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Essential Oils as Potential Biopesticides in the Control of the Genus Meloidogyne: A Review †

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Abstract: *Meloidogyne* spp., root-knot nematodes (RKN), are among the most economically damaging plant parasitic nematodes to horticultural and field crops, mainly due to their pathogenic effect, worldwide distribution and wide host range. RKN pest management relies on the use of commercial synthetic pesticides that kill or disrupt the feeding or reproductive behavior of nematodes, such as broad-spectrum fumigants and nervous system toxins. These active chemicals can cause negative environmental and public health impacts, and are feared to lead to resistance and immunity. As a sustainable alternative, the use of essential oils (EOs) as nematicides has shown great promise. These natural products are mostly biodegradable and subjected to less strict regulatory approval mechanisms for their exploration. The present work reviews the existing bibliography on the direct biological activity of EOs against RKNs. A total of 49 publications were identified reporting on anti-RKN activity of EOs, from 1995 to 2020. Plants from Lamiaceae and Compositae families make up more than 50% of the source material for EO extraction. The highest activities were reported for EOs of *Monarda*, *Artemisia*, *Filipendula* and *Satureja* genus. These taxa show potential to be further explored for highly active anti-RKN phytochemicals with practical applications in sustainable pest management strategies.

Keywords: *Artemisia*; compositae; essential oils; *Filipendula*; lamiaceae; *Meloidogyne*; *Monarda*; nematicide; *Satureja*; sustainable pest management; volatiles

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1. Introduction

In intensive agriculture, plant parasitic nematodes (PPNs) are a major problem for reducing plant growth and productivity. Depending on environmental and edaphic conditions, losses in agricultural fields can be extreme, as a result of direct PPN influence and/or indirectly by enabling infections with other opportunistic microbial pathogens. PPNs negatively impact worldwide crop yield, causing approx. 12% losses, which is more than twice those caused by insect pests [1]. The genus *Meloidogyne*, root-knot nematodes (RKN), comprises some of the most economically important species, responsible for extensive economical losses by reducing crop yield and product quality. These obligate endoparasites disrupt the plant host physiology by bypassing plant defenses and modifying root morphology. Inside the root, they establish specialized root structures (i.e., root galls), used by the RKN for feeding and reproduction [2]. These sites become energy sinks for photosynthates, leaving the host plant displaying nutritional stress symptoms.

RKN movement in the soil is slow, restricted only to a few meters per year, and dispersal commonly relies on human transportation of infested plants, plant products, in soil adhering to farm implements and on irrigation water [3]. Eggs are produced in masses surrounded by a gelatinous matrix that provides a barrier for water loss, adverse environmental conditions, and even biotic stress [4]. In the presence of adequate environmental conditions and chemical cues from the host, juveniles hatch and seek the roots of susceptible plants. Infection occurs at the elongation zone, where RKNs use the stylet to penetrate root tissues. Evading the plant immune response, they move intercellularly towards the root tip and then upward into the vascular cylinder to the differentiation zone, where the nematode feeding site is established [5]. By secreting a protein "cocktail" mainly composed of cell wall biosynthetic and degrading enzymes and even mobilizing plant produced enzymes, RKNs induce the formation of a feeding site, composed of five to seven redifferentiated cells distinguished from the neighboring by their increased volume, dense cytoplasm, numerous nuclei and small vacuoles [6]. These highly metabolically active giant cells develop cell wall ingrowths for rapid solute transport from the contiguous xylem elements, supplying nematodes with nutrients. Juveniles then undergo significant structural changes, molting into an adult sedentary stage. Pear-shaped adult females, with swollen bodies, begin producing the gelatinous matrix through six rectal glands, before and during egg laying [7]. The complexity of the RKN life cycle and the wide range of host plants they can parasitize turns pest management into a difficult task.

2. RKN Pest Management

With the onset of industrialization in modern agriculture and the mass monoculture of crops, the damaging effects of RKN diseases have increased dramatically requiring more effective means of control. Pest management is usually performed through non-chemical strategies, namely, natural host resistance and cultural controls, and chemical strategies, through the use of nematicides [8,9]. Chemical control employs the use of synthetic pesticides that kill or disrupt the feeding or reproductive behavior of nematodes, commonly broad-spectrum fumigants and nervous system toxins. Although highly efficient, these pesticides can show negative environmental and public health impacts, leading to several instances of banning on extremely hazardous pesticides [10]. Modern chemical control has become limited by the availability of active compounds and the emergence of resistance and immunity. This has prompted the search for cost-effective, environment friendly alternatives with high activity against the RKN. Phytochemical based strategies for RKN control have been successfully employed and several essential oils (EOs) have shown remarkable nematicidal activities, in some cases even surpassing those of commercial nematicides. EOs offer the advantage of being natural, biodegradable and subjected to less strict regulatory approval mechanisms for their exploration, due to a long history of use [11]. Chemically, EOs are comprised of terpenes (mainly mono-, sesquiterpenes and a few diterpenes) and phenolic compounds, such as phenylpropanoids, but other groups of compounds can also occur in relevant amounts. Biological activity of EOs is commonly the result of the combined effect of biologically active compounds with compounds that show no direct activity individually, but can influence resorption, rate of reactions and bioavailability of the active compounds. Furthermore, EO compounds can have additive, synergistic or antagonistic interactions towards anti-RKN activity. EOs display diverse biological activities which makes them desirable biopesticides, being able to regulate not just the targeted pest but also the opportunistic species and resistant strains [12,13].

Crossing the available information on EOs with activity against RKNs may provide important guidelines for future research on environment friendlier nematicidal compounds. In this respect, the present work reviews the existing bibliography on the direct biological activity of EOs against *Meloidogyne* spp., and summarizes the most important plant taxa.

3. Essential Oils as RKN Biopesticides

Research was performed with Web of Science® search engine, in all available databases, on published works reporting direct contact bioassays, using the topics "*Meloidogyne*" and "essential oil". Information on the family and species of the plant source used for EO extraction and respective EO half maximal effective concentration (EC_{50}), was collected when available.

A total of 49 works was retrieved reporting on the activity of EOs against RKNs, in direct contact assays. Plant sciences, entomology, food science technology, agronomy, biochemistry and molecular biology were the top 5 scientific areas of the journals that published these reports. Publications dated from 1995 to 2020, with 2020 being the year with the most publications (8) (Figure 1a). The listed publications were cited 1015 times, with an average of 21 citations per work (Figure 1b). Research interest has increased steadily since 2012 (Figure 1b).

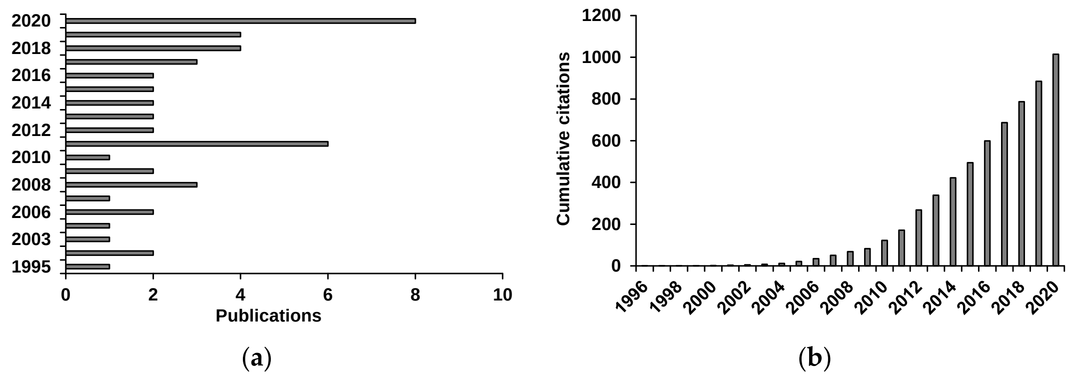

Figure 1. (**a**) Yearly number of reports on the activity of essential oils against root-knot nematodes and (**b**) yearly cumulative citation evolution of these reports.

EOs from 179 plant species, from a total of 29 families, were analyzed in over 900 direct contact bioassays. The most analyzed EOs belonged to plants of the Lamiaceae, Compositae, Poaceae and Myrtaceae families, from which over 70% of tested EOs were extracted (Figure 2a). The remaining 29% included families of plants known to be the source of important phytochemicals, such as the Rutaceae (6%), Apiaceae (4%) and Verbenaceae (4%).

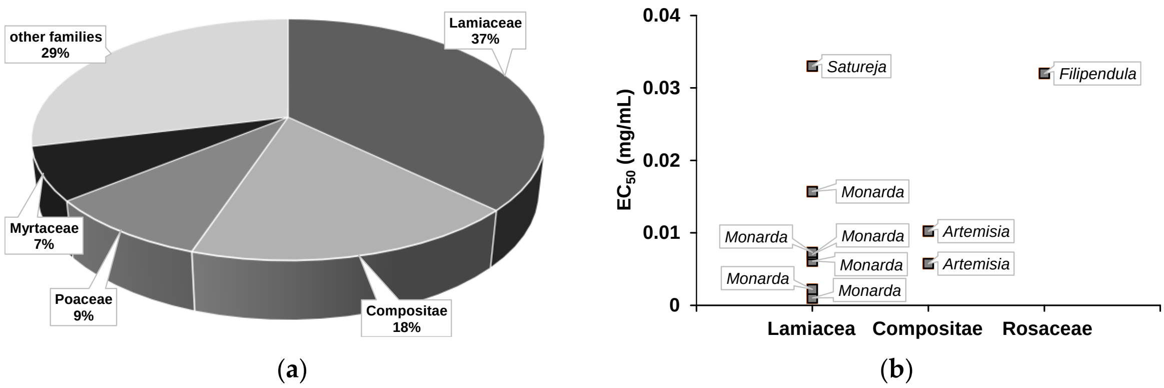

Figure 2. (**a**) Families of plants whose essential oils were extracted for biocidal assays on root-knot nematodes and (**b**) plant genus (■) of the most biologically active essential oils, organized by family and EC_{50}.

The EC_{50} values of the 10 most active EOs ranged from 0.001 to 0.030 mg/mL (Figure 2b). These EOs were extracted from plants of the genus *Monarda* (*M. didyma* and *M. fistulosa*), *Artemisia* (*A. nilagirica*), *Filipendula* (*F. ulmaria*) and *Satureja* (*S. montana*) [14–16].

These EOs showed chemical compositions mainly rich in monoterpenoids and phenylpropanoids, namely camphor, carvacrol, linalyl isovalerate, methyl salicylate, *o*-cymene, α-myrcene, α-thujone, β-caryophyllene oxide and γ-terpinene.

Future studies must explore the potential highly nematicidal EOs from Lamiaceae and Compositae families of plants, and give particular attention to the genus *Monarda* and *Artemisia*. The genus *Monarda* has 31 species and subspecies, while Artemisia has 530 (species accepted names according to The Plant List—http://www.theplantlist.org, accessed on).

Uncovering the mechanisms of action of EOs against RKN is an important step towards successfully establishing EOs as environmentally friendly nematicides. Essential oils have been reported to show diverse bioactivities, for ex. antibacterial, antiviral, antifungal, antimalarial, insecticide, insect repellent, antidepressant, anticancer, antimutagenic, hepatoprotective, anti-inflammatory, antioxidant, anticonvulsant, analgesic and antipyretic. In over 20,000 studies reporting EO biological activity, ca. 25% are performed on the antioxidant activity, 12% on antimicrobial activities, and 11% on insecticidal and insect repellent activities [17]. In future work, attention should be given to the interplay of reactive oxygen species between RKNs and plant host given that oxidative stress is known to play an important role in host susceptibility [18].

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