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In Retrospect: Nematicides in Plants

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ABSTRACT: Even while nematicidal compounds have their uses in agriculture, there are now legitimate worries that their overuse may increase biodegradation processes in soil, which would manifest as a decrease in the compounds' efficacy in the field and the evolution of resistance. Also, because of the ban on using methyl bromide, there is a pressing need for a reliable replacement for organophosporous and carbamate compounds like fosthiazate, fenamiphos, oXamyl, and aldicarb. In order to increase crop output while still preserving and contributing to agricultural sustainability, integrated pest control tactics have been used globally in recent years. Bionematicides, a kind of biopesticide, are a helpful tool in the arsenal of pest control methods. In particular, we have investigated the worldwide library for prospective nematicidal chemicals as part of our continuing investigation into natural nematicides of botanical origin. Here, we detail the chemical properties and structural foundation for the nematicidal action of plant metabolites.

KEYWORDS: *nematicidal compounds, biopesticides, bionematicides*

INTRODUCTION

Phytonematodes are among the most known crop pests, and their control is achieved mainly by cultural practices, crop rotation, and resistant cultivars, combined with a few available chemical nematicides that are still authorized. *Meloidogyne* sp. are probably the most notorious phytonematodes living in soil in protected areas. Inside the host tissues, *Meloidogyne* pass through an embryonic stage, four juvenile stages (J1−J4), and an adult stage (Figure 1). Juvenile *Meloidogyne* species hatch from eggs as second-stage juveniles (J2), while the first molt occurs within the egg. Newly hatched juveniles live for a short period of time in the rhizosphere of the host plants without feeding. Then J2s invade host root in the root elongation region and migrate until they find a place to settle and feed. In that area, parenchyma cells near the head of the J2 become multinucleate giant cells, from which the J2s and later the adults feed. After further feeding, the J2s undergo morphological changes, and then without further feeding, they molt three times and eventually become adults. In females, the reproductive system develops, and they can produce hundreds of eggs, while male adults leave the root and do not harm the host. The length of the life cycle is temperature-dependent.

The need for discovering less toxic and environmentally acceptable substitutes for commercial nematicides is amplified, creating a significant market opportunity for alternative and biorational products such as botanical nematicidals. However, the economic cost of research and registration of a prospective new synthetic nematicide is an enormous hurdle to overcome that the industry rarely sustains.[1] For this reason, at present there are only few commercial nematicides left in use, and their repeated applications lead to the enhancement of biodegrada- tion mechanisms in soil[2−4] and the development of pest resistance,[5] both expressed as a lack of efficacy under field conditions. It is therefore very important to study new and alternative nematode control methods[1] like the biorational pesticides by screening naturally occurring compounds in plants.[6,7]

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Since plants are long-lived stationary organisms, they must resist attackers over their lifetime by producing and exuding secondary metabolites. Research of phytochemicals has its roots in allelochemistry, involving the chemical-mediated interactions between a plant and other organisms in its environment.[1] The development of PSMs as tools in crop protection evolved through the observation of their activities when they were used in traditional practices and eventually by the identification of the active molecules as well as by the systematic screening of botanical families followed by biological tests in order to discover potential active molecules. Pyrethroids, synthetic molecules analogous to pyrethrum, and neem products (Meliaceae) are characteristic examples of commercial plant protection products based on botanical sources. The OECD (Organization for Economic Cooperation and Development) defines the botanical substances as semiochemicals, including chemicals involved in species communication (pheromones, but also plant extracts, plant volatiles, and natural oils) that exhibit pest control activities, while recently, the concept of biocontrol agents has been preferred to that of biopesticides.[8] Bioactive PSMs may be developed for use as pesticides themselves, or they can be used as model compounds for the development of chemically synthesized derivatives. Some botanicals used as pesticides pose less risk to humans and animals than their synthetic ancestorsdid, have a selective mode of action, are environmentally friendly, and avoid the emergence of resistant races of pest species and therefore can be used in integrated pest management (IPM) programs.[6] Stability concerns under field conditions have been raised as a result of sorption in the soil organic matter which results in the reduction of their

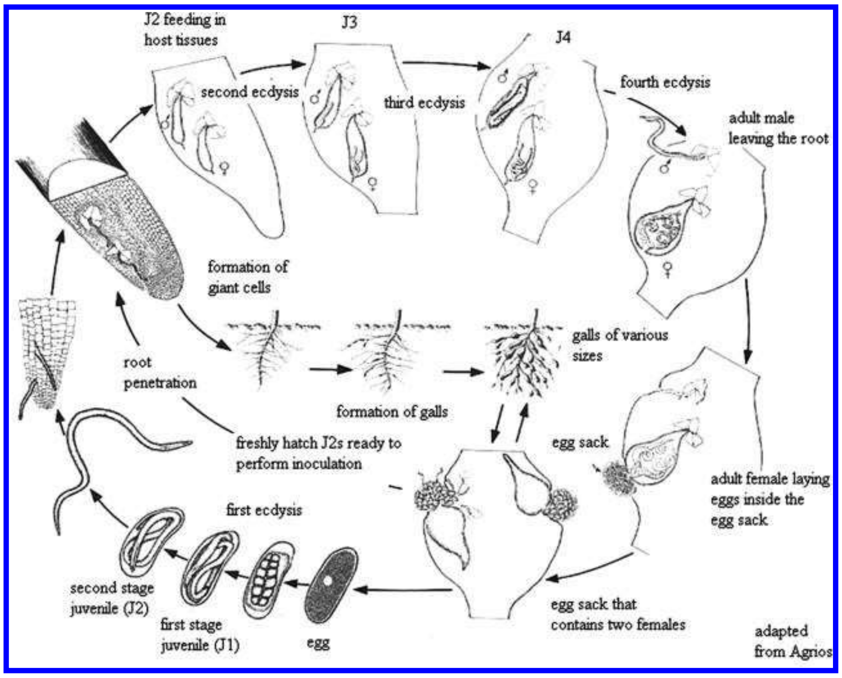

Figure 1. Biological cycle of *Meloidogyne* sp.

availability. Current studies investigate the encapsulation of essential oils as a potential controlled release vehicle with site-specific delivery to maximize the properties of the oils.[9] In recent years, the only commercial botanical registered for phytomenatodes control had been azadirachtin. This is a short review encompassing the main chemical classes of PSMs that have been used or have the potential of use as nematicides on crop protection, specifically against *Meloidogyne* species. We report on the natural substances of plant origin that have been found to exhibit, among others, nematicidal activity tested alone or in mixtures and the mode of action of single essential oil (EO) from *Eucalyptus meliodora*, exhibits high nematicidal activity (EC_{50} = 9 μg/mL).[13] Aldehydes and ketones such as *p*-anisaldehyde, benzaldehyde, *trans*-cinnamal- dehyde, (*R*)-(+)-pulegone, and furfural exhibit high nematicidal activities against *Meloidogyne javanica*. Specifically, the EC_{50} values of *trans*-cinnamaldehyde for juvenile immobilization and hatching inhibition in vitro were as low as 15 and 11.3 μL/L, respectively. In pot experiments, *trans*-cinnamaldehyde, furfural, and benzaldehyde at a concentration of 100 mg/kg greatly reduced the root galling of tomato. Under field conditions, soil treatment with *trans*-cinnamaldehyde (50 mL/m^2) reduced the

compounds against target pests (nematodes or others; if no data is available on nematodes), as well as on the current trend of use of the botanical nematicides in field practice along withtheir future perspective.

CHEMICAL CLASSES OF BOTANICALNEMATICIDALS

Aldehydes and Ketones. Aldehydes like phenols and alcohols induce cytotoxicity, damage the cellular and organelle membranes, act as prooxidants on proteins and DNA, and produce reactive oxygen species. The activity of *Melia*

galling index and increased the shoot weight of tomato plants.[14] In our previous studies, we have demonstrated that among oxygenated compounds, ketones were generally more active and that their activity against *M. incognita* exhibited EC_{50} values of 115 and 150 μg/mL for L-carvone and pulegone, respectively.[13,15] Similarly, (*E*,*E*)-2,4-decadienal, (*E*)-2-undece- nal, (*E*)-2-decenal, hexanal, nonanal, and furfural were provedas the most prominent nematicidal constituents of *Ailanthus altissima*. (*E*,*E*)-2,4-decadienal, (*E*)-2-decenal, and furfural showed the highest nematicidal activity against *M. javanica*, with $EC_{50/1d}$ values of 11.7, 20.43, and 21.79 mg/L,[16] while 2- undecanone EC_{50} values were calculated at 20.6 and 22.5 mg/L

azedarach against *Meloidogyne* sp. is attributed to the defatted

methanol fruit extract (polar fraction) and specifically to its organic acids, aldehydes, and alcohol contents.[10,11] *Meloidogyne* species live in soil in protected areas and usually reside at a fair distance from the target of nonfumigant nematicides. In fact, furfural exhibited the highest nematicidal activity similar to that of the commercial nematicide fosthiazate, both when J2s are immersed in test solutions and exposed to its vapors (fumigantactivity). Also, Rodriges-Kabana has reported on the strong nematicidal fumigant activity of furfural against *M. incognita*, when tested in greenhouse and microplot conditions,[12] but no correlation has been made so far with its contents in chinaberry. The fumigant activity is of extreme importance for a nematicide because it enhances its activity in the nontreated soil layers. The aromatic aldehyde benzaldehyde, found as a component of the

for *M. incognita* and *M. javanica*, respectively.[17] Finally, synergistic effects in suppressing initial and final soil populations of *M. arenaria* are reported when thymol is applied at 0, 50, 100, and 150 mg/kg to soil in combination with 0, 50,and 100 mg/kg benzaldehyde at 100 mg/kg.[18]

Alkaloids. Alkaloids are PSMs containing nitrogen atoms and are derived from various botanical families among which is Solacaneae. 2,5-Dihydroxymethyl-3,4-dihydroxypyrro- lidine is a pyrrolidine alkaloid contained in the genera *Loncocarpus* and *Derris*, exhibiting nematicidal activity. It is downwardly mobile in plant phloem, and its applications on plant foliar appendages decrease galling in roots, but the mode of action is under investigation.[19] *Tithonia diversifolia* (Hemsl.)

A. Gray, rich in alkaloids, suppresses egg hatching of *M.*

incognita by 98% from 2 days after incubation and 100%

inhibition at 9 days. *Tithonia* residue treatment at the rate of 30 tons/ha on yam (*Discoria rotundata*) in the greenhouse experiments significantly suppressed *M. incognita* (5000 eggs/ plant) reproduction, number of eggs, and juveniles, as well as galling.[20] 1,2-Dehydropyrrolizidine alkaloids (PAs), represent- ing a class of secondary plant metabolites that are active in defense against herbivores, are present in *Chromolaena odorata*,one of the most invasive weeds in Asia and Africa. In vitro studies demonstrate that pure PAs from *C. odorata* roots have nematicidal effects on *M. incognita*, even at concentrations of 70−350 mg/L. In vivo experiments show that mulch or cyanogenic plants have potential as nematicidal green manure.[30] The liquid extract (manipueira) obtained through the pressing of cassava roots for the production of starch and cassava flour is rich in proteins, carbohydrates, and several PSMs, thus exhibiting toxicity against nematodes and insects. Particularly, the leaves and roots of cassava are rich incyanogenic glycosides, namely, linamarin and lotoaustralin. The breakdown of linamarin by the enzyme linamarase is very rapid, releasing glucose and an intermediate cyanohydrin. At high pH or at high temperatures, the cyanohydrin decomposes spontaneously, producing a ketone together with volatile aqueous crude extracts from *C. odorata* roots reduce *M.*

hydrogen cyanide that is very toxic to a wide range of *incognita* infection on lettuce.[21] *Crotalaria* is a PA-producing plant that is used for nematode control since it yields different structural types of PAs, although of no conclusive ranking in toxicity. The effects are more pronounced for the tertiary than for the oxidized form. Additionally, large differences are organisms.[31] Soybean greenhouse experiments were conducted to evaluate the nematicidal activity of thymol at rates of 25− 250 mg/kg along with its activity when applied at 0, 50, 100,

and 150 mg/kg to soil in combination with 0, 50, and 100 mg/ kg benzaldehyde. When benzaldehyde was applied at 100 mg/observed in the susceptibility of different nematode species to PAs.[22] In pot experiments with the commercially available PA- containing plants *Ageratum houstonianum*, *Borago of f icinalis*, *Senecio bicolor*, and *Symphytum of f icinalis*, it was demonstrated that although *Meloidogyne hapla* is not repelled per se by these plants, the nematodes' juveniles development was completely suppressed on *A. houstonianum* and *S. bicolor*. In fact, the soil in which *A. houstonianum* and *S. bicolor* were cultivated and incorporated contained 200−400 times less nematodes than the soil treated with *Lycopersicon esculentum*.[22] The brimstone

(*Morinda lucida*) leaf crude extract (50 and 100% concen- trations) and brimstone leaf powder (1 and 2 t/ha), rich in saponins and flavonoids, significantly increase the number of leaves, plant height, number of branches, and fresh leaf and root weight of *Celosia argentea* (L.), and also significantly reduce the gall index due to *M. incognita*.[23] When *Acacia gummifera*, *Ceratonia siliqua*, *Ononis natrix*, *Tagetes patula*, and *Peganum harmala* were evaluated for their nematicidal effect through their aqueous extract used directly in the in vitro test, and the nematicidal effect ranged between 67% and 95%. *P. harmala* had an effect similar to that of the commercial nematicide (Vydate, a.i. oxamyl), while phytochemical analysis of this species revealed that this plant is rich in alkaloids. *A. gummifera* and *T. patula* extracts exhibited a high nematicidal effect of 84% and 82%, and they were found to contain significant concentrations of flavonoids. The extract of *O. natrix* and *C. siliqua* had a nematicidal effect against *Meloidogyne* spp., with 67% and 71% of mortality, respectively.[24] *Peganum harmala* aqueous extracts, rich in alkaloids, have an effect similar to that of the commercial nematicidal Vydate.[24]

Glycosides. **Cyanogenic glycosides are amino acid** derived PSMs present in more than 2500 plant species, playingan important role in plant defense against herbivores due to their bitter taste and release of toxic hydrogen cyanide. Upon tissue disruption (e.g., by chewing insects), the cyanogenic glucosides are released from the vacuoles and hydrolyzed by specific β-glucosidases to yield glucose, a ketone or an aldehyde, and toxic HCN. This process is called cyanogenesis and serves to facilitate a rapid nematicidal HCN release.[1,25–28] Cyanogenic glycosides, through the action of cyanide, prevent oxygen utilization by the inhibition of cytochrome oxidase.[29] Sudangrass cv. Trudan 8 has been demonstrated to suppress

the infection of vegetables by *M. hapla* due to hydrogen cyanide released from the degradation of the cyanogenic glucoside (dhurrin) during decomposition. This results in a reduction in severity of root gall infection up to 54%, which suggests that

kg, it showed synergistic effects in suppressing initial and final soil populations of *M. arenaria*, while significant reductions in root galling on soybean were attributable to thymol at ≥50 mg/ kg.[32] Treatment of tomato and cucumber plants with furostanol glycosides obtained from cell cultures of *Dioscorea deltoidea* Wall. decreased their susceptibility to infection by the root-knot nematode *M. incognita*. In treated plants, the fecundity of the nematode was decreased 5-fold, females were smaller, and the sex ratio shifted toward an increase in males.[33] In fact,furostanol glycosides extracted from *Dioscorea deltoidea* Wall. cell cultures under the conditions of biotic stress cause

nonspecific defense reactions resulting in the formation of systemic acquired resistance in tomato plants *Lycopersicon esculentum* Mill, evidenced by the comparison of changes in isoprene content (phytosterines, tomatin, and carotenoids) and in the rate of oxidative processes in the leaves and roots of intact and treated plants. This formation is presented by the enhancement in the photosynthetic apparatus pigment fund, pigments of the violaxanthin cycle in particular, by activation of the processes related to POL, and by the increase in peroxidaseactivity, which is an enzyme of antioxidant protection.[34] When the effects of certain plant steroids (belonging to furostanol glycosides or glycoalkaloids) and α-ecdysone were studied, onthe growth and development of *M. incognita*, it was shown thata steroid molecule exhibits significant nematicidal activity if it contains a carbohydrate moiety and an additional heterocycle in the steroid core. The maximum nematicidal activity is inherent in glycosides containing chacotriose as the carbohydrate moiety of the molecule.[35] The ethanol extract of *Arisaema erubescens* (Wall.) Schott tubers possess significant nematicidal activity against the root-knot nematode (*M. incognita*) due to its flavone-C-glycosides, namely, schaftoside and isoschaftoside. Both possess strong nematicidal activity against *M. incognita* (LC_{50} = 114.66 μg/mL and 323.09 μg/mL, respectively), while the crude extract of *A. erubescens* exhibited nematicidal activity against the root-knot nematode with an LC_{50} value of 258.11 μg/mL.[36]

Glucosinolates and Isothiocyanates. **Glucosinolates** (GLSs) are PSMs produced by mustards (*Brassica* and *Sinapis* sp.) and another genus of the order Capparales; they contain sulfur and nitrogen and β-D-thioglucose as well as sulphonated oxime moieties. These include thioglucosides, characterized by a side chain with varying aliphatic, aromatic and heteroaromatic carbon skeletons. Glucosinolates get converted into various degradation products (isothiocyanates, thiocyanates, and indoles) after cutting or chewing of the plant parts that contain

them because through this process, they come in contact with the vacuolar enzyme myrosinase (Myr). Biofumigation is a practice by which nematicidal isothiocyanates (ITCs) are released in soil after incorporating glucosinolate-containing plant material. This practice is considered an ecological substitution of the soil fumigation with toxic fumigants suchas methylbromide because these substances are fully biode- gradable and less toxic.[37,38] Glucosinolate degradation products

study, new genotypes of Brassicaceae are selected for high content in the roots of the glucosinolates generating these most active isothiocyanates, and their agronomic performances are verified under field conditions as catch crop plants.[52] According to Wu et al., some of the most potent ITCs compounds are allyl isothiocyanate (Allyl-ITC), acryloyl isothiocyanate (Ac-ITC), ethyl isothiocyanate (Et-ITC), benzyl thiocyanate (Bz-TC), benzyl isothiocyanate (Bz-ITC), 1-phenylethyl isothiocyanate

trigger the plant's defense mechanism, produce toxins, and (1-PE-ITC), and 2-phenylethyl isothiocyanate (2-PE-ITC),

create defensive barriers around the roots of the host plant, thus preventing harmful pathogens like fungi to enter the host (hyrpesensitive response).[39] The ITCs' (−N C S) fate in soil is fundamental for the efficacy of biofumigation. The maximum hydrolysis of the glucosinolates in the plant tissue that generates high isothiocyanate concentrations in the soil after incorporation is favored by maximum cell disruption, by addition of water, and by high soil temperatures. Residual glucosinolates are very weakly adsorbed, readily leached, and are microbially degraded and mineralized in soil. In contrast, isothiocyanates are strongly adsorbed by the organic matter in

soil, react strongly with soil compounds bearing a nucleophilic group, and are prone to volatilization losses and microbial degradation and mineralization minimizing the risks of persistence in the environment or leaching.[40] A formulated product named Dazitol, a commercialized nematicide in the USA, contains 4.37% ITCs extracted from plant material (mustard seeds).[41] However, metam sodium and dazomet, both being methyl isothiocyanate precursors, are rapidly degraded (85% in 10 days) in soils treated with these substances, indicating that there is an induced cross-accelerated degrada- tion with both fumigants.[42,43] During recent years, extensive reviews have concerned the chemical ecology of various *Brassica* toward parasitoids, predators, herbivores, and nemat- odes emphasizing GLSs and ITCs, their potential of integration in insect-pest management, and the physiological and biochemical implications underlying hydrolysis mecha- nisms.[44−47] Seed meals obtained from *Brassica juncea* 'Pacific

Gold', *B. napus* 'Dwarf Essex' and 'Sunrise', and *Sinapis alba*

'IdaGold' were found to exhibit nematode-suppressive abilities in *Pratylenchus penetrans* and *M. incognita* second-stage juveniles.[48] Currently, it has been found that 3-methoxybenzyl isothiocyanate, the predominant enzyme degradation product of glucosinolate glucolimnanthin contained in Meadowfoam (*Limnanthes alba* L.), was very toxic to *M. hapla* (EC_{50} = 2.5 ±

0.1 to 2.7 ± 0.1 mg/L) and care was taken to manipulate

meadowfoam seed meal to promote its production.[49] More- over, defatted seed meal application (*Raphanus sativus* ssp. *oleiformis* and *Eruca sativa* ssp. *oleiformis*), compared with oxamyl drip irrigation, limited nematode infestation and allowed cucumber roots with a lower root gall index (2.0 to

3.5 versus 3.5 to 4.5). The zucchini yield in the biocidal seed meal treated plot was 9% higher in the second month of harvesting due to the lower infestation of zucchini roots, and the harvesting time was one week longer with a final 14% total yield improvement.[50] It has been proven that cultivation

showing in vitro irreversible nematicidal activity against second- stage juveniles of *M. javanica*, following exposure for 72 h at concentrations as low as 5 μg/mL. In pot experiments, 1.0 mL of Allyl-ITC and 1.1 mL Ac-ITC per kg of soil inhibited *M. javanica* in a manner similar to or better than metam sodium at its recommended application dose. Similar results were obtained in the field experiments using 1.0 kg Allyl-ITC or

1.0 kg Ac-ITC per ha.[53] Nonetheless, the significant interference between biofumigation and biocontrol agents in the soil, presents challenges in combining these two environ- mentally friendly approaches to managing plant-parasitic nematodes. Specifically, it was found that although both the seed meals high in glucosinolates and the entomopathogenic nematodes *Steinernema* spp. reduced root-knot nematode damage to potato tubers and increased marketable tuber yields, their combination did not further improve the suppression of plant-parasitic nematodes.[54]

Limonoids, Quassinoids, and Saponins.

Limonoids are metabolically altered triterpenes and have a prototypical structure either containing or derived from a precursor with a 4,4,8-trimethyl-17-furanylsteroid skeleton. They can be found as constituent compounds in the order Rutales and more specifically in the families Meliaceae and Rutaceae, or less frequently in Cneoraceae and *Harrissonia* sp. of Simarouba- ceae.[55] To date, 300 limonoids are known, one-third of which (meliacins) is obtained from Meliaceae species (*Azadirachta indica* and *Melia azedarach*) corresponding to structurally rather complex substances.[56−60] The plant family Meliaceae (ma-

hogany family) has received much attention especially because of the presence of limonoid triterpenes[61] among which focus has been predominately on azadirachtin. Azadirachtin, a tetranortriterpenoid limonoid found in the Indian Neem tree (*Azadirachta indica* L., Meliaceae), is used for the production of a wide range of commercial formulations registered for nematode control.[62,63] Apart from azadirachtin, neem also contains more than 100 different limonoids exhibiting repellence, feeding deterrence, and insect growth inhibition activities.[61] In India, neem (*Azadirachta indica*) extracts have been introduced in pest management as a part of traditional practice for many years. It is of high importance that limonoids do not have direct negative effects on beneficial insects,[64,65] and for this reason, they can be combined in integrated pest management. Specifically, azadirachtin is classified as highly toxic to insects and mildly toxic to nontoxic to mammals due to the ability of mammalian cells to remove azadirachtin from the body.[66] Azadiractin is therefore classified as class IV (no

followed by soil incorporation of broccoli reduced *M. incognita*

mammalian toxicity) by the U.S. Environmental Protection damage in tomato.[51] For that which concerns the delineation of activity among ITC components, various studies have been made. In a study where 11 hydrolysis products of glucosinolates were tested for their nematicidal properties, 2-phenylethyl, benzyl, 4-methylthiobutyl, and prop-2-enyl isothiocyanate showed the stronger activity, with an LD_{50} at concentrations of 11, 15, 21, and 34 μM, respectively. On the basis of this

Agency (EPA); it is not persistent in the environment principally due to photodegradation;[67,68] it has no effects on skin sensitization and eye irritation, and is not mutagenic.[69] Moreover, azadirachtin is the most studied biopesticide because it exhibits a wide range of biological activities against agricultural pests and pathogens.[70] Its chemical structure elucidation took 18 years to solve, while its total synthesis

took almost 22 years.[66] Azadirachtin effects on insects are (i) antifeedancy due to deterrent effects on chemoreceptors; (ii) endocrine system disruptance (ecdysteroid and juvenile titers); and (iii) direct effects on tissues resulting in loss of fitness.[71] The insect growth regulation and development activities are caused by the decalin fragment of the molecule, while the hydroxyl-furan fragment affects the antifeedant effects.[72] Recently, it has been reported that azadirachtin induces a rapid increase in the mitotic index of insect cells, the appearance of many aberrant mitotic figures, and the prevention of polymerization in vitro of mammalian tubulin.[73] Although several reports suggest that neem products, such as seed powder, seed kernel powder, seed cake powder, dry leaf powder, and aqueous neem extracts, exhibit good efficacy against root-knot nematodes,[74–78] it seems that azadirachtin

activity, when used individually, is less fast and less high.[79] In fact, azadirachtin (Neemazal 1% EC, Intrachem Hellas) acts against *Meloidogyne* sp. at very high concentrations both concerning paralysis effects and biological cycle arrest (12.8 mg/L and 30.72 μg/g), and the recommended dose for nematode control in field does not provide adequate control.[80] According to our results, meliacins do not seem to be characteristic of nematicidal activity[81] contrary to Saha et al., sustaining synergism in a binary mixture (1:1) of azadirachtin and salannin, nimbin, and desacetylnimbin against *M. incognita* (LC_{50} 70.9 μg/mL).[82] *Melia azedarach* L. is another Meliaceae plant species, also known as chinaberry, demonstrating strong biofumigant properties when incorporated as a powder in *M. incognita* infested soil (EC_{50} = 0.34% w/w). Quassinoids and saponins also fall in the PSMs' category of triterpenoids, but they are much less studied contrary to limonoids. Quassinoids are the bitter principles of the Simaroubaceae family (*Quassia amara*, *Cassia camara*, and *Picrasma excelsa*) and constitute a group of structurally complex and highly oxygenated degraded triterpenes,[83] divided into five groups according to the basic skeleton (C-18, C-19, C-20, C-22, and C-25); they possess nematicidal properties,[1] while no data is available at present of their fate in the environment. Quassinoids act as non-competitive antagonists of the ionotropic GABA receptor to stabilize the closed conformation of the channel, resulting in the inhibition of the action of GABA.[84] The quassinoid fraction extracted from seeds of *Hannoa undulata* composed of a

surfactant properties, but they also possess significant nematicidal properties.[1,87–95] Saponins mainly consisting of triterpene glycosides of medicagenic acid are considered nematicidal agents,[96] and they act as membrane disruptants.[29] *Medicago sativa* L., alfalfa, is the most known plant species for its contents in saponins. In field conditions, soil amendments with 20 or 40 t/ha of a pelleted *M. sativa* meal increased tomato crop yield and reduced soil population densities and root galling of *M. incognita*.[97] *Tithonia diversifolia* (Hemsl.) A. water extract, yielding alkaloids and saponins, significantly inhibits *M. incognita* egg hatch by 98% from 2 days after incubation (DAI)

and was evidenced more with 100% inhibition at 9 DAI in the in vitro studies. *M. incognita* (5000 eggs/plant) reproduction, number of eggs and juveniles, and galling were significantly suppressed by *Tithonia* residue treatment at a rate of 30 tons/ ha on yam (*Discoria rotundata*) in a screen house.[98] A formulated product containing an extract from *Quillaja saponaria* (QL Agri 35 (QL)) decreased the convulsive movement of second stage juveniles of *M. incognita* after exposure for 8 days, and the most paralyzed juveniles were counted at the dose of 8 mg/L. There was also a gradual decrease in the number of juveniles emerging from egg masses of the same nematode species when the dose of *Q. saponaria* was increased from 0 to 8 mg/L.[99] Leaf and root meals from *Aster sedifolius* as well as the saponins extracted from the plant revealed nematicidal activity on *M. incognita*. Specifically, reproduction of the nematode was reduced by about 97% with 0.5 and 1 g/100 cm^3 soil of meals from leaves and roots.[100] Triterpenic saponins isolated from seeds of *Madhuca indica* and fruit pericarp from *Sapindus mukorossi* exhibited inhibitory effect against two phytoparasitic nematodes. Azadirachtin, salannin, nimbin, and desacetylnimbin were extracted from the seeds and oil of *Azadirachta indica* A. Juss. *M. indica* and *S. mukorossi* saponins were found to inhibit the movement of the preadult (J4) stage of *Rotylenchulus reniformis*, and the LC_{50} values were calculated at 68.8 and 181.9 μg/mL. Azadirachtin and the other limonoids affected the mobility of the secondary juvenile stage (J2) of *M. incognita* by 83.3 and 80.1%, respectively, at 0.5 mg/L. *M. indica* saponin (LC_{50} 220 μg/ mL) exhibited a potentiating effect in the presence of azadirachtin in a 1:3 ratio (LC_{50} 120.1 μg/mL). A binary

mixture (1:1) of azadirachtin and limonoids was found to show

mixture of three polycyclic lactones chaparrinone, glaucar- significant nematicidal activity against *M. incognita* (LC_{50} 70.9

ubolone, and klaineanone reduces the penetration and reproduction of *M. javanica.* Full inhibition of penetration occurred during three days of nematode exposure to a 5 mg/kg quassinoid solution in the soil−water, while soil amendment of crude powder of *H. undulata* seeds fully inhibited the reproduction of *M. javanica* on tomato roots.[85] Quassinoids, C19 or C20 compounds isolated from Simaroubaceae, revealed nematicidal activities against Diplogastridae (Nematoda). Of the various quassinoids tested, samaderines B and E displayed the most potent nematicidal activity with a minimum lethal concentration (MLC) of 2.0×10^{-5} M. The nematicidal activities of samaderines B and E were 15-fold greater than that of albendazole (3.0×10^{-4} M), 10-fold greater than that of

thiabendazole (2.0×10^{-4} M), and 7.5-fold greater than that of

avermectin (1.5×10^{-4} M). Thus, samaderines B and E may eventually be used as lead nematicides.[86] Saponins are triterpene glycosides obtained from *Quillaja saponaria*

(Quillajaceae) and various other plant species of the families Alliaceae, Asteraceae, Polygalaceae, and Agavaceae. Their side chains of hydrophilic carbohydrates provide them with

μg/mL) and *R. reniformis* (LC_{50} 91.2 μg/mL).[82] Saponins and flavonoid rich brimstone leaf, *Morinda lucida*, was tested for its nematoxic effects on root-knot nematode in the laboratory and screen house. Brimstone leaf crude extract (50 and 100% concentrations) and brimstone leaf powder (1 and 2 t/ha) were used. Brimstone leaf significantly reduced the gall index of *Celosia argentea* compared with the control.[101] Finally, *Cestrum parqui*, a shrub used in Tunisia as an ornamental plant, contains saponins and is highly toxic to the eggs of *M. incognita* as measured in vitro.[102] Saponins also induce nematicide effects on *Xiphinema index* raising concern in the culture of *Vitis vinifera*.[103] *Medicago sativa* L., alfalfa, is the most known plant species within the *Medicago* genus. The plant has been extensively studied for its content of saponins, mainly consisting of triterpeneglycosides of medicagenic acid, possess- ing several biological properties including biocidal activity on different soil microorganisms. Saponins from *M. sativa* have been found effective in vitro against the virus-vector nematode *Xiphinema index*, the root-knot nematode *M. incognita*, and the potato cyst parasite *Globodera rostochiensis*. The nematicidal efficacy differed among the three assayed nematode species, *G. rostochiensis* being the most susceptible to the active compounds from alfalfa.[95]

Organic Acids.

Vegetable oils contain large and heterogeneous quantities of saturated or unsaturated fatty acids, with medium to long esterified carbon chains, and esters of fatty acids with high molecular weight. In insects, they develop toxicity by inhalation and contact, suffocating by forming an impermeable film upon the cuticle. Some organic acids penetrate through the cuticle, disrupt the cellular membrane, and uncouple oxidative phosphorylation. Some fatty acids, such as oleic acid (C18), have their own insecticidal activities, whereas undecylenic (C11) acid has a lower toxicity but increases the activity of other insecticidal compounds.[8] Organic acids also act as nematicidals.[17]

Lantana camara Linn. var. *aculeata* is a poisonous plant, containing among others 11-oxo triterpenic acid. This compound was found to be active against root knot nematode *M. incognita* and showed an 85 to 90% mortality rate.[104] Seven constituents isolated from the aerial parts of *L. camara*, namely, pomolic acid, lantanolic acid, lantoic acid, camarin, lantacin, camarinin, and ursolic acid, were tested for nematicidal activity against the root-knot nematode *M. incognita*. Pomolic, lantanolic, and lantoic acids showed 100% mortality at 1 mg/ mL concentration after 24 h, while camarin, lantacin, camarinin, and ursolic acid exhibited 100% mortality at this concentration after 48 h. These results are comparable to those obtained with the conventional nematicide furadan (100% mortality at 1 mg/ mL concentration after 24 h).[105] Also lantanilic acid, camaric acid, and oleanolic acid isolated from the methanolic extract of the aerial parts of *L. camara* exhibited 98%, 95%, and 70% mortality, respectively, against *M. incognita* at 0.5% concen- tration. At this concentration, conventional nematicide furadan showed 100% mortality.[106]

Moreover, the nonessential amino acid L-3,4-dihydroxvphe- nylalanine (L-Dopa) was present at 6−9% in the seeds of *Mucuna* spp. When tested against the phytonematodes *M. incognita* and *H. glycines*, it exhibited nematicidal activity, and the LC_{50} values were calculated at 21 μg/mL and 0.17 μg/mL respectively.[107]

Phenolics, Flavonoids, and Quinones. According to a broad spectrum evaluation on the effects of phenylpropanoids on the behavior of *M. incognita*, repellents and motility inhibitors were found among the simple phenolic compounds. Flavonols stood out as repellent compounds, while they were, in their degraded form, also motility inhibitors. Salicylic acid was a strong attractant for *M. incognita*, but the compound was also nematicidal (LC_{50} of 46 μg/mL) and an irreversible inhibitor of hatching.[108] The nematicidal activity of phenolics has been previously reported.[1,28,80,109−112] Root leachates of a tropical weed named *L. camara*, used in combination with the plant growth-promoting rhizobacterium *Pseudomonas aerugino- sa* against *M. javanica*, significantly reduced nematode population densities in roots and subsequent root-knot infection, and enhanced plant growth. Even though a high concentration of root leachate slightly reduced *P. aeruginosa* colonization in the rhizosphere and inner root tissues, the nematicidal efficacy of the bacterium was unaffected. The root leachate of *L. camara* was found to contain phenolic contents, was found to be highly effective against *M. incognita* and *M. javanica*.[114] In vitro investigation of *Tagetes patula* L. flower polar extract against *Heterodera zeae* revealed activity based on the phenolic contents. In the nonpolar extract, a few fatty acids, their methyl esters, and thiophenes (including α- terthienyl) were detected. In studies of compounds obtained commercially, α-terthienyl and gallic and linoleic acids showed 100% mortality at concentrations of 0.125% after 24 h. Assessment of structure−activity relationships revealed that an increase in the number of hydroxyl groups in phenolic acids increased the activity; with fatty acids, activity depended on chain length and the number and position of double bonds.[115] Ethyl acetate extract of the branches of *Magnolia tripetala* exhibited nematicidal activity against *Bursaphelenchus xylophilus*, *Panagrellus redivivus*, and *Caenorhabditis elegans*. Two nem- aticidal phenolic compounds magnolol and honokiol were isolated from the extract based on bioassay-guided fractiona- tion. The median lethal concentrations (LC_{50}) of the isolated compounds were 149.3 and 63.7 mg/L, respectively, against *B. xylophilus*, 74.5 and 75.9 mg/L, respectively, against *P. redivivus*, and 64.7 and 57.8 mg/L, respectively, against *C. elegans* at 48 h.[116] *Chromolaena odorata* is a widespread weed found in humid the tropical south, Southeast Asia, and West Africa, exhibiting nematicidal properties due to its phenolics, alkaloid, and amino acids contents.[117] Ether-soluble phenolics from the chicory rhizome exhibited nematicidal activity.[118] In a green- house experiment, thymol, a phenolic monoterpene added in soil at 0, 50, 100, and 150 mg/kg, showed synergistic effects in suppressing initial and final soil populations of *M. arenaria* in combination with 100 mg/kg benzaldehyde, an aromatic aldehyde present in nature as a moiety of plant cyanogenic glucosides. Significant reductions in root galling and cyst formation on soybean were attributable to thymol at ≥50 mg/

kg.[32] The crude extract of *Arisana erubescens* exhibited

significant nematicidal activity against *M. incognita* with a LC_{50} value of 258.11 μg/mL, while the LC_{50} values of the phenolic compounds schaftoside and isoschaftoside contained in extracts were 114.66 μg/mL and 323.09 μg/mL, respectively.[119] *Caernohabditis elegans* and *C. brissage* treatment with flavones induced embryonic and larval lethality that was pronounced in early larval stages. Specifically, flavone (2-phenyl chromone) LD_{50} values were calculated at 100 μM for both nematode species.[120] *Acacia gummifera* and *T. patula* aqueous extracts, rich in flavonoids, suppressed *Meloidogyne* spp., at 84% and 82%, while the extract of *Ononis natrix* and *Ceratonia siliqua* had a nematicidal effect against *Meloidogyne* spp., with 67% and 71% of mortality, respectively.[24] The internal aerial tissues of *Polygonum senegalense* containing common flavonoids such as quercetin, kaempferol, luteolin, and their glycosides as well as the stomach ache medicine *Psiadia punctulata* (Compositae) from which novel methylated flavonoids, kaurene, and trachyloban diterpenes have been found exhibit nematicidal activities.[121] *Nothofagus alessandri* and *N. pumilio* exhibit nematicidal activity against *Caenorhabditis elegans*. The discovery of the phytoalexin, pinosylvin, in the leaves, raises the possibility that *Nothofagus* in general and *N. alessandri* in particular may have induced chemical defense mechanisms.[122] Nonetheless, a negative efficacy result was obtained when fractionation of the methanolic extract from *Gochnatia barrosii*

compounds, including *p*-hydroxybenzoic acid, vanillic acid,

Cabrera (Asteraceae) leaves resulted in the isolation of the

caffeic acid, ferulic acid, and a quercetinglycoside, 7-gluco- side.[113] The ethyl acetate fraction of the crude methanolic extract of *Viola betonicifolia*, rich in flavonoid and phenolic

flavonol glycoside *trans*-tiliroside kaempferol 3-*O*-β-D-(6″-*O*-*E*-*p*-coumaroyl)-glucopyranoside that lacked activity at 500 μg/ mL against *M. exigua* Goeldi larvae.[123] The Myrsinaceae are

well established ethno-anthelmintics, harbingers of long alkyl side chain benzoquinones. The main component of the subfamily Myrsinodae is embelin, while for the Maesodae it is maesaquinone together with its 5-acetyl derivative; the distribution of these benzoquinones by their alkyl side chain length or the presence/absence of a 6-methyl group is in accordance with morphological subfamily delimitation. The benzoquinones show nematicidal activity. Also, plants belong- ing to the Polygonaceae family are widely used as ethno- anthelmintics, and the common anthelmintic anthraquinones are obtained from various *Rumex* species while the naphthalenic acetogenin derivative, nepodin is more selectively distrib- uted.[121]

Piperamides. The PSMs produced by many species in the genus *Piper* are called piperamides among which capsaicin is obtained from the genus *Capsicum*, such as chili peppers (*Capsicum frutescens*, Mill.), and is characterized by nematicidal properties.[124,125]

Piperamides evoke contact toxicity and repellent and antifeedant activities, and at a biochemical level, they act as

neurotoxins, and they photodegrade.[126] As an emerging

2.10. Terpenes. Essential oils (EOs) are volatile, natural compounds with a strong odor, formed as PSMs by aromatic plants, exhibiting many biological activities. They are obtained by hydrodistillation, and they comprise heterogeneous mixtures of terpenes and terpenoids as well as other aromatic and aliphatic constituents, the biological actions of which are a very complicated concert of synergistic or antagonistic activities. Terpenes are formed structurally by coupling different numbers of isoprene units (5-carbon-base; C_5), and they may or may notcontain oxygen (terpenoids and terpenes). The main terpenoid classes are monoterpenes (C_{10}), sesquiterpenes (C_{15}), hemi- terpenes (C_5), diterpenes (C_{20}), triterpenes (C_{30}), and tetraterpenes (C_{40}).[136] Several factors can affect the chemical composition, toxicity, and bioactivity of the extracts such as the phenological age of the plant, percent humidity of the harvested material, and the method of extraction.[137] The broad spectrumof EO activities, ranging from insecticidal, antifeedant, repellent, oviposition deterrent, growth regulatory, and antivector activities, along with their wide availability from the flavor and fragrance industries, can make possible the commercializa- tion of essential oil-based pesticides, particularly for organic

biocide, very little data are available on the environmentalfate of capsaicin, but initial assessment suggests that it will bind to sediments.[127]

Polyacetylenes and Polythienyls, Section 2.9. The polyacetylenes and polythienyls found in Tagetes species, sometimes known as marigolds, are responsible for the plant's ability to serve as a nematicidal food source. 138 It's due to the high volume of While the interspecific toXicity of individual oils and compounds is highly idiosyncratic, the synergistic effect of EOs on many targets at once reduces the target species' resistance or adaptability. In addition to causing cytotoXicity and membrane destruction in cells and organelles, phenols and alcohols also have a number of other negative effects.

properties.1,128 Marigolds are used to incorporate prooXidants on proteins and DNA that have been infected with M. incognita, and to generate reactive fields of cowpeas or soybeans may help lower nematode populations, protecting crop yields from possible harm.

129 The oXygen species variation is an interesting (ROS). After being activated by light, furocoumarins are able to pass through a cell's membrane, protein, and DNA without causing any harm. effects of marigolds against nematicidal pests have been linked to the Singlet oXygen. There are times when essential oils and their Variables such as the cultivar of marigold employed, the species or races of target nematodes, the temperature, and the age of the marigold

plant all have a role in the success of nematode control.

130 Although marigold was effective in suppressing M. incognita when planted shortly after a crop sensitive to it, it had little effect on the beneficial soil mesofauna, such as free-living nematodes and soil mesoarthropods. 131 African marigold vermicomposts were shown to be very effective in lowering tomato infections caused by M. incognita. 132 When administered to tomato seedlings infected with root-knot nematodes, aqueous extracts of marigold roots enhanced plant height as well as leaf and fruit output compared to the control treatment. 133 Marigold (Tagetes patula L.) was tested against Meloidogyne (M. arenaria), M. hapla (13 populations), M. javanica (three populations), and M. incognita (46 populations) in order to identify the races and virulence groups of each Meloidogyne species in Spain and Uruguay. There was no difference in response to marigold between virulence groups of M. incognita, but there was a difference in behavior between and within populations of races A and B of M. hapla, demonstrating that screening the M. hapla population against which T. patula will be used is essential for making effective agronomic decisions. 134 Nematode-suppressing crops have a residual antagonistic effect on plant-parasitic nematodes, making them easier to manage in subsequent crops. Plant-parasitic nematode populations may be greatly reduced by alternating marigold with other decorative plants or nematode-suppressing cover crops, such as sunn hemp, with field or cash crops. nuclear and cytoplasmic mutagenicity; they operate on mitochondria and the respiratory system.

Since EOs often exhibit low mammalian toXicity and low environmental persistence, they are excluded from the standard data criteria for registration in the United States. 140 Most of the research on essential oils has focused on their effectiveness against insect and fungal agricultural pests140; this section of the article provides a brief overview of the worldwide literature on essential oils' nematicidal potential141. At a concentration of 1,000 L/L, the essential oils of Carum carvi, Foeniculum vulgare, Mentha rotundifolia, and Mentha spicata were nematicidal toward Meloidogyne javanica. Cucumber seedlings' root galling was decreased in pot tests when these EOs and those from Origanum vulgare, O. syriacum, and Coridothymus capitatus were miXed in sandy soil at concentrations of 100 and 200 mg/kg. 142 Essential oils from Eucalyptus citriodora, Eucalyptus hybrida, and Ocimum basilicum were shown to be nematicidal against Meloidogyne incognita, as were oils from Pelargonium graveolens, Cymbopogon martinii, Mentha arvensis, Mentha piperita, and Mentha spicata. Even at concentrations as low as 500 and 250 mg/L, respectively, the oils of eucalyptus (E. citriodora and E. hybrida) and Indian basil (O. basilicum) were extremely toXic. 143 The EO of Kadsura heteroclite is nematicidal against M. incognita with an LC50 value of 122.94 g/mL. The primary components of this EO are -eudesmol (17.56%) and 4-terpineol (9.74%). 144 Over 80% of juvenile Meloidogyne sp. are rendered paralyzed by the EOs of A. triphylla, L. juneliana, and L. turbinate at a concentration of 667 L/L. 145 The half-lethal concentration (EC50) of clove oil at which egg hatching is inhibited is 0.097% (v/v), whereas the EC50 for paralysis in juveniles in their second stage of development (J2) is 0.145%. Clove oil, at a concentration of 5.0%, has volatile

the percentage of nematode eggs that hatch in water by 30% and reduce the viability of hatched J2 by as much as a factor of 100. The EC50 value for clove oil in soil experiments is determined to be 0.192 percent. 146 Meloidogyne arteellia had a significantly lower hatching, J2 survival, and reproduction rate when exposed to 2, 4, 8, or 16 L/mL of EO from Chrysanthemum coronarium. 147 At 150 L/plant, both thyme and garlic EO significantly decrease root galling (2.82 0.47%) (5.53 1.68%) and produce the smallest egg masses (2.46 0.17 and 2.50 0.22). 148 All juvenile nematodes were killed and egg hatching was prevented at 12.5 g/mL after 24 hours of exposure to the miXture of Haplophyllum and Plectranthus EOs (1:1). This mixture was reported to be very toxic against M. javanica in vitro and was comparable in toxicity to carbofuran. 149 Origanum vulgare, Origanum dictamnus, Mentha pulegium, Melissa officinalis, Foeniculum vulgare, Pimpinela anisum, Eucalyptus meliodora, and Pistacia terebinthus all had EC50 values of less than 2 milliliters per milliliter when tested against M. incognita: 1.55, 1.72, 3.15, 6.15, 231, 269, 807 Paralysis of M. incognita and M. javanica (EC50/1d = 77.5 and 107.3 mg/L) is caused by the EO of Ruta chalepensis L. 17 Root-knot nematodes may be effectively combated by adding fragrant plant leftovers to the soil. In particular, tarragon, spearmint, and wild rocket crop residues result in high mortality of the tested pathogens, suggesting that they may be useful as organic amendments for the control of M. javanica. 150 Chrysanthemum coronarium EO applied on sterile cotton pellets at concentrations of 1040 L per 500 cm3 soil significantly decreased the reproduction rate of the nematode in pot trials with chickpea cv. PV 61. 147 Reduced root gall development was seen in tomatoes grown in soil treated with a mixture of Haplophyllum and Plectranthus EOs (1:1). 149 Interestingly, geraniol, eugenol, linalool, and peppermint oils at 1,500 mg oil/kg soil reduced the number of galls caused by M. arenaria without inducing any decrease in galling caused by M. incognita. Likewise, growing peppermint (Mentha piperita) and spearmint (M. spicata) accessions for 8 or 12 weeks in M. arenaria-infested soil before At concentrations of 1,000 and 1,500 mg/L, geraniol, linalool, and peppermint oil were all phytotoXic to tomato. 151 High nematicidal activity is also seen when specific components of essential oils are utilized. For M. incognita and M. javanica, the EC50 values for the essential oil of Ruta chalepensis L. are 20.6 and 22.5 mg/ L, respectively, indicating that this first-ranking volatile, 2-undecanone, is active at these concentrations. 17 Previous research has shown that oXygenated chemicals (alcohols and ketones) are typically more active than hydrocarbons, and that the activity against M. incognita diminishes from L-carvone to pulegone to trans-anethole to geraniol to carvacrol to thymol to estragole to terpinen-4-ol to -eudesmol. 13,15 In addition, borneol, carveol, citral, geraniol, and -terpineol, all of which include hydroXyl and carbonyl groups, have been shown to be highly nematicidal against M. incognita at concentrations as low as 250 mg/L by other researchers. Pot tests showed that 100 and 250 mg/kg of these monoterpenoids reduced root galling in tomato plants. 152 The nematicidal EO of Croton regelianus153 and Chenopodium ambrosioides (27.27%), of which ascaridole is the main ingredient, has potent nematicidal activity against M. incognita with LC50 values of 49.55 g/mL and 32.79 g/mL, respectively. 154 In particular, geraniol, thymol, and camphor are very effective against M. javanica J2s. after 72 hours of exposure, 91, 60, and 56 percent of the nematodes were dead, whereas cineole, menthol, and pinene showed no action. After 72 hours of exposure, carvacrol, thymol, and geraniol were the most lethal to M. incognita J2s, killing 100%, 90%, and 74% of the bacteria, respectively. When tested against M. incognita, cineole performed the worst. 155 MiXed in sandy soil at concentrations of 75 and 150 mg/ kg, it significantly reduced the root galling of cucumber seedlings, and Oka et al. found that carvacrol, t-anethole, thymol, and (+)-carvone have strong nematicidal potential against M. javanica, immobilizing the juveniles and inhibiting egg hatching at >125 L/L in vitro. The nematicidal action of the EOs and their constituents was confirmed at doses of 200 and 150 mg/kg, respectively, in in vitro pot tests. 142 Carvacrol, thymol, and linalool at low concentrations (1, 2, and 4 mg/L) fully stopped Meloidogyne incognita hatching. 156 The greatest reduction in root galling on tomato was achieved when thymol was applied as preplant fumigation through drip irrigation lines under polyethylene mulch at a rate of 73 kg/ha. This was done in conjunction with acibenzolar-S-methyl, which was primarily applied as a foliar spray at a concentration of 25 mg/L. (Lycopersicon esculentum). 157 There seems to be a complex web of interactions137,158 between the various terpene component compounds and how they contribute to the overall activity of an EO. It's worth noting that even if they don't have any effect on their own, the presence of inactive constituents is sometimes essential to attain complete toXicity in the active components. In descending order, the terpene pairings trans-anethole/geraniol, trans-anethole/eugenol, carvacrol/eugenol, and geraniol/carvacrol showed strong binary action (synergism) on M. incognita paralysis. 15 Therefore, it is crucial to comprehend the biological processes responsible for nematicidal EOs, as well as the synergy and antagonism interactions between the many components that make up an EO. The effects of interactions between nematicidal and non-nematicidal terpenes also need further study.

Results and Discussions 2.11.

Overall, there has been a significant shift in how IPM strategies are approached. Even though botanical nematicides show promise as tools for managing Meloidogyne spp., there is still much work to be done in defining their targets and mechanisms of action, as well as developing effective strategies for using them in the field. 159 The development of new nematicidal chemicals necessitates the acquisition of new information, and secondary metabolites from plants may play a crucial role in identifying promising molecules for chemical synthesis. One useful method for this goal is the plant metabolomic approach, which investigates plant metabolites as the byproducts of cellular activity.

Developing novel and ecologically friendly nematode control tactics requires a biochemical knowledge of the interaction between semio chemicals and root-knot nematodes, as well as the interactions between hosts and parasites.

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