et al. 2019; Chitwood-Brown et al. 2021).

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Several strategies to control Fol include cultural, biological, and chemical control, as well as host resistance, which is the most effective (Chitwood-Brown et al. 2021). Among the host-resistant strategies, grafting is an optional method that uses resistant genotypes as rootstock for susceptible scions (Kubota et al. 2008; Guan et al. 2012).

Grafting combines the desired characteristics of the scion and the rootstock, providing a rapid alternative method to classical breeding or transgenesis (Spanò et al. 2020). The desired rootstock should be compatible with the scion genotype and able to survive under unfavorable conditions, including abiotic and biotic stress (Louws et al. 2010). There have been several reports indicating that promising rootstocks can improve the agronomic traits of scions. For example, interspecific tomato rootstocks effectively increased fruit quality, contents of bioactive compounds, and yield of the high-value 'Corbarino' tomato landrace scion (Parisi et al. 2022). Plant growth, yield, and fruit physicochemical properties of eggplant scions showed better performance when grafted on the wild related rootstock of eggplant (Musa et al. 2021). Zhang et al. (2021) reported that tomato grafting with nitrogen use efficiency (NUE) rootstock improved nitrogen absorption and utilization and increased yield production at different nitrogen levels. The grafting of fresh-market tomato cultivars on *Ralstonia solanacearum*-resistant eggplant rootstocks showed a decreased wilting percentage and disease index. The yield of grafted tomatoes was higher than that of nongrafted and self-grafted tomatoes, but did not affect the quality of the fruit (Manickam et al. 2021). Similar research by Reyad et al. (2021) on grafted cucumbers found a significant decrease in fusarium wilt severity and improved plant growth. Resistant rootstocks exhibited an increase in the activity of peroxidase and polyphenol oxidase enzymes.

Successful grafting and graft-enhancing plant performance depend on the interaction and the level of compatibility between scion and rootstock, which may affect the formation of the graft union (Tedesco et al. 2022). Rootstock and scion that are genetically related will have increased graft success (Pina & Errea 2005; Zeist et al. 2018; Li et al. 2021).

Previously, we tested tomato germplasm for Fol resistance and found four tomato lines resistant to Fol (Thanyasiriwat et al., unpublished). These genotypes had the potential to be used as rootstocks for grafting. Therefore, this study aimed to evaluate scion growth, grafting compatibility, and Fol prevention of the intraspecific grafted tomatoes using the combination of Fol-resistant tomato rootstocks and SDT3, a susceptible tomato scion.

MATERIALS AND METHODS

Plant materials and growth condition

The experiment was conducted in a greenhouse condition. Four tomato accessions, LE314, LE472, LE482, and LE501, selected previously from tomato germplasm in the Tropical Vegetable Research Center (TVRC), Kasetsart University, Kamphaeng Saen Campus for their resistance to Fol race 1, were used as rootstocks (RS). A susceptible tomato cultivar, 'Sidathip 3' (SDT3), was used as a scion (SC). This cultivar is a table tomato fruit type with a small fruit size of 3 × 4 cm. The fruit weight is more than 20 g. The seeds of all Fol-resistant tomato accessions were sown directly into 50-cell plug trays filled with a ready-to-use mixture of the substrate (Kekkilä Professional, Finland). Eight days later, the seeds of SDT3 were sown similarly. The 21-day-old seedlings at the three- to four-true-leaves stage were transferred to a 6 × 8-inch plastic pot with a soil mixture (with topsoil and ready-to-use soil mixture 2 : 1 by volume). All seedlings were grown in a greenhouse for 30 days under the natural sunlight and temperature of 30–33 °C/25–28 °C (day/night). Seedlings were watered once a day.

Grafting procedure

Thirty days after germination, the susceptible SDT3 cultivar (SC) was grafted onto four Fol-resistant accessions, LE314, LE472, LE482, and LE501 (RS), using the cleft grafting method. The grafted plants were covered with transparent plastic to avoid water loss and grown in the greenhouse for two weeks. The grafted plants were watered

twice daily and supplemented with 20 g of dry pelleted fertilizer with N-P-K of 15-15-15 weekly until the 30-day. The experiment included intraspecific heterograft (SDT3/LE314, SDT3/LE472, SDT3/LE482, and SDT3/LE501) and self-grafted tomato plants SDT3/SDT3 and LE472/LE472). The plant survival rate (SR) evaluation and Fol inoculation detailed below were performed at 20 days after grafting (DAG). Evaluation of grafting compatibility was taken at 21, 28, 35, and 42 DAG. The samples of grafting points were collected at 4 and 15 DAG for gene expression analysis.

Grafting compatibility and scion growth measurements

Grafting compatibility was evaluated by measuring the diameter of the grafting point (GP), the scion (SC), and the rootstock (RS) at 1 cm above and below the grafting point using the formula (Zeist et al. 2018): GI = {[(GP − RS) + (GP − SC)/2] + (RS − SC)}/2.

The plant survival rate was calculated at 20 DAG as a percentage of surviving plants relative to the total number of grafted plants. The plant height (PH), measured from the base of the scion stem to the apex (cm), and the number of branches (NB) were evaluated at 21, 28, 35, and 42 DAG. The size of the fruit and fruit yield were evaluated at 45 DAG.

Peroxidase gene expression analysis

1 cm-long stem samples were collected at the grafting point of LE472/LE472 and SDT3/LE472 at 4 and 15 DAGs. Total RNA was extracted using TRIzol reagent (Invitrogen). The synthesis of complementary DNA (cDNA) was carried out using a 2-step RT-PCR Kit (Vivantis, Malaysia). Expression of the peroxidase gene was performed by qPCR. The primer sequences for the peroxidase gene (*Solyc02g084800.2*) were 5′-TTTGTTGAGGCTCCATTTCC-3′ and 5′-TTTGTGGGCATTCTTTCTCC-3′ (Wang et al. 2019). The selected primers of the housekeeping baseline gene, 18S rRNA (X51576), were 5′-GGGCATTCGTATTTCATAGTCAGA-3′ and 5′-GTTCTTGATTAATGAAAACATCCT-3′ (Mascia et al. 2010).

Two-fold serial dilutions were performed using cDNA from a representative sample to generate standard curves and threshold values (C_T) for a housekeeping gene (18S rRNA) and the gene of interest. A standard curve-based calculation method was used to estimate the efficiency of the primer with the following equation: Efficiency (%) = $[10^{(-1/\text{slope})} - 1] \times 100$. For gene expression analysis, the cDNA template was diluted to a 1 : 2 concentration. The real-time PCR reaction used in both the efficiency test and the analysis of gene expression was performed with the PCR mixture containing 1 µl of the diluted cDNA, 5 µl of 2X SensiFast SYBR NO-ROX mix (Meridian Bioscience), and 0.4 µl each of 10 µM Primer-F and Primer-R. The reaction of PCR was performed in triplicate for each cDNA sample, along with no template control in parallel to each gene. All reactions were processed in PCRmax ECO 48 REAL TIME PCR PLATE (PCRmax). The PCR reaction was performed in PCRmax Eco 48 real-time PCR (PCRmax). The 2-step cycle of the PCR condition consisted of enzyme activation at 95 °C for 2 min, followed by 40 cycles of denaturation at 95 °C for 5 s and annealing/extension at 60 °C for 20 s. The dissociation curve analysis was performed after 40 cycles to identify the presence of primer dimers and analyze the specificity of the reaction. The 18S rRNA gene was used as an internal control. The C_T data of homo- and heterografted tomatoes at each time point obtained from peroxidase gene amplification were normalized with those from 18S rRNA to give the relative gene expression. The fold changes in the target gene and the normalized to 18S rRNA samples, relative to homograft samples (LE472/LE472) at 4 or 15 DAG, were calculated for each sample using the $2^{-\Delta\Delta C_T}$ (Livak & Schmittgen 2001) method described previously (Mascia et al. 2010).

Fusarium wilt disease-resistant evaluation

The grafted and nongrafted plants at 20 DAG were inoculated with a suspension of spores from the Fol isolate TFPK401 race 1 in the concentration of 1×10^6 spore per ml using the root dip method.

The mock-inoculated plants were treated with autoclaved distilled water to serve as controls. The inoculated plants were transferred to 6 × 8 inch plastic pots with autoclaved and watered before transplantation. SDT3 (nongrafted) was used as a susceptibility control. The tested plants were grown in a greenhouse condition with natural sunlight. The disease severity score (DSS) and disease index (DI) were adopted from Marlatt et al. (1996) with some modifications. Symptoms were scored at the vegetative stage using a five-grade severity scale, with (1) denoting symptomless, (2) chlorotic plants, (3) chlorotic plants and wilting, (4) wilting plants, and (5) plant death. Disease scoring was recorded at 60 days post-inoculation (DPI) with SDT3 (nongrafted) as a susceptibility control, and disease symptoms were shown on a scale of 5. The DI was calculated using the following formula: $DI = [(ni \times si)/(N \times S)] \times 100$, where ni – number of wilting plants, si – disease severity score, N – total number of tested tomatoes, and S – highest disease severity score.

Experimental design and statistical analysis

The experiment was carried out using a completely randomized design (CRD). 10 biological replicates were used for measuring and evaluating the plant survival rate (SR), grafting compatibility, and Fol resistance. All data collected were subjected to analysis of variance (ANOVA) using Statistix 8.0. Means were compared using Tukey's mean comparison test ($p = 0.05$).

RESULTS

Grafting compatibility between scion and rootstocks

The percentage of successful grafting was observed after 20 DAG in intraspecific self-grafted tomatoes (SDT3/SDT3) and heterografted tomatoes (SDT3/LE314, SDT3/LE472, SDT3/LE482, and SDT3/LE501). In both graftings, 100% plant survival rate was observed. The rootstocks were compatible with the SDT3 scion genotype and demonstrated that the grafting condition was performed favored healing without interfering in the formation of the graft union (Fig. 1). There was an increase in GI in all grafted tomatoes ranging from 0.06–0.08 to 0.11–0.14 in the course of 21–42 DAG, but these differences did not differ significantly until 42 DAG, although self-grafted plants showed a slightly lower GI than heterografted ones (Table 1).

The intraspecific and interspecific grafting did not affect scion growth and fruit yield

The height of the scions of the self-grafted and heterografted genotypes grew consequently with time but did not differ significantly within term points (Fig. 2A). A similar pattern was observed in the number of branches (Fig. 2B). The average fruit size ranged from 2.75–3.27 cm × 3.17–3.66 cm and fruit yield ranged from 141.90 to 160.48 g per plant, showing no significant differences between grafting components (Table 2).

The expression of the peroxidase gene (*Solyc02g084800.2*) was upregulated in heterografted tomato

The relative expression of the peroxidase gene was analyzed in self-grafted LE472/LE472 and heterografted SDT3/LE472 at 4 and 15 DAG. The expression of the SDT3/LE472 sample increased threefold and was significantly higher than that of LE472/LE472 at 15 DAG (Fig. 3).

The influence of intraspecific rootstocks on the resistance against Fol

The results showed that all intraspecific rootstocks significantly reduced symptoms of fusarium wilt disease at 60 days post-inoculation. The heterografted plants showed a DSS of 1 and 0% of disease index (DI), compared to a self-grafted and nongrafted SDT3 showing 5 DSS and 100% DI (Fig. 4).

Figure 1. Successful grafting and graft union (white arrow) indicate the grafting compatibility between scion and different rootstock accessions at 42 DAG

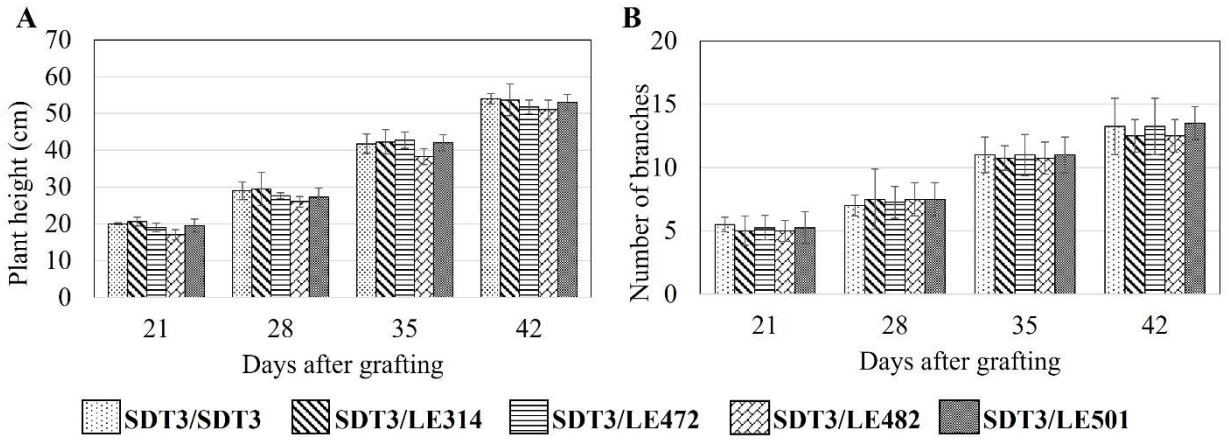

Figure 2. Plant height (A) and the number of branches, (B) of scion SDT3 grafted on SDT3 (self-grafted), and heterografted (SDT3/LE314, SDT3/LE472, SDT3/LE482, and SDT3/LE501)

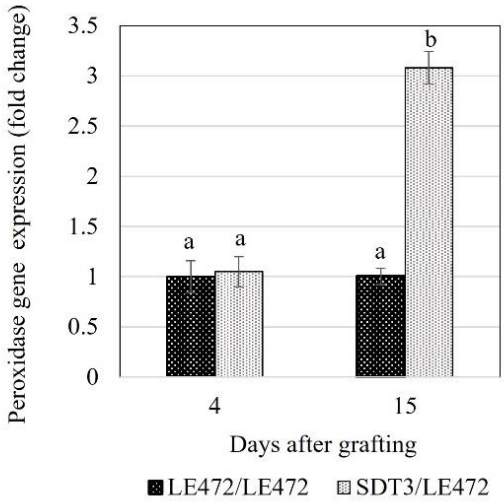

Figure 3. Expression level of peroxidase (*Solyc02g084800.2*) gene in self-grafted (LE472/LE472) and heterografted (SDT3/LE472) tomatoes at 4 and 15 DAG. The data were normalized using 18S rRNA gene to give the relative gene expression (mean ± SD), different letters above the bar are significantly different (p = 0.05), according to Tukey's test

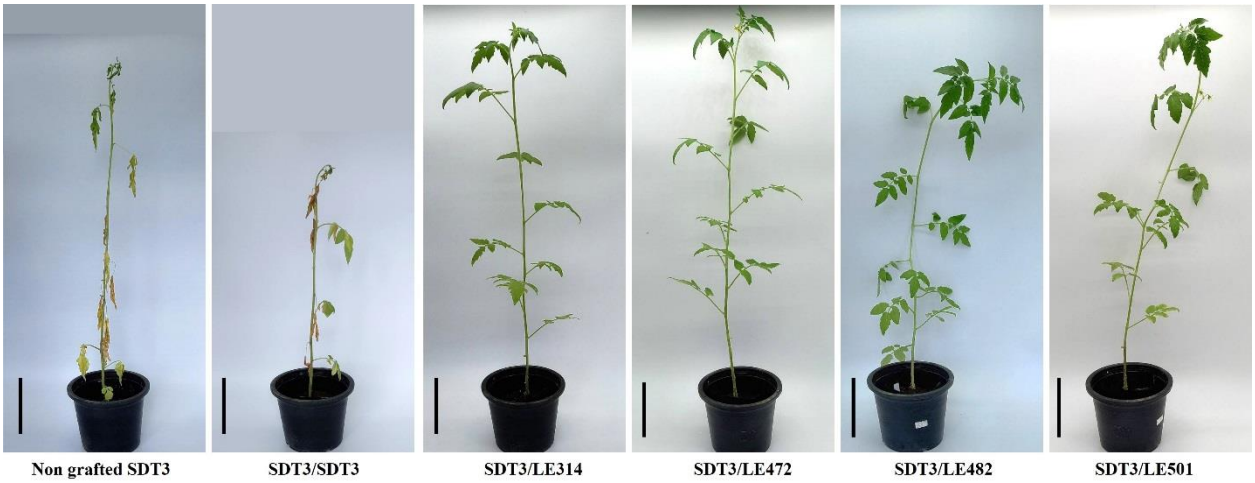

Figure 4. The disease symptoms of mock- and Fol-inoculated nongrafted SDT3, self-grafted (SDT3/SDT3), and heterografted (SDT3/LE314, SDT3/LE472, SDT3/LE482, and SDT3/LE501) at 60 DPI. The nongrafted and self-grafted SDT3 showed a DSS of 5. All heterografted tomatoes showed a DSS of 1 (scale bars = 10 cm)

Table 1. The grafting incompatibility (mean ± SD) between scion, SDT3, and four tomato rootstock accessions measured 21, 28, 35, and 42 DAG

Scion/rootstock combination	Days after grafting			
	21	28	35	42
SDT3/SDT3	0.06 ± 0.02	0.07 ± 0.01	0.09 ± 0.02	0.11 ± 0.00
SDT3/LE314	0.07 ± 0.01	0.07 ± 0.02	0.09 ± 0.00	0.14 ± 0.03
SDT3/LE472	0.08 ± 0.00	0.08 ± 0.01	0.11 ± 0.01	0.15 ± 0.03
SDT3/LE482	0.08 ± 0.00	0.10 ± 0.01	0.10 ± 0.02	0.12 ± 0.02
SDT3/LE501	0.08 ± 0.01	0.09 ± 0.00	0.11 ± 0.01	0.13 ± 0.02
F	ns	ns	ns	ns
CV (%)	16.91	16.84	15.65	20.79

F – the probability of F statistic from ANOVA, ns – nonsignificant differences

Table 2. Fruit size (cm) and yield (g per plant) of scion SDT3 grafted on different tomato rootstocks

Scion/rootstock combination	Fruit size (cm)		Fruit yield (g per plant)
	width	length	
SDT3/SDT3	2.95 ± 0.6	3.29 ± 0.5	151.73 ± 6.7
SDT3/LE314	3.01 ± 0.2	3.47 ± 0.2	157.36 ± 6.5
SDT3/LE472	3.27 ± 0.1	3.66 ± 0.1	160.48 ± 8.3
SDT3/LE482	3.27 ± 0.1	3.58 ± 0.2	156.25 ± 0.5
SDT3/LE501	2.75 ± 0.1	3.17 ± 0.2	141.90 ± 17.7
F	ns	ns	ns
CV (%)	9.77	9.39	7.08

F – the probability of F statistic from ANOVA, ns – nonsignificant differences

DISCUSSION

Successful grafting and graft-inducing plant behavior can depend on the interaction and the level of compatibility between the scion and the rootstock, which may or may not form a graft union (Tedesco et al. 2022). Our study showed 100% successful graft compatibility in both self-grafted and heterografted tomatoes, similar to the Zeist et al. (2018) report. The above authors reported that the intraspecific and self-grafts showed high compatibility, resulting in a high photosynthetic efficiency compared to grafting with other Solanum species. Moreover, when applied as rootstock, mini tomato transferred resistance to bacterial wilt to scions without changing fruit production. Kawaguchi et al. (2008) investigated graft incompatibility in solanaceous plants with varying graft combinations, including tomato, eggplant, and pepper. The results indicated that only tomato/tomato graftings were properly fused; scions were able to properly transfer assimilates, water, and minerals; and fruit production was not affected.

A previous report suggested that peroxidases play a role in lignification (Fernández-García et al. 2004). The peroxidases encoded by multigene families have been studied in many plant species (Quiroga et al. 2000). It was suggested that the cell wall-targeted peroxidase *TPX1* gene was involved in synthesizing lignin and suberin in tomato roots and aerial parts. Lignin is required for cell wall thickening, and the gene for lignin metabolism is expressed in grafted tissues (Xie et al. 2019). The last step in lignin synthesis is the oxidation of cinnamyl alcohols catalyzed by peroxidase. Total peroxidase activity increased in the xylem of grafted plants during stem development (Fernández-García et al. 2004) and wound healing (Yang et al. 2022). Fernández-García et al. (2004) observed a high level of lignin in tomato scions, which was correlated with the increase of peroxidase activity in the graft union. Wang et al. (2019) reported that the oxidative stress genes associated with ROS scavenging, such as peroxidases *Solyc02g084800* and *Solyc10g076240,* were upregulated, and *Solyc02g092580* was downregulated in heterografted tomatoes at 16 DAG. Our experiment found a similar result in the expression of the peroxidase gene (*Solyc02g084800.2*) that was upregulated in heterografted tomato (SDT3/LE472) at 15 DAG compared to the self-graft plant (LE472/LE472). Assunção et al. (2019) reported that oxidative stress genes, including polyamine oxidase, glutathione S-transferase, galactinol synthase, and peroxidases, were expressed with higher levels in the graft union of heterografted grapevine than in the self-grafted plants. Studies have shown the measurement of antioxidant enzymes at the graft union of different scion/rootstock combinations. The results indicated that the peroxidase activity in microcalli culturing in suspension (incompatible scion) was relatively higher than those of the pear control suspension (Nocito et al. 2010). In addition, the activity of peroxidase at the graft interface of incompatible grafts in *Prunus* spp. 4 and 8 months after grafting was higher than that of compatible grafts (Zarrouk et al. 2010).

The use of resistant tomato rootstocks in grafting is an effective strategy to control a wide range of soilborne pathogens: fungal and oomycete, bacterial, and nematode (Guan et al. 2012). The resistance mechanism between tomato and Fol has been investigated, indicating that the R genes conferred resistance to Fol, namely the *I* family (immunity) gene, including *I*, *I2*, *I3*, and *I7*. The host–pathogen interaction is cultivar/race specific (Srinivas et al. 2019; Chitwood-Brown et al. 2021). The rootstocks of selected tomato genotypes used in this study showed resistance to Fol race 1 and possibly were recognized by tomato accessions governing the *I* gene that had been incorporated from wild tomato *S. pimpinellifolium* (Gonzalez-Cendales et al. 2016; Prihatna et al. 2018). Specific combinations of genotypes within *Lycopersicon esculentum* applied as rootstock/stem are beneficial not only to building a rootstock-induced systemic defense against several soil pathogens but also for increase of vegetative growth, yield and fruit quality increase (Rivard & Louws 2008).

CONCLUSION

In this experiment, we suggested that selected tomato genotypes used as rootstocks are an excellent choice for the prevention of infection caused by Fol. The use of an intraspecific tomato/tomato graft combination was more advantageous over interspecific grafts, due to higher graft success and compatibility. In addition, the scion growth and yield production were similar to the self-grafted and nongrafted tomatoes. Taking into consideration from the literature that success in using resistant rootstocks for grafting susceptible cultivars depends on a specific combination of both genotypes, we advise experimentally testing the grafted plants for Fol protection under high disease pressure in field conditions.

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Disclosure statement

The authors declare no conflict of interest.

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