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Review

Recent Advances and Developments in the Nematicidal Activity of Essential Oils and Their Components against Root-Knot Nematodes

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Abstract: The *Meloidogyne* genus is widely recognized for its significant economic and scientific importance within the group of plant-parasitic nematodes. The chemical management of nematodes presents its challenges and heavily depends on employing soil fumigants containing toxic and costly nematicides. However, plant-derived essential oils offer promising alternatives, demonstrating a wide range of biological activities that affect nematodes through a range of mechanisms, including disrupting their nervous systems, inducing detrimental effects on plasma membrane permeability, penetrating the gelatinous matrix of nematode eggs, and disturbing intracellular redox status. Most of the extracted essential oils were predominantly sourced from the Lamiaceae family (32%), followed by Asteraceae (11%), Apiaceae (9%), and Poaceae (8%), and with genera *Thymus*, *Mentha*, *Ocimum*, *Artemisia*, *Cymbopogon* being the most common. The nematicidal activity of EOs primarily arises from their chemical groups, such as terpenes, phenylpropanoids, and organosulfur compounds. Among these, geraniol, carvacrol, limonene, eugenol, thymol, and pinene demonstrate the strongest nematicidal potential. The assessed EO efficacy was evaluated against 6 species belonging to the genus *Meloidogyne*. This review also provides knowledge of synergistic and antagonistic interactions of EO components. Synergistic interactions were identified between carvacrol and geraniol, as well as geraniol and eugenol, whereas binary combinations of carvacrol, γ-terpinene, and o-cymene exhibited reduced efficacy. Understanding how specific compounds interact can lead to the development of more potent and effective final products.

Keywords: *Meloidogyne*; bionematicides; green nematicides; nematode management

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1. Introduction

Plant-parasitic nematodes (PPNs) pose a significant challenge to crop production, with root-knot nematodes (RKNs) being particularly threatening to global food security [1]. The *Meloidogyne* genus is widely recognized for its significant economic and scientific importance within the group of plant-parasitic nematodes. These nematodes exhibit high plasticity and adaptability, thriving in diverse geographical areas such as tropical and subtropical regions, like Africa, Asia, North and South America, and Europe [2]. According to indications from the Intergovernmental Panel for Climate Change, elevated temperature and moisture levels may result in an increased rate of infection, development, and reproduction, which, in turn, leads to the shift of their abundance and geographic distribution [3]. The *Meloidogyne* infect monocotyledonous and dicotyledonous plant species, inducing transcriptional reprogramming in host cells, leading to the formation of giant cells, establishing a permanent feeding site within the plant host where they obtain nutrients while completing their parasitic lifecycles [1–4]. These nematodes are sedentary endoparasites with four prevalent species (*M. arenaria*, *M. hapla*, *M. incognita*,

and *M. javanica*). Recent research has revealed the existence of new species previously mistaken for one of the common four. Although the overall documented species count approaches 100, some of these species have more limited or poorly characterized host ranges [5]. Furthermore, *Meloidogyne* spp. can form dynamic disease complexes (MDCs) in conjunction with fungal and bacterial species, further exacerbating disease occurrences and, therefore, causing extensive damage to numerous vital crops globally, including tomato and coffee [6].

The primary focus of controlling nematodes is essentially preventive; the most reliable approaches involve implementing proper sanitation measures and selecting plant varieties that exhibit resistance. However, climatic variations induce diverse immune responses in plants, leading to the loss of resistance to pathogens in certain plant varieties under high-temperature conditions [7]. Existing infestations can be mitigated through fallowing, crop rotation, and soil solarization. However, these methods target nematodes in the top foot of the soil, providing short-term efficacy (for approximately a year) [8]. Chemical management of nematodes presents its challenges and heavily depends on employing soil fumigants containing toxic and costly nematicides. Moreover, these methods may not be suitable for some farming systems, such as organic or regenerative. Although chemical nematicides are currently necessary tools in agriculture, their extensive use has raised significant concerns regarding the enhancement of biodegradation mechanisms in the soil [9]. This could lead to reduced efficacy under field conditions. In addition, the toxicity of nematicides is of particular concern for those operating the application machinery and individuals at risk of exposure during chemical application. Moreover, pesticide residue monitoring may not always prevent the use of nematicides on crops too close to harvest, posing an additional risk [10]. Recently, the risks associated with manufacturing and utilizing these products have become evident, leading to increased regulatory scrutiny of hazardous substances (Class 1 pesticides, previously encompassing all nematicides). Consequently, several highly effective and widely used nematicides, such as methyl bromide, fenamiphos, and aldicarb, have faced severe restrictions. Furthermore, the expenses associated with introducing a novel chemical active ingredient to the US and European markets have been steadily rising each year and are presently estimated to exceed USD 250 million, marking a ten-fold increase compared to the costs observed during the 1960s [11,12]. This increase is accompanied by escalating registration costs and, as mentioned above, more stringent usage criteria. As a result, the prospect of developing conventional compounds (organophosphates or oxime carbamates) is doubtful if their toxicities are deemed to be high [13]. The convergence of these factors, coupled with a growing recognition of the importance of nematode control in agriculture, has raised awareness of the challenges posed by nematodes to crop damage. As agricultural practices intensify, soil degradation accelerates, and warmer climate conditions potentially worsen the problem, the agricultural sector is increasingly aware of the urgent need to address these issues [12].

In response to this challenge, farmers worldwide continue to adopt integrated pest management (IPM) strategies to optimize crop yield while maintaining sustainability in agriculture. Exploring natural compounds with reduced toxicity and minimal environmental impact has become necessary, including biodegradable nematicides that pose little to no harm to human health. Research has focused on biopesticides, particularly green nematicides, revealing promising prospects in pest management technology, progress, and practices that align with the pursuit of more eco-friendly and effective solutions. Benign alternative methods to chemical nematicides are anticipated to form a significant part of long-lasting crop protection strategies in the projected future [14]. In this context, the utilization of beneficial fungi (such as *Trichoderma longibrachiatum* and *T. asperellum*), beneficial bacteria (such as *Pseudomonas fluorescens* and *Bacillus firmus*), botanicals, and essential oils has gained attention as viable biological alternatives for nematode management [15]. Essential oils (EOs) exhibit a wide array of activities, including insecticidal, antifeedant, repellent, oviposition deterrent, growth regulatory, and antivector properties. They are nat-

ural, volatile substances characterized by their potent fragrance, originating from aromatic plants as plant secondary metabolites (PSMs). They are extracted through hydrodistillation and consist of diverse combinations of terpenes, terpenoids, and various aromatic and aliphatic compounds. The biological effects of the EOs result from complex interactions involving synergistic or antagonistic actions among constituents.

EOs impact nematodes through a range of mechanisms, including disrupting their nervous systems, inducing detrimental effects on plasma membrane permeability, penetrating the gelatinous matrix of nematode eggs, and disturbing intracellular redox status [16–18]. Due to their complex composition, essential oils can simultaneously affect multiple targets, therefore reducing the likelihood of target organisms developing resistance or adapting to the treatment. Additionally, the interspecific toxicity of individual oils and compounds varies significantly, making their effects highly idiosyncratic [19].

In a previous review conducted by Catani et al. [20], a comprehensive mapping of the extensive data on essential oils in agriculture against various species of PPNs was effectively presented, providing a thorough bibliometric analysis. In our study, our objective was to conduct a more in-depth investigation, narrowing the focus specifically to root-knot nematodes of the genus *Meloidogyne*. We aimed to complement their overview by providing a detailed exploration into the modes of action and interactions of EOs, with a specific examination of the nematicidal potential of their individual components. Additionally, our focus was on identifying the plant species serving as sources for each essential oil, highlighting components with the strongest nematicidal potential, exploring their mode of action, examining their synergistic and antagonistic interactions with other compounds, and discussing some limitations in EO commercialization. Through this approach, our goal was to present a holistic perspective on the potential of EOs in nematode management, acknowledging areas that warrant further investigation and development. We focus on recent advancements and new findings, as earlier literature on the subject has been thoroughly reviewed by other authors [21].

2. Categorization of Studies

We conducted a comprehensive literature search spanning the last 13 years (2009–2022) using reputable scientific databases, including Scopus, Web of Science, and Google Scholar. A total of 37 relevant research papers were identified, all focusing on the use of essential oils against *Meloidogyne* soil nematodes. The search strings utilized for our investigation included terms such as (“Essential Oil” or “EO”) and (“control of” or “against” or “biological nematicides”) and (“nematodes” or “*Meloidogyne*” or ‘’RKN” or “root-knot nematodes”). The collected data revealed a systematic classification based on plant botanical families as primary sources of EOs. Notably, plants belonging to the Lamiaceae family predominated, comprising 32% of the sources for EOs (Figure 1). Further categorization was based on the identification of the principal chemical components within the EOs responsible for their nematicidal properties. Overall, the reviewed experiments revealed the assessment of the EO efficacy against 6 species within the *Meloidogyne* genus (Figure 2).

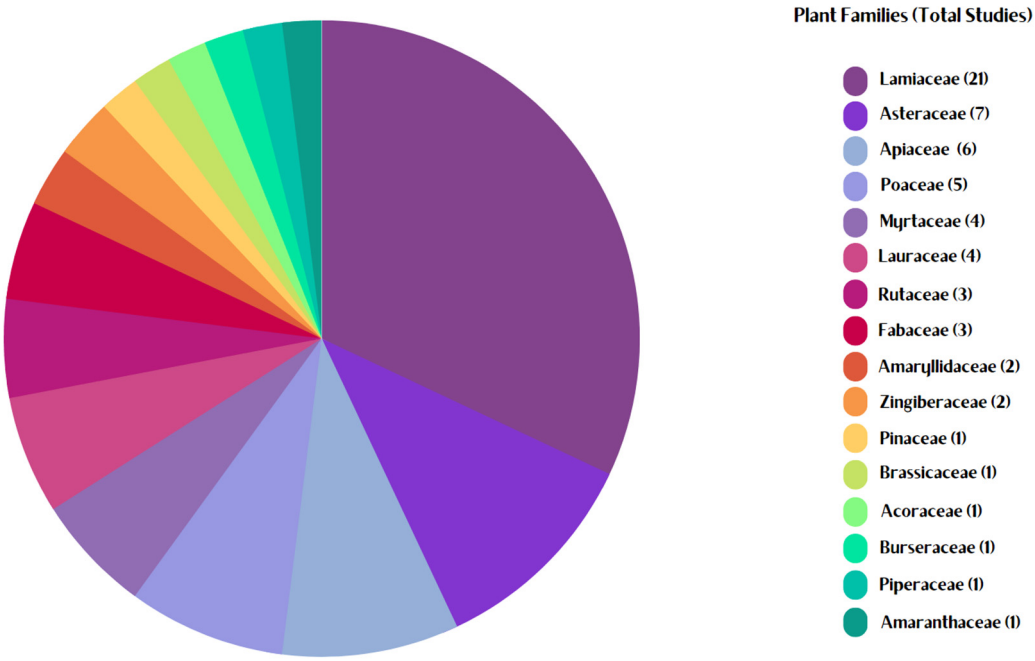

Figure 1. Botanical families identified as plant sources for nematode-controlling essential oils in the dataset.

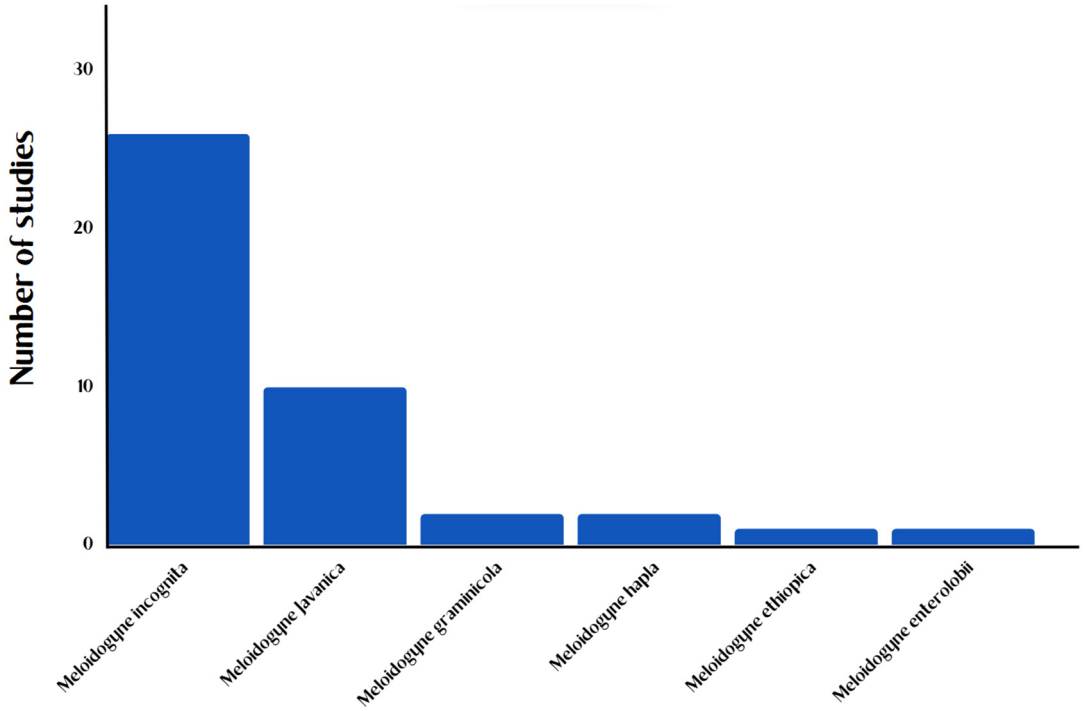

Figure 2. Number of nematicidal studies performed per Meloidogyne species (*M. incognita*, *M. Javanica*, *M. graminicola*, *M. hapla*, *M. ethiopica*, and *M. enterolobii*).

3. Essential Oils, Chemical Groups of Their Components, and Their Mode of Action

Over the last decade, there has been a particular interest in the nematicidal activity of plant EOs and their constituents [21]. The plant-derived substances have shown potential as a source of highly effective pesticidal compounds. They are regarded as an almost boundless reservoir of eco-friendly pest management solutions, with minimal impact on plant and human health, being easily biodegradable [22]. Essential oils comprise complex blends of volatile organic compounds naturally synthesized within various plant parts,

forming part of the plant's secondary metabolism. These metabolites, produced in response to various forms of biotic stress, play essential physiological roles, e.g., attracting pollinators, establishing symbiotic relationships, and providing structural components for lignified cell walls in vascular tissues. Additionally, they enhance ecological competitiveness, exerting diverse effects on the host plant and surrounding organisms [23]. A wide range of PSMs includes flavonoids, phenolic compounds, terpenes, and nitrogen-containing chemicals derived from primary compounds [24,25]. Although some PSMs are naturally produced and stored during regular plant growth, others are specifically synthesized in response to various stress conditions [22]. Essential oils are extracted from various plant parts like leaves, flowers, seeds, and bark. Extraction methods vary depending on the plant part used; steam distillation is the most common method due to its simplicity and cost-effectiveness. Other techniques include mechanical extraction, hydrodistillation, solvent extraction, supercritical CO_2 extraction, and subcritical water extraction [26–28]. The chemical composition, toxicity, and bioactivity of the extracts, in turn, can be influenced by several factors, such as the phenological age of the plant, the percent humidity of the harvested material, and the method of extraction [19].

The nematicidal activity of EOs primarily stems from their individual components, such as specific chemical compounds or bioactive molecules (Figure 3). In various experiments, most of the components tested as nematicides are terpenes. Terpenes are formed structurally by coupling different numbers of isoprene units (5-carbon-base; C5), and they may or may not contain oxygen (terpenoids and terpenes). The main terpene classes are monoterpenes (C10), sesquiterpenes (C15), hemiterpenes (C5), diterpenes (C20), triterpenes (C30), and tetraterpenes (C40). The lipophilic nature of essential oils, including their terpenoid components, has been associated with in vitro cytotoxic activity, primarily due to the presence of phenols, aldehydes, and alcohols [29]. Terpenes exhibit nematode-targeting mechanisms by disrupting plasma membrane permeability due to their lipophilic properties. This disruption compromises barrier function and leads to the leakage of cytoplasmic macromolecules in various organisms, including plant-parasitic nematodes [30]. An alternative hypothesis regarding their impact on plant nematodes suggests a biochemical interaction mechanism where plants release compounds that exhibit toxicity towards both microorganisms and nematodes. The mode of action of each terpene is different and is inextricably linked to its chemical structure. Certain monoterpenes have been found to disrupt the structure of biomolecules like polysaccharides, fatty acids, and phospholipids and can induce depolarization of mitochondrial membranes [31,32]. Furthermore, Kalaiselvi et al. [18] mentioned another mode of action where monoterpenes of the essential oil of *Artemisia nilagirica* disturb the intracellular redox status, activate the central signaling pathway of apoptosis, and induce DNA damage, ultimately leading to cell death. Additionally, other components of EOs with nematicidal effects, not belonging to the terpene group, include organosulfur compounds such as allyl isothiocyanate (AITC), diallyl disulfide (DADS), and diallyl trisulfide (DATS). These compounds influence nematodes' neurotransmission and chemosensing functions [17]. Phenylpropanoids, another group of components found in plant essential oils, show promising results against nematodes, including (e)-cinnamaldehyde, benzaldehyde, eugenol, and eugenol methyl ester. The well-characterized biosynthetic pathway of phenylpropanoids presents a promising target for enhancing nematode resistance, as enzymes involved in this pathway are induced in plants upon wounding or pathogen infection, including sedentary endoparasitic nematodes [33]. In more precise terms, oils containing phenylpropanoid aldehydes exert their effects against nematodes by impeding the activity of the V-ATPase enzyme. This enzyme, known as a vacuolar-type proton-translocating ATPase, is responsible for pumping protons across membranes and is energized by ATP hydrolysis. It plays critical roles in nematode nutrition, osmoregulation, cuticle synthesis, neurobiology, and reproduction [34]. Moreover, the presence of phenols, aldehydes, and alcohols in an EO can act against the nematode by oxidizing its cytoplasmic membranes [34].

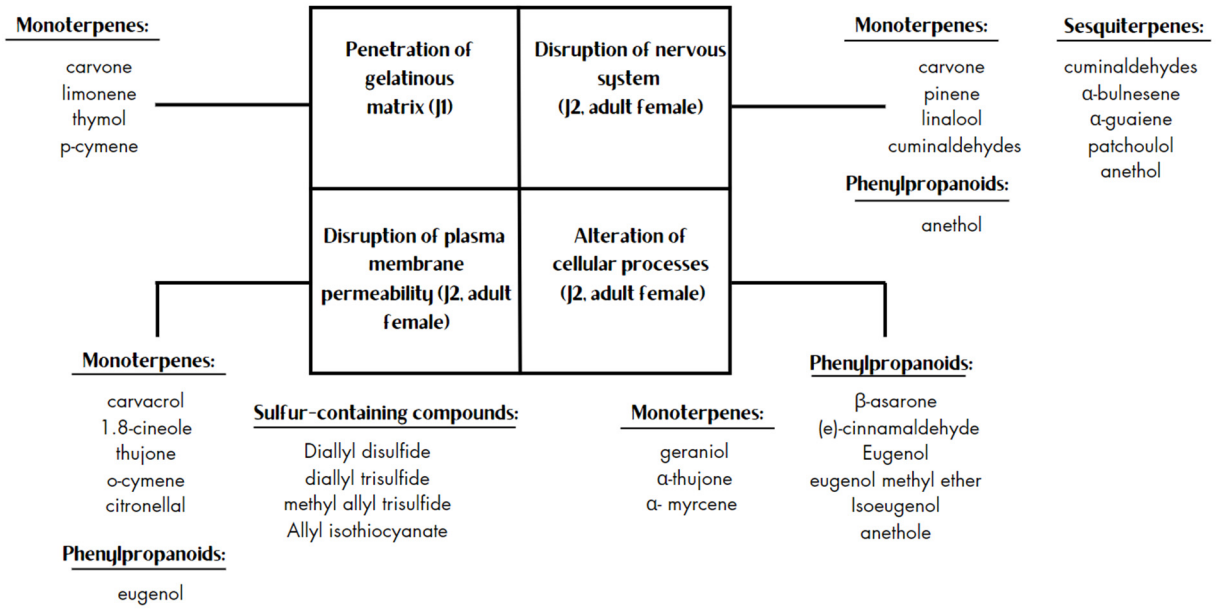

Figure 3. Compounds of EOs and their mode of action against root-knot nematodes.

Many of the extracted essential oils renowned for their diverse biological properties predominantly originate from the Lamiaceae family (Table 1). The Lamiaceae family encompasses 7530 species, including trees, shrubs, subshrubs, and herbs. It is globally distributed and utilized across various fields, such as medicine, pharmaceuticals, and the food industry [35,36]. Within this family, EOs derived from genera like *Thymus* (e.g., *Thymus vulgaris*), *Origanum* (e.g., *Origanum vulgare*), *Salvia* (e.g., *Salvia rosmarinus*), *Mentha* (e.g., *Mentha spicata*), and *Ocimum* (e.g., *Ocimum basilicum*), have exhibited strong insecticidal, acaricidal, fungicidal, herbicidal and nematicidal properties [36,37]. Mint (*Mentha* spp.) stands as one of the most extensively studied plants for EO extraction, followed by thyme (*Thymus* spp.) and basil (*Ocimum* spp.). Additionally, significant amounts of EOs were derived from Asteraceae, Apiaceae, and Poaceae botanical families, with genera like *Artemisia* and *Cymbopogon* being prominent EO sources (Table 2).

Table 1. Plant sources of the essential oils belonging to the family Lamiaceae, their components with nematicidal action in different experimental settings against *Meloidogyne* spp.

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
				Lamiaceae				
Lavandula Intermedia (3 species: *Abrialis*, *Cerioni* and *Sumiens*)	linalool	J2, eggs	J2 mortality, egg-hatching inhibition, reduction of galls, eggs	tomato	in vitro, pot, greenhouse, soil	*M. incognita*	EO: 24.9 $\mu g/mL^{-1}$, 1.2 $\mu g/mL^{-1}$, 17.4 $\mu g/mL^{-1}$.	[38]
Lavandula officinalis, *Mentha arvensis*, *Thymus serpyllum*, *Ocimum basilicum*		Galls, eggs	Reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]
Monarda didyma, *Monarda fistulosa*	γ-terpinene, o-cymene, carvacrol	Eggs, J2	J2 mortality, egg-hatching inhibition, reduction of galls and eggs in soil	tomato	in vitro, soil	*M. incognita*	EO: 1.0 $\mu L\ mL^{-1}$, 12.5 $\mu L\ mL^{-1}$ for 24 h (J2 mortality) 500 and 1000 $\mu g\ mL^{-1}$ for 24, 48 h (egg hatching)	[40]
Mentha longifolia	piperitone oxide	J2, eggs	J2 mortality, Egg hatch inhibition			*M. graminicola*	EO: 15.62 to 1000 ppm for 96 h	[41]
Mentha longifolia	i-menthone	Egg	Egg hatch inhibition		in vitro	*M. hapla*		[42]
Mentha spicata L.	carvone, limonene	J2, eggs	J2 mortality, reduction of galls and eggs	Coleus	in vitro, greenhouse	*M. javanica*	EO: 1000, 2000, 3000, 4000, and 5000 ppm (*v*/*v*) for 24 h, 48 h, 72 h	[43]
Mentha spicata L.		J2	J2 mortality, reduction of galls	pepper	in vitro, greenhouse, plastic house	*M. incognita*	EO: 5% (*v*/*v*) for 72 h	[44]
Mentha spicata	carvone	Egg	Egg hatch inhibition		in vitro	*M. hapla*		[42]
Menta piperita	carvone	J2	J2 mortality		in vitro	*M. hapla*		[42]
Nepeta cateria		J2	J2 mortality	banana	orchard	*M. incognita*	EO: 1.2 mL/L	[45]

Table 1. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
Basilicum L.	sabinene, myrcene, trans-caryophyllene	J2	J2 mortality, reduction of galls	pepper	in vitro, greenhouse, plastic house	*M. incognita*	EO: 5% (*v*/*v*) for 72 h	[44]
Ocimum sanctum L.	eugenol methyl ether	J2	J2 mortality		in vitro	*M. incognita*	EO: 1230 mg/L for 24 h	[46]
Ocimum basilicum	i-linalool	J2	J2 mortality		in vitro	*M. hapla*		[42]
Origanum onites	carvacrol	egg	Egg hatch inhibition		in vitro	*M. hapla*		[42]
Origanum onites	carvacrol	egg	Egg hatch inhibition		in vitro	*M. hapla*		[42]
Pogostemon cablin Benth	α-guaiene, patchoulol, α-bulnesene	J2	J2 mortality, J2 immobility		in vitro	*M. incognita*	EO: 250 μg/mL^{-1}, 31.25 μg/mL^{-1} for 24 h	[47]
Pogostemon cablin	α-guaiene	J2	J2 mortality, paralysis	pepper	in vitro, greenhouse, plastic house	*M. incognita*	EO: 387.77 μg mL^{-1} for 48 h	[48]
Salvia officinalis	thujone	egg	Egg hatch inhibition		in vitro	*M. hapla*		[42]
Thymus citriodorus	geraniol	J2, eggs	Biological cycle arrest, J2 paralysis, J2 mortality	tomato	in vitro, pot	*M. incognita*	EO: 50 μL kg^{-1} soil	[49]
Teucrium polium	limonene, α-pinene, β-pinene	J2	J2 mortality		in vitro	*M. incognita*	EO: 4000 and 8000 ppm (*v*/*v*) for 24 h	[50]
Thymus linearis Benth	thymol, carvacrol	J2, eggs	J2 mortality, Egg hatch inhibition		in vitro	*M. incognita*	Rainy season: 5 μL/mL for 72 h (J2 mortality), 2 μL/mL for 72 h (egg hatching) Winter season: 8 μL/m for 72 h (J2 mortality),2 μL/mL for 72 h (egg hatching)	[51]

Table 1. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
Thymus vulgaris L.	thymol, ρ-cymene	J2, eggs	J2 mortality, reduction of galls and eggs	Coleus	in vitro, greenhouse	*M. javanica*	EO: 1000, 2000, 3000, 4000, and 5000 ppm (*v*/*v*) for 24 h, 48 h, 72 h	[43]
Zataria multiflora		J2	J2 mortality	banana	orchard	*M. incognita*	EO: 1.2 mL/L	[45]

Table 2. Plant sources of the essential oils belonging to different botanical families, their components with nematicidal action in different experimental settings against *Meloidogyne* spp.

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
Acoraceae								
Acorus calamus	β-asarone	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 524.45 µg mL^{-1} for 24 h	[48]
Amaranthaceae								
Dysphania ambrosioides	(z)-ascaridole, e-ascaridole, p-cymene	Eggs, J2	J2 mortality, egg-hatching inhibition, reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 500 µg mL^{-1} for 48 h	[52]
Amaryllidaceae								
Allium sativum	diallyl disulfide (DADS), diallyl trisulfide (DATS), methyl allyl trisulfide	Eggs, J2	J2 mortality, egg-hatching inhibition	Tomato	in vitro, pots	*M. javanica*	EO: 0.025 µg mL^{-1} for 72 h Hydrolat: 0.125 µg mL^{-1} for 72 h	[53]
Allium sativum	diallyl disulfide (DADS), diallyl trisulfide (DATS)	Eggs, J2	J2 mortality, egg-hatching inhibition, reduction of galls and eggs	Tomato	in vitro, greenhouse, pots	*M. incognita*	EO: 500 µg mL^{-1} Components: 62 µg mL^{-1}	[53]
Anacardiaceae								
Schinus terebinthifolius	terpinen-4-ol, γ-terpinene, α-terpineol	Eggs, J2	J2 mortality, egg-hatching inhibition	lettuce	in vitro, field	*M. javanica*		[54]

Table 2. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
				Apiaceae				
Coriandrum sativum	linalool	J2	J2 mortality		in vitro, lab	*M. hapla*		[42]
Cuminum cyminum	γ-terpinen-7-al, α-terpinen-7-al, cumin aldehydes	J2, Eggs	J2 mortality, egg-hatching inhibition, J2 paralysis, egg differentiation, reduction of nematode population in soil	Tomato	in vitro, pots	*M. javanica*	EO: 62.5 µL/L, 2000 µL/L for 48 and 96 h of immersion	[55]
Daucus carota	carotol, daucol, daucene	J2, Eggs	J2 mortality, egg-hatching inhibition		in vitro	*M. incognita*	EO: 2500 ppm for 96 h	[56]
Ferula oopoda		J2	J2 mortality	Banana	Orchard	*M. incognita*	EO: 1.2 mL/L	[45]
Foeniculum vulgare	anethole	J2	J2 mortality		in vitro, lab	*M. hapla*		[42]
Ridolfia segetum	(z)-β-ocimene, β-pinene	J2, Eggs	J2 mortality, J2 mobility, and egg-hatching inhibition		in vitro, lab	*M. javanica*	EO: 16 µL/mL for 72 h	[57]
				Asteraceae				
Artemisia absinthium	borneol acetate, β-terpineol	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 937.52 µg mL^{-1} for 48 h	[48]
Artemisia absinthium	-	Galls, eggs	Reduction of galls and eggs	Tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]
Artemisia nilagirica	α-thujone, α-myrcene, linalyl isovalerate, camphor, caryophyllene oxide, eucalyptol	J2, Eggs	J2 mortality, egg-hatching inhibition, reduction of galls, eggs, and nematodes in soil	Tomato	in vitro, greenhouse	*M. incognita*	EO: 20 µg/mL for 48 h	[18]
Achillea santolina		J2	J2 mortality	Banana	Orchard	*M. incognita*	EO: 1.2 mL/L	[45]
Achillea wilhelmsii	1,8-cineole, limonene, α-pinene, β-pinene	J2	J2 mortality		in vitro	*M. incognita*	EO: 4000 and 8000 ppm (*v*/*v*) for 24 h	[50]

Table 2. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
Tanacetum falconeri Hook. f.	cis-dehydromatricaria ester-1	J2	J2 mortality		in vitro	*M. incognita*	EO: 1% (*w*/*v*) for 24 h	[58]
Tanacetum polium	(e)-caryophyllene, limonene, α-pinene, β-pinene	J2	J2 mortality		in vitro	*M. incognita*	EO: 4000 and 8000 ppm (*v*/*v*) for 24 h	[50]
				Brassicaceae				
Brassica nigra	allyl isothiocyanate (AITC)	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 47.7 μg mL^{-1} for 72 h	[17]
				Burseraceae				
Commiphora myrrha	furanoeudesm-1,3-diene, curcerene	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 1000 μg mL^{-1} for 24 h	[48]
				Fabaceae				
Piptadenia viridiflora	benzaldehyde	J2	J2 mortality		in vitro	*M. incognita*	EO: 1000 μg mL^{-1}, Component: 100 and 200 μg mL^{-1} for 48 h	[59]
Tephrosia toxicaria	β-caryophyllene, germacrene D, a-humulene, bicy-clogermacrene	Eggs, J2	J2 mortality, egg-hatching inhibition		in vitro	*M. javanica*/*M. enterolobii*	EO: 50, 100, 200, 400, 600, 800 μg mL^{-1} for 48 h	[60]
Trifolium incarnatum	(z)-3-hexenyl acetates, (Z)-3-hexane-1-ol, (E) -ocimene, furanoeudesm-1,3-diene	J2	J2 mortality, reduction of galls	chili pepper (*Capsicum annuum* L.)	in vitro, greenhouse, plastic house	*M. incognita*	EO: 3% and 5% (*v*/*v*) for 48 h	[44]

Table 2. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
				Hypericaceae				
Hypericum perforatum		Galls, eggs	Reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]
				Lauraceae				
Cinnamomum cassia	(e)-cinnamaldehyde	Eggs, J2	J2 mortality, J2 paralysis, reduction of galls and eggs	Soybean	in vitro, in greenhouse pots	*M. incognita*	EO: 62 μg/mL^{-1} Component: 208 μg/mL^{-1} for 48 h	[34]
Cinnamomum zeylanicum Blume	eugenol	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 391 mg/L for 24 h	[46]
Cinnamomum zeylanicum	(e)-cinnamaldehyde, eugenol	Eggs, J2	J2 mortality, egg-hatching inhibition, reduction of galls and eggs		in vitro, pots	*M. incognita*	EO: 49 μg/mL^{-1}, Components: 529 and 768 μg/mL^{-1} for 48 h	[59]
Laurus nobilis L.	linalool, 1, 8-cineole, α-pinene, β-pinene, α-terpinyl acetate	Eggs, J2	J2 mortality, egg-hatching inhibition		in vitro	*M. incognita*	EO: 0.80 μg/mL^{-1} for 96 h	[56]
				Myrtaceae				
Eucalyptus citriodora	citronellal	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 746.48 μg mL^{-1} for 24 h	[48]
Eucalyptus citriodora		Galls, eggs	Reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]
Melaleuca alternifolia	β-terpineol, γ-terpinene	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 404.13 μg mL^{-1} for 24 h	[48]
Myrtus communis	α-pinene, 1,8-cineol	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 932.65 μg mL^{-1} for 48 h	[48]
Syzygium aromaticum	eugenol	J2	J2 mortality		in vitro	*M. graminicola*	Component: 500 ppm for 48 h	[61]

Table 2. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
				Pinaceae				
Pinus nigra	a-pinene, c-verbenol	J2	J2 mortality		in vitro	*M. javanica*	EO: 1 µg mL^{-1} Compounds: 0.5 µg mL^{-1}	[62]
				Piperaceae				
Piper nigrum		Galls, eggs	Reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]
				Poaceae				
Cymbopogon flexuosus	citral	J2	J2 mortality		in vitro	*M. graminicola*	Component: 500 ppm for 48 h	[61]
Cymbopogon martinii	geraniol	J2	J2 mortality		in vitro	*M. graminicola*	Component: 500 ppm for 48 h	[61]
Cymbopogon nardus	citronellal, geraniol	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 325.41 µg mL^{-1} for 24 h	[48]
Cymbopogon schoenanthus (L.) *Spreng*	piperitone	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 524 mg/L for 24 h	[46]
Vetiveria zizanioides (L.) (extract)	sesquiterpene acid 3,3,8,8-tetramethyltricyclo[5.1.0.0(2,4)]oct-5-ene-5-propanoic acid, 6-isopropenyl-4,8a-dimeth yl-1,2,3,5,6,7,8,8a-octahydronaphthalen-2-ol		J2 mortality		in vitro	*M. graminicola*	EO: 0.95 mg/mL for 72 h	[63]
				Rutaceae				
Citrus bergamia		Galls, eggs	Reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]

Table 2. *Cont.*

Plant Source of the Essential Oil	Active Components	Target Life Stage	Mode of Action	Crop	Experiment	*Meloidogyne* spp.	Experiment Details	Author
Citrus reticulata	limonene	Eggs, J2	J2 mortality, egg-hatching inhibition		in vitro	*M. incognita*	Component: 1500 µg/mL^{-1} for 96 h	[16]
Citrus sinensis	l-limonene	J2	J2 mortality, J2 paralysis		in vitro	*M. incognita*	EO: 353.20 µg mL^{-1} for 24 h	[48]
				Verbenaceae				
Lippia citriodora	citral	Egg	Egg hatch inhibition		in vitro	*M. hapla*		[42]
				Zingibiraceae				
Hedychium coccineum	e-neradiol, davanone B, spathulenol, eucalyptol	Eggs, J2	J2 mortality, egg-hatching inhibition		in vitro	*M. incognita*	EO: 0.25 µg/mL for 24 h 1 µg/mL for 96 h	[64]
Zingiber officinale		Galls, eggs	Reduction of galls and eggs	tomato	in vitro, pots	*M. incognita*	EO: 3% and 5% (*v*/*v*)	[39]

The nematicidal effect of specific substances is closely linked to their chemical profile. The results indicate that compounds featuring hydroxyl (-OH) or methoxy (OCH_3) groups, such as linalool, geraniol, carvacrol, and thymol, exhibited a higher frequency of nematicidal action compared to those with an acetyl group (acetyleugenol). This finding implies that the positions of the double bond within the propenyl group and the position of the substituent in the geometrical isomer play crucial roles in determining the nematicidal activity. Furthermore, allylic alcohol and phenolic alcohols, such as carvacrol and geraniol, demonstrated more potent nematicidal properties compared to other alcoholic compounds containing a hydroxyl group [50]. To differentiate the impact of essential oils based on their specific chemical compositions, researchers conduct identification and quantification of the constituent compounds of essential oils that are responsible for nematoxicity. This analysis involves techniques such as gas chromatography–mass spectrometry (GC–MS), high-performance liquid chromatography (HPLC), and proton nuclear magnetic resonance (HNMR) alongside in vitro assays [50,65].

3.1. Geraniol

Geraniol, an alcohol monoterpene present in the essential oil of various herbs, has demonstrated synergistic effects when combined with other terpenes like trans-anethole, eugenol, and carvacrol, effectively reducing gall development at specific concentrations [66]. The efficacy of geraniol can be attributed to the position of the alcohol functional group, a critical factor significantly influencing the nematicidal potency of various compounds. Experiments conducted on tomato plants against *M. incognita* and *M. javanica* juveniles revealed the nematicidal potential of geraniol, causing paralysis and interrupting their biological life cycle. This effect was attributed to the high content of geraniol (44.06%) found in the EO derived from *Thymus citrodorus* [67]. Similarly, the EO of *Cymbopogon nardus*, also containing geraniol, induced mortality (LC50 within 72 h at concentrations below 50 g mL^{-1}) and immobility in over 50% of J2s at various concentrations. This compound exhibited efficacy against *M. ethiopica* juveniles, rendering them immobile within 24 h of exposure and maintaining their unresponsiveness throughout the experiment. Notably, geraniol initiated a 98.1% mortality rate after 24 h, ultimately leading to complete nematode mortality in subsequent assessments [68]. Furthermore, geraniol has shown significant nematicidal activity against *M. javanica*; at a concentration of 500 ppm, it induced 100% paralysis of J2s and inhibited egg hatching by approximately 70%. Sublethal doses (140 and 280 ppm) in pot experiments also reduced the number of nematode females in tomato roots to 59 and 56, respectively, while the control treatment exhibited 93 females per gram of root [66].

3.2. Carvacrol

Carvacrol, categorized as a monoterpenic phenol alongside p-cymene, constitutes essential components found in essential oils extracted from plants belonging to the Lamiaceae family. This botanical group is characterized by its rich aromatic compounds [69]. Carvacrol disrupts the normal functioning of certain receptors in nematodes, impairing movement and potentially explaining its nematicidal effect. This action is achieved through interaction with nicotinic acetylcholine receptors (nAChR) within the nematodes' neuromuscular system [69]. *Meloidogyne incognita* demonstrated significant sensitivity to carvacrol, the major compound in *Monarda didyma* and *Monarda fistulosa* EOs, exhibiting an LC50 value of 14.2 µg mL^{-1} after 24 h of treatment. This concentration resulted in an 82% mortality rate of J2 juveniles, along with a considerable inhibition of egg hatch, decreasing to just 4.1% after 48 h of exposure [40]. Carvacrol, a primary constituent of the from *Satureja hellenica* EO, displayed high efficacy against various developmental stages of both *M. incognita* and *M. javanica*. It induced over 80% paralysis in J2 juveniles after 24, 48, and 96 h of exposure and effectively inhibited egg differentiation even at a dose of 250 µL/L, without additional inhibition observed in higher doses [55]. *Origanum onites* exhibited high efficacy in inhibiting egg hatching (68.8%), which was attributed to their high carvacrol content [42].

Furthermore, Kabdal et al. (2022) reported significant outcomes of carvacrol on J2 mortality and egg hatching when testing *Thymus linearis* EO from two different seasons (winter season and rainy seasons) against *M. incognita*. Interestingly, slightly better results were observed during the winter season (showing 64% at 5 µL/mL after 72 h of exposure time) compared to the rainy season (showing 55.23% at 5 µL/mL after the same exposure time). The authors attributed the success of EO to higher percentages of carvacrol.

3.3. Eugenol

Eugenol, chemically known as 4-allyl-2-methoxyphenol ($C_{10}H_{12}O_2$), serves as the primary nematicidal compound found in *Ocimum sanctum* L., a plant belonging to the Lamiaceae family. It is also a major constituent of clove oil—*Syzygium aromaticum* (Myrtacaceae), *Laurus nobilis* L. (Lauraceae), and *Cinnamomum zeylanicum* (Lauraceae) [70]. In an in vitro study on *Laurus nobilis* L., eugenol was identified as the major component exhibiting strong nematicidal potential. Complete inhibition of egg hatch was observed at a concentration of 1.25 mg mL^{-1}, and at a lower concentration of 0.20 mg mL^{-1}, more than 50% mortality of *M. incognita* J2 juveniles was recorded within 24 h of immersion [56]. The EO derived from *Syzygium aromaticum*, with eugenol as its major compound comprising 87.1% of the oil's composition, demonstrated promising effects on the mortality of *M. gramincola* J2 juveniles [61]. Specifically, at a concentration of 500 ppm, the J2 mortality rate ranged from 93.75% to 98.75% over exposure durations of 24, 48, 72, and 96 h. Even when the concentration was significantly reduced to just 62.5 ppm, it still resulted in pronounced mortality rates (73.75% to 80.00%). As the predominant compound in cinnamon essential oil (*Cinnamomum zeylanicum*), eugenol exhibited moderate effectiveness in vitro against second-stage juveniles *Meloidogyne incognita*, considering the EC50 at 371 ± 70 mg/L after 24 h of exposure, and 216 ± 86 mg/L after 48 h of treatment [46]. The authors suggested that phenylpropanoid aldehydes, particularly eugenol, showed higher activity compared to acetate derivatives (acetyleugenol).

3.4. Linalool

Linalool, present in two enantiomeric forms, S-(+)- and R-(−)-linalool, is prominent in essential oils known for their diverse biological activities, including antimicrobial and antioxidant properties, as well as repellent effects on various crop-damaging insects [71]. Compared to other EO components, linalool exhibits moderate solubility in water (1590 mg L^{-1} at 25 °C) [72]. The tested EOs from three lavandin cultivars showed strong activity against *M. incognita* and *M. javanica*, highlighting the variation among sources and nematode species. The observed structure–activity relationships primarily depended on the chemical features of the dominant components [38]. For instance, the EO from cv *Rinaldi Cerioni* (65.82% of linalool) exhibited significantly higher toxicity compared to cv *Abrialis* (40.31%) and *Sumiens* (47.99%). All three varieties displayed nematicidal activity (J2 mortality exceeding 70%) following an 8-hour treatment, and it was attributed to the acyclic structure of linalool, the major component of lavandin cultivars. *Coriandrum sativum* EO, which was predominantly composed of linalool (81.3%), caused high mortality among *Meloidogyne hapla* J2 (69.3%) after 24 h. However, its effectiveness was comparatively lower than other acyclic alcohols, such as geraniol and citronellol [42].

3.5. Limonene

Limonene, a monocyclic monoterpene ($C_{10}H_{16}$), comprises two optical isomers: R-limonene (D-limonene) and S-limonene (L-limonene), each with distinct insecticidal and antimicrobial properties [27,73]. Limonene, as the major compound of *Citrus reticulata* peel EO, was the primary compound responsible for egg-hatching inhibition, as well as J2 mortality in *M. incognita*. Results revealed 87.45% egg-hatching inhibition at 1500 µg mL^{-1} after 96 h of exposure and 83.31% J2 mortality at the same concentration and exposure time [16]. Furthermore, limonene was a major compound in spearmint essential oil emulsion, causing a notable increase in the mortality percentage of *M. javanica* juveniles in a concentration-

depending manner. Specifically, at 4000 ppm, the mortality rate reached 78.9% within 24 h and 100% after 72 h of exposure [44]. Its presence was also detected in essential oils from various plants such as *Achillea wilhelmsii*, *Tanacetum polycephalum*, *Rutaceae Citrus reticulata*, *Citrus sinensis*, and *Teucrium polium*, and was identified as a key component responsible for their nematicidal activity when subjected to in vitro nematotoxicity tests [50]. Both concentrations of limonene (100 and 200 ppm) induced over 90% mortality in *M. incognita* J2 [50].

3.6. Thymol

Thymol has been found to enhance the innate immune response in nematodes, associated with specific parasitism-related signaling pathways and crucial regulatory genes [74]. Thyme EO emulsion extracted from *Thymus vulgaris* L. (Lamiaceae) was tested in vitro against second-stage juveniles *M. javanica*, and in vivo on coleus plants [43]. At a concentration of 5000 ppm, the emulsion achieved the highest mortality reduction (100%) within 24 h, primarily attributed to thymol. Thymol was also the major component of *Thymus vulgaris* EO (35.3%), with a relatively higher half-maximal effective concentration (EC50) of 4190 ± 816 mg/L after 72 h, suggesting a need for higher concentrations and longer exposure times for effective nematode control [46]. Extracted EO from *T. linearis*, mainly composed of thymol, demonstrated a dosage-dependent effect on *M. incognita*. At a low concentration of 2 µL/mL, it inhibited egg hatching by 38.72% after 72 h. Interestingly, higher concentrations (6 and 10 µL/mL) resulted in lower hatching percentages (36.58%) within the same exposure time. However, higher concentrations significantly increased J2 mortality, reaching 55.23% at 5 µL/mL after 72 h (from 19.80% at 1 µL/mL) [51].

3.7. Pinene

Pinene, a well-known group of monoterpenes ($C_{10}H_{16}$), is the primary constituent of turpentine extracted through resin distillation from various coniferous trees, notably those of the *Pinus* genus [75,76]. The two structural isomers, α-pinene and β-pinene, are also abundant in various herbs, including rosemary, parsley, basil, and even citrus peels, contributing to their distinctive aromas and properties [77–79]. The monoterpene hydrocarbon α-pinene was found in many essential oils when testing for the nematicidal activity of EO compounds. In vitro tests showed that α-pinene alone exhibited 79% *M. incognita* egg hatch inhibition at 1.50 mg mL^{-1} and caused over 50% J2 mortality at 0.20 mg mL^{-1} after 24 h. Also, it constituted a significant portion of the EO of bay leaf, which displayed high effectiveness in the same parameters (egg hatching and J2 mortality) against the same species. At a concentration of 1.00 mg mL^{-1} after 72 h, *Laurus nobilis* L. EO caused complete egg-hatching inhibition, while total J2 mortality was observed at 0.80 mg mL^{-1} after 96 h of immersion. It is hypothesized that the presence of α-pinene contributes to the effectiveness of bay leaf EO [56]. Similarly, being a major component of *Myrtus communis* (Myrtaceae) EO, α-pinene contributed to its effectiveness, showing results in J2 mortality and mobility. At a concentration of 879.40 µg mL^{-1}, the EO exhibited LC50 within 72 h and caused immobility in over 50% of *M. incognita* J2s at different concentrations [48]. Pinene was also one of the main components of the EOs of *Achillea wilhelmsii*, *Tanacetum polycephalum* (Asteraceae), and *Teucrium polium* (Lamiaceae), causing mortality in *M. incognita* J2s at concentrations of 4000 and 8000 ppm. In vitro tests with α-Pinene and β-Pinene alone caused the death of, and when tested alone, at a concentration of 100 ppm, exhibits over 80% J2 mortality, and at 200 ppm, over 90% after 24 h [39]. *Ridolfia segetum* (Apiaceae) EO demonstrated significant nematicidal activity (LC50 at 9269 µL/mL) against *Meloidogyne javanica*, effectively inhibiting both egg hatch (75.35% at 16 µL/mL) and the survival of J2 juveniles (71% immobility after 72 h at 16 µL/mL) [57]. A strong nematostatic effect was also observed, resulting in temporary or permanent paralysis, particularly in the case of J2 juveniles of *M. javanica*, and was attributed to the presence of the bioactive compound β-pinene.

3.8. Other Compounds

The monoterpenoid carvone is an efficient acetylcholinesterase inhibitor, displaying effectiveness against nematodes by disrupting their nervous system. Reports indicate that carvone can also exert depressive effects on the central nervous system of nematodes [16]. In Felek et al.'s [42] study, the nematicidal potential of EO from various plants was assessed for its efficacy against *Meloidogyne hapla*. The EO extracted from *Mentha piperita* exhibited the highest juvenile nematode mortality rate (93.2%), with carvone identified as its primary component (39.3%). One of the key components of EOs of *Eucalyptus citriodora* (81.9%) and *Cymbopogon nardus* (95.8%) is citronellal, an acyclic monoterpene aldehyde. In vitro tests against *M. incognita* highlighted citronellal as one of the most effective constituents for immobilizing and eliminating nematodes. In addition, in silico analysis suggests that citronellal (along with geraniol and β-terpineol) may possess a higher binding capacity, indicating its potential role in mediating the biological effects of EOs against nematodes [48]. Another compound displaying nematicidal properties is (e)-cinnamaldehyde, found in *Cinnamomum cassia* EO, effectively controlling *Meloidogyne incognita* in soybean plants. At a concentration of 62 μg mL^{-1}, it immobilized and killed 100% of J2 juveniles, surpassing the performance of the commercial nematicide carbofuran, which achieved only 63% nematode mortality at 173 μg mL^{-1} [34]. The primary component of *Cinnamomum zeylanicum* EO, (e)-cinnamaldehyde, exhibited substantial efficacy with an LC50/48 h value of 64 μg/mL, effectively inhibiting *M. incognita* hatching. This contrasts with the ineffectiveness of the chemical nematicide carbofuran, which had no impact on hatching in the same study [59]. The EO extracted from *S. terebinthifolius* green fruit, constituted of a high concentration of terpenes such as terpinene-4-ol, α-terpinene, γ-terpinene, and α-terpineol, led to an 82–86% reduction in *M. javanica* hatching and increased juvenile mortality by 300%. However, field application did not effectively control *M. javanica* in lettuce when infestation levels were high (555 J2/100 cm^3 of soil) [54]. Laquale et al. [40] reported on the nematicidal potential of γ-terpinene, which effectively controlled *M. incognita* in vitro and in soil. EOs of *Monarda fistulosa* and *M. didyma* demonstrated high toxicity against J2, with LC50 values as low as 7.0 μg mL^{-1} after just 4 h of exposure; immersion in a 12.5 μg mL^{-1} solution for 24 h, resulted in over 80% mortality. Additionally, concentrations of γ-terpinene (along with o-cymene) showed significant results in reducing egg hatching, particularly during the 48-h treatment. Interestingly, in soil experiments, the suppressive outcome of both essential oils at rates of 500 and 1000 μg kg^{-1} was statistically comparable to that of the treatment with Oxamyl.

4. Synergistic and Antagonistic Interactions among Essential Oil Components

Numerous compounds found in essential oils exhibit diverse mechanisms of action. The same chemical constituent may demonstrate distinct biological activity when included within a natural mixture compared to its isolated form. Therefore, natural compounds, when combined, can either enhance, complement, or attenuate each other [80]. Consequently, the utilization of these compounds together may result in various outcomes: zero interaction, synergy (where the response is greater than expected), or antagonism (where it is less) (Figure 4) [67,81]. Understanding the interaction between molecules is particularly crucial in agriculture, where effective bioactive substances are sought [82]. More specifically, recognizing the synergism of binary mixtures is essential for formulating artificial blends and developing new nematicides. The primary compounds found in the essential oils of *M. didyma* and *M. fistulosa*, namely carvacrol, γ-terpinene, and o-cymene, were investigated for their binary combinations, revealing reduced efficacy against *Meloidogyne* species. Notably, the combination of o-cymene and carvacrol at a 1:2 ratio resulted in the highest mortality rate at 31.5%, while the combination of γ-terpinene and carvacrol at a 1:2 ratio resulted in a mortality rate of 36.1%. Conversely, the combination of γ-terpinene and o-cymene at a 2:1 ratio exhibited the lowest mortality rate at 20.3%. This indicates the presence of antagonistic interactions among these compounds. Furthermore, both major and minor compounds within the EOs of *M. didyma* and *M. fistulosa* showed complex

synergistic and antagonistic effects, as demonstrated by their heightened toxicity against *M. incognita* (LC50 at 1 µg/mL for 24 h) compared to individual compound tests [40].

An additional interaction involving carvacrol is noted by Pardavella et al. [55], where the EO of *Satureja Hellenica* proved more effective against *M. incognita* than the corresponding hydrolat. One of the differences between the compounds of these two was the presence of p-cymene in the EO, which is crucial for nematicidal activity. This occurs due to its synergistic interaction with carvacrol; however, in this case, other substances, even in smaller quantities, might contribute synergistically. Furthermore, synergistic interactions were observed between carvacrol and geraniol, as well as between carvacrol and trans-anethole, showcasing the effectiveness of *Thymus citriodorus* EO and hydrosol against nematode paralysis [67].

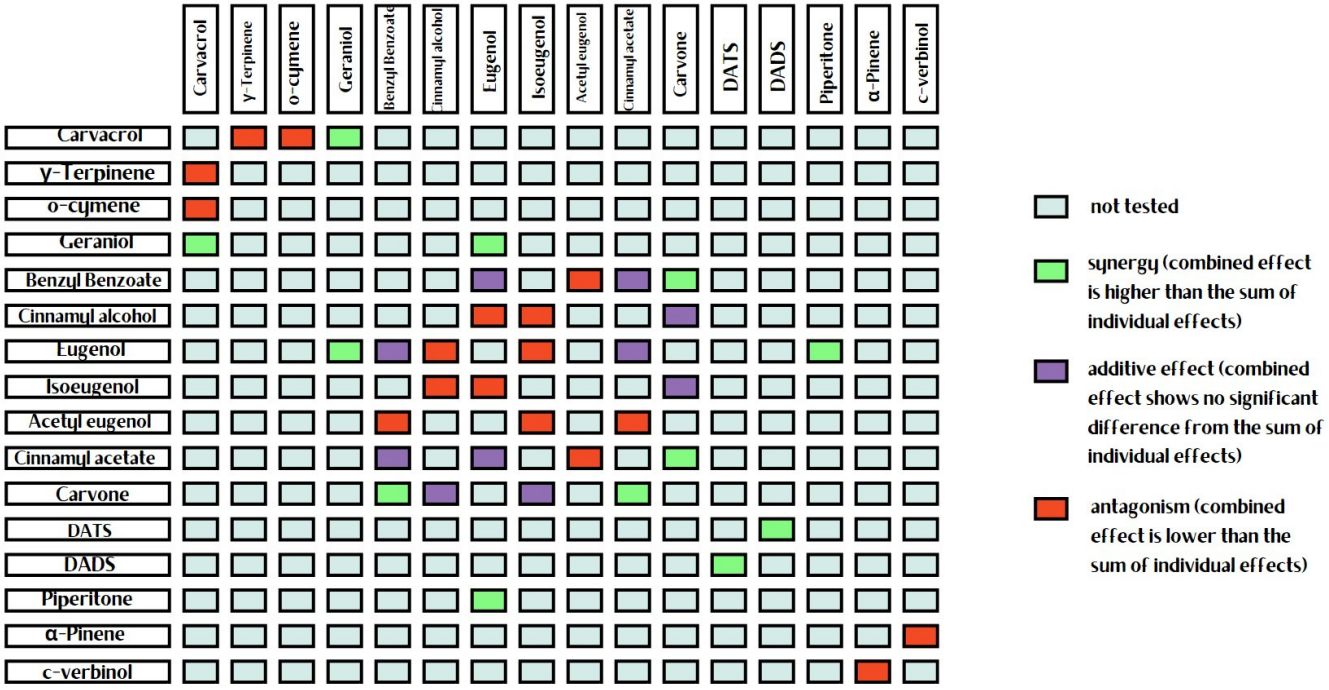

Figure 4. Synergistic and antagonistic interactions between the components of essential oils. Reported synergies were extracted from studies by [40,46,49,62,83].

Eloh et al. [46] conducted a study investigating compounds from the EOs of three plant species—*Ocimum sanctum*, *Cymbopogon schoenanthus Speng*, and *Cinnamomum zeylanicum Blume*. These compounds, primarily categorized as phenylpropanoids, displayed notable nematotoxicity, all exhibiting effectiveness (all showing EC50/48 h < 300 mg/L). The authors explored the synergistic potential of these compounds when combined with benzyl benzoate and carvone, a compound often associated with synergistic activities alongside EO components. Conversely, pairs that acted antagonistic were eugenol /isoeugenol, acetyl eugenol/ benzyl benzoate, cinnamyl alcohol/ eugenol, cinnamyl acetate/ acetyleugenol, cinnamyl alcohol/ isoeugenol, and acetyl eugenol/ isoeugenol. The components that showed additive effects were benzyl benzoate /eugenol, cinnamyl acetate/ eugenol, benzyl benzoate/ cinnamyl acetate, isoeugenol/ carvone, and cinnamyl alcohol/ carvone. Carvone showed synergistic activity with benzyl benzoate, methyl eugenol, and cinnamyl acetate. The synergistic nematicidal activity of carvone and phenylpropanoids may be explained by the differing modes of action between phenylpropanoids and terpenes. Although carvone effectively inhibits acetylcholinesterase, phenylpropanoids induce oxidative stress. The combination of these mechanisms has the potential to significantly enhance the nematicidal activity of the formulations [46].

Further synergy was documented in a study by Jardim et al. [83], where garlic EO displayed remarkable efficacy against J2 mortality and immobility, hatching inhibition, and

reduction of eggs and galls in soil. The two main components of the oil, diallyl trisulfide (DATS) and diallyl disulfide (DADS), were found to exhibit a synergistic effect. The combination of DADS and DATS immobilized and killed a larger number of J2s compared to the sum of their individual effects. Interestingly, when DADS and DATS were tested individually, they could not match the immobility or mortality values of the essential oil at proportional concentrations. However, when combined, their activity surpassed that of the essential oil. For instance, a 56 μg mL^{-1} solution of DATS + DADS (14 + 42 μg mL^{-1}, respectively) immobilized and killed 100% of J2s, while the essential oil at 62 μg mL^{-1} achieved 85.5% immobility and 82.3% mortality of J2s. These findings imply that other components of the EO interfere with the action of DADS and DATS against *M. incognita* J2.

A similar scenario was observed in the case of *Cymbopogon schoenanthus*, where the EO exhibited toxicity to *M. incognita* J2 with an EC50/72 h value of 288 mg/L after 24 h. However, its main compound, piperitone, failed to demonstrate any nematicidal activity at 500 mg/L. Hence, the nematotoxicity of the EO may be attributed to other single major components or synergistic interactions with piperitone [46]. The two major components of EO derived from black pine—α-pinene and c-verbenol—did not affect *M. javanica*, but the concentration of 1 μg/mL showed J2 mortality 81, 48%, indicating that synergies among the other minor components caused the nematicidal action [62].

5. Concluding Remarks and Future Perspectives

The tested essential oils from various botanical families, including Lamiaceae, Asteraceae, Apiaceae, Myrtaceae, and others, have demonstrated potential in nematicidal activity, particularly against RKN of the *Meloidogyne* genus. These effects are primarily attributed to the chemical composition of the EOs, where most of the compounds in reported experiments were mostly terpenes. Terpenes exhibit a broad occurrence across diverse plant species belonging to different plant families. Their nematicidal effect stems from their capability to disturb plasma membrane permeability, affect nematode nervous systems, disrupt intracellular redox balance, trigger apoptosis-related signaling pathways, and induce DNA damage. Studies report on nematicidal outcomes from the use of certain EOs derived from genera such as *Mentha*, *Citrus*, *Cymbopogon*, and *Thyme*, showcasing promising potential in inhibiting egg hatching, penetrating the gelatinous matrix of an egg, inducing juvenile paralysis, and increasing mortality rates. Notably, the biological activity of these EOs is often concentration-dependent, with variations influenced by the specific chemical properties of their constituents. For example, compounds like geraniol, carvacrol, linalool, pinene, eugenol, and other constituents of EOs exhibited great efficacy against *Meloidogyne* spp. in most experiments.

Incorporating EOs into pest management strategies, including nematode control, underscores the necessity for a nuanced understanding of their primary constituents, synergistic or antagonistic interactions, and the fundamental mechanisms that affect their effectiveness. Therefore, further knowledge is required on the synergies and antagonism of EO components, which is crucial for modifying them by adding synergistic natural compounds or blending them in optimal proportions. These modifications could lead to the development of more potent and effective final products, potentially impacting the market prices and enhancing benefits for users [46]. Interestingly, beyond the nematicidal potential, essential oils have demonstrated satisfactory results in various other parameters in a wide range of experimental settings. These oils exhibited insecticidal, antifungal, antibacterial, and herbicidal activity, as well as a positive effect on plant growth parameters. For instance, the antifungal potency of certain EOs derived from thyme, spearmint, black mustard, ginger, and fennel is attributed to their ability to penetrate and disrupt the fungal cell walls and cytoplasmic membranes, leading to their permeabilization and damage to the mitochondrial membranes, thus inhibiting fungal growth [17,44,57,64]. Moreover, EOs from *Juniperus communis*, *Pinus nigra*, *Abies alba*, and *Douglas fir* showed insecticidal activity, causing antifeedant symptoms and eventual death of aphids (*Aulacorthum solani Kalt*, *Rhopalosiphum padi*, *Myzus persicae*, *Phyllaphis fagi*) through tarsi, ingestion, or the

respiratory system [57,62]. Arya et al. [64] observed that EOs of *Hedychium coccineum Buch. Ham. ex Sm.* (ginger) showed effects against bacteria like *Staphylococcus aureus* and *Salmonella enterica serovar Typh*, and even herbicidal activity against *Raphanus raphanistrum subsp. Sativus* (radish) seeds. Moreover, the EO of basil and mint increased dry weight on pepper plants [44], and lavandin EO enhanced the root system and green biomass of tomato plants [38], indicating the growth-promoting potential of EOs.

Despite substantial research on botanicals for plant protection purposes, relatively limited attention has been directed toward exploring their potential in alternative formulations (except EOs), such as hydrosols, nanoemulsions, crude extracts, water extracts, or powders for nematode control. Although observations indicate variations in their effectiveness, the results between EOs and the mentioned formulations differ significantly. This discrepancy arises from significant differences in their chemical composition, even though they originate from the same plant source. For instance, nonpolar compounds in essential oils, due to limited solubility in water, cannot be detected in their hydrosols, demonstrating the importance of these distinctions) [55]. Identifying plant-derived compounds with potent nematicidal properties that may not be part of essential oil composition is critical. Aquatic extracts of *Achillea wilhelmsii*, *Tanacetum polycephalum*, and *Teucrium polium* predominantly contain polyphenols (such as gallic acid, catechin, and chlorogenic acid), which exhibit nematicidal activity, while they are absent in the respective EOs [50]. Moreover, experiments with nanoemulsions demonstrated their superiority over essential oils in nematode effects, owing to improved stability derived from reduced oil particle size [43]. Essential oils, with low water solubility and larger particle sizes, encounter difficulty interacting with cell membranes compared to nanoemulsion particles, enabling better access of essential oils to nematode cell membranes, thus leading to more effective nematode hindrance and eradication [44]. Moreover, employing essential oils in nanoemulsion form offers additional advantages, including the ability to disperse in irrigation water, rapid adhesion and penetration of plant roots, long-lasting presence in the soil, and effective nematode suppression [43].

Although the aromatic plant-based biopesticide market is expanding steadily, it remains a minor fraction of the global market. This limited representation can be attributed to their inconsistent performance and the scarcity of field studies evaluating their efficacy [25]. This raises the question: can different experimental settings influence the results? Hence, effective EOs and their active components tested in vitro must be evaluated in field conditions. Investigating terpenes' nematicidal effects proves complex due to the compounds' mixture in plant essential oils, which contain multiple constituents rather than isolated terpenes. Determining specific terpenes responsible for nematicidal activity becomes challenging, compounded by variations in nematode species, life stages, and environmental conditions across studies [84]. Furthermore, Kotsinis et al. [84] reported that the same compound, such as geraniol, successfully controlled *Meloidogyne* spp., but showed incompatibility with entomopathogenic nematode species (e.g., *Heterorhabditis* spp.). Research on EOs requires further exploration to consider factors affecting their efficacy, such as procedural errors affecting chemical composition, color variation, and unpleasant odors, diminishing overall quality, with factors like raw materials, plant parts, solvents, temperature, pressure, and time influencing these outcomes [36,85]. Understanding the potential phytotoxicity of high EO concentrations and their impact on beneficial nematode populations is crucial. Higher EO concentrations often yield better nematicidal results; however, only a limited number of studies have reported on their potential phytotoxic effects [86–89]. Moreover, studies suggest that EOs such as cinnamon, clove, garlic, peppermint, lemongrass, thyme, pine, and eucalyptus oils might adversely affect beneficial nematodes, compromising their survival and behavior [90].

Exploring appropriate technical formulations of EO-based nematicides, such as micro- or nano-encapsulation, to achieve controlled release and gradual degradation of the EO's active constituents is imperative. This approach would extend and enhance the nematicidal effectiveness of EO-based soil treatments while mitigating their high volatility, rapid

dispersion, and degradation [40]. As a result, standardized plant culture and EO extraction processes should be considered to produce commercial products with standardized compositions and nematicidal efficacy. Understanding how different EO compounds interact with nematodes, along with the challenges posed by natural EO properties, is crucial. This knowledge could lead to the creation of more effective and targeted natural insecticides in the future that are practical and environmentally beneficial.

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