



Host status of cultivated and wild *Fragaria* genotypes to the quarantine root-knot nematodes *Meloidogyne chitwoodi* and *Meloidogyne fallax*

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Abstract The quarantine root-knot nematodes *Meloidogyne chitwoodi* and *Meloidogyne fallax* pose a significant phytosanitary risk to agricultural production, yet little is known about their ability to reproduce on strawberry. This study evaluated the host status of cultivated and wild *Fragaria* genotypes to both nematode species under greenhouse conditions. Seven strawberry genotypes were assessed in two independent experiments differing in inoculum density and duration, representing one and two nematode generations. *Solanum lycopersicum* cv. Moneymaker served as a susceptible control. Nematode reproduction was determined using the reproductive factor ($RF = Pf/Pi$). Tomato supported high levels of reproduction of both nematode species, confirming inoculum viability. In contrast, all *Fragaria* genotypes consistently showed RF values below 1. *M. chitwoodi* reproduced only at very low levels (maximum $RF = 0.025$), whereas *M. fallax* showed no reproduction after one generation and only very limited reproduction after two generations (maximum $RF = 0.010$). Although occasional eggs and second-stage juveniles

were recovered from some strawberry plants, none of the evaluated genotypes supported nematode population increase. The results demonstrate that the tested *Fragaria* genotypes are poor hosts for both quarantine nematodes and may contribute to reducing population densities but should not be considered as eradication crops.

Keywords *Fragaria* × *ananassa* · *Fragaria vesca* · *Fragaria moschata* · Host suitability · Quarantine nematodes · Root-knot nematodes · Reproductive factor

Cultivated strawberry (*Fragaria* × *ananassa* Duch.) and woodland strawberry (*Fragaria vesca*) are grown worldwide and represent one of the most economically important berry crops (Porter et al., 2023; Shulaev et al., 2011). Despite their economic importance, strawberry production is frequently challenged by soil-borne pathogens and pests (Bozbuga et al., 2022). Among these, plant-parasitic nematodes (PPN) are of particular concern as they reduce plant vigor, yield, and fruit quality (Abd-Elgawad, 2019; Bozbuga et al., 2022; Samaliev & Mohamedova, 2011). Yield losses caused by PPN can be substantial and depend on nematode species, population density, environmental conditions, and host susceptibility. For example, annual yield losses of approximately 12% have been reported in strawberry production in Egypt (Abd-Elgawad, 2019). Among the nematodes associated

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with strawberry, root-knot nematodes (RKN; *Meloidogyne* spp.) are among the most widespread and economically important groups, occurring in major strawberry-producing regions worldwide (Brito et al., 2008; Samaliev & Mohamedova, 2011). *Meloidogyne* spp. are obligate, sedentary endoparasitic nematodes whose infective second-stage juveniles (J2) invade host roots at the root tip using their stylets, and migrate intercellularly towards the vascular cylinder (Caillaud et al., 2008). They establish within the vascular cylinder by inducing multinucleate giant cells that serve as permanent feeding sites. Giant cell induction results in the formation of root galling, which disrupts water and nutrient uptake and leads to reduced plant vigor, stunting, chlorosis, and decreased productivity of affected plants (Krezanoski et al., 2020; Talavera et al., 2019). In temperate regions, *M. hapla* is generally regarded as the predominant root-knot nematode species affecting strawberry. However, thermophilic species such as *M. incognita*, *M. javanica*, and *M. arenaria* have become increasingly important in warmer production areas and under protected cultivation systems, where they can cause severe damage to strawberry crops (Abd-Elgawad, 2019; Brito et al., 2008; Talavera et al., 2019). Particular attention has been given to the quarantine root-knot nematodes *Meloidogyne chitwoodi* and *Meloidogyne fallax*, which are adapted to temperate climates and represent a significant phytosanitary risk (EPPO, 2020 and 2025). Although most studies have focused on the impact of *M. chitwoodi* and *M. fallax* on their major hosts *Solanum tuberosum* (potato) and *Daucus carota* (carrot), their interaction with strawberry (*Fragaria* spp.) remains poorly understood. Previous studies have shown that host suitability differs among *Fragaria* species and cultivars. Wild relatives such as *F. vesca* generally exhibit reduced susceptibility, whereas some commercial cultivars can support nematode reproduction of several *Meloidogyne* species (Ruthes & Dahlin, 2024; Talavera et al., 2019). Because strawberry is propagated primarily through vegetative planting material, infected plants could contribute to the persistence and spread of quarantine nematodes. A better understanding of the host status of *Fragaria* spp. is therefore important for phytosanitary risk assessment and for developing effective management and breeding strategies against *M. chitwoodi* and *M. fallax*. Accordingly, this study evaluated the host status of cultivated and

wild *Fragaria* genotypes to *M. chitwoodi* and *M. fallax* by comparing nematode reproduction over one and two generations under greenhouse conditions.

To address this objective, two root-knot nematode populations were used: *Meloidogyne chitwoodi* Race 1, pathotype Roza (population MCB) and *Meloidogyne fallax* (population MFV), previously characterized morphologically and molecularly by Cabianca et al. (2026). Both populations were reared on tomato (*Solanum lycopersicum* cv. Moneymaker) under controlled greenhouse conditions at Agroscope, Switzerland. The following strawberry genotypes were evaluated: *Fragaria* × *ananassa* cvs. Ostara, Mara des Bois, Elsanta, Herz, Wädenswil 6, and F1 Sarian, *Fragaria moschata*, and *Fragaria vesca* cv. Alexandria. Tomato (*Solanum lycopersicum* cv. Moneymaker) was included as a susceptible control in both experiments.

Tomato plants were established from seed in germination trays containing commercial potting substrate and transplanted into 13-cm wide pots. Strawberry plants were obtained from seeds as described for tomato plants, or from mother plants by runner propagation and transplanted into 13-cm pots. All plants were grown individually in a 3:1 (v/v) silver sand:sandy loam soil mixture (29.2% silt) and maintained in a greenhouse at 20 ± 2 °C under a 16 h light: 8 h dark photoperiod. Plants were watered and fertilized with WUXAL Super (Hauert MANNA Duengerwerke GmbH, Nürnberg, Germany) as required throughout the experiment.

Two independent greenhouse experiments were conducted using both nematode species. In the first experiment, plants were inoculated with 7000 J2 per plant to evaluate nematode reproduction after a single generation, corresponding to approximately one nematode generation (820 DD5, Griffin, 1985). In the second experiment, plants were inoculated with 1500 J2 per plant and maintained for 1640 DD5, allowing for two nematode generations to develop. Each treatment consisted of five replicates per genotype ($n=5$) arranged in a completely randomized design.

At the end of each experiment, root systems were carefully removed from the pots and washed free of soil. Roots were cut into 1-cm pieces for nematode egg extraction using a sodium hypochlorite (NaOCl) extraction method adapted from Hussey and Barker (1973). Root fragments submerged in 1.5% NaOCl were vigorously shaken for 4 min. Subsequently, the

nematode egg suspension was immediately poured through sieves (900, 160, 50, and 25 μm) and thoroughly rinsed with tap water. Eggs and J2 retained on the 50 and 25- μm sieve were collected into 50-mL Falcon tubes and quantified using a counting slide with an inverted microscope (CKX53, Olympus Optical Co Ltd., Japan). The final nematode population (Pf) was calculated as the combined number of eggs and J2 from each root system. The reproductive factor (RF) was calculated according to Oostenbrink (1966) as $\text{RF} = \text{Pf} / \text{Pi}$, where Pi represented the initial inoculum density. Analysis of Variance (ANOVA) and Tukey's Honest Significant Difference (HSD) were performed on each experimental dataset in R (version 4.6.1).

Following one generation, the susceptible control, *S. lycopersicum* cv. Money-maker, supported extensive reproduction of both nematode species, with mean reproductive factors (RF) of 14.66 ± 2.04 for *M. chitwoodi* and 33.43 ± 10.49 for *M. fallax* (Table 1).

In contrast, reproduction on all tested *Fragaria* genotypes remained consistently low. Following inoculation with *M. chitwoodi*, only small numbers of eggs and J2 were recovered, resulting in RF values ranging from 0 to 0.005. The highest mean RF was recorded for cvs. Mara des Bois and Elsanta. *M. chitwoodi* failed to reproduce on cv. F1 Sarian. No eggs or J2 were recovered from any *Fragaria* genotype inoculated with *M. fallax*, resulting in RF of zero for all tested *Fragaria* genotypes. Statistical analysis

Table 1 Reproduction of *M. chitwoodi* (MCB) and *M. fallax* (MFV) on cultivated and wild *Fragaria* genotypes following one generation under greenhouse conditions

Plant genotype	RF – MCB (Mean $\pm$ SD)	RF – MFV (Mean $\pm$ SD)
<i>S. lycopersicum</i> cv. Money-maker	14.66 ± 2.04^a	33.43 ± 10.49^a
<i>F. \times ananassa</i> cv. Ostara	0.002 ± 0.004^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Mara des Bois	0.005 ± 0.004^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Elsanta	0.005 ± 0.007^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Wädenswil 6	0.002 ± 0.004^b	0.000 ± 0.000^b
<i>F. vesca</i> cv. Alexandria	0.001 ± 0.001^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. F1 Sarian	0.000 ± 0.000^b	0.000 ± 0.000^b
<i>F. moschata</i>	0.001 ± 0.002^b	0.000 ± 0.000^b

Letters indicate statistical significance groups according to HSD test

confirmed the significance of the difference between tomato and each strawberry cultivar RF value ($p < 1.8e^{-11}$). No statistically significant difference was observed between strawberry cultivars.

When the experiment was extended to allow two nematode generations, the overall results remained similar (Table 2). Tomato supported high levels of reproduction of both nematode species, with mean RF values of 17.70 ± 3.57 for *M. chitwoodi* and 11.93 ± 2.64 for *M. fallax*.

For *M. chitwoodi*, only isolated eggs and J2 were recovered, resulting in RF values ranging from 0 to 0.025. The highest mean RF was observed for cv. Ostara ($\text{RF} = 0.025 \pm 0.017$), while no reproduction was detected on cvs. Mara des Bois, F1 Sarian, and on *F. moschata*.

M. fallax reproduction was observed after two generations for cv. Wädenswil 6 and cv. Herz, albeit with few eggs or J2, corresponding to mean RF values of 0.010 ± 0.017 and 0.002 ± 0.004 , respectively. However, *M. fallax* failed to reproduce on the remaining *Fragaria* genotypes tested.

Across both experiments, all *Fragaria* genotypes maintained RF values below 1. Although occasional eggs and J2 were recovered from individual plants, none of the tested genotypes supported nematode population increase. As for the one-generation experiment, statistical analysis showed that the only significant difference was between control tomato and

Table 2 Reproduction of *M. chitwoodi* (MCB) and *M. fallax* (MFV) on cultivated and wild *Fragaria* genotypes following two generations under greenhouse conditions

Plant genotype	RF – MCB (Mean $\pm$ SD)	RF – MFV (Mean $\pm$ SD)
<i>S. lycopersicum</i> cv. Money-maker	17.70 ± 3.57^a	11.93 ± 2.64^a
<i>F. \times ananassa</i> cv. Ostara	0.025 ± 0.017^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Mara des Bois	0.000 ± 0.000^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Elsanta	0.008 ± 0.017^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Wädenswil 6	0.008 ± 0.017^b	0.010 ± 0.017^b
<i>F. vesca</i> cv. Alexandria	0.008 ± 0.017^b	0.000 ± 0.000^b
<i>F. \times ananassa</i> cv. Herz	0.004 ± 0.008^b	0.002 ± 0.004^b
<i>F. \times ananassa</i> cv. F1 Sarian	0.000 ± 0.000^b	0.000 ± 0.000^b
<i>F. moschata</i>	0.000 ± 0.000^b	0.000 ± 0.000^b

Letters indicate statistical significance groups according to HSD test

each strawberry cultivar RF value ($p < 2e^{-16}$), with no difference between RF values of *Fragaria* cultivars. In addition, no visible root galling was observed on any of the tested *Fragaria* genotypes during either experiment.

The consistently low reproductive factors observed across both experiments indicate that the evaluated *Fragaria* genotypes are poor hosts for *M. chitwoodi* and *M. fallax*. These findings are consistent with previous reports showing that host suitability varies considerably among *Meloidogyne* species and that strawberry is generally a less favourable host for several root-knot nematodes than many vegetable crops (Ruthes & Dahlin, 2024; Talavera et al., 2019). Similar differences in host suitability among temperate and tropical *Meloidogyne* species have also been reported in parsley, where host status depended on both the crop and the nematode species (Noskov et al., 2024). Our results further support the observation of Ruthes and Dahlin (2024), who reported reduced reproduction of several thermophilic *Meloidogyne* species on *Fragaria vesca* compared with *M. hapla*. Here, similarly low levels of reproduction were observed for the quarantine species *M. chitwoodi* and *M. fallax* across several commercial strawberry cultivars and wild *Fragaria* species. This also suggests that adaptation to temperate climates does not necessarily translate into high reproductive success on *Fragaria* spp., unlike the pattern reported for *M. hapla* (Ruthes & Dahlin, 2024). Taken together, these findings indicate that reduced host suitability may be a common characteristic of *Fragaria* germplasm for several *Meloidogyne* species, although the degree of susceptibility depends on both the strawberry genotype and the nematode species (Hammam et al., 2022; Ruthes & Dahlin, 2024; Talavera et al., 2019).

Despite the very low RF values, occasional eggs and J2 were recovered from some inoculated plants, particularly those infected with *M. chitwoodi*. This indicates that a small proportion of the nematode population was able to establish feeding sites, complete its life cycle, and produce offspring. Interestingly, for *M. fallax*, eggs and J2 were recovered only after two generations, and only from *F. × ananassa* cvs. Wädenswil 6 and Herz. Consequently, the *Fragaria* genotypes with RF values above zero cannot be considered true non-hosts but should instead be classified as poor hosts, as they substantially suppressed nematode reproduction without completely preventing

development. Similar classifications based on reproductive factor have recently been proposed for temperate *Meloidogyne* species on parsley (Noskov et al., 2024). This distinction is particularly important because even low levels of reproduction may allow nematode populations to persist and serve as a source of inoculum for subsequent crops. As commercial strawberry production commonly relies on vegetative propagation by runners, the occurrence of reproducing nematodes in strawberry plants may have phytosanitary implications if infected planting material facilitates the persistence and dissemination of these quarantine nematodes. Previous studies have shown that host suitability differs among *Meloidogyne* species and populations. For example, Ruthes and Dahlin (2024) reported limited reproduction of *M. incognita* on strawberry, whereas Hammam et al. (2019, 2022) demonstrated that *M. incognita* can cause severe damage in commercial strawberry production. Overall, these findings highlight that host suitability is influenced by *Meloidogyne* species and nematode population, and should therefore be assessed individually. The distinction between poor hosts and true non-hosts has important implications for the management of quarantine nematodes. Studies on spinach have similarly shown that crops supporting only limited nematode reproduction may nevertheless contribute to the persistence of *M. chitwoodi* populations under field conditions (Taning et al., 2022). Although cultivation of the tested strawberry genotypes could contribute to a sharp decline in *M. chitwoodi* and *M. fallax* populations, the recovery of reproducing individuals indicates that strawberry should not be regarded as an eradication crop for these quarantine nematodes. This study was conducted under controlled greenhouse conditions using a single population of each nematode species. Although the one- and two-generation experiments produced consistent results, additional nematode populations and field trials are needed to determine whether these findings hold under commercial production conditions. Even low levels of reproduction may allow small nematode populations to persist between cropping cycles and serve as a source of inoculum for future susceptible crops. Because both species are regulated quarantine pests in Europe, crops that suppress rather than completely prevent reproduction should be integrated with additional phytosanitary and management measures to minimise the risk of persistence and spread

(Björklund & Boberg, 2019; EPPO, 2020, 2025; van der Beek et al., 1998, 1999).

Taken together, these findings demonstrate that cultivated and wild *Fragaria* genotypes are poor hosts for *M. chitwoodi* and *M. fallax*. Although low levels of reproduction were observed on some genotypes, none supported an increase in nematode populations under controlled greenhouse conditions. While strawberry cultivation may contribute to reducing population densities of these quarantine nematodes, the occasional recovery of eggs and juveniles indicates that it cannot be relied upon for their eradication. These findings improve our understanding of host suitability in *Fragaria* and provide valuable information for phytosanitary risk assessment, as well as for future resistance screening and strawberry breeding programmes.

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Data availability All data generated or analysed during this study are included in this published article.

Declarations

Conflict of interest The authors declare no conflict of interest.

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