

Review

# Current Trends and Future Prospects in Controlling the Citrus Nematode: *Tylenchulus semipenetrans*

Anil Baniya <sup>1,†</sup>, Omar Zayed <sup>2,†</sup>, Jiranun Ardpairin <sup>3</sup>, Danelle Seymour <sup>2</sup> and Adler R. Dillman <sup>1,\*</sup>

<sup>1</sup> Department of Nematology, University of California, Riverside, CA 92521, USA; abaniya@ucr.edu

<sup>2</sup> Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, USA; omarz@ucr.edu (O.Z.); dseymour@ucr.edu (D.S.)

<sup>3</sup> Department of Microbiology and Parasitology, Faculty of Medical Science, Naresuan University, Phitsanulok 65000, Thailand; jiranuna61@nu.ac.th

\* Correspondence: adlerd@ucr.edu; Tel.: +1-9518273912

† These authors contributed equally to this work.

**Abstract:** Citrus nematode (*Tylenchulus semipenetrans*) is one of the dominant plant-parasitic nematodes in citrus-growing regions, resulting in an average yield loss between 10 and 30%. *Tylenchulus semipenetrans* is a sedentary semi-endoparasitic nematode that infects the roots of citrus trees, causing stunted growth, reduced fruit yield, and poor fruit quality; collectively this pathology and thus the disease caused is referred to as the slow decline of citrus. Despite its huge importance, the citrus nematode is regarded as a neglected parasite, and most research focuses on biological control and integrated pest management. Advancements in understanding the molecular mechanisms of other plant-parasitic nematodes, such as sedentary endoparasites with biological similarities to citrus nematodes, can be leveraged to gain deeper insights into the molecular mechanisms of citrus nematodes. In this review, we examine the biology, and integrated pest management of citrus nematodes, and explore future research directions toward understanding the role of genomics, gene-editing tools, and the molecular mechanisms of host-seeking and effectors used by other plant-parasitic nematodes to cause infection, which can serve as a foundation for future work in citrus nematode management.

**Keywords:** *Tylenchulus*; slow decline; nurse cell; integrated management; plant breeding; genomics; defense mechanism; effector; immunity

Academic Editor: Isabel Luci Pisa Mata da Conceição

Received: 10 December 2024

Revised: 28 January 2025

Accepted: 29 January 2025

Published: 31 January 2025

**Citation:** Baniya, A.; Zayed, O.; Ardpairin, J.; Seymour, D.; Dillman, A.R. Current Trends and Future Prospects in Controlling the Citrus Nematode: *Tylenchulus semipenetrans*. *Agronomy* **2025**, *15*, 383. <https://doi.org/10.3390/agronomy15020383>

**Copyright:** © 2025 by the authors. Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Many species of plant-parasitic nematodes (PPNs) are associated with citrus roots but very few of them can successfully reproduce and cause significant damage to the trees. Some of the major PPNs associated with citrus are *Tylenchulus semipenetrans*, *Pratylenchus coffee*, *Radopholus similis*, and *Meloidogyne* spp. Some of the minor species of PPNs that cause damage to citrus but only occur in small geographic areas are *Pratylenchus brachyurus*, *P. vulnus*, *Hemicycliophora arenaria*, *H. nudata*, *Paratrichodorus lobatus*, *P. minor*, *Xiphinema index*, and *X. brevicolle* [1]. While there are numerous nematode species that infect citrus, *T. semipenetrans* is the predominant pathogenic nematode in most citrus-growing regions and across a wide range of soil types, which may have contributed to *T. semipenetrans* being commonly referred to as citrus nematode [1–4]. It is estimated that citrus nematode infestation is present in 50–90% of citrus-growing orchards in California, Arizona, Florida, and Texas [5], resulting in an average yield loss of between 10% and

30%, depending on the level of infection [1,5–8]. *T. semipenetrans* is a sedentary endoparasitic nematode that infects the roots of citrus trees, causing stunted growth, reduced fruit yield, and poor fruit quality [9]. Additionally, the infection in citrus roots caused by *T. semipenetrans* can lead to subsequent invasions of plant pathogenic fungi and/or bacteria leading to additional damage to citrus trees [8].

Most studies of citrus diseases and pathogens focus on *Citrus tristeza virus* (CTV) (genus Closterovirus, family Closteroviridae), *Phytophthora* species (*P. citrophthora*, *P. parasitica*, *P. syringae*, and *P. hibernalis*), and Huanglongbing (HLB). HLB is also known as citrus greening, which is the most devastating disease of citrus [10–13]. Given the substantial losses caused in citrus production by CTV, *Phytophthora*, and HLB, these crucial pathogens have received significant research attention. Despite the absence of effective control measures for some of these pathogens, there is a thorough understanding of the molecular mechanisms of pathogenicity [10,12,14–17]. Due to the considerable threat these major pathogens pose to citrus crops, research on the impacts of PPNs tends to receive less attention in citrus.

The economic impact of *T. semipenetrans* infestations is significant but the genetic basis of *T. semipenetrans* pathogenicity and the response of citrus towards nematode infection remains poorly understood. It can be referred to as a neglected pathogen of citrus, as this nematode is not listed among the top 10 economically important parasitic nematodes in molecular plant pathology [18,19]. Most research on the citrus nematode has concentrated on integrated pest management and biological control. There is a lack of information on host-seeking behavior, molecular infection mechanisms, effector proteins, and potential targets for gene-editing tools to manage *T. semipenetrans*. However, substantial progress has been made in understanding these mechanisms in other PPNs with similar biology, such as the formation of specialized feeding sites and the sedentary nature of mature females in root-knot nematodes (*Meloidogyne* spp.) and cyst nematodes (*Heterodera* spp. and *Globodera* spp.). Advances in other PPNs have opened new avenues to address the challenges posed by *T. semipenetrans* in citrus, which share similar biology. A comparable strategy has been highly effective in identifying mechanisms and creating toolkits for studying animal parasites (*Strongyloides* spp., *Brugia malayi*, and *Ascaris suum*). These tools, originally adapted from the free-living model nematode *Caenorhabditis elegans*, are now poised for wider use [20]. Recent advances in genome sequencing, annotation, resistance breeding, integrated pest management, and molecular biology technologies further add new opportunities to unravel the genetic basis of citrus nematode pathogenicity and develop novel control strategies.

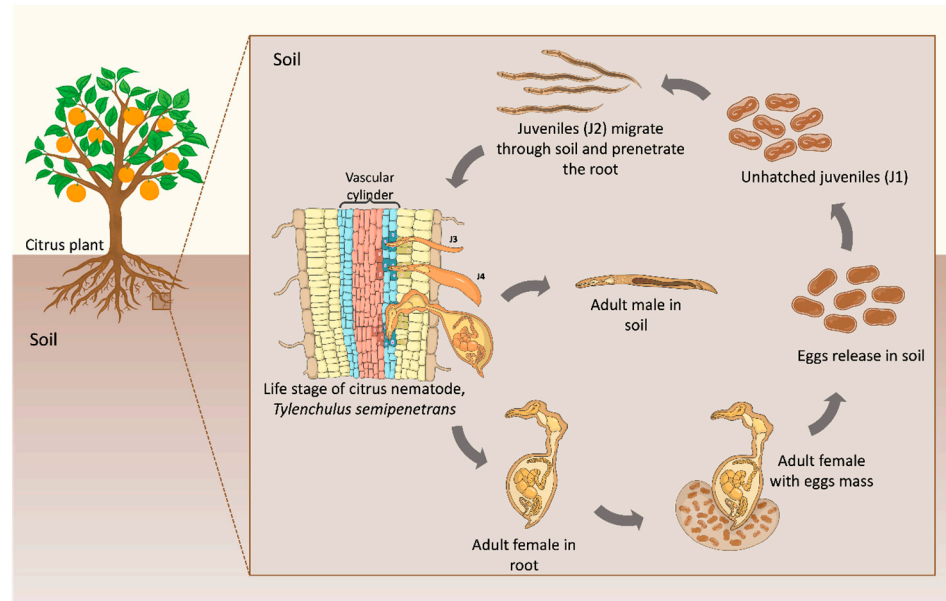
In this review, we will (i) outline the biology of nematodes, including symptoms of infection, advancements in assessing these parameters, and future directions to improve the accuracy of nematode infection estimation; (ii) highlight achievements in integrated pest management through the use of resistant varieties, chemical, cultural and biological control; (iii) explore potential future research areas enabled by nematode genomics and genome sequencing of *T. semipenetrans*; (iv) provide details on gene-editing tools for targeting *T. semipenetrans* in citrus; (v) outline the molecular mechanisms of host-seeking behavior in sedentary endoparasitic nematodes (*Meloidogyne* spp., *Heterodera* spp., *Globodera* spp.) that may be conserved in citrus nematodes; (vi) explore the molecular mechanisms of nematode-associated molecular patterns (NAMPs) and damage-associated molecular patterns (DAMPs) in host plants; and (vii) discuss nematode effectors and target proteins studied in *Meloidogyne* spp., *Heterodera* spp., and *Globodera* spp. that could serve as potential targets for *T. semipenetrans* management.

## 2. Biology and Symptoms of *Tylenchulus semipenetrans* Infection in Citrus

Infestation by *Tylenchulus semipenetrans* causes a disease called the 'slow decline' of citrus [3]. Second-stage juveniles (J2) of *T. semipenetrans* enter the root cortex, establish feeding sites, and become sedentary (Figure 1). Cortical cells at feeding sites develop into 6-10 specialized non-hypertrophied nurse cells. These cells have unique characteristics, including an expanded nucleus and nucleolus, and the central vacuole is replaced by cytoplasm [21,22]. Nematodes feeding on these nurse cells reduce the amount of water and nutrients available to the growing plant. When *T. semipenetrans* infects roots, and the roots are stained, the adult females appear as typical semi-endoparasites, with their anterior body section embedded in the root and the posterior, swollen region extending outside the root tissues (Figure 1). However, unlike root-knot nematode infections, no visible galls form on the citrus roots due to *T. semipenetrans* infestations, while root-knot nematode infections produce easily visible galls [3,23]. Morphologically, the mature female *T. semipenetrans* has a slender, irregular anterior body portion that stays embedded in the root tissues, while its smooth, swollen, and digitate posterior portion protrudes from the root surface (Figure 1). The excretory pore and vulva are located at the posterior end, whereas mature root-knot nematode females are pear-shaped. Both nematodes are approximately 0.01 inches long [24,25]. A new *T. semipenetrans* infection causes a gradual decline in tree quality, resulting in smaller, less productive, and weaker trees over time. However, when young citrus seedlings are transplanted into soil heavily infested with nematodes, poor tree growth is immediately evident after planting [9]. As the tree's growing conditions worsen, the effects of nematode parasitism become more pronounced [8,26–29].

Several studies have shown that infestation of *T. semipenetrans* negatively affects plant growth through several processes: Alteration of root physiology, reduction of photosynthesis, change in water and mineral status, and disruption of hormonal balance [1]. Broadly, *T. semipenetrans* infection symptoms can be classified into two categories: Above-ground and below-ground symptoms. The aboveground symptoms include leaf chlorosis and curling, poor growth, lack of vigor, small fruit, and leaf size, and twig dieback in severe cases [2,4,28]. The wilting of the tree is observed following early water stress and pronounced leaf shedding resulting in exposed branch terminals. Excess sodium may build in leaves under saline conditions [3,30].

In terms of below-ground symptoms, nematode-infected trees have fewer and shorter feeder roots with many rootlets. Feeder roots that have been substantially parasitized are slightly thicker than healthy roots and appear dirty because of soil particles sticking to gelatinous egg masses on the root surface [8]. Nematode feeding induces the loss of integrity at the epidermis and feeding sites in the cortex, and feeder roots decay quickly, allowing for secondary invasions by pathogens [2,8,31,32]. Mild nematode parasitism causes lesions in citrus roots, but severe infections cause cortical sloughing and root death [3,8].



**Figure 1.** The generalized life cycle of *T. semipenetrans*. Eggs are deposited in the soil or in egg masses. First-stage juveniles (J1) inside the eggs molt into second-stage juveniles (J2), hatch, and search for the host plant. Second-stage juveniles find the citrus roots and enter the root. The female J2 molts into the J3 and J4 stages and finally into the sedentary female. Female juveniles develop into mature females by feeding on the epidermis and outer layers of the cortical parenchyma in roots. As the immature female grows, it starts to penetrate the outer surface of the root and reaches the deeper cortical layers, though it typically does not reach the central cylinder, and sometimes the endodermis. Once settled, it establishes a permanent feeding site made up of specialized cells known as nurse cells, which provide essential nutrients. A mature female has a swollen posterior part of its body and protrudes from the root surface, while its elongated neck and head remain embedded in the cortex. Males, however, undergo the third stage of molting before departing from the egg mass, and they can reach adulthood within a week without feeding. Fully grown females produce eggs that are enclosed in a gelatinous matrix. The entire life cycle of the female, from egg-to-egg production, spans from four to eight weeks [33].

Most of the time symptoms may not be noticeable in lightly infected roots, allowing infected nursery stocks to go unnoticed [9]. Diagnosis of the disease is difficult as field symptoms are like physiological diseases or other plant diseases. Etiolation symptoms of the disease are often misdiagnosed as HLB. As a result, developing adequate detection techniques and identifying nematode damage thresholds is critical. Currently, for *T. semipenetrans*, the population density in soil is used to determine the damage level and is based on the number of nematodes observed per 100 g of soil. If the number of nematodes is less than 1600 per 100 gm of soil, then it is considered to have no economic damage. If the population is more than 1600 but less than 3600 per 100 g of soil, then it is at the Economic Damage Threshold (ET). If the population exceeds 3600 per 100 gm of soil sample, it is considered to have reached the Economic Injury Level (EIL) [34]. Determining damage thresholds for nematode population densities that affect tree growth is complex and dependent on various factors such as nematode aggressiveness, soil, rootstock susceptibility, management practices, seasonal variability of the nematode population, nematode-plant host interactions, and presence of other pathogens [1,7,9,23,26,29,35,36]. The technique currently used to determine the nematode threshold is outdated. With the advancement of new techniques, future research should focus on developing more sensitive methods to quantify nematodes, such as qPCR [37], artificial intelligence [38,39], and digital image analysis to identify and assess nematode populations, above and below-ground

symptoms, and predict the potential outbreak of disease before they cause economic damage [1,40–42]. The use of molecular techniques for nematode identification offers the advantage of precise identification and can be carried out by individuals with limited expertise in nematode morphology. However, it has the drawbacks of being costly and technically demanding [43].

### 3. Integrated Management Strategies for *Tylenchulus semipenetrans* in Citrus Production

#### 3.1. Breeding Strategies Against *Tylenchulus semipenetrans*

The use of resistant citrus cultivars is essential for an economical and environmentally friendly integrated nematode management strategy. Developing citrus varieties resistant to nematodes requires extensive knowledge of cultivars and their relatives. Additional important production issues include germplasm screening methods, sources of resistant germplasm in the primary, secondary, and tertiary gene pools, breeding strategies and methods, and growing and preservation resources over an extended period. Some efforts to develop citrus varieties that are resistant to citrus nematode have been initiated. Breeding against citrus nematode has primarily focused on the use of tolerant rootstocks, which can tolerate infection and maintain the health of the grafted scion. Several resistant rootstocks have been developed through conventional breeding, but the existence of several biotypes of *T. semipenetrans* that differ in their host preference and geographical distribution poses a limitation to rootstock selection. One of the widely used rootstocks is *Poncirus trifoliata*, which has been reported to exhibit tolerance to several citrus diseases [44–50]. Hybrids of *P. trifoliata* also provide tolerant rootstocks against citrus nematode [51–54]. The first and most common hybrids are Carrizo citrange (*Citrus sinensis* × *Poncirus trifoliata*) and ‘Swingle’ citrumelo (*Citrus paradisi* × *Poncirus trifoliata*) rootstocks that have been widely used in citrus production due to their tolerance to *T. semipenetrans* [55,56]. Swingle citrumelo is a commercially acceptable rootstock with a high degree of tolerance to most populations of *T. semipenetrans*. In Iran, *P. trifoliata*, Swingle citrumelo, and *Citrus aurantium* are recommended for managing *T. semipenetrans* [57]. In addition, hybrids of *P. trifoliata* × *Citrus reticulata* have inherited tolerance to *T. semipenetrans* [50,58]. Poorman orange (*Citrus* × hybrid of undetermined origin) × *P. trifoliata* hybrids were found to be tolerant to more than one biotype of *T. semipenetrans* [51,52]. In another study, Carrizo citrange, Savage citrange, and Yuma citrange [59] Citrumelo and grapefruit [60] were reported as tolerant to *T. semipenetrans* in Pakistan. In Western Australia, Troyer and Carrizo citrange are used as tolerant rootstock to citrus nematode [55]. The cultivars C22, C57, and C146 exhibited tolerance to the *T. semipenetrans* in Texas USA [61]. The rootstock Forner-Alcaide 5 is a selection of Cleopatra mandarin that exhibits tolerance to *T. semipenetrans* [62,63] (Supplementary Table S1).

There are three *T. semipenetrans* biotypes currently known: The citrus and Mediterranean biotypes which infect a wide range of citrus cultivars, and the *Poncirus* biotype which reproduces better on *P. trifoliata* and its hybrids [62,64]. However, any biotype can develop pathogenicity to any tolerant rootstocks [65], for example, populations of *T. semipenetrans* capable of reproducing well on Swingle citrumelo have been reported in Florida [66]. Also, a progressive adaptation of the nematode to reproduce on rootstocks previously described as moderately resistant (i.e., Troyer and Carrizo citranges) can occur because of their continuous cultivation [62]. The presence of high nematode levels at the time of planting or when interplanting moderately resistant and susceptible rootstocks can reduce their relative resistance level to *T. semipenetrans* [58]. For example, Carrizo citrange is currently more susceptible to *T. semipenetrans* in some areas than others [56].

### 3.2. Chemical Control Against *Tylenchulus semipenetrans*

For a long time, methyl bromide was the standard fumigant to manage soil-borne diseases including PPNs and weeds in high-value crops like vegetables and citrus [67]. After the phase-out of methyl bromide, some of the registered preplant nematicides to control *T. semipenetrans* are Metam Sodium, 1,3-Dichloropropene/Chloropicrin, and 1,3-Dichloropropene. Post-plant nematicides are Fluopyram and Oxamyl [1,68–70]. For chemical control of the PPNs, two types of nematicides are being used: Non-fumigants (Organophosphorus, Carbamate, Abamectin, Fluoroalkenyl) and fumigants (Isothiocyanates, halogenated aliphatic). The mechanism of action for these nematicides includes respiratory inhibition (Isothiocyanates, halogenated aliphatic), neurotoxicity (Organophosphorus, Carbamate, Abamectin), or interference of steroid metabolism (Fluoroalkenyl) [71]. Similarly, the fluorinated nematicide fluazaindolizine, with an unknown mode of action and very low mammalian toxicity, has shown promising results in controlling various species of PPNs, such as *M. incognita* and *T. semipenetrans*, even at non-lethal concentrations and with short-term exposure to the nematicide [72]. Most studies examining the effects of nematicides on root-knot nematodes suggest that their use does not prevent re-infection and instead leads to an increase in nematode resistance to these chemicals [73–76]. Therefore, finding new nematicidal targets should be a priority. The use of rootstock that is nematode-resistant or -tolerant can lessen the effects of the infection. If the planting location is infested with citrus nematodes, pre-plant fumigation is recommended despite using a tolerant rootstock [23]. Trees planted on fumigated orchard grounds often have higher fruit growth and yields. Post-plant nematicides are costly [23]. Growers should consider application costs, orchard age and health, and estimated crop loss [68]. Regular sampling of the nematode population might help evaluate the situation. If sampling indicates moderate to high population levels in established orchards, it may be advisable to consider the use of a nematicide [1]. When selecting a nematicide, it is vital to consider factors such as the properties of the pesticide, the timing of its application, persistence in the field, and its potential impact on honeybees, human health, and the environment [77].

### 3.3. Cultural and Biological Control Against *Tylenchulus semipenetrans*

Implementing good cultural practices and utilizing biological control agents can help reduce the negative impacts of chemical pesticides while effectively managing *T. semipenetrans* in a new orchard through exclusion. This can be accomplished by cultivating new transplants in uninfected soils [78–80], using nematode-free plant materials like cuttings and transplants [1,35], irrigation with uninfected water [81,82], and creating regulatory mechanisms through quarantine and certification programs [1,78,80,81,83]. Once a nematode infestation has been confirmed in a citrus grove, eradication measures should be implemented. Good crop husbandry can aid in the prevention of nematode infection. Growing citrus trees in suboptimal conditions can exacerbate the situation [1,26,84]. The management of citrus nematode is dependent on optimal orchard management [82]. Soil is another important limiting factor for citrus nematode. Some physicochemical soil variables like soil properties, organic matter, nutrition, fertilizer, and pH can support or hinder the development of high nematode populations either directly or indirectly [9,85–88]. The citrus nematode can attack around 75 plant species, predominantly in the Rutaceae family, with only a few non-rutaceous hosts such as grapevine, persimmon, lilac, and olive [82]. Because of its narrow host range, this nematode can be managed through proper orchard sanitation, equipment management, and low-volume irrigation or drip irrigation [1,8,89]. Some strategies, such as soil solarization, crop rotation, mulching, soil tillage, and weed control can have significant impacts on nematode management [1,8,23,90,91]. Soil biofumigation using Brassicaceae, green manure, botanical plant extracts, composts, animal manure plant debris, oilseed cakes, and crustacean shells are cheaper and

environmentally friendly alternatives to chemical pesticides nematode management but warrant further investigation [92–98]. The use of biological control measures to control *T. semipenetrans* is still in its infancy [82]. Several fungi and bacteria isolated from citrus fields have shown promising but varying effects in controlling the nematode [99–108]. Parasitic fungi used for plant-parasitic nematode control such as citrus nematodes include *Purpureocillium lilacinum* (previously known as *Paecilomyces lilacinus*), *Trichoderma* spp., mycorrhizae (*Glomus* spp.), and *Pochonia chlamydosporia*. Additionally, several nematophagous species, such as *Drechslerella dactyloides*, *Arthrobotrys superba*, *A. oligospora*, *Dactylaria leptospora*, *Da. brochopaga*, *Catenaria anguillulae*, *Dactylellina ellipsospora*, *Myzocyctum* spp., *Nematoconus concurrens*, and *Monacrosporium* spp., also target nematodes in citrus orchards. Among all the listed species *Trichoderma* spp. are among the most used fungi for combating citrus nematodes, there are currently few commercial products approved for use against citrus nematodes. These fungi decrease the number of J2 entering the roots, leading to fewer females in the citrus roots [6].

The harmful effects of several *Bacillus* spp. on PPNs have been demonstrated, with most studies focusing on the effectiveness of experimental spore formulations against *T. semipenetrans*. Like certain fungi, the production of hydrolytic enzymes such as cellulases, proteases, lipases, and  $\beta$ -glucanases is believed to contribute to their pathogenicity [6,109]. Several reports have shown that soil application of *B. subtilis*, either alone or mixed with compost, in greenhouse and field experiments resulted in the mortality of *T. semipenetrans* [6,110–112]. Similarly, *Pseudomonas fluorescens* has shown promising effects in controlling both *T. semipenetrans* and *Meloidogyne* spp. in citrus. The mode of action includes inducing systemic resistance in the host plants and producing various secondary metabolites, including pyoluteorin, 2,4-diacetylphloroglucinol (2,4-DAPG), hydrogen cyanide (HCN), phenazines, and pyrrolnitrin [6,113–115]. The fermentation product of *Streptomyces avermitilis* has demonstrated potential against plant-parasitic nematodes by targeting  $\gamma$ -aminobutyric acid receptors in nematodes, triggering an influx of chloride ions into their cells, which leads to immobility and death, particularly in the J2 stage of nematode [116–119]. The culture filtrate of *S. avermitilis* has been shown to reduce egg hatching of root-knot nematodes and increase J2 mortality. Furthermore, the use of abamectin, isolated from *S. avermitilis*, has proven effective in controlling citrus nematodes under field conditions, reducing their reproduction and increasing crop yield [116,120–122]. *Pasteuria penetrans* is a well-known parasite of *Meloidogyne* spp. The combined application of *P. penetrans* and *P. lilacinum* significantly reduced the citrus nematode population in citrus, as these bacteria parasitize the J2 and female stages [6]. In addition to bacteria and fungi used to control PPNs, some predatory mites (Acari: Mesostigmata) feed on parasitic nematodes. Several mite species like *Cosmolaelaps simplex*, *Gaeolaelaps aculeifer*, *Macrocheles matrius* have been shown to significantly reduce *T. semipenetrans* egg masses, limit the penetration of J2 larvae into citrus roots, and promote seedling growth under greenhouse conditions [6,123,124].

Some work has been initiated to study management strategies for the citrus nematode, but the currently employed strategy is inadequate to effectively manage it. Future research should focus on studying the genetic and molecular mechanisms of infection, developing resistant or tolerant rootstocks against a broad range of pathogens, and improving plant vigor through sustainable and environmentally friendly cultural techniques. Chemical nematicides are expensive and have a broader impact on non-target pests [125,126]. Growers should be encouraged to use resistant varieties and to employ safe, non-chemical alternatives whenever possible.

#### 4. Genomics of *Tylenchulus semipenetrans*: Unraveling the Genetic Basis of Citrus Nematode Pathogenicity

Despite being a ubiquitous pathogen of citrus, genomic and genetic aspects of the *T. semipenetrans* nematode infection remain unknown. The identification of potential nematocidal targets and the creation of long-lasting nematode control could be made possible by a greater understanding of the genome, comparative genomics, behavior, and physiology of these parasites [127,128]. *T. semipenetrans* feeds from the modified non-hypertrophied nurse cells for a prolonged period [22]. Citrus nematode and sedentary endoparasites such as root-knot nematodes and cyst nematode (CN) infective juveniles establish feeding sites in host roots, employing stylets to break the plant cell walls, inject salivary secretions, and withdraw nutrition [21,129–131]. Development of feeding sites occurs after the injection of secreted effector proteins produced in the nematode esophageal glands [18]. Given the substantial losses caused in citrus production by CTV, *Phytophthora*, and HLB, these crucial pathogens have received significant research attention [10–13]. Despite the absence of effective control measures for some of these severe pathogens, there is a thorough understanding of the molecular mechanisms of pathogenicity [10,12,14–17]. The evolutionary origins of PPN effectors, however, have received little attention. Initially, the focus of genomic and transcriptional analysis of PPNs was limited to the genomes of RKN and CN, as well as the transcriptome of the esophageal gland. Several essential effector protein genes were discovered because of this research [131–137]. However, as sequencing and bioinformatics capabilities improved, the focus of research shifted to other PPNs, particularly several migratory and sedentary nematodes [138–143]. Comparative analysis of sequenced PPNs reveals a high degree of conservation in their cell wall modifying effector proteins, which are believed to have been acquired through horizontal gene transfer from bacteria and fungi [144,145].

Given the importance of effector proteins in parasitism, one viable technique for combatting PPNs is to silence the expression of effectors and other important genes [146–150]. Functional genomic techniques like transgenesis, RNA interference (RNAi), and targeted mutagenesis are invaluable in studying the molecular mechanisms by which parasitic nematodes locate and infect their hosts. It may result in the development of measures that inhibit the parasitism caused by them [151–156]. A comprehensive understanding of the effector proteins of PPNs and their roles is crucial. The availability of several RKN genomes has increased the resources available for finding collections of putative effectors in these organisms [127,132,133,157–159]. Developing control strategies for parasitic nematodes, including *T. semipenetrans* infections, presents multiple challenges that cannot be dealt with by a single form of information. Nematode genomics, on the other hand, provides an extensive foundation that includes information on both genomic DNA (gDNA) and transcribed sequences (cDNAs). This valuable resource enhances basic and applied parasitic nematode research to unveil the genetic basis of citrus nematode pathogenicity. Information about the genomics of *T. semipenetrans* is scarce. Future research should focus on genomic analysis, which will be a unique resource to gain deeper insight into the genetic mechanisms behind nematode adaptation to phytoparasitism, which will aid in the development of effective nematode control strategies. Similarly, the availability of large-scale genomics allows for in-silico experiments and the identification of potential targets for future research.

#### 5. Gene Editing Tools for Targeting *T. semipenetrans* in Citrus

The CRISPR/Cas9 system is a versatile gene editing tool widely adopted for targeted genome modifications in various organisms, including plants. CRISPR/Cas has been successfully employed in several plant species to generate resistance against PPNs [160].



Employing CRISPR/Cas for the inactivation of genes that are induced during nematode infestation has been shown to reduce nematode infection; these genes have been reported in many plants [161,162]. The system consists of a Cas9/12 nuclease and a single guide RNA (sgRNA) that directs the nuclease to a specific target site in the genome. Upon binding to the target site, Cas protein introduces a double-strand break (DSB), which is repaired by the cell's endogenous repair machinery, often resulting in targeted gene disruption.

Recently, novel target genes have been identified that could play a role in the establishment of parasitism between RKN and the plant, especially plant nutrient transporters [161]. Inactivation of those genes by RNAi significantly reduced the degree of parasitism [163]. Thus, CRISPR/Cas9 is a promising strategy that has been shown to work in other systems to inactivate multiple target genes simultaneously. One study recently used soybean hairy roots to study the resistance response of knocking out two serine hydroxymethyltransferase genes, *GmSHMT08* and *GmSHMT05* to confirm the role of these genes in soybean cyst nematode (SCN) tolerance [164]. Similarly, another study confirmed that t-SNARE proteins are critical to resisting SCN infection using the CRISPR-Cas9 system [165]. Another study used CRISPR/Cas to knock out *MG1* and its interactor *MGBP1*, in rice and found that this increased susceptibility to *M. graminicola* [166]. *PR10/Bet v1*-like protein knockout in rice increased the susceptibility to *M. graminicola* [167]. Disrupting the function of the previous genes increased plant susceptibility, indicating that these genes are involved in plant tolerance. On the other hand, knocking out other genes increased plant tolerance, for instance, one study employed the CRISPR/Cas9 system to specifically induce targeted mutagenesis of the rice gene copper metallochaperone heavy metal-associated plant protein 04 (*OsHPP04*), and successfully obtained genetically stable homozygous rice mutants, which conferred enhanced resistance against root-knot nematode in rice [168]. Using CRISPR/Cas9 confirmed that *FERONIA*-like receptor kinase homologue in soybean *GmLMM1*, increased plant susceptibility to nematodes [169]. Other studies have found that W-box transcription factor (*SIWRKY45*) in tomatoes [170], MYB transcription factor (*SIMYB57*) in tomatoes [171], malate synthase in cucumber [172], auxin-responsive transcription factors *ARF8A* and *ARF8B* in tomatoes [173], and heavy metal-associated isoprenylated plant protein (*HIPP27*) in *Arabidopsis* all increased plant susceptibility to PPN infection [174]. Table 1 contains candidate genes that CRISPR could target to improve citrus resistance against nematodes.

Despite some developmental work on gene editing tools in root-knot nematodes and cyst nematodes, no work has been initiated to identify gene editing tools against citrus nematodes. Root-knot nematode, cyst nematode, and citrus nematode are closely related species from the same clade of the phylum Nematoda, with somewhat similar biology [175]. Root-knot nematodes and cyst nematodes are endoparasitic, while citrus nematodes are semi-endoparasitic. Both groups of nematodes have some form of host tissue manipulation for feeding. It has been experimentally verified that DNA-based CRISPR reagents might be directly imported from other systems. For example, Cas9 and sgRNA expression plasmids from *C. elegans* were used in the closely related *Caenorhabditis briggsae* [20]. Information about genes identified in RKN and cyst nematode might be directly applicable to citrus nematode biology. Future research should focus on testing those genes that have been validated in previous studies among closely related species of citrus-infecting nematodes.

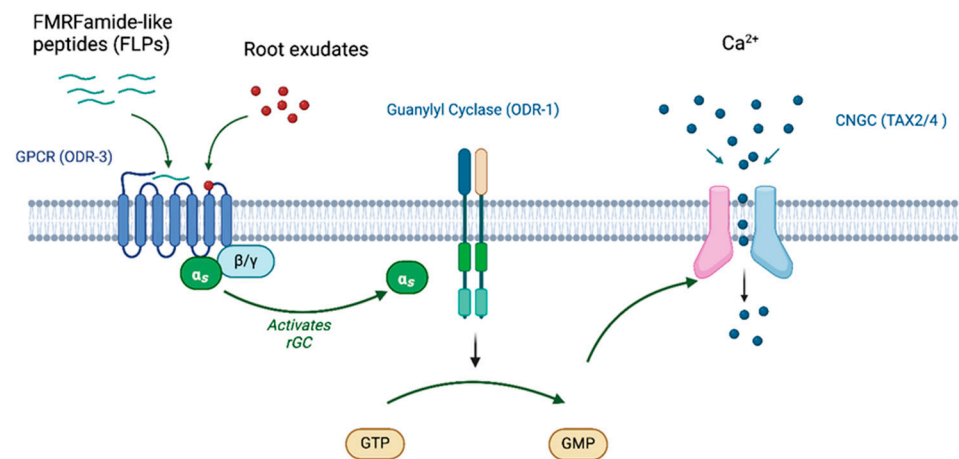
**Table 1.** Detailed list of genes from plants against nematodes and the homologs in citrus adopted from Dutta et al., 2023 [176].

Gene Name	Nematode Species	References	<i>C. reticulata</i>	<i>P. trifoliata</i>	<i>C. sinensis</i>
<i>AtRPE</i>	<i>Meloidogyne incognita</i>	[177]	Cre5g_011050	Pt3g006190	Cs_ont_5g039790
<i>AtETR1</i>			Cre5g_016860	Pt8g005340	Cs_ont_5g033030
<i>AtEIN2</i>	<i>Heterodera schachtii</i>	[178]	Cre6g_004920	Pt6g017960	Cs_ont_6g020590
<i>AtEIN3</i>			Cre2g_028110	Pt2g008350	Cs_ont_2g030110
<i>AtEIR1</i>			Cre4g_023270	Pt1g022280	Cs_ont_4g025100
<i>AtFH6</i>	<i>Meloidogyne incognita</i>	[179]	Cre1g_020750	Pt7g016330	Cs_ont_1g023750
<i>AtMAP65-3</i>	<i>Meloidogyne incognita</i>	[180]	Cre9g_021250	Pt9g017920	Cs_ont_9g024290
<i>AtPME3</i>	<i>Heterodera schachtii</i>	[181]	Cre1g_015230	Pt7g011540	Cs_ont_1g018180
<i>AtWRKY23</i>	<i>Heterodera schachtii</i>	[182]	Cre5g_040580	Pt3g035620	Cs_ont_5g006680
<i>AtADF2</i>	<i>Meloidogyne incognita</i>	[183]	Cre8g_014460	Pt8g009750	Cs_ont_8g003160
<i>AtbHLH25</i>	<i>Heterodera schachtii</i>	[184]	Cre1g_019860	Pt7g015470	Cs_ont_1g022810
<i>AtbHLH 27</i>			Cre4g_023460	Pt1g022100	Cs_ont_4g025270
<i>AtCCS52A1/B</i>	<i>Meloidogyne incognita, Heterodera schachtii</i>	[185]	Cre5g_010030	Pt3g007070	Cs_ont_5g040860
<i>AtKMD3</i>	<i>Meloidogyne incognita</i>	[186]	Cre5g_024520	Pt3g021540	Cs_ont_5g023080
<i>AtAAP1</i>			Cre3g_012800	Pt5g011300	Cs_ont_3g012730
<i>AtAAP2</i>	<i>Heterodera schachtii</i>	[187]	Cre1g_006010	Pt5g024470	Cs_ont_1g006440
<i>AtAAP8</i>			Cre3g_012800	Pt5g011300	Cs_ont_3g012730
<i>AtLBD16</i>	<i>Meloidogyne javanica</i>	[188]	Cre5g_035540	Pt3g030980	Cs_ont_5g011690
<i>AtFTRc</i>	<i>Meloidogyne javanica</i>	[189]	Cre6g_021980	Pt6g001900	Cs_ont_6g002310
<i>AtAAP6</i>	<i>Heterodera schachtii</i>	[190]	Cre8g_008840	Pt5g007900	Cs_ont_3g008880
<i>AtHIP27</i>	<i>Heterodera schachtii</i>	[191]	Cre1g_025260	Pt7g021360	Cs_ont_1g028570
<i>AtSUC2</i>	<i>Heterodera schachtii</i>	[192]	Cre3g_005950	Pt5g005340	Cs_ont_3g006170
<i>AtALF4</i>	<i>Meloidogyne javanica, Heterodera schachtii</i>	[193]	Cre4g_001860	Pt1g000410	Cs_ont_4g001890
Annexin	<i>Meloidogyne incognita</i>	[194]	Cre3g_010750	Pt5g009550	Cs_ont_3g010860
PUCHI	<i>Meloidogyne incognita</i>	[195]	Cre9g_003350	Pt9g003150	Cs_ont_9g003490
<i>AtGAPC1</i>	<i>Meloidogyne incognita</i>	[196]	Cre7g_021220	Pt3g010090	Cs_ont_7g022820
<i>AtABAP1</i>	<i>Meloidogyne incognita</i>	[197]	Cre9g_005030	Pt9g004780	Cs_ont_9g005150
<i>AtSmD1</i>	<i>Meloidogyne incognita</i>	[198]	Cre5g_004500	Pt3g005780	Cs_ont_5g046160
<i>AtADF3</i>	<i>Aphelenchoides besseyi</i>	[199]	Cre8g_014460	Pt8g009750	Cs_ont_8g003160
<i>AtYUC</i>	<i>Meloidogyne incognita, Heterodera schachtii</i>	[200]	Cre4g_003350	Pt1g005780	Cs_ont_4g003410
<i>AtPANC</i>	<i>Heterodera schachtii</i>	[201]	Cre5g_033760	Pt3g029210	Cs_ont_5g013390
<i>AtSWEET1</i>	<i>Meloidogyne incognita</i>	[202]	Cre3g_007760	Pt5g007110	Cs_ont_3g008000
<i>AtABI1/2/5</i>	<i>Heterodera schachtii</i>	[203]	Cre4g_021930	Pt1g023450	Cs_ont_4g023710
<i>AtCYP707A1/A4</i>			Cre6g_021150	Pt6g001140	Cs_ont_6g003200
<i>AtERN1</i>	<i>Meloidogyne incognita</i>	[204]	Cre2g_006010	Pt2g026820	Cs_ont_2g006310

## 6. Host-Seeking Behavior in Plant Parasitic Nematodes (PPNs)

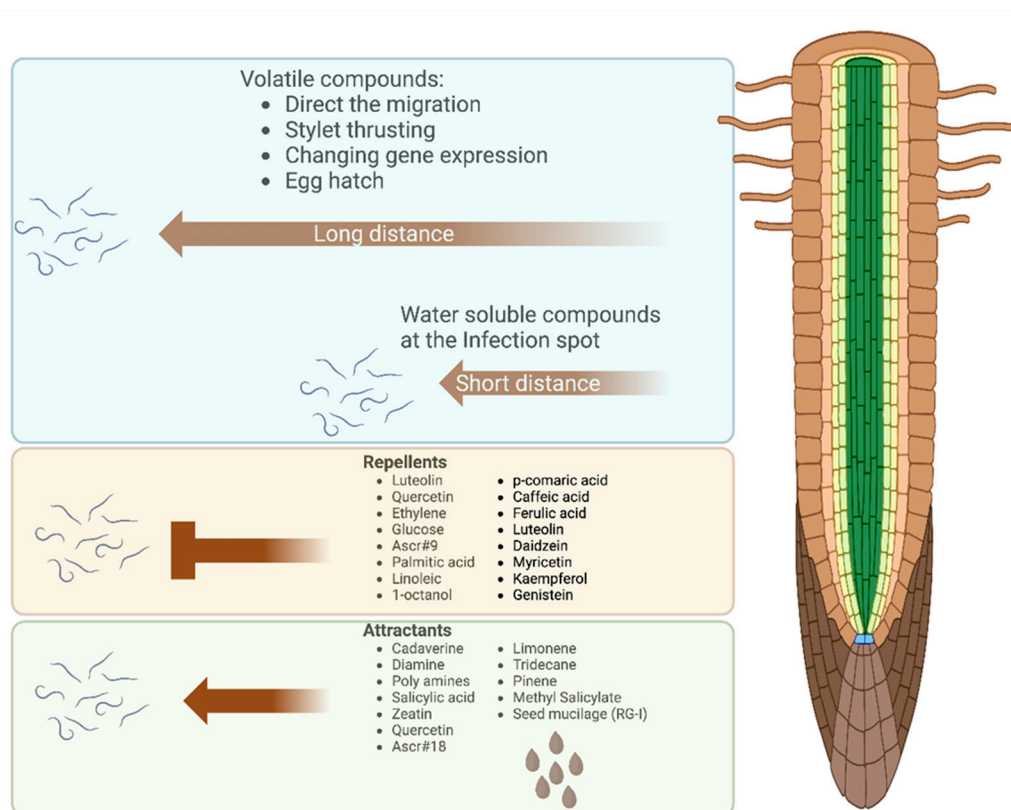
Nematodes use receptors and ion channels to sense small molecules in the surrounding environment and transduce the signals starting from receptors to ion channels. Among these receptors, G-protein coupled receptors (GPCRs) are significant as olfactory receptors that trigger cellular responses by interacting with intracellular heterotrimeric G proteins [205]. In *M. incognita*, putative homologs of four core *C. elegans* proteins for chemotaxis towards water-soluble and volatile chemicals were identified: *odr-1* (rGC), *odr-3* (GPCR), and *tax-2/tax-4* (cyclic nucleotide-gated ion channel). These genes exhibited the highest expression levels in infective juveniles [206]. Knocking down their expression via

RNAi altered nematode chemotaxis towards root exudates and other behaviors [206]. A similar expression pattern was noted for guanylate cyclase (rGC) homologs in SCN [207]. Screening the four proteins ODR-1, ODR-3, TAX-2, and TAX-4 against the proteomes of other PPNs such as *Meloidogyne*, *Heterodera*, and *Globodera* revealed the presence of orthologues with high similarity, indicating that these proteins are likely conserved across nematode species. The molecular mechanisms involved in sensing small molecules and transmitting signals, mediated by these proteins, might be a functional feature across nematode species including citrus nematode (Figure 2 and Supplementary File S1).



**Figure 2.** Different receptors and ion channels are used by plant-parasitic nematodes to sense their environment. The figure was created using Biorender.com.

The behavior of PPNs toward plant extracts, attractants, and repellants determines the interaction between PPNs and their host plants. While volatile compounds serve as long-distance cues for infective RKN juveniles to locate suitable hosts, water-soluble chemicals act as signaling cues within the root region [208]. Recent studies have identified various compounds, such as methyl salicylate, as significant attractants for nematodes in *Capsicum annum*, while others like certain flavonoids exhibit repellent effects [209]. The influence of ethylene on nematode behavior varies depending on the nematode species, with ethylene generally repelling RKN but showing less effects on cyst nematodes [208]. However, specific compounds often repel only particular nematode taxa in specific plant species, indicating the need for specific research about citrus root exudates to understand the spectrum of citrus nematode repellents and their mechanisms of action. Studies of citrus root metabolites under salt stress found a significant amount of palmitic acid, myristic acid, and linoleic acid, which have been previously reported as nematode-repellents [208]. This work highlights the need to test these compounds against citrus nematode. Also, erucic acid, oleic acid, and geraniol have been reported to have nematocidal effects [208] (Figure 3).



**Figure 3.** A summary of the general behavior of plant-parasitic nematodes toward plant extracts, attractants, and repellants that determine the interaction between PPN and their host plants. The top box in the figure illustrates the various cues nematodes use for sensing hosts over long and short distances. The middle box presents different plant-associated repellents, while the bottom box highlights various chemicals that serve as nematode attractants. The figure was created using Biorender.com.

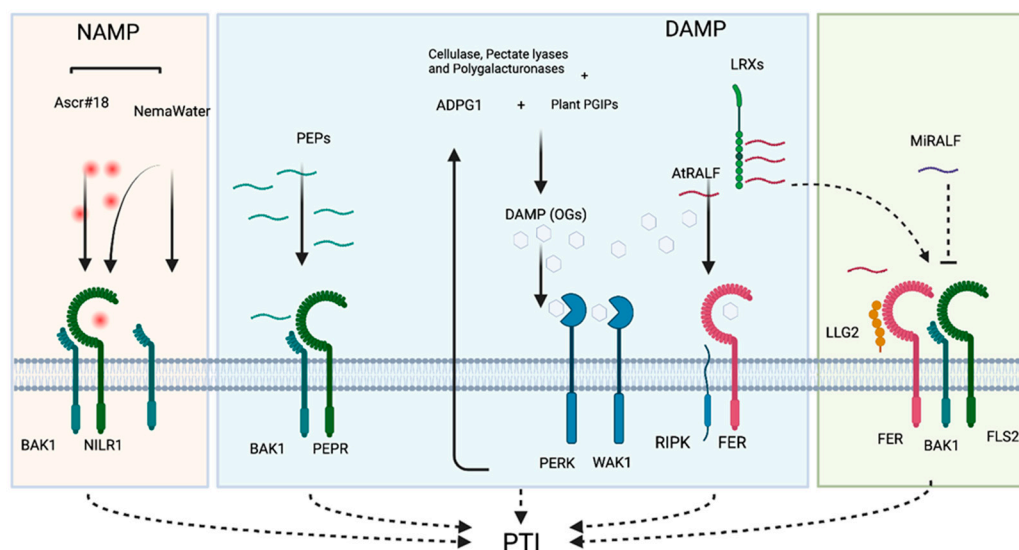
### 6.1. Perception of Nematode-Associated Molecular Patterns (NAMPs) and Damage-Associated Molecular Patterns (DAMPs) by the Host Plant

Damage-associated molecular patterns (DAMPs) represent an aspect of plant defense mechanisms against nematode infections [210]. These DAMPs can originate from various sources within the plant-nematode interaction such as stylet thrusts and nematode body movements [211]. PPNs employ several strategies to mitigate plant defenses by producing cell wall-degrading enzymes, including cellulases, pectate lyases, and polygalacturonases [212–214].

These enzymes facilitate the breakdown of plant cell walls, releasing fragments such as oligogalacturonides (OGs) that function as DAMPs. OGs are fragments resulting from the degradation of cell wall homogalacturonan (HG) [215]. Polygalacturonase-inhibiting proteins (PGIPs), are a class of cell wall proteins that inhibit the pectin-depolymerizing activity of polygalacturonase enzymes, leading to the accumulation of OGs [216]. These OGs can then serve as elicitors of plant immune responses via interactions with wall-associated kinases (WAKs). Studies have demonstrated the differential expression of PGIPs in response to nematode infection in various host genotypes, influencing susceptibility or resistance and OGs contribute to defense against cyst nematodes [217,218].

Proline-rich extensin-like receptor kinases (PERKs) have emerged as key players in the plant defense response against nematodes [219]. Their induction following infection by cyst nematodes (CNs) and root-knot nematodes (RKNs) suggests their involvement in plant-nematode interactions. Experimental evidence, including studies with *perk* mutants, confirmed the role of *perk* genes in attenuating nematode infection by recognizing OGs,

indicating their function as damage-triggered immune receptors. Plant elicitor peptides (PEPs) represent another facet of plant defense against nematodes. Derived from precursor proteins known as PROPEPs, these small peptides are perceived by membrane-bound receptors called PEP receptors (PEPRs). The PEP-PEPR system has been shown to contribute to defense against CNs, as evidenced by experiments with soybean seeds treated with PEPs resulting in reduced infection rates. However, this system does not appear to confer defense against RKNs, indicating specificity in the plant's response to different types of nematode infections [220] (Figure 4). Little is known about the perception of citrus nematodes by plants, but the same or similar pathways are likely used to detect root-knot nematodes, cyst nematodes, and citrus nematodes.



**Figure 4.** Overview of nematode-associated molecular patterns (NAMP) and damage-associated molecular patterns (DAMP) induced by nematodes in the plant because of nematode infection. The image illustrates the various enzymes secreted by nematodes to initiate plant infection, as well as the different receptors that recognize these enzymes and activate pathogen-triggered immunity in response.

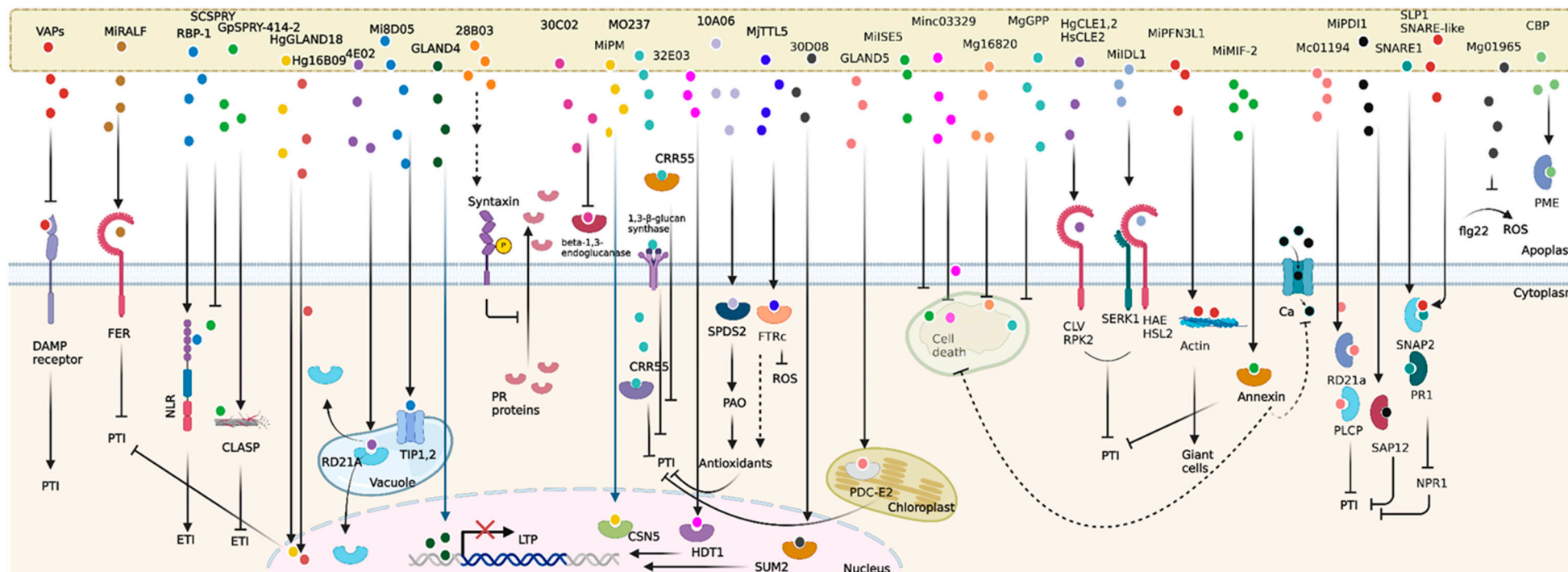
### 6.2. Nematode Effectors and Target Proteins

RKN and cyst nematode (CNs) have evolved parasitism mechanisms in plants, relying on the secretion of effector molecules. These effectors facilitate nematode invasion of the host root, suppressing plant defense responses, and reprogramming root cells to form feeding sites [221,222]. Effectors are mainly produced in the esophageal glands of nematodes and are delivered into plant cells through the stylet [223]. Effector identification has been significantly aided by advancements in sequencing technologies and genomic resources of nematodes. However, these resources are very limited in the case of the citrus nematode, as its genome has not yet been sequenced. Proteomic analyses have directly identified hundreds of proteins secreted by pre-parasitic and parasitic nematode stages [224,225]. Bioinformatic methods, based on the presence of signal peptides for secretory small proteins and peptides, the absence of a transmembrane domain, and the presence of the post-translation modification motifs like glycosylation sites are commonly used to predict candidate effector genes from nematode genomes and other pathogens [226]. Additionally, transcriptomic data have furthered our understanding of nematode gene expression dynamics during parasitism [227]. Previous studies have revealed that nematode effectors target various subcellular compartments within plant cells, including the apoplast, nuclei, and cytoplasm to promote the infection [221] (Figure 5).

Numerous effectors suppress plant immunity by interacting with host proteins involved in the PTI response, such as scavenging reactive oxygen species (ROS) or targeting pathogenesis-related (PR) proteins. Moreover, some effectors modulate plant hormone pathways, thereby promoting changes in hormonal balance that are favorable for nematode parasitism. Effector functions extend beyond immune modulation to directly influence plant gene expression, and the cellular processes involved in nematode-feeding site formation.

Effector proteins have been identified to interact with transcription factors, histones, splicing machinery, altering gene transcription and mRNA processing in host cells. These interactions facilitate the reprogramming of plant gene expression to support nematode parasitism. Furthermore, nematode effectors have been found to interfere with ubiquitin-related processes and suppress cell death responses and hypersensitivity (HR). Certain effectors mimic plant defense-related proteins to interfere with known defense signaling pathways are listed in Table 2.





**Figure 5.** Overview of characterized plant-parasitic nematode effectors and their plant targets. Effectors are secreted by the nematode’s stylet either into the apoplast or directly into the cytoplasm of the host cell. Several effectors target plants, influencing the regulation of reactive oxygen species (ROS) levels or their subsequent reactions. Some groups of effectors possess nuclear localization signals, enabling them to migrate to the nucleus of the feeding site. They can transport plant targets to the nucleus or interact with plant targets already present in the nucleus, thereby altering host responses. In certain interactions, the effectors target plant proteins associated with pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) or effector-triggered immunity (ETI). The figure was created using Biorender.com.

**Table 2.** List of effectors with their target protein in plants involved during interaction of plants and root-knot nematodes (*Meloidogyne* spp.) or plants with cyst-forming nematodes (*Heterodera* spp., and *Globodera* spp.).

A. Effectors Suppressing PTI through ROS Scavenging						
SN.	Effector Name	Nematode Species	Plant Host	Target Protein in Plants	Symptoms	References
1	MjTTL5	<i>Meloidogyne javanica</i>	Arabidopsis	AtFTRc	ROS scavenging	[189]
2	MjNEROS	<i>Meloidogyne javanica</i>	Tomato	ISP in electron transport chain	Suppression of ROS accumulation	[228]
3	MiPDI1	<i>Meloidogyne incognita</i>	Tomato	SAP12	Antioxidant activity	[229]

4	MiCTL1a	<i>Meloidogyne incognita</i>	Tomato	Catalase	Antioxidant enzyme interaction	[230]
5	MgMO289	<i>Meloidogyne graminicola</i>	Rice	OsHPP04	Decreased superoxide radicals in roots	[231]
6	Hs10A06	<i>Heterodera schachtii</i>	Arabidopsis	AtSPDS2	Spermidine production and ROS scavenging	[232]
7	29D09	<i>Globodera rostochiensis</i>	Potato	StHXK1 and StHXK7	Suppression of flg22-ROS production	[233]

**B. Effectors Targeting PR Proteins**

SN.	Effector Name	Nematode Species	Plant Host	Target Protein in Plants	Symptoms	References
1	MgMO237	<i>Meloidogyne graminicola</i>	Rice	OsGSC, OsCRRSP55, OsBetv1	Interaction with multiple PR proteins	[234]
2	Mc01194	<i>Meloidogyne chitwoodi</i>	Arabidopsis	PLCP RD21A	Targeting PLCP RD21A	[235]
3	Hg30C02	<i>Heterodera glycines</i>	Arabidopsis	AtPR2	Increased susceptibility to infection	[236]
4	Hs4E02	<i>Heterodera schachtii</i>	Arabidopsis	AtPR1, AtSNAP2	Suppression of PR protein expression	[237]
5	HsSNARE1	<i>Heterodera schachtii</i>	Arabidopsis	SHMT4	Cell wall-modifying enzyme regulation	[238]
6	HgSLP-1	<i>Heterodera glycines</i>	Soybean	Rhg1 $\alpha$ -SNAP	Resistance protein suppression	[239]
7	GrVAP-1	<i>Globodera rostochiensis</i>	Potato	Unknown	Inhibition of PR1 expression	[240]

**C. Effectors Involved in Feeding Site Formation by Modulating Cytoskeleton and Hormone Interference**

SN.	Effector Name	Nematode Species	Plant Host	Target Protein in Plants	Symptoms	References
1	MiPFN3	<i>Meloidogyne incognita</i>	Tomato	Actin	Favors parasitism	[241]
2	MiMSP32	<i>Meloidogyne incognita</i>	Arabidopsis	12-oxophytodienoate reductase 2 (OPR2)	Favors parasitism	[242]
3	8D05	Root-knot nematode	Arabidopsis	TIP-2	Facilitation of giant cell formation	[243]
4	GpSPRY-414-2	<i>Globodera pallida</i>	Potato	CLASP	Microtubule modification	[244]
5	Hs25A01	<i>Heterodera schachtii</i>	Arabidopsis	AUF1, CHS, eIF-2bs	Regulation of auxin levels	[245]
6	Hs2D01	<i>Heterodera schachtii</i>	Arabidopsis	HAESA (HAE)	Regulation of cell wall-modifying enzymes	[246]
7	Minc00344	<i>Meloidogyne incognita</i>	Soybean	Hub10	Interaction with microtubules in plant cells	[247]
8	Hs19C07	<i>Heterodera schachtii</i>	Arabidopsis	LAX3	Modulation of auxin signaling	[248]
9	HaGLAND5	<i>Meloidogyne incognita</i>	Arabidopsis	Pyruvate dehydrogenase subunit	Interference with SA-mediated defenses	[249]

**D. Effectors Modifying Plant Gene Expression**

SN.	Effector Name	Nematode Species	Plant Host	Target Protein in Plants	Symptoms	References
1	Mi16D10	<i>Meloidogyne incognita</i>	Arabidopsis	SCARECROW-like transcription factors	Modulation of ARF expression	[147]
2	MiEFF18	<i>Meloidogyne incognita</i>	Arabidopsis	SmD1	Alternate splicing modification	[198]
3	MiEFF1	<i>Meloidogyne incognita</i>	Arabidopsis	SCARECROW-like transcription factors	Interaction with transcription factors	[250]
4	MiRALFs	Root-knot nematode	Arabidopsis	FERONIA	Modulation of ABA response	[251]
5	7H08	<i>Meloidogyne incognita</i>	Arabidopsis	LTP gene expression	Induction of LTP gene expression	[252]
6	MaMSP4	<i>Meloidogyne arenaria</i>	Arabidopsis	$\beta$ -galactosidase 11, pectinesterase	Cell wall modification	[253]
7	Mg16820	<i>Meloidogyne graminicola</i>	Arabidopsis	DIP1	Induction of LTP gene expression	[254]
8	Hs30D08	<i>Heterodera schachtii</i>	Arabidopsis	Unknown	Interference with mRNA splicing	[192]
9	Hs32E03	<i>Heterodera schachtii</i>	Arabidopsis	HDT1, FKBP53	Altering histone acetylation	[255]
10	Hs4F01	<i>Heterodera schachtii</i>	Potato	Annexin	Interaction with oxidoreductase family	[256]
11	Hs10A07	<i>Heterodera schachtii</i>	Arabidopsis	IAA16	Modulation of ARF expression	[257]
12	HaVAP2	<i>Heterodera avenae</i>	Barley	CYPRO4-like protein	Interaction in the nucleus	[258]

**E. Effectors Suppressing ETI and HR**

SN.	Effector Name	Nematode Species	Plant Host	Target Protein in Plants	Symptoms	References
1	SPRYSEC-19	<i>Globodera rostochiensis</i>	Tomato	SW5F	Suppression of defense-related cell death	[259]
2	GpRbp-1	<i>Globodera pallida</i>	Potato	RanGAP2, UPL3	Suppression of HR	[260]
3	SPRYSEC-15	<i>Globodera pallida</i>	Potato	NRC2, NRC3	Inhibition of HR-associated cell death	[261]



Sedentary endoparasitic nematodes, such as RKN and CN, are thought to secrete hundreds of effectors. Comparisons of their effector repertoires indicate that while some are conserved across different genera, many are unique proteins with likely distinct roles at the plant-nematode interface [262]. Given the biological similarities between RKN, CN, and citrus nematodes, future research should focus on identifying and analyzing effectors conserved among these species. A key next step is the functional characterization of more citrus nematode effectors. Understanding how these effectors operate within cells, both individually and in combination, as well as identifying citrus-specific plant targets, will be crucial for advancing citrus nematode research.

## 7. Conclusions

Citrus is one of the most valuable agricultural commodities. However, these crops are constantly threatened by a variety of pests and diseases. The effect and mechanism of citrus nematode infection on citrus is an unexplored territory that is responsible for huge economic loss. A deeper understanding of various aspects of *T. semipenetrans* and citrus is crucial for addressing the intricate and evolving challenges posed by nematodes. Embracing resistant breeding allows for the development of citrus varieties with enhanced natural defenses against parasites, reducing the reliance on chemical pesticides and promoting sustainable agricultural practices. Genomic and molecular research unravels the intricate genetic mechanisms underlying resistance, facilitating targeted interventions and the identification of key molecular markers for breeding programs and potential key targets for nematode control. Integrated pest management approaches offer a holistic and environmentally friendly solution by combining biological, cultural, and chemical control methods, thereby minimizing the ecological impact of pest control practices. Recent research advancements on other sedentary endoparasitic nematodes, such as *Meloidogyne* and *Heterodera*, focus on key aspects of nematode biology that have long interested nematologists and parasitologists. These studies aim to uncover the genetic and molecular mechanisms underlying parasitism and interactions with host plants. The biology of these nematodes shares similarities with citrus nematodes. As we learn more about these species, it becomes evident that they utilize common developmental strategies to adapt to a wide range of environments. This shared biology suggests that insights gained from one species could be applicable to others. Such a multidisciplinary approach not only strengthens the resilience of citrus crops against pests but also supports long-term agricultural sustainability.

**Supplementary Materials:** The following supporting information can be downloaded at: [www.mdpi.com/xxx/s1](http://www.mdpi.com/xxx/s1), Supplementary Table S1: Tolerance and susceptibility of a wide range of rootstocks. The same rootstocks are tolerant in some areas or studies and sensitive in others, indicating adaptation of *T. semipenetrans* against the defense mechanism and/or the environmental conditions.[263]. Supplementary File S1: Phylogenetic analysis revealing the similarity of putative homologs of four essential *C. elegans* proteins involved in chemotaxis to water-soluble and volatile chemicals: *odr-1* (rGC), *odr-3* (GPCR), and *tax-2/tax-4* (cyclic nucleotide-gated ion channels), conserved in root-knot and cyst nematodes.

**Author Contributions:** A.B. and O.Z. Drafting and writing of the manuscript; A.B., O.Z., A.R.D., J.A. and D.S. conceptualizing of the review, writing different sections, and editing of the manuscript. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by USDA Farm Bill Multistate Project: W5185, California Department of Food and Agriculture (CDFA # 21-0001-052-SF), and the USDA National Institute of Food and Agriculture grant: 2022-70029-38471.

**Data Availability Statement:** No new data were created or analyzed in this study.

**Acknowledgments:** All the figures used in the manuscript are drawn using the Biorender.com application.

**Conflicts of Interest:** The authors declare no conflicts of interest.

## Abbreviations

Ascr	Ascaroside
BAK1	BRI1-Associated Kinase1
BKK1	BAK1-Like Kinase1
DAMP	Damage-associated molecular pattern
DORN1	Does not Respond to Nucleotides1
eATP	Extracellular adenosine triphosphate
EFR	Elongation factor Tu receptor
FLS2	Flagellin sensitive2
GPCRs	G-protein coupled receptors
HMGB	High mobility group box protein
JA	Jasmonic acid
MAMP	Microbe-associated molecular pattern
MAPK	Mitogen-activated protein kinase
NAMP	Nematode-associated molecular pattern
NMR	Nuclear magnetic resonance
OG	Oligogalacturonides
Pep	Plant elicitor peptide
PEPR	Pep receptor
PGIPs	Polygalacturonase-inhibiting proteins
PERKs	Proline-rich extensin-like receptor kinases
PRR	Pattern recognition receptor
ROS	Reactive oxygen species
SA	Salicylic acid
VAPs	venom allergen-like protein
WAK1	Wall-associated kinase1

## References

- Verdejo-Lucas, S.; Mckenry, M. V Management of the Citrus Nematode, *Tylenchulus semipenetrans*. *J. Nematol.* **2004**, *36*, 424–432.
- Crozzoli, R. Nematodes of Tropical Fruit Crops in Venezuela. In *Integrated Management of Fruit Crops Nematodes*; Ciancio, A., Mukerji, K.G., Eds.; Springer: Dordrecht, The Netherlands, 2009; Volume 4, pp. 63–84.
- Duncan, L.W. Nematode Parasites of Citrus. In *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture*, 2nd ed.; Luc, M., Sikora, R.A., Bridge, J., Eds.; CABI Publishing: Wallingford, UK, 2005; pp. 437–466, ISBN 0851997279.
- Ghaderi, R.; Hosseinvand, M. Non-Chemical Management of the Citrus Nematode, *Tylenchulus semipenetrans* (Nematoda: Tylenchulidae). In *Sustainability in Plant and Crop Protection, Vol 1: Organic Management*; Chaudhary, K.K., Meghvansi, M.K., Eds.; Springer: Cham, Switzerland, 2022; Volume 1, pp. 217–245.
- Esser, R.P.; Smith, G.T.; O'Bannon, J.M. *An Eleven Year Phytoparasitic Nematode Survey of Florida Citrus Grooves and Their Environs*; Florida Department of Agriculture and Consumer Services, Division of Plant Industry: Miami, FL, USA, 1993.
- Kumar, K.K.; Arthurs, S. Recent Advances in the Biological Control of Citrus Nematodes: A Review. *Biol. Control* **2021**, *157*, 104593. <https://doi.org/10.1016/J.BIOCONTROL.2021.104593>.
- Sorribas, F.J.; Verdejo-Lucas, S.; Forner, J.B.; Alcaidel, A.; Pons, J.; Ornat, C. Seasonality of *Tylenchulus semipenetrans* Cobb and *Pasteuria* sp. in Citrus Orchards in Spain. *J. Nematol.* **2000**, *32*, 622–632.
- Duncan, L.W. Managing Nematodes In Citrus Orchards. In *Integrated Management of Fruit Crops Nematodes*; Ciancio, A., Mukerji, K.G., Eds.; Springer: Dordrecht, The Netherlands, 2009; pp. 135–174.
- Duncan, L.W.; Cohn, E. Nematode Parasites of Citrus. In *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture*; Luc, M., Sikora, R.A., Bridge, J., Eds.; CAB International: Wallingford, UK, 1990; pp. 321–346, ISBN 9780851.
- Graham, J.; Feichtenberger, E. Citrus Phytophthora Diseases: Management Challenges and Successes. *J. Citrus Pathol.* **2015**, *21*–11 <https://doi.org/10.5070/C421027203>.

11. Hao, W.; Miles, T.D.; Martin, F.N.; Browne, G.T.; Förster, H.; Adaskaveg, J.E. Temporal Occurrence and Niche Preferences of *Phytophthora* spp. Causing Brown Rot of Citrus in the Central Valley of California. *Phytopathology* **2018**, *108*, 384–391.
12. Moreno, P.; Ambrós, S.; Albiach-Martí, M.R.; Guerri, J.; Peña, L. Citrus tristeza virus: A Pathogen That Changed the Course of the Citrus Industry. *Mol. Plant Pathol.* **2008**, *9*, 251–268. <https://doi.org/10.1111/J.1364-3703.2007.00455.X>.
13. Wang, N. The Citrus Huanglongbing Crisis and Potential Solutions. *Mol. Plant* **2019**, *12*, 607–609. <https://doi.org/10.1016/J.MOLP.2019.03.008>.
14. Folimonova, S.Y. Developing an Understanding of Cross-Protection by Citrus tristeza virus. *Front. Microbiol.* **2013**, *4*, 46301. <https://doi.org/10.3389/FMICB.2013.00076/BIBTEX>.
15. Gaikwad, P.N.; Sharma, V.; Singh, J.; Sidhu, G.S.; Singh, H.; Omar, A.A. Biotechnological Advancements in Phytophthora Disease Diagnosis, Interaction and Management in Citrus. *Sci. Hort.* **2023**, *310*, 111739. <https://doi.org/10.1016/J.SCI-ENTA.2022.111739>.
16. Thakuria, D.; Chaliha, C.; Dutta, P.; Sinha, S.; Uzir, P.; Singh, S.B.; Hazarika, S.; Sahoo, L.; Kharbikar, L.L.; Singh, D. Citrus Huanglongbing (HLB): Diagnostic and Management Options. *Physiol. Mol. Plant Pathol.* **2023**, *125*, 102016. <https://doi.org/10.1016/J.PMPP.2023.102016>.
17. Gottwald, T.R. Current Epidemiological Understanding of Citrus Huanglongbing. *Annu. Rev. Phytopathol.* **2010**, *48*, 119–139.
18. Jones, J.T.; Haegeman, A.; Danchin, E.G.J.; Gaur, H.S.; Helder, J.; Jones, M.G.K.; Kikuchi, T.; Manzanilla-López, R.; Palomares-Rius, J.E.; Wesemael, W.M.L.; et al. Top 10 Plant-Parasitic Nematodes in Molecular Plant Pathology. *Mol. Plant Pathol.* **2013**, *14*, 946–961. <https://doi.org/10.1111/MPP.12057>.
19. Kantor, M.; Handoo, Z.; Kantor, C.; Carta, L. Top Ten Most Important U.S.-Regulated and Emerging Plant-Parasitic Nematodes. *Horticulturae* **2022**, *8*, 208. <https://doi.org/10.3390/HORTICULTURAE8030208>.
20. Ward, J.D. Rendering the Intractable More Tractable: Tools from *Caenorhabditis elegans* Ripe for Import into Parasitic Nematodes. *Genetics* **2015**, *201*, 1279. <https://doi.org/10.1534/GENETICS.115.182717>.
21. Jones, M.G.K. Host Cell Responses to Endoparasitic Nematode Attack: Structure and Function of Giant Cells and Syncytia. *Ann. Appl. Biol.* **1981**, *97*, 353–372. <https://doi.org/10.1111/j.1744-7348.1981.tb05122.x>.
22. Palomares-Rius, J.E.; Escobar, C.; Cabrera, J.; Vovlas, A.; Castillo, P. Anatomical Alterations in Plant Tissues Induced by Plant-Parasitic Nematodes. *Front. Plant Sci.* **2017**, *8*, 1987. <https://doi.org/10.3389/FPLS.2017.01987/BIBTEX>.
23. Pretorius, M.C.; Le Roux, H.F. Nematode Pests of Citrus. In *Nematology in South Africa: A View from the 21st Century*; Fourie, H., Spaul, V.W., Jones, R.K., Daneel, M.S., De Waele, D., Eds.; Springer International Publishing: Berlin/Heidelberg, Germany, 2017; pp. 311–324, ISBN 9783319442105.
24. *Tylenchulus semipenetrans* (Citrus Root Nematode). In *PlantwisePlus Knowledge Bank*; CABI Publishing: Wallingford, UK, 2021.
25. Handoo, Z.A.; Nyczepir, A.P.; Esmenjoud, D.; Van Der Beek, J.G.; Castagnone-Sereno, P.; Carta, L.K.; Skantar, A.M.; Higgins, J.A. Morphological, Molecular, and Differential-Host Characterization of *Meloidogyne floridensis* n. sp. (Nematoda: Meloidogynidae), a Root-Knot Nematode Parasitizing Peach in Florida. *J. Nematol.* **2004**, *36*, 20–35.
26. Van Gundy, S.; Martin, J.P. Influence of *Tylenchulus semipenetrans* on the Growth and Chemical Composition of Sweet Orange Seedlings in Soils of Various Exchangeable Cation Ratios. *Phytopathology* **1961**, *51*, 146–151.
27. Van Gundy, S.D.; Kirkpatrick, J.D. Nature of Resistance in Certain Citrus Rootstocks to Citrus Nematode. *Phytopathology* **1996**, *54*, 419–427.
28. Verdejo-Lucas, S. Pre-Planting Solutions for the Slow Decline of Citrus Caused by *Tylenchulus semipenetrans*. In *Integrated Nematode Management: State-of-the-Art and Visions for the Future*; Sikora, R.A., Desaegeer, J., Molendijk, L., Eds.; CABI International: Wallingford, UK, 2021; pp. 174–181, ISBN 9781789247558.
29. Maafi, Z.T.; Ebrahimi, Y.; Anvari, F. Evaluation of the Resistance of Some Citrus Rootstocks to *Tylenchulus semipenetrans* in Mazandaran Province. *Iran. J. Plant Pathol.* **2000**, *36*, Pe189–Pe196.
30. Mashela, P.W.; Nthangeni, M.E. Osmolyte Allocation in Response to *Tylenchulus semipenetrans* Infection, Stem Girdling, and Root Pruning in Citrus. *J. Nematol.* **2002**, *34*, 273–277.
31. Hamid, G.A.; van Gundy, S.D.; Lovatt, C.J. Phenologies of the Citrus Nematode and Citrus Roots Treated with Oxamyl. In *Proceedings of the Sixth International Citrus Congress Middle-East, Tel Aviv, Israel, 6–11 March 1988; Volume 2*, pp. 993–1004.
32. Safdar, A.; Javed, N.; Aleem Khan, S.; Safdar, H.; Haq, I.U.; Abbas, H.; Ullah, Z. Synergistic Effect of a Fungus, *Fusarium semitectum*, and a Nematode, *Tylenchulus semipenetrans*, on Citrus Decline. *Pakistan J. Zool.* **2013**, *45*, 643–651.
33. Van Gundy, S.D. The Life History of the Citrus Nematode, *Tylenchulus semipenetrans* Cobb. *Nematologica* **1958**, *3*, 283–294.

34. Bozbuga, R.; Yildiz, S.; Yuksel, E.; Özer, G.; Dababat, A.A.; İmren, M. Nematode–Citrus Plant Interactions: Host Preference, Damage Rate and Molecular Characterization of Citrus Root Nematode *Tylenchulus semipenetrans*. *Plant Biol.* **2023**, *25*, 871–879. <https://doi.org/10.1111/PLB.13566>.
35. O'Bannon, J.H.; Radewald, J.D.; Tomerlin, A.T. Population Fluctuation of Three Parasitic Nematodes in Florida Citrus. *J. Nematol.* **1972**, *4*, 194.
36. Philis, I. Yield Loss Assessment Caused by the Citrus Nematode *Tylenchulus semipenetrans* on Valencia Oranges in Cyprus. *Nematol. Mediterr.* **1989**, *17*, 5–6.
37. Ruiz, M.; Vo, A.D.; Becker, J.O.; Roose, M.L. Real-Time PCR to Phenotype Resistance to the Citrus Nematode *Tylenchulus semipenetrans* Cobb. *Plants* **2023**, *12*, 2543. <https://doi.org/10.3390/PLANTS12132543/S1>.
38. Agarwal, S.; Curran, Z.C.; Yu, G.; Mishra, S.; Baniya, A.; Bogale, M.; Hughes, K.; Salichs, O.; Zare, A.; Jiang, Z.; et al. Plant Parasitic Nematode Identification in Complex Samples with Deep Learning. *J. Nematol.* **2023**, *55*, 20230045. <https://doi.org/10.2478/JOFNEM-2023-0045>.
39. Shabrina, N.H.; Lika, R.A.; Indarti, S. Deep Learning Models for Automatic Identification of Plant-Parasitic Nematode. *Artif. Intell. Agric.* **2023**, *7*, 1–12. <https://doi.org/10.1016/J.AIIA.2022.12.002>.
40. Duncan, L.W.; Ferguson, J.J.; Dunn, R.A.; Noling, J.W. Application of Taylor's Power Law to Sample Statistics of *Tylenchulus semipenetrans* in Florida Citrus. *J. Nematol.* **1989**, *21*, 707.
41. Pun, T.B.; Neupane, A.; Koech, R. Quantification of Root-Knot Nematode Infestation in Tomato Using Digital Image Analysis. *Agronomy* **2021**, *11*, 2372. <https://doi.org/10.3390/AGRONOMY11122372>.
42. Bock, C.H.; Poole, G.H.; Parker, P.E.; Gottwald, T.R. Plant Disease Severity Estimated Visually, by Digital Photography and Image Analysis, and by Hyperspectral Imaging. *CRC Crit. Rev. Plant Sci.* **2010**, *29*, 59–107. <https://doi.org/10.1080/07352681003617285>.
43. Bogale, M.; Baniya, A.; Digennaro, P. Nematode Identification Techniques and Recent Advances. *Plants* **2020**, *9*, 1260. <https://doi.org/10.3390/PLANTS9101260>.
44. Mathabatha, R.V.; Mashela, P.W.; Mokgalong, N.M.; Dube, Z.P. Potential Existence of Multiple *Tylenchulus semipenetrans* Biotypes in South Africa. *Acta Agric. Scand.* **2015**, *65*, 673–679. <https://doi.org/10.1080/09064710.2015.1044464>.
45. Mashela, P.W.; Mafeo, T.P.; Pofu, K.M.; Shimelis, H.A. *Tylenchulus semipenetrans* Biotype in Six Citrus-Producing Provinces of the Republic of South Africa. *Acta Hortic.* **2012**, *928*, 369–374. <https://doi.org/10.17660/ACTAHORTIC.2012.928.49>.
46. Kwaye, R.G.; Mashela, P.W.; Shimelis, H.; Mapope, N. Determination of *Tylenchulus semipenetrans* Biotype in Zebediela and Champagne, Republic of South Africa. *Plant Dis.* **2008**, *92*, 639–641. <https://doi.org/10.1094/PDIS-92-4-0639>.
47. Inserra, R.N.; Vovlas, N.; O'Bannon, J.H.; Esser, R.P. *Tylenchulus graminis* n. sp. and *T. palustris* n. sp. (Tylenchulidae), from Native Flora of Florida, with Notes on *T. semipenetrans* and *T. furcus*. *J. Nematol.* **1988**, *20*, 266.
48. Verdejo-Lucas, S.; Kaplan, D.T. The Citrus Nematode: *Tylenchulus semipenetrans*. In *Plant Resistance to Parasitic Nematodes*; Starr, J.L., Cook, R., Bridge, J., Eds.; CABI Publishing: Wallingford, UK, 2002; pp. 207–219. <https://doi.org/10.1079/9780851994666.0207>.
49. Reighard, G.L.; Loreti, F. Rootstock Development. In *The Peach: Botany, Production and Uses*; Layne, D., Bassi, D., Eds; CABI Publishing: Wallingford, UK, 2008; pp. 193–220. <https://doi.org/10.1079/9781845933869.0193>.
50. Legua, P.; Bellver, R.; Forner, J.B.; Forner-Giner, M.A.; Arthur, E.; Francisco, B. Trifoliata Hybrids Rootstocks for “Lane Late” Navel Orange in Spain. *Sci. Agric.* **2011**, *68*, 548–553. <https://doi.org/10.1590/S0103-90162011000500006>.
51. Gottlieb, Y.; Cohn, E.; Spiegel-Roy, P. Biotypes of the Citrus Nematode (*Tylenchulus semipenetrans* Cobb) in Israel. *Phytoparasitica* **1986**, *14*, 193–198.
52. Spiegel-Roy, P.; Vardi, A.; Elhanati, A.; Solel, Z.; Bar-Joseph, M. Rootstock Selections from a Poorman Orange X Poncirus trifoliata Cross. In *Citriculture, Proceedings of the Sixth International Citrus Congress: Middle-East, Tel Aviv, Israel, 6–11 March 1988*; Goren, R., Mendel, K., Goren, N., Eds.; Balaban: Rehovot, Israel, 1988. <https://doi.org/10.3/JQUERY-UI.JS>.
53. Uzun, A.; Gulsen, O.; Seday, U.; Yesiloglu, T.; Aka-Kacar, Y.; Tuzcu, O. Investigation of Genetic Relationships among Trifoliata Oranges and Their Hybrid Relatives Based on ISSR Markers. *Rom. Biotechnol. Lett.* **2011**, *16*, 6431.
54. Cuenca Ibanez, J. Mechanisms of Sexual Polyploidization and Inheritance in Triploid Citrus Populations. Ph.D. Dissertation, Universidad Politecnica de Valencia, Valencia, Spain, 2013.
55. Kevin Lacey; Foord, G.; Perth, S. *Citrus Rootstocks for Western Australia*; Department of Agriculture and Food Farmnote, 2006; Note: 155, South Perth, Australia
56. Sorribas, F.J.; Verdejo-Lucas, S.; Pastor, J.; Ornat, C.; Pons, J.; Valero, J. Population Densities of *Tylenchulus semipenetrans* Related to Physicochemical Properties of Soil and Yield of Clementine Mandarin in Spain. *Plant Dis.* **2008**, *92*, 445–450. <https://doi.org/10.1094/PDIS-92-3-0445>.

57. Ayazpour, K.; Aboutalebi, A.; Pakniyat, M. Evaluation of the Resistance of Some Citrus Rootstocks to the Citrus Nematode, *Tylenchulus semipenetrans*, in Fars Province, Iran. *Plant Protect. J.* **2009**, *1*, 289–296.
58. Verdejo-Lucas, S.; Galeano, M.; Sorribas, F.J.; Forner, J.B.; Alcaide, A. Effect on Resistance to *Tylenchulus semipenetrans* of Hybrid Citrus Rootstocks Subjected to Continuous Exposure to High Population Densities of the Nematode. *Eur. J. Plant Pathol.* **2003**, *109*, 427–433.
59. Iqbal, M.; Mukhtar, T.; Ahmad, R.; Khan, H. Relative Susceptibility/Resistance of Citrus Rootstocks to Citrus Nematode (*Tylenchulus semipenetrans*). *Pak. J. Nematol.* **2005**, *23*, 311–315.
60. Javed, J.; Javed, M.; Anwar, S.A.; Chohan, R.A. Population Dynamics of Citrus Nematode *Tylenchulus semipenetrans* in Citrus Orchards in Different Citrus Growing Districts of Punjab. *Pak. J. Phytopath.* **2008**, *19*, 90–93.
61. Louzada, E.S.; Del Rio, H.S.; Sétamou, M.; Watson, J.W.; Swietlik, D.M. Evaluation of Citrus Rootstocks for the High PH, Calcareous Soils of South Texas. *Euphytica* **2008**, *164*, 13–18.
62. Verdejo-Lucas, S.; Sorribas, F.J.; Forner, J.B.; Alcaide, A. Screening Hybrid Citrus Rootstocks for Resistance to *Tylenchulus semipenetrans* Cobb. *HortScience* **1997**, *32*, 1116–1119. <https://doi.org/10.21273/HORTSCI.32.6.1116>.
63. Galeano, M.; Verdejo-Lucas, S.; Sorribas, F.J.; Ornat, C.; Forner, J.B.; Alcaide, A. New Citrus Selections from Cleopatra Mandarin × *Poncirus trifoliata* with Resistance to *Tylenchulus semipenetrans* Cobb. *Nematology* **2003**, *5*, 227–234. <https://doi.org/10.1163/156854103767139725>.
64. Gottlieb, Y.; Cohn, E. Pinchas Spiegel-Roy Assessing Resistance of Citrus Rootstocks to *Tylenchulus semipenetrans* with Rooted Leaves. *Rev. Nématologie* **1987**, *10*, 119–121.
65. Baines, R.C.; Cameron, J.W.; Soost, R.K. Four Biotypes of *Tylenchulus semipenetrans* in California Identified, and Their Importance in the Development of Resistant Citrus Rootstocks. *J. Nematol.* **1974**, *6*, 63.
66. Duncan, L.W.; Inserra, R.N.; O'Bannon, J.H.; El-Morshedy, M.M. Reproduction of a Florida Population of *Tylenchulus semipenetrans* on Resistant Citrus Rootstocks. *Plant Dis.* **1994**, *78*, 1067–1071. <https://doi.org/10.1094/PD-78-1067>.
67. Regmi, H.; Desaegeer, J. Integrated Management of Root-Knot Nematode (*Meloidogyne* spp.) in Florida Tomatoes Combining Host Resistance and Nematicides. *Crop Prot.* **2020**, *134*, 105170. <https://doi.org/10.1016/J.CROPRO.2020.105170>.
68. Becker, J.O.; Westerdahl, B.B. Agriculture: Citrus Pest Management Guidelines/Nematodes. In *UC IPM Pest Management Guidelines: Citrus UC ANR Publication 3441*; University of California Agriculture and Natural Resources: Davis, CA, USA, 2018.
69. Klose, S.; Ajwa, H.A.; Browne, G.T.; Subbarao, K.V.; Martin, F.N.; Fennimore, S.A.; Westerdahl, B.B. Dose Response of Weed Seeds, Plant-Parasitic Nematodes, and Pathogens to Twelve Rates of Metam Sodium in a California Soil. *Plant Dis.* **2008**, *92*, 1537–1546. <https://doi.org/10.1094/PDIS-92-11-1537>.
70. Sweelam, M.E.; Omran, I.M.; Said, M.; Korah, A. Effect of Some Biological Nematicides Combined with Oxamyl in the Control of Citrus Nematode, *Tylenchulus semipenetrans*. *Egypt. J. Crop Prot.* **2021**, *16*, 1–10. <https://doi.org/10.21608/EJCP.2021.109799.1001>.
71. Antônio, L.; Kovaleski, M.; Deuner, C.C.; Bazh, E.; Minufya, A.; Antônio Ebone, L. Nematicides: History, Mode, and Mechanism Action. *Plant Sci. Today* **2019**, *6*, 91–97. <https://doi.org/10.14719/PST.2019.6.2.468>.
72. Wu, H.Y.; de Oliveira Silva, J.; Becker, J.S.; Becker, J.O. Fluazaindolizine Mitigates Plant-Parasitic Nematode Activity at Sublethal Dosages. *J. Pest. Sci.* **2021**, *94*, 573–583.
73. Maleita, C.; Esteves, I.; Chim, R.; Fonseca, L.; Braga, M.E.M.; Abrantes, I.; De Sousa, H.C. Naphthoquinones from Walnut Husk Residues Show Strong Nematicidal Activities against the Root-Knot Nematode *Meloidogyne hispanica*. *ACS Sustain. Chem. Eng.* **2017**, *5*, 3390–3398.
74. Ntalli, N.G.; Caboni, P. Botanical Nematicides: A Review. *J. Agric. Food Chem.* **2012**, *60*, 9929–9940.
75. Abdel-Rahman, F.H.; Alaniz, N.M.; Saleh, M.A. Nematicidal Activity of Terpenoids. *J. Environ. Sci. Health* **2012**, *48*, 16–22. <https://doi.org/10.1080/03601234.2012.716686>.
76. Meher, H.C.; Gajbhiye, V.T.; Chawla, G.; Singh, G. Virulence Development and Genetic Polymorphism in *Meloidogyne incognita* (Kofoid & White) Chitwood after Prolonged Exposure to Sublethal Concentrations of Nematicides and Continuous Growing of Resistant Tomato Cultivars. *Pest Manag. Sci.* **2009**, *65*, 1201–1207. <https://doi.org/10.1002/PS.1810>.
77. Roberts, P.A. Influence of Nematicides on Nematode Pathogens and Their Host Plants. In *Pesticide Interactions in Crop Production*; Altman, J., Ed.; CRC Press: Boca Raton, FL, USA, 2018; pp. 335–352, ISBN 9781351075459.
78. Abd-Elgawad, M.; McSorley, R. Movement of Citrus Nematode-Infested Material onto Virgin Land: Detection, Current Status and Solutions with Cost-Benefit Analysis for Egypt. *Egypt J. Agronematol.* **2009**, *7*, 35–48.
79. Abd-Elgawad, M.; El-Mougy, N.; El-Gamal, N.; Abdel-Kader, M.; Mohamed, M. Protective Treatments against Soilborne Pathogens in Citrus Orchards. *J. Plant Prot. Res.* **2010**, *50*, 477–484. <https://doi.org/10.2478/V10045-010-0079-0>.

80. Abd-Elgawad, M.; Koura, F.F.H.; Montasser, S.A.; Hammam, M.M.A. Distribution and Losses of *Tylenchulus semipenetrans* in Citrus Orchards on Reclaimed Land in Egypt. *Nematology* **2016**, *18*, 1141–1150. <https://doi.org/10.1163/15685411-00003020>.
81. Abd-Elgawad, M. Managing Nematodes in Egyptian Citrus Orchards. *Bull. Natl. Res. Cent.* **2020**, *44*, 41. <https://doi.org/10.1186/S42269-020-00298-9>.
82. Shokoohi, E.; Duncan, L.W. Nematode Parasites of Citrus. In *Plant Parasitic Nematodes in Subtropical and Tropical Agriculture*; Sikora, R.A., Coyne, D., Hallmann, J., Timper, P., Eds.; CAB International: Wallingford, UK, 2018; pp. 446–476.
83. Inserra, R.N.; Stanley, J.D.; O'Bannon, J.H.; Esser, R.P. Nematode Quarantine and Certification Programmes Implemented in Florida. *Nematol. Mediterr.* **2005**, *33*.
84. Tanha Maafi, Z.; Damadzadeh, M. Incidence and Control of the Citrus Nematode, *Tylenchulus semipenetrans* Cobb, in the North of Iran. *Nematology* **2008**, *10*, 113–122. <https://doi.org/10.1163/156854108783360096>.
85. O'Bannon, J.H. The Influence of an Organic Soil Amendment on Infectivity and Reproduction of *Tylenchulus semipenetrans* on Two Citrus Rootstocks. *Phytopathology* **1968**, *58*, 597–601.
86. Navas, A.; Nombela, G.; Bello, A. Caracterización de La Modalidad de Distribución de *Tylenchulus semipenetrans* En El Levante Español. *Nematropica* **1992**, *22*, 205–216.
87. Ardakani, A.S.; Tanha Mafi, Z.; Mokaram Hesar, A.; Mohammadi Goltappeh, E. Relationship between Soil Properties and Abundance of *Tylenchulus semipenetrans* in Citrus Orchards, Kohgiluyeh va Boyer-Ahmad Province. *J. Agri. Sci. Technol.* **2014**, *16*, 1699–1710.
88. Van Gundy, S.D.; Martin, J.P.; Tsao, P.H. Some Soil Factors Influencing Reproduction of the Citrus Nematode and Growth Reduction of Sweet Orange Seedlings. *Phytopathology* **1964**, *54*, 294–299.
89. Duncan, L.W.; Mashela, P.; Ferguson, J.; Graham, J.; Abou-Setta, M.M.; El-Morshedy, M.M. Estimating Crop Loss in Orchards with Patches of Mature Citrus Trees Infected by *Tylenchulus semipenetrans*. *Nematropica* **1995**, *25*, 43–51.
90. Esmenjaud, D.; Bouquet, A. Selection and Application of Resistant Germplasm for Grapevine Nematodes Management. In *Integrated Management of Fruit Crops Nematodes*; Ciancio, A., Mukerji, K.G., Eds.; Springer: Dordrecht, The Netherlands, 2009; pp. 195–214.
91. Pakniyat, M. Effective Control of Citrus Nematode (*Tylenchulus semipenetrans*) by Individual Canopy Soil Solarization of Infected Sweet Orange Trees. *Iran. J. Plant Pathol.* **2014**, *50*, Pe79–Pe93.
92. Ayazpour, K.; Hasanzadeh, H.; Arabzadegan, M.S. Evaluation of the Control of Citrus Nematode (*Tylenchulus semipenetrans*) by Leaf Extracts of Many Plants and Their Effects on Plant Growth. *Afr. J. Agric. Res.* **2010**, *5*, 1876–1880.
93. Elzawahry, A.; Elzawahry, A.M.; Mahran, A.M.A.; Sallam, M.A. Management of Citrus Nematode (*Tylenchulus semipenetrans*) by Certain Plant Species. *J. Phytopatho. P. Managem.* **2015**, *1*, 46–52.
94. Bello, A.; Arias, M.; López-Pérez, J.A.; García-Álvarez, A.; Fresno, J.; Escuer, M.; Arcos, S.C.; Lacasa, A.; Sanz, R.; Gómez, P.; et al. Biofumigation, Fallow, and Nematode Management in Vineyard Replant. *Nematropica* **2004**, *34*, 53–64.
95. Akhtar, M.; Malik, A. Roles of Organic Soil Amendments and Soil Organisms in the Biological Control of Plant-Parasitic Nematodes: A Review. *Bioresour. Technol.* **2000**, *74*, 35–47. [https://doi.org/10.1016/S0960-8524\(99\)00154-6](https://doi.org/10.1016/S0960-8524(99)00154-6).
96. T D'Addabbo The Nematicidal Effect of Organic Amendments: A Review of the Literature, 1982-1994. *Nematol Mediterr* **1995**, *23*, 299–306.
97. Rodríguez-Kábana, R. Organic and Inorganic Nitrogen Amendments to Soil as Nematode Suppressants. *J. Nematol.* **1986**, *18*, 129.
98. Mojtahedi, H.; Santo, G.S.; Hang, A.N.; Wilson, J.H. Suppression of Root-Knot Nematode Populations with Selected Rapeseed as Green Manure. *J. Nematol.* **1991**, *23*, 170.
99. Evans, D.; And, W.; Kaplan, D.T. Antagonists of Plant-Parasitic Nematodes in Florida Citrus. *J. Nematol.* **1990**, *22*, 567.
100. Martinelli, P.; Santos, J.; Sant'Anna, S. Nematophagous Fungi from Citrus Orchards in São Paulo and Goiás States. *Nematologia* **2009**, *33*, 123–131.
101. Gené, J.; Verdejo-Lucas, S.; Stchigel, A.M.; Sorribas, F.J.; Guarro, J. Microbial Parasites Associated with *Tylenchulus semipenetrans* in Citrus Orchards of Catalonia, Spain. *Biocontrol Sci. Technol.* **2007**, *15*, 721–731. <https://doi.org/10.1080/09583150500135941>.
102. Maafi, Z.T. Study of *Pasteuria penetrans* Group on Some Plant Parasitic Nematodes and Their Host Ranges in the North of Iran. *Iran. J. Plant Pathol.* **2000**, *36*, Pe221–Pe231.
103. Fattah, F.A.; Saleh, H.M.; Aboud, H.M. Parasitism of the Citrus Nematode, *Tylenchulus semipenetrans*, by *Pasteuria penetrans* in Iraq. *J. Nematol.* **1989**, *21*, 431.
104. El-Nagdi, M.; M Abd-Elgawad, M.M. Biological and Chemical Control of the Citrus Nematode, *Tylenchulus semipenetrans* (Cobb, 1913) on Mandarin in Egypt. *Egypt J. Biol. Pest Control* **2016**, *26*, 345–349.

105. Deepa, S.P.; Subramanian, S.; Ramakrishnan, S. Biomanagement of Citrus Nematode *Tylenchulus semipenetrans* Cobb on Lemon, Citrus Limonia L. *J. Biopesticides* **2011**, *4*, 205–207.
106. Walode, N.; Sinha, A.; Neog, P. Biological Control of Citrus Nematode, *Tylenchulus semipenetrans* on Citrus Jambhiri. *Indian J. Nematol.* **2008**, *38*, 244–246.
107. Labiadh, M.; Mhamdi, B.; Loulou, A.; Sadreddine, K. Impact of Rhizobacteria Community of Citrus Root on *Tylenchulus semipenetrans* and on Citrus Plant Growth. *Biocontrol Sci. Technol.* **2023**, *33*, 241–257. <https://doi.org/10.1080/09583157.2023.2175785>.
108. Kusakabe, A.; Wang, C.; Xu, Y.; Molnár, I.; Stock, S.P. Selective Toxicity of Secondary Metabolites from the Entomopathogenic Bacterium *Photorhabdus luminescens sonorensis* against Selected Plant Parasitic Nematodes of the Tylenchina Suborder. *Microbiol. Spectr.* **2022**, *10*, e02577-21.
109. El-Wahab, A.; Abd-El-Khair, H.; Koura, F. Effects Of Some Fungi And Bacteria As Bio-Control Agents Against Citrus Nematode *Tylenchulus semipenetrans* Cobb. *J. Appl. Sci. Res.* **2012**, *8*, 5436–5444.
110. Hanada, K.; Hu, Y.; Pan, F.; Chen, J.; Abd-Elgawad, M.M.M. Exploiting Plant–Phytonematode Interactions to Upgrade Safe and Effective Nematode Control. *Life* **2022**, Vol. 12, Page 1916 2022, 12, 1916, doi:10.3390/LIFE12111916..
111. El-Mohamedy, R.S.; A Hammam, M.M.; Abd-El-Kareem, F.; M Abd-Elgawad, M.M. Biological Soil Treatment to Control *Fusarium solani* and *Tylenchulus semipenetrans* on Sour Orange Seedlings Under Greenhouse Conditions *Int. J. ChemTech Res.* **2016**, *9*, 73–85.
112. A Hammam, M.M.; El-Mohamedy, R.S.; Abdel-Kareem, F.; M Abd-Elgawad, M.M. Evaluation of Soil Amended with Bio-Agents and Compost Alone or in Combination for Controlling Citrus Nematode *Tylenchulus semipenetrans* and Fusarium Dry Root Rot on Volkamer Lime Under Greenhouse Conditions *Int. J. ChemTech Res.* **2016**, *9*, 86–96.
113. Trivedi, P.C.; Malhotra, A. Bacteria in the Management of Plant-Parasitic Nematodes. In *Bacteria in Agrobiolgy: Disease Management*; Dinesh, K., Maheshwari, K., Eds.; Springer: Berlin/Heidelberg, Germany, 2013, pp. 349–377. [https://doi.org/10.1007/978-3-642-33639-3\\_13](https://doi.org/10.1007/978-3-642-33639-3_13).
114. Siddiqui, I.A.; Shaukat, S.S. Suppression of Root-Knot Disease by *Pseudomonas fluorescens* CHA0 in Tomato: Importance of Bacterial Secondary Metabolite, 2,4-Diacetylphloroglucinol. *Soil. Biol. Biochem.* **2003**, *35*, 1615–1623. <https://doi.org/10.1016/J.SOIL-BIO.2003.08.006>.
115. Défago, G.; Berling, C.H.; Burger, U.; Haas, D.; Kahr, G.; Keel, C.; Voisard, C.; Wirthner, P.; Wuethrich, B. Suppression of Black Root Rot of Tobacco and Other Root Diseases by Strains of *Pseudomonas fluorescens*: Potential Applications and Mechanisms. In *Biological Control of Soil-Borne Plant Pathogens*; Hornby, D., Ed.; CAB International: Kyoto, Japan; Oxon, UK, 1990; pp. 93–108.
116. El-Nagdi, W.M.A.; Youssef, M.M.A.; Hafez, O.M. Effects of Commercial Formulations of *Bacillus thuringiensis* and *Streptomyces avermitilis* on *Tylenchulus semipenetrans* and on Nutrition Status, Yield and Fruit Quality of Mandarin. *Nematol. Mediterr.* **2010**, *38*.
117. Martin, R.J.; Robertson, A.P.; Wolstenholme, A.J. Mode of Action of the Macrocyclic Lactones. In *Macrocyclic Lactones in Antiparasitic Therapy*; Vercruyse, J., Rew, R.S., Eds.; CAB International: Wallingford, UK, 2002; pp. 125–140. <https://doi.org/10.1079/9780851996172.0125>.
118. Sayed, A.; Saad, A.K.; Radwan, M.A.; Mesbah, H. Evaluation of Some Non-Fumigant Nematicides and the Biocide Avermectin for Managing *Meloidogyne incognita* in Tomatoes. *Pak. J. Nematol.* **2017**, *35*, 85–92.
119. Khalil, M.S. *Abamectin* and *Azadirachtin* as Eco-Friendly Promising Biorational Tools in Integrated Nematodes Management Programs. *Plant Pathol. Microbiol.* **2013**, *4*, 1–7. <https://doi.org/10.4172/2157-7471.1000174>.
120. Ruanpanun, P.; Chamswarng, C. Potential of Actinomycetes Isolated from Earthworm Castings in Controlling Root-Knot Nematode *Meloidogyne incognita*. *J. General Plant Pathol.* **2016**, *82*, 43–50.
121. Jayakumar, J. Bio-Efficacy of *Streptomyces Avermitilis* Culture Filtrates against Root Knot Nematode, *Meloidogyne incognita* and Reniform Nematodes, *Rotylenchulus reniformis*. *Karnataka J. Agri. Sci.* **2009**, *22*, 567–571.
122. El-Tanany, M.; El-Shahaat, M.; Khalil, M.S. Efficacy of Three Bio-Pesticides and Oxamyl against Citrus Nematode (*Tylenchulus semipenetrans*) and on Productivity of Washington Navel Orange Trees. *Egypt. J. Hort.* **2018**, *45*, 275–287. <https://doi.org/10.21608/ejoh.2018.3161.1060>.
123. Salehi, A.; Ostovan, H.; Modarresi, M. Evaluation of the Efficiency of *Gaeolaelaps aculeifer* in Control of Plant Parasitic Nematode *Tylenchulus semipenetrans* under Greenhouse Conditions. *J. Entomol. Nematol.* **2014**, *6*, 150–153.
124. Al-Rehiyani, S.; Fouly, A. *Cosmolaelaps simplex* (Berlese), a Polyphagous Predatory Mite Feeding on Root-Knot Nematode *Meloidogyne javanica* and Citrus Nematode *Tylenchulus semipenetrans*. *Pakistan J. Biol. Sci.* **2005**, *8*, 168–174. <https://doi.org/10.3923/pjbs.2005.168.174>.

125. Wada, S.; Toyota, K. Effect of Three Organophosphorous Nematicides on Non-Target Nematodes and Soil Microbial Community. *Microbes Environ.* **2008**, *23*, 331–336. <https://doi.org/10.1264/jsme2.ME08534>.
126. Grabau, Z.J.; Mauldin, M.D.; Habteweld, A.; Carter, E.T. Nematicide Efficacy at Managing *Meloidogyne arenaria* and Non-Target Effects on Free-Living Nematodes in Peanut Production. *J. Nematol.* **2020**, *52*, e2020-28. <https://doi.org/10.21307/JOFNEM-2020-028>.
127. Grynberg, P.; Togawa, R.C.; de Freitas, L.D.; Antonino, J.D.; Rancurel, C.; Costa, M.M.D.C.; Grossi-De-sa, M.F.; Miller, R.N.G.; Brasileiro, A.C.M.; Guimaraes, P.M.; et al. Comparative Genomics Reveals Novel Target Genes towards Specific Control of Plant-Parasitic Nematodes. *Genes* **2020**, *11*, 1–25. <https://doi.org/10.3390/GENES11111347>.
128. Li, J.; Todd, T.C.; Lee, J.; Trick, H.N. Biotechnological Application of Functional Genomics towards Plant-Parasitic Nematode Control. *Plant Biotechnol. J.* **2011**, *9*, 936–944. <https://doi.org/10.1111/J.1467-7652.2011.00601.X>.
129. Davis, E.; Aron, L.; Pratt, L.; Hussey, R. Novel Immunization Procedures Used to Develop Monoclonal Antibodies That Bind to Specific Structures in *Meloidogyne* spp. *Phytopathology* **1992**, *82*, 1244–1250.
130. Atkinson, H.J.; Harris, P.D.; Halk, E.J.; Novitski, C.; Leighton-Sands, J.; Nolan, P.; Fox, P.C. Monoclonal Antibodies to the Soya Bean Cyst Nematode, *Heterodera glycines*. *Ann. Appl. Biol.* **1988**, *112*, 459–469. <https://doi.org/10.1111/J.1744-7348.1988.TB02083.X>.
131. Davis, E.L.; Hussey, R.S.; Baum, T.J.; Bakker, J.; Schots, A.; Rosso, M.N.; Abad, P. Nematode Parasitism Genes. *Annu. Rev. Phytopathol.* **2003**, *38*, 365–396. <https://doi.org/10.1146/ANNUREV.PHYTO.38.1.365>.
132. Abad, P.; Gouzy, J.; Aury, J.M.; Castagnone-Sereno, P.; Danchin, E.G.J.; Deleury, E.; Perfus-Barbeoch, L.; Anthouard, V.; Artiguenave, F.; Blok, V.C.; et al. Genome Sequence of the Metazoan Plant-Parasitic Nematode *Meloidogyne incognita*. *Nat. Biotechnol.* **2008**, *26*, 909–915. <https://doi.org/10.1038/nbt.1482>.
133. McK Bird, D.; Williamson, V.M.; Abad, P.; McCarter, J.; Danchin, E.G.J.; Castagnone-Sereno, P.; Opperman, C.H. The Genomes of Root-Knot Nematodes. *Annu. Rev. Phytopathol.* **2009**, *47*, 333–351. <https://doi.org/10.1146/ANNUREV-PHYTO-080508-081839>.
134. Hewezi, T.; Baum, T.J. Manipulation of Plant Cells by Cyst and Root-Knot Nematode Effectors. *Mol. Plant Microbe Interact.* **2012**, *26*, 9–16. <https://doi.org/10.1094/MPMI-05-12-0106-FI>.
135. Rosso, M.N.; Hussey, R.S.; Davis, E.L.; Smant, G.; Baum, T.J.; Abad, P.; Mitchum, M.G. Nematode Effector Proteins: Targets and Functions in Plant Parasitism. In *Effectors in Plant-Microbe Interactions*; Martin, F., Kamoun, S., Eds.; John Wiley & Sons, Ltd.: Hoboken, NJ, USA, 2011; pp. 327–354, ISBN 9780470958223.
136. Haegeman, A.; Mantelin, S.; Jones, J.T.; Gheysen, G. Functional Roles of Effectors of Plant-Parasitic Nematodes. *Gene* **2012**, *492*, 19–31. <https://doi.org/10.1016/J.GENE.2011.10.040>.
137. Davis, E.L.; Hussey, R.S.; Mitchum, M.G.; Baum, T.J. Parasitism Proteins in Nematode–Plant Interactions. *Curr. Opin. Plant Biol.* **2008**, *11*, 360–366. <https://doi.org/10.1016/J.PBI.2008.04.003>.
138. Jacob, J.; Mitreva, M. Transcriptomes of Plant-Parasitic Nematodes. In *Genomics and Molecular Genetics of Plant-Nematode Interactions*; Jones, J., Gheysen, G., Fenoll, C., Eds.; Springer: Dordrecht, The Netherlands, 2011; pp. 119–138.
139. Gheysen, G.; Mitchum, M.G. How Nematodes Manipulate Plant Development Pathways for Infection. *Curr. Opin. Plant Biol.* **2011**, *14*, 415–421. <https://doi.org/10.1016/J.PBI.2011.03.012>.
140. Abad, P.; McCarter, J.P. Genome Analysis of Plant Parasitic Nematodes. In *Genomics and Molecular Genetics of Plant-Nematode Interactions*; Gheysen, G., Fenoll, C., Jones, J., Eds.; Springer Science & Business Media, B.V.: London, UK, 2011; pp. 103–117.
141. Rosso, M.N.; Jones, J.T.; Abad, P. RNAi and Functional Genomics in Plant Parasitic Nematodes. *Annu. Rev.* **2009**, *47*, 207–232. <https://doi.org/10.1146/ANNUREV.PHYTO.112408.132605>.
142. Chen, J.; Chen, S.; Xu, C.; Yang, H.; Achom, M.; Wang, X. A Key Virulence Effector from Cyst Nematodes Targets Host Autophagy to Promote Nematode Parasitism. *New Phytol.* **2023**, *237*, 1374–1390. <https://doi.org/10.1111/NPH.18609>.
143. Hu, L.J.; Wu, X.Q.; Ding, X.L.; Ye, J.R. Comparative Transcriptomic Analysis of Candidate Effectors to Explore the Infection and Survival Strategy of *Bursaphelenchus xylophilus* during Different Interaction Stages with Pine Trees. *BMC Plant Biol.* **2021**, *21*, 1–14. <https://doi.org/10.1186/S12870-021-02993-9/FIGURES/5>.
144. Haegeman, A.; Jones, J.T.; Danchin, E.G.J. Horizontal Gene Transfer in Nematodes: A Catalyst for Plant Parasitism? *Mol. Plant Microbe Interact.* **2011**, *24*, 879–887. <https://doi.org/10.1094/MPMI-03-11-0055>.
145. Danchin, E.G.J.; Rosso, M.N.; Vieira, P.; De Almeida-Engler, J.; Coutinho, P.M.; Henrissat, B.; Abad, P. Multiple Lateral Gene Transfers and Duplications Have Promoted Plant Parasitism Ability in Nematodes. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 17651–17656.
146. Baniya, A.; Joseph, S.; Duncan, L.; Crow, W.; Mengistu, T. The Role of *Caenorhabditis elegans* Sex-Determination Homologs, *Mi-sdc-1* and *Mi-tra-1* in *Meloidogyne incognita*. *Eur. J. Plant Pathol.* **2021**, *161*, 439–452. <https://doi.org/10.1007/S10658-021-02335-3/FIGURES/8>.



147. Huang, G.; Allen, R.; Davis, E.L.; Baum, T.J.; Hussey, R.S. Engineering Broad Root-Knot Resistance in Transgenic Plants by RNAi Silencing of a Conserved and Essential Root-Knot Nematode Parasitism Gene. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 14302–14306.
148. Niu, J.; Liu, P.; Liu, Q.; Chen, C.; Guo, Q.; Yin, J.; Yang, G.; Jian, H. Msp40 Effector of Root-Knot Nematode Manipulates Plant Immunity to Facilitate Parasitism. *Sci. Rep.* **2016**, *6*, 19443. <https://doi.org/10.1038/srep19443>.
149. Shi, Q.; Mao, Z.; Zhang, X.; Ling, J.; Lin, R.; Zhang, X.; Liu, R.; Wang, Y.; Yang, Y.; Cheng, X.; et al. The Novel Secreted *Meloidogyne incognita* Effector MiISE6 Targets the Host Nucleus and Facilitates Parasitism in *Arabidopsis*. *Front. Plant Sci.* **2018**, *9*, 252. <https://doi.org/10.3389/FPLS.2018.00252/BIBTEX>.
150. Wang, D.; Wu, F.; Xu, X.; Peng, D.; Duan, Y.; Peng, H.; Wu, H. The Function of HgLac in *Heterodera glycines* and Its Potential as a Control Target. *Pestic. Biochem. Physiol.* **2025**, *208*, 106225. <https://doi.org/10.1016/J.PESTBP.2024.106225>.
151. Gang, S.S.; Hallem, E.A. Mechanisms of Host Seeking by Parasitic Nematodes. *Mol. Biochem. Parasitol.* **2016**, *208*, 23–32. <https://doi.org/10.1016/J.MOLBIOPARA.2016.05.007>.
152. Morris, R.; Wilson, L.; Sturrock, M.; Warnock, N.D.; Carrizo, D.; Cox, D.; Maule, A.G.; Dalzell, J.J. A Neuropeptide Modulates Sensory Perception in the Entomopathogenic Nematode *Steinernema carpocapsae*. *PLoS Pathog.* **2017**, *13*, e1006185. <https://doi.org/10.1371/JOURNAL.PPAT.1006185>.
153. Maule, A.G.; McVeigh, P.; Dalzell, J.J.; Atkinson, L.; Mousley, A.; Marks, N.J. An Eye on RNAi in Nematode Parasites. *Trends Parasitol.* **2011**, *27*, 505–513. <https://doi.org/10.1016/J.PT.2011.07.004>.
154. Lilley, C.J.; Davies, L.J.; Urwin, P.E. RNA Interference in Plant Parasitic Nematodes: A Summary of the Current Status. *Parasitology* **2012**, *139*, 630–640. <https://doi.org/10.1017/S0031182011002071>.
155. Chaudhary, S.; Dutta, T.K.; Tyagi, N.; Shivakumara, T.N.; Papolu, P.K.; Chobhe, K.A.; Rao, U. Host-Induced Silencing of Mi-Msp-1 Confers Resistance to Root-Knot Nematode *Meloidogyne incognita* in Eggplant. *Transgenic Res.* **2019**, *28*, 327–340. <https://doi.org/10.1007/S11248-019-00126-5/FIGURES/6>.
156. Banerjee, S.; Banerjee, A.; Gill, S.S.; Gupta, O.; Dahuja, A.; Jain, P.K.; Sirohi, A. RNA Interference: A Novel Source of Resistance to Combat Plant Parasitic Nematodes. *Front. Plant Sci.* **2017**, *8*, 834. <https://doi.org/10.3389/FPLS.2017.00834/BIBTEX>.
157. Koutsovoulos, G.D.; Pouillet, M.; Elashry, A.; Kozłowski, D.K.L.; Sallet, E.; Da Rocha, M.; Perfus-Barbeoch, L.; Martin-Jimenez, C.; Frey, J.E.; Ahrens, C.H.; et al. Genome Assembly and Annotation of *Meloidogyne enterolobii*, an Emerging Parthenogenetic Root-Knot Nematode. *Sci. Data* **2020**, *7*, 324. <https://doi.org/10.1038/s41597-020-00666-0>.
158. Blanc-Mathieu, R.; Perfus-Barbeoch, L.; Aury, J.M.; Da Rocha, M.; Gouzy, J.; Sallet, E.; Martin-Jimenez, C.; Bailly-Bechet, M.; Castagnone-Sereno, P.; Flot, J.F.; et al. Hybridization and Polyploidy Enable Genomic Plasticity without Sex in the Most Devastating Plant-Parasitic Nematodes. *PLoS Genet.* **2017**, *13*, e1006777. <https://doi.org/10.1371/JOURNAL.PGEN.1006777>.
159. Opperman, C.H.; Bird, D.M.; Williamson, V.M.; Rokhsar, D.S.; Burke, M.; Cohn, J.; Cromer, J.; Diener, S.; Gajan, J.; Graham, S.; et al. Sequence and Genetic Map of *Meloidogyne hapla*: A Compact Nematode Genome for Plant Parasitism. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 14802–14807.
160. Langner, T.; Kamoun, S.; Belhaj, K. CRISPR Crops: Plant Genome Editing toward Disease Resistance. *Annu. Rev. Phytopathol.* **2018**, *56*, 479–512. <https://doi.org/10.1146/ANNUREV-PHYTO-080417-050158/CITE/REFWORKS>.
161. Kyndt, T.; Denil, S.; Haegeman, A.; Trooskens, G.; Bauters, L.; Van Crielinge, W.; De Meyer, T.; Gheysen, G. Transcriptional Reprogramming by Root Knot and Migratory Nematode Infection in Rice. *New Phytol.* **2012**, *196*, 887–900. <https://doi.org/10.1111/J.1469-8137.2012.04311.X>.
162. Gheysen, G.; Fenoll, C. Gene Expression in Nematode Feeding Sites. *Annu. Rev. Phytopathol.* **2002**, *40*, 191–219. <https://doi.org/10.1146/ANNUREV.PHYTO.40.121201.093719>.
163. Danchin, E.G.J.; Arguel, M.J.; Campan-Fournier, A.; Perfus-Barbeoch, L.; Magliano, M.; Rosso, M.N.; Da Rocha, M.; Da Silva, C.; Nottet, N.; Labadie, K.; et al. Identification of Novel Target Genes for Safer and More Specific Control of Root-Knot Nematodes from a Pan-Genome Mining. *PLoS Pathog.* **2013**, *9*, e1003745. <https://doi.org/10.1371/JOURNAL.PPAT.1003745>.
164. Kang, J. Application of CRISPR/Cas9-Mediated Genome Editing for Studying Soybean Resistance to Soybean Cyst Nematode. Ph.D. Thesis, University of Missouri--Columbia: Columbia, MO, USA, 2016.
165. Dong, J.; Zielinski, R.E.; Hudson, M.E. T-SNAREs Bind the Rhg1  $\alpha$ -SNAP and Mediate Soybean Cyst Nematode Resistance. *Plant J.* **2020**, *104*, 318–331. <https://doi.org/10.1111/tpj.14923>.
166. Wang, X.; Cheng, R.; Xu, D.; Huang, R.; Li, H.; Jin, L.; Wu, Y.; Tang, J.; Sun, C.; Peng, D.; et al. MG1 Interacts with a Protease Inhibitor and Confers Resistance to Rice Root-Knot Nematode. *Nat. Commun.* **2023**, *14*, 3354. <https://doi.org/10.1038/s41467-023-39080-6>.

167. Li, Z.; Huang, Q.; Lin, B.; Guo, B.; Wang, J.; Huang, C.; Liao, J.; Zhuo, K. CRISPR/Cas9-Targeted Mutagenesis of a Representative Member of a Novel PR10/Bet v1-like Protein Subfamily Significantly Reduces Rice Plant Height and Defense against *Meloidogyne graminicola*. *Phytopathol. Res.* **2022**, *4*, 1–13. <https://doi.org/10.1186/S42483-022-00143-Z/FIGURES/7>.
168. Huang, Q.; Lin, B.; Cao, Y.; Zhang, Y.; Song, H.; Huang, C.; Sun, T.; Long, C.; Liao, J.; Zhuo, K. CRISPR/Cas9-Mediated Mutagenesis of the Susceptibility Gene OsHPP04 in Rice Confers Enhanced Resistance to Rice Root-Knot Nematode. *Front. Plant Sci.* **2023**, *14*, 1134653. <https://doi.org/10.3389/FPLS.2023.1134653/FULL>.
169. Zhang, X.; Wang, D.; Chen, J.; Wu, D.; Feng, X.; Yu, F. Nematode RALF-Like 1 Targets Soybean Malectin-Like Receptor Kinase to Facilitate Parasitism. *Front. Plant Sci.* **2021**, *12*, 775508. <https://doi.org/10.3389/FPLS.2021.775508/BIBTEX>.
170. Huang, H.; Zhao, W.; Qiao, H.; Li, C.; Sun, L.; Yang, R.; Ma, X.; Ma, J.; Song, S.; Wang, S. SlWRKY45 Interacts with Jasmonate-ZIM Domain Proteins to Negatively Regulate Defense against the Root-Knot Nematode *Meloidogyne incognita* in Tomato. *Hortic. Res.* **2022**, *9*, uhac197. <https://doi.org/10.1093/HR/UHAC197>.
171. Zhao, W.; Liang, J.; Huang, H.; Yang, J.; Feng, J.; Sun, L.; Yang, R.; Zhao, M.; Wang, J.; Wang, S. Tomato Defence against *Meloidogyne incognita* by Jasmonic Acid-Mediated Fine-Tuning of Kaempferol Homeostasis. *New Phytol.* **2023**, *238*, 1651–1670. <https://doi.org/10.1111/nph.18837>.
172. Zhang, X.; Li, S.; Li, X.; Song, M.; Ma, S.; Tian, Y.; Gao, L. Peat-Based Hairy Root Transformation Using Rhizobium Rhizogenes as a Rapid and Efficient Tool for Easily Exploring Potential Genes Related to Root-Knot Nematode Parasitism and Host Response. *Plant Methods* **2023**, *19*, 1–13. <https://doi.org/10.1186/S13007-023-01003-3/FIGURES/5>.
173. Noureddine, Y.; Da Rocha, M.; An, J.; Médina, C.; Mejias, J.; Mulet, K.; Quentin, M.; Abad, P.; Zouine, M.; Favery, B.; et al. AUXIN RESPONSIVE FACTOR8 Regulates Development of the Feeding Site Induced by Root-Knot Nematodes in Tomato. *J. Exp. Bot.* **2023**, *74*, 5752–5766. <https://doi.org/10.1093/JXB/ERAD208>.
174. Dutta, T.K.; Vashisth, N.; Ray, S.; Phani, V.; Chinnusamy, V.; Sirohi, A. Functional Analysis of a Susceptibility Gene (HIPP27) in the *Arabidopsis thaliana*-*Meloidogyne incognita* Pathosystem by Using a Genome Editing Strategy. *BMC Plant Biol.* **2023**, *23*, 390. <https://doi.org/10.1186/S12870-023-04401-W/FIGURES/6>.
175. Smant, G.; Helder, J.; Govers, A. Parallel Adaptations and Common Host Cell Responses Enabling Feeding of Obligate and Facultative Plant Parasitic Nematodes. *Plant J.* **2018**, *93*, 686–702.
176. Dutta, T.K.; Ray, S.; Phani, V. The Status of the CRISPR/Cas9 Research in Plant–Nematode Interactions. *Planta* **2023**, *258*, 103. <https://doi.org/10.1007/s00425-023-04259-0>.
177. Favery, B.; Lecomte, P.; Gil, N.; Bechtold, N.; Bouchez, D.; Dalmaso, A.; Abad, P. RPE, a Plant Gene Involved in Early Developmental Steps of Nematode Feeding Cells. *EMBO J.* **1998**, *17*, 6799–6811. <https://doi.org/10.1093/EMBOJ/17.23.6799>.
178. Wubben, M.J.E.; Su, H.; Rodermel, S.R.; Baum, T.J. Susceptibility to the Sugar Beet Cyst Nematode Is Modulated by Ethylene Signal Transduction in *Arabidopsis thaliana*. *Mol. Plant-Microbe Inter.* **2007**, *14*, 1206–1212. <https://doi.org/10.1094/MPMI.2001.14.10.1206>.
179. Favery, B.; Chelysheva, L.A.; Lebris, M.; Jammes, F.; Marmagne, A.; De Almeida-Engler, J.; Lecomte, P.; Vaury, C.; Arkowitz, R.A.; Abad, P. *Arabidopsis* Formin AtFH6 Is a Plasma Membrane-Associated Protein Upregulated in Giant Cells Induced by Parasitic Nematodes. *Plant Cell* **2004**, *16*, 2529–2540. <https://doi.org/10.1105/TPC.104.024372>.
180. Caillaud, M.C.; Lecomte, P.; Jammes, F.; Quentin, M.; Pagnotta, S.; Andrio, E.; Engler, J.D.A.; Marfaing, N.; Gounon, P.; Abad, P.; et al. MAP65-3 Microtubule-Associated Protein Is Essential for Nematode-Induced Giant Cell Ontogenesis in *Arabidopsis*. *Plant Cell* **2008**, *20*, 423–437. <https://doi.org/10.1105/TPC.107.057422>.
181. Hewezi, T.; Howe, P.; Maier, T.R.; Hussey, R.S.; Mitchum, M.G.; Davis, E.L.; Baum, T.J. Cellulose Binding Protein from the Parasitic Nematode *Heterodera schachtii* Interacts with *Arabidopsis* Pectin Methyltransferase: Cooperative Cell Wall Modification during Parasitism. *Plant Cell* **2008**, *20*, 3080–3093. <https://doi.org/10.1105/TPC.108.063065>.
182. Grunewald, W.; Karimi, M.; Wieczorek, K.; Van De Cappelle, E.; Wischnitzki, E.; Grundler, F.; Inzé, D.; Beeckman, T.; Gheysen, G. A Role for AtWRKY23 in Feeding Site Establishment of Plant-Parasitic Nematodes. *Plant Physiol.* **2008**, *148*, 358–368. <https://doi.org/10.1104/PP.108.119131>.
183. Clément, M.; Ketelaar, T.; Rodiuc, N.; Banora, M.Y.; Smertenko, A.; Engler, G.; Abad, P.; Hussey, P.J.; De Almeida Engler, J. Actin-Depolymerizing Factor2-Mediated Actin Dynamics Are Essential for Root-Knot Nematode Infection of *Arabidopsis*. *Plant Cell* **2009**, *21*, 2963–2979. <https://doi.org/10.1105/TPC.109.069104>.
184. Jin, J.; Hewezi, T.; Baum, T.J. The *Arabidopsis* BHLH25 and BHLH27 Transcription Factors Contribute to Susceptibility to the Cyst Nematode *Heterodera schachtii*. *Plant J.* **2011**, *65*, 319–328. <https://doi.org/10.1111/J.1365-313X.2010.04424.X>.

185. de Almeida Engler, J.; Kyndt, T.; Vieira, P.; Van Cappelle, E.; Boudolf, V.; Sanchez, V.; Escobar, C.; De Veylder, L.; Engler, G.; Abad, P.; et al. CCS52 and DEL1 Genes Are Key Components of the Endocycle in Nematode-Induced Feeding Sites. *Plant J.* **2012**, *72*, 185–198. <https://doi.org/10.1111/J.1365-313X.2012.05054.X>.
186. Curtis, R.H.C.; Pankaj; Powers, S.J.; Napier, J.; Matthes, M.C. The Arabidopsis F-Box/Kelch-Repeat Protein At2g44130 Is Upregulated in Giant Cells and Promotes Nematode Susceptibility. *Mol. Plant-Microbe Inter.* **2012**, *26*, 36–43. <https://doi.org/10.1094/MPMI-05-12-0135-FI>.
187. Elashry, A.; Okumoto, S.; Siddique, S.; Koch, W.; Kreil, D.P.; Bohlmann, H. The AAP Gene Family for Amino Acid Permeases Contributes to Development of the Cyst Nematode *Heterodera schachtii* in Roots of *Arabidopsis*. *Plant Physiol. Biochem.* **2013**, *70*, 379–386. <https://doi.org/10.1016/J.PLAPHY.2013.05.016>.
188. Cabrera, J.; Díaz-Manzano, F.E.; Sanchez, M.; Rosso, M.N.; Melillo, T.; Goh, T.; Fukaki, H.; Cabello, S.; Hofmann, J.; Fenoll, C.; et al. A Role for LATERAL ORGAN BOUNDARIES-DOMAIN 16 during the Interaction *Arabidopsis*–*Meloidogyne* spp. Provides a Molecular Link between Lateral Root and Root-Knot Nematode Feeding Site Development. *New Phytol.* **2014**, *203*, 632–645. <https://doi.org/10.1111/NPH.12826>.
189. Lin, B.; Zhuo, K.; Chen, S.; Hu, L.; Sun, L.; Wang, X.; Zhang, L.H.; Liao, J. A Novel Nematode Effector Suppresses Plant Immunity by Activating Host Reactive Oxygen Species-Scavenging System. *New Phytol.* **2016**, *209*, 1159–1173. <https://doi.org/10.1111/NPH.13701>.
190. Pariyar, S.R.; Nakarmi, J.; Anwer, M.A.; Siddique, S.; Ilyas, M.; Elashry, A.; Dababat, A.A.; Leon, J.; Grundler, F.M.W. Amino Acid Permease 6 Modulates Host Response to Cyst Nematodes in Wheat and *Arabidopsis*. *Nematology* **2018**, *20*, 737–750. <https://doi.org/10.1163/15685411-00003172>.
191. Radakovic, Z.S.; Anjam, M.S.; Escobar, E.; Chopra, D.; Cabrera, J.; Silva, A.C.; Escobar, C.; Sobczak, M.; Grundler, F.M.W.; Siddique, S. *Arabidopsis* HIP27 Is a Host Susceptibility Gene for the Beet Cyst Nematode *Heterodera schachtii*. *Mol. Plant Pathol.* **2018**, *19*, 1917–1928. <https://doi.org/10.1111/MPP.12668>.
192. Verma, A.; Lee, C.; Morriss, S.; Odu, F.; Kenning, C.; Rizzo, N.; Spollen, W.G.; Lin, M.; McRae, A.G.; Givan, S.A.; et al. The Novel Cyst Nematode Effector Protein 30D08 Targets Host Nuclear Functions to Alter Gene Expression in Feeding Sites. *New Phytol.* **2018**, *219*, 697–713. <https://doi.org/10.1111/NPH.15179>.
193. Olmo, R.; Cabrera, J.; Fenoll, C.; Escobar, C. A Role for ALF4 during Gall and Giant Cell Development in the Biotic Interaction between *Arabidopsis* and *Meloidogyne* spp. *Physiol. Plant* **2019**, *165*, 17–28. <https://doi.org/10.1111/PPL.12734>.
194. Zhao, J.; Li, L.; Liu, Q.; Liu, P.; Li, S.; Yang, D.; Chen, Y.; Pagnotta, S.; Favery, B.; Abad, P.; et al. A MIF-like Effector Suppresses Plant Immunity and Facilitates Nematode Parasitism by Interacting with Plant Annexins. *J. Exp. Bot.* **2019**, *70*, 5943–5958. <https://doi.org/10.1093/JXB/ERZ348>.
195. Suzuki, R.; Yamada, M.; Higaki, T.; Aida, M.; Kubo, M.; Tsai, A.Y.-L.; Sawa, S. PUCHI Regulates Giant Cell Morphology During Root-Knot Nematode Infection in *Arabidopsis thaliana*. *Front. Plant Sci.* **2021**, *12*, 755610. <https://doi.org/10.3389/fpls.2021.755610>.
196. Truong, N.M.; Chen, Y.; Mejias, J.; Soulé, S.; Mulet, K.; Jaouannet, M.; Jaubert-Possamai, S.; Sawa, S.; Abad, P.; Favery, B.; et al. The *Meloidogyne incognita* Nuclear Effector MiEFF1 Interacts With *Arabidopsis* Cytosolic Glyceraldehyde-3-Phosphate Dehydrogenases to Promote Parasitism. *Front. Plant Sci.* **2021**, *12*, 641480. <https://doi.org/10.3389/FPLS.2021.641480/BIBTEX>.
197. Cabral, D.; Forero Ballesteros, H.; de Melo, B.P.; Lourenço-Tessutti, I.T.; Simões de Siqueira, K.M.; Obicci, L.; Grossi-de-Sa, M.F.; Hemerly, A.S.; de Almeida Engler, J. The Armadillo BTB Protein ABAP1 Is a Crucial Player in DNA Replication and Transcription of Nematode-Induced Galls. *Front. Plant Sci.* **2021**, *12*, 636663. <https://doi.org/10.3389/FPLS.2021.636663/BIBTEX>.
198. Mejias, J.; Bazin, J.; Truong, N.M.; Chen, Y.; Marteu, N.; Bouteiller, N.; Sawa, S.; Crespi, M.D.; Vaucheret, H.; Abad, P.; et al. The Root-Knot Nematode Effector MiEFF18 Interacts with the Plant Core Spliceosomal Protein SmD1 Required for Giant Cell Formation. *New Phytol.* **2021**, *229*, 3408–3423. <https://doi.org/10.1111/NPH.17089>.
199. Ding, S.; Cheng, X.; Wang, D.; Chen, C.; Yang, S.; Wang, J.; Xu, C.; Xie, H. *Aphelenchoides besseyi* Ab-FAR-1 Interacts with *Arabidopsis thaliana* AtADF3 to Interfere with Actin Cytoskeleton, and Promotes Nematode Parasitism and Pathogenicity. *Int. J. Mol. Sci.* **2022**, *23*, 12280. <https://doi.org/10.3390/IJMS232012280/S1>.
200. Suzuki, R.; Kanno, Y.; Abril-Urias, P.; Seo, M.; Escobar, C.; Tsai, A.Y.L.; Sawa, S. Local Auxin Synthesis Mediated by YUCCA4 Induced during Root-Knot Nematode Infection Positively Regulates Gall Growth and Nematode Development. *Front. Plant Sci.* **2022**, *13*, 1019427. <https://doi.org/10.3389/FPLS.2022.1019427/BIBTEX>.
201. Siddique, S.; Radakovic, Z.S.; Hiltl, C.; Pellegrin, C.; Baum, T.J.; Beasley, H.; Bent, A.F.; Chitambo, O.; Chopra, D.; Danchin, E.G.J.; et al. The Genome and Lifestage-Specific Transcriptomes of a Plant-Parasitic Nematode and Its Host Reveal Susceptibility Genes Involved in Trans-Kingdom Synthesis of Vitamin B5. *Nat. Commun.* **2022**, *13*, 6190. <https://doi.org/10.1038/s41467-022-33769-w>.

202. Zhou, Y.; Zhao, D.; Duan, Y.; Chen, L.; Fan, H.; Wang, Y.; Liu, X.; Chen, L.Q.; Xuan, Y.; Zhu, X. AtSWEET1 Negatively Regulates Plant Susceptibility to Root-Knot Nematode Disease. *Front. Plant Sci.* **2023**, *14*, 1010348. <https://doi.org/10.3389/FPLS.2023.1010348/BIBTEX>.
203. Różańska, E.; Krępski, T.; Wiśniewska, A. Mutations in Selected ABA-Related Genes Reduce Level of Arabidopsis Thaliana Susceptibility to the Beet Cyst Nematode *Heterodera schachtii*. *Plants* **2023**, *12*, 2299. <https://doi.org/10.3390/PLANTS12122299>.
204. Zhou, D.; Godinez-Vidal, D.; He, J.; Teixeira, M.; Guo, J.; Wei, L.; Van Norman, J.M.; Kaloshian, I. A G-Type Lectin Receptor Kinase Negatively Regulates Arabidopsis Immunity against Root-Knot Nematodes. *Plant Physiol.* **2023**, *193*, 721–735. <https://doi.org/10.1093/PLPHYS/KIAD253>.
205. Hilger, D.; Masureel, M.; Kobilka, B.K. Structure and Dynamics of GPCR Signaling Complexes. *Nat. Struct. Mol. Biol.* **2018**, *25*, 4–12. <https://doi.org/10.1038/s41594-017-0011-7>.
206. Shivakumara, T.N.; Dutta, T.K.; Chaudhary, S.; von Reuss, S.H.; Williamson, V.M.; Rao, U. Homologs of *Caenorhabditis elegans* Chemosensory Genes Have Roles in Behavior and Chemotaxis in the Root-Knot Nematode *Meloidogyne incognita*. *Mol. Plant Microbe Interact.* **2019**, *32*, 876–887. <https://doi.org/10.1094/MPMI-08-18-0226-R>.
207. Yan, Y.; Davis, E.L. Characterisation of Guanylyl Cyclase Genes in the Soybean Cyst Nematode, *Heterodera glycines*. *Int. J. Parasitol.* **2002**, *32*, 65–72. [https://doi.org/10.1016/S0020-7519\(01\)00315-0](https://doi.org/10.1016/S0020-7519(01)00315-0).
208. Sikder, M.M.; Vestergård, M. Impacts of Root Metabolites on Soil Nematodes. *Front. Plant Sci.* **2020**, *10*, 1792. <https://doi.org/10.3389/fpls.2019.01792>.
209. Kihika, R.; Murungi, L.K.; Coyne, D.; Ng'ang'a, M.; Hassanali, A.; Teal, P.E.A.; Torto, B. Parasitic Nematode *Meloidogyne incognita* Interactions with Different *Capsicum annum* Cultivars Reveal the Chemical Constituents Modulating Root Herbivory. *Sci. Rep.* **2017**, *7*, 2903. <https://doi.org/10.1038/s41598-017-02379-8>.
210. Choi, H.W.; Klessig, D.F. DAMPs, MAMPs, and NAMPs in Plant Innate Immunity. *BMC Plant Biol.* **2016**, *16*, 232. <https://doi.org/10.1186/s12870-016-0921-2>.
211. Sato, K.; Kadota, Y.; Shirasu, K. Plant Immune Responses to Parasitic Nematodes. *Front. Plant Sci.* **2019**, *10*, 479663. <https://doi.org/10.3389/FPLS.2019.01165/BIBTEX>.
212. de Boer, J.M.; Yan, Y.; Wang, X.; Smant, G.; Hussey, R.S.; Davis, E.L.; Baum, T.J. Developmental Expression of Secretory Beta-1,4-Endoglucanases in the Subventral Esophageal Glands of *Heterodera glycines*. *Mol. Plant Microbe Interact.* **1999**, *12*, 663–669. <https://doi.org/10.1094/MPMI.1999.12.8.663>.
213. Jaubert, S.; Laffaire, J.-B.; Abad, P.; Rosso, M.-N. A Polygalacturonase of Animal Origin Isolated from the Root-Knot Nematode *Meloidogyne incognita*. *FEBS Lett.* **2002**, *522*, 109–112. [https://doi.org/10.1016/s0014-5793\(02\)02906-x](https://doi.org/10.1016/s0014-5793(02)02906-x).
214. Vanholme, B.; Van Thuyne, W.; Vanhouteghem, K.; De Meutter, J.; Cannoot, B.; Gheysen, G. Molecular Characterization and Functional Importance of Pectate Lyase Secreted by the Cyst Nematode *Heterodera schachtii*. *Mol. Plant Pathol.* **2007**, *8*, 267–278. <https://doi.org/10.1111/J.1364-3703.2007.00392.X>.
215. Ferrari, S.; Savatin, D.V.; Sicilia, F.; Gramegna, G.; Cervone, F.; De Lorenzo, G. Oligogalacturonides: Plant Damage-Associated Molecular Patterns and Regulators of Growth and Development. *Front. Plant Sci.* **2013**, *4*, 41591. <https://doi.org/10.3389/FPLS.2013.00049/BIBTEX>.
216. Cheng, S.; Li, R.; Lin, L.; Shi, H.; Liu, X.; Yu, C. Recent Advances in Understanding the Function of the PGIP Gene and the Research of Its Proteins for the Disease Resistance of Plants. *Appl. Sci.* **2021**, *11*, 11123. <https://doi.org/10.3390/APP112311123>.
217. Shah, S.J.; Anjam, M.S.; Mendy, B.; Anwer, M.A.; Habash, S.S.; Lozano-Torres, J.L.; Grundler, F.M.W.; Siddique, S. Damage-Associated Responses of the Host Contribute to Defence against Cyst Nematodes but Not Root-Knot Nematodes. *J. Exp. Bot.* **2017**, *68*, 5949–5960. <https://doi.org/10.1093/jxb/erx374>.
218. Veronico, P.; Melillo, M.T.; Saponaro, C.; Leonetti, P.; Picardi, E.; Jones, J.T. A Polygalacturonase-Inhibiting Protein with a Role in Pea Defence against the Cyst Nematode *Heterodera goettingiana*. *Mol. Plant Pathol.* **2010**, *12*, 275–287. <https://doi.org/10.1111/J.1364-3703.2010.00671.X>.
219. Torres, J.L.L. Proline-Rich Extensin-like Receptor Kinases Mediate Damage-Triggered Immune Responses to Nematode Infections. In Proceedings of the IS-MPMI XVIII Congress, Glasgow, UK, 14–18 July 2019.
220. Lee, M.W.; Huffaker, A.; Crippen, D.; Robbins, R.T.; Goggin, F.L. Plant Elicitor Peptides Promote Plant Defences against Nematodes in Soybean. *Mol. Plant Pathol.* **2018**, *19*, 858–869. <https://doi.org/10.1111/mpp.12570>.
221. Mejias, J.; Truong, N.M.; Abad, P.; Favery, B.; Quentin, M. Plant Proteins and Processes Targeted by Parasitic Nematode Effectors. *Front. Plant Sci.* **2019**, *10*, 472968. <https://doi.org/10.3389/FPLS.2019.00970/BIBTEX>.
222. Bali, S.; Gleason, C. Unveiling the Diversity: Plant Parasitic Nematode Effectors and Their Plant Interaction Partners. *Mol. Plant Microbe Interact.* **2023**, *37*, 179–189. <https://doi.org/10.1094/MPMI-09-23-0124-FI>.

223. Jagdale, S.; Rao, U.; Giri, A.P. Effectors of Root-Knot Nematodes: An Arsenal for Successful Parasitism. *Front. Plant Sci.* **2021**, *12*, 800030. <https://doi.org/10.3389/FPLS.2021.800030/BIBTEX>.
224. Rehman, S.; Gupta, V.K.; Goyal, A.K. Identification and Functional Analysis of Secreted Effectors from Phytoparasitic Nematodes. *BMC Microbiol.* **2016**, *16*, 48. <https://doi.org/10.1186/s12866-016-0632-8>.
225. Tritten, L.; Ballesteros, C.; Beech, R.; Geary, T.G.; Moreno, Y. Mining Nematode Protein Secretomes to Explain Lifestyle and Host Specificity. *PLoS Negl. Trop. Dis.* **2021**, *15*, e0009828. <https://doi.org/10.1371/journal.pntd.0009828>.
226. Zeng, R.; Gao, S.; Xu, L.; Liu, X.; Dai, F. Prediction of Pathogenesis-Related Secreted Proteins from *Stemphylium lycopersici*. *BMC Microbiol.* **2018**, *18*, 191. <https://doi.org/10.1186/S12866-018-1329-Y/TABLES/5>.
227. Lu, M.R.; Lai, C.-K.; Liao, B.-Y.; Tsai, I.J. Comparative Transcriptomics across Nematode Life Cycles Reveal Gene Expression Conservation and Correlated Evolution in Adjacent Developmental Stages. *Genome Biol. Evol.* **2020**, *12*, 1019–1030. <https://doi.org/10.1093/gbe/evaa110>.
228. Stojilković, B.; Xiang, H.; Chen, Y.; Maulana, M.I.; Bauters, L.; Van de Put, H.; Steppe, K.; Liao, J.; de Almeida Engler, J.; Gheysen, G. The Nematode Effector Mj-NEROSs Interacts with Rieske's Iron-Sulfur Protein Influencing Plastid ROS Production to Suppress Plant Immunity. *New Phytol.* **2024**, *242*, 2787–2802. <https://doi.org/10.1111/NPH.19781>.
229. Zhao, J.; Mejias, J.; Quentin, M.; Chen, Y.; de Almeida-Engler, J.; Mao, Z.; Sun, Q.; Liu, Q.; Xie, B.; Abad, P.; et al. The Root-Knot Nematode Effector MiPDI1 Targets a Stress-Associated Protein (SAP) to Establish Disease in Solanaceae and *Arabidopsis*. *New Phytol.* **2020**, *228*, 1417–1430. <https://doi.org/10.1111/NPH.16745>.
230. Zhao, J.; Sun, Q.; Quentin, M.; Ling, J.; Abad, P.; Zhang, X.; Li, Y.; Yang, Y.; Favery, B.; Mao, Z.; et al. A *Meloidogyne incognita* C-Type Lectin Effector Targets Plant Catalases to Promote Parasitism. *New Phytol.* **2021**, *232*, 2124–2137. <https://doi.org/10.1111/NPH.17690>.
231. Song, H.; Lin, B.; Huang, Q.; Sun, L.; Chen, J.; Hu, L.; Zhuo, K.; Liao, J. The *Meloidogyne graminicola* Effector MgMO289 Targets a Novel Copper Metallochaperone to Suppress Immunity in Rice. *J. Exp. Bot.* **2021**, *72*, 5638–5655. <https://doi.org/10.1093/jxb/erab208>.
232. Hewezi, T.; Howe, P.J.; Maier, T.R.; Hussey, R.S.; Mitchum, M.G.; Davis, E.L.; Baum, T.J. Arabidopsis Spermidine Synthase Is Targeted by an Effector Protein of the Cyst Nematode *Heterodera schachtii*. *Plant Physiol.* **2010**, *152*, 968–984. <https://doi.org/10.1104/pp.109.150557>.
233. Jones, J.T.; Kumar, A.; Pylypenko, L.A.; Thirugnanasambandam, A.; Castelli, L.; Chapman, S.; Cock, P.J.A.; Grenier, E.; Lilley, C.J.; Phillips, M.S.; et al. Identification and Functional Characterization of Effectors in Expressed Sequence Tags from Various Life Cycle Stages of the Potato Cyst Nematode *Globodera pallida*. *Mol. Plant Pathol.* **2009**, *10*, 815–828. <https://doi.org/10.1111/J.1364-3703.2009.00585.X>.
234. Chen, J.; Hu, L.; Sun, L.; Lin, B.; Huang, K.; Zhuo, K.; Liao, J. A Novel *Meloidogyne graminicola* Effector, MgMO237, Interacts with Multiple Host Defence-Related Proteins to Manipulate Plant Basal Immunity and Promote Parasitism. *Mol. Plant Pathol.* **2018**, *19*, 1942–1955. <https://doi.org/10.1111/mpp.12671>.
235. Davies, L.J.; Zhang, L.; Elling, A.A. The Arabidopsis Thaliana Papain-like Cysteine Protease RD21 Interacts with a Root-Knot Nematode Effector Protein. *Nematology* **2015**, *17*, 655–666. <https://doi.org/10.1163/15685411-00002897>.
236. Hamamouch, N.; Li, C.; Hewezi, T.; Baum, T.J.; Mitchum, M.G.; Hussey, R.S.; Vodkin, L.O.; Davis, E.L. The Interaction of the Novel 30C02 Cyst Nematode Effector Protein with a Plant  $\beta$ -1,3-Endoglucanase May Suppress Host Defence to Promote Parasitism. *J. Exp. Bot.* **2012**, *63*, 3683–3695. <https://doi.org/10.1093/JXB/ERS058>.
237. Pogorelko, G.V.; Juvale, P.S.; Rutter, W.B.; Hütten, M.; Maier, T.R.; Hewezi, T.; Paulus, J.; van der Hoorn, R.A.L.; Grundler, F.M.W.; Siddique, S.; et al. Re-Targeting of a Plant Defense Protease by a Cyst Nematode Effector. *Plant J.* **2019**, *98*, 1000–1014. <https://doi.org/10.1111/tpj.14295>.
238. Zhao, J.; Liu, S. Beet Cyst Nematode HsSNARE1 Interacts with Both AtSNAP2 and AtPR1 and Promotes Disease in *Arabidopsis*. *J. Adv. Res.* **2023**, *47*, 27–40. <https://doi.org/10.1016/J.JARE.2022.07.004>.
239. Bekal, S.; Domier, L.L.; Gonfa, B.; Lakhssassi, N.; Meksem, K.; Lambert, K.N. A SNARE-Like Protein and Biotin Are Implicated in Soybean Cyst Nematode Virulence. *PLoS ONE* **2015**, *10*, e0145601. <https://doi.org/10.1371/JOURNAL.PONE.0145601>.
240. Lozano-Torres, J.L.; Wilbers, R.H.P.; Gawronski, P.; Boshoven, J.C.; Finkers-Tomczak, A.; Cordewener, J.H.G.; America, A.H.P.; Overmars, H.A.; Van 't Klooster, J.W.; Baranowski, L.; et al. Dual Disease Resistance Mediated by the Immune Receptor Cf-2 in Tomato Requires a Common Virulence Target of a Fungus and a Nematode. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 10119–10124.
241. Leelarasamee, N.; Zhang, L.; Gleason, C. The Root-Knot Nematode Effector MiPFN3 Disrupts Plant Actin Filaments and Promotes Parasitism. *PLoS Pathog.* **2018**, *14*, e1006947. <https://doi.org/10.1371/JOURNAL.PPAT.1006947>.

242. Verhoeven, A.; Finkers-Tomczak, A.; Prins, P.; Valkenburg-van Raaij, D.R.; van Schaik, C.C.; Overmars, H.; van Steenbrugge, J.J.M.; Tacke, W.; Varossieau, K.; Slootweg, E.J.; et al. The Root-Knot Nematode Effector MiMSP32 Targets Host 12-Oxophytodienoate Reductase 2 to Regulate Plant Susceptibility. *New Phytol.* **2023**, *237*, 2360–2374. <https://doi.org/10.1111/NPH.18653>.
243. Xue, B.; Hamamouch, N.; Li, C.; Huang, G.; Hussey, R.S.; Baum, T.J.; Davis, E.L. The 8D05 Parasitism Gene of *Meloidogyne incognita* Is Required for Successful Infection of Host Roots. *Phytopathology* **2013**, *103*, 175–181. <https://doi.org/10.1094/PHYTO-07-12-0173-R>.
244. Mei, Y.; Wright, K.M.; Haegeman, A.; Bauters, L.; Diaz-Granados, A.; Govere, A.; Gheysen, G.; Jones, J.T.; Mantelin, S. The *Globodera pallida* SPRYSEC Effector GpSPRY-414-2 That Suppresses Plant Defenses Targets a Regulatory Component of the Dynamic Microtubule Network. *Front. Plant Sci.* **2018**, *9*, 382626. <https://doi.org/10.3389/FPLS.2018.01019/BIBTEX>.
245. Pogorelko, G.; Juvale, P.S.; Rutter, W.B.; Hewezi, T.; Hussey, R.; Davis, E.L.; Mitchum, M.G.; Baum, T.J. A Cyst Nematode Effector Binds to Diverse Plant Proteins, Increases Nematode Susceptibility and Affects Root Morphology. *Mol. Plant Pathol.* **2016**, *17*, 832–844. <https://doi.org/10.1111/MPP.12330>.
246. Verma, A.; Lin, M.; Smith, D.; Walker, J.C.; Hewezi, T.; Davis, E.L.; Hussey, R.S.; Baum, T.J.; Mitchum, M.G. A Novel Sugar Beet Cyst Nematode Effector 2D01 Targets the Arabidopsis HAESA Receptor-like Kinase. *Mol. Plant Pathol.* **2022**, *23*, 1765–1782. <https://doi.org/10.1111/MPP.13263>.
247. Godinho Mendes, R.A.; Basso, M.F.; Fernandes de Araújo, J.; Paes de Melo, B.; Lima, R.N.; Ribeiro, T.P.; da Silva Mattos, V.; Saliba Albuquerque, E.V.; Grossi-de-Sa, M.; Dessaune Tameirao, S.N.; et al. Minc00344 and Mj-NULG1a Effectors Interact with GmHub10 Protein to Promote the Soybean Parasitism by *Meloidogyne incognita* and *M. javanica*. *Exp. Parasitol.* **2021**, *229*, 108153. <https://doi.org/10.1016/J.EXPPARA.2021.108153>.
248. Lee, C.; Chronis, D.; Kenning, C.; Peret, B.; Hewezi, T.; Davis, E.L.; Baum, T.J.; Hussey, R.; Bennett, M.; Mitchum, M.G. The Novel Cyst Nematode Effector Protein 19C07 Interacts with the Arabidopsis Auxin Influx Transporter LAX3 to Control Feeding Site Development. *Plant Physiol.* **2011**, *155*, 866–880. <https://doi.org/10.1104/PP.110.167197>.
249. Yang, S.; Pan, L.; Chen, Y.; Yang, D.; Liu, Q.; Jian, H. *Heterodera avenae* GLAND5 Effector Interacts with Pyruvate Dehydrogenase Subunit of Plant to Promote Nematode Parasitism. *Front. Microbiol.* **2019**, *10*, 445342. <https://doi.org/10.3389/FMICB.2019.01241/BIBTEX>.
250. Jaouannet, M.; Perfus-Barbeoch, L.; Deleury, E.; Magliano, M.; Engler, G.; Vieira, P.; Danchin, E.G.J.; Rocha, M.D.; Coquillard, P.; Abad, P.; et al. A Root-Knot Nematode-Secreted Protein Is Injected into Giant Cells and Targeted to the Nuclei. *New Phytol.* **2012**, *194*, 924–931. <https://doi.org/10.1111/j.1469-8137.2012.04164.x>.
251. Zhang, X.; Peng, H.; Zhu, S.; Xing, J.; Li, X.; Zhu, Z.; Zheng, J.; Wang, L.; Wang, B.; Chen, J.; et al. Nematode-Encoded RALF Peptide Mimics Facilitate Parasitism of Plants through the FERONIA Receptor Kinase. *Mol. Plant* **2020**, *13*, 1434–1454. <https://doi.org/10.1016/j.molp.2020.08.014>.
252. Barnes, S.N.; Wram, C.L.; Mitchum, M.G.; Baum, T.J. The Plant-Parasitic Cyst Nematode Effector GLAND4 Is a DNA-Binding Protein. *Mol. Plant Pathol.* **2018**, *19*, 2263–2276. <https://doi.org/10.1111/mpp.12697>.
253. Przybylska, A.; Wieczorek, P.; Obrepalska-Stepłowska, A. *Meloidogyne arenaria* Candidate Effector MaMsp4 Interacts with Maize (*Zea mays* L.) Proteins Involved in Host Defense Response and Cell Wall Modifications. *Plant Soil* **2023**, *491*, 501–523. <https://doi.org/10.1007/S11104-023-06130-3/FIGURES/1>.
254. Naalden, D.; Haegeman, A.; de Almeida-Engler, J.; Birhane Eshetu, F.; Bauters, L.; Gheysen, G. The *Meloidogyne graminicola* Effector Mg16820 Is Secreted in the Apoplast and Cytoplasm to Suppress Plant Host Defense Responses. *Mol. Plant Pathol.* **2018**, *19*, 2416–2430. <https://doi.org/10.1111/MPP.12719>.
255. Vijayapalani, P.; Hewezi, T.; Pontvianne, F.; Baum, T.J. An Effector from the Cyst Nematode *Heterodera schachtii* Derepresses Host RRNA Genes by Altering Histone Acetylation. *Plant Cell* **2018**, *30*, 2795–2812. <https://doi.org/10.1105/tpc.18.00570>.
256. Patel, N.; Hamamouch, N.; Li, C.; Hewezi, T.; Hussey, R.S.; Baum, T.J.; Mitchum, M.G.; Davis, E.L. A Nematode Effector Protein Similar to Annexins in Host Plants. *J. Exp. Bot.* **2010**, *61*, 235–248. <https://doi.org/10.1093/JXB/ERP293>.
257. Hewezi, T. Cellular Signaling Pathways and Posttranslational Modifications Mediated by Nematode Effector Proteins. *Plant Physiol.* **2015**, *169*, 1018–1026. <https://doi.org/10.1104/PP.15.00923>.
258. Luo, S.; Liu, S.; Kong, L.; Peng, H.; Huang, W.; Jian, H.; Peng, D. Two Venom Allergen-like Proteins, HaVAP1 and HaVAP2, Are Involved in the Parasitism of *Heterodera avenae*. *Mol. Plant Pathol.* **2019**, *20*, 471–484. <https://doi.org/10.1111/MPP.12768>.
259. Postma, W.J.; Slootweg, E.J.; Rehman, S.; Finkers-Tomczak, A.; Tytgat, T.O.G.; van Gelderen, K.; Lozano-Torres, J.L.; Roosien, J.; Pomp, R.; van Schaik, C.; et al. The Effector SPRYSEC-19 of *Globodera rostochiensis* Suppresses Mediated Disease Resistance in Plants. *Plant Physiol.* **2012**, *160*, 944–954. <https://doi.org/10.1104/PP.112.200188>.

260. Diaz-Granados, A.; Sterken, M.G.; Overmars, H.; Ariaans, R.; Holterman, M.; Pokhare, S.S.; Yuan, Y.; Pomp, R.; Finkers-Tomczak, A.; Roosien, J.; et al. The Effector GpRbp-1 of *Globodera pallida* Targets a Nuclear HECT E3 Ubiquitin Ligase to Modulate Gene Expression in the Host. *Mol. Plant Pathol.* **2020**, *21*, 66–82. <https://doi.org/10.1111/MPP.12880>.
261. Contreras, M.P.; Pai, H.; Selvaraj, M.; Toghiani, A.A.; Lawson, D.M.; Tumtas, Y.; Duggan, C.; Yuen, E.L.H.; Stevenson, C.E.M.; Harant, A.; et al. Resurrection of Plant Disease Resistance Proteins via Helper NLR Bioengineering. *Sci. Adv.* **2023**, *9*, eadg3861.
262. Vieira, P.; Gleason, C. Plant-Parasitic Nematode Effectors—Insights into Their Diversity and New Tools for Their Identification. *Curr. Opin. Plant Biol.* **2019**, *50*, 37–43. <https://doi.org/10.1016/J.PBI.2019.02.007>.
- 263 Ferris, H. Host Range of a Genus and Species of Plant-Feeding Nematodes Available online: <http://nemalex.ucdavis.edu/Nemabase2010/NematodePageHostRangeResults.aspx?NgenusNspec=Tylenchulus+semipenetrans> (accessed on 10 January 2023).

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.