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Research Papers

Deciduous fruit trees and grapevines as alternative crops in *Demathophora necatrix* (syn. *Rosellinia necatrix*) infested soils

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Summary. White root rot, caused by *Dematophora necatrix* (syn. *Rosellinia necatrix*), affects deciduous trees. A *D. necatrix* infection-distribution survey found widespread disease in apple and cherry orchards in northern Israel bordering a Mediterranean forest, although the forest trees were unaffected. Because cherry and apple orchards must be abandoned due to long fungal survival in infested soils, alternative deciduous fruit trees and grapevines were assessed for growth in these *D. necatrix*-infested orchards. In the field, grapevine rootstocks and the almond–peach rootstock GF-677 were most tolerant to *D. necatrix*-infested soil. Apple was the most sensitive crop, with the rootstock Hashabi being more tolerant than PI80 or MM104. The Mediterranean forest tree *Pistacia atlantica*, which can serve as a rootstock for pistachio, was as sensitive as kiwifruit and apple, and persimmon rootstock sensitivity was not different from grapevine. Those results show that beside the above mentioned crops, vineyards can also replace apple orchards in *D. necatrix*-infested soils and so broadens the list of possible crops for the local farmers in a Mediterranean climate at altitudes above 440 m above sea level. This has also been observed in a commercial 10-year-old vineyard of 'Shiraz' grapevines grafted on SO4 rootstock. The almond-peach rootstock GF-677 can also be grown in infested soil, but in commercial orchards requires additional treatment for adequate disease control.

Keywords. Apple rootstock, GF-677 almond–peach rootstock, grapevine rootstock, tolerant crops.

INTRODUCTION

The disease white root rot is caused by the ascomycete fungus *Dematophora necatrix* Hartig, (syn. *Rosellinia necatrix*). *Dematophora necatrix* is a soilborne pathogen that has been reported to infect 170 plant species from 30 families, including deciduous trees (apple, pear, plum and almond), olives, some citrus species, avocado, mango and macadamia (Pliego *et al*., 2011). Development of this disease occurs in sensitive trees, where the roots become covered with white mycelium and decay, the leaves turn yellow and fall, and the affected trees wither and die soon after symptom appearance. In Israel, apple and cherry orchards are mostly affected (Dafny-Yelin *et al.*, 2018). Infected trees do not recover and must be uprooted. Replacement of the infected trees in apple or cherry orchards where the soils are infested is not possible, so the land must be abandoned for production of these fruit.

In Japan, grapevine is considered to be very sensitive to *D. necatrix* infection (Arakawa *et al.*, 2002), but the plants can overcome infections with the use of fungicides (Kanadani *et al.*, 1998). In Israel, grapevines became infected after inoculation with *D. necatrix*, but in naturally infested soil under field conditions, no plants became infected (Sztejnberg and Madar, 1980).

Tolerance to white root rot has been shown in the apple rootstocks M7 and MM109 (Gupta and Verna, 1978). In addition, SangBum *et al.* (2000) showed that a *Malus sieversii* seed lot was resistant to a Korean *D. necatrix* isolate, where 32 out of 159 clones of *Malus* germplasm exhibited slow development of *D. necatrix* infections or had no necrotic symptoms. In avocado plants, Zumaquero *et al.* (2019) characterized expression of different genes in tolerant and susceptible avocado rootstocks.

In Israel, Sztejnberg *et al.* (1983) reported that persimmon was survived for 6 years in *D. necatrix* infested soil, without any signs of disease symptoms. Citrus and mango rootstocks, and *Passiflora edulis*, were also tolerant to the disease (Sztejnberg and Madar, 1980). Most of the infested soils in Israel are in the northern part of the country, at altitudes 440-1100 m above sea level (Dafny-Yelin *et al.*, 2018). This area is suitable for deciduous fruit trees and grapevines, but not for citrus or mango.

An infection-distribution survey by Dafny-Yelin *et al.* (2018) showed that white root rot was widespread in plots bordering a Mediterranean forest, but the infections did not appear to harm the trees in that forest. From farmer viewpoints, *Pistacia atlantica*, which grows in these forests, can be used as a rootstock for pistachio (Picchioni *et al.*, 1990).

The present research aimed to identify alternative crops that could be grown in *D. necatrix*-infested soils to broadens the list of possible crops for the local farmers.

MATERIALS AND METHODS

Plant material

The following rootstocks and crops were tested:

(i) apple rootstocks Hashabi 13-14, Malling Merton series MM104, MM109 and MM106, and PI80 from Pillnitzer 'Supporter' (a semi-dwarf apple rootstock from Pillnitz in Dresden). All apple plants were 2 years old at planting day, and was obtained from the Tesler Nursery, Moshav Nov, Israel, except for the apple plants in the Metula plot that were not grafted and were only 1 year old at planting day.

(ii) GF-677 rootstock, a peach–almond hybrid which can be used as a rootstock for almond and peach, was obtained from plant nurseries in Rosh HaNikra, Israel, and was 1 year old at planting day.

(iii) grapevine rootstocks 101-14 MGT, 110 Richter, 1103 Paulsen, 140 Ruggeri and SO4 (*Vitis labrusca*), all grafted with Cabernet Sauvignon (*Vitis vinifera*). Grapevine plants were 6 months old, from the Machmid Nursery in Umm al-Fahm, and the Dor-onn and Zimnavoda Nursery in Zikhron Ya'akov, Israel.

(iv) persimmon rootstocks *Diospyros virginiana* and *Diospyros lotus* were from Haskelberg Nursery, Kfar Vitkin, Israel, and were 2 years old.

(v) *Actinidia deliciosa* (kiwifruit) var. Hayward (not grafted, self-rooted) 1-year-old plants from Fuga Agricultural Marketing Ltd., Yesud HaMa'ala, Israel.

(vi) *Pistacia atlantica* forest trees (not commercial rootstocks), 1-year-old plants from KKL Nursery, Golani junction, Israel.

Resistant fruit crops and grapevines in naturally infested plots

Experimental plots were chosen based on the presence of dead apple trees with typical *D. necatrix* mycelia in the roots. Experimental trees were planted between the orchard trees (except in Mas'ada where the entire plot was replanted). During the years of the experiment, the nearby orchard trees (or the trees between the experimental trees) were also monitored for indication of active disease (data not shown).

The field experiment included five plots. These were:

(1) Cabernet Sauvignon vines grafted on five rootstocks, including 101-14 MGT, 110 Richter, 1103 Paulsen, 140 Ruggeri, and SO4, planted in Metula orchards (Lat. 35.569, Long. 33.278, altitude of 442 m above sea level) in June 2013 (distribution map presented in Supplementary Figure 1);

(2) mainly non-grafted rootstocks, including —GF-677 (used for peach and almonds), Hashabi 13-14 (for apples), persimmon rootstocks *D. virginiana* and *D. lotus*, and *P. atlantica*, along with self-rooted kiwifruit var. Hayward, planted in Metula next to plot (1) (above) in July 2013 (Supplementary Figure 2);

(3) grapevines, fruit and forest trees grown together, with the plant material the same as in Metula

(above) with one exception. Hashabi 13-14 apple rootstock was grafted with var. Starking (Scarlet-spur type). The experiment was planted in Mas'ada (Lat. 33.237, Long. 35.780, 1034 m above sea level) in March 2013 (Supplementary Figure 3);

(4) apple tree var. Sundowner was grafted on the five different apple rootstocks, including Hashabi, MM106, MM109, PI80, MM104 from Tesler Nursery, and was planted in Manara orchard (Lat. 33.187, Long. 35.543, 848 m above sea level) in March 2018. The fungicide Ohayo (a.i. 0.5% fluazinam) was applied on the day of planting, at the rate of 2 L of 5 g L^{-1} Ohayo per tree via irrigation (as recommended in Dafny-Yelin *et al*., 2019). Two additional applications of the fungicide were applied at 1.5 and 2.5 months after planting (Supplementary Figure 4);

(5) similar experiment to (4) (above), planted in Sasa orchard (Lat. 33.022, Long. 35.400, 830 m above sea level) in March 2018, with the following exceptions: (i) the apple tree variety was Cripps Pink , (ii) to give the trees in Sasa the good establishment conditions, soil solarization was carried out in the summer of 2017, a year before planting. Ohayo fungicide was applied on the day of planting and one additional application was applied 2.5 months after planting (Supplementary Figure 5).

The grapevines were trained vertically and pruned each year. The weight of pruned tissues from each plant was measured as an index of plant vigour. For the other plant species, trunk circumferences were measured as indices of plant vigour. In Mas'ada in the last year of experiments, grapevine yield parameters were measured at harvest. For the other crops, trunk circumferences and tree heights (except for kiwifruit and grapevine) were measured in each plot in the last experimental year. For all plants, in April to November, viability was recorded using the following key: 0 = dead plant, 1 = weak plant, 2 = healthy plant with no new vegetative growth, or 3 = healthy plant with normal development. Daily areas under the viability curves (AUC) were calculated based on ca. 20 monitoring times, at least five per year at minimum intervals of 1 month.

All experiments were planted in randomized blocks, in five (1st and 3rd plots) or six (2nd, 4th and 5th plots) replicates, except for *P. atlantica* in the 1st plot that was planted in six replicates, and 101-14 MGT and 110 Richter grapevine rootstocks that were planted in seven replicates. Plots 1 to 3 were planted in May 2013. Most replicates contained five trees, except for GF-677, which had four trees per replica. The trees were planted 0.5 m apart. Plots 4 and 5 were planted in March 2018. Each replica consisted of at least three trees (except for PI80 which had one tree in one of the replicas), and trees were planted *ca*. 1.5 m apart.

Statistical analyses

ANOVA and Pearson's chi-squared test for contingency analysis were carried out using JMP 13 software (SAS Institute, 2016). The statistical significance of treatment effects was determined using honestly significant difference (HSD), at $P \leq 0.05$, or Student's t-test [least significant difference (LSD), $P \leq 0.05$] for pairs. Normality (Shapiro–Wilk or Anderson–Darling tests) and homoscedasticity (Levene's test) of the results with or without square-root or Log+1 transformations were the conditions ($P > 0.05$) for running the ANOVA test; otherwise, non-parametric contingency analysis was performed. Where specified, Bonferroni corrections were applied to correct the critical alpha level, due to multiple chi-squared tests conducted. Effects of experimental blocks were also evaluated to estimate *D. necatrix* infection and aggressiveness in the orchards. In the apple rootstock experiment, contingency analysis was conducted only between the Hashabi–PI80 and Hashabi–MM104 pairs.

RESULTS

Comparisons between fruit crops and grapevines in naturally infested soils

To find potential alternative crops for farmers, and to give them the best alternatives based on farm geographical locations, comparisons between fruit crops and grapevines were made on two farms located in different geographical regions: (i) Metula in the Galilee region at 442 m above sea level, and (ii) Mas'ada in the Golan Heights at 1034 m above sea level. In the naturally infested soil in Mas'ada (Figure 1A), there were statistically significant differences between the crops in the number of wilting trees at the end of the experiment ($\chi^2 = 82.7577$, $P < 0.0001$), and no effect of block was detected ($\chi^2 = 10.7023$, $P = 0.0301$).

Almond and grapevine were the most resistant plants, with, respectively, 96.0% and 86.4% of plants still viable 5 years after planting. Almond was more tolerant than apple ($\chi^2 = 35.507$, $P < 0.0001$), kiwifruit ($\chi^2 = 18.015$, $P < 0.0001$), *P. atlantica* ($\chi^2 = 18.075$, $P < 0.0001$) and persimmon ($\chi^2 = 8.567$, $P = 0.034$). Persimmon plants showed 72.2 and 53.3% survival with *D. virginiana* and *D. lotus* rootstocks, respectively. Apple rootstocks were the most sensitive, with only 12% of the

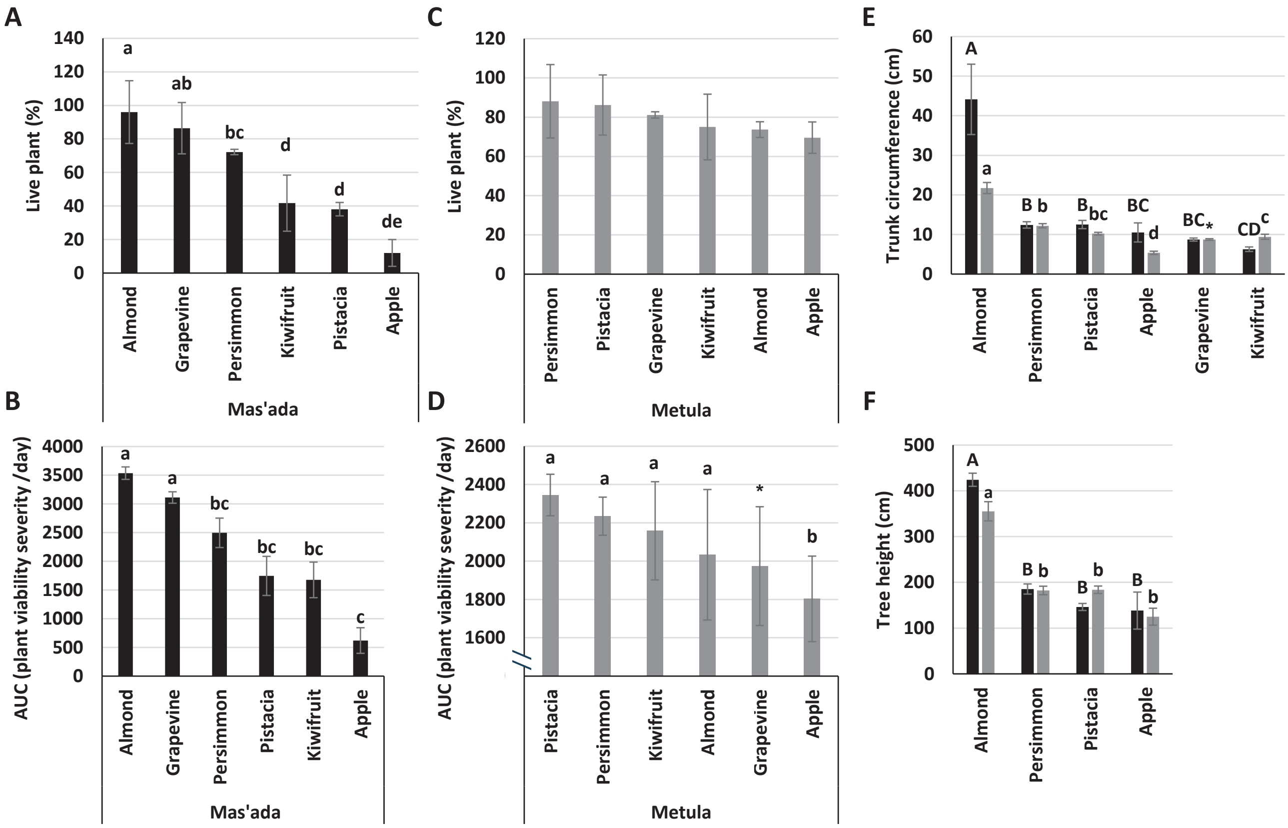

Figure 1. Mean parameters in *Dematophora necatrix*-infested soil for Mas'ada and Metula plants. (A) Percentage of live 5-year-old trees and (B) areas under the curves (AUC) for plant viability (0 = dead plant to 3 = live plant with good growth) over time (by days) in Mas'ada. Different letters indicate statistically significant differences ($P < 0.01$) between crops, as shown from contingency analyses, and Pearson tests after Bonferroni corrections, for 15 comparisons. (C) Mean percentages of live 3-year-old trees, and (D) mean AUC in Metula. Different letters accompanying the means indicate statistically significant differences ($P < 0.05$) between crop types, as indicated by contingency analyses, and Pearson tests without Bonferroni corrections. (E) Mean trunk circumferences of surviving trees. Black bars, Mas'ada plots; different uppercase letters indicate differences ($P < 0.05$) between crops as indicate from contingency analyses and Pearson tests after Bonferroni correction, for 15 comparisons. Gray bars, Metula plots; different lowercase letters indicate differences ($P < 0.05$) indicated from HSD after Log+1 transformations. (F) Mean tree heights. Black bar, Mas'ada plot; different letters indicate differences ($P < 0.05$) shown from HSD, after square root transformations. Gray bar, Metula plot; different letters indicate differences ($P < 0.05$), shown from contingency analyses, and Pearson tests after Bonferroni corrections, for six comparisons. Asterisks indicate that grapevines in Metula were not taken into consideration in the statistical analyses because they were planted in a separate plot nearby.

plants surviving after 5 years. Plant survival of *P. atlantica* and kiwifruit were, respectively, 38.1 and 40.0%, with no significant difference ($P > 0.05$) compared to the apple Hashabi rootstock (Figure 1A). AUC for plant viability per day gave statistically significant differences among crops ($\chi^2 = 88.9121$, $P < 0.0001$). Apple trees had the smallest AUCs, and almond and grapevine had the greatest, indicating that they were less sensitive than persimmon, *Pistacia*, kiwifruit and apple (Figure 1B).

In the Metula experiment the number of live apple plants was lowest (69.6%; Figure 1C), the number of live persimmon plants was highest (88.1%), while 26.3% of almonds and only 4.0% of Mas'ada plants were wilted. There was no significant difference ($\chi^2 = 4.8432$, $P = 0.3038$) between the crops for numbers of dead plants at the end of the experiment in 2015 (Figure 1C). For viability indices (AUC), there were significant differences between the crop types ($\chi^2 = 24.1618$, $P < 0.0001$), where apples had the lowest AUC values (lowest viability, and greatest severity), that were different from *Pistacia* (non-parametric comparison for each pair using the Wilcoxon method $P < 0.0001$), persimmon ($P < 0.0001$), kiwifruit ($P = 0.0098$), and almond ($P = 0.0234$), (Figure 1D). In Metula and in Mas'ada, block also had significant effects on AUC values ($\chi^2 = 88.9121$ for Metula and 13.4844 for Mas'ada, $P < 0.0001$, Wilcoxon test).

In the Metula and Mas'ada plots, at the end of the experiment (third and fifth years, respectively), trunk circumferences of GF-677 were greatest (mean = 217 mm for Metula, and 441 mm for Mas'ada (Figure 1E), and the trees were the tallest (mean = 3.55 m in the third year for Metula and 4.24 m in the fifth year for Mas'ada. (Figure 1F). This indicates suggests that the disease affected plant growth differently based on the host sensitivities to *D. necatrix*, but that the pathogen did not kill the plants. No effect of block on plant height ($P > 0.05$) was detected in Metula or Mas'ada. However, in Mas'ada, there was a significant effect of block on the trunk circumference (after square root transformation, F = 5.9485, $P = 0.0013$).

Most of the plants that wilted died in the first year, up to 72% of the apple trees in Mas'ada. In general, for all crops, most of the trees died in the first 3 years. In Mas'ada, only a single plant or no plant from each crop wilted in the fourth year, and no wilting was seen in the fifth year of the study (Table 1). In grapevine, 78–92% of the plants were healthy after years 3 and 5 of the experiment. The main damage occurred in the first or second years of the study. For rootstock 1103 Paulsen in Mas'ada, and SO4 in Mas'ada and Metula, plant death was observed in less than 5% of the rootstocks after the second year of the study.

In Mas'ada, no statistically significant differences were observed between grapevine rootstocks for mean trunk circumference ($\chi^2 = 4.9029$, $P = 0.2974$), pruning weight ($\chi^2 = 4.0556$, $P = 0.3985$), yield (F = 1.0463, $P = 0.3872$), or AUC ($\chi^2 = 4.1664$, $P = 0.3840$; Table 2). In Metula, there were no effects on mean trunk circumference (F = 3.3069, $P = 0.0135$) or AUC for plant viability per day ($\chi^2 = 1.8664$, $P = 0.7603$). However, statistically significant differences were detected for mean pruning weights (F = 7.2734, $P < 0.0001$). Plants grafted on the 1103 Paulsen rootstock had greater pruning weights than plants grafted on the 110 Richter rootstock (F = 3.3867, $P = 0.0120$), with no effect of block (F = 0.568, $P = 0.7243$) or the block × crop interactions (F = 1.4983, $P = 0.2082$; Table 2).

Table 1. Mean proportions Sensitivity of fruit trees and grapevines to *D. necatrix* in naturally infested soil in the orchard. Dead plants were calculated as percentage of live plants at the beginning of each year.

Crop	Rootstock	Percentage of dead plants each year (dead plants/live plants at the beginning of the year)				
		2013	2014	2015	2016	2017
Mas'ada						
Almond	GF-677	0.0 (0/25)	0.0 (0/25)	4.0 (1/25)	0.0 (0/24)	0.0 (0/24)
Apple	Hashabi	72.0 (18/25)	14.3 (1/7)	50.0 (3/6)	0.0 (0/3)	0.0 (0/3)
Grapevine	101-14 MGT	8.0 (2/25)	0.0 (0/23)	0.0 (0/23)	0.0 (0/23)	0.0 (0/23)
	110 Richter	8.0 (2/25)	0.0 (0/23)	0.0 (0/23)	0.0 (0/23)	0.0 (0/23)
	1103 Paulsen	8.0 (2/25)	0.0 (0/23)	4.4 (1/23)	4.5 (1/22)	0.0 (0/23)
	140 Ruggeri	8.0 (2/25)	0.0 (0/23)	0.0 (0/23)	0.0 (0/23)	0.0 (0/23)
	SO4	4.0 (1/25)	4.2 (1/24)	4.3 (1/23)	0.0 (0/22)	0.0 (0/22)
Kiwifruit	Hayward	37.5 (9/24)	6.7 (1/15)	14.3 (2/14)	7.7 (1/13)	0.0 (0/12)
Persimmon	*D. virginiana*	11.1 (2/18)	6.3 (1/16)	13.3 (2/15)	0.0 (0/13)	0.0 (0/13)
	D. lotus	33.3 (5/15)	10.0 (1/10)	11.1 (1/9)	0.0 (0/8)	0.0 (0/8)
Pistacia	*atlantica*	38.1 (8/21)	15.4 (2/13)	27.3 (3/11)	0.0 (0/8)	0.0 (0/8)
Metula						
Almond	GF-677	26.32 (5/19)	0.0 (0/14)	0.0 (0/14)		
Apple	Hashabi	4.35 (1/23)	27.3 (6/17)	0.0 (0/16)	n.d.	n.d.
Grapevine	101-14 MGT	7.40 (2/27)	8.0 (2/25)	0.0 (0/23)	n.d.	n.d.
	110 Richter	25.00 (7/28)	4.8 (1/21)	0.0 (0/21)	n.d.	n.d.
	1103 Paulsen	21.4 (6/28)	0.0 (0/22)	0.0 (0/22)	n.d.	n.d.
	140 Ruggeri	7.4 (2/27)	0.0 (0/25)	0.0 (0/25)	n.d.	n.d.
	SO4	10.7 (3/28)	8.0 (2/25)	4.4 (1/23)	n.d.	n.d.
Kiwifruit	Hayward	12.5 (3/24)	4.8 (1/21)	10.0 (2/20)	n.d.	n.d.
Persimmon	*D. virginiana*	5.9 (1/17)	6.3 (1/16)	0.0 (0/15)	n.d.	n.d.
	D. lotus	0.0 (0/25)	12.0 (3/25)	0.0 (0/22)	n.d.	n.d.
Pistacia	*atlantica*	6.9 (2/29)	3.7 (1/27)	3.9 (1/26)	n.d.	n.d.

n.d., not detected.

Table 2. Mean plant growth indices of different live grapevine rootstocks in a soil that was naturally infested with *Dematophora necatrix*, at the end of 2017 in Mas'ada (n = 15 to 23 plants) and 2015 in Metula (n = 20 to 25 plants). The AUC for plant vitality / day calculated for all tested plants (n=24-25 plants in Mas'ada, n=30 plants in Metula).

Grapevine	Yield weight (g)	Trunk circumference (cm)	Pruning weight (kg)	AUC
Mas'ada (2017)				
101-14 MGT	904.9 ± 188.7	100.0 ± 7.14	1.3 ± 0.3	3220.0 ± 188.2
110 Richter	533.8 ± 122.5	74.8 ± 10.0	0.6 ± 0.1	2706.0 ± 302.6
1103 Paulsen	595.5 ± 130.0	101.0 ± 4.4	1.0 ± 0.1	3196.0 ± 188.6
140 Ruggeri	961.5 ± 205.0	82.8 ± 9.7	0.9 ± 0.2	3162.0 ± 215.5
SO4	836.5 ± 178.4	76.7 ± 9.4	0.7 ± 0.1	3286.0 ± 188.7
Metula (2015)				
101-14 MGT	998.4 ± 114.4	86.0 ± 4.6	2.4 ± 0.2 ab	2038.4 ± 148.5
110 Richter	1162.0 ± 125.8	91.1 ± 5.1	1.8 ± 0.2 c	1780.3 ± 176.8
1103 Paulsen	1251.65 ± 167.7	93.5 ± 4.2	2.7 ± 0.2 a	1901.2 ± 170.0
140 Ruggeri	1042.48 ± 132.6	84.9 ± 4.6	1.8 ± 0.2 bc	2069.0 ± 152.4
SO4	865.52 ± 121.0	82.1 ± 4.5	1.9 ± 0.2 bc	2081.8 ± 129.9

Different letters indicate significant difference by LSD ($P < 0.05$).

Comparison between apple rootstocks in naturally infested soils

To find potential solutions for growers who wish to continue growing apples, apple rootstocks were compared in naturally infested soil in two field plots located 22 km apart at similar altitude in the Galilee region. Hashabi was the most tolerant rootstock, with 82% (18 of 22) healthy trees in Manara and 87% (20 of 23) in Sasa. PI80 and MM104 were the most sensitive rootstocks, with 50% (eight of 16) PI80 trees surviving and 48% (ten of 21) of MM104 trees surviving. In Manara, statistically significant differences were found between Hashabi and PI80 ($\chi^2 = 4.34$; $P = 0.0372$) and Hashabi compared to MM104 ($\chi^2 = 5.532$; $P = 0.0187$), but not between blocks ($P > 0.05$). In addition, among the viable trees, Hashabi had an additional benefit in the infested soil compared to the other rootstocks, in terms of growth parameters of trunk circumference and tree height. In Sasa, MM109 and MM104 had the greatest growth parameters (Figure 2). There were no effects of block or rootstock × block interaction in either plot ($P > 0.05$).

DISCUSSION

This study examined the sensitivity of fruit crops and grapevine species to the pathogenic fungus *D. necatrix* in Mas'ada and Metula, with emphasis on species suitability for growth in the north of Israel, in the Golan Heights and in Galilee regions.

In the naturally *D. necatrix*-infested orchards, according to measures of trunk diameter and plant height, the GF-677 rootstock, which can be grafted with stone fruit trees such as peach and almond, produced the largest trees in the experimental plot. This is the first study to demonstrate that GF-677 rootstock can be grown in *D. necatrix*-infested soils. As a result, several infested commercial apple orchards in Metula were replaced in recent years with nectarine or peach trees on the GF-677 rootstock. In two of the three commercial plots, no tree mortality was seen for 2 years, and the trees developed normally. The third plot was monitored for 8 years after the crop replacement, and the orchard remained well-developed. However, each year, *ca*. 8 to 9% of the trees were replaced, similar to previous findings by Sztejnberg and Madar (1980). They observed that peach and almond species are very susceptible to *D. necatrix* in pots. Pinochet (2010) also reported that peaches grafted on GF-677 rootstock are very sensitive to *D. necatrix*, with an observed 18% mortality rate of trees growing in infested soil. The present study results showed that the GF-677 rootstock was less sensitive than the apple Hashabi rootstock, and can be grown in soil infested with *D. necatrix*, but additional steps must be taken to deal with the disease, such as solar treatments (Sztejnberg *et al*., 1987) or use of pesticides (Gupta and Gupta, 1992; Dafny-Yelin *et al*., 2019). In addition, more peach rootstocks should be tested in Israel to find better ones, as Pinochet (2010) reported that Replantpac (Rootpac R), a plum–almond hybrid rootstock, was suitable for replanting in *D. necatrix*-infested soils.

The grapevines in the field experiment survived, with approx. 85% surviving and mortality decreased each year. These results were similar to those of Sztejnberg and

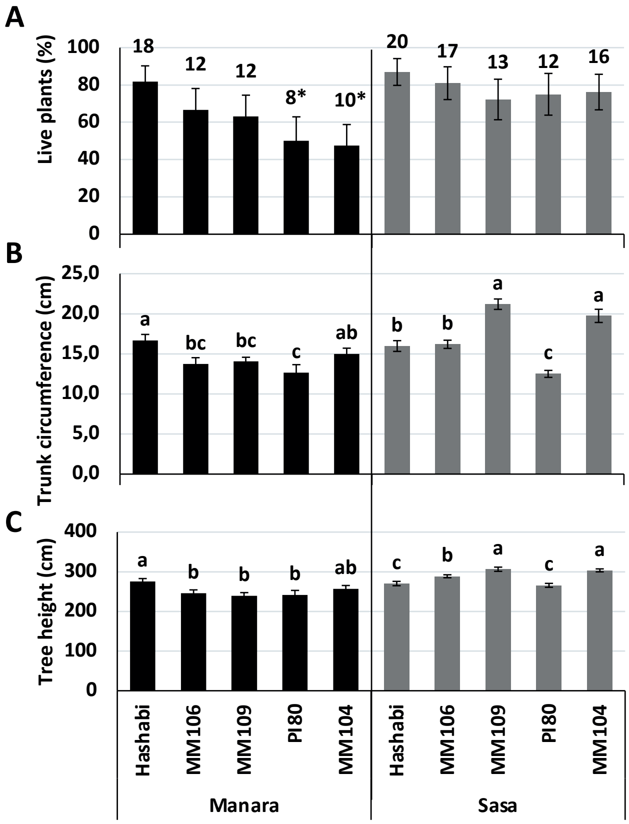

Figure 2. Mean apple rootstock parameters in *D. necatrix*-infested soils in Manara and Sasa. (A) Health of 5-year-old apple trees on different rootstocks (planted in March 2018, and tested in September 2022). The numeral above each column is the number of trees that survived. Asterisks indicates differences ($P < 0.05$) compared to the Hashabi survivors in each plot (contingency analyses). (B) Mean trunk circumferences of surviving trees. Different letters indicate differences ($P < 0.01$) between rootstocks in each plot (LSD tests). (C) Mean tree heights. Different letters indicate differences ($P < 0.05$) between rootstocks in each plot. Black histograms, Manara plots; gray histograms, Sasa plots.

Madar (1980), who showed that vines on different rootstocks were not damaged for 2 years in a naturally infested agricultural area. Mansoori and Dorostkar (2008) reported that most seedlings derived from *Vitis vinifera* and hybrid varieties died within 150 d in artificially infested pots, and the varieties were defined as susceptible. In contrast, seedlings of 'Bidaneh Sephid Gazvin' and 'Bidaneh Ghermez Gazvin' remained alive. Wine grapes in Israel are grown in areas where white root rot occurs in apple and cherry (Dafny-Yelin *et al.,* 2018), but no mortality occurs in grapevine plots as a result of the disease. This may be due to the low levels of irrigation applied in vineyards (500 to 2500 m^3 ha^{-1} per season (Zahavi, personal communication), compared to the *ca.* 10-fold greater irrigation rates applied for apple and cherry (Peres *et al.*, 2018).

In parallel to the experiments reported here, a study was carried out in Moshav Margaliot, where there was high infestation of cherry trees grafted on MM2 rootstock. In the summer of 2013, the farmer replaced this crop with a Shiraz scion grafted on the SO4 rootstock. Ten years after planting, the plot has remained healthy, bearing fruit, and no vines have been damaged by white root rot (Dafny-Yelin, personal communication).

Apple is known to be very susceptible to *D. necatrix* infections (Gupta, 1978; Sztejnberg *et al.*, 1987; Dafny-Yelin *et al.*, 2018; 2019), in agreement with the present study results in Mas'ada, where 88% of the apple trees (variety Starking Scarlet-spur, grafted on Hashabi rootstock) had died after the third year. In the Metula plot, the Hashabi rootstock was much less sensitive than in the Mas'ada plot, with less than a third of the trees having died during the same period.

Growth parameters of all plants that survived till the end of the experiment were monitored. Although these parameters of the various host species cannot predict plant survival, they can provide estimates of crop fitness in infested plots. The apple plants that survived in Metula developed at a lower rate than expected after 3 years, where healthy plants did not develop new growth and reached an average height of 1.25 m and trunk circumference of ca. 5 cm. This contrasted with GF-677 which developed new growth, and reached 3.5 m height and trunk circumference of more than 20 cm. In Metula, 27% of the trees wilted, whereas in Mas'ada, only 4% of the plants died. These differences may be due to other factors that affect plant and fungal development, such as irrigation regimes, the root system volumes, and soil type and depth. The interaction of rootstock and scion could also affect rootstock sensitivity, as the apple trees in Metula were not grafted. Rootstock–scion interactions are important because auxin, the growth regulator produced in the shoots, has effects on root development and elongation (Soumelidou *et al.*, 1994; Hooijdonk *et al.*, 2010).

Sharma *et al.* (2013) assessed resistance of apple rootstocks in a pot trial with artificially infested soil, and showed that the commercial rootstocks MM106, M4, M9, M26, M27 and M7 were very sensitive to *D. necatrix* infection. Gupta and Verma (1978) showed that M7 and MM109 were partially resistant in the field 500 d after infection. In the present study, similarly to Sharma *et al.* (2013) in naturally infested soil, none of the apple rootstocks exhibited immune reactions. However, apple trees that were grafted on Hashabi were less sensitive than those on the other assessed rootstocks in two plots (Figure 2). The trees were less damaged in Sasa than in Manara probably because the soil in Sasa had been solarized before planting. Solarization has been found useful for young trees under Israel's climatic conditions (Sztejnberg *et al*., 1987), and in other areas in the world where apples (Gupta, 1978; Kanadani *et al*., 1998) or avocado (López-Herrera and Zea-Bonilla, 2007; Arjona-López *et al*., 2020) are grown in infested soils. In healthy Israeli plots, Hashabi plants had the optimum rootstock for apple growth (Assaf, 1995), and in the *D. necatrix*-infested plot in Manara, this rootstock gave the best performance as indicated by trunk circumference. The semi-dwarf rootstock PI80 was the weakest, as expected, with the least mean trunk circumference and tree height (Figure 2, and Fischer, 1996). However, since introduction of new apple rootstocks, Hashabi is no longer commonly used in commercial orchards.

Persimmon survived in the Metula experimental plots at an average of *ca.* 90%, greater survival than for the other crops; in Mas'ada, survival rate of Metula was less than for almond trees, but similar to that for grapevines. Sztejnberg *et al.* (1983) reported survival of persimmon trees for 6 years with no signs of disease, suggesting that this was due to high phenol contents in the roots of this species.

Kiwifruit is a *D. necatrix*-sensitive crop (Pliego *et al*., 2011). In the present study, kiwifruit was found to be less susceptible to the pathogen than apple. Similar to grapevine, kiwifruit is grown in Israel in plots that are close to infected apple and cherry orchards (Dafny-Yelin *et al*., 2018), and no mature kiwifruit plots with mortality due to *D. necatrix* have been seen. This suggests that kiwifruit can overcome the white root rot in commercial plots.

Overall, grapevine and peach rootstocks were the most tolerant of *D. necatrix* soil infestations, without any significant differences between the assessed rootstocks. Apple was the most sensitive crop. Among apple rootstocks, Hashabi was more resistant to *D. necatrix* infections than PI80 or MM104 rootstocks. Kiwifruit and *Pistacia* were as sensitive as apple, while persimmon rootstock sensitivity did not differ significantly from that of the grapevine rootstocks.

CONCLUSIONS

This study has demonstrated the relative sensitivity of different fruit crop species (including grapevine) to the pathogenic fungus *D. necatrix*, in different regions of Israel. Grapevines commercial rootstocks and the almond-peach rootstock GF-677 had promising tolerance to *D. necatrix*-infested soil, offering an alternative for orchard replacement, particularly in the northern regions of Israel such as the Golan Heights and Galilee areas. Despite susceptibility to white root rot in controlled experiments, GF-677 exhibited resilience in commercial orchards, although additional disease management practices were required in the field. The present study also highlighted the importance of selecting appropriate host rootstocks, with Hashabi showing greatest resistance among apple varieties. The necessity for crop replacements for management of soilborne diseases underscores the challenges faced by farmers, necessitating further research to identify optimal rootstocks for sustainable agriculture in *D. necatrix*-infested areas. The present study has contributed valuable insights for agricultural practices aimed at mitigating the impacts of soil-borne pathogens on fruit crop production in Israel.

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AUTHOR CONTRIBUTIONS

Mery Dafny-Yelin and Tirtza Zahavi conceived the study, the experimental design and the data analyses; Jehudith Clara Kohavi-Moy and Shlomit Dor conducted data collection; Shlomi Kfir took care of the experiment plots; Mery Dafny-Yelin wrote the first draft of the manuscript of this paper; and all authors commented on all previous versions of the manuscript. Amber Hill and Tirtza Zahavi reviewed and edited the manuscript of the paper, and all the authors read and approved the final manuscript.

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