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Helminth Molecules in Crop Protection and Agriculture: A Systematic Review of Bioactive Compounds, Mechanisms, and Field Efficacy

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Abstract

Plant-parasitic nematodes (PPNs) are among the most damaging agricultural pathogens, causing annual global crop losses estimated at $358 billion. Conventional chemical nematicides pose significant environmental and health risks, driving the urgent search for sustainable alternatives. Helminths—particularly nematodes—produce a diverse arsenal of bioactive molecules with potential agricultural applications. This systematic review synthesizes current knowledge on helminth-derived bioactive compounds, their molecular mechanisms, and field efficacy. We examine: (i) effector proteins that suppress host plant defenses and manipulate cellular signaling; (ii) nematode-associated molecular patterns (NAMPs), particularly ascaroside #18 (ascr#18), which triggers pattern-triggered immunity (PTI) through the NILR1 receptor and primes plant defense; (iii) secondary metabolites with direct nematicidal activity from plants and fungi; and (iv) entomopathogenic nematodes (EPNs) as biological control agents. The review highlights the intricate interplay between plant immunity, hormonal regulation, and nematode parasitism, including the emerging understanding of reactive oxygen species (ROS) manipulation by nematode effectors. We evaluate translational challenges and integration potential for sustainable crop protection strategies.

Keywords: Helminth Molecules; Parasitic nematodes; Effector proteins; Nematode-associated molecular patterns (NAMPs); Ascaroside #18; Pattern-triggered immunity (PTI); Entomopathogenic nematodes (EPNs); Biological control; Crop protection; Sustainable agriculture.

1. Introduction

Plant-parasitic nematodes represent one of the most significant constraints to global agricultural productivity, with over 4,100 described species [1]. Root-knot nematodes (Meloidogyne spp.), cyst nematodes (*Heterodera* and *Globodera* spp.), and lesion nematodes (*Pratylenchus* spp.) are the most economically damaging, with infestations sometimes resulting in total crop failure [2,3]. These obligate biotrophic parasites invade plant roots, causing mechanical damage, nutrient depletion, and increased susceptibility to secondary pathogens [4,5]. Traditional nematode management has relied heavily on chemical nematicides, including organophosphates, carbamates, and fumigants [6]. However, these compou-nds pose serious environmental and health risks, including soil contamination, groundwater pollution, and toxicity to non-target organisms [7]. The develop-ment of nematicide resistance in PPN populations has further compromised chemical control efficacy [8]. Recent research has highlighted that agroecological crop protection practices generally reduce risks of parasitic diseases, unlike conventional agrochemical-based practices which tend to increase them [2].

Helminths, particularly nematodes, produce a diverse array of bioactive molecules that mediate their interactions with hosts and the environment [4]. These molecules include effector proteins that suppress plant defenses, enzymes that modify host tissues, and secondary metabolites with antimicrobial and nematicidal properties [5]. Understanding these molecules offers opportunities for developing novel, environmentally sustainable crop protection strategies [9]. Entomopathogenic nematodes from the genera Heterorhabditis and Steinernema have emerged as promising biological control agents, providing effective pest management without the ecological costs of chemical pesticides [10,11].

This systematic review aims to synthesize current knowledge on helminth molecules with applications in crop protection, focusing on bioactive compounds, mechanisms of action, and field efficacy.

2. Methodology

2.1 Search Strategy

A systematic literature search was conducted using PubMed, Scopus, Web of Science, Google Scholar, and ScienceDirect databases for articles published between 2000 and 2026 [12]. Search terms included combinations of: "helminth molecules," "nematode effectors," "bioactive compounds," "crop protection," "nematicidal activity," "plant defense," "entomopathogenic nematodes," "ascarosides," "pattern-triggered immunity," and "sustainable agriculture."

2.2 Inclusion Criteria

Studies were included if they: (1) investigated helminth-derived molecules with potential agricultural applications; (2) reported bioactivity against plant pests or pathogens; (3) elucidated mechanisms of action at the molecular level; or (4) evaluated field efficacy [13]. Both laboratory and field studies were considered. Open-access and peer-reviewed sources from MDPI, PubMed Central, Elsevier, Springer, Nature, and APS journals were prioritized.

2.3 Data Extraction

Extracted data included helminth species, molecule type, target organism, mechanism of action, efficacy metrics, experimental conditions, and field performance data. Quality assessment was performed using standar-dized criteria for biological and agricultural research.

Results

3.1 The Molecular Battlefield: Plant Immunity and Nematode Effectors

Plants and nematodes are engaged in intricate evolutio-nary arms races [14]. Plants have evolved sophisticated defense strategies, including pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) [5,15]. Nematodes counter with a diverse arsenal of molecular effectors that suppress, redirect, or exploit these defenses [6]. A central battleground is the regulation of reactive oxygen species (ROS) and their signaling—core components of plant immunity that nematodes have evolved to manipulate [17].

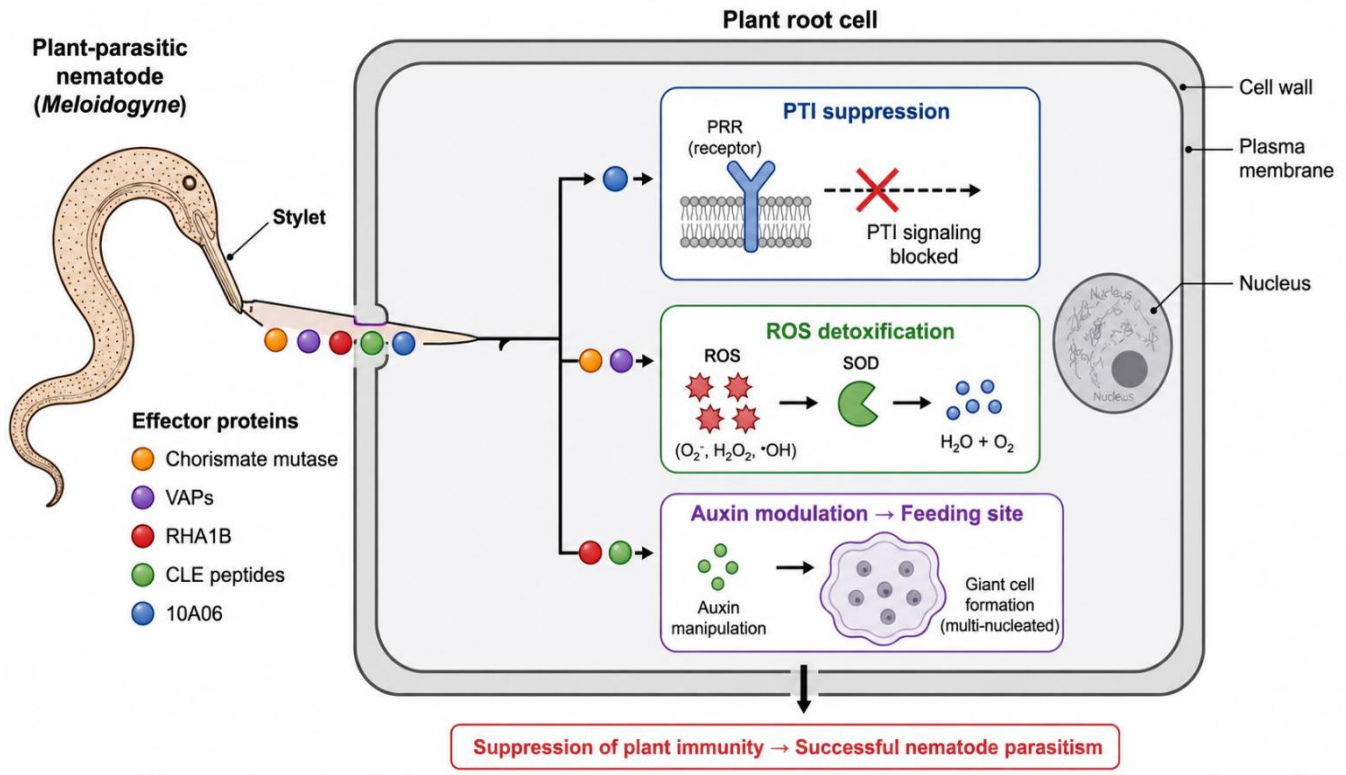

Fig. 1 Nematode Effector-mediated suppression of plant immunity [4,5,18,32-37]

3.1.1 Pattern-Triggered Immunity and NAMPs

PTI relies on specialized pattern recognition receptors (PRRs) that sense conserved molecular signatures—pathogen-associated molecular patterns (PAMPs), damage-associated molecular patterns (DAMPs), and nematode-associated molecular patterns (NAMPs) [15,17].

The best-characterized NAMP is ascaroside #18 (ascr#18), a glycolipid pheromone widely conserved across free-living and parasitic nematodes [18,19]. Initially identified in Ascaris lumbricoides, ascr#18 is abundant in infective juveniles of several plant-parasitic species [20]. When applied exogenously, ascr#18 triggers PTI and enhances resistance to nematodes and microbial pathogens in diverse plants, including Arabidopsis, tomato, potato, and barley [18,19].

Recent research identified NILR1 (NEMATODE-INDUCED LEUCINE-RICH REPEAT-RLK1) as the immune receptor for ascr#18 [21]. The potato NILR1 (StNILR1) directly binds ascr#18 with a dissociation constant (Kd) of ~1.79 µM, mediating immune signaling and resistance against the potato cyst nematode Globodera pallida [22]. Importantly, StNILR1 functions as a dual receptor, recognizing both ascr#18 and the plant hormone brassinosteroid (BR) to activate two different physiological outputs—PTI and BR response [23]. Ascr18/BR-StNILR1 signaling requires the coreceptor StBAK1 [21].

Defense priming by ascr#18 is associated with the formation of open chromatin in regulatory regions of defense genes, providing extended protection with minimal fitness costs [18]. However, recent research reveals that ascr#18 triggers an immune response that differs from typical PTI features—no reactive oxygen species burst or defense-related growth inhibition is observed [18]. Instead, ascr#18 acts by repressing auxin signaling, downregulating auxin transport genes (AUX1, SAUR69, IAA27) involved in nematode feeding site formation [19,24].

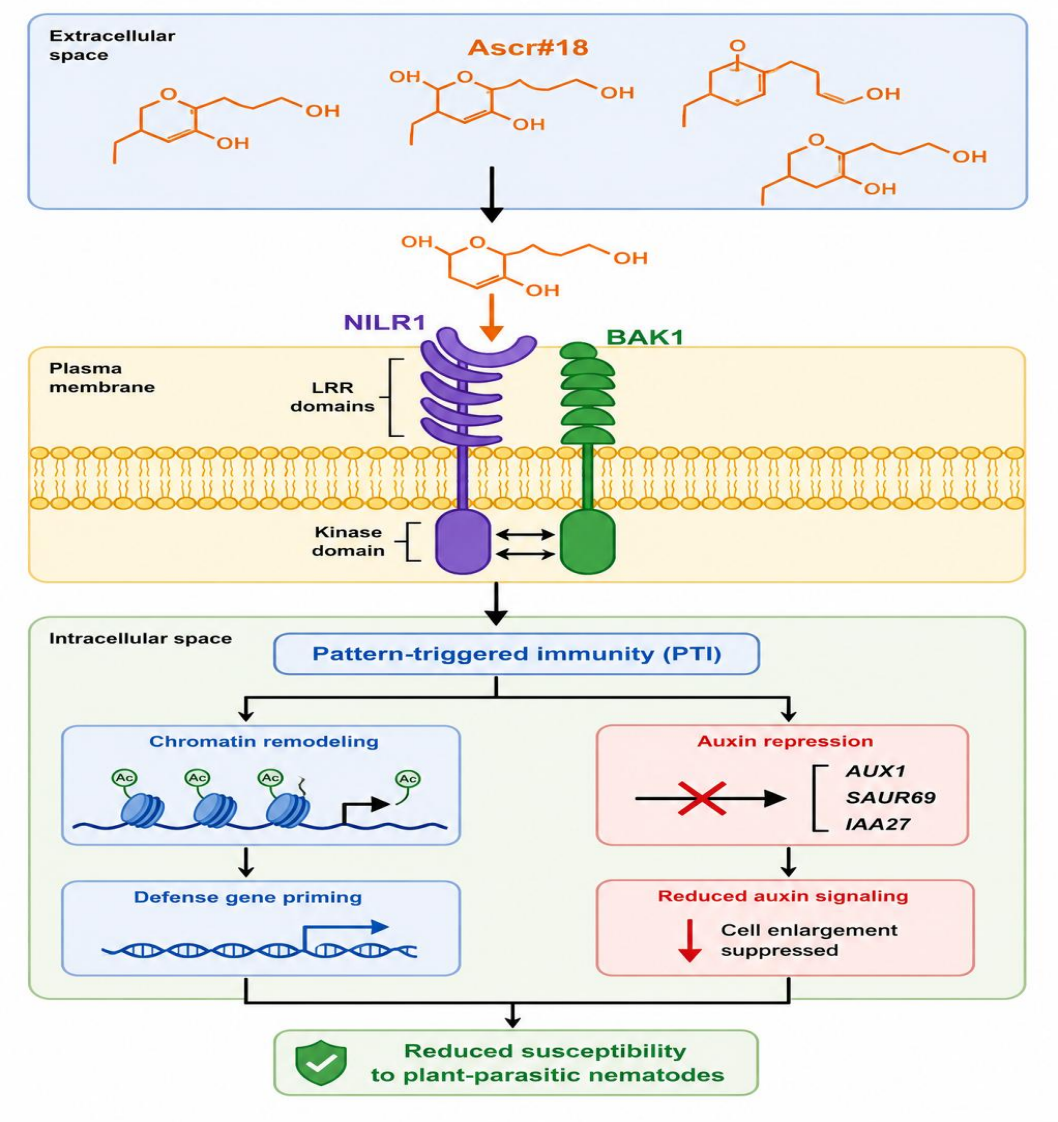

Fig 2. NAMP-triggered plant defence via NILR1 receptor [18-23]

3.1.2 ROS Manipulation by Nematode Effectors

Reactive oxygen species play critical roles during initial nematode infection [17]. ROS cause direct oxidative damage to invading nematodes and function as key signaling molecules that activate downstream defense responses, including cell wall reinforcement through cross-linking of structural components and induction of localized programmed cell death [17,25].

Sedentary PPNs have evolved specialized effectors to suppress ROS production and signaling [17]. These effectors can:

- Suppress ROS bursts directly [17]
- Detoxify reactive molecules via enzymes such as superoxide dismutases (SODs) [26]
- Manipulate host pathways to reduce immune responses [16,27]

PPNs inject effectors into host cells that interfere with ROS production at multiple levels—from direct enzymatic scavenging to sophisticated hijacking of host signaling pathways [17].

3.1.3 Effector Proteins and Host Manipulation

PPNs use their stylet to secrete effector proteins into plant cells, inducing the development of specialized feeding structures—giant cells in root-knot nematodes and syncytia in cyst nematodes [5,9].

The nematode secretome contains three main categories of effectors [5]:

- Cell wall-degrading enzymes (CWDEs)—cellulases, pectate lyases, polygalacturonases, and expansins—facilitating penetration and migration through root tissues
- Effectors inducing feeding site development—modifying host metabolism to establish compatible interactions
- Suppressors that inhibit plant resistance responses

3.2 Bioactive Compounds with Nematicidal Activity

A range of secondary metabolites from plants and fungi show potent nematicidal effects [28,29]. A comprehend-sive review identified 262 plant-based metabolites with nematicidal activities isolated from 35 plant families and 65 plant species [8]. Table 2 summarizes representative compounds with their activities [28,29,30].

Essential oils containing linalool, thymol, carvacrol, cinnamaldehyde, and eucalyptol have also demonstrated promising nematicidal activity through inhibition of egg development and increased larval mortality [29]. However, field efficacy can be limited by volatility and phytotoxicity, which advanced formulation techniques (micro- and nano-encapsulation) can address [29].

3.3 Entomopathogenic Nematodes as Biological Control Agents

EPNs of the genera Heterorhabditis and Steinernema are obligate parasites of insect pests, offering environmentally safe alternatives to chemical insecticides [10,11]. Extensive global surveys have cataloged more than 100 species of Steinernema and 20 species of Heterorhabditis [10].

The EPN life cycle involves a mutualistic association with enteric bacteria—Xenorhabdus (for Steinernema) and Photorhabdus (for Heterorhabditis) [11,35]. The infective juveniles (IJs) carry bacteria in their intestines. Upon entering an insect host, IJs release bacteria that produce toxins, immunosuppressive factors, and antimicrobial compounds, killing the host within 24-48 hours and creating a nutrient medium for nematode development [10,35].

EPN behavioral strategies vary [36]:

- Cruisers (e.g., H. bacteriophora) actively seek hosts via chemical cues
- Ambushers (e.g., S. carpocapsae) remain stationary and attach to passing hosts
- Intermediate species (e.g., S. feltiae) combine both strategies

Table 1. Key effector families in plant-parasitic nematodes

Effector Family	Source Nematode	Function	References
Chorismate mutase	M. javanica, G. pallida	Suppresses SA defense	[31]
VAPs	Multiple PPNs	Suppresses basal immunity	[32]
CLE peptides	CNs, RKNs	Manipulates cell differentiation	[33]
RHA1B	G. pallida	Ubiquitinates NILR1	[23]

CNs, cyst nematodes; RKNs, root-knot nematodes; VAPs, venom allergen-like proteins

Table 2. Representative bioactive compounds with nematicidal activity

Compound	Source	Target	Mechanism	Activity	References
ascr#18	PPNs	H. schachtii	PTI/auxin suppression	Priming active	[23,24]
Alkaloids	Evodia rutaecarpa	M. incognita	Cellular disruption	LC_{50}=73.55 µg/mL	[28]
Omphalotin	Basidiomycetes	M. incognita	Ion-channel modulation	Selective activity	[27]

PPNs, plant-parasitic nematodes

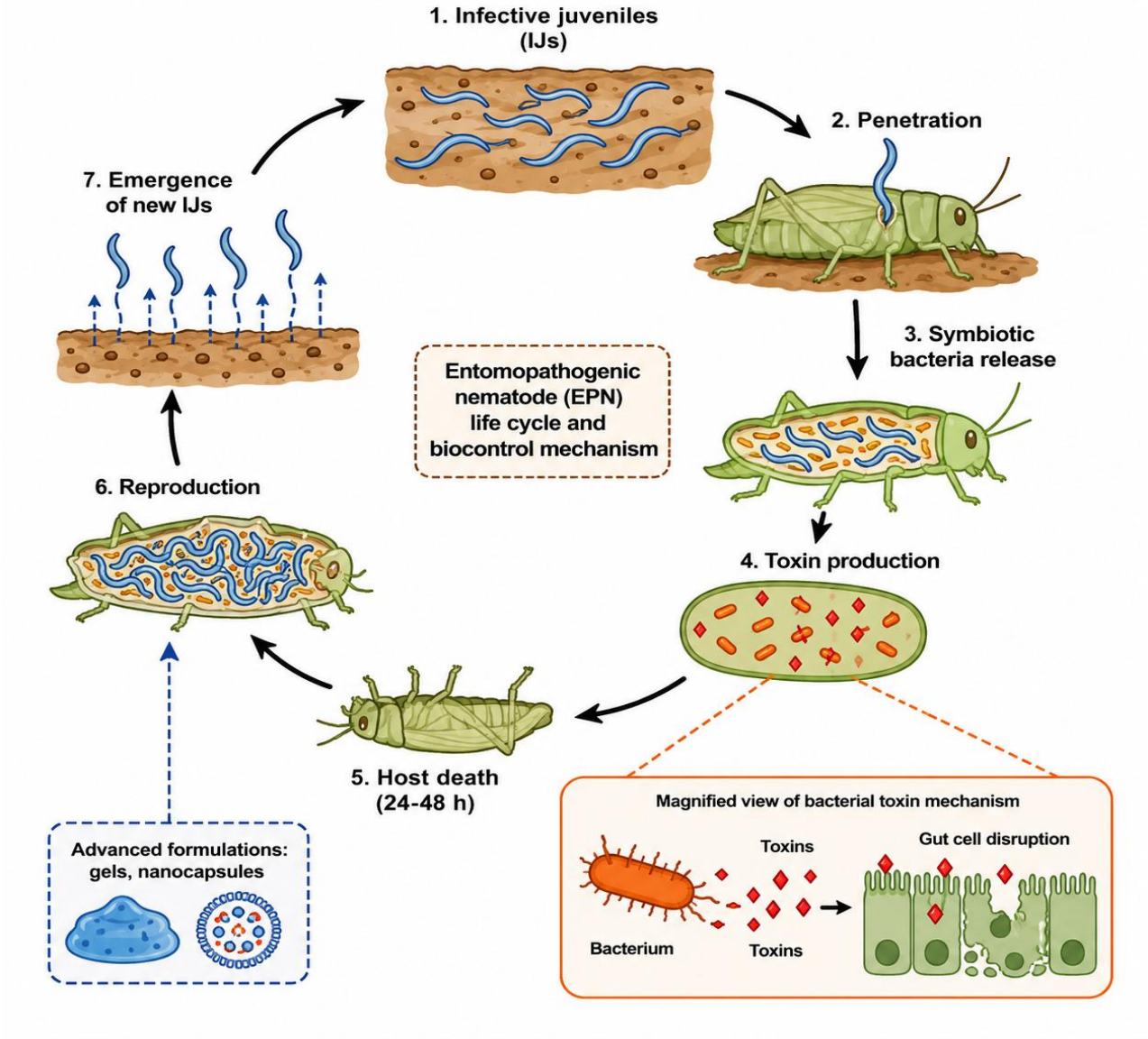

Fig 3. Entomopathogenic Nematodes as Biological Control life cycle [10,11,35,36,39,41,42]

3.3.1 Factors Affecting EPN Field Performance

EPN efficacy is significantly influenced by abiotic and biotic factors [10,11]:

Factor	Optimal Range	Impact	References
Temperature	20-30°C	<10°C reduces infectivity; >32°C impairs reproduction	[37,38]
Soil moisture	Field capacity	Essential for IJ movement	[10]
UV radiation	Minimal exposure	Rapidly inactivates IJs	[10,39]

IJ, infective juveniles

Table 3. Field efficacy of entomopathogenic nematode formulations

EPN Species	Symbiont	Target Pest	Formulation	Efficacy	References
S. feltiae	*X. bovienii*	*F. occidentalis*	Gel-based granules	72-85% mortality	[10,42]
H. bacteriophora	*P.luminescens*	*Popillia japonica*	Nanocapsule spray	68% reduction	[10,43]

Cold-tolerant species like S. feltiae, S. arenarium, and H. bacteriophora can withstand temperatures as low as −22°C, −14°C, and −19°C, respectively [37]. Heat stress triggers accumulation of trehalose, enhancing thermotolerance in some strains [38,40].

Field Efficacy of EPN Formulations

Advances in formulation technology—including water-dispersible granules, calcium alginate capsules, gel carriers, and nanoparticle formulations—have enhanced EPN stability, shelf-life, and field efficacy [10,11,41]. EPN formulated and applied as insect cadavers show higher efficacy than aqueous suspensions [41].

4. Discussion

4.1 Mechanisms of Helminth Molecule Activity

Helminth molecules operate through multiple complementary mechanisms in crop protection contexts [4]:

- Immune Suppression: Effector proteins suppress plant immunity by interfering with PTI and ETI pathways [5]. The interaction between nematode VAPs and host PLCPs, and RHA1B-mediated NILR1 degradation, exemplify sophisticated parasitic strategies [23,27].
- Defense Elicitation: NAMPs such as ascr#18 activate plant defenses through NILR1dependent PTI, priming immune genes via chromatin remodeling [18]. However, recent research reveals a novel defense mechanism based on suppression of auxin signaling rather than classical PTI activation [19,24]. This aligns with the observation that nematode feeding site development is heavily dependent on auxin modulation [33].
- Direct Toxicity: Plant- and fungal-derived compounds (alkaloids, terpenoids, omphalotin, polydosetins) directly affect nematode viability through membrane disruption, ionchannel modulation, or interference with reproduction [28,29,34].
- Bacterial Toxin Production: EPN-associated bacteria produce insecticidal compounds that kill hosts rapidly, with EPNs acting as vectors and delivery systems [11,35].

4.2 ROS Signaling: A Central Battleground

A critical finding from recent research is the centrality of ROS manipulation in plant-nematode interactions [17]. ROS play dual roles—as direct antimicrobial agents and as signaling molecules activating downstream defenses [25]. Nematodes have evolved sophisticated effectors to suppress ROS at multiple levels, from detoxification enzymes to hijacking host signaling pathways [17,27]. Understanding these interactions offers opportunities for developing strategies that enhance plant ROS responses while countering nematode suppression [17].

4.3 The Challenge of Field Translation

Despite promising laboratory results, field application faces significant challenges [10,11]:

- Environmental Factors: Temperature fluctuations, soil moisture variability, UV radiation, and desiccation affect EPN survival and infectivity [10]
- Biotic Interactions: Soil microbiota, predators, and parasitoids can reduce EPN populations [10]
- Formulation Stability: Maintaining IJ viability during storage and application remains challenging [41]
- Application Methods: Optimal timing, dosage, and delivery (soil injection, foliar spray, trunk injection) require site-specific adaptation [39]

Integration into Sustainable Agriculture

Helminth-based approaches align with agroecological crop protection principles [2]. Integration with integrated pest management (IPM) programs, combining biological control, resistant cultivars, and cultural practices, offers the most promising approach for long-term nematode management [43]. Recent advances in genetic engineering, including CRISPR/Cas9 for developing nematode-resistant crops, complement helminth-based strategies [44].

5. Conclusion

Helminth molecules—effector proteins, NAMPs, secondary metabolites, and EPN symbiont toxins—provide a diverse arsenal for crop protection [4]. Key conclusions:

- Effector Research Reveals Vulnerabilities: Studies of nematode effectors, particularly those manipulating ROS and auxin signaling, identify targets for resistance breeding and novel control strategies [5,16,12].
- NAMPs Offer Prophylactic Potential: Ascaroside #18 primes plant defenses through NILR1-dependent mechanisms and represses auxin signaling, reducing nematode susceptibility [18,19,24]. Field retention of priming activity demonstrates practical potential [18].
- Bioactive Compounds Show Promise: Plant- and fungal-derived nematicidal compounds provide leads for biopesticide development, with some showing selective activity against target species [28,29,34].
- EPNs Are Ready for Application: Entomopathogenic nematodes have proven field efficacy against major insect pests, with next-generation formulations enhancing practical utility [10,11,41].

Future Research Priorities

- Characterizing unknown NAMPs present in nematode secretions [17]
- Elucidating the interplay between PTI, ETI, and hormonal signaling in nematode resistance [5,15]
- Optimizing EPN formulations and application methods for diverse agro-ecological conditions [10,41]
- Integrating helminth-based approaches with genetic engineering (CRISPR/Cas9) for durable resistance [44]
- Evaluating long-term ecological impacts and potential for resistance development [45]

Helminth-inspired solutions can significantly reduce reliance on synthetic pesticides, contributing to a more sustainable and resilient food system while addressing global food security challenges [2,43].

Conflicts of interest: The authors stated that no conflicts of interest.

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